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ESTRUTURA DA MACROFAUNA E PRODUÇÃO SECUNDÁRIA BENTÔNICA EM HABITATS VEGETADOS E NÃO VEGETADOS DE ESTUÁRIOS TROPICAIS NA ECORREGIÃO MARINHA LESTE DO BRASIL

VITÓRIA
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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Oceanografia Ambiental da Universidade Federal do Espírito Santo, como requisito parcial para obtenção do título de Mestre em Oceanografia Ambiental.
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RESUMO

Ecossistemas estuarinos, compostos por diferentes habitats que incluem florestas de mangue e planícies de maré, possuem alta produtividade e uma diversa comunidade de organismos bentônicos. Esses habitats são espacialmente heterogêneos resultando em variações na densidade, biomassa e produção secundária de organismos bentônicos, porém, essas escalas de variabilidade são pouco conhecidas em estuários tropicais. Para avaliar as variações espaciais na produção secundária, biomassa, densidade e composição da macrofauna nos manguezais (vegetado) e nas planícies de maré lamosas adjacentes (não vegetadas), foi utilizado um protocolo espacial hierárquico, permitindo determinar quais escalas espaciais foram significantes para cada descritor das assembleias. Três estuários tropicais localizados na Ecorregião Marinha Leste do Brasil foram amostrados na região mesohalina nas escalas espaciais de sítios, plots e réplicas em ambos os habitats. Mudanças nas assembleias bentônicas, na biomassa, na densidade e na produção secundária ocorreram principalmente entre habitats, com algumas diferenças entre estuários. No estuário do Benevente, os habitats não vegetados apresentaram maior produção secundária, biomassa e densidade da macrofauna, o que ocorreu devido à dominância de Kalliapseudidae (Tanaidacea). Porém, os outros dois estuários, Baía de Vitória e estuário do Piraquê-Açu, apresentaram padrões opostos na biomassa e produção secundária da macrofauna, com valores mais altos nos manguezais, o que é consistente com estudos anteriores em habitats vegetados de estuários. A composição taxonômica das assembleias bentônicas foi mais similar entre os habitats vegetados dos estuários, e relacionada à maior biomassa de detritos e matéria orgânica sedimentar total nestes habitats. Oligochaeta e Capitellidae dominaram nos habitats vegetados, enquanto habitats não vegetados apresentaram diferentes dominâncias entre estuários. Mollusca e Crustacea exibiram maior biomassa e foram responsáveis por grande parte da produção secundária nos estuários avaliados, com exceção do habitat não vegetado do estuário do Benevente, onde Kalliapseudidae foi a família com maior produção.

Palavras-chave: Estuários, Macrofauna, Produção secundária, Manguezal, Planície de maré.

ABSTRACT

Estuarine ecosystems, composed by various habitats, including mangrove forests and tidal flats, support high productivity and a diverse community of benthic organisms. These habitats are spatially heterogeneous resulting in variable density, biomass and secondary production of benthic organisms, but the scales of their variability are poorly known in tropical estuaries. To assess the spatial variability of benthic macrofaunal secondary production, biomass, density and composition on mangroves (vegetated) and adjacent tidal flats (unvegetated), a nested protocol was used allowing determining what spatial scales were significant to each assemblage descriptor. Three tropical estuaries located in the Eastern Marine Ecoregion of Brazil were sampled (larger spatial scale) on one mesohaline region in both habitats at the scales of sites, plots and replicates (local scales). Changes in benthic assemblage composition, biomass, density and secondary production occurred mainly between habitats, with some differences among estuaries. At Benevente estuary, unvegetated habitats had higher macrofaunal secondary production, biomass and density, due to the dominance of Kalliapseudidae (Tanaidacea). However, the other two estuaries exhibited opposite patterns of macrofaunal biomass and secondary production, with higher values within mangrove forests which is consistent with previous observations in vegetated habitats from other estuaries. Taxonomic composition (family level) of benthic assemblages was more similar between vegetated habitats among estuaries, and related to higher sedimentary detritus biomass and total sedimentary organic matter in these habitats. Oligochaeta and Capitellidae dominated vegetated habitats, whereas unvegetated habitats exhibited variable dominance between estuaries. Mollusca and Crustacea exhibited higher biomass and were responsible for most of the secondary production at the studied estuaries, except at unvegetated habitat in Benevente estuary, where Kalliapseudidae was the family with higher production.

Keywords: Estuaries, Macrofauna, Secondary production, Mangroves, Tidal flats.

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CAPÍTULO 1

Introdução geral

Estuários e manguezais sustentam ecossistemas dinâmicos e produtivos (Kennish, 2002; McLusky, Elliott, 2004; Lee, 2008). Ecossistemas estuarinos possuem importantes funções ecológicas e socioeconômicas, incluindo: exportação de nutrientes e material orgânico para a região costeira; proteção das zonas costeiras contra tempestades, inundação e erosão; ciclagem de nutrientes; áreas de reprodução e berçário de várias espécies de importância ecológica e comercial; fornecimento de recursos, como peixes e mariscos, para as comunidades locais; acúmulo de matéria orgânica no solo e consequente enterramento de carbono; entre outros (Alongi, 1998; McLusky, Elliott, 2004; Kristensen et al., 2008; Adhikari et al., 2009; Soares et al., 2012; Lee et al., 2014). Ambientes estuarinos também são ricos em fontes de alimento que se acumulam nos sedimentos, principalmente sob a forma de detritos, proporcionando comunidades bentônicas abundantes (McLusky, Elliott, 2004; Nagelkerken et al., 2008).

Comunidades bentônicas em estuários e manguezais são formadas por diversos grupos, e compostas em grande parte por caranguejos, poliquetas, oligoquetas e moluscos, entre outros (Kristensen, 2008; Lee, 2008; Nagelkerken et al., 2008). A macrofauna bentônica é um importante componente do ecossistema estuarino e é um elemento estruturante das cadeias alimentares (Herman et al., 1999). Entre as funções desempenhadas por esses organismos está o processamento da matéria orgânica, bioturbação, modificações nas propriedades do sedimento e aeração, ciclagem de nutrientes e ainda são fontes de alimento para outros organismos (Lee, 1998; Kristensen, 2008; Kristensen et al., 2008; Nagelkerken et al., 2008).

Um importante parâmetro para o estudo da dinâmica do ecossistema é a produção das populações macrobentônicas (Dolbeth et al., 2005), que pode ser definida como a quantidade de tecido elaborada por unidade de tempo em determinada área (Waters, Crawford, 1973; Downing, 1984). A produção é uma das principais vias de fluxo de energia, sendo o meio pelo qual a energia torna-se disponível para ser transmitida entre níveis tróficos no ecossistema (Tumbiolo, Downing, 1994; Petracco, 2008). A produção é função do crescimento dos indivíduos, do número de coortes, do recrutamento e da mortalidade, e assim, a produção está diretamente relacionada ao ciclo de vida das espécies (Waters, Crawford, 1973; Petracco, 2008). Portanto, a produção secundária também reflete outras propriedades ou processos das populações e interações bióticas, assim como as condições ambientais em que os organismos estão inseridos (Dolbeth et al., 2012). A produção secundária bentônica também responde a fatores ambientais que variam espacialmente, como a carga de nutrientes e a produção primária. Esses fatores podem variar espacialmente entre estuários, podendo gerar diferentes produções entre eles (Edgar, Barrett, 2002). A produção secundária pode ser utilizada também como uma ferramenta para avaliar a condição do ecossistema e os impactos de atividades antrópicas e mudanças ambientais (Dolbeth et al., 2012).

O objetivo do estudo e os recursos disponíveis podem influenciar na escolha do método utilizado para estimar a produção secundária. Os métodos clássicos utilizados para estimar a produção secundária são baseados na identificação de coortes, taxa de crescimento e tamanho dos organismos, o que é impraticável de ser utilizado na avaliação da comunidade como um todo, devido ao fato de serem procedimentos demorados e dispendiosos (Sprung, 1993; Tumbiolo, Downing, 1994). Nesse contexto, modelos empíricos foram estabelecidos para estimar a produção (Edgar, 1990; Tumbiolo, Downing, 1994; Brey, 2001), com alguns estudos demonstrando resultados satisfatórios através da utilização desses métodos (Wilber, Clarke 1998; Dolbeth et al., 2005). Entre esses métodos está o método empírico proposto por Edgar (1990), que requer pouco esforço relativo de amostragem e é aplicável para ecossistemas estuarinos com temperaturas entre 5 e 30ºC.

A análise da distribuição espacial dos organismos bentônicos é essencial para identificar e entender as escalas dos processos que influenciam a distribuição da macrofauna (Underwood, Chapman, 1996). Diferentes fatores controlam a distribuição, a abundância e a produção dos organismos estuarinos nesses ambientes. Entre eles podemos citar a salinidade, disponibilidade de oxigênio, composição do sedimento, concentração de nutrientes, interações ecológicas, disponibilidade de alimento, entre outros (McLusky, Elliott 2004). Dessa forma, a abundância, composição, produção e biomassa da macrofauna bentônica podem apresentar variações de distribuição espacial em diferentes escalas dentro do estuário e entre estuários (Edgar, Barrett, 2002).

A distribuição da fauna também pode ser alterada pela presença de vegetação. Na região entre-marés de estuários encontram-se habitats bentônicos vegetados (e.g. marismas, bosques de mangue) e habitats não vegetados adjacentes (e.g. lamosos, arenosos ou areno-lamosos). Em razão da presença de raízes, troncos e outras estruturas vegetais, áreas vegetadas apresentam-se como habitats mais complexos, que oferecem maior estabilidade sedimentar (Lana, Guiss, 1991; Pagliosa, Lana, 2005). Desta forma, a presença de vegetação pode provocar mudanças na abundância e diversidade bentônica, além das tramas tróficas das espécies entre áreas vegetadas e não vegetadas (Lana, Guiss, 1991; Yu et al., 1997; Pagliosa, Lana, 2005). Em algumas áreas vegetadas, a macrofauna bentônica pode apresentar aumento na abundância, produção, diversidade e riqueza de espécies, quando comparadas a áreas adjacentes sem vegetação (Edgar et al., 1994; Heck et al., 1995; Bostrom, Bonsdorff, 1997; Netto, Lana, 1999; Kon, et al., 2010).

