IVAN RODRIGO ABRÃO LAURINO

Effects of environmental changes on sandy beach biodiversity: what we can learn with small-scale patterns and processes?

São Paulo
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A thesis submitted to the Instituto Oceanográfico of the Universidade de São Paulo in partial fulfilment for the degree of Doctor of Science, Oceanography, with emphasis in Biological Oceanography.

Advisor: Prof. Dr. Alexander Turra

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Aprovado em: 15/07/2022

Versão Corrigida

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Dedico essa obra à minha família e amigos que sempre estiveram comigo ao longo dessa jornada. Em especial, minha mãe Júnia e minha namorada Tamiris.

AGRADECIMENTOS

Agradeço ao meu orientador e professor, Dr. Alexander Turra, pelos anos de convivência e dedicação, os quais me fizeram crescer profissionalmente, cientificamente e intelectualmente, graças às suas contribuições.

Agradeço a todas as agências de fomento que contribuíram financeiramente.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

Ademais, sou grato à Fundação Boticário e à FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), as quais também contribuíram financeiramente para a execução do presente trabalho.

Agradeço a toda equipe do Laboratório Manejo, pela companhia e ajuda de sempre, em especial ao Guilherme e ao Hélio, pelas contribuições em diferentes capítulos do presente trabalho, participando de forma fundamental no meu crescimento e amadurecimento científico.

Agradeço aos técnicos do IO, em especial o Tomás, por toda a ajuda com as análises laboratoriais, e aos membros da CPG do IO, sempre muito prestativos e eficientes.

Agradeço, de coração, a todos os colegas que foram comigo para as coletas de campo. Sem vocês nada seria possível!

Por fim, agradecimentos especiais vão para toda a minha família, principalmente a minha mãe Júnia, que sempre me deu todo o suporte necessário para seguir esse longo caminho acadêmico. Agradecimentos mais que especiais também vão para minha namorada Tamiris, que, além da grande ajuda acadêmica ao longo do desenvolvimento do trabalho, também me apoiou constantemente, dia após dia, com muito carinho, amor e compreensão.

RESUMO

LAURINO, Ivan Rodrigo Abrão. **Efeitos de mudanças ambientais na biodiversidade de praias arenosas:** o que podemos aprender com padrões e processos de pequena escala?. 2022. 119 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2022.

Praias arenosas são ecossistemas altamente apreciados pela humanidade. A distribuição e estrutura da biodiversidade praial, bem como sua interação com o meio físico, são componentes indispensáveis para o funcionamento das praias e sua provisão de serviços ecossistêmicos. Contudo, praias arenosas são vulneráveis às mudanças climáticas e à urbanização, pressões que ameaçam sua biodiversidade. Na presente contribuição, testamos os efeitos de múltiplas mudanças ambientais no comportamento, distribuição, estrutura e relações ecológicas da biodiversidade praial. Com esse objetivo, realizamos uma série de experimentos de campo, em pequena escala, nas praias do litoral norte de São Paulo, Brasil. Exploramos os efeitos de inundações, da redução da salinidade, de estruturas urbanas costeiras e do aumento de detritos de tempestades nas praias. Testamos as respostas da macrofauna bentônica frente a essas pressões avaliando o comportamento de espécies, a riqueza taxonômica e funcional de comunidades, sua abundância e biomassa, assim como sua função como presas para aves. Descobrimos que inundações simuladas induzem o deslocamento vertical descendente de poliquetas (i.e., *Scolelepis*) e isópodes (i.e., *Excirolana armata*), alterando sua distribuição na coluna de sedimento. Para *E. armata*, tal deslocamento é menor em inundações de água doce do que de água salgada, sugerindo uma influência da salinidade no comportamento deste isópode. Reduções de salinidade também diminuem a riqueza da comunidade e a probabilidade de poliquetas formarem manchas (principalmente *Scolelepis*) próximo a córregos de entrada de água doce nas praias. As estruturas urbanas (i.e., muros de casas no supralitoral), por sua vez, reduziram a abundância e biomassa da macrofauna, influenciando também sua composição e estrutura funcional. Em particular, a abundância de poliquetas e moluscos no infralitoral, a abundância e biomassa do coleóptero *Phaleria testacea* e a ocorrência de predadores e espécies de grande porte (> 80mm) foram os padrões mais impactados pelas estruturas urbanas. *P. testacea* também foi a espécie mais afetada pelos detritos de tempestade, apresentando agregações nos detritos, embora não tenhamos encontrado evidencias de que tal agregação funcione como uma fonte de presas para aves em curto prazo na área estudada. Ademais, tal agregação foi um fenômeno fortemente associado aos detritos naturais (i.e., algas e folhas), não ocorrendo em detritos plásticos. Concluímos que a macrofauna bentônica das praias estudadas é sensível a múltiplas mudanças ambientais, como inundações, mudanças de salinidade, urbanização e alterações no aporte de detritos de tempestade. Os efeitos que notamos na biodiversidade podem desencadear, em longo prazo, importantes impactos ecossistêmicos no funcionamento das praias, os quais devem ser posteriormente avaliados. Por fim, defendemos que o uso de abordagens de pequena escala podem ser importantes ferramentas para a conservação, gerando indicadores precoces, subletais (e.g., deslocamento vertical), úteis para aprimorar a avaliação de cenários futuros e programas de monitoramento.

Palavras-chave: Macrofauna. Experimentos em campo. Indicadores precoces.

ABSTRACT

LAURINO, Ivan Rodrigo Abrão. **Effects of environmental changes on sandy beach biodiversity:** what we can learn with small-scale patterns and processes?. 2022. 119 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2022.

Sandy beaches are coastal ecosystems largely appreciated by human society. The distribution and structure of beach biodiversity and its interaction with the physical environment are essential components for the beach's functioning and the provision of ecosystem services. However, sandy beaches are also vulnerable to multiple threats such as climate changes and urban development, pressures that jeopardize their biodiversity. In the present contribution, we test the effects of multiple environmental changes on beach biodiversity's behavior, distribution, structure, and ecological relationships. With this goal, we carried out a series of small-scale field experiments on the beaches of the northern coast of São Paulo, Brazil. We explored the effects of flooding, salinity reduction, coastal armoring (i.e., backshore seawalls), and the increase of storm-stranded debris (i.e., wrack) on the beach ecosystem. We tested the responses of benthic macrofauna to these pressures by evaluating the behavior of species, the taxonomic and functional richness of communities, their abundance and biomass, as well as their function as prey for birds. We found that simulated flooding induces the downward vertical displacement of polychaetes (i.e., *Scolelepis*) and isopods (i.e., *Excirolana armata*), changing the macrofauna distribution in the sediment column. We also noted a weaker downward displacement with freshwater than with saltwater floods for *E. armata*, suggesting a salinity influence on the behavior of this isopod. Salinity reductions also decreased the community richness and the probability of polychaetes forming high-abundance patches (mainly *Scolelepis* patches) close to freshwater streams on the beach. Coastal armoring, in turn, reduced the abundance and biomass of beach macrofaunal assemblages and influenced their composition and functional structure. Particularly, the abundance of subtidal polychaetes and molluscans, the abundance and biomass of the coleopteran *Phaleria testacea*, and the occurrence of predators and large body size species (> 80mm) were the patterns most impacted by coastal armoring. The coleopteran *P. testacea* is also the main species affected by the storm-stranded debris, presenting aggregations under wrack. However, there was no evidence that such aggregation could work as a prey hotspot for birds in the short term, considering the study area. Additionally, these aggregations under wrack were a phenomenon strongly associated with natural debris (i.e., algae and leaves), not occurring in plastic debris. We conclude that the macrobenthic biodiversity of the sandy beaches studied is sensitive to environmental changes, especially flooding events, salinity reductions, urban development, and changes in the storm-stranded wrack. The biodiversity changes evidenced here can induce, in the long-term, important ecosystem impacts on the functioning of beaches, which should be further assessed. Finally, we argue that the use of small-scale approaches can be important tools for conservation, generating early proxies (i.e., sublethal biological indicators, such as vertical displacement), useful to improve the assessment of future scenarios and monitoring programs.

Keywords: Macrofauna. Field experiments. Early proxies.

SUMMARY

1. GENERAL INTRODUCTION: SANDY BEACHES IN A CHANGING WORLD

1.1 Global and local changes in the coastal zone

The coastal zone is characterized by remarkable ecosystems that support great biodiversity and fundamental human uses. Ecosystems services from the coastal zone include climatic regulation, food provision, and coastal protection, besides their inherent and crucial values for recreational activities and the wellbeing of the society (Peterson & Lubchenco 1997; Ward et al. 2022). Not surprisingly, about a third of the world's human population lives less than 100 km from the coast, where many large cities and important socio-economic and cultural activities are concentrated (Melet et al. 2020). Due to their unique geographic location, between oceanic and continental drivers (Defeo et al. 2021), the coastal zone is also greatly affected by continental and oceanic processes and pressures such as climate change, urbanization, and pollution (Lu et al. 2018). Therefore, coastal ecosystems and their biodiversity are daily exposed to global, regional, and local changes that are threatening their provision of services and their benefits to people.

The predicted climate changes are the major global threat that the coastal zone is currently submitted. As a result of the ocean warming and the glaciers melting, the sea level has risen at a global rate of 1.7 ± 0.3 mm/year since 1950 (Nicholls & Cazenave 2010). This rate has been intensifying and reached a global average of ~ 3.0 ± 0.4 mm/year since 1993 (Nicholls & Cazenave 2010), with more than 7.0 cm of total sea-level rise between 1993 and 2017 (Nerem et al. 2018). As the world warms, the sea level rises and the ocean also has more energy to convert to extreme climate events such as cyclones and, consequently, storms, which have been increasing in intensity and frequency in the last years (Elsner et al. 2008; Lin & Emanuel 2015; Yin et al. 2018). Coastal erosion and retraction are the principal results of these changes, leading to losses of ecosystems, habitats, and species across the coastal zone (Slott et al. 2006; Vousdoukas et al. 2020; Defeo et al. 2021; Defeo & Elliott 2021). Extreme changes in the annual regimes of rainfall and temperature also happen associated with these global changes, promoting long and intense rainy periods with floods or long drought periods, with significant pressures on coastal biodiversity, ecosystems, and cities (Harris et al. 2018; Yin et al. 2018; Oliveira-Gomes & Bernardino 2020).

Local pressures also occur with intense human impacts on the coastal zone and its ecosystems. Coastal urbanization, industrialization, predatory tourism, overexploitation of marine resources, and pollution are the principal local threats that which the coastal ecosystems and their biodiversity are submitted (Defeo et al. 2021; Defeo & Elliott 2021). Urbanization and industrialization directly promote local losses of natural habitats and, summed to unplanned tourism, they act as local sources of pollution and contamination (Lu et al. 2018; Defeo et al. 2021; Defeo & Elliott 2021). An important and worrying fact is that the local changes have great synergism with the ongoing global changes, given that the human disturbances reduce the resilience of the coastal zone to the predicted climate changes (Defeo & Elliott 2021). As an example, the coastal squeeze is promoting losses of coverage of coastal ecosystems due to the cumulative and synergistic pressures of urban development and the erosion from the increasing sea level and storminess (Orlando et al. 2019; Scapini et al. 2019; Defeo et al. 2021). In this sense, global and local changes act together in the coastal zone, meaning that the current threats to the coastal ecosystems need to be understood as a trans-scalar problem.

In a recent and timely contribution, Defeo & Elliott (2021) presented the ‘triple whammy’ of coasts under threat, which summarizes, in a trans-scalar and illustrative way, the principal threats and changes that the coastal zone is submitted nowadays. For the authors, the first ‘whammy’ is the increasing urbanization and industrialization in the coastal zone, also connected to coastal pollution and contamination. The second ‘whammy’ is the increasing use of marine resources, which includes the use of coastal space (e.g., degrading natural ecosystems) and the uncontrolled use of biodiversity (i.e., overfishing). The third ‘whammy’ is the increasing effects of climate change, which regards the increase of the global-change drivers (e.g., ocean warming) summed to the local changes that reduce coastal resistance and resilience (i.e., loss of natural habitats). Defeo & Elliott (2021) highlighted that the ‘triple whammy’ is potentialized as more people are moving to the coast searching for their services and benefits, which generates a contradiction given that these services and benefits are also threatened by the ‘triple whammy’. In other words, the disorderly search for coastal goods has damaged the essential ecosystemic grounds that support these goods and ultimately can eliminate the features that previously encouraged this search (Butler 1980). This contradiction is much more intense in complex coastal ecosystems of great human appreciation, such as sandy beaches.

1.2 Sandy beaches as complex coastal ecosystems

To an inattentive observer, a sandy beach may seem similar to a marine desert, devoid of life, when compared to other coastal ecosystems such as rocky shores and mangroves. This may be one of the reasons for the delay in beginning the studies about the ecology of sandy beaches, which began only 50 years after the first studies on rocky shores (Mclachlan & Defeo

2017). In contrast to this apparent negligence by science, sandy beaches have always been the most used coastal ecosystem by humans, from a recreational point of view. Nowadays, we know that behind this beautiful and seemingly simple seascape, there is unique and fragile biodiversity and complex ecological processes taking place, which are fundamental for the maintenance of the ecosystem services and their use by humans.

Beach ecosystems are a segment of the Littoral Active Zone (LAZ), a geomorphic transitional system between the marine and the terrestrial environments (Mclachlan & Defeo 2017; Scapini et al. 2019; Fanini et al. 2021a). The LAZ also includes the surf zone and the foredunes, two systems that surround the beaches and are in constant interaction with them (Fig. 1.1). Such interaction takes the form of sedimentary movements, which are made by the waves in the transition between the beach and the surf zone; or by the winds in the transition between the beach and the foredunes (Mclachlan & Defeo 2017).

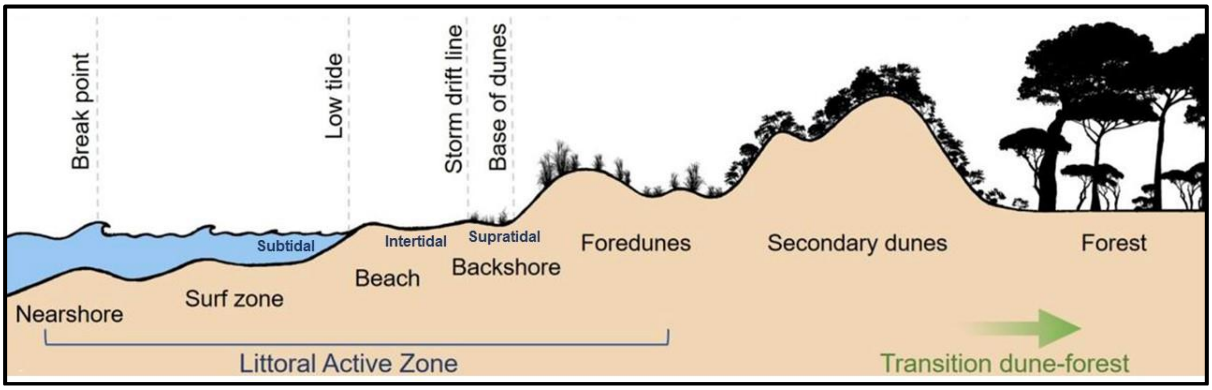

Figure 1.1. Scheme of the Littoral Active Zone. Font: modified from Scapini et al. (2019), based on Mclachlan & Defeo (2017).

Together with the waves and winds, the tides also can regulate the sedimentary movement while also creating distinct beach zones: 1) The subtidal zone (sublittoral), the area always submerged and covering the beach inferior limit and all the surf zone; 2) The intertidal zone (midlittoral), beach area submerged during the high tide period and emerged during the low tide period; 3) The supratidal zone (supralittoral), beach area mostly emerged and located on the beach backshore, the transition between the upper beach limit and the foredunes (Amaral et al. 2016). The storm drift line, a segment usually occupied by stranded debris (e.g., algae, leaves, etc.), divides the intertidal and supratidal zones of the beach (Fig. 1.1).

Sandy beaches can be classified by different criteria according to their physical environment. Considering the tide range, beaches can be classified from microtidal (range < 2m) to megatidal (range > 8m) (Mclachlan & Defeo 2017). Microtidal beaches are wave-dominated beaches (i.e., more influenced by waves than tides) and can be classified into three morphodynamic states related to their capacity to absorb the wave's energy: reflective (low capacity); intermediate (middle capacity); and dissipative (high capacity) (Wright & Short, 1984). These morphodynamic states can reflect in the sedimentary properties and the face slope of the beach. In general, the sand is coarser and the beach face slope is steeper on reflective beaches (Defeo & McLachlan 2005). The coastal position of the beach also can influence its sediment grain size and face slope. Sheltered beaches (or protected beaches) usually have a lower influence of waves than ocean-exposed beaches, so the first also could have finer sediments and flatter face slopes (Wright & Short, 1984). Beaches also can be classified as estuarine beaches, located within estuaries and with great freshwater influence; or oceanic beaches, located outside estuaries and with great saltwater influence. Although oceanic beaches are located outside estuaries, they can be associated with river mouths and freshwater inputs, which can influence beach biodiversity (Lercari & Defeo 2006). In fact, a combination of factors, such as sediment properties, beach face slope, and salinity, among several others, are fundamental to regulating the biodiversity patterns and processes on sandy beaches.

Beach biodiversity is mainly represented by the macrobenthic community, which includes polychaetes, molluscans, and arthropods (including crustaceans and insects). The composition, abundance, biomass, and richness of these communities vary across beach zones and also among beach types. The across-zone distribution of the macrofauna (zonation pattern) is related to their abilities to live submerged or emerged and deal with wave action (McLachlan & Jaramillo 1995). Accordingly, the subtidal zone is occupied mainly by molluscans (e.g., bivalves), some crustaceans, and polychaetes not adapted to air exposure (McLachlan & Jaramillo 1995). Contrary, the intertidal zone is occupied by many polychaetes, crustaceans, and mollusks adapted to great tide variations. The supratidal zone is only inhabited by terrestrial and semi-terrestrial organisms very resistant to long emerged periods and desiccation (e.g., coleopterans, talitridae amphipods, some cirolanid isopods, and ghost crabs). The zonation pattern is usually clearer and more complex on dissipative beaches, where the beach profile is larger and flatter than reflective ones (Jaramillo et al. 1993; McLachlan & Jaramillo 1995). Species composition and richness also change among beach types. Reflective beaches usually have poorer intertidal biodiversity in comparison to dissipative beaches (Checon et al. 2018). Even considering beaches of the same type, steep slopes with coarse sediments are related to low diversity and abundance of intertidal macrofauna (Defeo & McLachlan 2005) (Fig. 1.2).

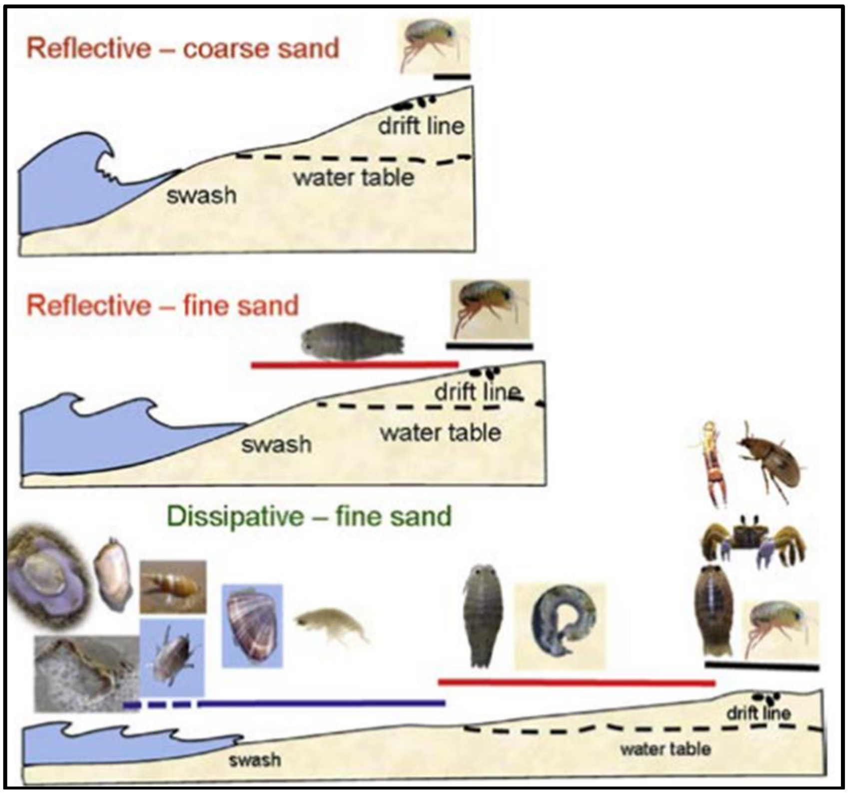

Figure 1.2. Scheme of the zonation pattern of the macrobenthic community on different beach types. Font: Mclachlan & Defeo (2017), based on Jaramillo et al. (1993) and McLachlan & Jaramillo (1995).

Besides the macrobenthic community, the fish community is also an important component of the beach biodiversity, working as a top predator on the subtidal and intertidal (during high tides) zones of the beaches (e.g., Takahashi et al. 1999). Similarly, the birds also have a great role as top predators on the intertidal and supratidal zones of the beaches (e.g., Schlacher et al. 2017). Other important biodiversity groups in sandy beaches include the epibenthic megafauna, the planktonic community, the microphytobenthos, the benthic meiofauna, and the microbiota (Fanini et al. 2020). Each species of each one of these groups can present different distributional and behavioral patterns, linked to different processes in distinct trophic web positions, which ultimately support many functions and services in the beach ecosystem (Mclachlan & Defeo 2017). For instance, many macrofaunal species, such as some polychaetes and crustaceans, are deposit-feeders or scavengers and have an important function for the organic matter and nutrient recycling on beaches (Welsh et al. 2003; Murray et al. 2017; Gómez et al. 2018). Other molluscans and crustaceans are filtering suspend-feeders and promote water purification (Hily et al. 1991; Vozzo et al. 2021). Some of these invertebrates are directly edible, serve as bait for fishing, or are even prey for commercially important fish or ecologically important birds (e.g., Takahashi et al. 1999; Schlacher et al. 2017; Mclachlan & Defeo 2017). This means that, directly or indirectly, the beach biodiversity patterns and processes are connected to ecosystem functions and services. In this sense, the threats that affect biodiversity or the physical environment that support it are also threats to the functioning of beaches and the services they provide. This illustrates how sandy beaches are complex systems and, therefore, understanding their vulnerability to threats can be a challenging task.

