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GUILHERME NASCIMENTO CORTE

FAUNA DE FUNDO NÃO-CONSOLIDADO DA BAÍA DO ARAÇÁ, LITORAL NORTE DE SÃO PAULO

SOFT-BOTTOM BENTHIC FAUNA OF ARAÇÁ BAY, NORTHERN COAST OF SÃO PAULO

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RESUMO

Ecossistemas costeiros fornecem bens e serviços essenciais e sustentam uma grande variabilidade genética e taxonômica. Entretanto, apesar de sua importância, esses ecossistemas encontram-se entre os mais impactados e ameaçados ao redor do globo. Para que esses ecossistemas sejam preservados é fundamental o conhecimento sobre os processos que determinam suas caraterísticas ecológicas. Nesse contexto, essa tese teve como objetivo investigar as comunidades bentônicas macro- e meiofaunais que habitam os sedimentos da baía do Araçá, São Sebastião, SP, e as suas relações com o ambiente. Diferentes métodos de coletas foram utilizados e a fauna foi coletada desde a região entremarés até mais de 20 m de profundidade. Foi constatado que eventos de larga escala relacionados às mudanças climáticas podem provocar significativas mudanças nas características ecológicas da baía (capítulo 1). Também foi observado que a influência de processos espaciais pode ser preponderante nessas comunidades e que essa influência é dependente da capacidade de dispersão das espécies (capítulo 2). A análise conjunta da macro- e meiofauna mostrou que os dois grupos possuem padrões similares em suas comunidades e que são estruturados por variáveis ambientais semelhantes (capítulo 3). Entretanto, o padrão de riqueza de espécies e abundância de indivíduos nessas comunidades foi contrastante, o que destaca que estratégias de conservação e manejo não devem ser baseadas apenas em um desses grupos. De maneira geral, os resultados apresentados nessa tese complementam diversos trabalhos que destacaram a influência de variáveis físico-químicas na fauna bentônica marinha de substratos não-consolidados e demonstram que processos espaciais e eventos extremos podem exercer grande influência na estruturação e manutenção dessas comunidades.

ABSTRACT

Coastal ecosystems provide essential goods and services and maintain a large biodiversity. However, despite their importance, these ecosystems are among the most threatened around the globe. To preserve these ecosystems is essential to understand the processes that determine their ecological characteristics. In this regard, this thesis aimed to investigate the macro- and meiofaunal benthic communities inhabiting the soft-bottom of Araçá Bay, São Sebastão, SP, as well as their relationship with the environment. Different sampling methods were used and fauna was collected from the intertidal zone to more than 20 m deep. It was observed that large-scale events related to climate change can cause significant changes in the ecological features of the bay (Chapter 1). It was also observed that the influence of spatial processes can be predominant in these communities, and that this influence is dependent on the dispersal abilities of species (Chapter 2). The analysis of macro- and meiofauna showed that the two groups have similar patterns and are structured by similar environmental variables (Chapter 3). Their patterns of species richness and abundance, however, were contrasting, which highlights that conservation and management strategies should not be based on only one of these groups. Overall, the findings of this thesis complement several works that highlighted the influence of physical and chemical variables in the marine benthic fauna inhabiting soft-bottom coastal ecosystems, and demonstrate that spatial processes and extreme events can exert great influence on the assembling and maintenance of these communities.

Sumário

Introdução

Comunidades ecológicas são heterogêneas no tempo e espaço, e estruturadas pela ação combinada de diferentes variáveis (Menge and Olson 1990, Levin 1992, Leibold et al. 2004). Variáveis ambientais como temperatura, altitude e profundidade, por exemplo, determinam a ocorrência de espécies em uma escala mais ampla, enquanto o tipo de sedimento e interações biológicas podem sobrepor essas variáveis em uma escala mais local (Defeo and McLachlan 2005). A isso, soma-se a influência da história evolutiva e de variáveis espaciais, as últimas principalmente relacionadas à capacidade de dispersão das espécies (Holyoak et al. 2005).

Entender como essas variáveis atuam na formação e manutenção dos padrões de biodiversidade é um dos principais objetivos em estudos ecológicos (MacArthur et al. 1967, Levin 1992, Hubbell 2001). Esse conhecimento é essencial para a compreensão da dinâmica dos ecossistemas (Spruzen et al. 2007) e elemento chave para a implementação de programas de monitoramento e manejo (Thrush et al. 1997, Ysebaert and Herman 2002, Soares-Gomes and Pires-Vanin 2003). Somente por meio dessas informações podemos elaborar melhores previsões sobre futuras mudanças ambientais oriundas da ação humana, assim como preservar bem e serviços ecossistêmicos fundamentais. No entanto, a compreensão dos processos responsáveis pelos padrões de biodiversidade é ainda um dos desafios centrais na ecologia de comunidades (Leibold et al. 2004, Mason et al. 2013, Heino et al. 2014).

Esse desafio é ainda maior em ecossistemas marinhos, sobretudo devido à menor disponibilidade de informação sobre esses ambientes. Esse menor conhecimento resulta em baixa representatividade em discussões sobre temas fundamentais, como respostas biológicas às mudanças climáticas e quais áreas seriam adequadas para preservação (Hoegh-Guldberg and Bruno 2010, Webb and Poloczanska 2011, Schoeman et al. 2014). Consequentemente, observam-se falhas na conservação desses ecossistemas, colocando em perigo a sua biodiversidade e bens e serviços (Costello et al. 2010, Tittensor et al. 2010, Poloczanska et al. 2013).

Entre os ambientes marinhos, os ecossistemas costeiros, caracterizados pela interação entre terra e mar, fornecem uma ampla gama de serviços ecossistêmicos, como filtragem de água, ciclagem de nutrientes, proteção da linha de costa e conservação da biodiversidade, além de sustentar uma grande variabilidade genética e taxonômica (Defeo et al. 2009, Barbier et al. 2011). Entretanto, esses ecossistemas encontram-se entre os mais impactados e ameaçados ao redor do globo (Halpern et al. 2007, Barbier et al. 2011).

Nesse contexto, essa tese tem como objetivo caracterizar a estrutura das comunidades presentes em um ecossistema costeiro complexo, assim como tentar compreender as variáveis e processos que as influenciam. Especificamente, o foco está nas comunidades macrobentônicas que habitam os sedimentos (fundo não consolidado) da baía do Araçá, São Sebastião, SP, um dos ecossistemas mais ricos em diversidade biológica da costa de São Paulo (Amaral et al. 2010, Amaral et al. 2015).

O que é conhecido sobre comunidades bentônicas de fundo raso não consolidado?

Comunidades bentônicas marinhas de fundo raso não consolidado são parte fundamental dos ecossistemas costeiros, sendo um dos elementos estruturais da teia alimentar (Ysebaert and Herman 2002, Spruzen et al. 2007). Essas comunidades são caracteristicamente heterogêneas em distribuição e abundância (Defeo and McLachlan 2005, Gray and Elliott 2009) e, de maneira geral, estruturadas por variáveis físico-químicas, como tipo de sedimento, teor de oxigênio e hidrodinâmica. Interações biológicas exercem menor influencia nessas comunidades, entretanto, sua importância é aumentada em ambientes onde a ação de ondas e correntes é mais amena, como praias dissipativas e planícies de marés (ambientes planos, com sedimento mais fino e que sofre menor influência da energia das ondas) (Defeo and McLachlan 2005).

Em consequência da forte influência de variáveis ambientais nas comunidades bentônicas marinhas de fundo raso não consolidado, variações ambientais podem ocasionar mudanças significativas em sua estrutura. Assim, perturbações que modifiquem as características sedimentares, como alterações na linha de costa e ondas de maior energia associadas às tempestades, podem afetar a fauna bentônica e modificar o padrão de dominância das espécies (Schlacher et al. 2007, Defeo et al. 2009). Contaminação por poluentes químicos e orgânicos também pode alterar essas comunidades, muitas vezes ocasionando a extinção local de várias espécies e fazendo com que apenas espécies tolerantes consigam habitar a área contaminada.

O que é pouco conhecido sobre comunidades bentônicas de fundo raso não consolidado?

Ainda há muito a se compreender sobre as comunidades bentônicas que habitam os sedimentos das regiões costeiras. Embora seja conhecido que essas comunidades serão afetadas por mudanças climáticas, pouco se sabe sobre os reais efeitos dessas mudanças. A maior parte das pesquisas relacionadas aos efeitos das mudanças climáticas em regiões costeiras investiga tolerância de espécies individuais às mudanças no regime de temperatura e pH (Schoeman et al. 2014). Distúrbios em grandes escalas como tempestades, por exemplo, são difíceis de serem replicados e, por isso, são pouco investigados. Sabe-se que a ação de ondas de maior energia associadas às tempestades podem aumentar os processos erosivos e modificar as características morfodinâmicas das regiões costeiras (Short 2000, Alves and Pezzuto 2009). Entretanto, poucas informações sobre sua influência na fauna estão disponíveis, o que impossibilita um melhor entendimento dos seus efeitos e a elaboração de previsões mais realistas.

A influência de variáveis espaciais relacionadas à dispersão das espécies que habitam os sedimentos costeiros é outra importante lacuna a ser preenchida. O conhecimento das taxas de dispersão e padrões de colonização é fundamental para compreender como as comunidades se desenvolvem, bem como para entender a dinâmica de recuperação após distúrbios ou avaliar a resiliência de comunidades ecológicas (Pilditch et al. 2015). Durante muito tempo, acreditou-se que ecossistemas marinhos pudessem ser considerados ambientes abertos por que o ambiente é conectado pela coluna d’água (Gray and Elliott 2009). Entretanto, estudos têm mostrado que as taxas de trocas larvais podem ser limitadas e os níveis de auto-recrutamento elevados em ecossistemas marinhos, favorecendo a influência de variáveis espaciais na estruturação dessas comunidades (Lundquist et al. 2004, Quillien et al. 2015, Gerwing et al. 2016). Estudos recentes também têm demonstrado que a dispersão na fase adulta pode ser tão ou mais eficiente que a dispersão larval (Valanko et al. 2010a, b, Pilditch et al. 2015).

Estudos conjuntos que investiguem a fauna bentônica de maneira mais holística também são encontrados em número reduzido. A maioria dos estudos sobre a fauna em sedimentos marinhos, especialmente no Brasil, é realizada de maneira compartimentalizada, analisando separadamente a fauna da região entremarés e do sublitoral, ou somente grupos específicos, como a macro ou a meiofauna. Dessa maneira, é necessário que mais trabalhos examinem a biodiversidade bentônica de maneira integrada e qual a influencia do ambiente sobre eles.

Estrutura da tese

A partir das informações apresentadas, essa tese foi estruturada em três capítulos mais considerações gerais. Cada capítulo buscou investigar um dos tópicos destacados na seção anterior. Assim, o capítulo 1 investiga como processos de larga escala associados às mudanças climáticas podem afetar as comunidades macrofaunais da região entremarés. Especificamente, o capítulo trata da influência de tempestades sobre essa fauna. No segundo capítulo é examinada a influência de variáveis ambientais, bióticas e espaciais na estruturação das comunidades macrofaunais. Buscou-se entender quais as variáveis são mais importantes e se esse padrão é constante no tempo e dependente da capacidade de dispersão das espécies. O capítulo três analisa os padrões de distribuição da macro e meiofauna da Baía do Araçá, desde a região entremarés até a profundidade de 25 m. A congruência entre os dois grupos foi examinada com o intuito de investigar se um grupo pode ser usado como substituto para o outro em estudos de conservação e manejo. Por fim, os resultados dos três capítulos são explorados de maneira sucinta nas considerações finais.

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Capítulo 1

Effects of storms on habitat heterogeneity and beta diversity in marine soft-sediments

Abstract

Storms can result in strong modifications in coastal soft-sediments, with powerful waves increasing erosive processes and changing the habitat features. Climate change projections highlight that storms might have their frequency and intensity increased in the near future. Thus, it is necessary to understand ecological responses to severe storms in order to avoid or mitigate harmful effects on coastal ecosystems. Here, we combine hydrographic, sediment and biological data to test a set of hypothesis and predictions about the ecological impacts of storms on macrobenthic assemblages inhabiting intertidal soft-sediments of Araçá Bay, a sheltered tidal flat in Southeast Brazil. We found that storms reduced species richness, abundance and biomass of macrobenthic assemblages. We also found that β diversity is higher after storms; however, local contribution to β diversity is lower, indicating that areas within the bay are less unique in their biological composition. Overall, our results suggest that storms may affect biodiversity and ecosystem services of coastal soft-sediment ecosystems. Future studies should test our hypothesis and predictions in different areas in order to advance the knowledge of how future climate change will impact coastal ecosystems.

Introduction

Human-induced climate change is now firmly established as a scientific reality (McMichael et al. 2006, IPCC 2014). Many of the observed changes since the 1950s are unprecedented over decades to millennia, and global temperature is projected to rise over the 21st century under all assessed scenarios (IPCC 2014). Impacts from recent climate-related extremes, such as heat waves, droughts, floods and cyclones, are observed across all continents and oceans, and it is very likely that these will become more intense and frequent in many regions (Baker et al. 2008, IPCC 2014). Nevertheless, impacts of climate change on ecosystems are still underinvestigated, and there is a clear research need to understand these impacts and identify strategies to mitigate harmful effects (Hulme 2009, IPCC 2014, Schoeman et al. 2014).

The need for studies about climate-change impacts is further enhanced for marine ecosystems, where the effects of climate change are still largely overlooked relatively to terrestrial systems (Dugan et al. 2010, Hoegh-Guldberg and Bruno 2010, Poloczanska et al. 2013, Schoeman et al. 2014). Besides the reduced number of studies, much of the climate-related research in marine systems has focused on the responses of individual species to changes in ocean temperature and chemistry (Baker et al. 2008, Schoeman et al. 2014, Ortega et al. 2016). To some degree, this focus is appropriate since these factors may alter the physiological functioning, behaviour, and demographic traits of organisms (Defeo et al. 2009). However, a growing body of work is demonstrating that relationships between environmental changes and individual species, although important, are not enough to predict many important aspects of future biological and ecosystem functioning changes (Doney et al. 2012, Schoeman et al. 2014, Sydeman et al. 2014, Stuart-Smith et al. 2015). In this regard, variation of abundances or biomass in species assemblages related to environmental conditions would be the best response variable available to estimate the impact of changes in ecosystems (Legendre et al. 2010, Doney et al. 2012, Legendre and Gauthier 2014).

Among the natural disturbances related to climate change, large-scale extreme events, such as storms, can result in strong modifications in marine coastal ecosystems (Jaramillo et al. 1987, Schlacher et al. 2007, Defeo et al. 2009, Harris et al. 2011). Although storms are short in duration, they are considered a dominant process along many shores and can exert broad and long-term impacts on benthic assemblages (Jaramillo et al. 1987, Posey et al. 1996, Rakocinski et al. 2000). Storms are usually accompanied by increases in sea level, allowing waves to continue towards the coast unaffected by structures that usually reduce coastal erosion, such as reefs and longshore sand bars. As a consequence, large amounts of sediment and associated benthic invertebrates can be removed during storm events (Commito et al. 1995, Norkko et al. 2001, Alves and Pezzuto 2009). Additionally, storms can also change coastal soft-sediments by carrying sediment from the continent to the sea. Climate change projections highlight that storms will likely increase in frequency and intensity (IPCC 2014), resulting in changes in ecosystems service and biodiversity at coastal ecosystems (Defeo et al. 2009, Dugan et al. 2010, Schoeman et al. 2014). Nevertheless, our knowledge about the ecological implications of storm impacts is still limited, precluding actions to mitigate harmful effects. It is therefore essential to investigate ecological responses to severe storms in order to preserve coastal ecosystems (Walker et al. 2008, Alves and Pezzuto 2009, Harris et al. 2011).

The unpredictable nature of storms, however, often precludes a rigorous experimental design to specifically tests for their effects (Harris et al. 2011). This is especially true for intertidal soft-sediments, which have a very restricted time frame for sampling since field work needs to be done at spring tides to avoid contamination by tidal migrants (Schlacher et al. 2008). Due to these difficulties, studies on the general influence of storms on soft-sediments benthic communities are often hampered by a lack of information on community composition before or for long periods after the storm event (Posey et al. 1996). Moreover, the large extent of storms usually prevents the designation of appropriate control areas. As an alternative, one effective approach to advance the knowledge of the ecological implications of the disturbance related to severe storms on soft-sediments benthic communities is to refine a priori conceptual predictions and hypotheses against field data (Harris et al. 2011). This research strategy offers an opportunity to identify trends in ecosystem response, and maximizes the accuracy of updated forecasts (Baker et al. 2008, Schoeman et al. 2014).

Here, we combined hydrographic, physical and biological data to assess the ecological impacts of storms on macrobenthic assemblages inhabiting intertidal soft-sediments of Araçá Bay, a sheltered tidal flat in Southeast Brazil. Specifically, we aim to test a set of *a priori* hypotheses and predictions against field observations gathered in periods before and after the study area was struck by severe storms.

Our first hypothesis is that wave action associated with storms would transport and mix large volumes of sediments, resulting in homogenization of sediment features. We therefore predict that habitat heterogeneity (i.e. environmental variability among sampling stations) would be reduced (prediction 1) and macrobenthic assemblages would be influenced by different environmental variables after storms (prediction 2). Further, as observed for different groups (e.g. tropical trees, Condit et al. (2002); sublittoral macrofauna, Hewitt et al.

(2005); birds, Veech and Crist (2007)), we predict that a reduction in habitat heterogeneity would result in reduction of β diversity in macrobenthic assemblages (i.e., more homogeneous environment would result in more homogeneous assemblages) (prediction 3). We also predict that disturbances related to storms would result in mass-mortality events and, consequently, decrease of biomass and number of species and individuals (prediction 4). Moreover, due to the expected mass-mortality events, the changes in β diversity should be more related to loss of species richness than to turnover of species (prediction 5). Since we are analyzing only one site over a short temporal scale, we recognise that it is not possible to test these predictions unequivocally. However, given the unpredictable nature and large extent of storms, as well as the likely increase in their frequency and intensity, we consider necessary to advance the understanding of storms effects by identifying trends in ecosystem response.

Material and Methods

Study area and sampling

This work was done at Araçá Bay (23º 49’S, 45º 24’W), a heterogeneous and biodiverse rich environment (with more than 1300 invertebrates and vertebrates registered) located in the Marine Protected Area of the Northern coast of São Paulo State, Southeast Brazil (Amaral et al. 2015). Araçá bay is very sheltered, situated in the central area of the São Sebastião Channel. In this area, currents are highly influenced by the wind, and meteorological frontal systems may increase the speed of currents eightfold (Kvinge 1967, Fo 1990, Castro and Miranda 1998). With large part of its area being flooded and dried due to tidal oscillations, Dottori et al. (2015) also show the influence of subtidal oscillations controlling the physical properties and the quality of waters that reach the Araçá Bay.

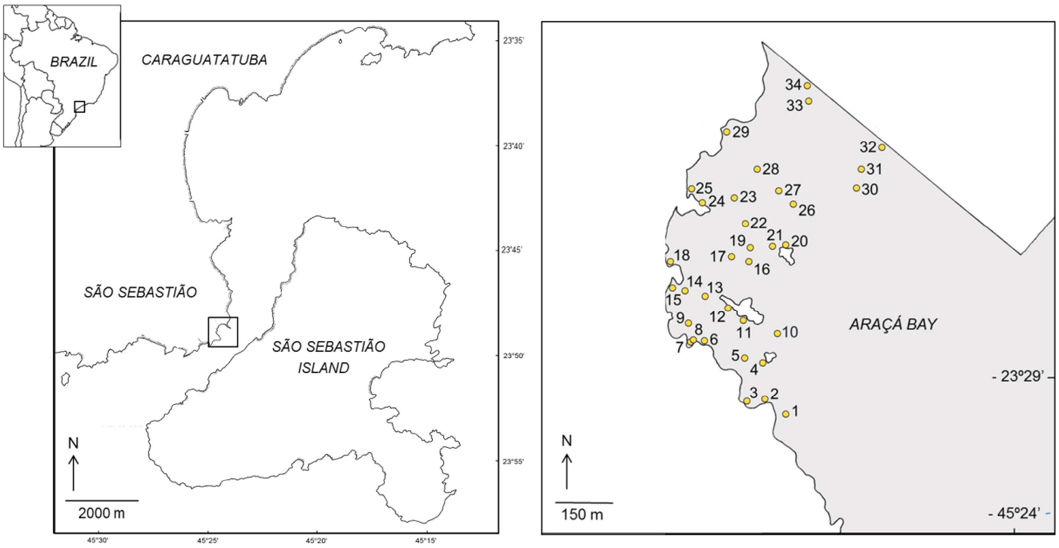

Fig. 1 - Map showing the location of the study area and the spatial distribution of sampling sites in the intertidal area of Araçá Bay.

Sampling was performed on four occasions, 25 September 2011, 5 February 2012, 7 May 2012 and 29 July 2012, in the intertidal area of Araçá Bay. At the first sampling occasion, 34 locations (hereafter sampling stations) were selected attempting to cover the greatest diversity of habitats (i.e. different sediment types in different depth zones of the tidal flat). The position of all sampling stations was registered and the same locations were sampled on next three sampling events. At each sampling station, we collected three sediment samples using a 20-cm diameter core until 20 cm deep for biological data, and one sediment sample using a 3 cm diameter core to a depth of 20 cm for grain size analyses.

On 6 May 2012 and 18 July 2012, unusually large storms - reported as a tornado by the Brazilian media in May (Monteiro 2012, Torrezan 2012) - hit São Sebastião. Torrential rain and strong winds flooded roads and damaged many houses and tourist amenities nearby Araçá Bay in both periods. We sampled the study area on the first spring tide following both storms (one day interval in May and 11 days in July). These two sampling events are hereafter referred as “after storm” samplings, whereas the first two are called “no storm”.

Biological and environmental data

Each biological sample was immediately sieved through a 0.3 mm mesh. The fauna retained was sorted into taxonomic groups and fixed in 70% ethanol. Subsequently, all individuals were identified to the lowest taxonomic level possible.