Apesar de sua importância, ambientes estuarinos são afetados por diversas perturbações e impactos antrópicos, com potenciais impactos na estrutura e dinâmica das comunidades e na alteração dos habitats (Kennish, 2002; Lee et al., 2014). Problemas ambientais resultam do desenvolvimento urbano desordenado e do crescimento da população em regiões costeiras, causando poluição, contaminações químicas e perda ou alteração dos habitats estuarinos (Kennish, 2002). Mudanças climáticas, causando, por exemplo, aumento da temperatura, alteração nos padrões de precipitação, aumento do nível do mar, e alteração na ocorrência de eventos climáticos extremos como enchentes ou secas, também podem alterar a dinâmica estuarina e provocar respostas complexas das assembleias bênticas (Dolbeth et al., 2012; Bernardino et al., 2015). A resposta da biota ao estresse ambiental é um resultado integrado de processos diretos ou indiretos, que podem ser refletidos em mudanças na densidade, diversidade e produção das populações e comunidades. As mudanças climáticas associadas a impactos antrópicos podem interagir para produzir impactos na biodiversidade e no funcionamento do ecossistema, o que por sua vez, terão implicações no ecossistema e nos sistemas econômicos e sociais que dependem deles (Cardoso et al., 2008). É importante que sejam detectadas alterações no ambiente estuarino, para que sejam adotadas medidas de remediação e de gestão, que podem ser importantes para a recuperação do ecossistema (Kennish, 2002; Cardoso et al., 2008).

O Brasil possui um extenso litoral com diversos estuários desde a região tropical equatorial no norte do país, até regiões subtropicais no sul. Apesar desta ampla área e da importância dos ecossistemas estuarinos e de seus organismos, poucos estudos de produção secundária foram realizados e publicados no Brasil (Bernardino et al., 2016). De maneira geral, estudos de densidade e composição das comunidades bentônicas são mais comuns em estuários e manguezais, enquanto estudos de produção secundária são escassos (Alongi, 2002; Lee, 2008), e não foram encontrados estudos comparando produções secundárias de comunidades bênticas entre manguezais e habitats não vegetados. A produção secundária da macrofauna bentônica é também uma importante medida da comunidade além de outros parâmetros mais estudados, como abundância, riqueza e diversidade. Tendo em consideração a importância e as ameaças a esses ecossistemas, e os poucos estudos relativos a esses temas, a quantificação da produção secundária e as variações espaciais da macrofauna bentônica no presente estudo serão importantes para entender a composição e as diferenças espaciais e entre estuários da fauna de ecossistemas estuarinos da Ecorregião Marinha Leste do Brasil.

Neste contexto, o objetivo do presente trabalho foi avaliar a produção secundária, densidade, biomassa e composição das comunidades bentônicas em diferentes escalas espaciais, através de uma amostragem hierárquica, em manguezais e planícies de maré (habitats vegetado e não vegetado, respectivamente) de três estuários do Espírito Santo, localizado na Ecorregião Marinha Leste do Brasil. Este estudo permitirá compreender padrões espaciais de produção secundária e na estrutura da fauna bentônica, diferenciando ecossistemas vegetados e não vegetados, além de contribuir para o conhecimento da macrofauna bentônica em estuários do Espírito Santo.

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CAPÍTULO 2

Spatial heterogeneity in macrofaunal structure and secondary production in mangrove and tidal flat habitats of tropical estuaries within the Eastern Marine Ecoregion of Brazil

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Abstract

Estuarine ecosystems, composed by various habitats, including mangrove forests and tidal flats, support high productivity and a diverse community of benthic organisms. These habitats are spatially heterogeneous resulting in variable density, biomass and secondary production of benthic organisms, but the scales of their variability are poorly known in tropical estuaries. To assess the spatial variability of benthic macrofaunal secondary production, biomass, density and composition on mangroves (vegetated) and adjacent tidal flats (unvegetated), a nested protocol was used allowing determining what spatial scales were significant to each assemblage descriptor. Three tropical estuaries located in the Eastern Marine Ecoregion of Brazil were sampled (larger spatial scale) on one mesohaline region in both habitats at the scales of sites, plots and replicates (local scales). Changes in benthic assemblage composition, biomass, density and secondary production occurred mainly between habitats, with some differences among estuaries. At Benevente estuary, unvegetated habitats had higher macrofaunal secondary production, biomass and density, due to the dominance of Kalliapseudidae (Tanaidacea). However, the other two estuaries exhibited opposite patterns of macrofaunal biomass and secondary production, with higher values within mangrove forests which is consistent with previous observations in vegetated habitats from other estuaries. Taxonomic composition (family level) of benthic assemblages was more similar between vegetated habitats among estuaries, and related to higher sedimentary detritus biomass and total sedimentary organic matter in these habitats. Oligochaeta and Capitellidae dominated vegetated habitats, whereas unvegetated habitats exhibited variable dominance between estuaries. Mollusca and Crustacea exhibited higher biomass and were responsible for most of the secondary production at the studied estuaries, except at unvegetated habitat in Benevente estuary, where Kalliapseudidae was the family with higher production.

Keywords: Estuaries, Macrofauna, Secondary production, Mangroves, Tidal flats.

2.1 Introduction

Estuaries are productive ecosystems that commonly support large densities and biomass of benthic organisms (Kennish, 2002). The benthic macrofauna is an important component of estuarine ecosystems, including mangrove forests and tidal flats, as they are involved in many trophic and biogeochemical processes (Herman et al., 1999; Kristensen and Kostka, 2005). Macrofaunal organisms are important as sedimentary trophic links with major effects on sediment bioturbation and recycling of nutrients and organic matter (Ysebaert et al., 1998; Herman et al., 1999; Nilsen et al., 2006; Kristensen, 2008; Kristensen et al., 2008). Benthic assemblages are heterogeneous along estuarine ecosystems reflecting multiple community responses to environmental variables including salinity, sediment composition, organic matter and variable habitats present within estuaries (Edgar and Barrett, 2002; Morais et al., 2016).

The benthic secondary production is one important ecological parameter to understand ecosystem dynamics as it allows energy flow estimates within ecosystems and represents the formation of community biomass by growth through time (Dolbeth et al., 2005; Benke, 2010; Dolbeth et al., 2012). As a result, total secondary production reflects both population dynamics (biomass, life span and body-size) and also biotic interactions and environmental variability within ecosystems (Waters and Crawford, 1973; Dolbeth et al., 2012). Environmental changes affects secondary production in marine ecosystems. Temperature, food, nutrient and oxygen availability, and also habitat heterogeneity including variations in sediment grain size and vegetation can have an effect on production (Edgar et al., 1994; Heck et al., 1995; Edgar and Barrett, 2002; Dolbeth et al., 2003). For example, temperature can influence growth rates and reproduction, leading to an increase in production in warmer waters (Tumbiolo and Downing, 1994). In estuaries, plant cover, which is a proxy of spatial heterogeneity and habitat complexity, can increase food availability and shelter (Lana and Guiss, 1991), resulting in increased abundance, biomass and production of macrofauna when compared to unvegetated areas (Lana and Guiss, 1991; Heck et al., 1995; Dolbeth et al., 2007). In mangroves, higher densities of benthic invertebrates have been reported compared to adjacent unvegetated tidal flats (Sheridan, 1997), which are possibly linked to the presence of vegetation (i.e. source of food) and canopy shade providing cooler and wetter surface substrate (Kon et al., 2010).

Estuaries and mangroves are subject to many human impacts, such as eutrophication, habitat loss and climate change (Alongi, 2002; Bernardino et al., 2015). Benthic secondary production can be used to represent the functional responses of fauna subjected to long-term environmental and local anthropogenic impacts (Benke, 2010; Dolbeth et al., 2012). For example, excessive nutrient and sewage inputs to estuaries lead to eutrophication that affects production in different ways (Kennish, 2002). Initially, nutrient enrichment can promote algal blooms that temporarily enhance macrofauna production and abundance, but post-bloom periods can cause collapse of the system and decline of community production (Dolbeth et al., 2003; Dolbeth et al., 2012). In addition, eutrophication can also lead to hypoxia events or increase its extent and severity, producing an adverse effect in benthic biomass and production that can have negative consequences for the whole system (Sturdivant et al., 2014). Climate change is also a concern issue, as it can increase the frequency and intensity of extreme climate events such as temperature rise, floods and droughts (Dolbeth et al., 2011). With predicted changes in precipitation and temperature, estuaries may face strong abiotic changes with impacts on benthic ecosystems (Bernardino et al., 2015). These changes in climate can directly affect benthic secondary production and also cause indirect effects by changing primary production (Dolbeth et al., 2011; Dolbeth et al., 2012).

The spatial patterns of secondary production in mangroves and unvegetated estuarine tidal flats are largely unknown, especially for tropical estuaries (Alongi, 2002; Lee, 2008). In South America, although the Brazilian coast has hundreds of estuarine systems, benthic production has only been evaluated on epibenthic assemblages (i.e. crabs and gastropods), on the Amazon Ecoregion, or focused on specific populations in some localities (Pagliosa and Lana, 2000; Koch and Wolff, 2002; Costa and Soares-Gomes, 2015; Bernardino et al., 2016). These studies highlight the importance of secondary production as a tool to assess the effects of environmental change in benthic organisms and reinforce the importance of macrofauna in mangroves.

Given the importance of benthic assemblages to estuarine ecosystems, and increasing human and climatic pressures, understanding spatial patterns of benthic secondary production in estuaries is invaluable to monitoring and conservation of these areas (Alongi, 2002; Kennish, 2002). This study investigated benthic secondary production, biomass and abundance at variable spatial scales in vegetated and unvegetated habitats from three tropical estuaries on the Eastern Marine Ecoregion of Brazil. We tested the hypothesis that spatial variations in benthic communities occurs at variable scales, both within vegetated and unvegetated habitats (scales of habitat), and among estuaries (scales of estuary). These changes will likely reflect variable nutrient or organic matter input to benthic assemblages, which would increase secondary production in estuaries with higher organic availability.