1.3 Key threats to sandy beaches in the 21st century

As sandy beaches are a coastal ecosystem largely appreciated and used by humans, they are also under several threats. The classical threats include unplanned recreational activities (i.e., predatory tourism), sewage pollution, and the overexploitation of biodiversity resources (Schlacher et al. 2008; Defeo et al. 2009). These key threats have been intensified since the beginning of the 21st century and concerns about other threats such as climate change, urban development, and the increase of marine litter emerged (Schlacher et al. 2008; Defeo et al. 2009; Amaral et al. 2016; Fanini et al. 2020; Defeo et al. 2021). Such concerns are justified considering that the isolated and, mainly, synergistic effects of all these threats jeopardize the recreational potential of these ecosystems (Krelling et al. 2017) and, even worse, they can lead to the disappearance of many beaches around the world until the end of the century (Vousdoukas et al. 2020).

The climate changes are undoubtedly a central threat to sandy beaches in the current century (Fig. 1.3). In addition to the increase in the intensity and frequency of extreme climate events, such as storminess, sea-level rise tends to promote beach erosion, flooding the upper beach zones and squeezing the beach area, with consequent loss of habitats and species (Hubbard et al. 2013; Orlando et al. 2019; Scapini et al. 2019; Defeo et al. 2021). It is predicted that about 15% of the world's beaches are at risk of suffering a retraction (i.e., coastline erosion) of 100 m until 2050, with significant losses of the beach area or even the disappearance of short beaches (Vousdoukas et al. 2020). If we consider the projections until 2100, 40% of the world's beaches tend to suffer such retraction (Vousdoukas et al. 2020). Extreme storms also have great potential to change morphodynamics, sediment grain size, and face slopes of the beaches, ultimately affecting the connected biodiversity patterns (e.g., Lucrezi et al. 2010; Machado et al. 2016). Changes in the rainfall regime, which threatens biodiversity due to the influence of rainfall on water salinity, have also been observed globally. Rainfall increase, for instance, is especially worrisome for beaches associated with freshwater sources such as estuaries, streams, and drainage channels, which could promote freshwater floods with beach salinity changes during long rainy periods (Scapini et al. 2019).

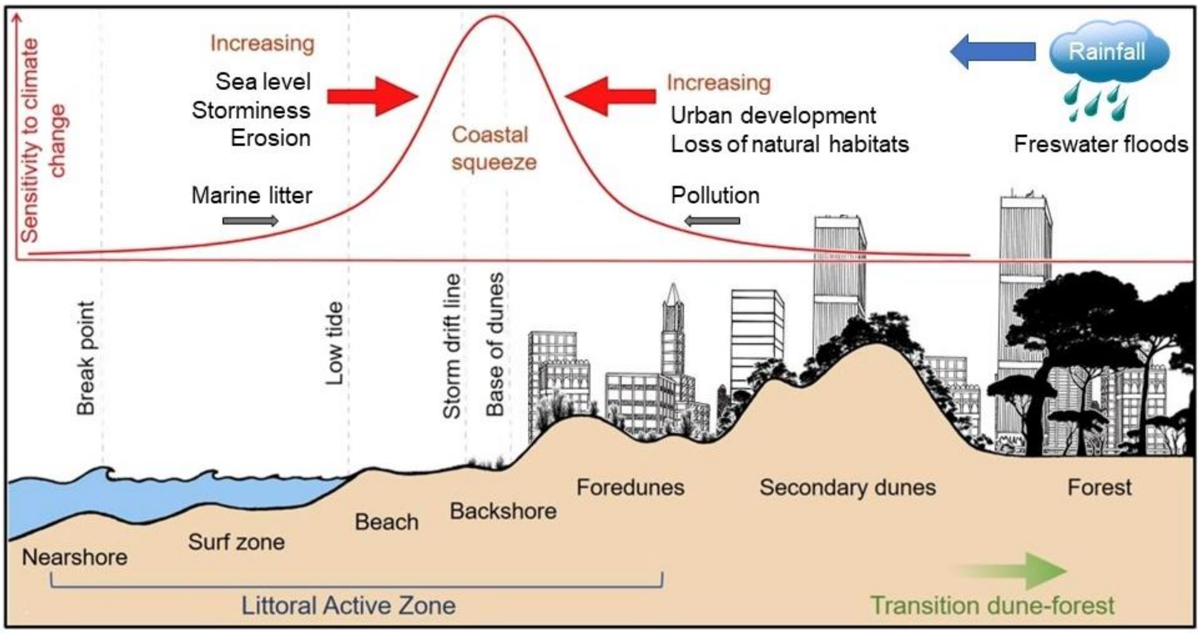

Figure 1.3. Scheme of the Littoral Active Zone with the key threats to sandy beaches in the 21st century. Font: modified from Scapini et al. (2019), based on Mclachlan & Defeo (2017).

The urban development and consequent increase in coastal pollution sum with climate change as a central threat to sandy beaches (Fig. 1.3). The man-made structures (e.g., buildings, walls, houses, roads) directly replace the beach backshore, the dunes, and the coastal vegetation, which increase the sensitivity of the beach to climate changes, especially to the coastal squeeze and erosion (Schlacher et al. 2008; Scapini et al. 2019; Cooper et al. 2020; Defeo et al. 2021). Moreover, coastal pollution and marine litter, especially plastic litter, have been strongly growing in recent decades with a potential synergism with climate change (Defeo et al. 2021; Fanini et al. 2021b; Tekman et al. 2022). Beached plastic debris is increasing and tends to amplify as storms intensify, considering that these weather events have a high capacity to bring marine debris to beaches (Pattiaratchi & Wijeratne 2019; Defeo et al. 2021). Furthermore, sewage pollution in coastal freshwater sources (e.g., estuaries), summed to the rainfall increase in some regions, would cause not only salinity changes but also drastic impacts on sandy beaches, including eutrophication (Defeo et al. 2009). Beach biodiversity, their functions, and associated ecosystem services are at risk in this scenario, which ultimately highlights the need for urgent conservation strategies to guarantee the current and future uses of sandy beaches by humans.

1.4 Looking forward to supporting conservation

The trans-scalar and integrated nature of the current coastal threats connected to the complexity of ecological and social processes of the sandy beaches turn the conservation of these ecosystems a great challenge. The different threats, their interactions, and their effects on the beach ecosystem are often site-dependent and still poorly understood, requiring studies to build a solid basis for conservation and adaptation actions on local and global scales (Fanini et al. 2020; Defeo & Elliott 2021). For this, understanding biodiversity patterns and processes on sandy beaches and how they are vulnerable to distinct threats is an important first step to assessing how and what ecosystem services and human uses could be at risk (Amaral et al. 2016). As remarked by Underwood et al. (2000), we cannot advance in understanding the ecological processes of biodiversity without first understanding their patterns. In this same logic, we cannot understand the vulnerability of ecosystem services and their uses on beaches without first understanding the vulnerability of the processes and patterns that lie behind them.

In this regard, hypothesis-testing approaches aiming to understand the effect of key environmental changes in biodiversity patterns and processes can be a useful conservation tool. However, such approaches must investigate the effects of specific drivers that are linked to the key threats highlighted above. This includes the effects of alterations in physical parameters that are sensitive to climate changes (e.g., changes in salinity, grain size, and beach slope), the effects of key human impacts (e.g., presence of urban infrastructure or marine litter), and their synergistic effects (Fanini et al. 2020; Defeo & Elliott 2021). It is also important to understand the effects of these drivers on biodiversity patterns and processes that support important ecosystem services on the beaches. It includes patterns of taxonomic and functional richness (e.g., functional diversity), specific faunal behaviors linked to ecosystem functions (e.g., sediment bioturbation), food web processes (e.g., predation), and ecological patterns of functional groups (e.g., deposit-feeders, scavengers, etc.). The relationship between these drivers, patterns, and processes is testable on beaches around the world and could assist in understanding the present and modeling the future.

To accomplish this goal, the best-case scenario is to implant long-term monitoring programs across large spatial scales, allowing us to understand how the drivers connected to the threats are affecting the biodiversity patterns and processes on the beaches (Amaral et al. 2016). However, such programs take a long time to generate the first responses and their standardized implementation and permanence on a large spatial scale is quite difficult and expensive. An alternative strategy, potentially less costly and with faster responses, is the use of small-scale field experiments. Simple experimental designs could be useful to understand the relationship between specific drivers and beach biodiversity responses in the short term and on a local scale, besides being the baseline for stimulating experimental macroecology studies. Such approaches can be natural experiments (e.g., Gandara-Martins et al. 2015; Laurino et al. 2021), using the natural small-scale variation of a specific driver (e.g., an environmental gradient of salinity or grain size). Manipulative-controlled experiments also can be applied with this goal, manipulating the drivers (i.e., the stressors) on the field (e.g., Schlacher et al. 2016; Pardal-Souza et al. 2017). The results of these experiments (natural or manipulative) could generate proxies and indicators that could be further used in large-scale monitoring programs and local management strategies (e.g., Laurino et al. 2021). Furthermore, these proxies coming from appropriate experimental designs can be extrapolated to larger spatial scales, respecting their limitations, and also can assist future predictions and modeling. Evidently, such small-scale approaches are not a substitute for large-scale monitoring programs, but they can serve as a practical and useful complement aiming to deal with the multiple threats that jeopardize sandy beach ecosystems today and in the coming years.

1.5 General goal

In the present contribution, we designed a series of small-scale field experiments (natural and manipulative) intending to test the effects of key environmental changes on sandy beach biodiversity. We explored the effects of specific drivers connected to environmental changes such as the increasing sea level, rainfall, storminess, urbanization, and marine litter. We tested the responses to these drivers in biodiversity patterns and processes potentially important for the support of beach ecosystem services. It includes behavioral patterns, taxonomic and functional richness, abundance and biomass patterns, and also food web processes (i.e., predation). The results of the experiments were discussed in a wide and ecosystemic perspective, aiming to support further vulnerability analysis regarding the beach ecosystem services and novel conservation strategies.

2. CHAPTER I: FLOODING AFFECTS VERTICAL DISPLACEMENT OF INTERTIDAL MACROFAUNA: A PROXY FOR THE POTENTIAL IMPACTS OF ENVIRONMENTAL CHANGES ON SANDY BEACHES

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Abstract

In the context of global environmental changes, sea level rise is expected to cause long-term floods in upper zones of sandy beaches, while increased rainfall may intensify freshwater floods with extreme salinity reductions. However, the effects of these changes on benthic macrofauna behavior, especially the species vertical displacement, remain largely overlooked in sandy beach ecology. Here, we used natural and manipulative experiments to evaluate whether the predicted effects of saltwater and freshwater floods would affect the distribution of beach macrofauna within the sediment column (i.e., vertical distribution). We first tested the effects of natural tidal flooding by analyzing the upper beach macrofauna at different depths within the sediment column during low and high tide periods. Then, we simulated saltwater and freshwater floods in manipulative experiments to examine their effects on the vertical distribution of the semiterrestrial crustacean *Excirolana armata* within the sediment. We observed that the macrofauna was concentrated closer to the sediment surface layer during low tide and in deeper areas during high tide. We also found that both saltwater and freshwater floods induced a movement of *E. armata* towards deeper layers of the sediment; yet this effect was dependent on salinity given that fewer individuals reached deeper sediment layers during freshwater floods. Overall, our results show that floods induce movements of sandy beach macrofauna within the sediment column, thereby changing the vertical distribution of benthic species. It is possible that these changes may affect ecological processes and services provided by sandy beach biodiversity such as bioturbation, biomass production and the flux of energy. In this regard, we suggest that future studies focus on the understanding of behavioral responses of macrofauna as a proxy for the impacts of global environmental changes, attempting to upscale their ecological consequences from the short to long-term effects.

Keywords: Beach macrofauna, tide, salinity, field experiments, sea level rise, rainfall.

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* *Published paper*: https://doi.org/10.1016/j.ecss.2020.106882

2.1 Introduction

Sandy beach macrofauna are a major component of coastal biodiversity and trophic webs. Given its strong association with sediments, changes in the abiotic environment strongly influence macrofaunal communities and populations (McLachLan & Defeo 2013; Carcedo et al. 2017). Environmental variables such as sediment grain size (Defeo & McLachLan 2005), wave action (McLachLan & Defeo 2013), tidal range (Schlacher & Thompson 2013) and salinity (Jorge-Romero et al. 2019) determine the distribution and species richness of sandy beach communities. At a population level, these variables may strongly influence the abundance and life-history of sandy beach species (Defeo & McLachLan 2005), regulating behaviors such as burrowing activity (Dugan et al. 2000), feeding strategy (Checon et al. 2020) and across-shore movements (Scapini 1992; Yannicelli et al. 2001), which highlights the importance of recognizing the effects of environmental changes on sandy beach biodiversity.

Nevertheless, very few studies have been dedicated to understanding how environmental changes influence the distribution and displacement behavior of macrofauna species in the vertical dimension of sandy beaches (i.e., throughout the sediment column). In fact, the number of studies on the vertical distribution in sandy beach sediment is so limited that this dimension has been recently called the “forgotten dimension” in sandy beach ecology (Celentano et al. 2019). Despite being largely overlooked, vertical macrofaunal movements can alter environmental processes and services, such as sediment bioturbation related to nutrient recycling (Murray et al. 2017) and the availability of macrofauna as food for vertebrate predators (Touhami et al. 2018). Therefore, investigating changes in the vertical distribution of sandy beach biota is important to better understand species responses to small-scale environmental variations and also to reveal behaviors with potential effects on the ecosystem level.

Tide floods are examples of environmental disturbances with the potential to sharply modify environmental conditions and influence the activities and behaviors of sandy beach species. Water saturation influences sediment penetrability (McLachlan & Defeo 2017), thereby directly affecting the vertical displacement of the macrofauna (Sassa et al. 2011; 2014). Moreover, high tidal floods may benefit macrofaunal species by reducing thermal stress and increasing food availability (Pincebourde et al. 2008). On the other hand, tidal floods may also increase the exposure of intertidal macrofauna to aquatic predators (Phillips 1977; Checon et al. 2020). Considering the periodic influence of tidal floods and the mobile substrate on the intertidal zone of sandy beaches, intertidal species exhibit specific adaptations to this condition

(Scapini et al. 2014). Nevertheless, the distribution of each species across the shore is related to their specific needs and physiology (Rossano et al. 2008; Scapini et al. 2014). While species inhabiting low intertidal areas are more adapted to submersed conditions, upper intertidal species are adapted to less frequent tidal floods (i.e., mainly during spring tides) and display semiterrestrial life strategies (Bergamino et al. 2012). With the predicted global change scenarios, including sea level rise and increased storminess (Hinkel et al. 2015), it is expected that the upper beach zones will experience more frequent floods associated with greater inundation episodes (Alfredini et al. 2008). Therefore, it is important to understand how upper intertidal species may be affected and the possible implications for ecosystem functioning.

In addition to tidal floods, freshwater floods can also affect benthic macrofauna. Rainfall directly or indirectly (i.e., through river floods) increases the sediment freshwater input in sandy beaches and, similarly to what is expected for tidal floods, influences sediment penetrability. Freshwater input also reduces the salinity of the sediment interstitial water, which may affect the behavior of macrofaunal species, such as the substrate choice, rhythms of activity and orientation (Scapini 1979; Fanini et al. 2012; 2017; Scapini et al. 2019). Moreover, drastic reductions in salinity can increase osmotic stress and promote the mortality of less tolerant species (Felder 1978). In the long term, this may lead to a decrease in macrofaunal diversity and abundance, as observed in beaches with reduced-salinity sites (Bergamino et al. 2009; Gandara-Martins et al. 2015; Jorge-Romero et al. 2019). Considering that both tidal (seawater) and rainfall (freshwater) floods are expected to modify sediment penetrability, one can also expect that they may influence the vertical movement and thus the distribution of beach macrofauna. Nevertheless, differences in salinity could trigger different physiology-related behavioral responses in faunal displacement (Houck & Drickamer 1996).

Understanding the ecological effects of different types of floods on sandy beach macrofauna is therefore an important step to effectively manage and preserve coastal biodiversity. In this context, natural and manipulative experimental field approaches are important for understanding the response of biodiversity in the face of an environmental change scenario (Schlacher et al., 2008). In this work, we evaluated the potential impacts of saltwater and freshwater floods on the vertical displacement of beach macrofauna at community and population levels. Considering that water changes the physical properties of the sediment (Sassa et al. 2014) and the potential influence of salinity on the macrofaunal behavior (Scapini 1979), we tested the following hypotheses: (1) the natural tidal floods induce short-term vertical movements in macrofaunal assemblages, resulting in different patterns of vertical distribution at the low and high tide periods; (2) freshwater floods induce a stronger displacement response in sandy beach populations than the saltwater floods due the negative effects of salinity reduction, resulting in organisms concentrating in deeper layers of the sediment as a strategy to avoid osmotic stress. For the population approach, we selected the semiterrestrial crustacean *Excirolana armata* (Isopoda: Cirolanidae) as a model species. We based our choice on the fact that this species has high burrowing ability (Yannicelli et al. 2002) and is one of the most abundant species tied to the substrate in the upper intertidal zones of the southern Atlantic beaches (Ribetti & Roccatagliata 2006; Amaral et al. 2016). This species is also commonly found on beaches with riverine influx, and population biomass reductions are evident in sites with greater freshwater influence (Lozoya & Defeo 2006; 2010), although the behavioral impacts of salinity on this species have not yet been registered (Fanini et al. 2017).

2.2 Materials and methods

2.2.1 Study area

The southeastern coast of Brazil features a variety of tropical sandy beaches vulnerable to anticipated local and global environmental changes. According to the Brazilian Climate Change Panel (PBMC 2016), the Southeast Region of Brazil has been exposed to sea level rise with averages ranging from 1.8 to 4.2 mm per year since the 1950s. On the coast of Sao Paulo state, in particular, the sea level rose approximately 30 cm in the last century, which was three times higher than the global average for the same period (PBMC 2016). The sea level is expected to rise approximately 1.5 m in some coastal cities of Sao Paulo state until 2100, dramatically reducing the width of the sandy beaches and causing coastal squeeze (Alfredini et al. 2008). This sea level rise has also been accompanied by an increase in precipitation in the region, with more frequent cases of extreme rainfall events in the coastal cities of Sao Paulo (Cavalcanti et al. 2017). The data from the National Institute of Meteorology indicate the occurrence of extreme rainfall (100 mm during a two-hour period) on the north coast of Sao Paulo during January 2019 (INMET 2019). In this sense, the southeastern coast of Brazil is facing strong environmental changes and is a good model area for the present study.

To test our hypotheses, experiments were developed at Dura Beach (23°29'37.9"S/45°10'19.3"W), Ubatuba city, on the northern coast of Sao Paulo state. This subtropical sandy beach is morphologically sheltered and classified as a microtidal (tidal range < 2 m) dissipative beach (Rocha et al. 2010). Dura Beach is composed predominantly of very fine sand and shows a beach topography with a low slope (Marconi & Abrahão 1975; Rocha et al. 2010), features that favor the establishment of benthic macrofauna species (McLachlan & Dorvlo, 2005). In addition, this beach has no nearby buildings or fixed structures for commerce, thereby lowering the risk of human interference on the experiments throughout the study.

2.2.2 Sampling and experimental design

2.2.2.1 Community level

To test our first hypothesis, we established a rectangular sampling area of 150 m in length (parallel to the waterline) and 10 m in width (perpendicular to the waterline) in the upper intertidal zone. Then, 50 points (sampling units) were randomly marked inside this area with stakes. We assessed the vertical distribution of the upper intertidal macrobenthic community in the sampling area comparing two extreme tidal periods: 1) daytime peak of the spring low tide (standardized at ~ 09:00 a.m.), without water into the upper intertidal zone; and 2) daytime peak of the spring high tide (standardized at ~ 03:00 p.m.), with water into the upper intertidal zone. Twenty-five marked points were randomly selected for sampling at low tide, and the other twenty-five were selected for sampling at high tide. To encompass the temporal variability of the tidal effects, the 50 points were randomly divided and grouped into three consecutive sampling days. Each day had a balanced number of samples for the low and high tide periods.

The macrofauna were collected using a PVC cylindrical corer (15 cm in diameter) inserted 20 cm into the sediment. Each macrofauna sample was divided into three layers of different sediment depths: 1) surface: between 0 and 3.5 cm in depth; 2) middle: between 3.5 and 7.0 cm in depth; and 3) deep: from 7.0 to 20.0 in depth. The choice of these specific depth intervals was based on pilot activities in which we evaluated the sediment layers that would possibly provide the best visualization of the faunal displacement. The sediment layers were sieved into a set of two overlapping sieves (1.0 mm and 0.5 mm meshes), and the retained organisms were preserved in 70 % alcohol until identification to the lowest possible taxonomic level.

2.2.2.2 Population level

To test our second hypothesis, we experimentally simulated floods with saltwater (salinity = 33) and freshwater (salinity = 0) and evaluated their effects on the vertical distribution of the isopod *Excirolana armata*. Two distinct experimental approaches were simultaneously performed: 1) The natural-density experiment, which started with the organisms in their natural (i.e., non- manipulated) vertical position and abundance values; 2) The controlled-density experiment, which started with the organisms being added in standardized abundances (10 individuals per replicate) and in the same vertical position of the sediment (surface: 0 cm deep).

We set up the experiments along a 300 m long transect (parallel to the waterline) in the upper intertidal zone. For the natural-density experiment, we selected 42 points within the occurrence areas of the organism (sites with evident trails) in the transect. For the controlled-density experiment, a total of 48 points were selected along the transect where no trails of *E. armata* were identified, considering that the organisms would be added later in standardized abundances. For both experiments, the points were randomly divided in a balanced way into three experimental treatments: 1) “freshwater”; 2) “saltwater”; and 3) "control". Thus, 14 replicates per treatment were dedicated to the natural-density experiment, and 16 replicates were dedicated to the controlled-density experiment.

At each replicate, we buried a cylindrical PVC corer of 15 cm in diameter and 20 cm in height. For the controlled-density experiment, we sampled individuals of *Excirolana armata* on the same beach but outside the experimental transect. We selected individuals approximately 3 mm in length, a size found for juveniles in the region (Petracco et al. 2010), and without sex differentiation (males and females were included randomly). Then, we added 10 *E. armata* individuals to the internal sediment surface of each sampler for all points selected for the controlled-density experiment. For both experiments, we covered the upper opening of all samplers with mesh (1 mm) to prevent the escape of the organisms. Next, we set up a metal stand around the sampler and suspended a plastic pot (volume of 1.5 liters) on top of the stand to add water for the treatments. Three small holes (~ 2 mm in diameter) were drilled into the bottom of the pots to simulate constant dripping in each experiment when fresh and saltwater was added to the pot. We standardized a 10 cm distance between the bottom of the suspended pot and the surface of the buried sampler, avoiding excessive shading of the sediment surface inside the sampler (Fig. 2.1).