The sediment samples were oven-dried at 60°C and passed through a series of sieves to determine the mean grain size (Folk and Ward 1957). Organic matter content was determined by the weight differences between samples that were dried at 60°C for 24 h and then incinerated at 550°C for 6 h. Calcium carbonate content was obtained by HCl 10% treatment. The sediment temperature and interstitial water salinity were measured *in situ* with a digital thermometer and a refractometer, respectively. Daily sea temperature data were obtained from CEBIMar, the Marine Biology Center from University of São Paulo, situated 2 km from Araçá.

Data on waves

The height, period and power of the local waves were estimated daily for the entire sampling period (September 1, 2011 to October 31, 2012) based on the regional offshore wave information extracted from the global wave generation model WaveWatch III (NCEP/NOAA) (Tolman 1997). With the aim of assessing storm conditions for the area, wave information for the period of interest has been extracted at a point over the continental shelf south of the São Sebastião channel (24.5 S; 45.5 W).

The daily mean wave height and period were calculated from eight daily values. In order to account for the synergy of wave height and period, the wave power P was estimated by: $P = \rho\ g^2H^2T/32\pi$, where ρ is water density (1,027 kg/m3), g the acceleration due to gravity (9.81 m/s2), H the wave height (m), and T the wave period (s). P is given in watts per meter (W/m) (Herbich 2000).

Data analysis

Prediction 1: Habitat heterogeneity would be reduced after storms

To investigate changes in habitat heterogeneity among sampling periods, we computed the multivariate dispersions among sampling stations in terms of the environmental variables based on Euclidean distances to centroids for normalized data. In this analysis, higher heterogeneity among sampling stations would result in higher multivariate dispersions (Anderson 2006). Then, we used a test for homogeneity of multivariate dispersions (Anderson and Walsh 2013) to check if habitat heterogeneity varied among sampling periods. We also performed a principal component analysis (PCA) on normalised environmental data to evaluate how environmental features varied trough time. PCA and tests for homogeneity of multivariate dispersions (PERMDISP routine) were done in Primer 6 (Anderson et al. 2008).

Prediction 2: macrobenthic communities are influence by different environmental variables after storms

To determine which environmental variables were the most significant to explain variation in macobenthic communities in each sampling period, we regressed the community matrix on the environmental dataset through a Redundancy Analisys with stepwise selection procedure. We used sediment fractions (mud, fine sand, coarse sand and pebble), mean diameter, sorting, calcium carbonate and organic matter content, salinity and depth as explanatory variables. Mean diameter, coarse sand and pebble percentages were excluded from the analysis to keep the variation inflation factor lower than 3 (Zuur et al. 2010). Before analyses, fractions were logit transformed (Warton and Hu) and sorting, salinity and depth were standardized. The Hellinger transformation was used in the community matrix to reduce the importance of large abundances (Legendre and Gallagher 2001). RDA analyses were done in the R environment using the package vegan (Oksanen et al. 2013).

Prediction 3: reduction in habitat heterogeneity affects β diversity in macrobenthic communities

We used two different approaches to determine β diversity: (1) the multivariate dispersion considering the average dissimilarity from individual observation units to their group centroid (Anderson 2006, Anderson et al. 2011), and (2) directly calculating the total variance of the site-by-species community data matrix (Legendre and De Caceres 2013). The first method is useful to test for differences among areas or times through a multivariate test for homogeneity in dispersions (i.e. higher dispersions would be related to higher β diversity) (Anderson et al. 2011). The second approach has the advantage of allowing the partition of the total variance of the community composition data into additive components: (i) Species Contribution to β Diversity (SCBD), which indicates which species exhibit large variations across the study area, and (ii) Local Contribution to β Diversity (LCBD), which represents the contribution of individual sampling units to the overall β diversity (i.e. the degree of uniqueness of the sampling units in terms of community composition *sensu* Legendre and De Cáceres 2013). Here, large LCBD values indicate sites that have strongly different species compositions.

To test if the β diversity varied in time, differences in β-diversity among the sampling periods were tested using a test for homogeneity of multivariate dispersions (Anderson et al. 2008). Tests were done on the basis of Bray-Curtis (abundance, forth root transformed) resemblance measuresusing the PERMDISP routine, Permanova+ add-on in Primer 6 (Anderson et al. 2008). The total variance of the site-by-species community data and SCBD and LCBD were calculated in the R environment using the function beta.div (Legendre and De Cáceres 2013).

Prediction 4: Storms result in mass-mortality events

We inferred mass-mortality from declines in species richness, abundance and biomass. Species richness and abundance were analyzed using two expressions: (1) the cumulative α diversity, which is the total number of species recorded in the total number of sampling stations per sampling period (cumulative alfa diversity can be viewed as the gamma (γ) diversity for each period); and (2) the average α diversity ($\overline{\alpha}$), which is the which is the mean number of species (individuals) per sampling station in each period. The same approach was used to calculate the cumulative and average abundance. To investigate changes in biomass, we selected twenty-four species which corresponded to more than 95% of the total of individuals collected in all sampling events (Annex 1). At each sampling occasion, about one third of the individuals of each one of those species were randomly selected. Larger individuals (mainly molluscs and crustaceans) were weighed individually, whereas biomass of small species was determined by pooling all individuals of the same species per sampling date. The soft tissue of individuals was thus dried at 80°C until it reached a constant weight, yielding the shell-free dry mass (SFDM). The SFDM was then ignited in a muffle furnace at 550°C for 5 h to estimate the ash-free dry mass (AFDM) (Urban and Campos 1994). Mean individual biomass ($\overline{w}$) was determined dividing the AFDM by the number of individuals weighed. Thus, the number of individuals of each species in each sampling station was multiplied by their mean individual biomass to achieve biomass values per sampling station.

Temporal variability on species richness, abundance and biomass of macrobenthic assemblages were assessed through generalized linear models (Bolker et al., 2009). We tested for differences between sampling periods considering time as a fixed factor and sampling stations as replicates. Candidate models using zero-inflated negative binomial and Poisson distribution were adjusted (Zuur et al. 2009). Model parameters were estimated by Markov Chain Monte Carlo (MCMC) simulation, using package glmmADMB (Fournier et al. 2012, Skaug et al. 2012) of the R Program. Corrected Akaike information criteria (AICc), LogLikelihood scores and Akaike weights (AICw) were used in model inferences (Burnham and Anderson 2002). We also used the R package mvabund (Wang et al. 2012) to test for months differences on the multivariate abundances using generalised linear models (GLM) with Poisson distribution. The same package was used to produce a plot to visualize differences.

Prediction 5: changes in β diversity should be more related to loss of species than to turnover of species.

To test this prediction, we used the partitioning framework developed by Podani and Schmera (2011) and Carvalho et al. (2012), where β diversity (βtotal) is partitioned in β diversity explained by replacement (turnover) of species alone (βrepl) and β diversity explained by species loss/gain (richness differences, βrich). This analysis was done with the R package BAT– Biodiversity Assessment Tool (Cardoso et al. 2015).

Results

Environmental characterization

Environmental characteristics for the four sampling periods are presented in Table 1. Seawater temperature varied seasonally, with warmer waters during summer (February 2012) and cooler waters in winter (July 2012). Salinity was higher in September 2011 and lower in July 2012. Within each period, salinity was more variable in February 2012. No great variation in organic matter content was recorded. Sediment features varied throughout the study period, and the content of silt and clay and fine sand in the sediment increased from September 2011 to July 2012, whereas the coarser fractions of sediment decreased (Table 1, Figure 2).

Table 1. Environmental variables across the sampling periods. Numbers in parenthesis correspond to standard deviation.

	September/11	**February/12**	**May/12**	**July/12**
Temperature (^oC)	21.91 (±1.40)	27.24 (±1.03)	25.04 (±1.22)	20.35 (±0.54)
Salinity	32.26 (±1.96)	31.68 (±5.01)	30.59 (±3.92)	29.94 (±3.55)
Mean diameter (phi)	2.47 (±0.70)	2.68 (±0.69)	2.72 (±0.54)	2.79 (±0.64)
Silt and clay (%)	4.18 (±3.66)	4.73 (±3.37)	4.80 (±3.65)	5.71 (±5.29)
Fine sand (%)	68.49 (±18.65)	73.47 (±19.49)	74.09 (±16.36)	74.73 (±17.77)
Coarse sand (%)	16.83 (±16.85)	12.88 (±15.43)	11.10 (±11.89)	10.46 (±14.93)
Peebles (%)	6.18 (±8.60)	3.73 (±6.84)	3.19 (±5.21)	3.16 (±6.07)
Organica matter (%)	1.63 (±0.75)	1.68 (±1.20)	1.72 (±0.89)	1.86 (±1.28)
$CaCO_3$ (%)	4.88 (±2.52)	4.43 (±2.59)	3.76 (±2.73)	3.48 (±1.86)
Power of waves (3 days)	19.7 (±0.09)	16.0 (±0.10)	32.1 (±0.06)	29.3 (±0.06)
(7 days)	13.2 (±0.15)	13.9 (±0.32)	47.8 (±0.21)	20.0 (±0.21)
(14 days)	31.5 (±0.15)	14.8 (±0.30)	52.0 (±0.19)	47.5 (±0.19)
Height of waves (3 days)	1.48 (±0.31)	1.60 (±0.10)	1.87 (±0.21)	1.64 (±0.06)
(7 days)	1.85 (±0.44)	1.39 (±0.31)	2.27 (±0.49)	1.35 (±0.45)
(14 days)	1.79 (±0.43)	1.48 (±0.30)	2.26 (±0.38)	1.91 (±0.81)

Power of waves (KW/s); Height of waves (m)

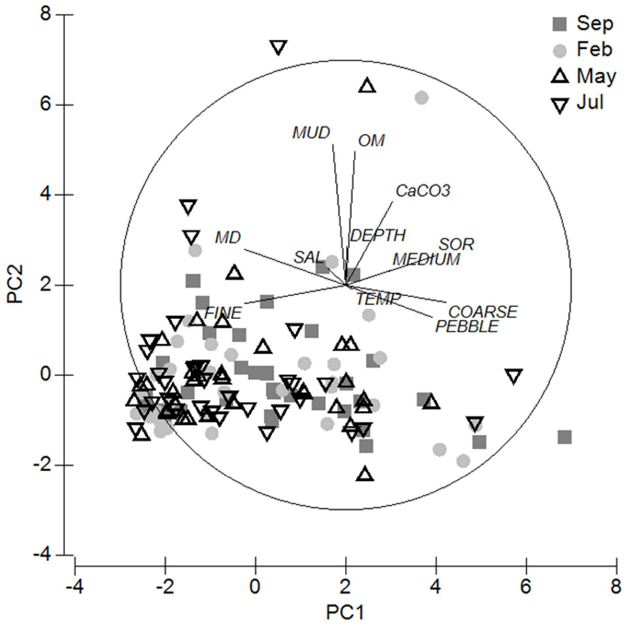

Figure 2 - Biplot of PCA analysis using environmental variables from the Araçá Bay. (FINE) fine sand percentage, (MD) mean diameter, (SAL) salinity, (MUD) mud, (OM) organic matter content, (CaCO3) calcium carbonate content, (DEPTH) depth, (MEDIUM) medium sand percentage, (TEMP) temperature, (SOR) sorting coefficient, (COARSE) coarse sand percentage, (PEEBLE) peeble percentage.

Because macrobenthic communities may show a delayed response to a change in environmental conditions, we analysed the wave data from time windows of three, seven and 14 days before each sampling period. For all time wondows, waves were more powerful before samplings in May and July 2012 (Table 1, Figure 3). These values are related to the offshore wave climate and are an indication of energetic events in the region of Araçá Bay.

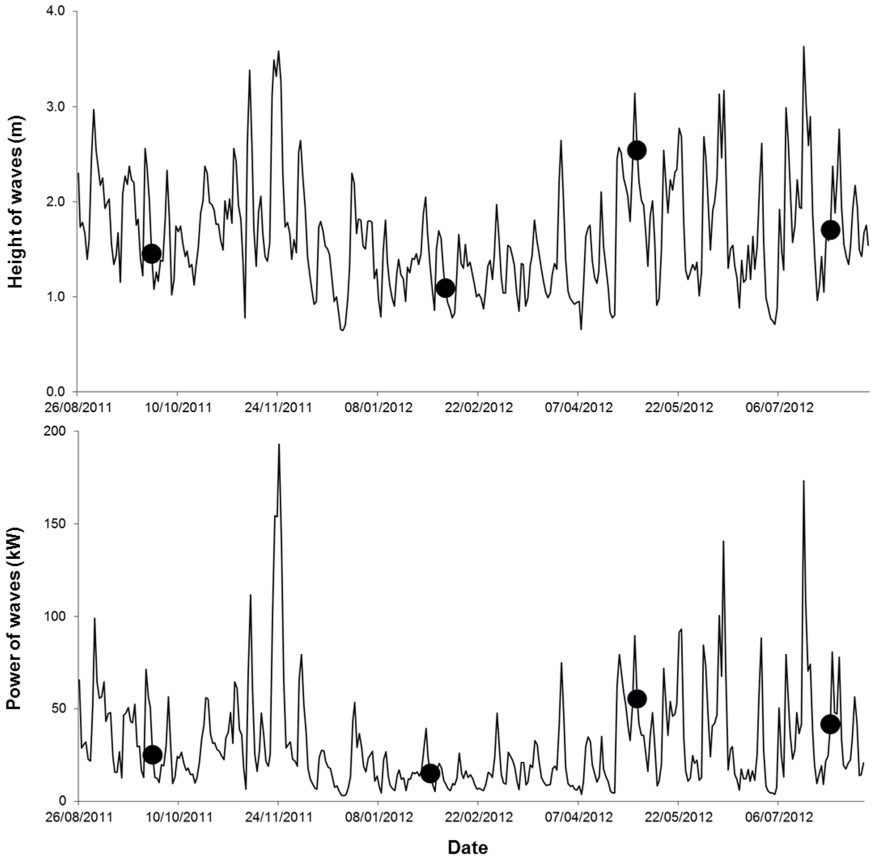

Fig. 3 – Wave height and wave power from 30 days before the first sampling period until 15 days after the last sampling period.

Prediction 1: Habitat heterogeneity would be reduced after storms

Sediment was slightly more homogeneous among sampling stations in May and July 2012, as showed by the more clustered pattern in the ordination axis (Figure 3) and the lower mean distance to centroid in the multivariate dispersion analyses ($\bar{d}$: September 2011 = 29.6, February 2012 = 30.4; May 2012 = 25.8; July 12 = 27.6). These differences, however, were not enough to be detected in the multivariate dispersion analysis (Table 2).

Tab. 2 – Pairwise comparisons of environmental and biotic characteristics of each month.

	Environment		**Biological**	
Groups	**t**	**P**	**t**	**P**
Sept x Feb	0.26	0.83	0.21	0.86
Sept x May	12.84	0.24	**23.41**	**0.03**
Sept x Jul	0.61	0.60	0.95	0.419
Feb x May	15.02	0.22	19.58	0.07
Feb x Jul	0.82	0.52	11.27	0.289
May x Jul	0.54	0.66	**37.68**	**0.001**

Prediction 2: macrobenthic communities are influence by different environmental variables after storms

Overall, macrobenthic communities were influenced by similar environmental variables on periods before and after storms. Depth was important in all four periods analysed, whereas sediment features was relevant in three periods (Table 3).

Table 3. Results of forward selection in RDA performed on macrofaunal and meiofaunal datasets.

Month	Selected variable	AIC	F	P
September 2011				
Macrofauna (11.89%; P = 0.008)	Fine sand	-19.91	2.69	0.01
	Depth	-20.69	2.64	0.01
February 2012				
Macrofauna (12.82%; P = 0.001)	Salinity	-20.96	2.55	0.005
	Depth	-21.31	2.22	0.01
	Fine sand	-21.26	1.77	0.04
May 2012				
Macrofauna (13.90%; P = 0.002)	Depth	-14.44	4.14	0.005
	Fine sand	-14.61	2.04	0.04
July 2012				
Macrofauna (16.99%; P = 0.001)	Depth	-18.16	2.82	0.01

Prediction 3: reduction in habitat heterogeneity reduces β diversity in macrobenthic communities

Contrary to our expectation, total β diversity was higher in May 2012 (Tables 2 and 4) and no pattern in β diversity changes could be related to the influence of storms. Nonetheless, β diversity values depended on the method used. The multivariate dispersion to the group centroid (Anderson 2006, Anderson et al. 2011) indicated that β diversity was lower in July 2012, however, the direct calculation of the total variance of the site-by-species community data matrix (Legendre and De Caceres 2013) showed that β diversity was lower in February 2012. An inverse relationship was observed between β diversity and the LCBD values, which were lower in May 2012 (Table 4, Figure 4). The crustacean *Monokalliapseudes schubarti*, the polychaetes *Capitella* spp, *Armandia hossfeldi*, *Scoloplos* sp. and *Laeonereis culveri*, and the gastropod *Olivella minuta* were the species that had higher SCBD values.

Table 4. Total number of individuals (Ind) and diversity indices in all sampling periods. A: total abundance; $\bar{A}$: average number of individuals per sampling station; γ: gamma diversity; $\bar{\alpha}$: average alpha diversity; $\bar{d}$: multivariate dispersion to the group centroid; β (SS): β diversity according the total variance community data;LCDB: local contribution to β diversity; B: biomass

	A	$\bar{A}$	γ	$\bar{\alpha}$	$\bar{d}$	*β (SS)*	LCBD	B
Sep 11	9606	280.6 (±358.5)	83	14.4 (±5.4)	44.2	0.55	1.39-6.97	20.7 (±0.7)
Feb 12	13228	389.1 (±343.4)	79	11.9 (±5.1)	44.8	0.38	0.72-11.96	14.2 (±0.4)
May 12	3828	112.6 (±233.2)	65	9.8 (±3.9)	49.6	0.68	1.68-3.99	11.1 (±0.5)
Jul 12	6722	197.7 (±245.4)	66	12.4 (±3.9)	41.9	0.58	1.86-4.60	16.6 (±0.4)

B: gAFDM per 3.2 m^2 (total area sampled per month)

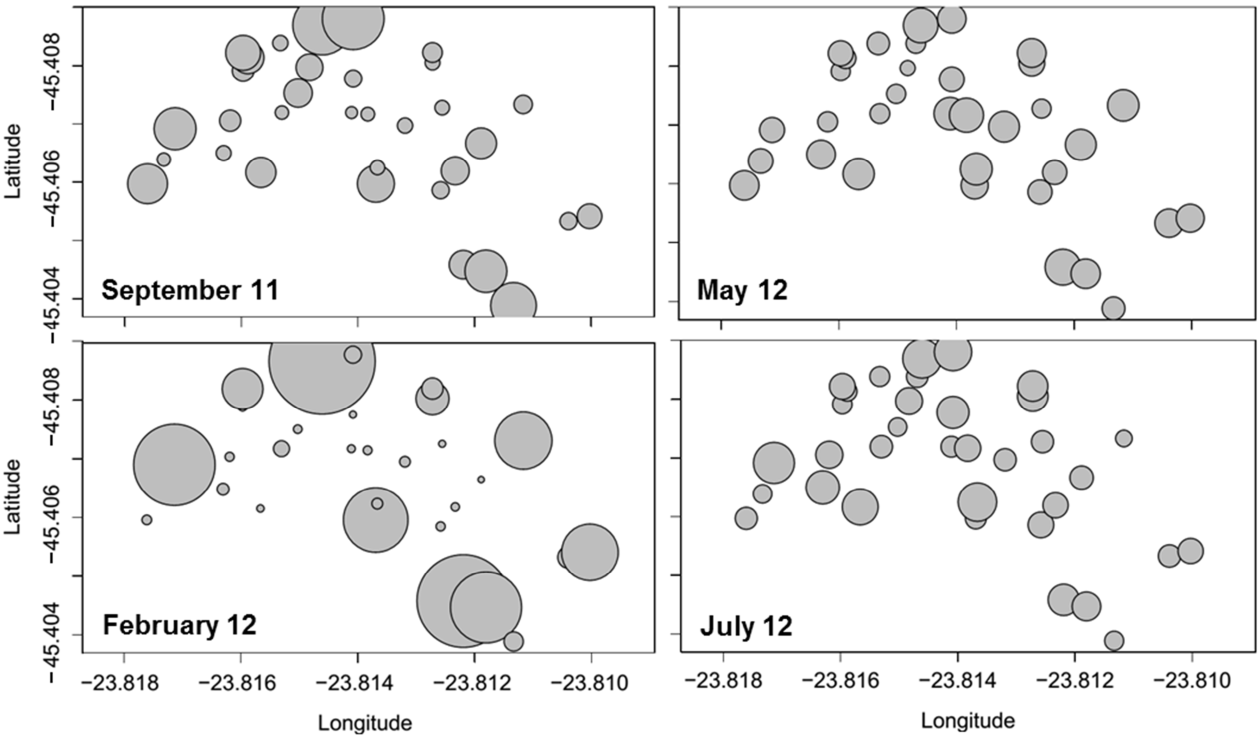

Fig. 4 – Local contribution to β diversity (LCBD) in all sampling events. Circles correspond to the proportion of LCBD of each sampling station. Sum of all circles in each period correspond to 100%.

Prediction 4: Storms would result in mass-mortality events

From differences in species richness, abundance and biomass (Tables 4 and 5, Figure 5), we inferred that mass-mortality event might have occurred in May 2012, when was observed a reduction of more than 70% of individuals from the sampling before (Annex 1). Differences on the multivariate abundances were also detected, with lower values in May and

July (Wald test $_{(3,\ 132)}$ = 110.1; P<0.001). The declines in abundance and biomass reductions were greatly influenced by changes in the population of the crustacean *Monokalliapseudes schubart*, which had a decrease of almost 95% of infividuals between February and May 2012 (Figure 6 - Annex 2).

Table 5 - Results from generalized linear models fitted for species richness, abundance and biomass of macrobenthic assemblages of Araçá Bay.