2.2 Material and methods

2.2.1 Study area

The study was carried out in three tropical estuaries along southern area of the Eastern Marine Ecoregion of Brazil (Spalding et al., 2007; Figure 1). The northernmost estuary, Piraquê-Açu and Piraquê-Mirim estuarine system (PAE; 19°57’S 40°09’W) is covered by extensive and well-developed mangrove forests with an area of over 12 km^2 (Sroczyńska et al., 2012). The Vitória Bay estuarine system

(VIB; 20º16’S 40º20’W) is the largest estuary on the region within a densely populated metropolitan area and is considered an area with critical level of degradation (Diegues, 1999). VIB is subject to discharge of untreated domestic sewage from the surrounding cities and its estuarine margins are largely urbanized for habitational and harbor facilities (Carmo et al., 1995; Jesus et al., 2004; Grilo et al., 2013). The estuary has extensive mangrove forests despite the intense urbanization of the region with an area of approximately 18 km^2 (Jesus et al., 2004). The southernmost estuary, Benevente (BEN, 20º48'S 40º39'W), has well preserved mangrove forests that cover an area of approximately 4.6 km^2 with minor urban settlement (Vale and Ferreira, 1998; Pereira et al., 2009; Petri et al., 2011). Mangrove forests of the three estuaries are composed by *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana* species (Zamprogno et al., 2016; Vale and Ferreira, 1998) and all three estuaries are characterized by a microtidal regime, with semidiurnal tides.

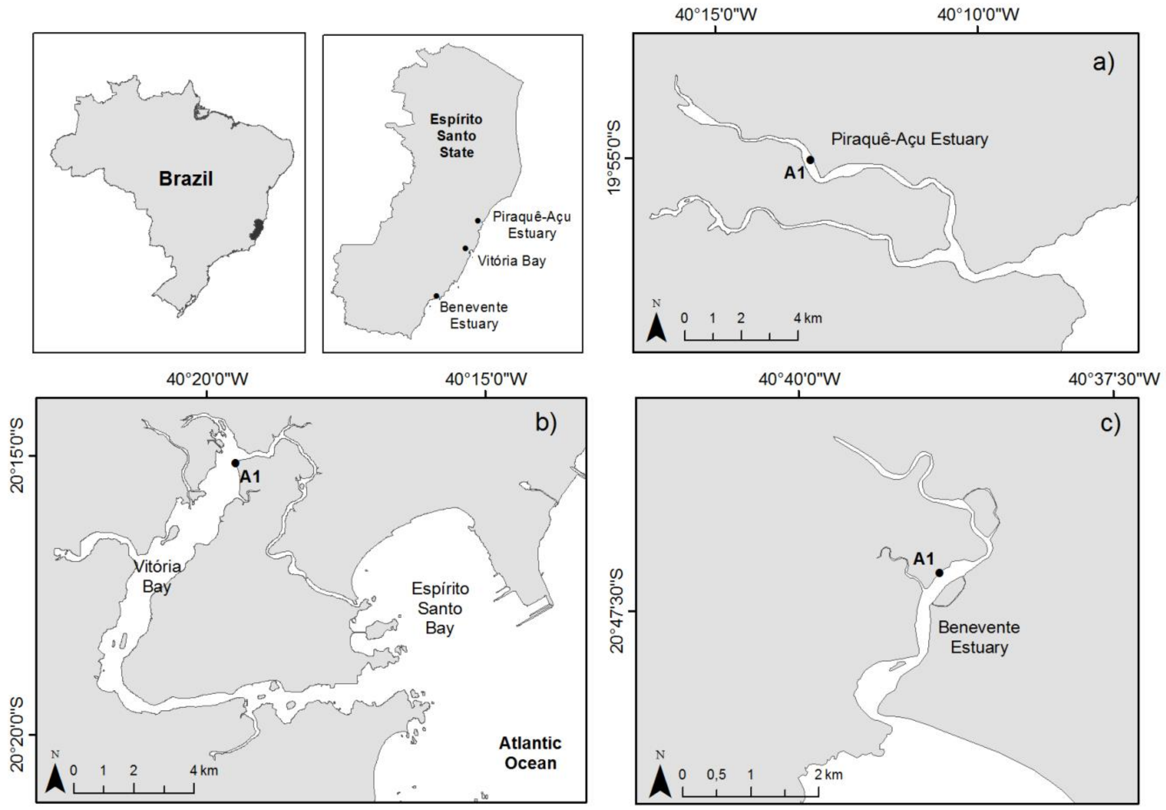

Figure 1. Study area indicating the three sampled estuaries and study areas. (a) Piraquê-Açu estuary, (b) Vitória Bay, (c) Benevente estuary.

2.2.2 Sampling and sample processing

Benthic macrofaunal assemblages were sampled on a nested spatial design on vegetated (V - mangrove forests) and unvegetated (NV - tidal flats) habitats on the mesohaline zone (salinity ranging between 18 and 5; Venice System, 1958) in the three estuaries. The objective of this study was to analyze the spatial variations in macrofauna, so, samples were collected in one sampling event that occurred in August and September 2014, corresponding to the dry season. Each area was divided in two sites separated by at least 100 m containing adjacent vegetated and unvegetated habitats. Three sampling plots were randomly established in each habitat and site, parallel to the waterline and separated by tens of meters (10^1 m). Three replicate faunal samples were sampled within each plot, distanced by approximately 1 meter from each other, using a PVC corer with 15 cm diameter and to a sediment depth of 10 cm (0.0177 m^2 area). Additionally, one composite sediment sample was collected at each plot for sediment analysis (grain size, TOM and chlorophyll-a), by mixing three samples of 7 cm diameter and 5 cm depth. Superficial water temperature and salinity were measured in each sampling area.

Faunal samples were preserved in 4% formalin and posteriorly washed through a 1 mm sieve and the retained material was stored in 70% alcohol. In the laboratory, samples were sieved through a stacked series of sieves (1, 1.4, 2, 2.8 and 4 mm), using the methods described by Edgar (1990a). Macrofauna was sorted in each sieve size and identified at family level, considering that this level of identification is satisfactory to identify differences in macrofaunal assemblages (Warwick, 1988; Chapman, 1998; Olsgard et al., 1998). During sorting of samples, the plant material was separated for plant biomass (plant detritus and living roots) determination (dry weight) after drying at 60°C during 48 hours.

Sediment subsamples were treated with hydrogen peroxide (H_2O_2), to eliminate organic matter, and mud content was determined by wet sieving samples through a 0.063 mm mesh size. After drying, the sediment >0.063 mm was sieved through a series of sieves and grain size was classified following the Wentworth scale (Suguio, 1973). Sediment total organic matter (TOM) content was estimated by weight loss after combustion at 500ºC during 4 hours. Chlorophyll-*a* (Chl-*a*) and phaeopigments were extracted from the sediment with acetone and analyzed using a spectrophotometer before and after acidification with HCl (Lorenzen, 1967).

2.2.3 Faunal biomass and secondary production

The macrofauna was wet weighed within each taxonomic group, generally family, by each sieve size (1, 1.4, 2, 2.8 and 4 mm) after identification. Macrofaunal biomass (mg wet weight m^{-2}) was converted into ash-free dry weight (mg AFDW m^{-2}) using the conversion factors compiled in Brey (2001) and Brey et al. (2010). For taxa with no conversion factor available, a conversion factor was selected from the highest taxonomic level. Shells of mollusks were excluded from biomass estimation. Conversion factors from Brey (instead of estimate by methodology used by Edgar (1990a)) were chosen to avoid overestimation of AFDW and consequently of production, mainly in the larger sieve size, since some individuals with elongated bodies and low weights were retained in the sieves.

The secondary production of benthic macrofauna was estimated using the general equation $P=0.0049*B^{0.80}*T^{0.89}$ of Edgar (1990a), which relates daily macrobenthic production P (μg day^{-1}) to ash-free dry weight B (μg) and water temperature T (°C). Temperature was standardized at 23.5°C, which was the mean water temperature measured in the estuaries during faunal sampling. Production was calculated for each taxon (Polychaeta, Oligochaeta, Kalliapseudidae, Other Crustacea, Mollusca and Others) within each sieve size and total production per sample was calculated as the sum of these values. The P/B ratio for each habitat in each estuary was calculated from mean production divided by the mean macrofaunal biomass and is a measure of biomass turnover rate (Dolbeth et al., 2012).

2.2.4 Data analysis

The spatial variability in benthic macrofaunal abundance, biomass and secondary production were evaluated at multiple scales and habitats using a nested and orthogonal analysis of variance (ANOVA). Habitat was defined as a fixed factor and orthogonal to spatial factors (estuary, site, plot). Spatial factors were treated as random and included three estuaries, sites (N=2) nested in estuary, plots (N=3) nested in site and samples (N=3) collected at plots. Spatial differences on sediment properties and plant biomass were assessed by ANOVA across scales of estuary and site (nested in estuary), due to the lack of sample replication at plots. This ANOVA also included habitat factor orthogonal to spatial factors since both vegetated and unvegetated habitats were sampled. A Cochran's test was performed previously to each ANOVA to assess heterogeneity of variances and when necessary data was transformed. A posteriori Student-Newman-Keuls (SNK) tests were applied on the factors or interactions significantly different in ANOVA to determine the differences.

Differences on macrofaunal assemblages were assessed by Permutational Multivariate Analysis of Variance performed with 9999 permutations (PERMANOVA; Anderson et al., 2008). A non-metric multidimensional scaling (nMDS) performed using Bray-Curtis dissimilarity matrix and square-root transformed data was used to visualize variation in macrofauna assemblages. To identify the taxa that most contributed to dissimilarities among habitats was used a Similarity Percentage (SIMPER) analysis. The relationships between environmental variables (TOM, Chl-*a*, Mud, plant biomass) and abundance of macrofauna were investigated using a Canonical Correspondence Analysis (CCA). In this analysis, the abundance of the top 5 dominant taxa (comprising over 90% of total abundance) was used, instead of complete data of abundance, to generate a clearer graph. The sum of abundance data of macrofauna replicates samples were used so that the number of samples from abundance and environmental variables were the same.

All statistical analyses were performed in the software R (R Core Team, 2015) and PERMANOVA was carried out using the software PRIMER 6 (Clarke and Gorley, 2006) with the PERMANOVA+ add-on package (Anderson et al., 2008).