We established 21 additional random points at the upper intertidal zone (along the transect where the other points were established) to characterize the abiotic system of the experiments. At these points, we set up the same experimental structure described above and subjected them to the same three treatments (7 points per treatment). However, for these additional points, we drilled three holes on the side of each sampler (before burying it) and attached rubber hoses to the holes to sample the sediment interstitial water after the experiments were completed. Each hole was drilled at the height on the corer that was equivalent to the three different sediment depths used in this study (surface, middle and deep). The end of the hose in contact with the sampler sediment (internal) had an attached porous filtering stone while the other end (external) was attached to a syringe for subsequent suction of the interstitial water.

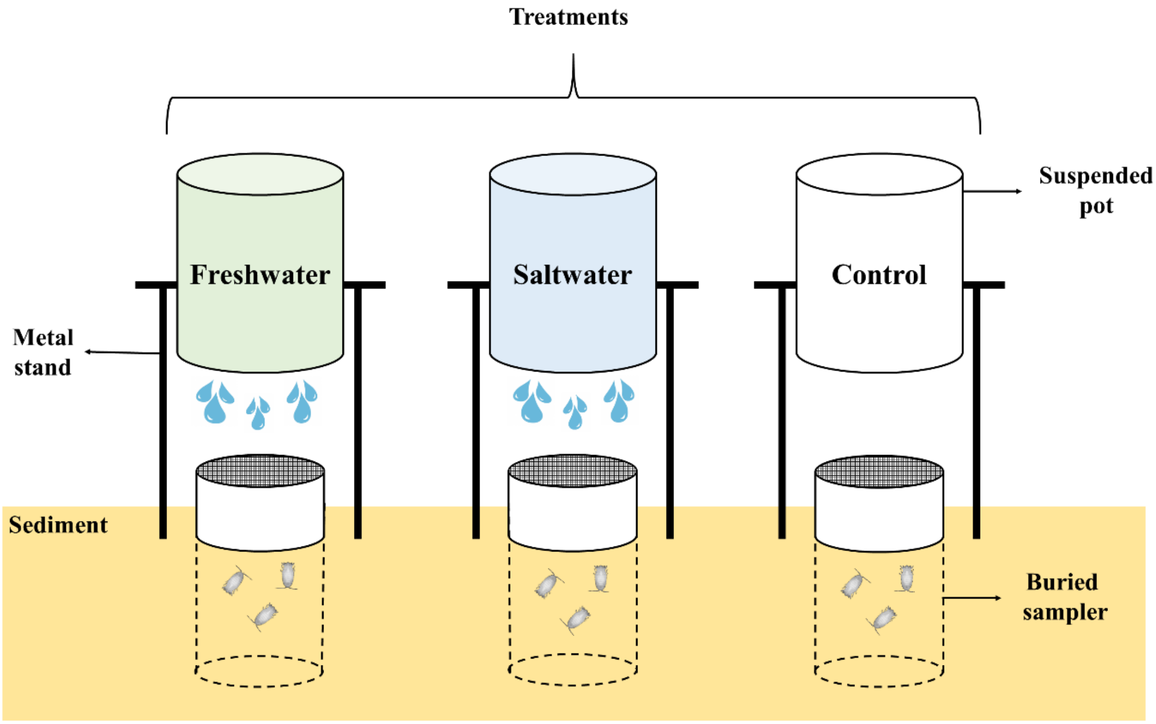

Figure 2.1. Experimental design applied to test the effects of the infiltration of water with different salinities on the vertical distribution of *Excirolana armata*. The experiment had three treatments: 1) simulated freshwater flooding (salinity = 0); 2) simulated saltwater flooding (salinity = 33); and 3) control, not manipulated (salinity in natural conditions ~ 25). The flooding in freshwater and saltwater treatments was conducted using suspended pots with holes drilled in the bottom, from which the water dripped onto the internal sediment surface of samplers buried in the upper intertidal zone of Dura Beach (Ubatuba, SP, Brazil).

We performed the experiments during the dry season of 2019 (July) and we started running the experiments at the peak of low tide (09:00 a.m.). At the “freshwater” treatment of both the experiments and additional points, we added water with zero salinity (collected in a natural source of drinking water without human treatment) in the suspended pot above the buried sampler. At the points that were in the “saltwater” treatment group, we added seawater with salinity equal to 33. At the "control" treatment points, the suspended pots remained empty throughout the experiment (Fig. 2.1). We standardized the addition of 0.75 liters of water into each suspended pot every 15 minutes during the experiments, which dripped through the holes in the bottom of the pot into the buried sampler. The water formed a 2 cm flood layer on the internal sediment surface of each sampler, allowing a continuous water infiltration flow into the sand. In total, we added 3 liters of water at each point in the “freshwater” and “saltwater” treatments, and the experiment lasted 1 hour. Both the experiment time and the water amount added were chosen based on pilot experiments in which we identified these values as the most appropriate and practicable considering the need to assemble and disassemble the experiment before high tide approached the experimental setting.

At the end of the experiment, we measured the salinity of the sediment interstitial water at the 21 established additional points using a hand-held optical refractometer (model brix with accuracy of 0.1). Simultaneously, the corers were dug up from all points of both experiments, and the internal sediment samples were divided into the three evaluated layers of sediment depths (surface, middle and deep). For both experiments, we sifted each sample as described in the previous section and recorded the abundance of *Excirolana armata* individuals at each depth for all points of each treatment and experiment.

Of the 21 additional points, we selected 9 (three from each treatment) for evaluation of sedimentary characteristics at the three different depths. In the field, we measured the sediment temperature at the different depths for each sample using a digital thermometer (accuracy of 0.1 ºC). Then, we froze the samples for further laboratory analysis of the organic matter, carbonates and grain size. We measured the organic matter content of the sediment by assessing the weight loss of the dried samples (60 °C for 24 h) after incineration (550 °C for 6 h). The carbonate content was determined by comparing the dry weight of the sediment before and after acid treatment (10 % HCl). Grain size analysis was performed by sieving the dry sediment following the procedure of Suguio (1973), and the sediment parameters (i.e., mean grain size) were obtained following Folk & Ward (1957).

2.2.3 Data analysis

For hypothesis 1, generalized linear mixed models (GLMMs) were designed to test our prediction that the distribution of macrofauna community within the sediment (response variable: individuals per sampled sediment layer) depended on the tidal period (low and high tide). We applied an adjusted Poisson distribution model (logarithmic linking function) that was suitable for counting data (O´Hara & Kotze 2010), which was checked for overdispersion. We assessed the effects of the interactions between two fixed predictor factors: 1) “depth” (three levels) and 2) “tide” (two levels). Considering the dependence between the different depths of the same sediment sample, we included a random covariate named “point” (50 levels) and its interaction with the factor “depth” to pair the depths of the same point in the model. The factor "time" (three levels: 1st, 2nd and 3rd sampling day) was also included in the model as a random covariate. Subsequently, we assessed the effects of the different factors and interactions using a likelihood ratio test (LRT with chi-square statistic), and we assessed the quality of fit of the model using the Akaike information criterion (AIC). In the case of a significant interaction between the “tide” and “depth” factors ($p<0.05$), we applied Tukey's post hoc pairwise comparisons to identify the interaction levels among these factors.

In the experiments (hypothesis 2) to verify which abiotic parameters differed between the experimental treatments and depths, we performed an analysis of variance (ANOVA) with repeated measurements for each abiotic parameter. Each analysis had two fixed factors: 1) “depths” (three levels paired in repeated measurements) and 2) “treatments” (three levels). Tukey's post hoc pairwise comparison was performed for each parameter that varied significantly with any of the factors ($p<0.05$). We log-transformed the data to comply with the assumption of normality and homoscedasticity.

For each experimental approach, we used a GLMM (Poisson distribution) to test our prediction that the abundance of *Excirolana armata* individuals within the sediment depths (response variable) depended on the observed treatment. In the models, we evaluated the interaction between the two fixed predictor factors: 1) “depths” (three levels) and 2) “treatments” (three levels). For the natural-density experiment, similar to the previous analysis (hypothesis 1), we included the “point” random factor (42 levels) and its interaction with the “depth” factor in the model to match the dependent depths of the same samples. For the controlled-density experiment, we applied the same model described above; however, the "point" factor presented 48 levels, and the isolated effect of the "treatment" factor was not considered, as the organism’s abundance was standardized between the treatments. For both experiments, the LRT test was also applied, and the model’s quality of fit was evaluated by the AIC. Tukey's post hoc pairwise comparison was also performed in case of interaction with significant effect ($p<0.05$) between the “depth” and “treatment” factors.

2.3 Results

2.3.1 Community level

A total of 408 macrofaunal individuals were collected, 210 during low tide and 198 during high tide. The macrobenthic community was composed of the species *Scolelepis* sp. (Annelida; Polychaeta), *Excirolana armata* and *Excirolana braziliensis* (Crustacea; Isopoda) during both tidal periods. The average community abundance was 8.40 ± 8.48 (standard deviation) per sample at low tide and 7.92 ± 9.60 per sample at high tide.

Differences in macrobenthic abundance in each sediment depth depended on tidal period (Tab. 2.1). The values indicated a behavior of vertical displacement towards the bottom of the sediment with the rising tide (Fig. 2.2). The abundance in the surface and middle layers was higher at low tide, while the average abundance in the deep layer was higher at high tide (Fig. 2.2). In fact, the macrobenthic abundance in the deep sediment layer was less than half of that observed in the other layers during low tide. In contrast, during high tide, the sediment surface layer had the lowest abundance value compared to those of the other layers (Fig. 2.2). Individuals of *Scolelepis* sp. (73.96 % of total abundance) and *Excirolana armata* (15.63 % of total abundance) were responsible for the observed differences of vertical distribution. The percentage of individuals of both species in the deep layer tripled during the high tide, while *Excirolana braziliensis* (10.41 % of total abundance) had approximately 80 % of the individuals in the sediment surface layer in both tide periods.

Table 2.1. Generalized linear mixed models (GLMMs) designed to test whether the abundance of benthic macrofauna (response variable) throughout the sediment depths depends on the tidal period (low and high tide). The full model presented had two fixed predictor factors: 1) "depth" (surface, middle and deep) and 2) "tide" (low and high). The random factors considered were 1) "point" (50 levels) and 2) "time" (1st, 2nd and 3rd sampling day). The reduced models compared to the full model tested the effects of different factors (fixed and random) and interactions. For each model, the Akaike information criteria (AIC), deviance, chi-square statistic of the likelihood ratio test (LRT), and the p-value of the test (bolded when significant) are presented.

Effects	**Generalized linear mixed models (GLMM)**			
	AIC	**Deviance**	**LRT (Chi)**	**p**
Full model	606.99	580.99	-	**-**
Fixed factors				
"tide" x "depths"	613.54	591.54	10.55	**0.005**
"tide"	613.19	593.19	1.64	0.200
"depths"	616.67	598.67	7.13	**0.028**
Random factors				
"point" x "depths"	708.54	692.54	111.55	**<0.001**
"point"	834.11	820.11	239.13	**<0.001**
"time"	611.83	587.83	6.84	**0.009**

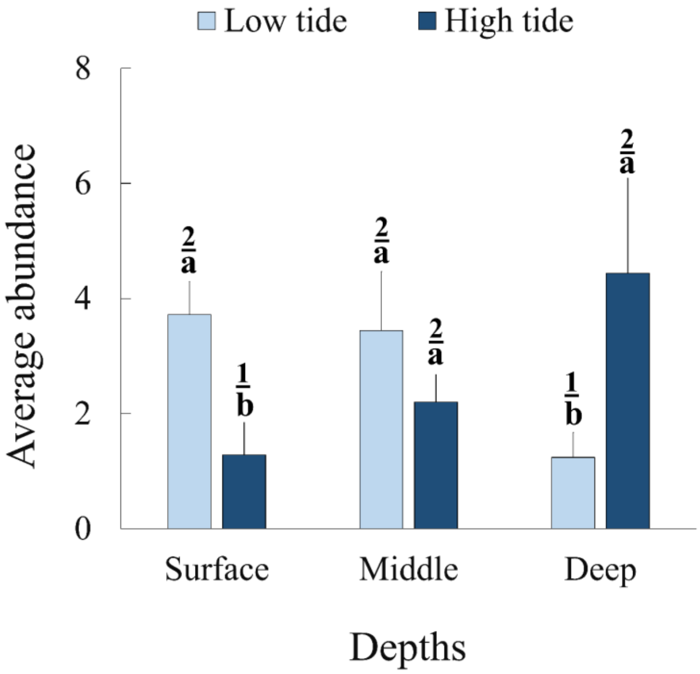

Figure 2.2. Average abundance (and standard error) of benthic macrofauna per sample observed at three different sediment depths (Surface: between 0 and 3.5 cm; Middle: between 3.5 and 7.0 cm; Deep: between 7.0 and 20.0 cm) and during two different periods of tide (low and high). Different letters indicate significant differences observed in the average abundance between tidal periods: "a" represents abundance values significantly higher than "b", when comparing the tidal periods within each depth. The different numbers indicate significant differences observed in the average abundance between depths: "2" represents abundance values significantly higher than "1", when comparing the depths within each tidal period. Pairwise comparisons from Tukey test ($p<0.05$).

2.3.2 Population level

Salinity was the only environmental variable that varied between the different experimental treatments (Tab. 2.2). The “freshwater” treatment presented an average salinity of 4.9 ± 2.02 (standard deviation), while in the “saltwater” and “control” treatments, the salinity was significantly higher, with averages of 30.4 ± 2.46 and 25.2 ± 8.7, respectively. No variation in salinity between depths was observed in any of the three treatments (Tab. 2.2). The organic matter and carbonate contents in the sediment varied between depths but did not depend on treatments (Tab. 2.2). The organic matter presented lower values in the middle layer (0.68 ± 0.29 %) compared to the surface (1.30 ± 0.38 %) and deep (0.90 ± 0.35 %) layers. The percentage of carbonates presented lower values in the deep layer (5.59 ± 2.60 %) compared to the surface layer (6.55 ± 1.70 %) and the middle layer (5.99 ± 1, 47 %). The average sediment temperature observed was 28.11 ± 0.93 °C, while the average grain size (diameter) observed for the sediment was 3.32 ± 0.09 ϕ, which confirmed the predominance of very fine sand on the beach.

Table 2.2. Analysis of variance (ANOVA) with repeated measurements performed to verify which abiotic parameters differed between experimental treatments and depths. The analyses were performed separately for five parameters: 1) salinity of the sediment interstitial water; 2) sediment temperature (ºC); 3) percentage of organic matter in the sediment (%); 4) average diameter of sediment grain (ϕ); and 5) percentage of carbonates in the sediment (%). Each analysis had two fixed factors: 1) "treatments" (three levels: freshwater, saltwater and control); 2)"depth" (three levels paired in repeated measurements: surface, middle and deep). For each analysis, the degree of freedom (df), mean square (MS), F statistic and p-value of the test (in bold when significant) are shown.

	Treatments effects			
	df	**MS**	**F**	**p**
Salinity	2	22.296	104.9	**<0.001**
Temperature (ºC)	2	0.002	3.1	0.119
Organic matter (%)	2	0.126	3.2	0.115
Grain size (ϕ)	2	0.004	1.9	0.228
Carbonates (%)	2	3.719	0.3	0.754

	Depth effects			
	df	**MS**	**F**	**p**
Salinity	2	0.017	0.2	0.835
Temperature (ºC)	2	0.003	2.2	0.152
Organic matter (%)	2	1.130	8.2	**0.006**
Grain size (ϕ)	2	0.001	1.9	0.193
Carbonates (%)	2	2.097	4.7	**0.031**

In the natural-density experiment, the abundance of *Excirolana armata* throughout the sediment depths depended on the treatment (Tab. 2.3), indicating a distinct effect of different floods on the vertical movements. In the saltwater treatment, a greater number of individuals displaced towards the bottom of the sediment than in the freshwater and control treatments (Fig. 2.3). However, a greater number of individuals were found in the middle sediment layer in the freshwater treatment than in the other treatments. (Fig. 2.3). In the controlled-density experiment, we did not observe an evident pattern of displacement. Although a movement tendency from the sediment surface to the sediment middle layer was observed in the "freshwater" and "saltwater" treatments, only the latter induced a significant downward displacement when compared to the control treatment. Approximately 30 % of the organisms in the saltwater treatment reached the middle sediment layer, while in the freshwater and control treatments, only 15 % and 5 % of the individuals, respectively, occurred in this layer (Fig. 2.4). This fact suggests a weaker downward displacement with freshwater input than with saltwater input.

Table 2.3. Generalized linear mixed models (GLMMs) designed to test whether the abundance of *Excirolana armata* (response variable) throughout the sediment depths depended on the experimental treatment applied in two experimental approaches (natural-density and controlled-density experiments). The full model presented for each experiment had two fixed predictor factors: 1) "depths" (surface, middle and deep); 2) "treatments" (freshwater, saltwater and control). The random factor considered was "point". The reduced models compared to the full models tested the effects of different factors (fixed and random) and interactions. For each model, the Akaike information criteria (AIC), deviance, chi-square statistic of the likelihood ratio test (LRT), and the p-value of the test (bolded when significant) are presented.

Natural-density experiment	**Generalized linear mixed model (GLMM)**			
	AIC	**Deviance**	**LRT (Chi)**	**p**
Full model	341.43	311.43	-	**-**
Fixed factors				
"treatments" x "depths"	349.53	327.53	16.10	**0.003**
"treatments"	348.00	330.00	2.47	0.291
"depths"	359.77	341.77	14.24	**0.001**
Random factors				
"point" x "depths"	349.19	329.19	17.76	**0.003**
"point"	351.53	333.53	22.10	**0.001**

Controlled-density experiment	**Generalized linear mixed model (GLMM)**			
	AIC	**Deviance**	**LRT (Chi)**	**p**
Full model	456.46	426.46	-	**-**
Fixed factors				
"treatments" x "depths"	478.51	456.51	30.05	**<0.001**
"depths"	545.94	527.94	71.43	**<0.001**
Random factors				
"point" x "depths"	462.17	442.17	15.71	**0.008**
"point"	460.17	442.17	15.71	**0.015**

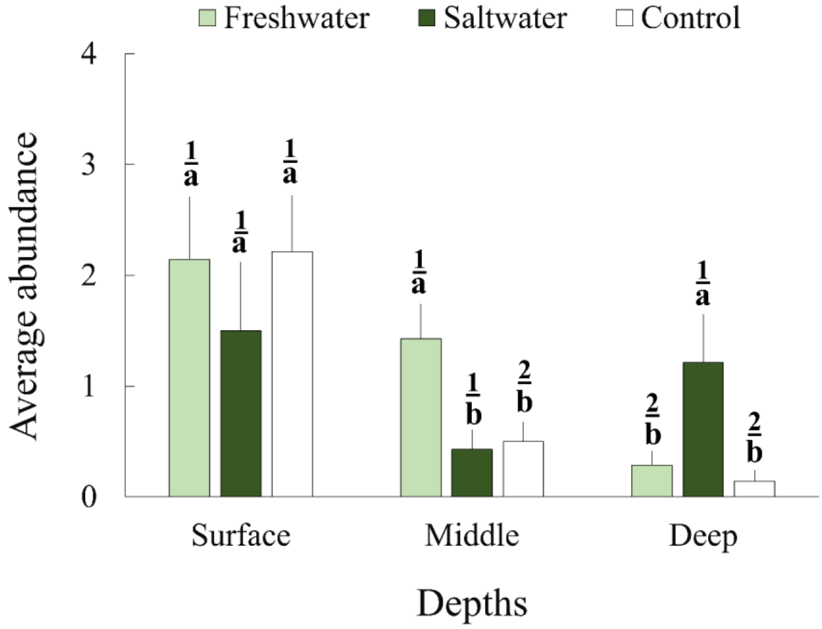

Figure 2.3. Average abundance (and standard error) of *Excirolana armata* per sample observed at three different sediment depths (Surface: between 0 and 3.5 cm; Middle: between 3.5 and 7.0 cm; Deep: between 7.0 and 20.0 cm) in the natural-density experiment. The experiment had three treatments: 1) simulated freshwater flooding (salinity = 0); 2) simulated saltwater flooding (salinity = 33); and 3) control, not manipulated (natural salinity ~ 25). Different letters indicate significant differences observed in the average abundance between the treatments: "a" represents abundance values significantly higher than "b", when comparing the treatments within each depth. The different numbers indicate significant differences observed in the average abundance between depths: "2" represents abundance values significantly lower than "1", when comparing the depths within each treatment. Pairwise comparisons from Tukey test (p<0.05).

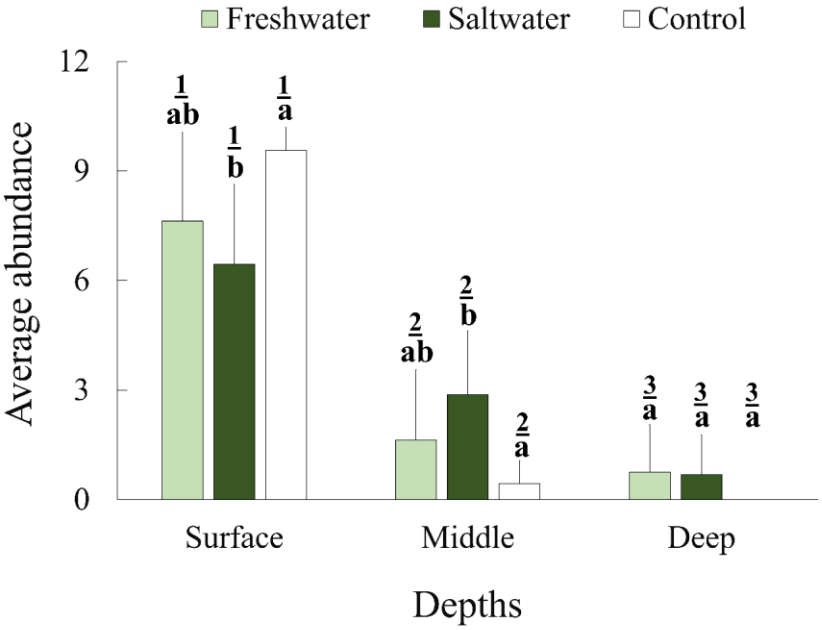

Figure 2.4. Average abundance (and standard error) of *Excirolana armata* per sample observed at three different sediment depths (Surface: between 0 and 3.5 cm; Middle: between 3.5 and 7.0 cm; Deep: between 7.0 and 20.0 cm) in the controlled-density experiment. The experiment had three treatments: 1) simulated freshwater flooding (salinity = 0); 2) simulated saltwater flooding (salinity = 33); and 3) control, not manipulated (natural salinity ~ 25). Different letters indicate significant differences observed in the average abundance when comparing the treatments within each depth: "a" represents abundance values significantly higher than "b"; “ab” represents intermediate values not different of “a” and “b”. The different numbers indicate significant differences observed

in the average abundance when comparing the depths within each treatment: "2" represents abundance values significantly lower than "1"; “3” represents values significantly lower than “1” and “2”. Pairwise comparisons from Tukey test ($p<0.05$).