	Estimate	**SE**	**Z-Value**	**P-value**
Richness				
(Intercept)	2.66	0.06	44.88	
February	-0.19	0.08	-2.21	**0.03**
May	-0.37	0.09	-3.99	**<0.001**
July	-0.13	0.09	-1.55	0.12
Abundance				
(Intercept)	5.62	0.14	39.24	
February	0.16	0.18	0.85	0.40
May	-0.58	0.20	-2.87	**<0.01**
July	-0.18	0.19	-0.93	0.36
Biomass				
(Intercept)	6.41	0.16	39.49	
February	-0.37	0.23	-1.64	0.10
May	-0.62	0.23	-2.71	**<0.001**
July	-0.21	0.23	-0.96	0.34

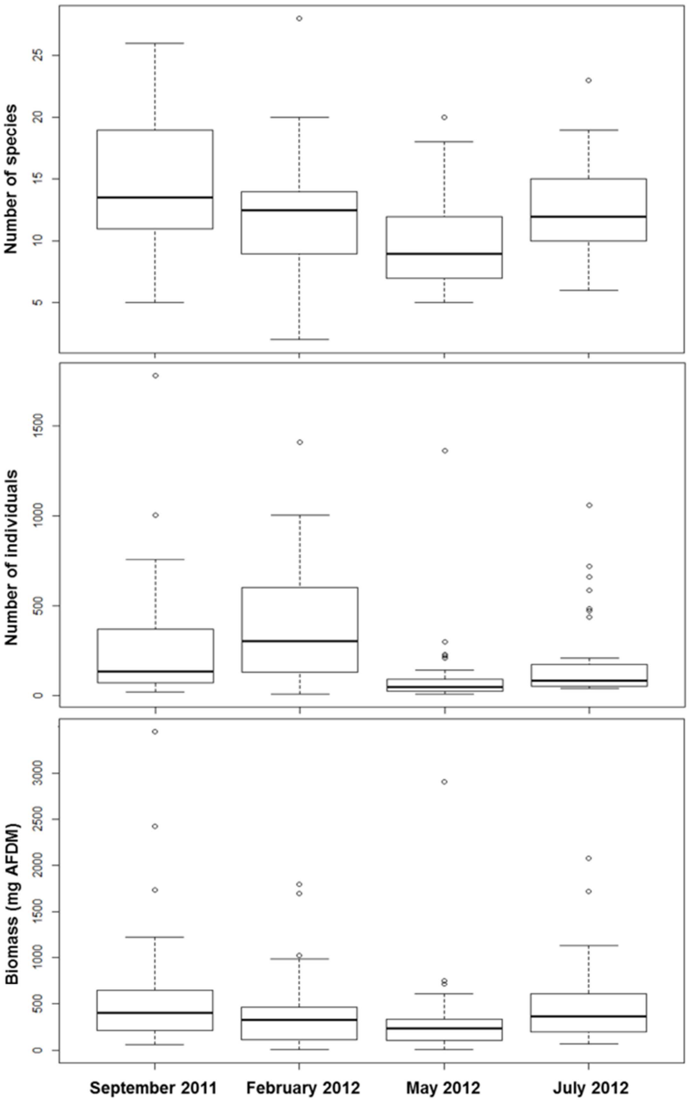

Fig. 5 - Boxplot of number of species, abundance and biomass of macrobenthic organisms in Araçá Bay during the study period.

Prediction 5: changes in β diversity should be more related to loss of species than to turnover of species.

The analysis of β diversity between months showed that strong differences were observed between periods, and these differences were stronger between periods no storm and after storms. Moreover, as expected, most of this variation was related to loss of species loss (Table 4).

Tab. 4 – Β diversity among different sampling envents (months). Values inside the brackets correspond to the fraction of β diversty related to species replacement (Brepl) and species loss/gain (Brich).

	Sep	**Feb**	**May**
Feb	Bt = 0.45; Brepl = 0.20; Brich = 0.25		
May	Bt = 0.83; Brepl = 0.33; Brich = 0.50	Bt = 0.79; Brepl = 0.13; Brich = 0.66	
Jul	Bt = 0.72; Brepl = 0.50; Brich = 0.22	Bt = 0.73; Brepl = 0.32; Brich = 0.41	Bt = 0.47; Brepl = 0.05; Brich = 0.42

Discussion

Most of previous works about the influence of storms on coastal soft-sediment ecosystems have showed that storms may have stronger impacts on environmental characteristics than on macrobenthic assemblages (Saloman and Naughton 1977, Cochôa et al. 2006, Alves and Pezzuto 2009, Harris et al. 2011). Our results, however, suggest the opposite trend. As observed by Sola and Paiva (2001) in a sheltered sandy beach in Rio de Janeiro, Brazil, we found that storms did not deeply affected the habitat features of Araçá Bay, but changed its biodiversity patterns.

Overall, two of our five *a priori* predictions were supported. We found that species richness, abundance and biomass of macrobenthic organisms declined after the first storm (predictions 4 and 5). However, we did not find strong evidence for the hypothesis that storms would reduce habitat heterogeneity (prediction 1). Furthermore, the prediction that macrobenthic assemblages would be influenced by different environmental variables after storms (prediction 2) was not supported. Since we did not find strong evidence for changes in habitat heterogeneity, our third prediction, i.e. reduction in habitat heterogeneity reduces β diversity, was also not confirmed.

The lack of strong modifications in environmental features of Araçá Bay in periods after storm is likely related to the sheltered characteristics of the area. The magnitude of erosive processes related to storms depends on the morphodynamic state of the environment, and the same wave climate acting on different morphodynamic conditions produces different responses in terms of morphological changes (Short 2000). In this regard, exposed-reflective environments are more susceptible to enhanced hydrodynamic processes, whereas a much higher amount of wave energy is necessary to affect sheltered environments with wide and flat intertidal areas where a larger amount of wave energy is dissipated (Short 2000, Di Domenico et al. 2014). In this regard, the characteristics of Araçá Bay (i.e. a wide tidal flat and sheltered by São Sebastião Island) are likely to protect the area from wave action, therefore preventing the occurrence of strong changes in its habitat features. Notwithstanding, a slightly homogenization of sediment was observed in periods after storms, as well as an increase of the fraction of fine sand. Similar results were reported by Sola and Paiva (2001) and Gallucci and Netto (2004) after the passage of cold fronts over coastal soft-sediment ecosystems in Southeast and South Brazil, respectively.

Although changes in habitat heterogeneity after storms were not sufficient to be detected by statistical analyses, β diversity was higher in May. Despite the increased β diversity, the LCBD values were more similar in May, which indicates that different sites within the bay contributed more evenly to total beta diversity after storms. This result implies that assemblages varied in a constant way, and none of them had strongly different species compositions. Therefore, macrobenthic assemblages were more similar in periods after storm probably a consequence of increased hydrodynamic processes which may directly influence macrobenthic assemblages (Sola and Paiva 2001). In tidal systems such as Araçá Bay, dispersion of individuals is promoted by regular tide-mediated currents and also by stochastic wave-driven resuspension events (Valanko et al. 2010). When these conditions are present, coastal environments become more turbulent and variable, with intense offshore-directed currents and high rates of cross-shore sediment transport (Delgado and Defeo 2004, Masselink and Puleo 2006). Thus, it is reasonable to infer that larger waves and faster currents associated to storms might have changed the spatial patterns and homogenized macrobenthic communities. Additionally, it is also possible that the increased hydrodynamic related to storms may have washed away many individuals, resulting in the observed decrease of abundance, species richness and biomass in May. Transportation of sediment and associated fauna due to wind-induced waves or tidal currents has been reported as a likely determinant of short-term temporal variations in local community composition (Armonies 2000).

Shifts in the abundance of species also reinforce the hypothesis that many macrofaunal individuals were washed away due to increased waves and water circulation. Decrease in the number of less mobile and shallow burrower species, such as the polychaete *Isolda pulchella* and the bivalve *Anomalocardia brasiliana*, after the first storm suggest that they might have be removed with the top layer of sediment. Furthermore, the most impressive change in abundance is related to the tanaidacean *Monokalliapseudes schubarti* (a decrease of 95% in abundance in May 2012), which usually builds shallow tubes and is very sensitive to environmental changes (Nucci et al. 2001, Pagliosa and Barbosa 2006). Similar result was registered by Sola and Paiva (2001), which reported a significant decrease of tanaidaceans after the passage of storms in Rio de Janeiro, Brazil. *Monokalliapseudes schubarti* – and tanaidaceans in general - is an important component of macrobethic soft-bottom intertidal and shallow water communities in South America and, due to its high abundance and continuous reproduction, is an important food resource to higher thropic levels (Leite et al. 2003, Fonseca and D'Incao 2006). The significant reduction of this species resulted in decreases in biomass, and suggests that storms may affect the trophic status of marine coastal ecosystems.

It is important to highlight, however, that many factors can contribute to the mortality of macrofaunal organisms. Besides episodic events such as storms, which induce an increase of mortality due to physical disturbances, mortality may be natural due to ageing process, death of animals after spawning and high rate of natural mortality among recent recruits to the benthos (Brey 1999). Moreover mortality may be enhanced by seasonal changes in the environmental (e.g., temperature, organic matter, salinity) and biotic features (e.g. seasonal changes in number of predators, parasites and diseases) (Brey and Gage 1997). Due to the lack of replication at the temporal scale, we cannot unequivocally disentangle storms effects from seasonal effects. To hinder this situation, the austral fall and winter are usually associated to an increase in the occurrence of extra-tropical cyclones in the Southern hemisphere. These cyclones are accompanied by frontal systems, commonly known as cold fronts, which form extensive regions on oceans with uniform winds over 10 m/s (Stech and Lorenzzetti 1992). These winds are usually associated with precipitation and produce high energy waves which usually hit the West coast of continents, including South America (Stech and Lorenzzetti 1992, Castro and Miranda 1998, Cochôa et al. 2006). In this scenario, storms may be an additional seasonal factor that shape coastal ecosystems and contribute to their dynamic nature.

Regardless of being a major influence or one additional variable shaping coastal ecosystems and their assemblages, storms seems to cause more pronounced changes on macrobenthic biodiversity in the short-term. Even though we have sampled Araçá Bay on the first spring tide following two storms, differences in environmental and biotic characteristics were stronger after the first storm, when the sampling was done after a one day interval. Moreover, very strong waves hit São Sebastião in November 2011, but no difference in macrobenthic assemblages were detected between samplings done on September 2011 and February 2012. In a coastal soft-sediment ecosystem in South Brazil, Gallucci and Netto (2004) found that abundance and number of species of macrobenthic organisms declined during the passage of a cold front, but all values were back to pre-frontal conditions 24 h later. Similarly, Schlacher and Thompson (2013) observed that wave height and maximum wave height had a better correlation with changes in macrobenthic assemblages on a very short time window (up to 1 day). Taken together, these results indicate that intertidal macrobenthic assemblages show high resilience and may quickly recover from short-term and unpredictable environmental disturbances related to storms.

Even though soft-sediment macrobenthic communities may show strong resilience, it is important to consider that this property of ecological systems is dependent on the biological organization, as well as the frequency and intensity of disturbances (Thrush et al. 2008). On the past decades, theoretical and empirical evidence suggests that declines in diversity is expected to reduce ecosystem stability (i.e. resistence and resilience) because less diverse communities are less likely to contain species, or functional groups, that are capable of differential response which could act as buffers against dramatic changes in population dynamics (Hutchinson 1959, Tilman 1996, McCann 2000). Moreover, a growing body of evidence has been showing that cumulative or multiple stressor effects can lead to the loss of resilience and an increased risk of regime shift (Thrush et al. 2008, Thrush et al. 2009). The partition of beta diversity and the temporal analysis of species richness showed that changes after storms are mainly a consequence of species loss. These results suggest important implications for management and conservation of coastal ecosystems, with frequent and intense storms being likely to reduce diversity and also the resilience of marine soft-sediments.

Despite the limitations of this study associated to the unpredictable nature and large extent of storms, our results suggest that storms have a direct impact on macrobenthic assemblages and, in a less extent, may also change habitat features of a sheltered coastal ecosystem. The magnitude of those effects, however, probably depends on the morphodynamic characteristics of the environment and the cumulative impact of storms. Since climate change projections highlights that storms will likely have their frequency and intensity increased in the near future (Baker et al. 2008, IPCC 2014), to properly investigate these phenomenon and how they influence the organization of ecological assemblages is of great importance for conservation and management purposes (Harris et al. 2011). In this regard, to investigate our set of *a priori* hypotheses and predictions in other areas can be important for the development of a forecasting ability to identify storm effects. This approach would allow the anticipation or prevention of unwanted regime shifts which may compromise the ecological importance, multiple uses and economic values of coastal ecosystems.

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Annex 1

Table 5. Total number of individuals and relative proportion of species registered at each sampling. Species written in bold correspond to those used in biomass analysis.

	September 2011		**February 2012**		**May 2012**		**July 2012**	
	N ind	**Freq (%)**	**N ind**	**Freq (%)**	**N ind**	**Freq (%)**	**N ind**	**Freq (%)**
Edwardisia	0	0.00	0	0.00	19	0.50	2	0.03
Neritina virginea	**11**	**0.12**	**5**	**0.04**	**14**	**0.37**	**14**	**0.21**
Cerithium atratum	**85**	**0.89**	**14**	**0.11**	**43**	**1.12**	**41**	**0.61**
Nassarius vibex	4	0.04	5	0.04	1	0.03	0	0.00
Olivella minuta	**176**	**1.84**	**34**	**0.26**	**99**	**2.59**	**103**	**1.53**
Bulla striata	0	0.00	5	0.04	0	0.00	0	0.00
Nucula semiornata	2	0.02	4	0.03	2	0.05	1	0.01
Phacoides pectinata	1	0.01	0	0.00	1	0.03	1	0.01
Diplodonta punctata	1	0.01	0	0.00	1	0.03	5	0.07
Diplodonta patagonica	0	0.00	1	0.01	0	0.00	0	0.00
Solen tehuelchus	0	0.00	1	0.01	0	0.00	0	0.00
Eurytellina lineata	**50**	**0.52**	**15**	**0.11**	**6**	**0.16**	**20**	**0.30**
Tellina sp 1	2	0.02	0	0.00	0	0.00	1	0.01
Tellina sp 2	1	0.01	0	0.00	0	0.00	1	0.01
Strigilla pisiformis	3	0.03	1	0.01	3	0.08	1	0.01
Macoma sp	7	0.07	2	0.02	2	0.05	1	0.01
Semele sp 1	0	0.00	0	0.00	2	0.05	0	0.00
Abra sp1	1	0.01	0	0.00	0	0.00	1	0.01
Ervilia nitens	3	0.03	0	0.00	0	0.00	0	0.00
Tagelus plebeius	1	0.01	3	0.02	0	0.00	1	0.01
Tagelus divisus	4	0.04	2	0.02	1	0.03	0	0.00
Donax gemmula	1	0.01	0	0.00	0	0.00	0	0.00
Iphigenia brasiliana	0	0.00	0	0.00	0	0.00	1	0.01
Gouldia cerina	2	0.02	0	0.00	0	0.00	0	0.00
Chione cancellata	2	0.02	1	0.01	2	0.05	0	0.00
Chione subrostrata	0	0.00	1	0.01	0	0.00	0	0.00
Anomalocardia brasiliana	**91**	**0.95**	**91**	**0.69**	**74**	**1.93**	**94**	**1.40**
Protothaca pectorina	0	0.00	0	0.00	1	0.03	0	0.00
Tivela mactroides	0	0.00	0	0.00	0	0.00	1	0.01
Pitar fulminatus	0	0.00	1	0.01	0	0.00	0	0.00
Clyclinella tenuis	5	0.05	0	0.00	0	0.00	0	0.00
Corbula caribaea	13	0.14	5	0.04	0	0.00	4	0.06
Corbula sp 1	9	0.09	6	0.05	2	0.05	7	0.10
Sphenia antillensis	0	0.00	1	0.01	0	0.00	0	0.00
Periploma ovata	0	0.00	3	0.02	0	0.00	0	0.00
Nemertinea sp 1	25	0.26	0	0.00	12	0.31	1	0.01
Sipuncula sp 1	3	0.03	0	0.00	1	0.03	0	0.00

(cont.)

(cont.)

Phyllodoce mucosa	5	0.05	3	0.02	0	0.00	0	0.00
Eteone alba	2	0.02	0	0.00	0	0.00	0	0.00
Hermundura tricuspis	**47**	**0.49**	**53**	**0.40**	**34**	**0.89**	**54**	**0.80**
Sigambra grubii	6	0.06	1	0.01	3	0.08	10	0.15
Sigambra tentaculata	2	0.02	0	0.00	1	0.03	1	0.01
Ancistrosyllis jonesi	0	0.00	0	0.00	0	0.00	2	0.03
***Syllis* sp 1**	**113**	**1.18**	**126**	**0.95**	**29**	**0.76**	**14**	**0.21**
Laeonereis culveri	**391**	**4.10**	**128**	**0.97**	**51**	**1.33**	**392**	**5.83**
Glycinde multidens	**46**	**0.48**	**25**	**0.19**	**18**	**0.47**	**36**	**0.54**
Goniada litorea	3	0.03	6	0.05	2	0.05	3	0.04
Hemipodia simplex	0	0.00	1	0.01	1	0.03	1	0.01
Diopatra dexiognatha	1	0.01	0	0.00	0	0.00	0	0.00
Diopatra aciculata	7	0.07	6	0.05	2	0.05	0	0.00
Mooreonuphis lineata	0	0.00	2	0.02	0	0.00	2	0.03
Onuphis eremita oculata	0	0.00	1	0.01	0	0.00	0	0.00
Dorvillea sp 0	2	0.02	1	0.01	0	0.00	0	0.00
Marphysa sebastiana	**52**	**0.54**	**36**	**0.27**	**36**	**0.94**	**32**	**0.48**
Nematonereis hebes	0	0.00	3	0.02	0	0.00	3	0.04
Scoletoma tetraura	3	0.03	13	0.10	5	0.13	0	0.00
***Scoloplos (leodamas)* sp 1**	**359**	**3.76**	**201**	**1.52**	**111**	**2.90**	**278**	**4.14**
***Haploscoloplos* sp 1**	**215**	**2.25**	**6**	**0.05**	**5**	**0.13**	**33**	**0.49**
Naineris setosa	**14**	**0.15**	**71**	**0.54**	**4**	**0.10**	**10**	**0.15**
***Protoaricia* sp 1**	**38**	**0.40**	**55**	**0.42**	**18**	**0.47**	**2**	**0.03**
Aricidea (Aricidea) fragilis	16	0.17	3	0.02	6	0.16	6	0.09
Aricidea (Allia) albatrossae	0	0.00	1	0.01	0	0.00	0	0.00
Aricidea cf wassi	0	0.00	0	0.00	0	0.00	18	0.27
Scolelepis squamata	**55**	**0.58**	**122**	**0.01**	**48**	**1.25**	**148**	**2.20**
Scolelepis texana	0	0.00	0	0.00	1	0.03	0	0.00
Dispio uncinata	1	0.01	0	0.00	0	0.00	1	0.01
Dispio remanei	0	0.00	1	0.01	2	0.05	0	0.00
Prionospio steenstrupi	0	0.00	0	0.00	5	0.13	19	0.28
Paraprionospio pinnata	1	0.01	0	0.00	0	0.00	0	0.00
Boccardia polybranchia	2	0.02	1	0.01	0	0.00	0	0.00
Bocardiella ligerica	0	0.00	2	0.02	0	0.00	0	0.00
Polydora nuchalis	2	0.02	38	0.29	0	0.00	1	0.01
Polydora websteri	4	0.04	4	0.03	0	0.00	0	0.00
Polydora sp 1	0	0.00	3	0.02	0	0.00	0	0.00
Polydora sp 2	0	0.00	1	0.01	0	0.00	0	0.00
Magelona nonatoi	1	0.01	0	0.00	0	0.00	0	0.00
Magelona californica	2	0.02	0	0.00	0	0.00	0	0.00
Magelona papilicornis	2	0.02	4	0.03	14	0.37	33	0.49
Magelona variolamellata	1	0.01	0	0.00	1	0.03	1	0.01

(cont.)

(cont.)