2.3 Results

2.3.1 Sediment properties and plant material

The sediment was predominantly mud in all estuaries and habitats (Figure 2). The measured superficial water salinity in the sampling areas were 8 in BEN, 16 in

VIB and 15 in PAE and are corresponding to the mesohaline zone (Venice System, 1958). The sediment mud content, mean grain size and total organic matter differed significantly among sites and in the interaction between habitat and site representing spatial variation at local scales (Table 1). Chl-*a* and phaeopigments differed significantly between habitats and estuary, respectively, with higher sediment Chl-*a* at unvegetated habitats (SNK, $p < 0.05$) and lower phaeopigments in the BEN estuary (SNK, $p < 0.001$) (Table 1; Figure 2). Plant biomass differed significantly among estuaries and in the interaction between habitat and site (Table 1). VIB had over 2 times higher total plant biomass (4217 ± 3097.6 $g.m^{-2}$) if compared to the BEN and PAE estuaries (592 ± 516.5 $g.m^{-2}$ and 1663.2 ± 1206.2 g.m¯2, respectively). Plant biomass in vegetated habitats was composed of living roots and detritus, while unvegetated habitats only presented detritus.

Table 1. ANOVA results for sediment properties and plant material. H = habitat, E = estuary, S = site, df = degrees of freedom, MS = mean square. Significant values in bold.

		Mean grain size			**Mud content**			**TOM**		
Source	**df**	**MS**	**F**	***p***	**MS**	**F**	***p***	**MS**	**F**	***p***
H	1	0.64	0.680	0.50	710.88	1.813	0.31	1244.64	4.448	0.17
E	2	5.11	3.474	0.17	4190.30	4.729	0.12	283.85	1.596	0.34
HxE	2	0.95	0.635	0.59	392.01	0.465	0.67	279.85	5.528	0.10
S(E)	3	1.47	6.115	**0.003***	886.16	8.709	**0.0004***	177.85	11.505	**<0.0001**
HxS(E)	3	1.49	6.204	**0.003***	843.80	8.293	**0.0006***	50.62	3.275	**0.04**
Residual	24	0.24			101.75			15.46		

		Chlorophyll-a			**Phaeopigments**			**Plant biomass**		
Source	**df**	**MS**	**F**	***p***	**MS**	**F**	***p***	**MS**	**F**	***p***
H	1	39.04	24.060	**0.04***	0.06	0.160	0.73	90,50	6,448	0,13
E	2	27.90	1.944	0.29	4.02	479.926	**0.0002**	79,93	60,220	**0,004**
HxE	2	1.62	1.447	0.36	0.35	2.915	0.20	14,03	1,727	0,32
S(E)	3	14.35	1.487	0.24	0.01	0.030	0.99	1,33	1,525	0,23
HxS(E)	3	1.12	0.116	0.95	0.12	0.437	0.73	8,13	9,337	**0,0003**
Residual	24	9.65			0.28			0,87		

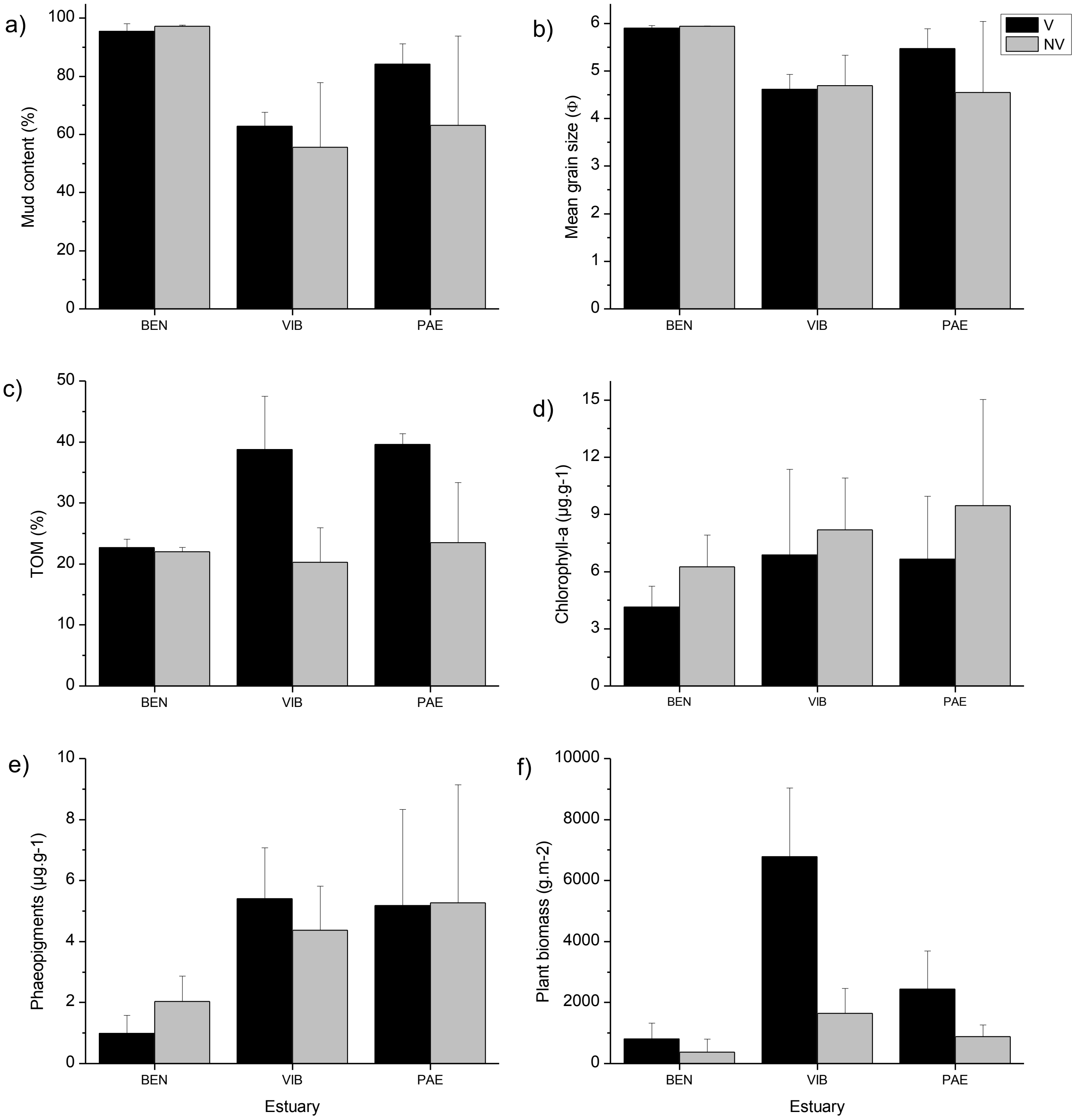

Figure 2. Sediment properties and plant material at sampled estuaries. Means (±SD) of (a) mud content (%), (b) mean grain size (Φ), (c) TOM (%), (d) chlorophyll-a (µg.g^{-1}), (e) phaeopigments (µg.g^{-1}) and (f) plant biomass in DW (dry weight) (g.m^{-2}). V = vegetated habitat, NV = unvegetated habitat.

2.3.2 Macrofaunal density, biomass and secondary production

A total of 18,036 individuals belonging to 37 taxa were sampled at the three estuaries. Total macrofaunal density was significantly different at the plot and estuary spatial scales, and in their interactions with habitat (Table 2). The BEN estuary exhibited higher macrofaunal density in unvegetated habitats (SNK, $p < 0.01$), but this pattern was opposite to the VIB and PAE estuaries that had higher densities in vegetated habitats, although, the differences were not statistically significant (Figure 3). Macrofaunal densities varied over 40-fold between unvegetated habitats at BEN and PAE estuaries (33,022 ± 14,709 ind.m^{-2} and 784 ± 641 ind.m^{-2}, respectively; Figure 3). Kalliapseudidae (Tanaidacea) was dominant in unvegetated tidal flats at BEN estuary, whereas Polychaeta and Oligochaeta were more abundant in similar habitats at PAE and VIB estuaries. Vegetated habitats in the three estuaries had higher densities of Oligochaeta and Polychaeta (Figure 4).

Significant differences in macrofaunal biomass and estimated secondary production were observed only in the interaction between habitat and estuary (Table 2). Biomass and production followed patterns of macrofaunal density and were higher at unvegetated habitats in BEN, contrasting with higher values in vegetated habitats at the other two estuaries (SNK, $p < 0.05$; Figure 3). The lowest macrofaunal biomass (100.7 ± 206.4 mg AFDW m^{-2}) and production (3.4 ± 5.2 mg m^{-2} day^{-1}) were observed at unvegetated tidal flats in the PAE estuary (Figure 3).

The contribution from each macrofaunal group to total assemblage biomass and secondary production varied greatly between estuaries and habitats and, in some cases, these groups were different from groups with higher densities (Figure 4). Large individuals including Mollusca (mainly Bivalvia) and Crustacea (mainly crabs - Brachyura), contributed greatly to benthic biomass and production in vegetated habitats at the three estuaries despite their low density (Figure 4; Figure 5). At vegetated habitats in VIB estuary, Mollusca (mainly Mytilidae and Solecurtidae) contributed to most of the biomass and production (65% and 48%, respectively), with Oligochaeta and Polychaeta representing second and third groups respectively. At vegetated habitats of the PAE estuary, Mollusca and Crustacea were the most representative groups in biomass (mainly Mytilidae and Panopeidae) and production. Crustaceans (mainly Ocypodidae) contributed to over 70% of the macrofaunal biomass and production at V habitats in BEN estuary with Polychaeta as the second group.

In general, biomass and production of estuarine habitats were mainly derived from large size classes (Figure 5). Vegetated habitats had over 50% of its production from large size classes (> 4 mm), whereas unvegetated habitats had variable contribution (30-75%) of other size classes from 1 to < 4 mm (Figure 5). At unvegetated habitats in VIB and PAE estuaries, Mollusca (mainly Solecurtidae) and Polychaeta (mainly Capitellidae) were the groups that most contributed to biomass and production (Figure 4). Kalliapseudidae was the dominant taxa in BEN unvegetated habitat and contributed greatly to biomass and production (95% and 92%, respectively; Figure 4).