2.4 | Discussion

Flood events significantly change the sedimentary environment of sandy beach ecosystems and are expected to influence benthic macrofauna behavior, especially the vertical displacement of organisms. However, this topic remains largely overlooked in sandy beach ecology. Our results provide empirical evidence that flood events are an important driver of the vertical distribution of benthic sandy beach fauna, with burrowing species moving from the surface to deep layers of the sediment when exposed to both natural tidal floods and experimental water inflow. Moreover, we showed that freshwater and saltwater inflows generated distinct effects on the vertical distribution, indicating distinct displacement responses for macrofauna in the face of different flood events.

The movement of macrofaunal organisms to deeper layers of the sediment under flood scenarios is likely associated with changes in sediment properties. During low tide or in treatments without flooding (control), macrofaunal organisms were concentrated in the surface sediment, which is a pattern that has already been registered in other beaches and tidal flats (Touhami et al. 2018; Celentano et al. 2019). Very fine sandy sediments, such as those in the study area, and low water content during the low tide period induce high sand compaction that can prevent organisms from accessing deeper sediment layers (Yannicelli et al. 2002). On the other hand, the water inflow at high tide increases the sediment water saturation and penetrability, thereby reducing the physical barriers that prevent vertical movement and favoring burrowing activity and the occupation of deeper sediment layers by macrofaunal species with high mobility (Sassa et al. 2011; 2014). This is the case for *Scolelepis* sp. (dominant species found) that can move vertically through tubes (Pardo & Amaral 2004) and for *Excirolana armata*, which has a greater displacement ability than congeneric species as *Excirolana braziliense*s (Yannicelli et al. 2001; 2002); these factors may have facilitated the vertical movements found here for these species.

The species recorded and tested here, however, depend on the ability to stay at the surface as they feed upon the organic material concentrated in the surficial sediment layer (Pardo & Amaral 2004; Bergamino et al. 2012). Thus, it is likely that the water inflow provides cues that force species to migrate towards deeper sediment layers to avoid unsuitable conditions, such as be caught by a rogue swash and find themselves exposed to passive transportation.

Moreover, on the sediment surface, macrofauna are exposed to aquatic predators at high tide, and the strategy of hiding in deeper sediments is a common defense adaptation already recorded for several species, such as fiddler crabs (e.g., Jennions et al. 2003; De Grande et al. 2018), hermit crabs (Kuhlmann 1992), beach gastropods (Phillips 1977; Checon et al. 2020) and isopods (Ejdung 1998). This may explain the downward migration observed here and the similarity between the effects of the natural tidal flood and the saltwater treatment in the experiments. However, our results are limited in proving such behavior, and experiments controlling sensory cues (i.e. with and without predator chemical cues) are needed to support this hypothesis.

Contrary to our expectations, the freshwater input generated a weaker displacement when compared to saltwater flooding. This result may be associated with activity reduction due to osmotic stress, a common effect registered for other beach crustaceans (Posey 1987). Nonetheless, Fanini et al. (2017) showed that salinity changes did not affect the behavior of *E. armata* (i.e., habitat choice), suggesting that this species has a strong physiological compensation mechanism. In this regard, the weaker downward movement of *E. armata* with freshwater floods may represent a response to avoid a moderate hydrodynamic turbulence in the surface sediment, which is common during rainfall and usually weaker than the turbulence promoted by saltwater floods (i.e. swash and rising tide).

Despite the differences between saltwater and freshwater input, both induced a downward vertical displacement in the macrofauna, suggesting the potential of tidal and rainfall floods to displace the organisms from the sediment surface. In the current environmental change scenario, sea level rise contributed to submerging larger areas of sandy beaches during the past decades (Orlando et al. 2019). Moreover, extreme weather events, including storms, would intensify beach erosion and coastal squeeze, especially in urbanized beaches subjected to coastal armoring (Dugan et al. 2008). This could first result in a response migration by some species towards the supratidal zone (Vanagt et al. 2008; Scapini et al. 2019). However, in urbanized beaches subjected to coastal squeeze, the horizontal migration of macrofauna is not possible due to the loss of the upper intertidal and supratidal habitats (Hubbard et al., 2013; Scapini et al. 2019). Based on our observations, macrofaunal species would be displaced to deeper sediment layers on these beaches, a fact that may change ecosystem processes such as bioturbation, connected to nutrient recycle and energy flux across coastal trophic food webs (Murray et al. 2017). Considering the importance of the sediment surface (the richest sediment layer in organic matter) for the feeding strategy of many sandy beach species, including the ones studied here, such effects can compromise their survival, growth and reproduction in the short term. In the long term, ecosystem service losses are a possibility considering that a strong reduction in biomass production would be expected. Furthermore, the presence of these organisms on the sediment surface during low tide periods represents a food source for predatory birds (Kuwae et al. 2010; Schlacher et al. 2017; Touhami et al. 2018). Based on our observations, a reduction in such availability is possible in long rainfall periods, potentially jeopardizing the biomass export service performed by the beaches.

In conclusion, our results show that both saltwater and freshwater floods can induce downward vertical movements of macrofaunal species within the sediment column. This change in the vertical distribution of sandy beach fauna could be a proxy for potential changes in important processes and services such as bioturbation and provision of food for coastal species in higher trophic levels. Yet, the long-term consequences of this short-term evidence have not been investigated and must be explored in future approaches. A second question arising is how these environmental and behavioral changes will combine with anthropic impacts such as coastal urbanization, which current strongly threaten sandy beaches. Further studies also should replicate our hypothesis with different species, different sediment types (i.e., beaches with coarse sand, where percolation is different) and different spatial-temporal scales. Overall, our findings reinforce that assessing macrofauna behaviors could be a promising approach to the development of wide perspectives and shed light on some ecological processes that are still poorly understood, with important implications for the beach functioning.

3. CHAPTER II: THE THREAT OF FRESHWATER INPUT ON SANDY BEACHES: A SMALL-SCALE APPROACH TO ASSESS MACROFAUNAL CHANGES RELATED TO SALINITY REDUCTION

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Abstract

Increased rainfall has become a key threat in recent decades for subtropical coastal regions. On sandy beaches that are associated with streams and rivers, the intensification of freshwater inputs is expected to reduce the salinity of interstitial waters and affect benthic biodiversity. Large freshwater gradients are promoted by river mouths and also change beach morphodynamic and sediment organic contents, which are covariates that have hindered the understanding of salinity-specific effects on benthic species in previous studies. Here, we aimed to assess how salinity reduction affects macrobenthic communities at small spatial scales to control the effects of environmental covariates. We assessed the macrofaunal spatial changes across few-meters gradients of freshwater influence (30 m) that were promoted by small streams (~2 m wide) within three subtropical beaches in southeastern Brazil. Our results showed that salinity was the only environmental factor that explained the macrofaunal variations across such small-scale gradients. We noted that salinity reductions decrease the overall macrobenthic abundance and richness in the first 15 m close to streams. Such variations are associated with changes in polychaete abundance (mainly *Scolelepis squamata*), which form larger patches with 1200 to 2800 individuals/m² only at sites with high salinity (greater than 25). We also found that a salinity reduction from 33 to 20 may promote a decrease of 85% in polychaete abundance near the streams. Nevertheless, salinity reductions did not affect crustacea abundance across the gradient. In the current global change context, these results suggest that freshwater input has great potential to impact polychaete patches, reduce macrobenthic biomass and secondary production and thus threaten important beach functions and services, such as bioturbation and food provision for the top predators.

Keywords: Climate change, benthic, rainfall, polychaeta patches, stream, *Scolelepis*.

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* *Published paper*: https://doi.org/10.1016/j.marenvres.2021.105459

3.1 Introduction

Environmental changes in sandy beaches currently occur all over the world and have great potential to impact the resident biodiversity and ecosystem services provided (Schoeman et al. 2014; Amaral et al. 2016). For instance, freshwater input on sandy beaches that is related to estuaries, streams or drainage canals can change the physical environment and consequently influence the intertidal macrobenthic populations and communities (Lercari et al. 2002; Lercari & Defeo 2003; 2006; 2015). In the current global change scenario, increased rainfall and storms are predicted for some subtropical regions (Marengo et al. 2010; Bernardino et al. 2015; Cavalcanti et al. 2017; IPCC 2021). Despite the globally predicted sea level rise and groundwater salinization (Vineis et al. 2011), these regions would experience different salinity changes depending on their spatial scales and associated processes, such as river outflow at the beaches. At local scales, the increased rainfall can increase freshwater input and promote salinity reductions at sandy beach sites that are associated with intermittent drainage and river discharges (McLachlan & Turner 1994; Cisneros et al. 2011; Scapini et al. 2019). Thus, the changes in freshwater input and salinity could represent key threats to the biodiversity and services of sandy beaches, which need further attention in the current global change context.

By definition, a natural or anthropogenic process with potential to impact a species or an ecosystem target, causing degradation or other environmental impairment (in the present or in the future) could be considered a threat (Salafsky et al. 2008; Bland et al. 2017). Salinity reduction that is promoted by freshwater input on sandy beaches, therefore, could be a threat for these ecosystems since salinity is indicated as a determinant driver for macrofaunal changes in some cases (Lercari et al. 2002; Lercari & Defeo 2003; 2006). At the individual level, salinity reductions can change macrofaunal behaviors such as habitat choice and vertical displacement within the sediment (Fanini et al. 2012; Laurino et al. 2020a) and promote osmotic stress and increased mortality in less tolerant species (Felder 1978; Charmantier & Charmantier-Daures 1994). At the population and community levels, salinity reductions can impact macrofaunal abundances and richness (Lercari & Defeo 2006; Orlando et al. 2020) and change population structures (Lercari & Defeo 1999) and species compositions (Bergamino et al. 2009). Salinity also affects sandy beach functions at the ecosystem level, as reductions in biomass production and predator abundance are observed for low-salinity sites (Jorge-Romero et al. 2019).

However, assessing the effects of freshwater input on sandy beaches can be misleading since salinity reductions are autocorrelated with the changes in beach morphodynamics and food supplies for macrobenthic communities. Freshwater inflow could promote sediment deposition or erosion by changing the mean grain sizes and beach face slopes, which are parameters that are strongly related to macrofaunal richness and abundance (Santos et al. 1991; Lercari & Defeo 2006; Chaouti et al. 2008). Furthermore, freshwater sources can improve food availability (e.g., organic matter) for macrofaunal species (Chaouti et al. 2008; Bergamino et al. 2012) and also influence their occurrence and abundance (Bergamino et al. 2009; Cisneros et al. 2011). Freshwater input on beaches is thus connected to a complex range of environmental changes that makes it challenging to identify whether the macrofaunal changes are actually related to salinity reductions or to a combination of the effects of the autocorrelated environmental parameters.

Here, we are interested in evaluating the specific effects of salinity reduction on the ecological patterns of sandy beach intertidal macrofauna, decreasing the multiple effects of the correlated drivers by using a small-scale approach. In fact, observations at different spatial scales can improve the assessment of distinct environmental parameters and their effects on sandy beach macrofauna (Defeo et al. 1997). Considering the freshwater input, large-scale approaches that have used river gradients across scales of kilometers are useful to understand the integrated effects of salinity and morphodynamic changes on macrofauna. According to Lercari & Defeo (2006), species richness and abundance levels are lower close to river mouths because the beach slopes are steeper and the salinities are lower compared to more distant sites. Other approaches that use gradients with smaller scales (e.g., hundreds of meters), in turn, can manage the morphodynamic spatial variations and can be used to provide a better understanding of the relationship between salinity and macrofauna. At this scale, Gandara-Martins et al. (2015) noted an increase in species richness and abundance with the salinity increase at sites more distant from a washout, but the morphodynamic conditions were relatively stable only in the first meters of the gradient. For more distant sites, the sediment grain sizes tended to be coarser, and the macrofaunal abundance and diversity tended to decrease (Gandara-Martins et al. 2015).

Considering this background, small-scale approaches that use a spatial gradient of freshwater influence of few meters (10-30 m) seem to be an appropriate strategy to understand the specific relationships between salinity and macrofaunal changes. This is especially true given that the gradients that are formed by small streams (~2 m wide), which could promote sudden changes in salinity across a few meters without altering the morphodynamic and organic supply of the surroundings. Such approaches could therefore support predictions of the ecological impacts of future freshwater input and local salinity reductions on sandy beach ecosystems due to both freshwater flooding and outcrops of low salinity groundwater. In this context, we aimed to assess how salinity reductions that are connected to freshwater input on subtropical sandy beaches affect macrofaunal patterns using a small-scale approach. Specifically, we aimed to evaluate the variations in the intertidal macrofaunal community for gradients of tens of meters of freshwater influence that are promoted by small streams flowing across the beach. We expected that the effects of salinity changes in the macrofauna would be evidenced at this small scale, where the morphodynamics and organic supplies would have smaller variations (and effects) than the salinities across the gradient. Then, considering this scale, we hypothesized that the macrofaunal richness and abundance would be negatively affected by salinity reductions, with significant decreases present closer to streams.

3.2 Materials and methods

3.2.1 Study area

The southeastern coast of Brazil contains subtropical sandy beaches that are strongly threatened by the current global environmental changes, where increases in total rainfall and freshwater input are predicted for the coming years (Marengo et al. 2010; Bernardino et al. 2015; IPCC 2021). In fact, the 2020 rainy period (February) had the greatest recorded rainfall in the coastal cities of this region (e.g., ~900 mm in 30 days, INMET 2020). The north coast of São Paulo, in particular, has a variety of sandy beaches that are associated with freshwater sources, such as manmade or natural drainage channels. These sources cause them to be highly vulnerable to the current increases in rainfall and, consequently, freshwater input. Based on this, we chose the northern coast of São Paulo, southeastern Brazil, as a model area for the present study (Fig. 3.1-A and B).

Specifically, three sandy beaches were selected for the study: Boracéia, Baleia and Dura (Fig. 3.1-C). All of them are microtidal (tidal range < 2 m) dissipative beaches, with wide and flat beach profiles (~ 130 m) and predominance of fine sediments (De Mahiques et al. 2016). Each beach selected has similar small freshwater streams (e.g., ~ 2 m wide; ~ 7 cm deep) that permanently flow across the beach, and can represent an appropriate model of freshwater input within the spatial scale of tens of meters (Fig. 3.1-D).

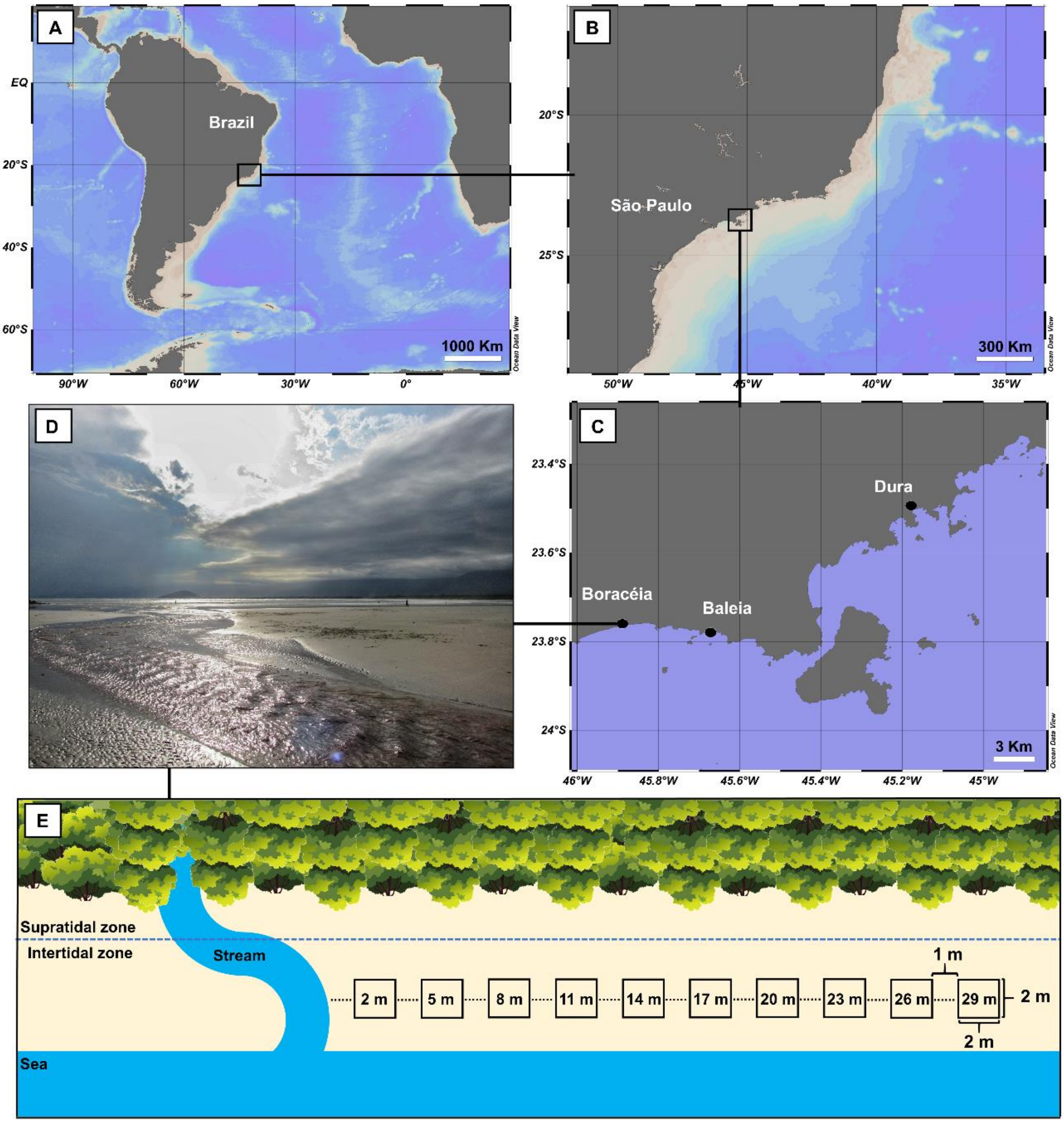

Figure 3.1. Study area and sampling design. **A)** South America, with southeastern Brazil highlighted; **B)** Southeastern Brazil, with the northern coast of São Paulo highlighted; **C)** Northern coast of São Paulo, with the three subtropical sandy beaches that were selected for sampling; **D)** Photographic record of the freshwater stream that is located on Boracéia Beach; **E)** Scheme of the applied sampling design with the ten sampling sites (2 x 2 m quadrats) and their respective distances from the stream (scheme out of scale).

3.2.2 Sampling and laboratory procedures

At the three beaches selected, we established a rectangular sampling area 30 m long (parallel to the shoreline) and 2 m wide (perpendicular to the shoreline) at the middle intertidal zone of adjacent to the stream. We considered the middle intertidal zone as the central area between the spring low-tide line (on the border with the subtidal zone) and the spring high-tide line (on the border with the supratidal zone). Within this area, ten sampling sites (2 x 2 m quadrats 1 m apart) were established across a distance gradient from the stream that were toward the southwest and parallel to the shoreline (Fig. 3.1-E). The midpoints of each sampling site were located at distances from the stream that were 2 m, 5 m, 8 m, 11 m, 14 m, 17 m, 20 m, 23 m, 26 m and 29 m (Fig. 3.1-E).

We first characterized the salinity gradients that were induced by each stream for the three selected beaches by performing salinity measurements of the interstitial waters of the sediments across the sampling sites. We started taking measurements from near the edge of the stream (first site, 2 m distant), which aimed to assess the spatial limits of the freshwater percolation of the surroundings of the streams across the total extent of the sampling area (until the last site, 29 m distant). In this step, we sampled the sediment interstitial water by suction using a syringe that was connected to a tube with a filtering stone at the end, which was in contact with the sediment surface (~ 5 cm deep, three random subsamples per site). Immediately after sampling, we measured the salinity of each subsample with an optical refractometer (accuracy of 0.5) and determined the salinity value for each site, which was the average of the subsamples.

Simultaneously, we measured the beach slope at each sampling site by using two rulers and a measuring tape (following Emery 1961). Next, we collected one sediment sample per site and froze for further laboratory analyses of grain size and organic matter content. Finally, we obtained three random replicates of macrofaunal samples (sampling units) at each site, which totaled 30 samples per beach (90 samples in total). Each sample was collected using a cylindrical PVC corer with dimensions of 15 x 20 cm (diameter x depth). All of the described sampling procedures occurred across three days during the peak of the spring low tide (daytime) in September 2020 with a quasi-synoptic approach, without rain between the sampling days.

The macrofauna samples were sieved with a set of two overlapping sieves (1.0 and 0.5 mm mesh). The retained species were preserved in 70% alcohol until identification to the lowest possible taxonomic level. In the laboratory, the sediment samples were defrosted, dried (60°C for 48 h) and weighed. Grain size analysis was performed by sieving the dry sediment following the procedure of Suguio (1973) and Folk and Ward (1957). Then, we measured the organic matter content of the sediment by assessing the weight loss of the dried sediment after incineration (550 °C for 6 h).

3.2.3 Data analysis

We used linear mixed models (GLMMs) to evaluate the relationships among the macrofaunal patterns and environmental parameters across the assessed gradients. First, we applied a model that was adjusted to the negative binomial family (logarithmic linking function), which is suitable for count data with overdispersion (Bolker 2008), by using the total abundance per sampling unit as the response variable. Then, using species richness per sampling unit as the response variable, we applied a second linear mixed model that was adjusted to the Gaussian family (identity linking function), which was better adjusted than negative binomial or Poisson distributions for this case when considering the Akaike Information Criterion (AIC). Next, we performed a GLMM (negative binomial) that was specific to the abundance of each principal taxonomic group found, which aimed to evaluate the possible relationships among the environmental parameters and specific macrofaunal groups.

The environmental parameters that were considered as predictors (fixed factors) in all models were the salinity of the interstitial sediment water, sediment organic content and beach morphodynamics, which were assessed through the Beach Index (BI). We calculated the BI of each sampling site for use in the models as a morphodynamic indicator by considering the grain sizes and beach slopes that were measured for each sampling site (following McLachlan and Dorvlo 2005). Therefore, low BI values indicate sampling sites with high hydrodynamism (high energy), which are characterized by coarser sediments and steeper slopes (McLachlan and Dorvlo 2005). We included the categorical covariable "beach" (three levels that were associated with the three beaches) as a random factor to consider the possible differences among beaches in the models. We chose to use "beach" as a random factor (and not a fixed factor) because we were interested in investigating a general pattern that was stronger than the variations among the beaches. For this reason, the beaches were selected as replicas with standardized morphodynamic features and similar streams.

To evaluate the effect of each environmental parameter on the macrofaunal patterns, we applied the likelihood ratio test (LRT) with the chi-square statistic for each model. The LRT compared the full model (including all predictors) with the reduced models (excluding the predictor of interest) to assess which predictors provided significant losses of model likelihood when excluded from the full model (considering $p<0.05$). We also calculated the AIC for each model (both full and reduced models) to assess their fits with and without the different predictors tested.