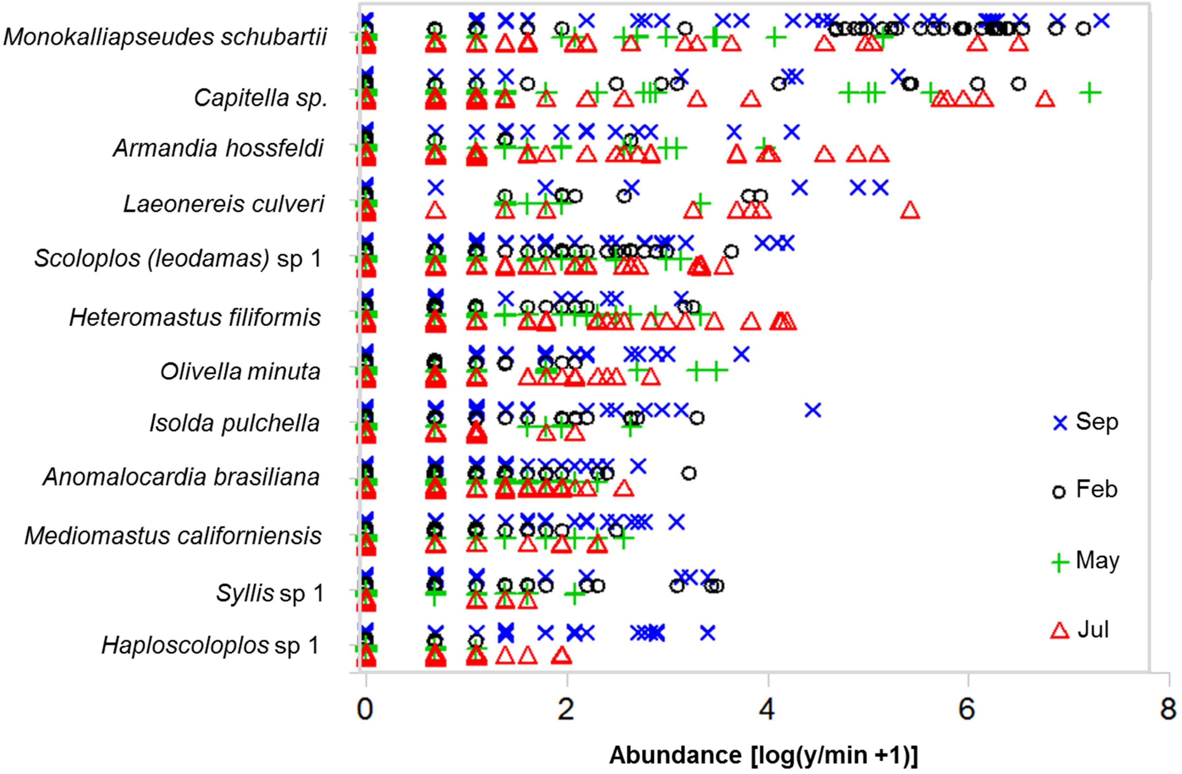
Poecilochaetus perequensis	0	0.00	0	0.00	1	0.03	2	0.03
Poecilochaetus australis	1	0.01	1	0.01	4	0.10	1	0.01
Poecilochaetus sp 1	0	0.00	5	0.04	0	0.00	0	0.00
Sternaspis capilata	0	0.00	0	0.00	35	0.91	3	0.04
Cirriformia tentaculata	26	0.27	4	0.03	0	0.00	0	0.00
Cirriformia filigera	6	0.06	32	0.24	0	0.00	10	0.15
Cirriformia punctata	2	0.02	0	0.00	0	0.00	0	0.00
Armandia hossfeldi	182	1.91	20	0.15	144	3.76	686	10.21
Armandia agilis	7	0.07	0	0.00	5	0.13	14	0.21
Armandia polyophtalama	6	0.06	0	0.00	0	0.00	0	0.00
Capitella spp	**364**	**3.81**	**1670**	**12.62**	**2136**	**55.80**	**2460**	**36.60**
Heteromastus filiformis	**69**	**0.72**	**99**	**0.75**	**145**	**3.79**	**406**	**6.04**
Mediomastus californiensis	**136**	**1.43**	**51**	**0.39**	**59**	**1.54**	**39**	**0.58**
Notomastus hemipodus	3	0.03	3	0.02	6	0.16	4	0.06
Notomastus lobatus	1	0.01	1	0.01	0	0.00	0	0.00
Scyphoproctus sp 1	13	0.14	38	0.29	0	0.00	0	0.00
Clymenella dalesi	2	0.02	2	0.02	0	0.00	1	0.01
Owenia fusiformis	3	0.03	2	0.02	1	0.03	3	0.04
Owenia brasiliensis	0	0.00	0	0.00	1	0.03	0	0.00
Isolda pulchella	**199**	**2.09**	**114**	**0.86**	**36**	**0.94**	**27**	**0.40**
Lioimia medusa	0	0.00	1	0.01	0	0.00	0	0.00
Nicolea uspiana	0	0.00	0	0.00	0	0.00	1	0.01
Terebellides anguicomus	1	0.01	5	0.04	1	0.03	1	0.01
Oligochaeta	0	0.00	20	0.15	11	0.29	0	0.00
Alpheus nittingi	0	0.00	1	0.01	0	0.00	0	0.00
Upogebia brasiliensis	0	0.00	0	0.00	0	0.00	1	0.01
Upogebia vasquezi	0	0.00	0	0.00	1	0.03	0	0.00
Upogebia paraffins	0	0.00	1	0.01	0	0.00	0	0.00
Ogyrides alphaerostris	1	0.01	0	0.00	0	0.00	0	0.00
Caridae sp 1	5	0.05	0	0.00	0	0.00	0	0.00
Dendobranchiata	0	0.00	0	0.00	0	0.00	1	0.01
Processa bermudensis	1	0.01	0	0.00	2	0.05	0	0.00
Pagurus criniticornis	**4**	**0.04**	**4**	**0.03**	**4**	**0.10**	**8**	**0.12**
Clibanarius vittatus	**0**	**0.00**	**0**	**0.00**	**1**	**0.03**	**0**	**0.00**
Clibanarius antillensis	**0**	**0.00**	**1**	**0.01**	**0**	**0.00**	**4**	**0.06**
Pinnixa chaetopterana	0	0.00	2	0.02	0	0.00	1	0.01
Callinectes danae	4	0.04	1	0.01	1	0.03	1	0.01
Panopeus occidentalis	1	0.01	2	0.02	1	0.03	0	0.00
Ocypodidae	1	0.01	0	0.00	0	0.00	0	0.00
Uca leptodactyla	1	0.01	0	0.00	0	0.00	0	0.00
Amphipoda sp 1	0	0.00	1	0.01	0	0.00	0	0.00
Monokalliapseudes schubartii	**6583**	**68.99**	**9988**	**75.51**	**541**	**14.13**	**1647**	**24.50**

(cont.)

(cont.)

Ophiuroidea sp 1	4	0.04	0	0.00	2	0.05	0	0.00
Holothuroidea sp 1	10	0.10	0	0.00	0	0.00	0	0.00
Cephalochordata sp 1	10	0.10	0	0.00	5	0.13	0	0.00
Total	9542	100	13227	99	3828	100	6722	100

Annex 2


Monokalliapseudes schubartii
Capitella sp.
Armandia hossfeldi
Laeonereis culveri
Scoloplos (leodamas) sp 1
Heteromastus filiformis
Olivella minuta
Isolda pulchella
Anomalocardia brasiliana
Mediomastus californiensis
Syllis sp 1
Haploscoloplos sp 1
× Sep
o Feb
+ May
△ Jul
0
2
4
6
8
Abundance [log(y/min +1)]

Capítulo 2

Dispersal ability affects the relative importance of environmental and spatial processes on marine macrobenthic communities

Abstract

Community ecology has traditionally assumed that the distribution of species is mainly influenced by environmental processes. There is however, growing evidence that environmental (habitat characteristics and biotic interactions) and spatial processes (factors that affect a local assemblage regardless of environmental conditions - typically related to dispersal and movement of species) interactively shape biological assemblages. A metacommunity, which is a set of local assemblages connected by dispersal of individuals, is spatial in nature and can be used as a straightforward approach for investigating the interactive and independent effects of both environmental and spatial processes. Here, we examined (i) how environmental and spatial processes affect the metacommunity structure of marine macroinvertebrates inhabiting the intertidal sediments of a biodiverse sandy-muddy tidal flat, and (ii) whether these effects are constant through time. We also investigated (iii) whether the relative importance of those processes depends on the dispersal abilities of organisms. We found that these macrobenthic assemblages are influenced by each of environmental and spatial variables; however, this influence changes through time and may be affected by stochastic events, such as storms. Moreover, we found that the influence of environmental and spatial processes varied according to the dispersal capabilities of organisms, and less effective dispersers, i.e. species with non-planktonic larvae and adults with reduced mobility, are more affected by spatial processes. These findings highlight that accounting for spatial processes and differences in species life histories is important to better understand species distribution and coexistence patterns in intertidal soft-sediments.

Introduction

Community ecology has historically focused on a single spatial scale assuming that biological assemblages are mainly structured by local interactions (Paine 1969, Connell 1980, 1983) and environmental features (Janzen 1967, Pianka 1981, Logue et al. 2011). On the past decades, however, an increasing body of work has been showing that spatial processes, which includes all factors that affect a local assemblage regardless of environmental conditions - typically related to dispersal and movement of species (Leibold et al. 2004, Heino et al. 2015), may also strongly influence local assemblages (e.g. Underwood 1994, Goncalves-Souza et al. 2014, Leibold and Loeuille 2015).

The metacommunity approach is an effective conceptual tool to investigate the interplay of environmental and spatial processes driving the composition and distribution of species (Cottenie 2005, Holyoak et al. 2005). A metacommunity is defined as a set of local assemblages that are linked by dispersal of potentially interacting species and is regulated by both environmental and spatial processes (Wilson 1992, Leibold et al. 2004). Although it is a straightforward approach to evaluate the interactive way these processes affect biological communities, there are few broad generalizations because most investigations around metacommunity processes were done in freshwater habitats (Logue et al. 2011), with few or no tests for other systems. Accordingly, the results until now are likely contingent to the system and the spatial extent studied. As dispersal is the fuel supplying organisms to local assemblages, the dispersal ability of organisms is also a central issue for deriving general theoretical predictions (Hájek et al. 2011, Grönroos et al. 2013, Heino 2013, Landeiro et al. 2014).

It has been suggested that the relative role of spatial processes increase with increasing spatial extent because fewer species are able to disperse across broad geographical scales (Cottenie 2005, Árva et al. 2015). Moreover, organisms with efficient and active dispersal can be less limited by spatial processes because of their higher ability to track environmental variability. On the other hand, spatial processes should be more important for poor and passive dispersers because of their reduced dispersal capacity. Therefore, a crucial element in metacommunity theory is the interaction between dispersal and environmental variability. As a consequence, the relative role of environmental and spatial processes may change over time due to seasonal changes in the environmental variables (Thrush et al. 2010, Datry et al. 2015) or to stochastic factors such as disturbance events and random supply of individuals

(Vanschoenwinkel et al. 2013, Gerwing et al. 2016). Notwithstanding, temporal changes in the metacommunity dynamics is still largely overlooked (Heino et al. 2015).

The application of the metacommunity approach can be especially useful in marine systems (Heino et al. 2015), where (1) all the patches are characterized as open systems, and thus they are virtually linked to each other via dispersal (Gray and Elliott 2009), and (2) species have different dispersal capabilities, varying from organisms able to disperse only a few centimeters to other that disperse thousands of kilometres (Shanks 2009, Pilditch et al. 2015). Macrobenthic invertebrates, for example, disperse across all life-history stages, ranging from species with reduced dispersal rates (absence of pelagic larval stages and adults with reduced mobility), to species that can reach great distances from their parents (with long-lived planktonic larval stages and high motile adults) (Thorson 1950, Whitlatch et al. 1998, Valanko et al. 2010). Nevertheless, very few studies have applied the metacommunity approach to marine systems (Heino et al. 2015), where most studies investigated the responses of organisms to physicochemical variables (de Juan and Hewitt 2011, Quillien et al. 2015).

In intertidal marine soft-sediments, considerable research has shown the influence of environmental variables, such as sediment type, salinity, wave action, tide, and exposure time to air on the distribution of benthic macrofauna (e.g. Lercari and Defeo 1999, Gray 2002, Thrush et al. 2005a). As a consequence, most models explaining patterns of intertidal marine soft-sediment assemblages assume that they are driven mainly by environmental processes (e.g. McLachlan 1990, McLachlan et al. 1993, Defeo and McLachlan 2005). Moritz et al. (2013) and Heino et al. (2015), however, argue that the high dispersal rates observed in marine ecosystems may homogenise assemblages at neighbouring localities, therefore, favoring spatial variables. Recently, Quillien et al. (2015) and Gerwing et al. (2016) supported this hypothesis by showing that spatial processes were important in structuring soft-sediment intertidal assemblages. These studies also showed that patterns of intertidal soft-sediment assemblages vary through time, reflecting changes in habitat heterogeneity, species population dynamics and disturbances.

We examined the relative importance of environmental and spatial processes on marine macrobenthic invertebrates inhabiting the intertidal sediments of a biodiverse and environmentally heterogeneous sandy-muddy tidal flat. The data set consisted of 34 locations distributed over approximately 0.22 Km^2 (largest distance between two locations about 850 m), a small scale when compared to other studies which investigated the role of spatial and environmental processes in coastal ecosystems (e.g. Moritz et al. (2013) investigated polychaete subtidal assemblages in approximately 15,400 km^2, whereas Gerwing et al. (2016) studied tidal flats with up to 56 Km distance in between). Due to the high influence of environmental variables and the high dispersal rates expected for macrobenthic fauna, as well as the relatively small scale analysed, we expected that environmental processes should exert a major control in the metacommunity dynamics (prediction 1). We also accounted for differences in species life histories and investigated whether the influence of spatial and environmental variables in marine macrobenthic communities are contingent on the dispersal abilities of organisms. As observed in other systems (e.g. fens, Hájek et al. 2011; lakes, Heino 2013; streams, Grönroos et al. 2013), we expected that the relative importance of environmental processes should decrease (and spatial processes increase) from stronger (species with planktonic larvae and motile adults) to weaker dispersers (species with nonplanktonic larvae and sessile or discretely motile adults) (prediction 2).

Methods

Study area and sampling

This work was done at Araçá Bay (23º 49'S, 45º 24'W), located in the Marine Protected Area of the Northern coast of São Paulo State, Southeast Brazil (Figure 1). Araçá Bay has a wide intertidal area (approximately 300 m wide) and is characterized as a heterogeneous and biodiverse rich environment, with more than 300 species of marine macroinvertebrates (Amaral et al. 2015). These features provide an ideal test system to investigate the relative contribution of spatial and environmental processes to community variation.

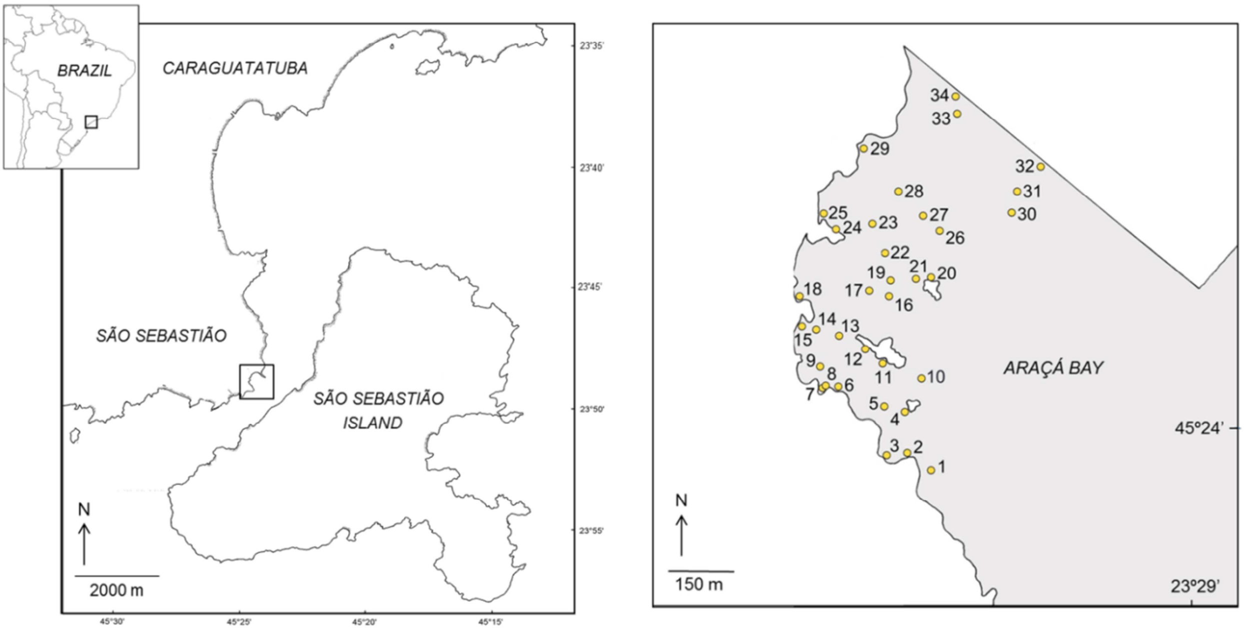


Fig. 1. Map showing the location of the study area and the spatial distribution of sampling sites in the intertidal area of Araçá Bay.

To avoid inconsistent conclusions about the metacommunity dynamics based on a single point in time, we sampled the tidal flat four times during a whole year and analyzed the influence of environmental and spatial processes for each period. Sampling was done in September 2011 and February, May and July 2012 in the intertidal area of Araçá Bay. As a measure of metacommunity structure, we used the species composition of assemblages inhabiting different locations in the whole intertidal area of Araçá Bay. This is typically a measure of beta-diversity that is defined as the variation in the identities (and their abundances, when considered) of species among sites (*sensu* Anderson et al. 2011). Any effect of environmental and spatial processes on metacommunity structure means that the variation in species composition is associated with either (or both) processes (see definitions below). We selected 34 locations (hereafter sampling sites) attempting to cover the greatest diversity of habitats (i.e. different sediment types in different depth zones of the tidal flat); the same locations were sampled at each period. At each sampling site, three sediment samples using a 20 cm diameter core of 20 cm depth were collected for biological data. An additional sediment sample was collected using a 3 cm diameter core until 20 cm deep for sediment analyses. Each biological sample was placed in a plastic bag and taken to the laboratory, where they were immediately sieved with a 0.3 mm mesh. The fauna retained were sorted in taxonomic groups and fixed in

70% ethanol. Subsequently, all individuals were further identified to the lowest taxonomic level possible. Since we were interested in spatial processes occurring at regional scale (i.e. within the bay), for each sampling period, all biological samples from a location were pooled for the analyses.

Dispersal ability groups

To investigate if the influence of environmental and spatial variables on macrobenthic assemblages depend on their dispersal abilities we divided the species in 4 dispersal ability groups (DAG) according to their development mode and motility in juvenile and adult phases: (1) species with planktonic larvae and motile adults (DAG1), (2) planktonic larvae and discretely motile adults (e.g. tube builders, DAG2), (3) non-planktonic larvae and motile adults (DAG3), and non-planktonic larvae and discretely motile adults (DAG4) (Appendix 1). We used Fauchald & Jumars’ (1979) and Jumars’ et al. (2014) ordinal scheme of motile and discretely motile focused on feeding biology. In this scheme, a motile species moves to eat, whereas a discretely motile species may feed without moving (often with the help of extensible siphons, tentacles or palps and ambient sediment transport) and can stay in place indefinitely, but remains capable of moving. We considered species with planktonic larvae and adults with reduced mobility (DAG2) as more effective dispersers than species with nonplanktonic larvae and motile adults (DAG3); Whitlatch et al. (1998) have showed that movement of juvenile and/or adult life-stages across the seabed usually occurs at smaller scales than before settlement. Therefore, we expected the importance of the spatial variables to increase from DAG1 to DAG4. It is important to highlight, however, that the importance of larval and adult dispersal in marine sediments has been subject of a constant debate and some authors argue that the post-settlement dispersal can be even more important than pre-settlement dispersal (see Pilditch et al. (2015) and references therein). Within each DAGs, there is probably much among-species variation (e.g. lecitotrophic and planktotrophic larvae were both considered planktonic even though they may differ in time spent in water column, and there is obvious differences in the locomotion way of several species considered motile). Nevertheless, due to the relatively small scale of this study, these variations should not be strong enough to cause differences in dispersal routes and the ability to actively search for environmentally suitable sites among species of the same group.

Information about the development mode and mobility of species was thus gathered from expert knowledge, peer-reviewed literature and publicly available databases (Appendix

1). When the information about some species was not available, we relied on information from higher taxonomic levels.

Environmental variables

We used sediment characteristics (percentages of silt and clay, fine sand, coarse sand, pebble, organic matter and $CaCO_3$), temperature, depth and interstitial water salinity of each location as environmental variables. Coarse sand and pebble content were highly correlated to each other and inversely correlated with fine sandy particles. Therefore, they were excluded from the analysis to keep the variation inflation factor lower than 3 (Zuur et al. 2010). The particle size distribution was determined by sieving sediment, (oven-dried at 60°C) through a series of sieves (Folk and Ward 1957). Organic matter content was determined by the weight differences between samples that were dried at 60°C for 24 h and then incinerated at 550°C for 6 h. Calcium carbonate content was obtained by HCl 10% attack. Interstitial water salinity and temperature were measured *in situ* with a refractometer and a digital thermometer, respectively. All variables were standardized to mean of zero and unit variance (z-transformation) to account for their different scales of measurement that can affect some statistical analysis.

Statistical analysis

We used Principal Coordinates of Neighbor Matrices (PCNM eigenfunctions; Borcard and Legendre 2002) to generate spatial variables (proxy for spatial processes) used as explanatory variables in Canonical models (Dray et al. 2006). PCNM are a form of Moran's eigenvector maps (Legendre et al. 2010) and were generated following the procedures described in Borcard and Legendre (2002) and Dray et al. (2006). We computed PCNM eigenvectors from a pairwise Euclidean (geographic) distance matrix between the 34 sampling locations. The longest distance connecting two locations in a minimum spanning tree was used as a threshold to truncate the distance matrix. Whereas locations separated by distances lower than the threshold were connected, those more distant than the threshold were disconnected in a neighbor matrix.

After we generate the spatial variables, we assessed the importance of spatial and environmental variables on metacommunity structure by applying permutation tests (10000 permutations) on redundancy analysis (RDA) model. We implemented a forward selection procedure with double stopping criteria (Blanchet et al. 2008, Legendre and Legendre 2012) to select only the environmental and spatial variables (PCNMs) that significantly explained the variance in the metacommunity structure. Further, we used a variation partitioning procedure (Peres-Neto et al. 2006) applied to the redundancy analysis (partial RDA) to disentangle species response to environmental and spatial variables (retained PCNMs) (Legendre and Legendre 2012). In this analyses, the total percentage of variation in the species data is decomposed into pure (independent) and shared (interactive) contributions of two sets of predictors (i.e., environmental and spatial variables) and can be attributed to different fractions based on adjusted fractions of variation (R_{adj}^2): total explained variation [a + b + c], environmental variation [a + b], spatial variation [b + c], environmental variation without the spatial fraction [a], spatial variation without the environmental fraction [c], the common fraction of variation [b] shared by environmental (E) and spatial predictors (S), and the residual fraction of variation not explained by E and S [d] (Peres-Neto et al. 2006). Despite some recent criticism (Gilbert and Bennett 2010, Smith and Lundholm 2010), this analytical technique remains valuable to identify common and unique contributions to model prediction and hence better address the question of the relative influences of the groups of independent variables considered in a regression model (P. Peres-Neto, pers. comm., 5 September 2015).