The mean estimated community annual production to biomass ratio (P/B) varied among estuaries and habitats. The highest P/B ratio was observed at unvegetated flats at PAE estuary (12.6 y^{-1}), whereas vegetated habitats in this estuary had the lowest P/B ratio (5.3 y^{-1}). BEN and VIB estuaries had relatively similar values of P/B between habitats, (6.4 and 6.5 y^{-1}; 7.5 and 9.3 y^{-1} for V and NV habitats, respectively).

Table 2. ANOVA results for macrofaunal abundance, biomass and secondary production. H = habitat, E = estuary, S = site, P = plot, df = degrees of freedom, MS = mean square. Significant values in bold.

		Density			**Biomass**			**Secondary production**		
Source	**df**	**MS**	**F**	***p***	**MS**	**F**	***p***	**MS**	**F**	***p***
H	1	311266.70	0.253	0.66	0.20	0.369	0.61	6.43	0.421	0.58
E	2	689817.25	19.504	**0.02**	0.32	4.388	0.13	8.95	5.596	0.10
HxE	2	1230614.84	23.040	**0.02**	0.54	20.178	**0.02**	15.29	26.162	**0.01**
S(E)	3	35368.39	1.372	0.30	0.07	3.427	0.05	1.60	2.982	0.07
P(S(E))	12	25774.72	4.120	**<0.0001**	0.02	1.400	0.19	0.54	1.616	0.11
HxS(E)	3	53413.02	1.431	0.28	0.03	1.061	0.40	0.58	0.990	0.43
HxP(S(E))	12	37327.63	5.967	**<0.0001**	0.03	1.682	0.09	0.59	1.779	0.07
Residual	72	6255.48			0.01			0.33		

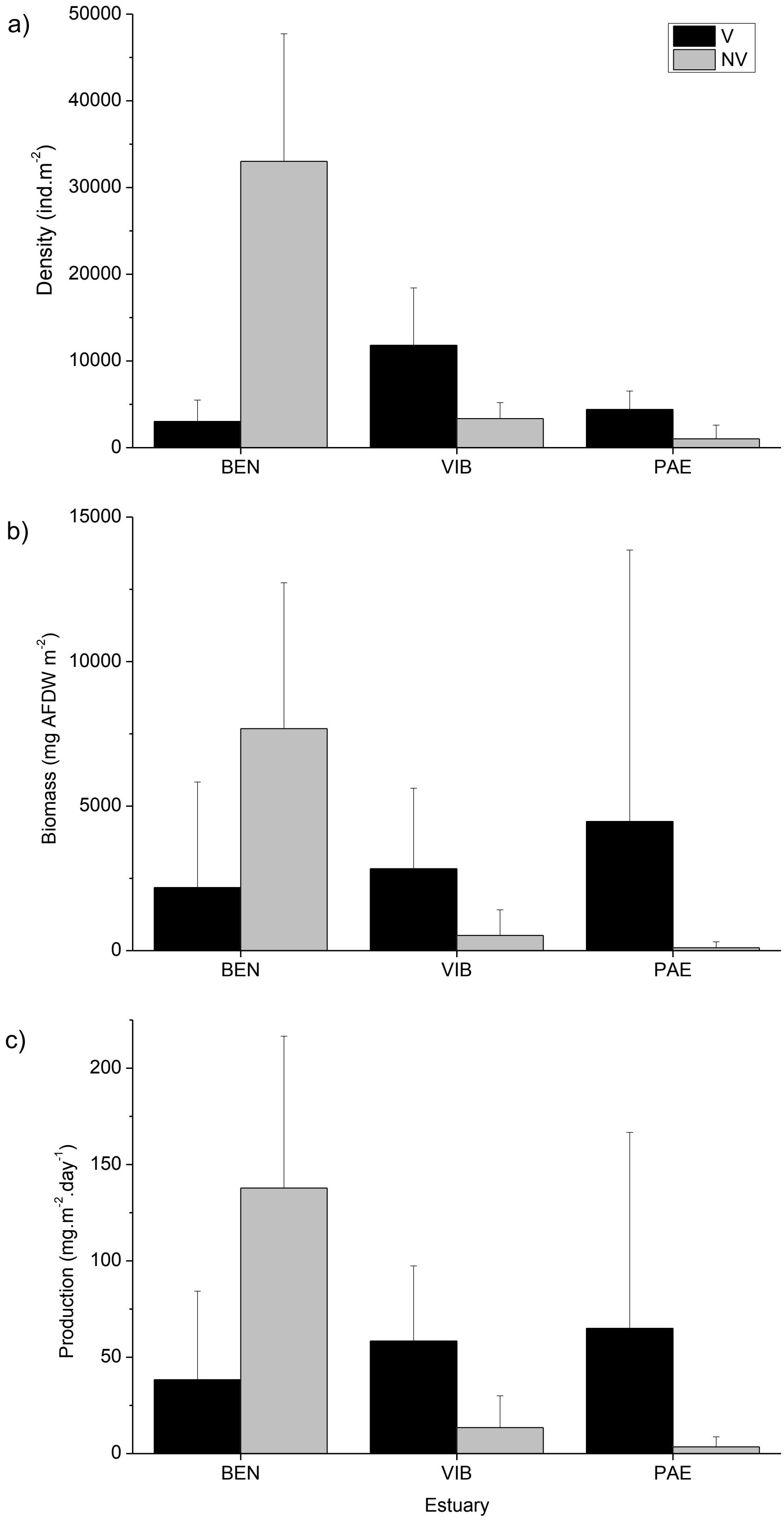

Figure 3. Macrofauna at sampled estuaries. Means (±SD) of (a) abundance (ind.m^{-2}), (b) biomass (mg AFDW m^{-2}) and (c) production (mg m^{-2} day^{-1}). V = vegetated habitat, NV = unvegetated habitat.

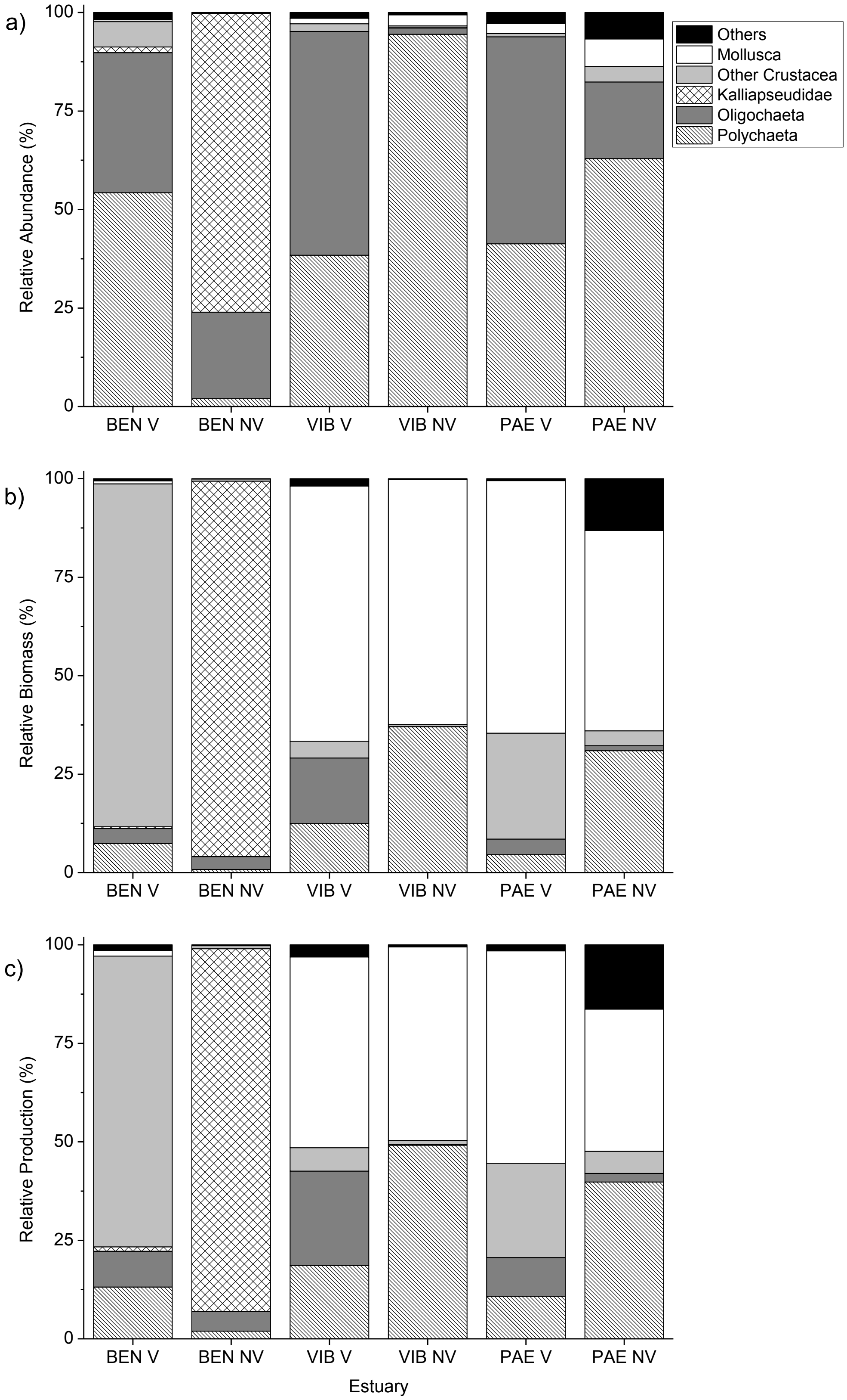

Figure 4. Relative (a) abundance, (b) biomass and (c) production of macrofauna groups at sampled estuaries. V = vegetated habitat, NV = unvegetated habitat.