For the macrofaunal groups that exhibited significant relationships with salinity, we used a probabilistic distribution model that was adjusted to the negative binomial family. In this step, we evaluated the cumulative probability (upper tail) to find the specific intervals of abundance values in scenarios with different salinities. We constructed probabilistic curves for the scenarios with salinities equal to 33, 30, 27, 25, 22, 19, and 16 by evaluating the probability of finding abundance values between 0 and 50 individuals per sample (i.e., between 0 and 2825 individuals/m^2) in the different salinity scenarios. The model parameters were estimated by the maximum likelihood method using the negative log-likelihood function (Bolker 2008). We perform all data analysis using the open software R and the packages "lme4", "MASS" and "bbmle" (script available as supplementary material - Appendix A).

3.3 Results

We observed salinity gradients for the adjacencies of the streams by considering the three sampled beaches; the lowest mean values were observed close to the streams and highest mean values were found far from the streams (Fig. 3.2). Specifically, the salinity gradients varied between 9 and 30 on Boracéia Beach, between 1 and 35 on Baleia Beach and between 6 and 35 on Dura Beach. On average, we noted that salinity was usually ~4.5 times greater when comparing the farthest site (29 m) with the closest site (2 m). The mean values of the Beach Index (BI) tended to be slightly lower at sites that were farther from the streams than at sites closer to the streams. In general, we observed that the BI values decreased by ~5% from the closest site to the farthest site of the streams (Fig. 3.2). Higher values of sediment organic content were observed at the three sites that were far from the streams, which represented an increase of ~30% when comparing the closest site with the farthest site. Nevertheless, nonlinear variations were generally observed for the organic contents across the sites (Fig. 3.2).

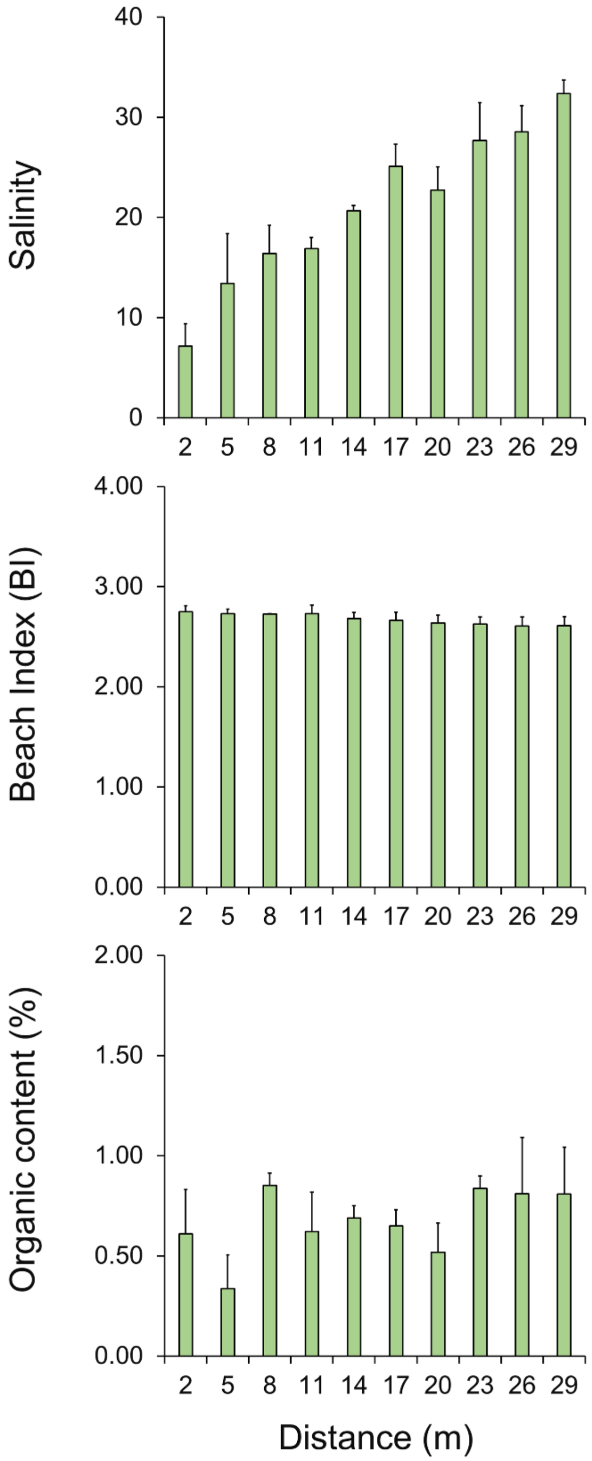

Figure 3.2. Salinities of the sediment interstitial waters, beach index and sediment organic contents that were recorded on the adjacencies of the small freshwater streams that flow on three beaches of southeastern Brazil (mean ± standard error between the tree beaches). The midpoints of the ten sampling sites (2 x 2 m quadrats, 1 m apart) were located at different distances from the streams: 2, 5, 8, 11, 14, 17, 20, 23, 26 and 29 m from the streams.

With regard to the intertidal macrofauna, we found a total of seven species and 543 individuals when considering the three beaches and all assessed sampling sites. Polychaeta were the dominant group, with four species (e.g., *Scolelepis squamata*, *Hemipodia californiensis,* *Ophelina cylindricaudata* and *Glycera* sp.) and 364 individuals in total and were followed by crustacea with two isopod species (e.g., *Excirolana armata* and *Excirolana braziliensis*) and 177 individuals in total. Mollusca was the least-observed group, with only two individuals of the bivalvia *Donax hanleyanus*. The Boracéia beach exhibited the highest abundance values, with 381 individuals (e.g., 280 polychaetas, 99 crustaceans and 2 molluskans), and was followed by Dura (102 individuals; 64 polychaetas and 38 crustaceans) and Baleia (60 individuals; 20 polychaetas and 40 crustaceans). In general, the polychaeta *S. squamata* was strongly dominant in its abundance (total: 340 individuals) and was followed by the crustacea *Excirolana armata* (total: 160 individuals).

We observed that the community abundances and richness varied across the sampling sites, with low mean values usually found closer to the streams (Fig. 3.3). For instance, in the first 15 m nearest the streams, the abundances reached a maximum of 621 individuals/m², while 15 m farther from the streams, we found abundances that reached a maximum of 2938 individuals/m². Similarly, the sampling units with three or more species were usually found between 15-30 m from the streams, considering that polychaeta species such as *Hemipodia californiensis*, *Ophelina cylindricaudata* and *Glycera* sp. were rarely found on the first 20 m from the streams. In fact, polychaeta was the main group responsible for the variations in the macrofaunal communities across the sites, given that this group showed an abrupt increase in abundance (principally related to *Scolelepis squamata*) between 15-30 m from the streams. On the other hand, crustacea showed low abundance variations across the sites, and the two isopod species were found across all gradients (Fig. 3.4).

Salinity was the environmental factor that explained the variations in macrofaunal patterns adjacent to the streams (Tab. 3.1). We noted that the community abundances and richness were positively related to increases in salinity. This positive relationship was also observed for the polychaeta abundances, while the crustacea abundances were not affected by the salinity gradients (Tab. 3.1; Fig. 3.4). We also observed that the abundances of the main faunistic groups (polychaeta and crustacea) varied among the beaches, although such differences were not reflected by distinct community abundances or richness between the beaches (Tab. 3.1).

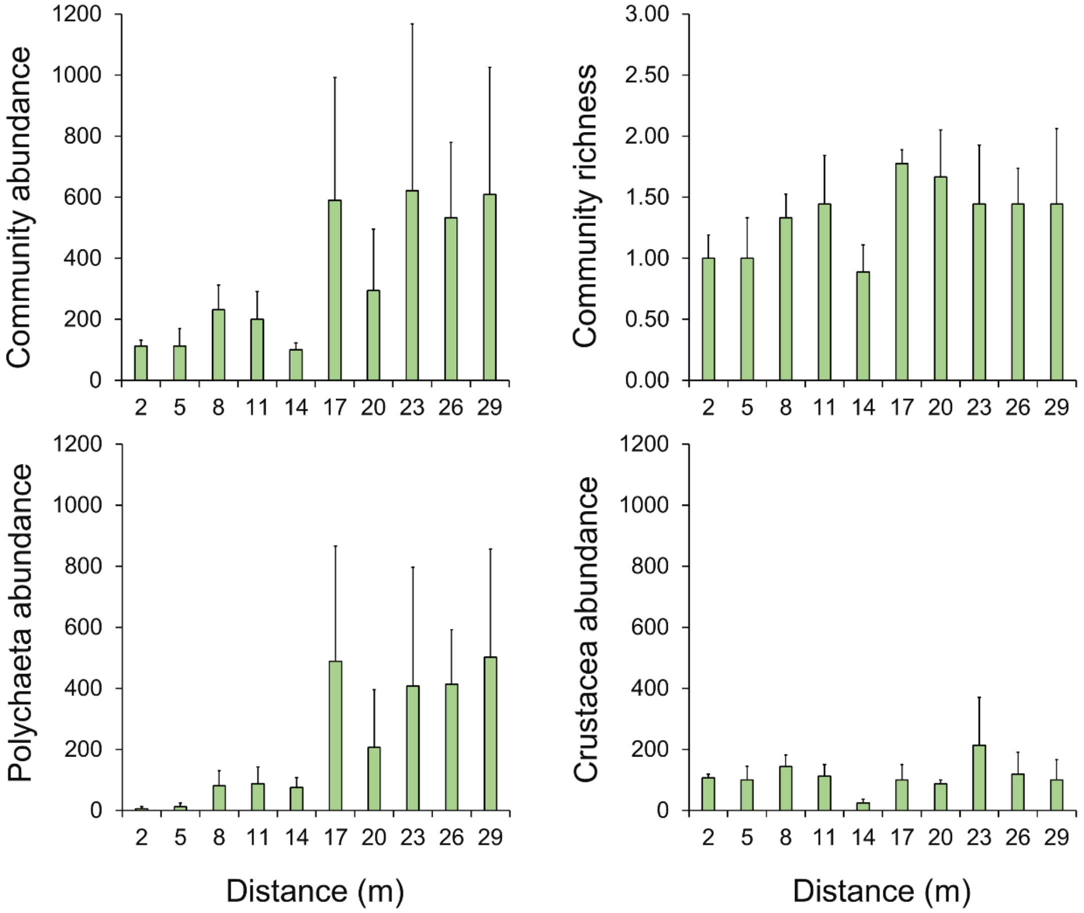

Figure 3.3. Macrofaunal community abundance (individuals/m^2) and species richness (species per sample unit) and polychaeta and crustacea abundances (individuals/m^2) that were recorded at the adjacencies of small freshwater streams that flow to three beaches of southeastern Brazil. The values are the mean ± standard error considering three replicates per site of each beach (n = 9 per site, in total). The midpoints of the ten sampling sites (2 x 2 m quadrats, 1 m apart) were located at different distances from the streams: 2, 5, 8, 11, 14, 17, 20, 23, 26 and 29 m from the stream.

The relationship between polychaeta abundance and salinity is not linear but appears as an exponential curve with an abrupt abundance increase for salinities greater than 25 (Fig. 3.4). In this regard, the samples with large peaks in polychaeta abundances, considering 1200 individuals/m^2 or more, were obtained only at sites with salinities greater than 25 (Fig. 3.4). Furthermore, a salinity reduction from 33 to 20 (i.e., at 29 m to 14 m distant from the stream) was accompanied by a decrease of ~85% in the polychaete abundances in this area of influence (Fig. 3.3; Fig. 3.4).

Table 3.1. Generalized linear mixed models (GLMMs) applied to test the effects of multiple predictors (environmental drivers) on the macrofaunal patterns across small-scale gradients of freshwater influence by considering the small freshwater streams (~2 m wide) that flow on three beaches of southeastern Brazil. The response variables tested were community abundance, species richness and polychaeta and crustacea abundances. The fixed factors considered predictors were the salinity of the sediment interstitial water, sediment organic content and beach morphodynamics (beach index), while "beach" was the random factor (three levels). For each predictor, the Akaike Information Criterion (AIC), the chi-square statistic (Chi) of the likelihood ratio test and the p-value of the test (in bold when significant) are presented.

Community	**Abundance**			**Richness**		
	AIC	**Chi**	**p**	**AIC**	**Chi**	**p**
Full Model	480.70	-	-	229.99	-	-
Salinity	485.43	6.73	**0.009**	232.44	4.45	**0.035**
Organic Content	478.73	0.03	0.866	231.49	3.50	0.061
Beach Index (BI)	478.74	0.03	0.852	228.07	0.08	0.783
Beach (random)	481.42	2.72	0.099	230.45	2.74	0.098

Groups	**Polychaeta**			**Crustacea**		
	AIC	**Chi**	**p**	**AIC**	**Chi**	**p**
Full Model	342.51	-	-	343.76	-	-
Salinity	356.47	15.96	**<0.001**	342.97	1.22	0.270
Organic Content	340.54	0.03	0.868	342.03	0.27	0.602
Beach Index (BI)	343.47	2.96	0.085	343.06	1.30	0.254
Beach (random)	344.41	4.76	**0.029**	347.03	5.27	**0.022**

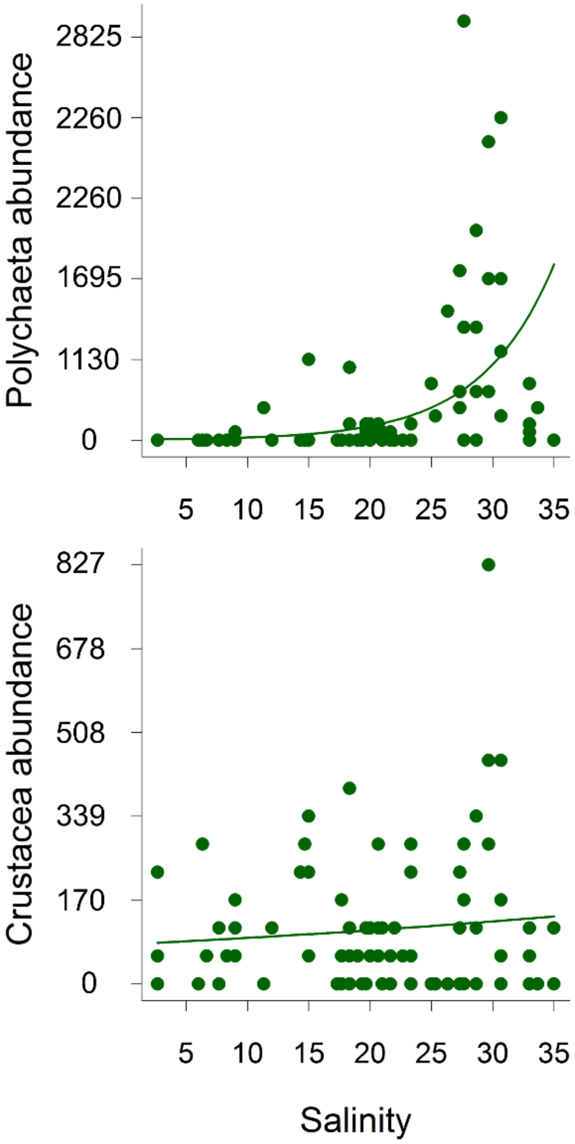

Figure 3.4. Relationships among the polychaeta and crustacea abundances and salinity of the sediment interstitial water that were recorded on the adjacencies of small freshwater streams that flow on three beaches in southeastern Brazil. The green dots represent the observed abundances per sample unit (converted to individuals/m^2), and the green line represents the abundances predicted by the models (negative binomial family).

Accordingly, in the probabilistic curves created, we observed that the probabilities of finding larger values of polychaeta abundances were higher in the scenarios with higher salinities (Fig. 3.5). For instance, the probability of finding 565 or more polychaetas/m² was approximately 25% for the scenario with salinity equal to 30, while for the scenario with salinity equal to 25, this probability decreased by half (Fig. 3.5). Additionally, we observed that the probability of finding large patches of polychaetas (with 2260 individual/m² or more) dropped to near zero for the scenarios with salinities lower than 30 (Fig. 3.5).

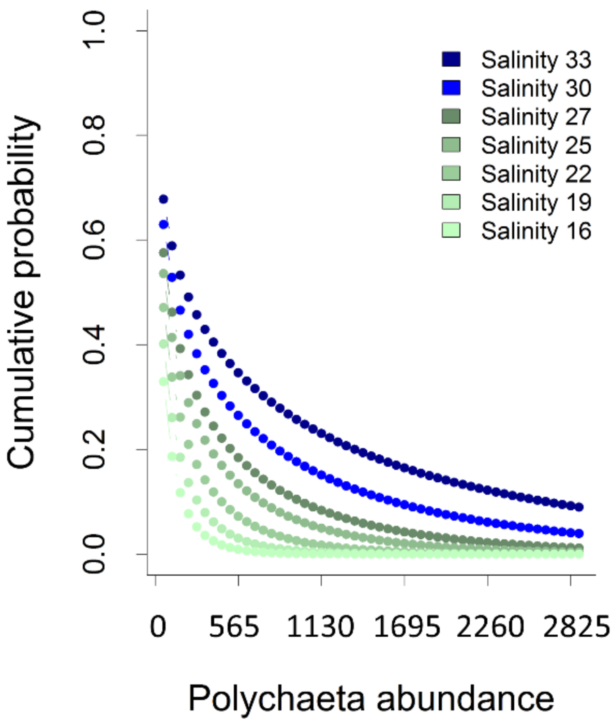

Figure 3.5. Cumulative probability curves (upper tail) showing the probabilities of finding specific intervals of polychaeta abundance values (between 0 and 2825 individual/m²) in different salinity scenarios (salinities between 33 and 16). The curves were calculated from a probabilistic distribution model that was based on the collected data and adjusted to the negative binomial family, with parameters that were estimated by the maximum likelihood method.

3.4 Discussion

We hypothesized that the salinity reductions promoted by freshwater inputs on sandy beaches would negatively affect the abundances and richness of the macrobenthic communities. In fact, at a small spatial scale, we observed that salinity was the only driver that influenced macrofaunal patterns, while the morphodynamic and organic matter factors did not have any effects. We observed that the community abundances and richness decreased with salinity reductions, which corroborates our hypothesis. Such changes are mainly due to the polychaetes, which form large patches with 1200 to 2800 individuals/m² only for sites with high salinities (greater than 25). Therefore, our results indicated that salinity reductions have the potential to decrease the community species richness and probability of polychaetes forming high-abundance patches on the studied beaches.

The polychaeta patches that were under high salinity that were found in this study were mainly associated with the species *Scolelepis squamata*. This species and others of the same genus are common on Atlantic beaches and are known to be tolerant to salinity variations (Rizzo & Amaral 2001; Ocaña et al. 2020). For instance, Santos et al. (1991) revealed that *Scolelepis* *gaucha* occurred at different salinities on a beach in southern Brazil but tends to show lower abundances close to streams. The cited study mentions that this species can be twice as abundant in areas with salinities between 24 and 30 when compared to areas with salinities between 14 and 24. However, the authors claim that these differences are not associated with salinity but rather are associated with morphodynamic variations that are related to stream erosion (Santos et al. 1991). Additionally, patches of *Scolelepis* can also be observed in areas with moderate freshwater influence (salinity ~20) on the beaches of Uruguay, although such peaks in abundance are explained by the high levels of organic matter in the area and not by salinity (Bergamino et al. 2009). Based on our data, by comparing sites with similar morphodynamics and low variations in organic matter, reduced salinity was demonstrated to be a key driver that controlled *Scolelepis* abundances and polychaete patch formation. Even though we found this species across almost the entire salinity gradient, which confirmed its expected salinity tolerance, high salinities seem to favor the success of recruitment (and/or individual survival) by generating hot spots of abundance. The same is valid for the other polychaeta species that were observed in the studied beaches, which were mainly found in sites with high salinity. Therefore, our results demonstrated the potential of freshwater input to impact species richness in polychaeta assemblages, which clarifies the results of other studies (Lercari & Defeo 2003; Bergamino et al. 2009) and highlights the specific impacts of decreased salinity on the abundance and generation of patches.

On the other hand, the crustaceans, which were mainly represented by the isopod *Excirolana armata* on the beaches assessed here, did not change their abundances in response to salinity reductions. Previous evidence has revealed that this isopod can occur with low abundances and biomass in sites under reduced salinity (Lozoya & Defeo 2006; 2010; Fanini et al. 2017). Conversely, *E. armata* was also demonstrated to be the dominant species at sites close to freshwater sources (Gandara-Martins et al. 2015), which could be related to the terrestrial organic provisions that are usually important for its diet (Bergamino et al. 2012). Moreover, *E. armata* is a highly substrate-specific species that is not well adapted to high-energy conditions with coarser sediments (Defeo et al. 1997; Lozoya & Defeo 2010). As a result, its higher tolerance to changes in other parameters, such as salinity, may ensure the maintenance of *E. armata* (Lozoya & Defeo 2010; Fanini et al. 2017). This could be the explanation for the pattern noted in this study, given that *E. armata* occurred across all sampling gradients despite the salinity changes. This adaptation may also be related to the life-history traits of the species, such as the presence of carapaces and egg brooding, which could favor osmotic control and the survival of recruits (Lozoya & Defeo 2006). Based on these factors, in conditions with no morphodynamic or organic content changes, freshwater inputs that are followed by salinity reduction do not seem to be a threat to this species.

Considering our results and the increased rainfall scenario for the study area (Marengo et al. 2010; IPCC 2021), beaches with freshwater sources could impact their macrobenthic communities due to possible future freshwater floods and groundwater outcrops. The increased freshwater flow of sources such as rivers will cause site-dependent changes (Bernardino et al. 2015), which make it difficult to project how much the salinity levels that are associated with each freshwater source would decrease for each beach. Despite these uncertainties, our results suggested that small salinity changes can result in large decreases in polychaeta abundances. We showed that any salinity value below 30 drastically reduced the probability of finding polychaete patches (Fig. 3.5). Furthermore, the streams evaluated here showed, on average, freshwater percolation with the potential to reduce the salinity by 13 units (from 33 to 20) for distances up to 15 m from the streams. These salinity reductions were accompanied by a decrease of ~85% in polychaete abundances.

To understand the potential consequences of such changes, let us consider Boracéia as an example, which is a beach strongly dominated by polychaetes. It is possible to find approximately 35 small streams (intermittent or permanent) across its entire extension (8000 m). Given that each stream reduces the salinity by 13 units for 15 m and, speculating that this effect is similar on both sides of the stream (summing a total of 30 m of influence per stream), a total of 1050 m of the beach extension, equivalent to 13.12% of the beach, could currently be losing 85% of its polychaete abundance. This simple exploratory estimation illustrates how small streams could be impactful at beach scales. However, the southeastern Brazil is characterized by a rainy season between November and April (Bernardino et al. 2015), period not encompassed on our sampling approach. The rainy season can have more than the triple of the rainfall volume than the dry period here evaluated (Laurino et al. 2020b). Thus, this effect can be intensified considering that the streams are dynamic and change their flows and along-shore reaches depending on rainfall regimes. A scenario in which there is higher pluviosity in the rainy season and/or the rainy period is longer throughout the year would amplify such effects. In this sense, future studies considering the temporal scale, with replication during the dry and rainy seasons, across several years and different streams, are needed to complement our finds and improve these estimations.