The partial RDAs were run for each dispersal mode group and for the whole community together for the four sampling periods. We transformed the total counts of species using the Hellinger transformation (Legendre and Legendre 2012) to homogenize variation among species abundances and make data more appropriate to be analyzed by linear ordination methods (Peres-Neto et al. 2006). To investigate temporal differences, all analyses were done separately for each sampling event. All analyses were undertaken in the R environment using vegan (Oksanen et al. 2013) and fields (Furrer et al. 2009) packages.

Results

Environmental characterization

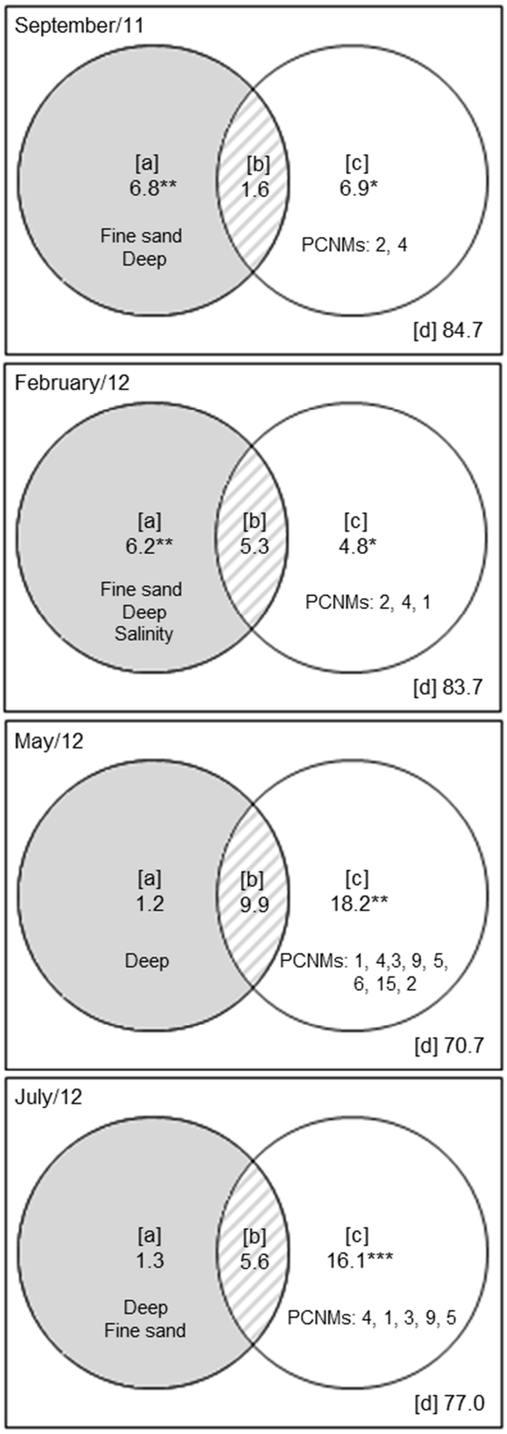
Seawater temperature varied seasonally, with warmer waters (27.2°C) during summer (February 2012) and cooler waters (20.4°C) in winter (July 2012). Salinity was greater in September 2011 and lower in July 2012. No great variation in organic matter content was recorded. Sediment features varied throughout the study period, and the content of silt and clay and fine sand in the sediment increased from September 2011 to July 2012, whereas the coarser fractions of sediment decreased (Appendix 2).

Biotic characterization

One hundred and twenty four macrobenthic species were recorded in this study (Appendix 1). Polychaetes, molluscs and crustaceans made up 94% of the total number of species (polychaetes: 67 species, molluscs: 34 species, crustaceans: 18 species). Species with planktonic larvae and sessile adults (DAG2) were the most representative group (n = 54), followed by species with planktonic larvae and motile adults (DAG1; n = 47), species with non-planktonic larvae and sessile adults (DAG 4, n = 12) and species with non-planktonic larvae and motile adults (DAG 3, n = 4) (Table 2). Seven species were not included in the analysis because we could not properly include them in a DAG.

Relative importance of environmental and spatial processes on metacommunity structure

When all species were analyzed together, both environmental and spatial processes significantly affected the macrobenthic metacommunity structure. Nevertheless, a stronger spatial pattern was observed in three of the four periods analysed (Figure 2). Sediment type, depth and salinity were the three environmental variables that most influenced species composition. The number of spatial variables retained for the partial RDA model ranged from 2 in September 2011 to 8 in May 2012. The shared variation by environmental and spatial predictors [b] was higher in May (Figure 2).



* $P < 0.05$; ** $P< 0.01$; *** $P < 0.001$

Figure 2. Variation partitioning results for macrobenthic assemblages considering all species. Results based on a partial redundancy analysis. Values shown are adjusted R^2.

The relative importance of environmental and spatial processes, however, was highly dependent on the dispersal ability of each group (Table 2). The group of the strongest dispersers (i.e. species with high motility in larval and adult stages, DAG 1) showed significant pure environmental control in three of the four samplings. In contrast, assemblages with reduced dispersal capabilities (i.e. nonplanktonic larvae and discretely motile adults, DAG 4) were only influenced by spatial variables (Table 1). Groups with intermediate dispersal capabilities (i.e., DAG 2 and DAG 3) did not show a clear pattern, being significantly influenced by spatial and/or environmental variables in only one period.

Table 1. Number of species and percentage of variation attributable to different fractions in each dispersal ability group

	DAG1	**DAG2**	**DAG3**	**DAG4**
September				
Species	39	32	4	8
Environment	**11.5**	-	06.2	-
Shared	09.1	-	18.6	-
Space	16.8	-	**21.4**	-
Unexplained	62.6	-	53.8	-
February				
Species	33	31	5	10
Environment	**05.2**	**16.1**	-	-
Shared	00.9	06.1	-	-
Space	**19.0**	**04.8**	-	-
Unexplained	74.9	73.0	-	-
May				
Species	33	27	4	3
Environment	00.6	**-**	-	0.00
Shared	11.5	-	-	02.3
Space	**10.2**	-	-	**54.0**
Unexplained	77.7	-	-	43.7
July				
Species	29	27	4	7
Environment	**02.8**	-	-	0.00
Shared	05.9	-	-	02.6
Space	**10.2**	-	-	**48.7**
Unexplained	81.1	-	-	49.7

Environment: pure environmental variation; Shared: spatially-structured environmental variation; Space: pure spatial variation; Unexplained: variation not explained by any set of explanatory variables. (DAG1) species with planktonic larvae and motile adults, (DAG2) planktonic larvae and discretely motile adults, (DAG3) nonplanktonic larvae and motile adults, and (DAG4) nonplanktonic larvae and discretely motile adults.Bold numbers correspond to statistically significant ($P<0.05$) values. (-) indicates that no environmental or spatial variable significantly explained the variance in the species composition matrix, therefore the variation partitioning procedure was not applied.

Discussion

Each of environmental and spatial processes affected the soft sediment macrobenthic assemblages. Nonetheless, contrary to our first prediction, spatial variables were better predictors (i.e., they explained higher variance) of metacommunity structure. This pattern, however, changed through time and was contingent on the dispersal ability of each group. Supporting our second prediction, environmental processes were more important for stronger disperses, whereas spatial processes were more relevant for weaker disperses.

The observed low importance of the independent environmental effect on the soft-sediment macrobenthic assemblages of Araçá Bay is novel. Metacommunity theory assumes that the relative role of environmental and spatial processes in the assembly of local communities depends on the spatial scale investigated. Because dispersal of species are not expected to be limited at small spatial scales, it is predicted that fine-scale (e.g. within a bay) spatial distributions of species are primarily determined by environmental processes (Cottenie 2005, Meutter et al. 2007, Árva et al. 2015). This would be expected for macrobenthic invertebrates inhabiting intertidal soft-sediments because most species can disperse during larval and adult phases, and several studies have documented that their species composition and abundances respond mainly to physical and biotic characteristics of the environment (McLachlan 1990, Defeo and McLachlan 2005, de Juan and Hewitt 2014). Our results, however, show some divergence from these findings. Although we observed that environmental processes are indeed important in structuring macrobenthic assemblages, we also revealed that the most substantial part of spatial distribution of macrobenthic organisms in Araçá Bay was related to spatial processes. Similarly, Quillien et al. (2015) and Gerwing et al. (2016) also found that spatial processes are relevant in structuring marine soft sediment assemblages, whereas Shanks (2009) found that many marine species larvae can disperse a short distance only (< 1 km), and Becker et al. (2007) showed that coastal mussel larvae, previously thought to dispersed hundreds of kilometers, are retained within a few kilometers of their natal origin.

Several authors have pointed out that the variation accounted by spatial processes may arise from two main sources: it can be attributed either to some spatially structured unmeasured environmental variables or pure spatial processes related to dispersion (e.g. Legendre and Legendre 2012, Landeiro et al. 2014, Provete et al. 2014). Although we included most environmental variables that are commonly found to affect the species distribution of soft sediment macrobenthic assemblages (i.e., sediment, depth and salinity), many others were not considered. Physical forces such as local currents and small-scale turbulent processes in the water column are known to affect recruitment of marine invertebrates (Abelson and Denny 1997, Lundquist et al. 2004) and, therefore, may contribute significantly to their spatial patterns. Oxygen and nitrogen content in the sediment is also another important environmental factor that was not considered here. Thus, it is likely that the environmental control observed here is underestimated and is important that future studies on macrobenthic assemblages include other variables than sediment type, depth and salinity. Nevertheless, the low percentage of variation explained by the common fraction of variation shared by environmental and spatial predictors (fraction b) is an indicative that spatial processes are indeed an important structuring factor in this system.

The importance of spatial processes on the macrobenthic assemblages of Araçá Bay is further supported by the different influence of environmental and spatial variables on organisms with different dispersal abilities (DAGs). As expected in the second prediction, stronger disperses responded strongly to environmental processes, whereas weaker disperses were more influenced by spatial processes. In this regard, our results show that dispersal capabilities vary depending on species traits, suggesting that species with planktonic larvae and mobile adults are better able to track environmental variability than species with nonplanktonic larvae and adults with reduced mobility. Since stronger dispersers may spread over extended area, they may also have larger and more evenly dispersed stock of potential colonizers than species with reduced dispersal capabilities. Consequently, it can be expected that better dispersers are less sensitive to habitat loss. On the other hand, species with nonplanktonic larvae and less mobile adults would be more impacted by habitat degradation due to its reduced mobility (Landeiro and Magnusson 2011, Siqueira et al. 2012).

The lack of a strong spatial or environmental signature in the DAG2 and DAG3 in three of four periods suggests that these groups do not show strong dispersal limitation, but also that their dispersal characteristics are too weak to track environmental variability. Historically, marine ecologists have emphasized the importance of pelagic larvae as the primary agents of dispersal for macrobenthic invertebrates (Whitlatch et al. 1998, Becker et al. 2007, Pilditch et al. 2015). This view stems from the fact that these larvae can disperse in very high numbers, and through large areas, with currents before settling. In soft-sediment systems, however, dispersal continues after larval settlement, and recent investigations have been showing that post-settlement dispersal are likely to be similar to pelagic larval dispersal because of continued, frequent, small-scale dispersal over longer periods (Pilditch et al. 2015). Our results do not show which dispersal strategy (pre- or post-settlement) is more efficient, but clearly demonstrate that both are relevant to structure soft- sediment macrobenthic assemblages.

Although development mode and adult mobility seem to be decisively important to dispersal capabilities of macrobenthic species, other traits may also exert strong influence. Number and size of eggs and/or larvae have been pointed as a determinant for distance traveled and potential of recolonization (Lundquist et al. 2004). Whereas large number of larvae is expected to reach greater distances due to random processes, small larvae (or eggs) are expected to have reduced fall velocity and stay more time within the water column, thus being transported long distances to colonize far away habitats. Larval behavior may also have exert strong importance on structure of marine macrobenthic metacommunities, as studies are accumulating that demonstrate that many larvae are capable of swimming to orient themselves (Metaxas 2001, Kingsford et al. 2002, Shanks 2009). It can be speculated that these larvae/species can actively search for suitable habitats, thus favoring environmental processes, or staying close to the bottom where currents are much slower, therefore favoring spatial processes (Shanks 2009). Information on these topics, however, is still lacking and should be addressed in future studies.

We also found that the relative importance of spatial and environmental processes changed through time. The temporal changes in metacommunity dynamic observed at Araçá Bay were mainly related to the importance of spatial processes. The percentage of variation explained by spatial processes increased in the last two samplings, which can be related to seasonal changes in biotic features (e.g. seasonal changes in recruitment patterns or number of predators) or to stochastic events which induce physical disturbances in the environment. Days before the last two samplings, Araçá Bay was struck by unusually large storms, which increased waves height and power (Corte et al. in prep). In tidal systems as our study area, dispersion of individuals is promoted by regular tidal-mediated currents and also by wave-driven resuspension events (Valanko et al. 2010). Therefore, it is reasonable to infer that the storms that affected the study area in May and July 2012 increased dispersal rates in macrobenthic assemblages. This increased dispersal, in turn, might have changed spatial patterns of abundance and affected the metacommunity dynamic of macrobenthic species. These findings suggest that storms might change spatial patterns of abundance of macrobenthic species and exert significant impacts on the metacommunity dynamic of intertidal soft-sediments. However, the limitations of this study (only one area investigated) preclude a rigorous test for storm impacts on metacommunity dynamics of soft-sediment assemblages, and our results may be viewed as insights for future studies.

Marine macrobenthic organisms are considered good dispersers because their dispersal happens before and after larval settlement (Whitlatch et al. 1998, Pilditch et al. 2015). It was expected therefore that environmental processes would exert a major role on their metacommunity structure. Our results, however, show that macrobenthic asssemblages may be primarily influenced by spatial processes even at small scales (less than 1 Km^2). In this regard, it is evident that broader consideration of the roles of spatial processes should enhance understanding the ways macrobenthic assemblages are structured (Thrush et al. 2005b, Zajac et al. 2013). This can be especially important for coastal ecosystems, where alongshore currents with reduced velocities and changes in the wind direction can keep the larvae closer to shore (Shanks 2009). By comparing groups of species varying in dispersal ability, we found that the relative influence of environmental and spatial variables is dependent of species dispersal capabilities. Therefore, accounting for differences in species life histories, specifically mode of species development, is important to better understand species distribution and coexistence patterns in intertidal soft-sediments. Since we showed that the influence of spatial and environmental processes is not consistent through time, it is also important that future studies replicate sampling in time so the influence of seasonal and stochastic factors on macrobenthic metacommunities can be unveiled.

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Annex 1

Species investigated in this study and their dispersal ability group (DAG).

Species	Adult Motility	Larval Motility	DAG	Reference
Cnidaria				
Edwardsia sp. 1	sessile	planktonic	2	Brusca et al. (2003).
Nemertea				
Nemertea sp. 1	-	-	-	-
Mollusca				
Abra sp.1	mobile	planktonic	1	(1)
Anomalocardia brasiliana	sessile	planktonic	2	Mouëza et al. (1999)
Bulla striata	mobile	nonplanktonic	3	Berrill (1931)
Cerithium atratum	mobile	planktonic	1	Houbrick (1971)
Chione cancellata	sessile	planktonic	2	Morsan and Kroeck (2005)
Chione subrostrata	sessile	planktonic	2	Morsan and Kroeck (2005)
Corbula caribaea	sessile	plankfeed	2	(1)
Corbula sp.1	sessile	plankfeed	2	(1)
Cyclinella tenuis	sessile	planktonic	2	Morsan and Kroeck (2005)
Diplodonta patagonica	sessile	planktonic	2	Raven (2013)
Diplodonta punctata	sessile	planktonic	2	Raven (2013)
Donax gemmula	mobile	plankfeed	1	Carstensen et al. (2010)
Ervilia nitens	sessile	planktonic	2	Raven (2013)
Eurytellina lineata	sessile	planktonic	2	Webb (1986)
Gouldia cerina	sessile	planktonic	2	Morsan and Kroeck (2005)
Iphigenia brasiliana	sessile	plankfeed	2	Webb (1986)
Macoma sp.	sessile	planktonic	2	Webb (1986); Carstensen et al. (2010)
Nassarius vibex	mobile	planktonic	1	Scheltema (1965)
Neritina virginea	mobile	planktonic	1	Crandall (1999)
Nucula semiornata	sessile	planktonic	2	(1)
Olivella minuta	mobile	planktonic	1	Edwards (1968)
Periploma ovata	sessile	planktonic	2	Raven (2013)
Phacoides pectinata	sessile	planktonic	2	Raven (2013)
Pitar fulminatus	sessile	planktonic	2	Morsan and Kroeck (2005)
Protothaca pectorina	sessile	planktonic	2	Morsan and Kroeck (2005)
Semele sp. 1	sessile	planktonic	2	Raven (2013)
Solen tehuelchus	sessile	planktonic	2	Raven (2013)
Sphenia antillensis	sessile	planktonic	2	(1)
Strigilla pisiformis	sessile	planktonic	2	Webb (1986)
Tagelus divisus	sessile	planktonic	2	Morsan and Kroeck (2005)
Tagelus plebeius	sessile	planktonic	2	Morsan and Kroeck (2005)
Tellina sp. 1	sessile	planktonic	2	Webb (1986)

Tellina sp. 2	sessile	planktonic	2	Webb (1986)
Tivela mactroides	sessile	planktonic	2	Morsan and Kroeck (2005)
Oligocaheta				
Oligochaeta	-	-	-	-
Polychaeta				
Ancistrosyllis jonesi	mobile	planktonic	1	Blake (1975)
Aricidea (Allia) albatrossae	mobile	planktonic	1	(2)
Aricidea (Aricidea) fragilis	mobile	planktonic	1	(2)
Aricidea cf. wassi	mobile	planktonic	1	(2)
Armandia agilis	mobile	planktonic	1	(1)
Armandia hossfeldi	mobile	planktonic	1	(1)
Armandia polyophtalama	mobile	planktonic	1	(1)
Boccardia polybranchia	sessile	planktonic	2	(1)
Boccardiella ligerica	sessile	planktonic	2	(1)
Capitella spp	mobile	planktonic	1	Rouse and Pleijel (2001)
Cirriformia filigera	sessile	planktonic	4	(1)
Cirriformia punctata	sessile	planktonic	4	(1)
Cirriformia tentaculata	sessile	planktonic	4	(1)
Clymenella dalesi	sessile	planktonic	2	(1)
Diopatra aciculata	sessile	nonplanktonic	4	Rouse and Pleijel (2001) ; (3)
Diopatra dexiognatha	sessile	nonplanktonic	4	Rouse and Pleijel (2001) ; (3)
Dispio remanei	sessile	planktonic	2	(1)
Dispio uncinata	sessile	planktonic	2	(1)
Dorvillea sp.	mobile	planktonic	1	(1)
Eteone alba	mobile	planktonic	1	(1)
Glycinde multidens	mobile	planktonic	1	(1)
Goniada litorea	mobile	planktonic	1	(1)
Haploscoloplos sp. 1	mobile	planktonic	1	Giese and Pearse (2012)
Hemipodia simplex	mobile	planktonic	1	(3)
Hermundura tricuspis	mobile	planktonic	1	Jumars et al. (2015)
Heteromastus filiformis	mobile	planktonic	1	(1)
Isolda pulchella	sessile	planktonic	2	Hernández-Alcántara and Solís-Weiss (2009)
Laeonereis culveri	mobile	planktonic	1	Mazurkiewicz (1975)
Loimia medusa	sessile	nonplanktonic	4	Rouse and Pleijel (2001); (3)
Magelona californica	sessile	planktonic	2	(1)
Magelona nonatoi	sessile	planktonic	2	(1)
Magelona papilicornis	sessile	planktonic	2	(1)
Magelona variolamellata	sessile	planktonic	2	(1)
Marphysa sebastiana	sessile	planktonic	2	(1)
Mediomastus californiensis	mobile	planktonic	1	(3)

Mooreonuphis lineata	sessile	planktonic	4	Rouse and Pleijel (2001); (3)
Naineris setosa	mobile	planktonic	1	Giangrande and Petraroli (1991)
Nematonereis hebes	mobile	nonplanktonic	3	Rouse and Pleijel (2001); (3)
Nicolea uspiana	sessile	nonplanktonic	4	(3)
Notomastus hemipodus	mobile	planktonic	1	(1)
Notomastus lobatus	mobile	planktonic	1	(1)
Onuphis eremita oculata	sessile	nonplanktonic	4	(3)
Owenia brasiliensis	sessile	planktonic	2	Brusca et al. (2003)
Owenia fusiformis	sessile	planktonic	2	Brusca et al. (2003)
Paraprionospio pinnata	sessile	planktonic	2	(1)
Phyllodoce mucosa	mobile	planktonic	1	Brusca et al. (2003)
Poecilochaetus australis	sessile	planktonic	2	(1)
Poecilochaetus perequensis	sessile	planktonic	2	(1)
Poecilochaetus sp. 1	sessile	planktonic	2	(1)
Polydora nuchalis	sessile	planktonic	2	(1)
Polydora sp.1	sessile	planktonic	2	(1)
Polydora sp.2	sessile	planktonic	2	(1)
Polydora websteri	sessile	planktonic	2	(1)
Prionospio steenstrupi	sessile	planktonic	2	(1)
Protoaricia sp. 1	mobile	nonplanktonic	3	Rouse and Pleijel (2001); (3)
Scolelepis sp.1	sessile	planktonic	1	(1)
Scolelepis squamata	sessile	planktonic	1	(1)
Scolelepis texana	sessile	planktonic	1	(1)
Scoletoma tetraura	mobile	planktonic	1	Ghodrati Shojaei et al. (2015)
Scoloplos (leodamas) sp. 1	mobile	nonplanktonic	1	(1)
Scyphoproctus sp. 1	-	-	-	-
Sigambra grubii	mobile	planktonic	1	Achari (1975)
Sigambra tentaculata	mobile	planktonic	1	Achari (1975)
Sternaspis capilata	mobile	planktonic	1	(3)
Syllis sp.1	mobile	nonplanktonic	3	Rouse and Pleijel (2001); (3)
Terebellides anguicomus	sessile	nonplanktonic	4	Rouse and Pleijel (2001); (3)
Sipuncula				
Sipuncula sp. 1	sessile	planktonic	2	Brusca et al. (2003)
Crustacea				
Alpheus nuttingi	mobile	planktonic	1	Brusca et al. (2003)
Amphipoda sp.1	sessile	nonplanktonic	4	Lopes and Masunari (2004); Leite (1996)
Callinectes danae	mobile	planktonic	1	Branco and Masunari (2000)
Caridae sp.1	mobile	planktonic	1	Brusca et al. (2003)
Clibanarius antillensis	mobile	planktonic	1	Varadarajan and Subramoniam (1982); Sant'Anna et al. (2009)
Clibanarius vittatus	mobile	planktonic	1	Varadarajan and Subramoniam (1982); Sant'Anna et al. (2009)

Dendobranchiata	mobile	planktonic	1	Rupert et al. (2004)
Monokalliapseudes schubartii	sessile	nonplanktonic	4	Pennafirme and Soares-Gomes (2009); Leite et al. (2003)
Ocypodidae	mobile	-	-	-
Ogyrides alphaerostris	mobile	planktonic	1	Packer (1985)
Pagurus criniticornis	mobile	planktonic	1	Negreiros-Fransozo and Hebling (1987)
Panopeus occidentalis	mobile	planktonic	1	Harvey and Epifanio (1997)
Pinnixa chaetopterana	sessile	planktonic		
Processa bermudensis	mobile	planktonic	1	Martínez-Mayén and Román-Contreras (2013)
Uca leptodactyla	mobile	planktonic	1	Yamaguchi (2001)
Upogebia brasiliensis	sessile	planktonic	2	De Oliveira et al. (2014)
Upogebia paraffins	sessile	planktonic	2	De Oliveira et al. (2014)
Upogebia vasquezi	sessile	planktonic	2	De Oliveira et al. (2014)
Echinodermata				
Holothuroidea sp. 1	-	-		-
Ophiuroidea sp. 1	-	-		-
Chordata				
Cephalochordata sp. 1	-	-		-

(1) www.genustraithandbook.org.uk
(2) http://www.sealifebase.org
(3) http://polychaetes.lifewatchgreece.eu/

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Annex 2

Table 1. Species richness, abundance of individuals and selected environmental variables across the sampling periods (±SD).