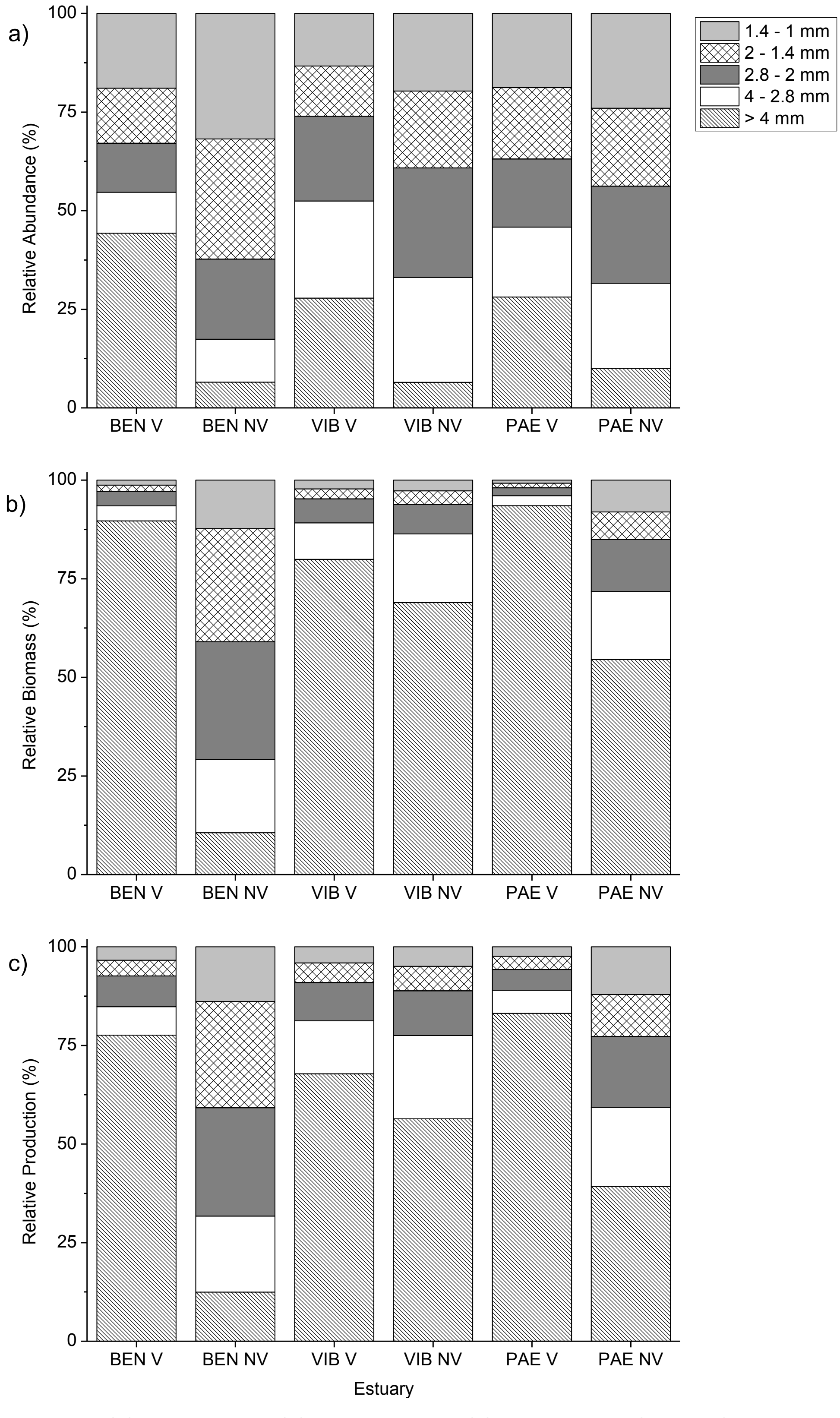

Figure 5. Relative (a) abundance, (b) biomass and (c) production of macrofauna size classes at sampled estuaries. V = vegetated habitat, NV = unvegetated habitat.

2.3.3 Assemblage composition

Numerically dominant taxa had distinct patterns between vegetated and unvegetated habitats, and between estuaries (Table 4). The numerically dominant taxa in vegetated habitats in the three estuaries were Oligochaeta and Capitellidae (>60%). Unvegetated habitats at BEN estuary were dominated by Kalliapseudidae and Oligochaeta (>90%). Spionidae and Capitellidae (>80%) were more abundant in unvegetated habitat at VIB, and Capitellidae and Oligochaeta (almost 70%) in unvegetated habitat at PAE. Differences in dominant taxa at unvegetated habitats indicate that BEN and VIB have dominance of particular families and that some taxa can be found at the three estuaries with variable densities.

The macrofaunal assemblage composition was significantly different in most spatial scales analyzed (PERMANOVA; Table 3). These significant differences occurred in the interaction among habitat and all the spatial scales analyzed (estuary, site and plot) and the spatial scales within estuaries (site and plot). Faunal distribution patterns in nMDS ordination evidenced differences between unvegetated and vegetated habitats in all the estuaries (Figure 6). And is also evidenced the differences in the samples within each habitat, what occurred mainly in unvegetated habitats. Macrofaunal assemblages between unvegetated habitats had lower similarity between estuaries, if compared to vegetated habitats, which were more similar among estuaries.

Dissimilarities were high (>70%) between habitats inside each estuary and among estuaries in the unvegetated habitat. Lower dissimilarities were found among estuaries in the vegetated habitats and similarity in this habitat was mainly due to Oligochaeta and Capitellidae (contribution of approximately 70%; SIMPER). Kalliapseudidae, Oligochaeta and Capitellidae were the taxa that most contributed to the observed differences among habitats in BEN. Oligochaeta, Spionidae, Capitellidae and Nereididae were the taxa that most contributed to the observed differences among habitats in VIB. Oligochaeta, Capitellidae, Nereididae and Pilargidae were the taxa that most contributed to the observed differences among habitats in PAE (SIMPER, Appendix Table A). Dissimilarity between unvegetated habitats among estuaries occurred mainly by Kalliapseudidae and Spionidae between BEN and VIB, by Kalliapseudidae and Oligochaeta between BEN and PAE, and by Spionidae and Capitellidae between VIB and PAE (SIMPER, Appendix Table B).

Table 3. PERMANOVA results calculated from the Bray–Curtis dissimilarity matrix for the macrofauna communities at the different scales investigated. H = habitat, E = estuary, S = site, P = plot. Significant values in bold.

Source	df	MS	Pseudo-F	P(perm)
H	1	34861	1.895	0.23
E	2	24587	5.153	0.06
S(E)	3	4771.7	3.025	**0.0001**
HxE	2	18394	4.366	**0.02**
P(S(E))	12	1577.5	2.414	**0.0001**
HxS(E)	3	4213.5	2.593	**0.0016**
HxP(S(E))	12	1625	2.486	**0.0001**
Residual	72	653.61		

Table 4. Mean density (ind.m^{-2}) and relative abundance (%) of the most representative taxa in vegetated (V) and unvegetated (NV) habitats in sampled estuaries.

BEN V			**BEN NV**		
Taxa	**Density (±SD)**	**Rel. abundance**	**Taxa**	**Density (±SD)**	**Rel. abundance**
Oligochaeta	1070 (862)	36	**Kalliapseudidae**	25028 (18207)	76
Capitellidae	728 (501)	24	**Oligochaeta**	7235 (13440)	22
Polychaeta sp1	355 (1002)	12	**Capitellidae**	276 (291)	0.8
Ampharetidae	348 (423)	12	**Nereididae**	182 (181)	0.6

VIB V			**VIB NV**		
Taxa	**Density (±SD)**	**Rel. abundance**	**Taxa**	**Density (±SD)**	**Rel. abundance**
Oligochaeta	6701 (5356)	57	**Spionidae**	2323 (1628)	69
Capitellidae	2288 (1967)	19	**Capitellidae**	505 (390)	15
Nereididae	1073 (1126)	9	**Nereididae**	248 (250)	7
Spionidae	549 (1013)	5	**Pilargidae**	82 (89)	2

PAE V			**PAE NV**		
Taxa	**Density (±SD)**	**Rel. abundance**	**Taxa**	**Density (±SD)**	**Rel. abundance**
Oligochaeta	2307 (1510)	53	**Capitellidae**	512 (949)	50
Capitellidae	1252 (655)	29	**Oligochaeta**	201 (320)	19
Nereididae	242 (142)	6	**Nemertea**	50 (75)	5
Pilargidae	113 (140)	3	**Pilargidae**	41 (121)	4

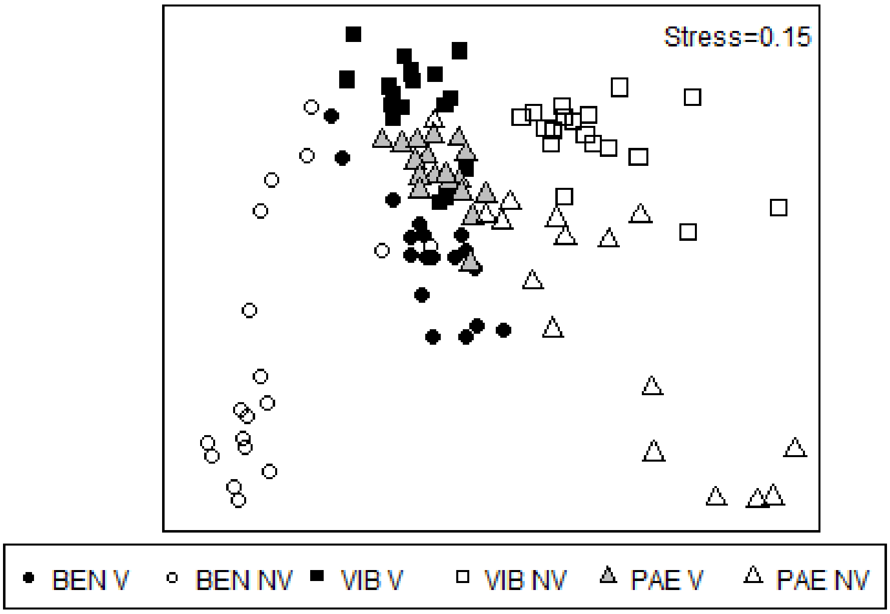

Figure 6. Non-metric multidimensional scaling (nMDS) ordination plot of community data from vegetated (V) and unvegetated (NV) habitats in studied estuaries.