The increased rainfall that is associated with salinity reductions could thus place the polychaete patches on beaches that are associated with artificial or natural freshwater sources at risk. Polychaete patches, mainly those associated with *Scolelepis*, are responsible for high biological production on the sandy beaches where they occur (Santos 1994) and serve as an important food source for fishes and birds (Speybroeck et al. 2007; Van Tomme et al. 2014). Moreover, the presence of *Scolelepis* patches can facilitate colonization by other species, such as non-opportunistic nematodes (Maria et al. 2011). The periodic vertical movements exhibited by *Scolelepis* within sediments that are related to tidal cycles (Laurino et al. 2020a) and its feeding behavior alternations from deposit feeder to suspensive feeder (Pardo & Amaral 2004) foster bioturbation and organic flux in the beaches. Therefore, a decrease in polychaete patches could promote significant changes in beach functioning and services, which must be investigated in future upscaling approaches aiming understand these possible risks not assessed here. To this end, future investigations also could explore the recovery time and the tolerance of *Scolelepis* to salinity changes in different temporal scales, aiming verify if the effects here observed are equal for intermittent and permanent water flows, and if they last per days or years.

In summary, we conclude that salinity reductions have great potential to decrease macrobenthic richness and abundance by reducing the probability of polychaetes forming patches on subtropical sandy beaches. In this regard, our approach could be replicated in other regions to better explore these relationships with other species and for other beach types. In a climate change context, our findings provide an alert for subtropical beaches with freshwater sources in regions with predicted rainfall increases, point out the potential risks of salinity reduction to the biodiversity parameters that are strongly connected to ecosystem functions and services. This potential risks also need to be formal analyzed in future approaches, considering the temporal dimension and other ecosystem components, such as the meiofauna and fishes communities. This is important based in the fact that freshwater inputs also can promote positive changes as the nutrient and organic matter supply for the beach (e.g. Bergamino et al. 2012); thus it could be a potential threat for some species or groups, but not for others. We also call special attention to the risks of constructing artificial freshwater sources (urban drains) on sandy beaches, which is an action that could intensify the predicted climate change impacts. Finally, we emphasize that small-scale approaches are useful to understand the relationships among biodiversity and specific drivers, which can generate insights for understanding the potential impacts of climate change in coastal ecosystems.

4. CHAPTER III: DOES COASTAL ARMORING AFFECT BIODIVERSITY AND ITS FUNCTIONAL COMPOSITION ON SANDY BEACHES?

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Abstract

Sandy beaches are increasingly squeezed due to the construction of backshore man-made structures (i.e., coastal armoring) and current global changes. Coastal armoring impacts beach sediment dynamics, inducing erosion and habitat loss, threatening biodiversity processes and the functional roles of sandy beach organisms. Here, we examine how the abundance, taxonomic richness, and functional richness of sandy beach fauna are affected by coastal armoring. We compared macrobenthic infaunal communities on five armored beaches (with backshore urban structures) and five vegetated beaches (not-armored). We also evaluated the abundance and biomass of upper-beach arthropods using pitfall traps, comparing armored and vegetated segments within the beaches. Infaunal richness and abundance were lower at armored beaches, mainly in the subtidal zones, because of a reduction in polychaete and molluscan abundance. There was no difference in overall functional richness between the armored and vegetated beaches. Nevertheless, we found that functional groups such as small suspension feeders were more associated with armored beaches, while large-bodied species and predators were more frequent at vegetated beaches. Pitfall traps showed that coastal armoring also reduced the abundance of the upper-beach coleopteran Phaleria testacea, leading to a loss of biomass. Therefore, our data suggest that coastal armoring can influence the functional composition of sandy beach biodiversity and significantly impact macrobenthic abundance and biomass.

Keywords: Coastal squeeze; benthic macrofauna; sea-level rise; functional traits; seawall.

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* *Unpublished paper*

4.1 Introduction

Sandy beaches are one of the most used and valued ecosystems by human society, representing 31% of the world's ice-free shoreline (Luijendijk et al. 2018). More people use sandy beaches than any other coastal ecosystem, and they sustain many economies worldwide, owing to activities such as tourism and fisheries (Klein et al. 2004, Schlacher et al. 2007). Beach ecosystems also shelter unique biodiversity that maintains essential functions and services such as nutrient cycling, food provision, and coastal protection (Schlacher et al. 2008; Amaral et al. 2016). However, increasing coastal urbanization and the current climate change scenario have raised concerns regarding the sustainability of beach ecosystems, including their biodiversity (Schoeman et al. 2014; Luijendijk et al. 2018; Defeo et al. 2021).

The projected sea-level rise and increased frequency and intensity of extreme storm events are expected to submerge and erode a substantial proportion of the world's sandy coastline, possibly leading to the disappearance of half the world's beaches (Vousdoukas et al. 2020). This global scenario combines with local pressure from coastal urbanization, which modifies the environmental characteristics of sandy beaches and negatively affects their biodiversity (Costa & Zalmon 2017; Costa et al. 2020; Orlando et al. 2020), thereby impairing beach ecosystem function in the short and long term (Reyes-Martínez et al. 2015; Schooler et al. 2017; 2019). Understanding how these global (e.g., climate change effects) and local (e.g., urbanization) impacts can affect beach biodiversity is therefore a key challenging step to supporting management and conservation strategies (Turra et al. 2013; Defeo et al. 2021).

Over the past few decades, the sea level has been rising worldwide at a rate of 2.9 mm per year since 1993 and could reach an average global increase of 65 cm by 2100 (Nerem et al. 2018). This increase may lead to coastline retraction exceeding 100 m by the end of the century in some regions, such as the southeastern coast of South America (Vousdoukas et al. 2020). Extreme storm events are also expected to increase in intensity and frequency in the coming years (Elsner et al. 2008; Lin & Emanuel 2016), potentializing beach erosion and retraction and modifying biodiversity patterns (Corte et al. 2017). Nevertheless, sandy beaches have the adaptive capacity to migrate landward, if they provide appropriate space associated with a natural backshore. Without artificial barriers, the natural sediment transportation across the beach-dunes system is maintained and the beach can migrate landward as the sea level rises (Slott et al. 2006; Cooper et al. 2020). The removal of backshore natural habitats and construction of man-made structures such as roads and seawalls, however, affect the natural dynamics of the littoral active zone (LAZ) (Dethier et al. 2016) and prevent sandy beach migration. As a result, these changed sandy beaches become trapped in a coastal squeeze scenario, which may lead to the loss of their intertidal and upper habitats (Scapini et al. 2019; Defeo et al. 2021).

In this context, the construction of man-made coastal structures (i.e., seawalls, bulkheads, and groins), a process called coastal armoring, has been highlighted as a great source of impact on sandy beaches and their biodiversity, especially for benthic resident species (Walker et al. 2008; Nourisson et al. 2018; Jaramillo et al. 2021). Coastal armoring changes beach sediment dynamics, inducing erosion and habitat loss, which is usually followed by a reduction in the number of individuals of macrofaunal species, mainly in the upper intertidal and supratidal zones (Dugan et al. 2008; 2018; Jaramillo et al. 2021). These impacts are likely prominent for supratidal arthropod fauna since backshore artificial structures may replace upper-beach habitats essential for populations of this group (Lucrezi et al. 2009; Bessa et al. 2013; Costa et al. 2022). The combined effect of coastal armoring and climate change can, therefore, intensify coastal squeeze, flooding upper beach zones and inducing extirpations of many macrofaunal species (Hubbard et al. 2013; Orlando et al. 2019).

Although the above cited studies have illustrated the coastal armoring effects on sandy beach species, a complete investigation including communities across all beach tidal zones and considering the faunal functional diversity has not been performed thus far. By using organism traits, such as body size, feeding guild, and dispersal capacity (e.g., larval type and adult motility), it is possible to determine which traits are most vulnerable to environmental changes and to better understand how environmental changes may alter the functions performed by local biodiversity (Petchey & Gaston 2006). This information could then be used to project how coastal armoring may affect the functional diversity and composition of sandy beach fauna. Additionally, this functional approach can provide valuable insights useful to understanding the integrated effects of local urbanization and global changes on beach ecosystems (Schooler et al. 2017).

In this study, we thoroughly sampled (i.e., from subtidal to supratidal zones) a set of 30 beach areas located on ten sandy beaches with and without backshore structures (seawalls) to investigate the influence of coastal armoring on the biodiversity patterns and functional composition of sandy beach ecosystems. Specifically, we first tested the hypothesis that coastal armoring would reduce the abundance, taxonomic richness, and functional richness of macrobenthic sandy beach assemblages. We also aimed to test the effects of coastal armoring on the abundance and biomass of arthropod populations in the upper beach zone (supratidal zone). This knowledge can provide information on the effects of backshore structures on vulnerable species as well as enhance understanding of their influence on the functioning of sandy beach ecosystems.

4.2 Materials and methods

4.2.1 Study area

This study was carried out on the north coast of the State of São Paulo, southeastern Brazil (Fig. 4.1-A). Although coastal urbanization is a general problem in Brazil, the southeastern coast can be highlighted for its high levels of urbanization, with negative effects on sandy beaches and their biodiversity already evident (Amaral et al. 2016; Costa & Zalmon 2017; 2019, Shah Esmaeili et al. 2021). The coast of the state of São Paulo is also highly vulnerable to the predicted climate change, with several areas showing increasing erosion and beaches at risk of disappearing due to coastal squeeze (Alfredini et al. 2008; Furlan et al. 2011; Zanetti et al. 2016). Furthermore, the study area has a large number of beaches (~ 200) along a relatively short coastline (~ 170 km), making it a suitable region to test our hypotheses with limited latitudinal variation.

4.2.2 Community-level approach

We selected a total of ten sandy beaches to evaluate the effects of coastal armoring on the abundance, taxonomic and functional richness of the macrobenthic community (Fig. 4.1-A). Five of the selected beaches have man-made structures on the backshore, mainly from houses and retaining walls from the beachfront, partially or completely replacing original vegetation or dunes on the coastline. The other five beaches selected have a natural backshore, without man-made structures and with original vegetation connected to the supratidal zone.

The vegetation of all vegetated beaches selected was characterized by "*Restinga*", a type of coastal tropical moist broadleaf forest, with a predominance of shrubs and small trees. To avoid confounding variables associated with urbanization that could obscure the observed patterns and the comparisons between beaches, we excluded beaches with direct sewage input from our sampling design. Furthermore, we aimed to select only beaches with narrow profiles, with ~ 50 m in across-shore width between the extreme high and low tide lines, since narrow beaches tend to be more vulnerable to high water events such as storm waves.

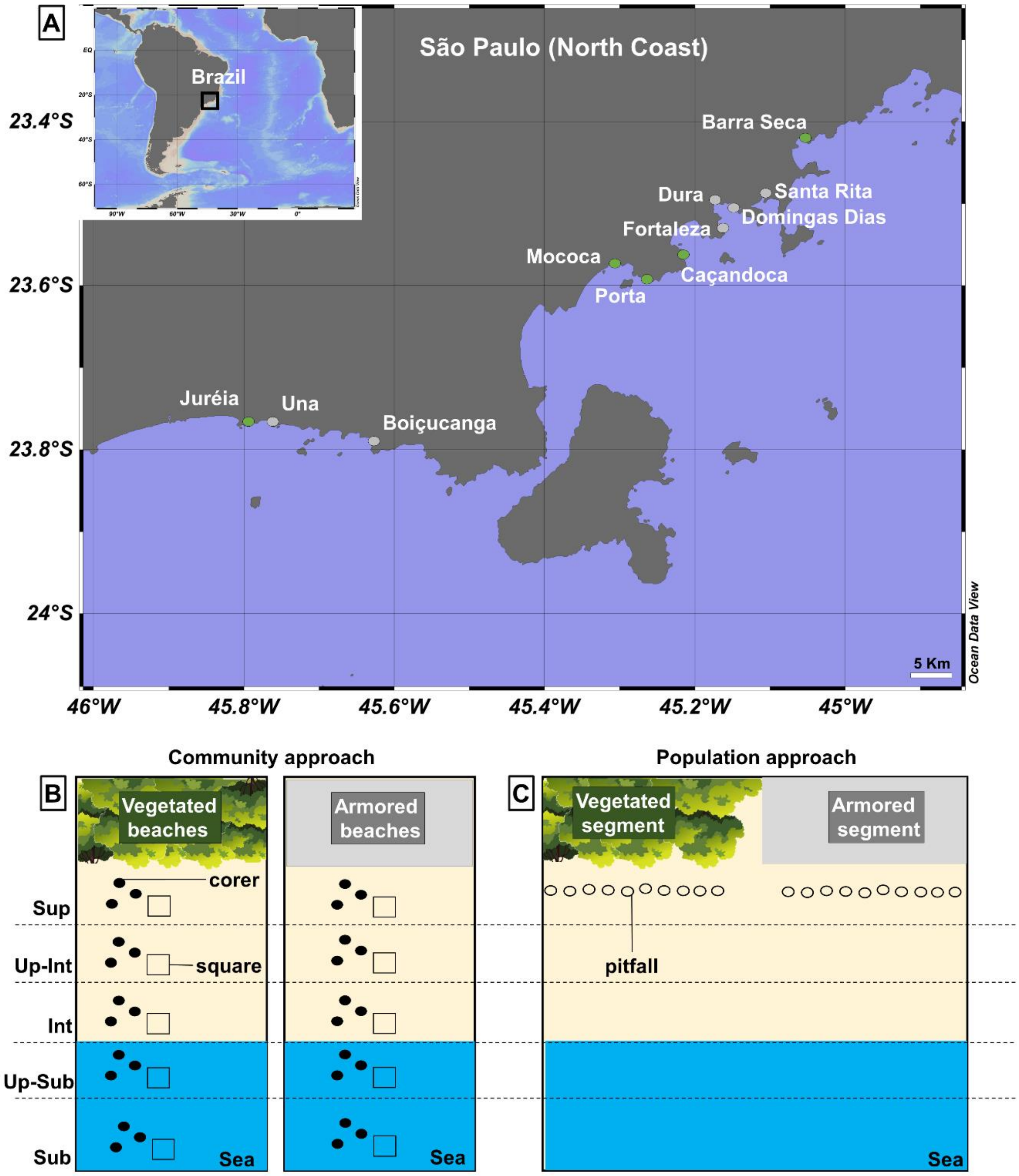

Figure 4.1. A) Study area located on the north coast of the State of São Paulo, southeastern Brazil with the beaches selected for the study. Green dots indicate the five vegetated beaches used for the community-level approach. Gray dots indicate the armored beaches selected. Only Dura was not used for the community-level approach and Dura and Santa Rita were the beaches selected for the population-level approach. B) Scheme of the sampling design applied for the community-level approach for vegetated and armored beaches. The scheme shows the sampling area divided into five tidal zones: 1) Supratidal zone (Sup); 2) Upper intertidal zone (Up-Int); 3) Intertidal zone (Int); 4) Upper subtidal zone (Up-Sub) and 5) Subtidal zone (Sub). For each tidal zone, three macrofauna samples were collected with a corer, and another sample was collected with a square sampler (scheme out of scale). C) Scheme of the sampling design applied for the population-level approach considering the comparison of vegetated and armored segments within the beaches. A total of 20 pitfall traps were installed per beach to sample the supratidal fauna, 10 traps were installed on the armored segment, and 10 traps were installed on the vegetated segment (scheme out of scale).

The beaches had lengths varying from ~ 500 to ~1500 m. We standardized sampling in three beach areas, one close to each beach edge (opposite sides of a beach embayment) and one in the middle of the beach, following Corte et al. 2022. We always keep a minimum distance of 150 m between the areas. For each area, we delimited five tidal zones across the beach profile: (1) Supratidal zone, area mostly dry; (2) Upper intertidal zone, area flooded only during the peak of spring high tide; (3) Intertidal zone, area exposed only during the peak of spring low tide; (4) Upper subtidal zone, permanently flooded area of ~ 0.5 m in depth during spring low tide; and (5) Subtidal zone, permanently flooded area of ~1.5 m in depth during spring low tide (Fig. 4.1-B).

To control the potential confounding influence of beach type (i.e., dissipative, reflective, or intermediate stages), we performed a morphodynamic characterization of each sampling area. To do so, we measured the entire beach profile of each sampling area and calculated the beach face slope (following Emery 1961). We also collected sediment samples at each zone of each area (15 samples per beach) for further analyses of grain size. With this information, we calculated the Beach Index (BI) (McLachlan & Dorvlo 2005), which is a metric to characterize beach morphodynamic states, where higher values indicate beaches toward more dissipative states and lower values indicate beaches toward more reflective states.

At each sampling area, three macrofauna samples were collected with a corer (15 cm in diameter), and another sample was collected with a 0.5 x 0.5 m square sampler per tidal zone (Fig. 4.1-B). While corers are the most commonly used samplers for macrofauna species on sandy beaches, larger square samplers are better suited to collecting species with large body sizes. All samples were collected up to 20 cm deep and wrack was avoided during beach sampling in the upper beach zones (to avoid confounding effects). Sampling events occurred during spring low-tide periods in a four-month interval between March and June 2019 (beaches were randomly sampled during this period).

At the laboratory, macrofauna samples were sieved (1.0 and 0.5 mm mesh sizes), and the individuals were preserved in 70% alcohol and later identified to the lowest possible taxonomic level. The sediment samples collected were dried (60 °C for 48 h), and grain size analysis was performed by sieving the dry sediment into twelve granulometric fractions, which were individually weighed and used to calculate the mean grain diameter size following Folk & Ward (1957).

4.2.3 Population-level approach

We evaluated the direct effects of man-made backshore structures on two supratidal arthropods: (1) the insect *Phaleria testacea* (Coleoptera, Tenebrionidae) and (2) the crustacean

Atlantorchestoidea brasiliensis (Amphipoda, Talitridae). We chose these two species because they are common on southeastern Atlantic beaches, are easy to sample and are representatives of the two principal arthropod groups of the supratidal zone (coleopterans and crustaceans) (Amaral et al. 2016).

We replicated the sampling design on two sandy beaches with the backshores partially armored (also presenting some not-armored segments) and with different morphodynamic characteristics: Dura (dissipative, with a wide and plain beach profile) and Santa Rita (intermediate, with a narrow and steep beach profile). At each beach, we delimited a sampling area on the supratidal zone of ~ 45 m in length (parallel to the shoreline) and ~ 8 m in width (perpendicular to the shoreline, covering all supratidal extension). At both beaches, the selected area had half of its backshore armored by a man-made wall, and the other half had natural vegetation (Fig. 4.1-C). We sampled both species using pitfall traps installed in the sand of both treatments (armored and vegetated segments) of both beaches. We maintained a transition zone of 5 m in length between the two segments without traps to ensure spatial independence between the treatments armored and vegetated. With the same intention, we also ensured a minimum distance of 2 m between neighboring traps. We used this small-spatial scale approach, as it is useful for testing the effect of a specific driver on benthic fauna (Laurino et al. 2020a; Laurino & Turra 2021), allowing the isolation of the parameter of interest (wall presence, in this case) from the other confounding factors, such as differences in wave exposure and inputs of organic matter (Fig. 4.1-C).

A total of 20 traps were installed per beach with 10 traps set on the armored segment and 10 traps set on the vegetated segment (Fig. 4.1-C). All traps were installed side by side, parallel to the shoreline, and at the same distance (2 m) from the backshore (both armored and vegetated). Following Schlacher et al. (2017), the pitfall traps were cups with an opening diameter of 7.5 cm and height of 11 cm. We fully buried each trap on the sand, leaving their openings level with the sediment surface. Next, we filled 75% of the internal volume of each trap with a solution of seawater and detergent to prevent the escape of the captured organisms. Sampling occurred for 12 hours at night, opening the traps at 6 pm and closing them at 6 am. After the traps were closed, they were removed from the sand, and their content was filtered through a mesh of 0.5 mm, retaining the captured organisms. Next, we estimated the supratidal face slope of the sampling area on both segments of both beaches (five measurements per segment) using two rulers of 1.5 m and a measuring tape (following Emery 1961). We also sampled the sediment of the sampling area (five samples per segment) to further analyze grain size, water content, and organic content. Sampling was performed once in March 2021, and weather conditions remained stable during its running time (i.e., without rain or strong winds).

At the lab, we confirmed the taxonomic identification of the two target species sampled, counted their abundance per trap, and estimated their biomass per trap. For the biomass analyses, all individuals were dried on an oven (60 °C) for 24 hours, weighed, and then incinerated in a muffle (550 °C) for 6 hours. The ash-free dry weight was the parameter used for biomass estimates per trap for both species. The sediment grain size was obtained by the same procedure carried out in the community-level analysis. Sediment water content was registered as the difference between the sediment weight before and after drying on the oven (60 °C for 48 hours). Organic content was determined from the difference in the sediment weight before and after incineration in the muffle (550 °C for 6 hours).

4.2.4 Data analysis

4.2.4.1 Community-level approach

To assess the effects of coastal armoring on the macrobenthic community, we calculated the abundance (number of individuals), taxonomic richness (number of taxa), and functional richness (functional space occupied by the community, a proxy of the functional diversity) for each sampling area of each beach (sampling units: N =30). We also calculated the abundance of the three most common taxonomic groups found on sandy beaches: Polychaeta, Arthropoda, and Mollusca. All these parameters were calculated by combining all samples collected at all tidal zones at each sampling area. Except for functional richness, all these parameters were also calculated separately by tidal zone.

Functional richness was estimated based on the method described in Corte et al. (2021). Accordingly, we first collected (from online databases) data on six macrofaunal traits related to the functional role of the taxa found: (1) depth position in the sediment (vertical distribution); (2) maximum length of body size; (3) feeding guild; (4) adult motility; (5) lifespan; and (6) larval dispersal potential. These traits were subdivided into different modalities to encompass their range of variation (see Supplementary material – Appendix B). To quantify the affinity of each taxon for each modality, we applied fuzzy coding (Chevene et al. 1994) with scores ranging from 0 (no affinity for the modality) to 3 (complete affinity for the modality). We used this matrix of taxa by traits to further calculate the functional richness and the Community-Weighted Mean trait value (CWM) per sampling unit. The CWM is a metric of which traits exert a dominant effect on ecosystem processes, which is adequate to demonstrate shifts in individual functional traits within communities due to environmental selection (Ricotta and Moretti, 2011). Functional richness was considered only by pooling the tidal zones (not separately by tidal zones) because we aimed that the calculation encompasses all the modalities of functional traits existing in the area, including the fauna of the entire beach profile.