	September 2011	**February 2012**	**May 2012**	**July 2012**
Richness (S)	80	81	65	64
Abundance	9606	13.228	3.828	6.722
Temperature (^{o}C)	21.91 (±1.40)	27.24 (±1.03)	25.04 (±1.22)	20.35 (±0.54)
Salinity	32.26 (±1.96)	31.68 (±5.01)	30.59 (±3.92)	29.94 (±3.55)
Silt and clay (%)	4.18 (±3.66)	4.73 (±3.37)	4.80 (±3.65)	5.71 (±5.29)
Fine sand (%)	68.49 (±18.65)	73.47 (±19.49)	74.09 (±16.36)	74.73 (±17.77)
Coarse sand (%)	16.83 (±16.85)	12.88 (±15.43)	11.10 (±11.89)	10.46 (±14.93)
Peebles (%)	6.18 (±8.60)	3.73 (±6.84)	3.19 (±5.21)	3.16 (±6.07)
Organica matter (%)	1.63 (±0.75)	1.68 (±1.20)	1.72 (±0.89)	1.86 (±1.28)
$CaCO_3$ (%)	4.88 (±2.52)	4.43 (±2.59)	3.76 (±2.73)	3.48 (±1.86)

Capítulo 3

Strong cross-taxon congruence does not imply in similar responses to environmental variables in marine benthic communities.

Abstract

Cross-taxon congruence, i.e. the degree to which patterns in assemblage structure in a set of sites are similar among different taxonomic groups, has being suggested as an important tool in conservation planning and biodiversity monitoring. In spite of its importance and potential applicability, the effectiveness of this approach is still largely overlooked and no consensus has been achieved thus far. Here, we assessed if macro- and meiofaunal communities inhabiting marine soft-sediments show concordant variation in a biodiverse coastal ecosystem. Patterns of assemblages' structure of the two groups were strongly correlated, and both assemblages were influenced by similar environmental variables. Nevertheless, the direction of this influence was different for each group and macro- and meiofauna taxonomic richness and abundance were inversely correlated. These opposing patterns of abundance and richness between the assemblages show that strong concordance may emerge even when different taxonomic groups show contrasting trends and highlight that caution should be take when using cross-taxon congruence in biodiversity assessment and conservation planning.

Introduction

Biodiversity loss is currently a major threat to the structure and functioning of ecosystems (Chapin III et al. 2000, Larsen et al. 2012). Over the past few decades, the accelerating extinction rates have induced an increasing effort into assessing biodiversity. The limited funding for conservation, the lack of taxonomic specialists and the time-consuming work to sample and identify organisms (Myers et al. 2000, Heino 2010, Vieira et al. 2015), however, usually preclude a complete biodiversity assessment. To reconcile the opposite forces of complexity and practicality, it is therefore necessary a reduction of the multiplicity associated with biodiversity into fast and cost effective measures that can be used for biodiversity conservation and monitoring (Siqueira et al. 2012).

One alternative to provide practical, less costly, and more quickly obtainable measures for biodiversity is to base broad-scale assessments on a well-known surrogate taxa whereby an indicator group is used to indicate the condition of the overall biodiversity of an ecosystem (Paavola et al. 2006, Dolph et al. 2011). Studies testing the effectiveness of surrogate groups have generally been based on indicator species, genera or familes (Dufrêne and Legendre 1997, Sánchez-Fernández et al. 2006, Heino 2010). More recently, however, researches started to investigate cross-taxon congruence based on community structure as an alternative for predicting variation in the biodiversity (Jackson and Harvey 1993, Paavola et al. 2006, Bini et al. 2007a, Vieira et al. 2015).

Cross-taxon congruence (also known as community concordance) corresponds to the degree to which different communities show similar patterns across varied environments. This is expected to happen when different communities respond to the same ecological processes, and is an indicative of the validity of surrogate taxa for conservation planning and monitoring purposes (Jackson and Harvey 1993, Bini et al. 2007b). In spite of its importance and potential applicability, cross-taxon congruence is still largely overlooked (Siqueira et al. 2012, Vieira et al. 2015). As a consequence, no consensus has been achieved thus far for this approach. While some studies have found that cross-taxon congruence bears great promise for bioassessment (Paavola et al. 2006, Sánchez-Fernández et al. 2006, Bini et al. 2007b), others have not found strong concordance between different taxonomic groups, suggesting a lack of support for this approach (Heino 2010, Vieira et al. 2015).

In aquatic ecosystems, studies evaluating cross-taxon congruence have been mostly realized with freshwater communities inhabiting streams, lakes and ponds (e.g.: (Jackson and Harvey 1993, Heino et al. 2003, Larsen et al. 2012). Marine ecosystems, despite their large biodiversity and endangered situation (Halpern et al. 2007, Defeo et al. 2009), have been neglected and the number of studies that investigated suitable surrogates for mapping and predicting marine biodiversity is very restricted. For instance no study has investigated the community concordance among marine benthic assemblages thus far.

In marine soft-bottom ecosystems, benthic species are composed from a wide taxonomic and functional diversity. This fauna is commonly divided based on size, being macrofauna (> 0.5 mm) and meiofauna (> 0.044 mm, < 0.5 mm) essential for ecosystems services such as nutrient cycling, as well as relevant food source for higher thropic levels (Danovaro et al. 2007, Bonaglia et al. 2014). These groups interact in soft-sediments (e.g. predation, facilitation process) and some meiofaunal organisms are early stages of macrofaunal ones (referred to as temporary meiofauna; (Hentschel and Jumars 1994, Zeppilli et al. 2015). The study of marine benthic communities, however, has traditionally been conducted independently, focusing on only one of their components (Fonseca and Netto 2006), and there are rarely data for multiple taxa in the same area to allow comparisons (Sutcliffe et al. 2012).

To evaluate the efficacy of the surrogacy approach for marine benthic fauna and to provide useful information that can be used to design effective biological monitoring programmes in coastal marine ecosystems, we studied a biodiverse marine soft-bottom ecosystem and investigated whether macro- and meiofaunal assemblages exhibit concordant patterns of community structure in three different periods. Further, we inspected whether both groups show similar patterns of abundance and species richness. Since a reliable surrogate group should also respond to similar processes that maintain other taxonomic groups (Heino 2010, Vieira et al. 2015), we also investigated the influence of environmental variables on macro- and meiofaunal assemblages.

Material and Methods

Study area

This work was done at Araçá Bay (23º 49’S, 45º 24’W), a wide intertidal flat (534.500 m^2) located in the central area of the São Sebastião Channel, state of São Paulo, Southeast Brazil (Fig. 1). This area has a gentle slope reaching a maximum depth of 30 meters onwards the channel. The tides range from average levels of 2.06 m (maximum) to -0.04 m (minimum) (Gubitoso et al. 2008).

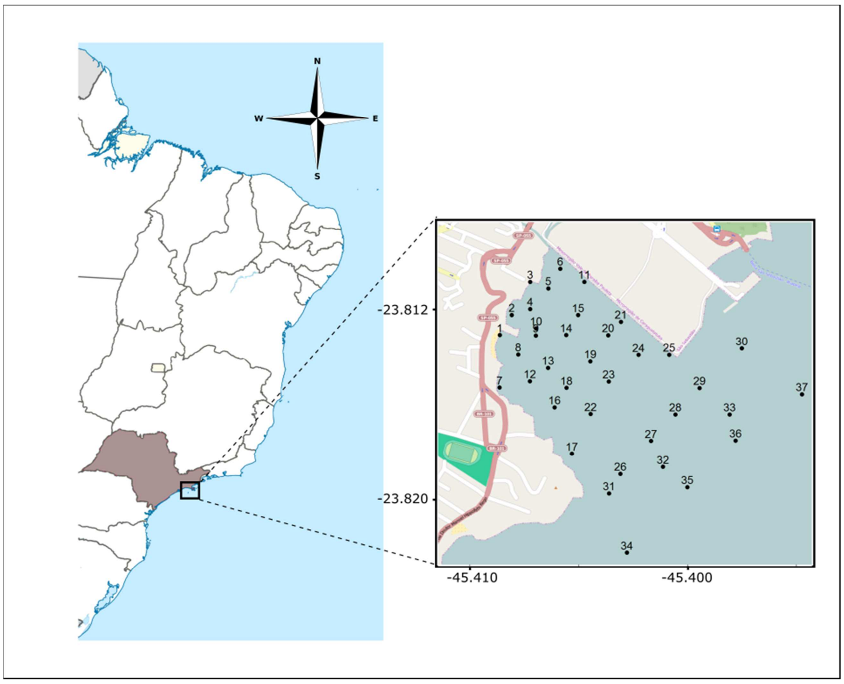

Fig.1 – Study Area. Map of the sampling sites in Araçá Bay, state of São Paulo – Brazil.

Sampling

Sampling was performed on October 2012, February 2013 and June 2013. Samples were taken during the low tide from thirty-seven geo-referenced sites arranged on an irregular sampling grid, from the intertidal to approximately 30 m deep (Fig. 1). At each sampling site, samples were collected simultaneously for the investigation of macrofauna, meiofauna, microphytobenthos, microbiota and granulometry.

For macrofauna analysis, four sediment samples were taken using a PCV corer of 10 cm diameter and 20 cm deep. Each sample was placed in a plastic bag and taken to the laboratory, where they were sieved with a 0.3 mm mesh. The fauna retained was sorted in taxonomic groups and fixed in 70% ethanol. Posteriorly, all individuals were identified to the species level.

For meiofauna analysis, one sediment sample was taken using a PVC corer of 2.5 cm in diameter and 5 cm deep. Samples were immediately fixed in 4% formaldehyde. In the laboratory, samples were washed through a 45 µM mesh sieve and extracted by flotation with Ludox TM 50 (specific density 1.18) (Heip et al. 1985). The retained material was stored in formaldehyde 4% and stained with Rose Bengal. Meiofauna was counted and identified under a stereomicroscope. Copepoda, Kinorhynca and Tardigrada were grouped into higher taxa, whereas Nematoda was identified to genus level and further separated into morphospecies. From each sample, a total of 100 nematodes were randomly picked, evaporated slowly in anhydrous glycerol and mounted on permanent slides for identification. After identification, the proportion of each taxon per sample was multiplied by the total number of individuals per sample to achieve the total number of individuals of each species.

For microphytobenthic analyses, five samples of the top 1cm of the sediment were taken using a corer measuring 2 cm in diameter and conditioned in dark bottles. These samples were kept on ice and stored at -20°C. Microphytobenthic analyses were performed from the estimate biomass of phaeopigments. These pigments were extracted from each sample with 10mL 100% acetone together with 0.07g $MgCO_3$ for 24h in the dark at 4° C. Absorbance was read at optical densities of 750, 665 and 430nm in a spectrophotometer, before and after acidification with 1N HCl, according to Plante-Cuny (1978). The calculation to obtain the content of phaeopigments were performed by using the equations of Plante-Cuny (1973). The microbiota analyses were performed from the direct count of heterotrophic bacteria, cyanobacteria and heterotrophic nanoflagellates (larger than 8.0 µm, see Caron et al. (1991)). In the lab, 20g of each sediment samples were diluted 10-fold with sterile seawater and vortexed during 5 minutes. The supernatant was stored in sterile flasks containing 5% formaldehyde (final concentration) and kept under refrigeration (Hobbie et al. 1977). For heterotrophic bacteria and cyanobacteria, aliquots were filtered onto 0.2-µm Nucleopore Black membrane, stained with DAPI (Porter and Feig 1980) and counted under epifluorescence microscope using ultraviolet and green lights, respectively. Aliquots for heterotrophic nanoflagellates were filtered onto 8µm Nucleopore Black (Caron et al. 1991), stained with DAP for six hours and then filtered onto 2µm Nucleopore black. Nanoflagellates were quantified by epifluorecence microscopy under ultraviolet light.

One additional sample of sediment was taken for granulometric analysis using a corer of 3 cm diameter and 20 cm deep. The granulometric analysis of the sediment collected was carried out using the routine sieving and pipetting techniques described by Suguio 1973 and sediment parameters were obtained using SysGran software, version 3.0 (Camargo 2006) in accordance with the classifications of Folk and Ward (1957).

Data analysis

To evaluate the similarity in distribution (spatial) patterns of community composition between macro- and meiofaunal assemblages (biological datasets), we first applied a log (y + 1) transformation to abundance data of each assemblage to minimize the effect of extreme values. We then computed a Principal Coordinates Analyses (PCoA) for each assemblage using the Bray-Curtis dissimilarity as the distance measure. Then, we compared the ordination patterns generated with a Procrustes Rotation Analysis (Jackson and Harvey 1993, Peres-Neto and Jackson 2001). Briefly, Procrustes Analysis tries to match the position of each sampling station in one multivariate space (defined here by the first three CA axes of the macrofauna data) to the position of the same sampling station in a second multivariate space (the first three CA axes of the meiofauna data), thereby assessing the degree to which both assemblages have similar patterns. The resultant statistic (residual sum-of-squares statistics - m^2) is then transformed into the r statistic ($r = \sqrt[2]{1 - m^2}$), which is a measure of the community congruence. The statistical significance of r was assessed with a Monte Carlo randomization method, using 10000 permutations. We also performed a Principal Coordinates Analyses (PCoA) for the environmental data using the Euclidean dissimilarity as the distance measure. Sediment parameters (coarse sand, fine sand and mud), orbital velocity of waves, depth, total organic carbon, microphytobenthos (phaeopigments), microbiota (heterotrophic bacteria, cyanobacteria and nanoflagellates), and the number of species and individuals of the 'other' taxonomic group (i.e. macrofauna data for the meiofauna analysis and *vice versa*) were used as environmental variables. Orbital velocity of waves was highly correlated with depth. Therefore, orbital velocity was excluded from the analysis to keep the variation inflation factor lower than 3 (Zuur et al. 2010).

The vector residuals given by the Procrustes Analysis represents the lack of fit of ordination scores for an individual sample, with low values indicating strong concordance (Paavola 2006). To inspect whether the congruence between macro- and meiofaunal assemblages is influenced by explanatory variables, we related the residuals of the Procrustes Analysis between the macro-and meiofaunal datasets to the variables measured with Pearson correlation coefficients.

We used generalized additive models (Zuur 2009) to investigate the effect of time and environmental variables on species richness and abundance of macro- and meiofaunal assemblages. Time was considered a fixed factor with three levels accounting for the three sampling periods. As environmental variables, we used the same used in Procrustes analyses in addition to the number of species and individuals of the 'other' taxonomic group (i.e. macrofauna data for the meiofauna analysis and *vice versa*). Candidate models using negative binomial and Poisson distribution, with correction for zero inflation, were adjusted using penalized cubic regression splines (Zuur et al., 2009). Models were validated following the protocol proposed by Zuur et al. (2009).

We used principles from theoretic information (Burnham and Anderson 2002) to select the best model predicting species richness and abundance of macro- and meiofauna.

First, we ran models comprising all combinations of predictors (excluding interactions) totaling 4096 possible candidate models. Then, we compared multiple models using corrected Akaike Information Criteria (AICc), logLikelihood scores and Akaike weights (AICw). Akaike weights measure the relative likelihood of a model being the best for the given data (Cardoso et al. 2016), which is a straight-forward procedure in a multimodel inference routine (Burnham and Anderson 2002). For inferences, we excluded models with dAICc scores (AICc value from the best model – AICc value of a candidate model) >4. We used the evidence ratio, the ratio of Akaike weights between the best model and a candidate model, as a measure of support for each individual model (Burnham and Anderson 2002). The evidence ration can be understood as the difference in the likelihood of different models in explaining the variation in the data. In this regard, an evidence ratio equal to 5 means that one model is five times more likely to explain variation in the data than the other. On the other hand, an evidence ratio close to one means that both models have similar probability to explain variation in the data.

If a variable was not included in the best model, this should not suggest that it is of no importance (Cardoso et al. 2016). The relative importance of each variable used to estimate species richness and abundance of macro- and meiofauna abundance was calculated as the sum of the AICw over all of the models in which the variable appears (Burnham and Anderson 2002).

All analyses were undertaken in the R environment (R Development Core Team 2013) using vegan (Oksanen et al. 2013), mgcv (Wood 2012) and MuMin (Barton and Barton 2015) packages.

Results

We recorded a total of 359 taxa (161 macrofauna and 198 meiofauna). The crustacean *Monokalliapseudes schubarti* and the polychaetes *Capitella* spp and *Armandia hosfeldi* were the most abundant macrofaunal species, whereas copepods and nematodes *Terschellingia* spp., *Dorylaimopsis* spp. and *Comesoma* spp. were the most abundant meiofaunal taxa.

Significant and strong (>0.8) concordance between macrofaunal and meiofaunal assemblages was recorded in all three periods (Table 1).

Table 1. Results of the Procrustes analyses evaluating the relationships between macro- and meiofaunal assemblages and between these assemblages and the environmental variables. P values are given in brackets.

	Macro		
	Oct/12	Feb/13	Jun/13
Meio	0.83 (<0.001)	0.83 (<0.001)	0.81 (<0.001)

The residuals of the Procrustes Analysis between the macro-and meiofaunal datasets were positively correlated with coarse sand and gravel, and negatively correlated with depth, total organic carbon and heterotrophic bacteria content (Table 2).

Table 2. Correlation between residuals of the Procrustes Analyses between macro- and meiofaunal datasets and the variables analysed. Significant values (<0.05) are in bold.

	r	**P**
Environmental		
Depth	**-0.27**	**<0.01**
Gravel (%)	**0.21**	**0.03**
Coarse sand (%)	**0.21**	**0.03**
Fine sand (%)	0.01	0.95
Mud (%)	**0.19**	**0.05**
Sorting	0.06	0.52
Phaeopigments	-0.06	0.58
Het. bacteria	-0.15	0.13
Cyanobacteria	**-0.22**	**0.03**
Nanoflagellates	-0.03	0.78
Organic carbon	**-0.22**	**0.02**

The number of species of macrofauna within Araçá Bay was better predicted using a generalized additive model of water depth, fine sand and abundance of meiofauna (Annex). The model explained 60.1 % of the variance in benthic samples (adjusted $r^2 = 0.469$). The results of the model showed no difference among sampling time. Depth and fine sand were included in all models selected, and thus had an importance of 1.0. Abundance of meiofauna was the third most important predictor, with importance value of 0.45. The evidence ratio

(1.19) between the best model and a model containing only depth and fine sand (rank = 3) indicated that both have virtually the same probability of being the best model.

Depth was also an important predictor for number of macrofaunal individuals with importance of 1.0. The second predictor was number of meiofaunal species (importance of 0.64), followed by nanoflagellates and fine sand (importance of 0.46 and 0.39, respectively) (Annex). The additive model regression explained 65.7% of the variance in meiofauna richness whitin Araçá Bay (adjusted $r^2 = 0.251$). The results of the additive model showed that time was not important for explaining variance in abundance of macrofauna. The evidence ratio (1.11) between the best model and a model containing only depth and meiofaunal species (rank = 3) indicated that both have the same probability to explain variation in the data.

The best model for predicting meiofaunal species richness included depth and coarse sand, with importance of 0.97 and 0.32, respectively (Annex). The model explained 61.2% of the variance in meiofauna richness whitin Araçá Bay (adjusted $r^2 = 0.517$). No difference among sampling time was recorded. The evidence ratio (1.27) between the best model and a model containing only depth (rank = 4) indicated that both have similar probability of being the best model, and highlights the importance of depth in explaining meiofaunal species richness.

Meiofauna abundance showed the most complex model. It was best predicted by depth, fine sand, nanoflagellates, number of macrofaunal species, coarse sand and mud content. The additive model regression explained 41.5 % of the variance in meiofauna richness whitin Araçá Bay (adjusted $r^2 = 0.258$). Depth, fine sand and nanoflagellates were included in all models selected, and thus had an importance of 1.0 (Annex). Number of macrofaunal species was also included in almost all models (importance 0.97). Coarse sand and mud content also showed high importance (0.77 and 0.72, respectively). As observed for macrofauna, the results of the additive model showed that time was not important for explaining variance in number of individuals of meiofauna.