2.3.4 Relationships between sediment properties and macrofauna

Macrofaunal densities were related to sediment mud content, TOM, plant biomass and Chl-*a*, with the first and second canonical axes explaining 26% and 17.2% of the variation in the data, respectively (CCA; Figure 7). These relationships also explained the differences in assemblage composition between vegetated and unvegetated habitats. Vegetated habitats of the three estuaries were related to higher TOM content, higher plant biomass and to higher abundances of Oligochaeta and Capitellidae. Unvegetated habitats were more heterogeneous between estuaries, with VIB NV habitats exhibiting higher Chl-*a* and dominated by Spionidae, whereas at PAE Capitellidae was dominant. At BEN, Kalliapseudidae were abundant at sediments with high mud content and relative low plant biomass and TOM content.

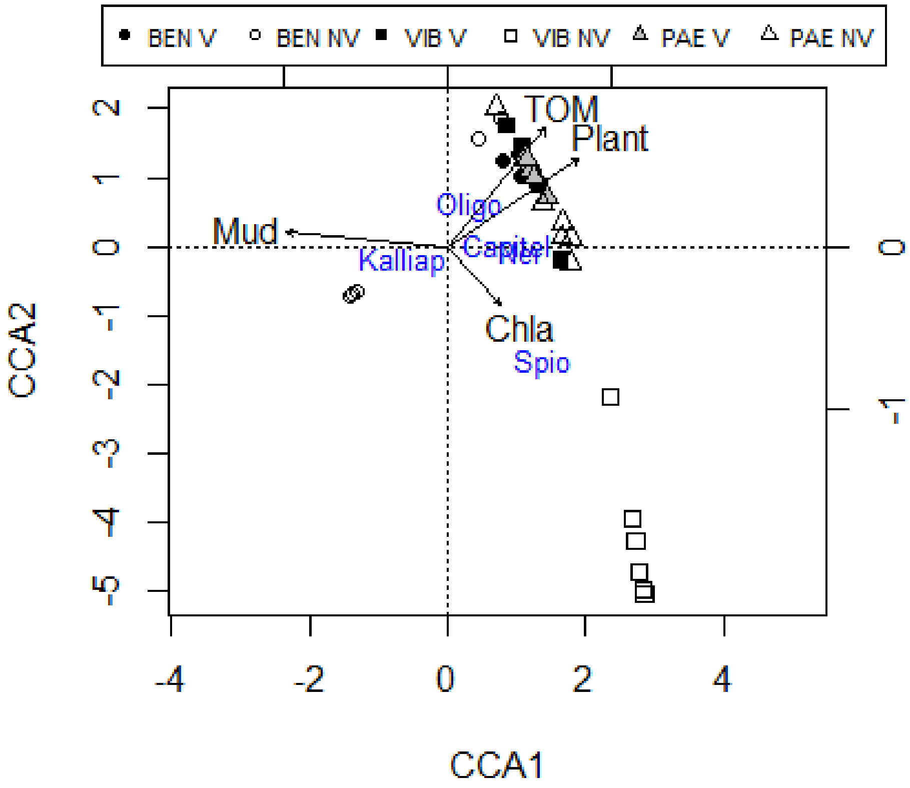

Figure 7. Canonical correspondence analysis (CCA) for most abundant taxa and environmental variables. Families indicated in CCA: Kalliap = Kalliapseudidae, Capitel = Capitellidae, Ner = Nereididae, Spio = Spionidae, Oligo = Oligochaeta. Environmental variables included: TOM = total organic matter, Mud = mud content, Plant = plant biomass, Chla = Chlorophyll-a.

2.4 Discussion

Mangrove forests occur in tropical and subtropical estuaries adjacent to tidal flats and the presence of vegetation may lead to modifications in water circulation and sedimentation (Lana et al., 1997; Alongi, 2002). In the present study, significant variations occurred at small spatial scales in mud content, TOM and plant biomass and no significant differences were found in the sediment properties and plant biomass in the interaction between habitat and estuary, despite general higher values of TOM and plant biomass were found in vegetated habitats. In the Southeastern Marine Ecoregion of Brazil, estuarine habitats were also not distinct with respect to sediment mud content, mean grain size and TOM (Lana et al., 1997). However, in Florida, significant differences were found in sediment properties between vegetated mangroves and unvegetated areas, with mangroves presenting higher organic and mud contents (Sheridan, 1997).

In other estuaries of the Eastern Marine Ecoregion of Brazil there was a similar predominance of fine sediments in mangroves as observed in this study, with similar to lower organic matter content (Costa et al., 2015). In intertidal areas of other estuaries in the Eastern Marine Ecoregion of Brazil, the total sedimentary organic matter was always lower than 25% and mud was predominant (Mariano and Barros, 2014), with comparable values from unvegetated habitats in this study. But the values of TOM and mud content from the present study were higher if compared to mangrove areas and tidal flats in Southeastern Marine Ecoregion of Brazil, Rio Grande Marine Ecoregion and to Florida (Lana et al., 1997; Sheridan, 1997; Netto and Galluci, 2003; Colpo et al., 2011). Mangrove trees composition and mangrove age are important in dynamics of organic matter and in organic content (Marchand et al., 2003; Zamprogno et al., 2016), and may be partially responsible for those regional differences.

Macrofaunal density, assemblage composition, biomass and secondary production exhibited variable patterns of spatial change between tropical estuaries in the Eastern Marine Ecoregion of Brazil. We observed marked changes in macrofaunal densities between the estuaries, but with inconsistent patterns between vegetated and unvegetated habitats. At the BEN estuary, these changes were due to the high dominance of Kalliapseudidae in unvegetated habitats which was related to higher mud content. Peaks of abundance of tanaidaceans have been previously reported at unvegetated habitats within subtropical estuaries with patchy distributions (Lana and Guiss, 1991; Leite et al., 2003; Pagliosa and Barbosa, 2006; Pennafirme and Soares-Gomes, 2009). The absence of this group at the PAE and their very rare occurrence in VIB estuaries (0.1%) indicate that the presence and dominance of these tanaidaceans are likely a result of both sedimentary composition and lower organic content (Nucci et al., 2001; Leite et al., 2003). In contrast to our expectations, vegetated and unvegetated habitats at PAE and VIB estuaries had statistically similar macrofaunal densities. This pattern is different from other estuaries with higher densities of macrofauna in mangroves if compared to adjacent unvegetated habitats (Schrijvers et al., 1995; Sheridan, 1997; Yu, et al., 1997), however, the inverse pattern was also reported in New Zealand, with lower densities in mangroves (Alfaro, 2006).

Direct comparisons among studies are difficult due to variations in sampling methodologies and different sieve mesh sizes. However, macrofaunal densities in mangrove areas in this study can be considered higher than mangroves in Kenya (tropical) and lower than mangroves in Florida (subtropical, Table 5). Macrofaunal abundance from the Rio Grande Marine Ecoregion of Brazil and New Zealand are similar to the reported values from this study. Tidal flats in this study presented variable densities between BEN and PAE and VIB. Benthic densities in unvegetated BEN tidal flats can be considered higher than other Marine Ecoregions of Brazil but tidal flats in PAE and VIB were within the range of other estuaries (Table 5). But when considering that mesh size used in the present study (1 mm) is bigger than the other studies, differences may be found, as the densities could increase in the present study if was used a similar mesh size from other studies.

Table 5. Macrofaunal densities (ind.m^{-2}) reported in mangroves and tidal flats in different tropical (*), subtropical (**) and temperate (***) estuaries.

Location	**Density (ind.m−2)**	**Habitat**	**Mesh size**	**Reference**
Rio Grande Marine Ecoregion of Brazil	Maximum 7,250	Mangrove**	0.5 mm	Netto and Galluci, 2003
Kenya	Total densities from 265 to 4,125 (mean of 1,933)	Mangrove*	1 mm	Schrijvers et al., 1995
Florida	22,591 - 52,914	Mangrove**	0.5 mm	Sheridan, 1997
New Zealand	About 8,000	Mangrove***	0.5 mm	Alfaro, 2006
Eastern Marine Ecoregion of Brazil	Values generally < 1,000 and maximum values of approximately 6,000	Tidal flats*	0.5 mm	Mariano and Barros, 2014
Southeastern Marine Ecoregion of Brazil	Values of approximately 500 to values around 3,000	Tidal flats**	0.5 mm	Morais et al., 2016
Eastern Marine	3,013	Mangrove BEN*	1 mm	Present study
Ecoregion	11,802	Mangrove VIB*		
of Brazil	4,391	Mangrove PAE*		
(Mean values)	33,023	Tidal flat BEN*		
	3,349	Tidal flat VIB*		
	1,033	Tidal flat PAE*		

Macrofaunal assemblages varied significantly between habitats and estuaries, with higher similarity within mangrove forests. Dominant groups from mangrove forests were composed mainly by Oligochaeta and Capitellidae, despite the differences in urbanization among estuaries. These taxa are typically dominant in in sediments with high organic content and detritus, and are widely present at other tropical and subtropical mangroves (Schrijvers et al., 1995; Sheridan, 1997; Netto and Lana, 1999; Dittmann, 2001; Netto and Galluci, 2003; Demopoulos and Smith, 2010). Mangrove derived detritus are nutritionally poor food sources and few groups of fauna are adapted to digesting this material (Lee, 2008). So, detritus can also have indirect effects in composition and abundance of macrofauna, which is also responding to the presence of habitat complexity due to the presence of vegetation cover (Netto and Lana, 1999; Netto and Galluci, 2003).

Macrofaunal assemblages of estuarine habitats may exhibit different responses and sensitivity to urbanization, due to intrinsic differences among habitats and their associated assemblages or in response to variable levels of disturbance (Lindegarth and Hoskin, 2001). Unvegetated habitats were highly dissimilar between estuaries with distinct dominant macrofaunal families, which may indicate lower tolerance to pollutants and higher disturbance rates. Kalliapseudidae was dominant in BEN and the presence of this family may be related to the sediment (explained above) and the lower level of urbanization of this estuary, as this family was previously found in higher densities in estuarine protected areas (Pagliosa and Barbosa, 2006). Spionidae were dominant in VIB and Capitellidae in PAE and the dominance of these families are typically observed in organically enriched areas (Mariano and Barros, 2014). VIB is a heavily polluted region with uncontrolled discharge of untreated domestic sewage (Grilo et al., 2013), and the PAE estuary has lower urbanization but still with detectable organic pollutants (Bernardino, unpublished data). These differences indicate that the macrofauna of each estuary show some degree of differentiation, which may be related to local impacts, but also some taxa can be found at all studied estuaries. Other tropical estuaries in Eastern Marine Ecoregion of Brazil also reported particularities in subtidal benthic assemblages in the estuaries, with some similar taxa (Barros et al., 2012).