We applied generalized linear mixed models (GLMMs) to test whether morphodynamics varied by comparing armored and vegetated beach areas, using the beach index as the response variable. We also applied GLMMs to assess how the macrofauna community descriptors were affected by the backshore conditions (armored and vegetated). In this step, the response variables used in each model, considering the tidal zones combined (sampling area as sampling unit: three per beach, 15 armored and 15 vegetated) were abundance (one model for the total community and the other three models for each main taxonomic group), taxonomic richness, and functional richness. The models considering abundances and taxonomic richness were adjusted to the negative binomial family (logarithmic linking function), which is suitable for counting data (Bolker 2008). The model considering functional richness was adjusted to the Gaussian family (identity linking function), as this parameter is a continuous variable. Separate models per tidal zone were also designed for abundance (total community and main taxonomic groups) and taxonomic richness.

Each model includes the predictor “Backshore condition”, a fixed factor with two levels (armored and vegetated). To control for the effect of morphodynamic characteristics (i.e., beach type), we included the “Beach Index” (BI) as a continuous covariable (fixed factor). All models include the interaction between the “Backshore condition” and “Beach Index” to test whether the morphodynamic effects on fauna may be different for armored and vegetated treatments. We also included a random factor "Beach" in each model, to consider the three sampling areas that were within the same beach. Next, all models were subjected to a likelihood ratio test (LRT) with the chi-square statistic to identify which fixed predictors provided significant losses of likelihood (considering $\alpha = 0.05$) when excluded from the full models (Bolker 2008).

To explore which taxa were most influenced by the presence of man-made structures on the backshore, we performed redundancy analysis (RDAs) with two components (two-axis) considering the abundance of the most plentiful and frequent species found as response variables. To avoid many zeros from being included in the data matrix, some species were combined into higher taxonomic levels (genera, family, class, etc.). As many polychaete taxa were abundant and frequent, one exclusive RDA was conducted for the polychaete taxa and another was conducted for arthropoda and molluscan taxa. Then, to observe which biological traits were most influenced by coastal armoring, we developed an RDA including all modalities of all functional traits evaluated. In this case, the RDA included the single-trait CWM values at each sampling area as response variables. We included two explanatory variables for all RDAs designed: (1) Coastal armoring (categorical variable) and the (2) BI (continuous variable). Significant effects of the explanatory variables on the response variables were tested considering $\alpha = 0.05$.

4.2.4.2 Population-level approach

We designed generalized linear models (GLMs) to assess differences in the environmental features, abundance, and biomass of the target species between armored and vegetated segments. To test the variation in the environmental parameters, response variables used include the supratidal face slope, sediment grain size, sediment-water content, and sediment organic content. To test for macrofaunal variations, response variables used include the abundance and biomass of the two selected species (*Phaleria testacea* and *Atlantorchestoidea brasiliensis*). All models include two fixed factors as predictors: (1) "Backshore condition" at two levels (armored and vegetated) and (2) "Beach" at two levels (the Dura and Santa Rita Beaches). We also include the interaction between these two factors as a predictor in all models to observe whether the armoring effect was dependent on the beach assessed. Pitfall traps were considered replicates (n = 10 per segment, 20 per beach; the total with two beaches: n = 20 armored and 20 vegetated).

Each model was adjusted to the family that provided a lower Akaike Information Criterion (AIC), indicating a higher likelihood (Bolker 2008). Accordingly, the models considering face slope and sediment-water content were adjusted to the log-normal family, while the abundance models (for both species) were adjusted to the negative binomial family. All other models (sediment organic content, grain size, and biomass of both species) were better fitted to the Gaussian family. All models were submitted to the LRT with the chi-square statistic to identify the effects of the predictors ($\alpha = 0.05$). In the case of significant effects observed for the interaction, we designed pairwise comparisons (z-statistic) of all levels of both factors.

4.3 Results

4.3.1 Community-level approach

The morphodynamic characteristics of the beaches selected showed that most of the beaches presented intermediate stages (beach index between 1.5 and 2.5). We noted similar characteristics for armored and vegetated beaches (Table 4.1), without significant differences in the beach index (BI) comparing both backshore conditions (Chi: 0.148; p = 0.701). In summary, the BI of the armored beaches presented a mean of 1.91 (minimum: 1.49; maximum: 2.31), while the BI mean of the vegetated beaches was 1.96 (minimum: 1.72; maximum: 2.26).

Table 4.1. Morphodynamic characterization of the beaches selected, including the beach face slope, the sediment grain size, and the beach index of five armored and five vegetated beaches. M: mean; SD: standard deviation.

	Armored beaches									
	Boiçucanga		Una		Fortaleza		Domingas Dias		Santa Rita	
	M	SD	M	SD	M	SD	M	SD	M	SD
Face slope (m)	8.05	0.71	12.79	4.31	24.20	3.14	12.73	0.33	15.45	3.17
Grain size (ϕ)	1.36	0.43	1.51	0.56	2.69	0.12	2.32	0.35	2.52	0.16
Beach Index	1.57	0.10	1.78	0.23	2.25	0.06	1.93	0.05	2.03	0.08
	Vegetated beaches									
	Mococa		Jureia		Barra Seca		Porta		Caçandoca	
	M	SD	M	SD	M	SD	M	SD	M	SD
Face slope (m)	8.91	0.72	9.95	0.18	19.90	3.25	14.67	0.87	19.16	6.16
Grain size (ϕ)	2.17	0.18	3.38	0.01	2.66	0.31	2.00	0.18	1.70	0.44
Beach Index	1.75	0.03	1.94	0.01	2.16	0.11	1.94	0.05	2.00	0.07

We found a total of 58 taxa and 746 individuals at the 30 sampling areas (see Supplementary Material for the complete list of taxa). Polychaeta was the dominant group, with 26 taxa and 417 individuals in total, followed by arthropods, with 15 taxa (11 crustaceans; 4 insects) and 245 individuals (192 crustaceans; 53 insects) in total. Mollusca occurred with 13 taxa (9 bivalves; 4 gastropods) and 69 individuals (30 bivalves; 39 gastropods). The polychaete *Scolelepis squamata*, *Scoloplos treadwelli* and the isopod *Excirolana braziliensis* were highly dominant in abundance (339 individuals among the three species), representing almost 50% of the total macrofaunal abundance found.

Considering the fauna of the whole beach profile, the abundance of the macrobenthic community was dependent on the backshore conditions and was also influenced by the BI (Table 4.2; Fig. 4.2). Abundance was higher on the vegetated beaches (35 ± 5.17 [mean ± standard error]) than on the armored beaches (15 ± 2.05) (Fig. 4.2). Abundance was also positively correlated with the BI values, indicating higher abundance at sites with flatter profiles and finer sediments (Fig. 4.2). This pattern was heavily influenced by polychaetes (Table 4.2; Fig. 4.2), which presented abundance levels almost three times higher at vegetated beaches (20.6 ± 5.09) than on the armored beaches (7.2 ± 1.53). However, the effects of the backshore in the polychaetes were dependent on the BI values (Table 4.2), since the main polychaete differences in abundance, comparing armored and vegetated backshores, were noted on the beaches with high BI values (>2) (Fig. 4.2). Taxonomic and functional richness, and arthropods and mollusks abundance, in turn, did not show differences comparing armored and vegetated beaches or any effect of the BI (Table 4.2; Fig. 4.2).

Table 4.2. Likelihood ratio test (LRT) with the chi-square statistic (Chi) and p values (in bold when significant) applied from generalized linear mixed models (GLMMs) designed considering the macrofaunal parameters observed on ten beaches of southeastern Brazil. The response variables of each model, pooling all tidal zones per beach area, include the community abundance, taxonomic richness, functional richness, and abundance of the three main macrofaunal groups found (Polychaeta, Arthropoda, and Mollusca). The fixed predictors considered in the models include the “Backshore condition” (armored and vegetated), the “Beach Index” (BI), and the interaction between these two factors.

Predictors	**Total Community**		**Taxa Richness**		**Functional Richness**	
	Chi	p	Chi	p	Chi	p
Backshore	7.80	**<0.001**	2.48	0.115	0.01	0.937
BI	5.54	**0.018**	2.07	0.150	3.41	0.064
Backshore x BI	0.12	0.724	0.06	0.803	0.25	0.617
	Polychaeta		**Arthropoda**		**Mollusca**	
	Chi	p	Chi	p	Chi	p
Backshore	0.47	0.492	0.14	0.707	1.00	0.316
BI	4.73	**0.029**	0.44	0.506	1.51	0.218
Backshore x BI	27.50	**<0.001**	0.01	0.976	0.50	0.478

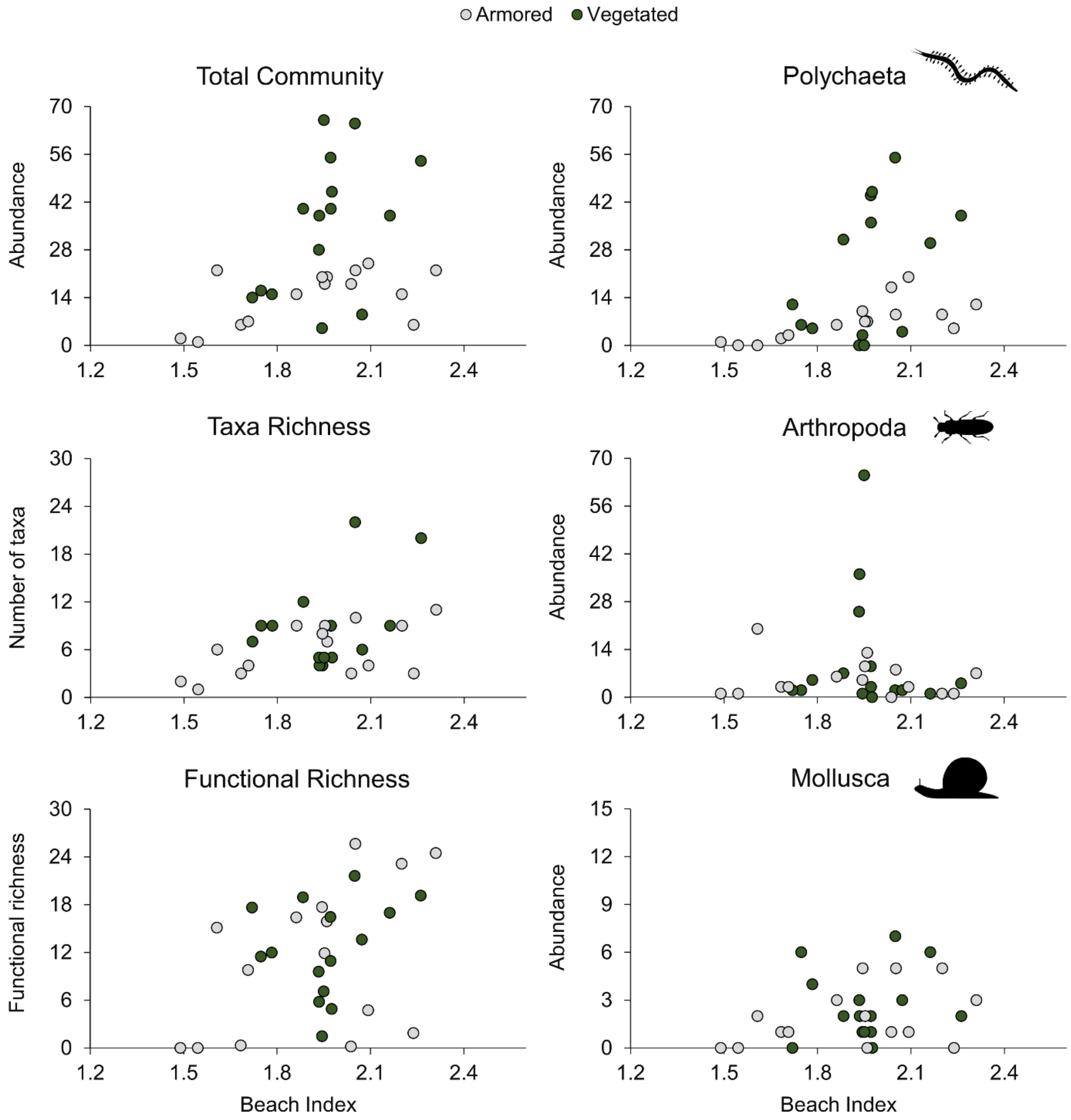

Figure 4.2. Total community abundance, taxonomic richness, functional richness, and the abundance of the three main macrofaunal groups found (Polychaeta, Arthropoda, and Mollusca) on ten beaches of southeastern Brazil with distinct backshore conditions (five beaches armored and five beaches vegetated). Three areas were sampled per beach, pooling samples for five tidal zones, totaling 30 dots (sampling areas) for each graphic. Morphodynamic variations among sampling areas are represented by the beach index (x-axis), and the backshore conditions of each sampling area are indicated by different colors (green: backshore vegetated; gray: backshore armored).

Observing the tidal zones separately, we noted an overall pattern of lower richness and abundance of the community and the main faunal groups on armored beaches than on vegetated beaches (Fig. 4.3). These differences were evident in the lower beach zones, with values significantly low for molluscans and taxa richness in the subtidal zone of armored beaches (Table 4.3; Fig. 4.3). Total abundance of the community and polychaetes abundance also followed this pattern, with values significantly low in the upper subtidal zone of armored beaches (Table 4.3; Fig. 4.3). Arthropods were the main responsible for the lower abundance in the upper beach zones of armored beaches compared to the vegetated beaches (Fig. 4.3), although no significant effect was detected (Table 4.3).

Table 4.3. Likelihood ratio test (LRT) with the chi-square statistic (Chi) and p values (in bold when significant) applied from generalized linear mixed models (GLMMs) designed considering the macrofaunal parameters observed on ten beaches of southeastern Brazil. The response variables of each model, for each tidal zones evaluated, include the community abundance, taxonomic richness, and abundance of the three main macrofaunal groups found (Polychaeta, Arthropoda, and Mollusca). Dashes indicate that Mollusca was not found in the Supratidal and Upper intertidal zones while Polychaeta did not occur in the Supratidal zone. The fixed predictors considered in the models include the "Backshore condition" (armored and vegetated), the "Beach Index" (BI), and the interaction between these two factors.

	Total Community		**Taxa Richness**		**Polychaeta**		**Arthropoda**		**Mollusca**	
Supratital	Chi	p	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	0.72	0.395	0.02	0.868	-	-	0.07	0.792	-	-
BI	1.23	0.267	0.13	0.717	-	-	0.01	0.956	-	-
Backshore x BI	0.47	0.490	2.41	0.120	-	-	3.17	0.074	-	-

	Total Community		**Taxa Richness**		**Polychaeta**		**Arthropoda**		**Mollusca**	
Upper intertidal	Chi	p	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	0.13	0.720	0.09	0.762	1.84	0.174	0.91	0.341	-	-
BI	0.12	0.727	0.08	0.771	7.10	**0.007**	0.70	0.401	-	-
Backshore x BI	0.97	0.322	0.08	0.766	0.94	0.332	0.77	0.379	-	-

	Total Community		**Taxa Richness**		**Polychaeta**		**Arthropoda**		**Mollusca**	
Intertidal	Chi	p	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	0.94	0.331	0.02	0.901	1.04	0.307	0.78	0.376	0.57	0.447
BI	26.90	**<0.001**	1.77	0.183	34.30	**<0.001**	0.16	0.685	0.09	0.766
Backshore x BI	3.37	0.070	0.28	0.595	7.58	**0.006**	0.21	0.644	0.01	0.990

	Total Community		**Taxa Richness**		**Polychaeta**		**Arthropoda**		**Mollusca**	
Upper subtidal	Chi	p	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	4.10	**0.043**	1.63	0.201	5.28	**0.021**	0.27	0.602	0.84	0.359
BI	1.47	0.225	0.68	0.411	2.28	0.131	0.49	0.482	0.35	0.551
Backshore x BI	0.11	0.739	0.77	0.768	0.01	0.938	0.32	0.569	0.84	0.359

	Total Community		**Taxa Richness**		**Polychaeta**		**Arthropoda**		**Mollusca**	
Subtidal	Chi	p	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	3.21	0.072	3.89	**0.049**	1.38	0.240	0.01	0.921	5.47	**0.019**
BI	4.72	**0.029**	5.33	**0.021**	4.13	**0.042**	0.01	0.906	3.70	0.054
Backshore x BI	0.29	0.592	0.10	0.747	2.01	0.156	0.01	0.944	0.08	0.400

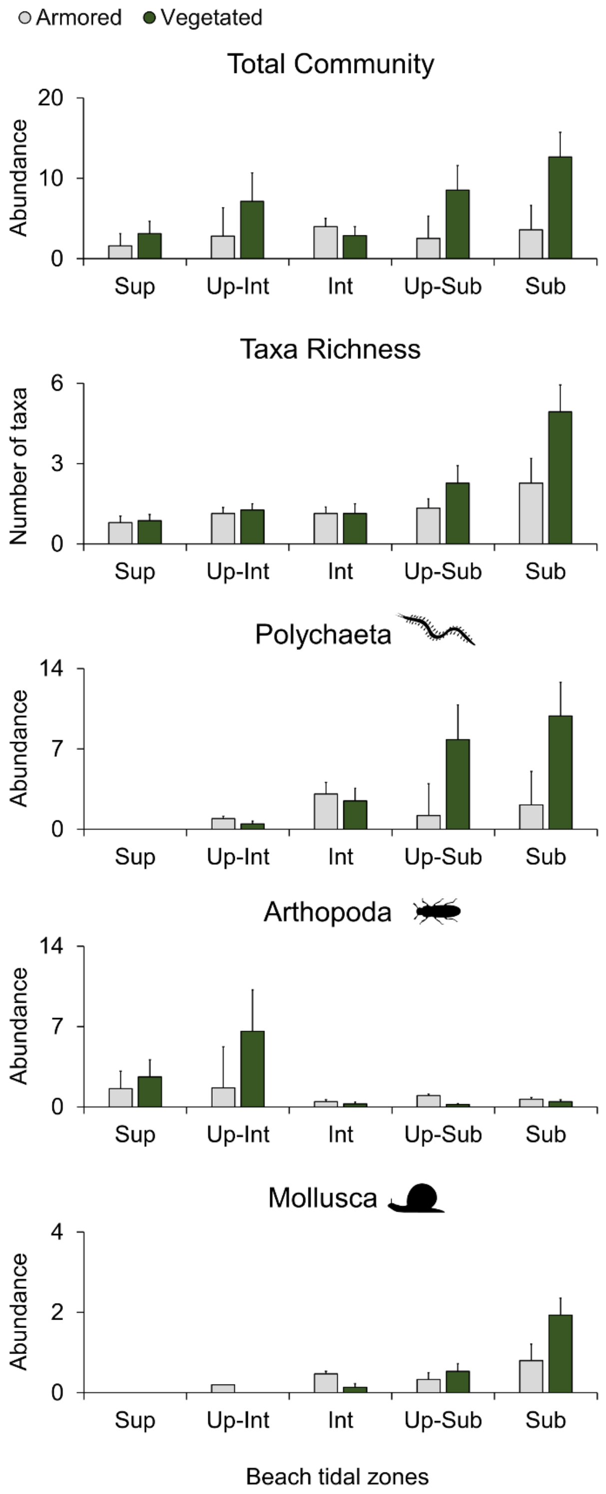

Figure 4.3. Total community abundance, taxonomic richness, and the abundance of the three main macrofaunal groups found (Polychaeta, Arthropoda, and Mollusca) across five tidal zones: 1) Supratidal zone (Sup); 2) Upper intertidal zone (Up-Int); 3) Intertidal zone (Int); 4) Upper subtidal zone (Up-Sub) and 5) Subtidal zone (Sub). Ten beaches of southeastern Brazil were sampled in total, with distinct backshore conditions (green: five beaches with backshore vegetated; gray: five beaches with backshore armored).

The species most negative related to the coastal armoring were polychaetes such as *Scoloplos treadwelli* (family Orbiniidae), *Armandia hossfeldi* and *Armandia maculata* (family Opheliidae) and *Dispio uncinata* (family Spionidae) (Fig. 4.4). Although the RDA axes showed low explanation power, these polychaetes occurred with abundances at least three times higher on the vegetated beaches than on the armored beaches. Other abundant polychaete species, such as *Scolelepis squamata*, were more strongly correlated with the BI than with the backshore conditions (Fig. 4.4). We did not detect any significant effects of coastal armoring and the BI on arthropods and mollusks, considering the RDAs; however, we noticed some tendencies related to specific taxa, such as higher levels of gastropods, amphipods, and coleopterans on vegetated beaches and bivalves in flatter areas (higher BI) (Fig. 4.4).

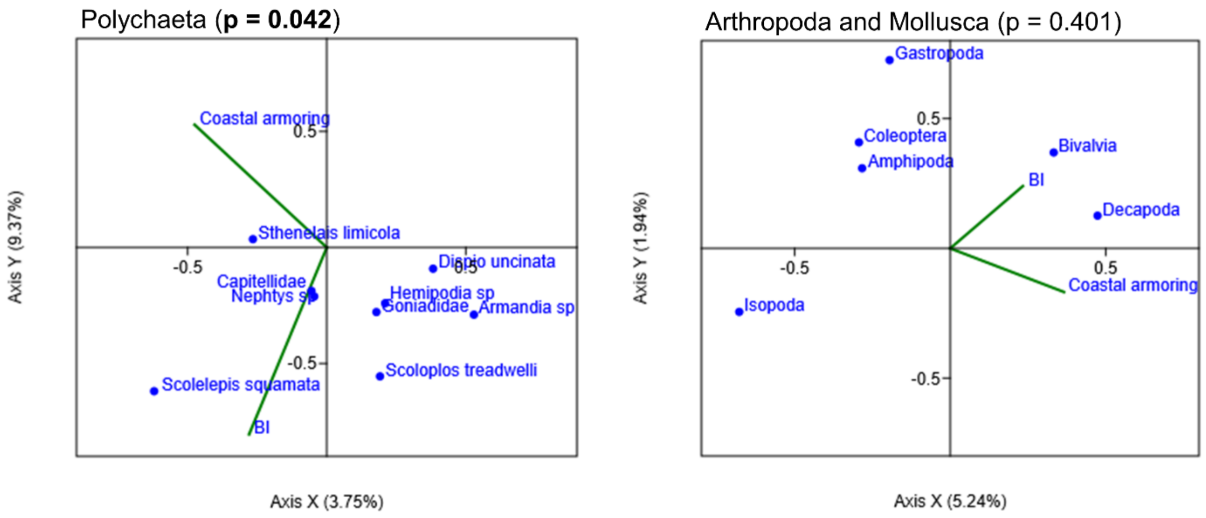

Figure 4.4. Redundancy analysis (RDA) of the abundance of the principal taxa found by evaluating their relationships with the backshore conditions (coastal armoring) and the beach index (BI) on ten sandy beaches in southeastern Brazil. Bolded p-values indicate significant effects of the explanatory variables (combining coastal armoring and BI) on the response variables (fauna).