Relationships between the species richness and abundance of macro and meiofaunal assemblages and the selected predictors (variables with an importance > 0.3) are shown in Fig. 2 and 3.

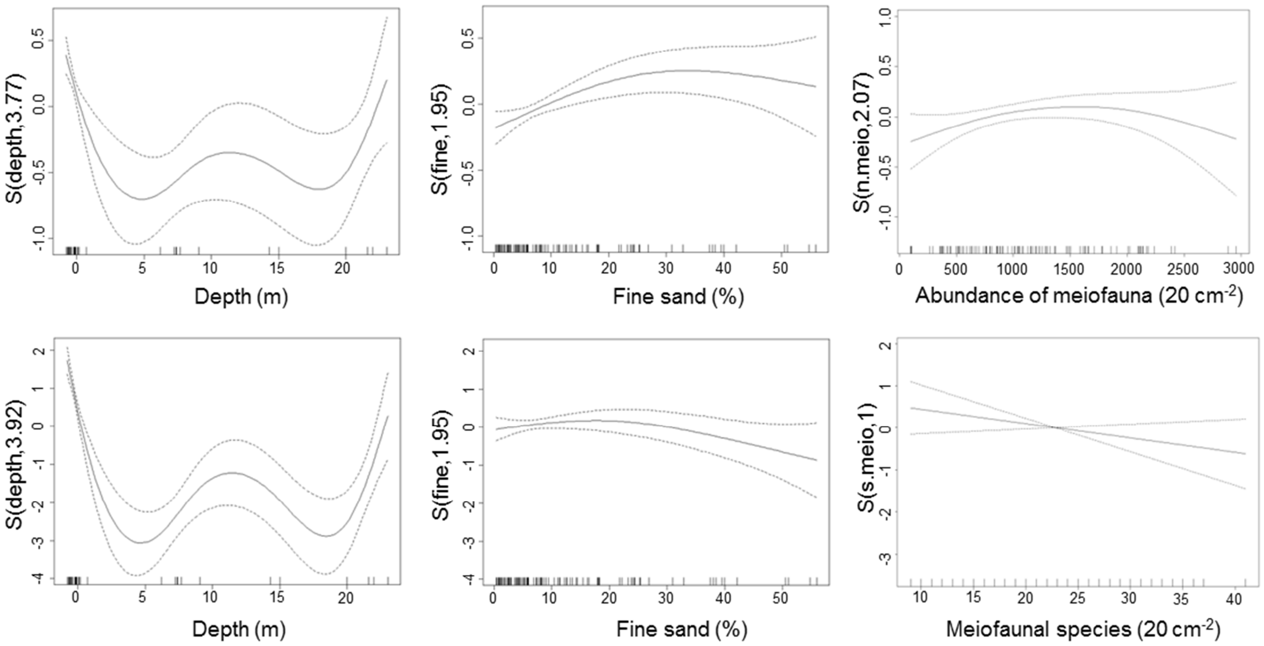

Figure 2 - Smoothers curves (S) showing the relationship (solid line) between species richness (top row) and abundance (bottom row) of macrofaunal assemblages and the variables with an importance value greater than 0.3 in models predictions. Dashed lines indicate standard errors of the smooth curve. The ‘rug plots’ on the x-axis indicate the range of variables over which measurements were taken. Numbers after the variable name on the y-axis represent estimated degrees of freedom.

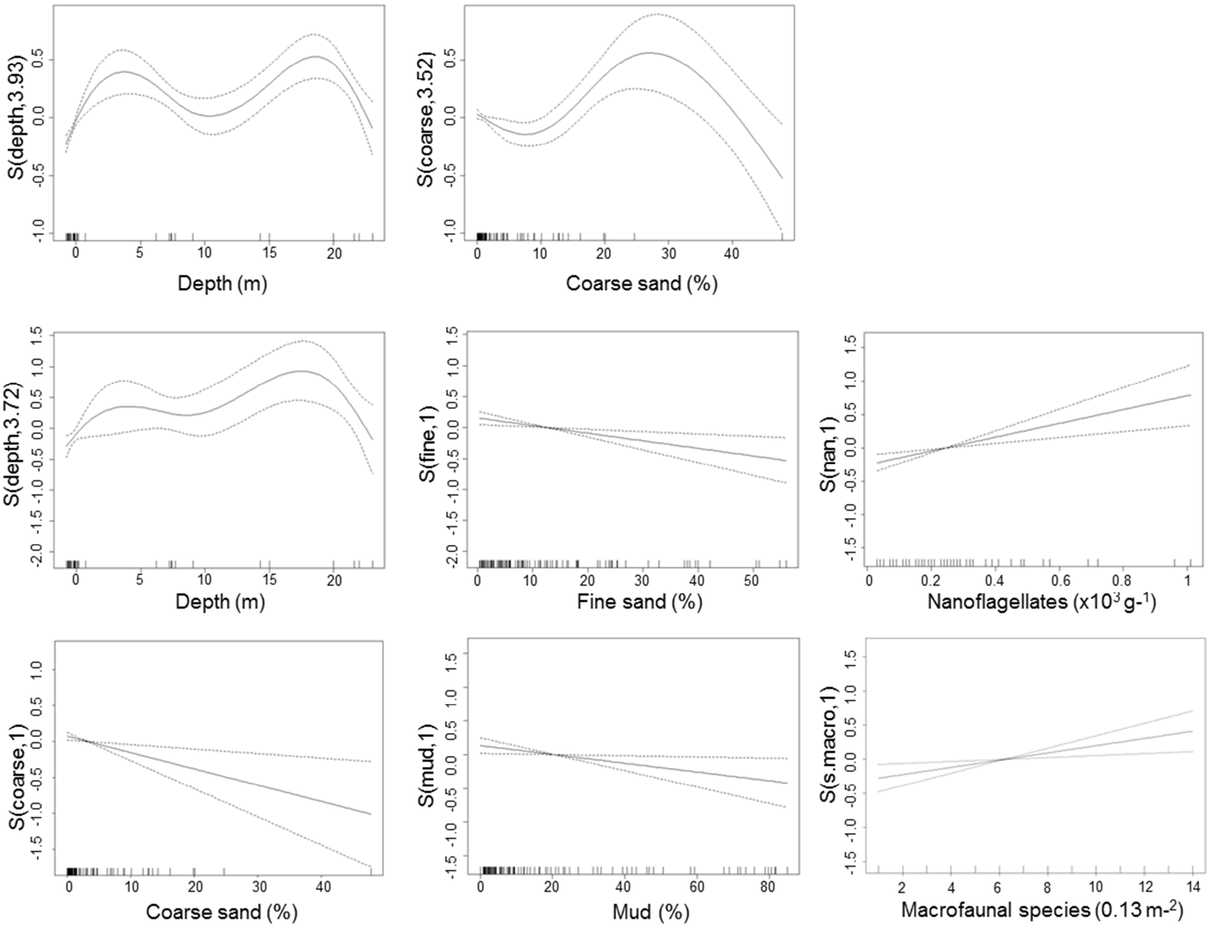

Figure 3 - Smoothers (S) curves showing the relationship (solid line) between species richness (top row) and abundance (middle and bottom row) of meiofaunal assemblages and the variables with an importance value greater than 0.3 in models predictions. Dashed lines indicate standard errors of the smooth curve. The ‘rug plots’ on the x-axis indicate the range of variables over which measurements were taken. Numbers after the variable name on the y-axis represent estimated degrees of freedom.

Discussion

Our results bring important implications for the use of the surrogacy approach in biodiversity assessments. Several studies have pointed out that strong and time-invariant congruence between different taxonomic groups might be an indicative that surrogate groups are relevant for biodiversity surveys (e.g. (Paavola et al. 2006, Bini et al. 2007b, Lopes et al. 2011). The logic behind it is that strong cross-taxon congruence implies that different groups exhibit very similar patterns; therefore, it would be reasonable to expect that all groups show similar trends in community parameters, and conservation programs could be based in a single taxonomic group. Our results, however, clearly demonstrate that strong concordance patterns may emerge even when different taxonomic groups exhibit contrasting trends in species richness and abundance, and suggests that cross-taxon congruence should be used with caution for conservation planning and monitoring purposes.

Macro- and meiofaunal assemblages were influenced by the same set of environmental variables, a result that help to understand the strong concordance between both groups. Depth and sediment type were the most important variables structuring both assemblages. The importance of these variables on community structure of marine benthic fauna is well-know and has been shown by several authors (e.g. (Flach et al. 2002, Defeo and McLachlan 2005, Pusceddu et al. 2014). Depth is a potentially important variable because it is associated with wave disturbance on sediment and determines other factors such as the amount and nature of light and phytoplankton-derived food reaching the seabed, sediment type and the stability of physico-chemical factors (Vanaverbeke et al. 2011). Sediment type, in turn, directly affects the spatial and structural conditions of the interstitial matrix and indirectly determines the physical and chemical environment of the sediment. Using the site-specific residuals from the ProTest analyses, we were able to reinforce the influence of depth and sediment type. Since a large amount of residuals imply weaker concordance, stronger concordance between macro- and meiofaunal assemblages is expected to occur at deeper areas with higher food availability and fine sediments.

It is important to stress, however, that although macro- and meiofaunal assemblages were influenced by similar environmental variables, the direction of this influence was different for each group. This was especially true for the depth gradient, where the two groups showed opposed trends. Macrofaunal assemblages had lower numbers of species and individuals in areas of 5 m depth and 15-20 m depth, whereas these areas had higher number of species and abundance of meiofaunal organisms.The non-linear nature of the relationships might be explained by hydrodinamic processes. A noticeable decrease in macrofauna abundance is expected on the shallow areas of the sublitoral due to the hydrodynamic stress on the surf zone (Janssen and Mulder 2005, Dolbeth et al. 2007). In this area, the wave action constant rework and move the sediment, limiting the residence of macrobenthos (Janssen and Mulder 2005). On the other hand, McIntyre (1971) and McLachlan et al. (1981) suggested that meiofauna is not so negatively affected by the increases in hydrodynamic stress than the macrofauna. The decrease in macrofaunal abundance and richnessin depth between 15 and 20 m is probably related to the stronger currents observed most frequently in the bottom layer of the São Sebastião Channel (Dottori et al. 2015). Sediment type is also an important factor in the establishment of benthic communities andt macro- and meiofaunal assemblages may show different responses to this variable (Fonseca and Netto (2006). Our results suggest that macro- and meiofauna are affected in different ways by the physical processes controlling coastal soft-bottom environments and may show contrasting distribution patterns in a depth gradient, especially at the surf zone of shallow sublitoral.

In addition to the environmental variables, biological interactions may also be important in structuring these assemblages and determining their congruence. Taxonomic composition and abundance of the other group was important in explaining macro and meiofaunal. The potential importance of biological interactions in structuring macro- and meiofauna assemblages has been discussed for a long time (McIntyre 1968, Watzin 1983, Warwick and Gee 1984) and it is not surprising. Macro- and meiofaunal species are closely connected to each other in soft-sediments and several authors have pointed out that direct interactions such as predation and competition exert a strong influence on their patterns and result on inverse relationships (Peterson 1982, Tita et al. 2000, Danovaro et al. 2007). Usually, meiofaunal assemblages are positively linked to the local bacterial production and organic matter content, but negatively affected by macrofaunal activity (Albertelli et al. 1999, Flach et al. 2002, Zeppilli et al. 2015). Meiofaunal organisms such as predator nematodes, in turn, are also expected to adversely affect macrofaunal assemblages by predating their larvae (especially polychaete) and inhibiting macrofaunal settlement (Watzin 1983, Danovaro et al. 1995, Dahms et al. 2004).

Taking into account the relatively small scale investigated here (less than 1 km^2), the strong concordance registered between macro- and meiofauna is rather surprising. Most studies that investigated congruence between different taxonomic groups at more local scales did not find solid concordance, mainly due to the lack of pronounced environmental gradients (Heino 2010, Dolph et al. 2011). According to Paavola et al. (2006), studies confined at small scales would imply strongly concordant patterns only if the environment is controlled by a single dominant gradient. In terrestrial environments, such dominant gradient would be observed in function of altitude, which would originate parallel shifts in the community composition of all taxonomic groups involved (Ormerod et al. 1994, Paavola et al. 2006). In marine ecosystems, such predominant gradients are likely to emerge from a depth gradient, and this fact can help to explain the strong concordance observed in this study. Even though our study area do not comprises a large extent, it encompasses a gradient from 0 to more than 20 m in depth. This gradient includes a wide range of habitats such as areas that are exposed to air during low tide, areas more influenced by wave action, and more stable habitats which are constantly submerged. Therefore, it is possible that stronger environmental gradients occur in smaller spatial scales in marine coastal ecosystems than in other aquatic environments, fact that would enhance community concordance.

Our results have important consequences to management and conservation strategies and programs. We showed that macro- and meiofaunal assemblages exhibited significant and strong concordance in spatial distribution in all periods analysed. Additionally, we found that both groups were influenced by the same set of explanatory variables. Therefore, an interpretation of our results based only on the cross-congruence approach suggests a high potential for the use of macrofauna as a surrogate for meiofauna (and *vice-versa*). However, a quick look at abundance and species distribution patterns of both groups reveals that, despite their strong concordance, macro- and meio fauna showed opposite diversity trends. These results are likely due to an interaction between biotic interactions and different responses to environmental gradient. Thus, we strongly recommend that studies evaluating community concordance investigate not only the congruence results but also the nature of the relationships of each assemblage with environmental variables and among assemblages.

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Annex

Top models adjusted for the species richness and abundance of macro- and meiofauna ordered by AICc value. All remaining models have dAIC > 4 and AICw < 0.001. Fine sand (fine), coarse sand (coarse), mud, heterotrophic bacteria (bact), cyanobacteria (cyan), total organic carbon (toc), phaeopigments (phaeop), number of macrofaunal species (s.macro), number of macrofaunal individuals (n.macro), number of meiofaunal species (s.meio), number of meiofaunal individuals (n.meio), depth, nanoflagellates (nanof), time (sampling period). Estimated degrees of freedom of each model (df), loglikehood (loglik), corrected Akaike value (cAIC), Delta Akaike (dAIC) and Akaike weights (AICw).

Rank	Model	df	logLik	AICc	dAIC	AICw
Number of species of macrofauna						
1	fine + n.meio + depth	11	-234.643	494.8	0	0.051
2	fine + cyan + n.meio + depth	12	-233.679	495	0.28	0.045
3	fine + depth	7	-239.120	495.1	0.35	0.043
4	fine + mud + depth	9	-236.995	495.6	0.8	0.034
5	fine + toc + depth	8	-238.104	495.6	0.85	0.033
6	fine + cyan + depth	8	-238.311	495.8	1.01	0.031
7	fine + mud + toc + depth	10	-235.859	496	1.21	0.028
8	fine + toc + n.meio + depth	12	-234.004	496.1	1.39	0.026
9	fine + depth + s.meio	9	-237.415	496.2	1.48	0.024
10	fine + bact + depth	8	-238.594	496.3	1.54	0.024
11	fine + mud + n.meio + depth	12	-233.195	496.3	1.56	0.023
12	fine + cyan +toc + depth	9	-237.315	496.4	1.6	0.023
13	fine + cyan + toc + n.meio + depth	13	-233.087	496.6	1.83	0.021
14	fine + bact + n.meio + depth	12	-234.420	496.7	1.9	0.02
15	fine + mud + depth + s.meio	11	-235.647	496.7	1.95	0.019
16	fine + mud + cyan + depth	10	-236.587	496.8	2	0.019
17	fine + n.meio + depth + s.meio	12	-234.516	497	2.21	0.017
18	fine + n.meio + nanof + depth	12	-233.911	497	2.22	0.017
19	fine + mud + bact + depth	10	-236.646	497	2.24	0.017
20	fine + n.meio + depth + time	13	-233.265	497	2.25	0.017
21	fine + bact + toc + n.meio + depth	9	-237.662	497	2.27	0.016
22	fine + phaeop + n.meio + depth	12	-234.566	497.2	2.4	0.015
23	fine + mud + cyan + n.meio + depth	13	-232.710	497.2	2.41	0.015
24	fine + mud + toc + n.meio + depth	13	-232.292	497.2	2.49	0.015
25	fine + cyan + depth + s.meio	10	-236.718	497.3	2.51	0.015
26	fine + depth + time	9	-237.812	497.3	2.56	0.014
27	fine + cyan + phaeop + n.meio + depth	13	-233.568	497.4	2.61	0.014
28	fine + phaeop + depth	8	-239.111	497.4	2.68	0.013
29	fine + bact + cyan + n.meio + depth	13	-233.629	497.4	2.68	0.013
30	fine + cyan + n.meio + depth + s.meio	13	-233.648	497.5	2.72	0.013
31	fine + toc + depth + s.meio	10	-236.713	497.5	2.77	0.013
32	fine + cyan + toc + depth	9	-238.030	497.6	2.81	0.013
33	fine + mud + n.meio + depth + s.meio	13	-233.243	497.6	2.85	0.012

34	fine + mud + bact + toc + depth	11	-235.621	497.7	2.95	0.012
35	fine + coarse + depth	11	-235.735	497.7	2.97	0.012
36	fine + cyan + n.meio + nanof + depth	13	-232.932	497.7	2.99	0.012
37	fine + mud + cyan + toc + depth	11	-235.685	497.8	3.03	0.011
38	fine + nanof + depth	9	-238.501	497.8	3.04	0.011
39	fine + mud + toc + depth + s.meio	12	-234.983	497.9	3.14	0.011
40	fine + cyan + nanof + depth	10	-237.287	497.9	3.16	0.011
41	fine + bact + depth + time	10	-236.781	497.9	3.16	0.011
42	fine + bact + depth + s.meio	10	-237.174	497.9	3.18	0.01
43	fine + mud + phaeop + depth	10	-237.009	498	3.21	0.01
44	fine + toc + phaeop + depth	9	-238.105	498	3.25	0.01
45	fine + cyan + phaeop + depth	9	-238.286	498.1	3.36	0.01
46	fine + bact + toc + n.meio + depth	13	-233.814	498.2	3.42	0.009
47	fine + coarse + toc + depth	12	-234.880	498.2	3.49	0.009
48	fine + mud + bact + n.meio + depth	13	-233.118	498.3	3.56	0.009
49	fine + bact + cyan + toc + depth	10	-237.094	498.3	3.57	0.009
50	fine + coarse + cyan + n.meio + depth	13	-233.168	498.4	3.61	0.008
51	fine + mud + nanof + depth	11	-236.557	498.4	3.65	0.008
52	fine + mud + toc +phaeop + depth	11	-235.866	498.4	3.67	0.008
53	fine + mud + cyan + depth + s.meio	12	-235.283	498.5	3.73	0.008
54	fine + bact + depth + time	10	-237.225	498.5	3.76	0.008
55	fine + toc + n.meio + depth + time	14	-232.609	498.5	3.77	0.008
56	fine + cyan + toc + depth + s.meio	11	-235.992	498.6	3.82	0.008
57	fine + mud + bact + depth + s.meio	12	-235.535	498.6	3.84	0.008
58	fine + toc + n.meio + depth + s.meio	13	-233.983	498.6	3.86	0.007
59	fine + toc + phaeop + n.meio + depth	13	-233.947	498.6	3.88	0.007
60	fine + mud + bact + cyan + depth	11	-236.359	498.7	3.9	0.007
61	fine + cyan + toc + nanof + depth	11	-236.277	498.7	3.91	0.007
62	fine + phaeop + depth + s.meio	10	-237.419	498.7	3.92	0.007
63	fine + toc + n.meio + nanof + depth	13	-233.287	498.7	3.93	0.007
64	fine + bact + phaeop + depth	9	-238.598	498.7	3.94	0.007
65	fine + mud + cyan + toc + n.meio + depth	14	-232.052	498.7	3.97	0.007

Rank	Model	df	logLik	AICc	dAIC	AICw
Number of individuals of macrofauna						
1	fine + depth + s.meio	8	-468.286	955.9	0	0.03
2	nanof + depth + s.meio	7	-469.369	956.1	0.16	0.028
3	depth + s.meio	6	-470.544	956.1	0.19	0.027
4	fine + depth	7	-469.876	956.8	0.9	0.019
5	cyan + depth + s.meio + time	12	-463.921	956.9	0.98	0.018
6	mud + nanof + depth + s.meio	9	-467.966	957	1.08	0.017
7	fine + nanof + depth + s.meio	9	-467.800	957.1	1.2	0.016
8	fine + depth + s.meio + time	10	-466.439	957.2	1.28	0.016
9	cyan + depth + time	11	-465.610	957.3	1.36	0.015
10	nanof + depth	6	-471.198	957.4	1.5	0.014
11	depth	5	-472.344	957.4	1.52	0.014
12	toc + nanof + depth + s.meio	9	-467.711	957.6	1.67	0.013
13	cyan + nanof + depth + s.meio	8	-468.971	957.7	1.78	0.012
14	toc + nanof + depth	8	-468.996	957.7	1.84	0.012
15	mud + depth + s.meio	8	-469.635	957.8	1.87	0.012
16	fine + phaeop + depth + s.meio	9	-468.068	957.8	1.93	0.011
17	fine + nanof + depth + s.meio + time	11	-465.777	957.8	1.95	0.011
18	cyan + nanof + depth + time	12	-464.749	957.8	1.95	0.011
19	fine + mud + depth + s.meio	9	-467.843	957.9	1.98	0.011
20	n.meio + nanof + depth + s.meio	8	-469.088	957.9	2.01	0.011
21	nanof + depth + s.meio + time	9	-467.853	957.9	2.01	0.011
22	toc + depth + s.meio	8	-469.554	958	2.06	0.011
23	phaeop + depth + s.meio	7	-470.329	958	2.08	0.011
24	phaeop + nanof + depth + s.meio	8	-469.150	958	2.08	0.011
25	fine + mud + nanof + depth + s.meio	10	-466.806	958	2.11	0.01
26	toc + depth	7	-470.633	958.1	2.17	0.01
27	fine + toc + depth	9	-468.483	958.1	2.17	0.01
28	mud + nanof + depth + s.meio + time	11	-465.869	958.1	2.2	0.01
29	toc + nanof + depth + s.meio + time	11	-465.321	958.1	2.2	0.01
30	fine + nanof + depth	8	-469.476	958.1	2.21	0.01
31	fine + toc + depth + s.meio	10	-467.457	958.1	2.24	0.01
32	fine + phaeop + depth	8	-469.417	958.2	2.26	0.01
33	mud + nanof + depth	8	-469.711	958.2	2.34	0.009
34	fine + bact + depth + s.meio	9	-468.234	958.3	2.36	0.009
35	fine + cyan + depth + s.meio	9	-468.276	958.3	2.38	0.009
36	fine + n.meio + depth + s.meio	9	-468.282	958.3	2.41	0.009
37	fine + depth + time	9	-468.247	958.3	2.43	0.009
38	fine + coarse + depth + s.meio	9	-468.314	958.3	2.45	0.009
39	fine + cyan + depth + time	13	-464.036	958.4	2.46	0.009
40	fine + toc + depth + s.meio + time	12	-464.594	958.4	2.48	0.009
41	n.meio + depth + s.meio	7	-470.524	958.4	2.49	0.009
42	cyan + depth + s.meio	7	-470.534	958.4	2.52	0.008
43	coarse + depth + s.meio	7	-470.479	958.4	2.53	0.008
44	bact + depth + s.meio	7	-470.545	958.4	2.54	0.008