In addition to the differences among habitats, the density and composition of macrofauna also presented significant differences in the small spatial scales within estuaries (among plots), as a result of patchy distribution. The variability in small scales was previously reported (Chapman and Tolhurst, 2004). Mean grain size, mud content, TOM and plant biomass also varied in small spatial scales within estuaries, and likely work as drivers of the variations in density and composition of macrofaunal assemblages. The sediment composition and detritus biomass may also have an important role at smaller scales by creating microhabitats (Netto and Galluci, 2003), but at larger scales salinity and primary productivity are also important (Edgar and Barrett, 2002; Pagliosa and Barbosa, 2006; Barros et al., 2012).

Macrofaunal biomass and secondary production were higher in vegetated habitats at PAE and VIB suggesting that mangrove forests are an important source of organic material to the local benthic assemblages. This result is consistent with other studies, where vegetated habitats were characterized by higher benthic secondary production and biomass in relation to unvegetated habitats (Edgar, 1990b; Sprung, 1994; Heck et al., 1995; Dolbeth et al., 2003). As well as in the density, important characteristics of vegetated habitat also seems to influence biomass and secondary production, as the presence of vegetation can increase number of microhabitats, protection from predators and food resources (Edgar, 1990b; Kon et al., 2010). However, BEN estuary had a distinct pattern, with higher biomass and production at unvegetated habitats, due to the higher densities of Kalliapseudidae. Despite their smaller individual sizes, biomass and production were high. This family presents continuous reproduction and fast growth, with temporal variation in abundance and peaks of reproduction (Fonseca and D'Incao, 2003; Leite et al., 2003; Pennafirme and Soares-Gomes, 2009) and seems to be benefited by characteristics of unvegetated habitats. As in this study, this family was previously found mainly in unvegetated habitat (Lana and Guiss, 1991) and a hypothesis for the occurrence of higher densities in this habitat is that roots present in the vegetated habitats can be physical barriers to tube building (Leite et al., 2003).

In New Zealand, the intertidal estuary production of approximately 10 mg AFDW m^{-2} day^{-1} was reported, however, this estimation only considered macrofauna between 0.5 and 8.0 mm (Cowles et al., 2009). Higher production was found in the present study in BEN NV and VIB NV (138 and 13 mg AFDW m^{-2} day^{-1}, respectively) and at unvegetated habitat at PAE production was lower (4 AFDW m^{-2} day^{-1}). However, comparisons between studies are difficult due to differences in sampling procedures. Macrofaunal biomass and production were driven by several distinct taxonomic groups in distinct size classes. In unvegetated habitats at BEN estuary Kalliapseudidae had higher biomass and production. This family is a deposit and suspension feeder, consuming detritus, and is consumed by fishes, birds and other crustaceans (Lana and Guiss, 1991; Pagliosa and Barbosa, 2006; Pennafirme and Soares-Gomes, 2009), so, this family is an important link in the food chain in estuaries and this high production seems to be important for the estuarine system in BEN. In vegetated habitats, Mollusca and Crustacea contributed to most of the biomass and production in all estuaries despite relative low densities. Mytillidae was the family with higher contribution to biomass in mangroves of VIB and PAE and, besides the importance for the estuary, can be used as food resource for humans (Nishida and Leonel, 1995). Two species of this family (Genus Mytella) dominated intertidal assemblages in VIB on a previous study (Nalesso et al., 2005), what contrasts with the present study, where low densities were found. Crustacea in vegetated habitats were composed by crab families, which are typically found in mangroves and have important functions in this habitat. Crabs are ecosystem engineers, act in nutrient remineralization, are bioturbation agents by burrowing activity, ingest and modify litter and probably contribute to primary production in mangroves by maintaining nutrients in the system (Koch and Wolff, 2002; Cannicci et al., 2008; Kristensen, 2008; Kristensen, et al., 2008; Kristensen et al., 2012).

The P/B ratio, which is a measure of biomass turnover rate (Dolbeth et al., 2012), was variable between habitats and estuaries. At PAE and VIB estuaries, the P/B ratio was higher or slightly higher in unvegetated habitats suggesting higher turnover rates of benthic production at tidal flats (Edgar et al., 1994; Sprung, 1994). The lower P/B ratio in vegetated habitats occurred due to the higher dominance of Bivalvia and Crustacea (crabs) that are larger individuals with slow growth rates and longer life spans (Sprung, 1994; Edgar and Barrett, 2002). The P/B ratio is important as an indicator of sustainable exploitation of populations and also indicates that small species, with higher P/B ratios, can replace their biomass in a short time, allowing these species to be more resilient to environmental perturbations (Tumbiolo and Downing, 1994).

Mangroves provide essential processes and services for estuarine systems. However, despite the importance of mangroves in estuaries, these habitats and estuarine systems as a whole are threatened by urbanization, habitat loss and impacts by climate change. As shown in this study, mangroves are important habitats for supporting secondary production within VIB and PAE estuaries and are inhabited by distinct benthic communities in relation to unvegetated habitats. The loss of mangrove forests or general alterations in estuaries due to the climate change, for example, temperature and sea level rise, changes in the frequency of floods and droughts events, may change estuarine dynamics, what probably will affect macrofauna and secondary production, with some implications to the whole estuarine system (Cardoso et al., 2008; Bernardino et al., 2015). Responses of macrofauna can be complex due to variable characteristics of organisms and estuaries, and the different spatial trends in climate change, distinct rates of warming and changes in rainfall (Bernardino et al., 2015). The study of benthic communities and secondary production are important to the knowledge of actual functioning of estuarine systems and can be used as a background for future researches in this context.

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Appendix A. Supplementary data

Supplementary Table A

Similarity percentages (SIMPER) analysis with contribution (%) for each taxa that most contributed to dissimilarities among habitats in each estuary at the cutoff level 80%.

BEN V - BEN NV			
Species	**Av.Diss**	**Contrib%**	**Cum.%**
Kalliapseudidae	39,24	51,95	51,95
Oligochaeta	12,36	16,36	68,31
Capitellidae	3,8	5,03	73,34
Ampharetidae	3,79	5,02	78,36
Polychaeta sp1	3,4	4,5	82,86

VIB V - VIB NV			
Species	**Av.Diss**	**Contrib%**	**Cum.%**
Oligochaeta	21,25	32,28	32,28
Spionidae	10,31	15,66	47,94
Capitellidae	7,4	11,24	59,18
Nereididae	5,72	8,69	67,87
Pilargidae	2,64	4,01	71,88
Polychaeta sp2	2,2	3,34	75,21
Bivalvia not ID	2,09	3,18	78,39
Sipuncula	1,95	2,96	81,35

PAE V - PAE NV			
Species	**Av.Diss**	**Contrib%**	**Cum.%**
Oligochaeta	20,02	27,98	27,98
Capitellidae	13,2	18,44	46,42
Nereididae	7,22	10,09	56,51
Pilargidae	4,21	5,89	62,4
Ampharetidae	4,07	5,69	68,09
Nemertea	3,89	5,44	73,52
Bivalvia not ID	2,64	3,69	77,21
Spionidae	2,63	3,67	80,88

Supplementary Table B

Similarity percentages (SIMPER) analysis with contribution (%) for each taxa that most contributed to dissimilarities in NV habitats among estuaries at the cutoff level 80%.

BEN NV - VIB NV

Species	Av.Diss	Contrib%	Cum.%
Kalliapseudidae	41,34	48,25	48,25
Spionidae	13,7	15,99	64,24
Oligochaeta	12,6	14,71	78,95
Capitellidae	3,48	4,06	83,01

BEN NV - PAE NV

Species	Av.Diss	Contrib%	Cum.%
Kalliapseudidae	49,96	56,29	56,29
Oligochaeta	15,05	16,95	73,24
Capitellidae	5,24	5,91	79,15
Nereididae	3,6	4,05	83,2

VIB NV - PAE NV

Species	Av.Diss	Contrib%	Cum.%
Spionidae	30,31	38,92	38,92
Capitellidae	11,2	14,38	53,29
Nereididae	7,96	10,22	63,51
Oligochaeta	5,61	7,2	70,71
Bivalvia not ID	4,65	5,97	76,69
Pilargidae	4,43	5,69	82,37

CAPÍTULO 3

Conclusões finais

Os resultados deste estudo mostraram a influência dos habitats na composição, densidade, biomassa e produção secundária da macrofauna bentônica nos estuários estudados. Porém, algumas diferenças foram observadas entre os estuários. Habitats não vegetados no estuário do Benevente apresentaram um padrão diferente dos outros estuários, devido à alta densidade e à dominância da família Kalliapseudidae (Tanaidacea). Dessa forma, os habitats não vegetados demonstraram um importante papel na produção secundária no estuário do Benevente. O estuário do Piraquê-Açu e a Baía de Vitória apresentaram um padrão inverso, com maior biomassa e produção nos habitats vegetados, o que confirma outros estudos que demonstraram a importância desses habitats para um aumento da densidade, biomassa e produção secundária bentônica em estuários.

As assembleias bentônicas dos habitats vegetados foram mais similares entre os estuários. Em geral, os grupos da fauna que apresentaram maiores densidades nos habitats vegetados foram diferentes dos grupos que mais contribuíram para a biomassa e produção, porém em ambas as situações, esses grupos são comumente encontrados em manguezais. A composição da macrofauna entre os habitats não vegetados apresentou maior variação entre os estuários, com diferentes famílias apresentando maiores densidades em cada estuário.

Apesar da importância dos estuários e dos manguezais, esses ecossistemas são ameaçados pela urbanização, perda de manguezais e por impactos das mudanças climáticas, com consequentes impactos para as comunidades bentônicas. Portanto, o estudo das comunidades bentônicas e suas produções secundárias são importantes para o conhecimento atual desses ecossistemas e poderá ser uma base para estudos futuros.