45	coarse + nanof + depth + s.meio	8	-469.389	958.4	2.55	0.008
46	bact + nanof + fine + nanof + s.meio	8	-469.367	958.4	2.55	0.008
47	toc + nanof + depth + time	10	-466.857	958.5	2.59	0.008
48	fine + toc + nanof + depth + s.meio + time	13	-463.462	958.5	2.59	0.008
49	fine + toc + nanof + depth + time	12	-464.845	958.5	2.6	0.008
50	fine + toc + depth + time	11	-465.944	958.5	2.62	0.008
51	phaeop + nanof + depth	7	-470.664	958.6	2.74	0.008
52	phaeop + depth	6	-471.772	958.6	2.75	0.008
53	cyan + nanof + depth	7	-470.638	958.6	2.75	0.008
54	nanof + depth + time	8	-469.462	958.7	2.81	0.007
55	fine + bact + depth	8	-469.636	958.8	2.89	0.007
56	mud + phaeop + nanof + depth + s.meio	10	-467.671	958.9	2.97	0.007
57	fine + n.meio + depth	8	-469.714	958.9	2.97	0.007
58	fine + toc + nanof + depth + s.meio	11	-466.347	958.9	2.98	0.007
59	mud + toc + nanof + depth	10	-468.183	958.9	3	0.007
60	depth + s.meio + time	8	-469.570	958.9	3.01	0.007
61	mud + depth	7	-471.346	959	3.06	0.006
62	mud + toc + nanof + depth + s.meio	10	-467.302	959	3.07	0.006
63	fine + nanof + depth + time	10	-467.654	959	3.08	0.006
64	fine + mud + depth	9	-469.527	959	3.13	0.006
65	fine + toc + nanof + depth	10	-467.674	959	3.14	0.006
66	fine + mud + nanof + depth + s.meio + time	12	-464.663	959.1	3.16	0.006
67	fine + phaeop + nanof + depth	10	-467.570	959.1	3.16	0.006
68	toc + phaeop + nanof + depth	9	-468.481	959.1	3.18	0.006
69	fine + cyan + depth	8	-469.858	959.1	3.19	0.006
70	mud + cyan + nanof + depth + s.meio	10	-467.744	959.1	3.2	0.006
71	bact + cyan + depth + s.meio + time	13	-463.731	959.1	3.23	0.006
72	cyan + toc + depth + time	13	-464.443	959.1	3.23	0.006
73	n.meio + nanof + depth + s.meio + time	10	-467.207	959.1	3.24	0.006
74	fine + cyan + nanof + depth + s.meio	10	-467.735	959.1	3.24	0.006
75	mud + n.meio + nanof + depth + s.meio	10	-467.884	959.2	3.26	0.006
76	fine + coarse + depth	8	-469.893	959.2	3.28	0.006
77	fine + bact + depth + s.meio + time	11	-466.312	959.3	3.37	0.006
78	fine + mud + depth + s.meio + time	11	-466.050	959.3	3.42	0.005
79	mud + nanof + depth	10	-467.550	959.3	3.44	0.005
80	fine + cyan + depth + s.meio	11	-466.249	959.4	3.47	0.005
81	mud + phaeop + nanof + depth	9	-469.054	959.4	3.48	0.005
82	coarse + mud + nanof + depth + s.meio	10	-467.970	959.4	3.49	0.005
83	cyan + n.meio + depth + s.meio + time	13	-463.843	959.4	3.51	0.005
84	toc + phaeop + nanof + depth + s.meio	10	-467.420	959.4	3.52	0.005
85	fine + phaeop + depth + s.meio + time	11	-466.317	959.4	3.52	0.005
86	bact + cyan + nanof + depth + s.meio	10	-467.948	959.4	3.53	0.005
87	fine + n.meio + nanof + depth + s.meio	10	-467.794	959.4	3.53	0.005
88	fine + phaeop + nanof + depth	9	-468.992	959.5	3.57	0.005
89	fine + toc + phaeop + depth	10	-467.991	959.5	3.6	0.005
90	fine + bact + nanof + depth + s.meio	10	-467.737	959.5	3.6	0.005

91	cyan + phaeop + depth + time	12	-464.991	959.5	3.61	0.005
92	toc + phaeop + fine + nanof	8	-470.197	959.5	3.62	0.005
93	bact + nanof + depth	7	-471.090	959.5	3.63	0.005
94	fine + bact + nanof + depth + s.meio + time	12	-465.579	959.5	3.64	0.005
95	cyan + phaeop + nanof + depth + s.meio	9	-468.692	959.5	3.64	0.005
96	bact + nanof + depth + s.meio + time	10	-467.414	959.5	3.65	0.005
97	bact + depth	6	-472.269	959.6	3.67	0.005
98	cyan + phaeop + depth + s.meio + time	13	-463.586	959.6	3.67	0.005
99	mud + toc + depth	8	-469.993	959.6	3.68	0.005
100	fine + mud + phaeop + depth + s.meio	11	-467.266	959.6	3.68	0.005
101	fine + coarse + nanof + depth + s.meio	10	-467.833	959.6	3.69	0.005
102	toc + depth + s.meio + time	10	-467.562	959.6	3.71	0.005
103	mud + toc + depth + s.meio	9	-469.156	959.6	3.71	0.005
104	cyan + depth	6	-472.290	959.6	3.72	0.005
105	coarse + cyan depth + s.meio + time	13	-463.768	959.6	3.72	0.005
106	cyan + toc + nanof + depth	9	-468.896	959.6	3.74	0.005
107	n.meio + depth	6	-472.324	959.7	3.76	0.005
108	fine + mud + phaeop + nanof + depth + s.meio	11	-466.351	959.7	3.76	0.005
109	mud + phaeop + depth + s.meio	9	-469.159	959.7	3.77	0.005
110	n.meio + nanof + depth	7	-471.161	959.7	3.77	0.005
111	cyan + toc + nanof + depth + s.meio	10	-467.733	959.7	3.77	0.005
112	coarse + depth	7	-472.191	959.7	3.8	0.004
113	cyan + n.meio + nanof + depth + s.meio	9	-468.759	959.7	3.82	0.004
114	coarse + nanof + depth	7	-471.211	959.7	3.84	0.004
115	coarse + cyan + depth + time	12	-465.591	959.8	3.88	0.004
116	toc + n.meio + nanof + depth + s.meio	11	-467.335	959.8	3.88	0.004
117	depth + time	7	-471.206	959.8	3.92	0.004
118	cyan + phaeop + nanof + depth	8	-470.043	959.8	3.92	0.004
119	mud + cyan + depth + time	12	-465.618	959.8	3.93	0.004
120	phaeop + n.meio + nanof + depth + s.meio	9	-468.840	959.8	3.93	0.004
121	cyan + n.meio + nanof + depth + s.meio + time	12	-464.973	959.8	3.95	0.004
122	cyan + toc + depth + s.meio	9	-469.277	959.8	3.95	0.004
123	fine + coarse + depth + s.meio + time	11	-466.518	959.8	3.95	0.004
124	bact + cyan + depth + time	12	-465.649	959.9	3.97	0.004
125	fine + n.meio + depth + s.meio + time	11	-466.526	959.9	3.98	0.004
126	bact + toc + nanof + depth + s.meio + time	13	-464.564	959.9	3.99	0.004

Rank	Model	df	logLik	AICc	dAIC	AICw
Number of species of meiofauna						
1	coarse + depth	9	-327.736	676.5	0	0.076
2	n.macro + depth	5	-332.366	676.5	0.04	0.075
3	toc + depth	6	-330.942	676.8	0.35	0.064
4	depth	5	-332.179	677	0.47	0.06
5	phaeop + depth	6	-331.761	678.3	1.85	0.03
6	coarse + toc + depth	10	-327.009	678.4	1.92	0.029
7	coarse + bact + depth	10	-327.467	678.4	1.95	0.029
8	fine + n.macro + depth	6	-332.290	678.6	2.06	0.027
9	coarse + cyan + depth	10	-327.513	678.6	2.09	0.027
10	n.macro + nanof + depth	6	-332.263	678.7	2.16	0.026
11	coarse + nanof + depth	10	-327.573	678.7	2.2	0.025
12	bact + depth	6	-331.940	678.8	2.28	0.024
13	mud + n.macro + depth	6	-332.352	678.8	2.31	0.024
14	fine + coarse + depth	10	-327.680	678.9	2.36	0.024
15	bact + depth + depth	6	-333.003	678.9	2.41	0.023
16	coarse + mud + depth	10	-327.737	679	2.47	0.022
17	toc + phaeop + depth	8	-330.447	679	2.47	0.022
18	mud + depth	6	-332.029	679	2.49	0.022
19	cyan + depth	7	-331.906	679	2.53	0.022
20	toc + n.macro + depth	8	-330.228	679.1	2.58	0.021
21	fine + toc + depth	7	-330.888	679.1	2.6	0.021
22	toc + nanof + depth	7	-330.920	679.2	2.66	0.02
23	fine + depth	6	-332.128	679.2	2.67	0.02
24	mud + toc + depth	7	-330.938	679.2	2.68	0.02
25	nanof + depth	6	-332.157	679.2	2.73	0.02
26	coarse + n.macro + depth	11	-327.257	679.6	3.1	0.016
27	cyan + toc + depth	8	-330.466	679.6	3.14	0.016
28	n.macro + depth + s.macro	7	-331.623	679.6	3.14	0.016
29	bact + toc + depth	8	-330.467	679.8	3.26	0.015
30	phaeop + depth + s.macro	7	-331.997	679.9	3.39	0.014
31	coarse + mud + n.macro	8	-330.465	680	3.46	0.014
32	coarse + mud + phaeop	7	-331.922	680.1	3.56	0.013
33	cyan + phaeop + depth	7	-331.454	680.1	3.61	0.013
34	fine + coarse + n.macro + depth	10	-328.800	680.2	3.67	0.012
35	fine + bact + n.macro + depth	7	-331.982	680.2	3.71	0.012
36	coarse + cyan + toc + depth	11	-326.859	680.3	3.78	0.012
37	bact + cyan + depth	7	-331.992	680.4	3.88	0.011
38	coarse + depth + time	11	-327.104	680.4	3.9	0.011
39	phaeop + n.macro + depth	8	-331.153	680.4	3.95	0.011
40	coarse + toc + nanof + depth	11	-326.917	680.4	3.95	0.011
41	mud + bact + n.macro + depth	7	-332.032	680.5	3.96	0.011
42	cyan + n.macro + depth	8	-331.056	680.5	3.97	0.011
43	bact + n.macro + depth	8	-331.012	680.5	3.99	0.01

Rank	Model	df	logLik	AICc	dAIC	AICw
Number of individuals of meiofauna						
1	fine + coarse + mud + nanof + depth + s.macro	10	-777.025	1578.5	0	0.193
2	fine + coarse + mud + n.macro + nanof + depth + s.macro	11	-776.745	1580.5	1.92	0.074
3	fine + mud + nanof + depth + s.macro	9	-779.197	1580.6	2.04	0.07
4	fine + coarse + mud + cyan + nanof + depth + s.macro	11	-776.674	1580.7	2.2	0.064
5	fine + coarse + mud + phaeop + nanof + depth + s.macro	11	-776.872	1580.8	2.27	0.062
6	fine + coarse + mud + toc + nanof + depth + s.macro	11	-776.945	1580.9	2.38	0.059
7	fine + coarse + mud + bact + nanof + depth + s.macro	11	-777.039	1581.1	2.57	0.053
8	fine + coarse + nanof + depth + s.macro	9	-779.656	1581.2	2.64	0.052
9	fine + nanof + depth + s.macro	8	-780.928	1581.6	3.01	0.043
10	fine + coarse + cyan + nanof + depth + s.macro	10	-778.602	1581.6	3.04	0.042
11	fine + coarse + nanof + depth + s.macro + time	11	-777.374	1581.7	3.2	0.039
12	fine + cyan + nanof + depth + s.macro	9	-779.871	1581.9	3.35	0.036
13	fine + coarse + toc + nanof + depth + s.macro	11	-778.451	1582	3.5	0.034
14	fine + coarse + mud + nanof + depth + s.macro + time	12	-776.189	1582.1	3.5	0.033
15	fine + mud + phaeop + nanof + depth + s.macro	10	-778.762	1582.2	3.69	0.03
16	fine + coarse + cyan + toc + nanof + depth + s.macro	11	-777.396	1582.2	3.69	0.03
17	fine + coarse + mud + nanof + depth	9	-780.406	1582.3	3.8	0.029
18	fine + mud + cyan + nanof + depth + s.macro	10	-778.849	1582.4	3.84	0.028
19	fine + mud + n.macro + nanof + depth + s.macro	10	-778.895	1582.5	3.91	0.027

Considerações finais

Esta tese investigou como diferentes processos e variáveis estruturam comunidades bentônicas que habitam os sedimentos de regiões costeiras. Por meio de coletas realizadas na região entremarés e sublitoral, foi comprovada a influência de variáveis ambientais, como tipo de sedimento e profundidade, algo já bastante conhecido. Entretanto, foi observado também que eventos de larga escala relacionados às mudanças climáticas podem provocar significativas mudanças nas características ecológicas de ambientes costeiros (capítulo 1), e que a influência de variáveis espaciais pode ser preponderante nessas comunidades (capítulos 2 e 3).

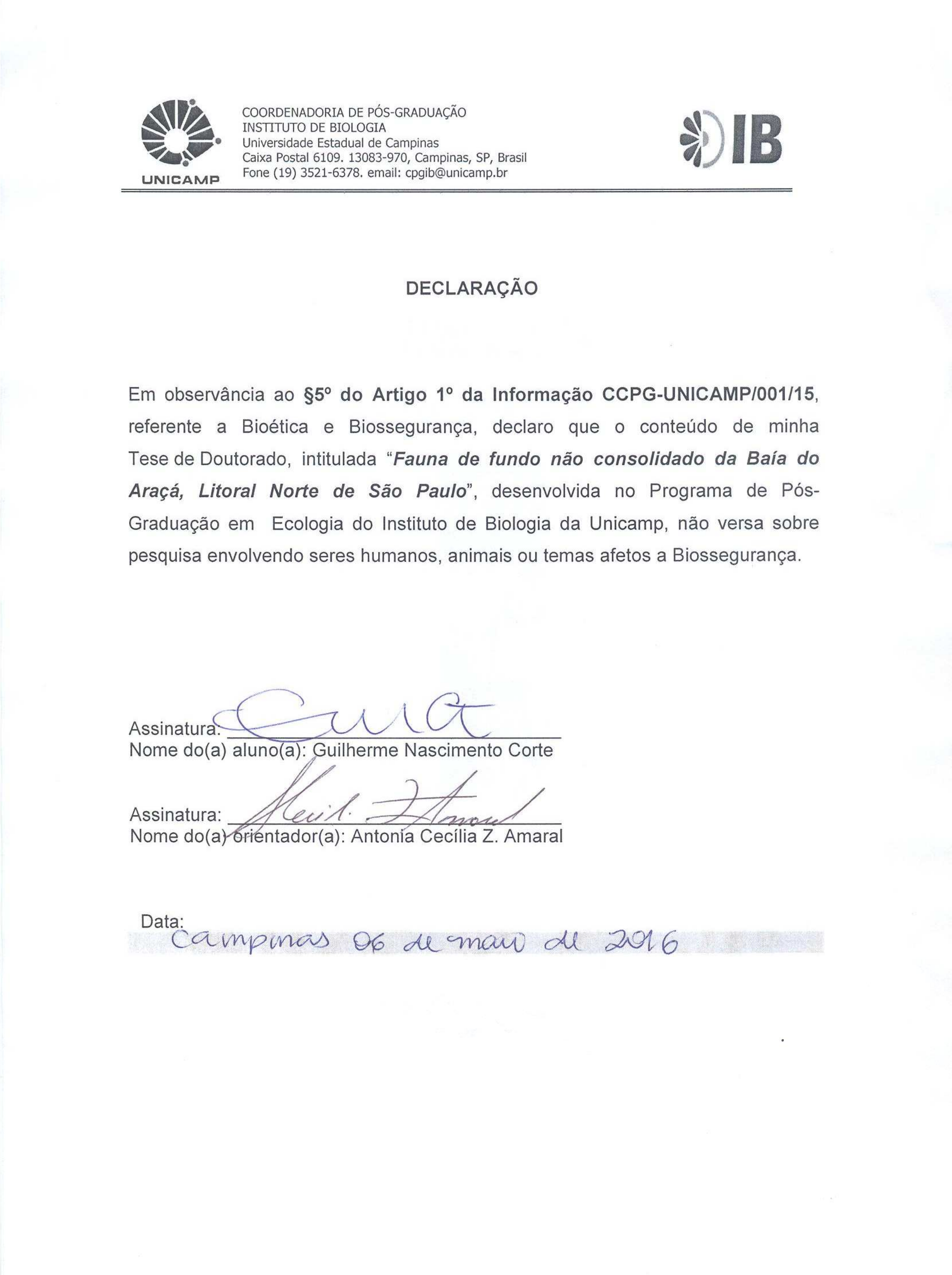
Possivelmente, a forte influência de eventos climáticos extremos e de variáveis espaciais em comunidades bentônicas de fundo não consolidado deve-se ao caráter móvel dessa fauna. Diferente do observado em outros sistemas, uma propriedade importante dessas comunidades é que as espécies que as constituem não são permanentemente fixas ao substrato e muitas ocorrem em grande abundância, o que pode resultar em maiores taxas de dispersão (capítulo 2). Além disso, a dispersão dessas espécies é facilitada pela ação de ondas e correntes de maior intensidade, variáveis que podem alterar o padrão de diversidade nesses ambientes (capítulo 1).

O fato das espécies bentônicas de fundo não-consolidado não se fixarem permanentemente no substrato, entretanto, não significa que essas espécies tem capacidade similar de dispersão. Os resultados obtidos no capítulo 2 demonstram que a estrutura espacial da fauna macrobentônica é contingente da capacidade de dispersão de cada espécie, sendo que espécies com maior mobilidade (dispersão larval e adultos móveis) sofrem menos influência de variáveis espaciais, i.e. são mais influenciadas pelo ambiente por que essas espécies podem se mover por distâncias maiores e, consequentemente, têm mais chances de se estabelecer em locais com características mais favoráveis. Os resultados do capítulo 2 também demonstraram que a estrutura espacial e a influência do ambiente são variáveis no tempo. Tal resultado não pode ser considerado surpreendente, uma vez que ecossistemas costeiros sofrem a constante influência de ondas e marés e estão entre os mais dinâmicos. Entretanto, esses resultados destacam que caracterizações desses ecossistemas não devem ser baseadas em coletas pontuais.

Enquanto os resultados apresentados nos capítulos 1 e 2 destacam como as comunidades bentônicas podem ser variáveis, o capítulo 3 aborda a estabilidade na concordância entre comunidades macro- e meiofaunais. Os resultados obtidos demonstram que a macro- e a maiofauna possuem padrões similares em suas comunidades e que os dois grupos são estruturados por variáveis ambientais semelhantes. Esses resultados podem ter implicação para estudos de manejo e conservação, sugerindo que um grupo pode ser usado como substituto para o outro. Entretanto, o padrão de riqueza e abundância nessas comunidades foi contrastante, o que destaca que a identificação de locais de maior valor em biodiversidade não deve ser realizada levando em consideração apenas um desses grupos.

De maneira geral, os resultados apresentados nessa tese destacam que processos espaciais e eventos extremos podem exercer grande influência na fauna bentônica marinha de substratos não-consolidados. Esses tópicos têm recebido mais atenção nos últimos anos, entretanto, o número de estudos é ainda bastante reduzido. A congruência entre diferentes grupos bentônicos é outro assunto pouco explorado e que deve ser mais investigado, sobretudo devido a sua potencial aplicabilidade em planos de conservação e manejo. Outro tópico ainda pouco explorado, porém essencial para compreender dos padrões da fauna bentônica, é a real conectividade em ambientes marinhos. Em ecologia, a validação empírica da capacidade de dispersão das espécies é fundamental, entretanto, informações precisas sobre a capacidade de dispersão das espécies bentônicas é extremamente reduzida. Dessa maneira, futuro estudos devem investigar a real capacidade de dispersão das espécies marinhas. Tal conhecimento proporcionará uma melhor compreensão da dinâmica desses ecossistemas e, consequentemente, que sejam tomadas medidas mais efetivas contra impactos, e planos de manejo mais eficientes sejam estabelecidos.

Anexos



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Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "***Fauna de fundo não consolidado da Baía do Araçá, Litoral Norte de São Paulo***", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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Campinas 06 de maio de 2016

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Comissão Central de Pós-Graduação
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