The distribution of functional traits also showed significant variations associated with the coastal armoring and the BI values (Fig. 4.5). We found that the backshore conditions were mainly related to variations in depth position, body size, feeding guild, and adult motility (Fig. 4.5). In this regard, coastal armoring was negatively related to large body size species (>80 mm), manly predators with high-marine motility and deep vertical distribution (> 8cm in depth). Accordingly, armored beaches sheltered species with more affinity to the sediment subsurface (0 to 3 cm in depth) and small body size (5 to 20 mm). Suspension feeders were also found to be mainly associated with the armored beaches, while the distribution of other feeding modalities (i.e., scavengers) was most related to BI variation. Similarly, the BI also influenced adult motility (i.e., low-marine), lifespan modalities, and larval dispersal potential (Fig. 4.5).

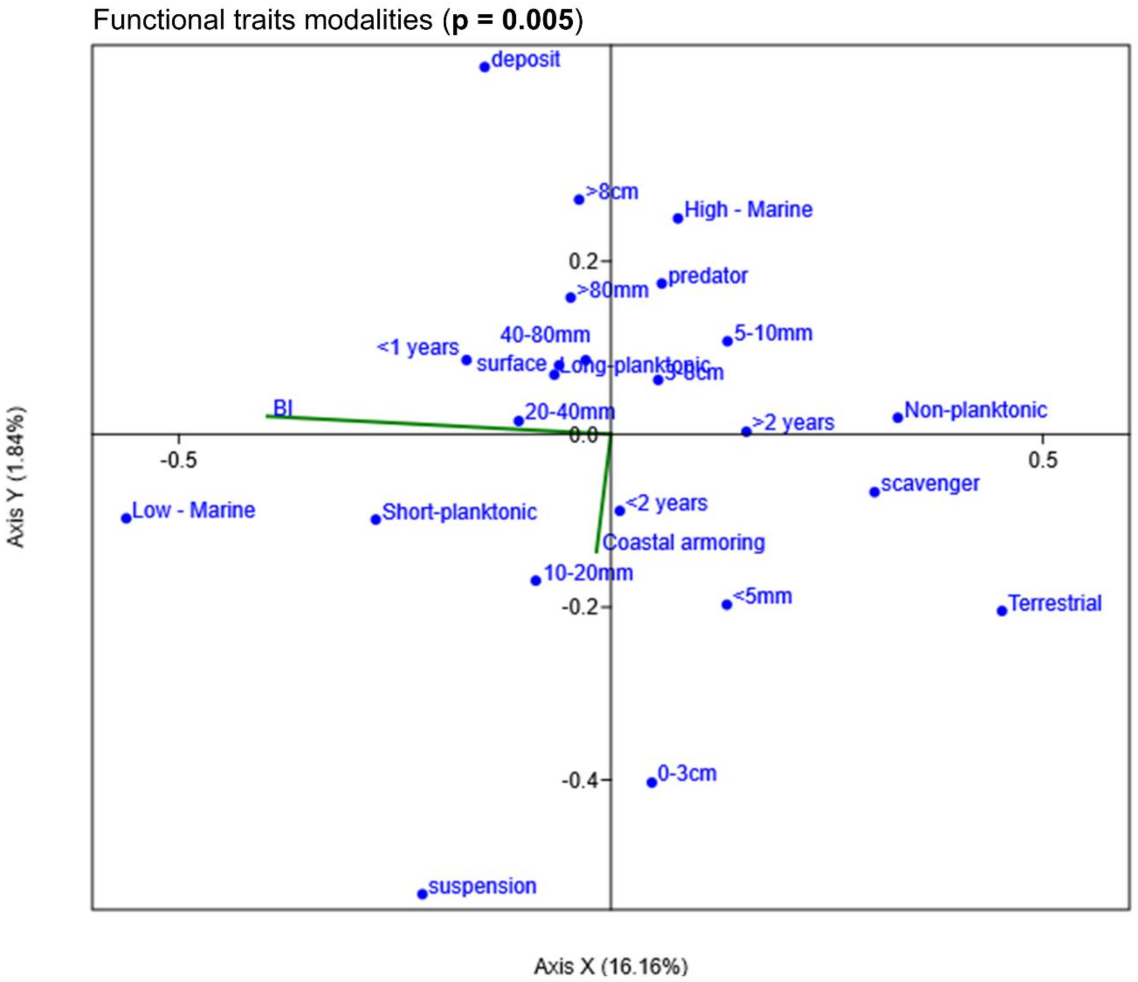

Figure 4.5. Redundancy analysis (RDA) of the functional macrofaunal traits evaluating the effects of the backshore conditions (coastal armoring) and the beach index (BI), as explanatory variables, in the trait modalities of the macrobenthic community on ten sandy beaches in southeastern Brazil. The RDA included the Community-Weighted Mean trait value (CWM) per sampling unit of each modality, related to each trait, as response variables. The functional traits considered, and their respective modalities, were: (1) depth position in the sediment (surface, 0-3cm, 3-8cm, and >8cm); (2) maximum length of body size (<5mm, 5-10mm, 10-20mm, 20-40mm, 40-80mm, and >80mm); (3) feeding guild (deposit, suspension, scavenger, and predator); (4) adult motility (Low – marine, High – marine, and Terrestrial); (5) lifespan (<1 year, >1 years, and >2 years); and (6) larval dispersal potential (Short-planktonic, Long-planktonic, and Non-planktonic). The bolded p-value indicates the significant effects of the explanatory variables (combining coastal armoring and BI) on the response variables (trait modalities).

4.3.2 Population-level approach

Considering the environmental features of the sampling areas, the supratidal face slope was the only variable that did not vary between beaches but varied between backshore conditions (Table 4.4). For both beaches, we noted that the armored segment presented steeper slopes than the vegetated segments (Fig. 4.6). Sediment grain size, in turn, varied between beaches (Table 4.4), with coarser sediments (i.e., lower ϕ values) found on Santa Rita Beach than on Dura Beach. However, only Santa Rita Beach showed coarser sediments on the armored segment than on the vegetated segment (Fig. 4.6). Conversely, only Dura Beach showed differences in sediment-water content when comparing backshore conditions, with drier sediments on the armored segment. Sediment organic content was the only variable that did not change between beaches or backshore conditions (Table 4.4; Fig. 4.6).

Table 4.4. Likelihood ratio test (LRT) with the chi-square statistic (Chi) and p values (in bold when significant) applied from generalized linear models (GLMs) designed considering the environmental features and macrofaunal parameters observed in the sampling area. The response variables of each model include the supratidal face slope, sediment grain size, sediment-water content, sediment organic content, and the abundance and biomass of two macrofaunal species: the coleopteran Phaleria testacea and the amphipod Atlantorchestoidea brasiliensis. The predictors considered in the models include the "Backshore condition" (armored and vegetated), "Beach" (the Dura and Santa Rita Beaches), and interactions between these two factors.

	Supratidal face slope		**Sediment grain size**		**Sediment water content**		**Sediment organic content**	
	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	12.436	**<0.001**	14.805	**<0.001**	11.165	**<0.001**	1.996	0.158
Beach	2.079	0.149	69.837	**<0.001**	8.682	**0.003**	0.015	0.902
Backshore x Beach	2.094	0.148	10.323	**0.001**	16.404	**<0.001**	0.903	0.342

	***P. testacea* (abundance)**		***A. brasiliensis* (abundance)**		***P. testacea* (biomass)**		***A. brasiliensis* (biomass)**	
	Chi	p	Chi	p	Chi	p	Chi	p
Backshore	5.299	**0.021**	0.007	0.932	3.807	0.051	32.942	**<0.001**
Beach	21.790	**<0.001**	6.796	**0.009**	70.317	**<0.001**	69.551	**<0.001**
Backshore x Beach	0.017	0.895	0.094	0.759	18.864	**<0.001**	7.414	**0.006**

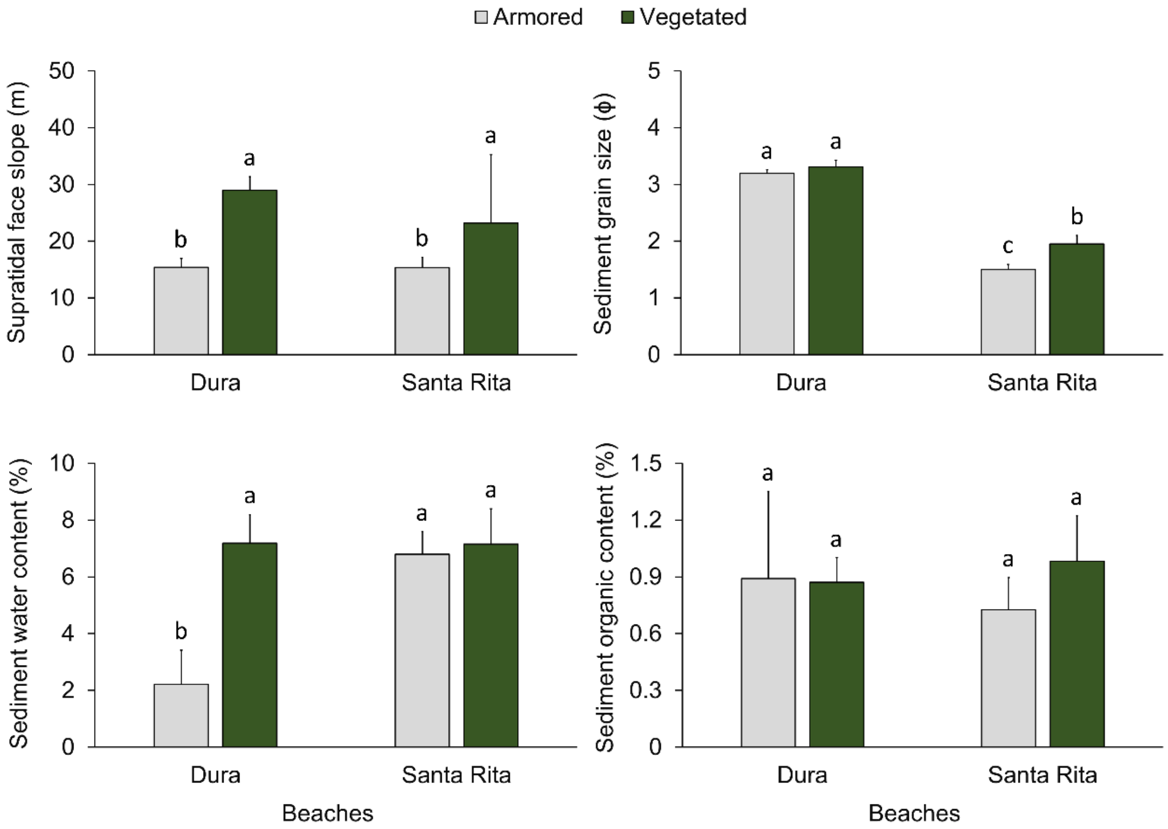

Figure 4.6. Environmental features measured in the sampling area selected for the population-level approach on the supratidal zone of two beaches in southeastern Brazil (Dura and Santa Rita), comparing two backshore conditions (armored and vegetated segments). Values include the mean and standard error per beach segment (n = 5 per segment). Letters indicate differences between backshore conditions and between beaches detected in the pairwise comparisons for each parameter evaluated. For all comparisons (across the two beaches and backshore conditions within and between beaches), "a" indicates values significantly higher than "b"; "c" indicates values significantly lower than "a" and "b".

With regard to the macrofaunal parameters, we found that the coleopteran *Phaleria testacea* showed higher abundance in the vegetated than in the armored segments, also presenting higher abundance at Santa Rita Beach than at Dura Beach (Table 4.4; Fig. 4.7). For biomass, this species was found at higher level in the vegetated segment than in the armored segment, mainly on Santa Rita Beach (Table 4.4; Fig. 4.7). The amphipod *Atlantorchestoidea brasiliensis* also showed higher abundances at Santa Rita Beach than at Dura Beach (Fig. 4.7) but without differences between the backshore conditions at both beaches (Table 4.4; Fig. 4.7). In terms of biomass, this species showed differences between beaches depending on backshore conditions (Table 4.4). In this regard, only the vegetated segment presented higher biomass values at Santa Rita Beach than at Dura Beach, without a clear armoring effect found when comparing the segments inside the beaches (Fig. 4.7).

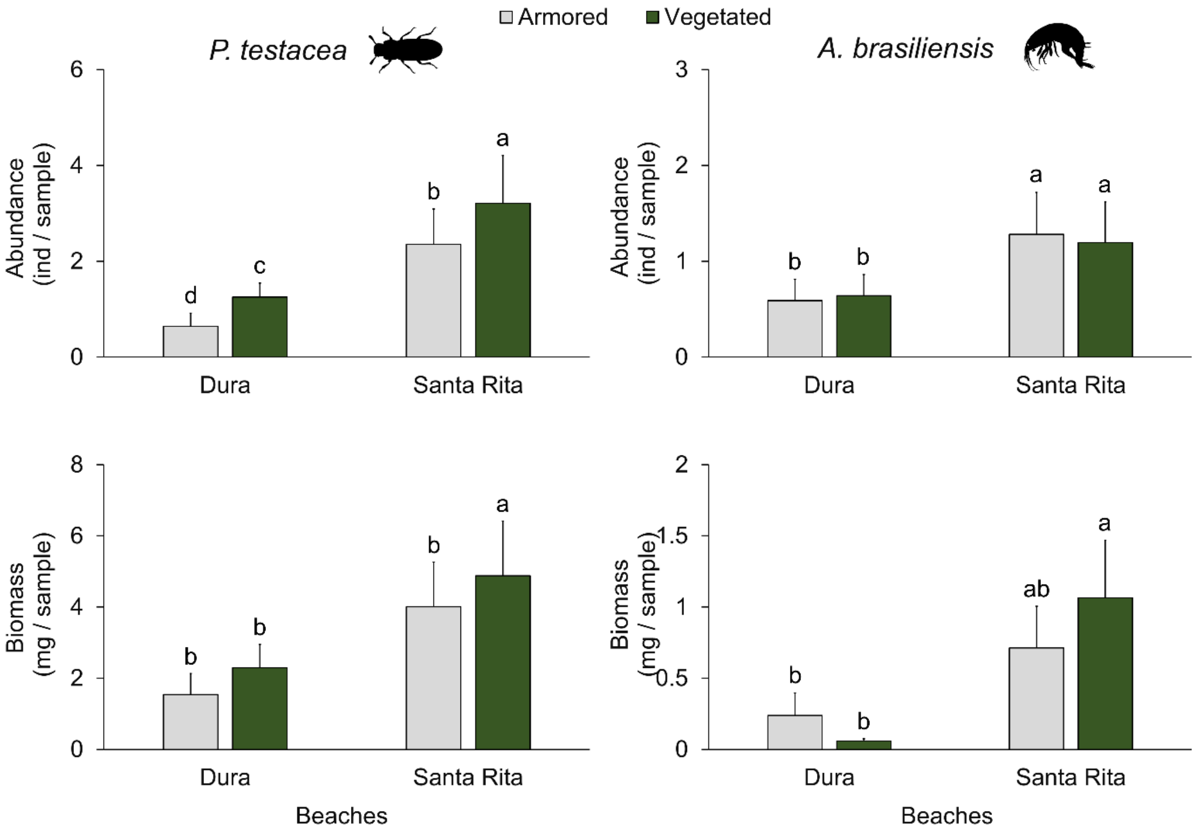

Figure 4.7. Abundance and biomass registered in the population-level approach. Two macrofaunal species were considered (the coleopteran *Phaleria testacea* and the amphipod *Atlantorchestoidea brasiliensis*) on the supratidal zone of two beaches in southeastern Brazil (Dura and Santa Rita), comparing two backshore conditions (armored and vegetated segments). Values are the mean and standard error per beach segment, transformed by log(x+1) and using pitfall traps as samples (n = 10 per segment). Letters indicate differences between backshore conditions and between beaches detected in the pairwise comparisons for each parameter of each species evaluated. For all comparisons (across the two beaches and backshore conditions within and between beaches), “a” indicates values significantly higher than “b”; “ab” indicates intermediate values not different from “a” or “b”; “c” indicates values significantly lower than “a”, “b” and “ab”; and “d” indicates values significantly lower than “a”, “b”, “ab”, and “c”.

4.4 Discussion

In this study, we hypothesized that coastal armoring would reduce beach biodiversity, including its abundance and taxonomic and functional components. We found that macrobenthic abundance decreased at armored beaches, mainly because of a reduction in the abundance of subtidal polychaetes and molluscans when compared to vegetated beaches. Taxonomic richness was lower on armored beaches than on vegetated beaches, an effect mainly noted for the subtidal zone. The overall functional richness of the macrobenthic community was not reduced by coastal armoring, but we noted differences in the main biological traits associated with armored and vegetated beaches. Populations of the coleopteran *Phaleria testacea* also presented lower numbers in armored than vegetated beach segments, which led to a reduction in total biomass. Therefore, our results suggest that although coastal armoring alone does not reduce macrofauna functional diversity, it may reduce the abundance and biomass of sandy beach assemblages and influence their functional composition.

Previous studies have shown that coastal armoring impacts are usually related to a loss of upper beach arthropods, such as the ghost crab *Ocypode quadrata*, isopods, amphipods, and insects (Lucrezi et al. 2009; Sobocinsk et al. 2010; Hubbard et al. 2013; Heerhartz et al. 2015; Jaramillo et al. 2021). However, these studies mainly focus on upper intertidal and supralittoral biodiversity, as these habitats are directly impacted by the construction of man-made structures on the backshore. By investigating the influence of coastal armoring across the whole terrestrial-marine gradient of sandy beaches, we were able to show that subtidal polychaetes and molluscans are also vulnerable taxa. A possible explanation for this reduction in armored beaches is that these habitats are less resilient to disturbances than vegetated and natural beach segments. As the natural balance of sediment transport across the littoral active zone is disrupted in armored beaches (Dethier et al. 2016), their physical characteristics and biological assemblages are more strongly affected by natural disturbances (e.g., waves) and extreme climatic events (e.g., storms) and have less recovery capacity compared to beaches with natural backshores and dunes (Lucrezi et al. 2010; Witmer & Roelke, 2014; Machado et al. 2016). As a result of this chronic disturbance, armored beaches seem to shelter less abundant communities than vegetated beaches.

The population approach (pitfall traps) reinforces that armored beach segments could be under chronic disturbance, presenting lower abundances and biomass of *Phaleria testacea* than vegetated beach segments. Both beaches evaluated showed steeper face slopes on armored segments than on vegetated segments, which usually signals an intensification of the erosion process due to extreme climatic events or even due to natural chronic wave energy, intensified by reflection of the armoring (Lucrezi et al. 2010; Machado et al. 2016). Santa Rita Beach is narrower than Dura Beach with a higher level of interaction between the seawater and the armoring, which makes it more susceptible to flooding and more affected by coastal armoring (Vousdoukas et al. 2020; Jaramillo et al. 2021). This can explain why the lower biomass of *P. testacea* on the armored than the vegetated segment was mainly observed on Santa Rita Beach. Another possible explanation is that *P. testacea* is indirectly affected by the reduction of beach wrack caused by the coastal armoring. Coleopterans tenebrionids such as *P. testacea* are deposit-scavenger insects that feed on organic debris present in wrack patches (Colombini et al. 2002; Olabarria et al. 2007). Previous studies have shown that coastal armoring alters the amount of beach wrack due to the disruption of the marine-terrestrial connection, which ultimately constrains wrack-associated invertebrates (Heerhartz et al. 2014; 2015). In addition to improving beach resilience, backshore vegetation also seems to play an important role in the retention of sediment moisture in some cases, as we observed for Dura Beach. Sediment water content is usually positively related to the abundance of supratidal arthropods because high moisture prevents desiccation (e.g., Lucrezi et al. 2009), which may have contributed to the reduction in abundance observed on the armored segment of this beach. However, the amphipod *Atlantorchestoidea brasiliensis* was not affected by coastal armoring on either beach. This means that the effect of coastal armoring seems to be species dependent and may also vary with beach features.

This species-dependent effect of coastal armoring implies distinct sensitivities of the species and, consequently, different functional compositions between vegetated and armored beaches. For instance, abundant species with large body sizes, such as *Scoloplos treadwelli*, and with high-marine motility, such as *Armandia* sp., and predators such as *Hemipodia* sp. and the family Goniadidae were negatively related to coastal armoring, which contributed to a high affinity of the vegetated beach community with these trait modalities. Predatory species, with large body sizes and high-marine motility, are common in the lower zones of the beach, which was most impacted by coastal armoring in the present work. A recent study on southeastern Brazil showed that beach subtidal zones sustained the most complex benthic community in the across-shore beach gradient, but were also the most impacted by urbanization (Corte et al. 2022), which can explain the impacts on the functional traits connected to this zone. Conversely, suspension feeders with small body sizes were more associated with armored beaches, suggesting that they are less sensitive to coastal armoring. These are mainly small decapods of the family Pinnotheridae (mainly *Austinixa aidae*). Areas under high erosion, which armored beaches are more prone to, are usually dominated by suspension feeders, mainly because the erosion process contributes to nutrient suspension in the water column (MacMillan et al. 2017). These patterns suggest that although armored and vegetated beaches have the same values of functional richness, they present different dominant groups connected to distinct traits, signaling that such beaches may provide different functions and ecosystem services.

The vegetated beaches evaluated here seem to be central to organic matter transfer in sandy beach ecosystems for the study area. Our results show that a vegetated backshore on beaches can sustain high-abundance communities, with high biomass populations and species that could reach larger body sizes than those on armored beaches. Based on this, we can assume that the service of biomass stock and transfer is better performed by vegetated beaches and could be highly vulnerable to coastal armoring. This assumption is supported not only by our data but also by a set of works identifying reductions in benthic abundance and biomass as one of the most noticeable coastal armoring impacts on sandy beaches (Lucrezi et al. 2009; Dugan et al. 2008; Sobocinsk et al. 2010; Dugan et al. 2018; Jaramillo et al. 2021). This loss of transference of benthic biomass on armored beaches can be accompanied by a reduction in the abundance of top predators such as shorebirds that feed on benthic species (Dugan et al. 2008). We also noted differences in the main feeding strategies for the benthic community related to coastal armoring, which also suggests a more complex food web on vegetated beaches due to the occurrence of predatory polychaetes. In fact, coastal development and other human disturbances have great potential to have negative implications for trophic functioning on sandy beaches (Reyes-Martínez et al. 2015; Costa et al. 2017). This suggests that more than causing a loss of benthic abundance and biomass, coastal armoring could impact organic matter flux across the food web. Despite these human impacts, armored beaches may still sustain important biological functions and services. For instance, suspension feeders, which have a higher prevalence on armored beaches, are critical to the filtration and purification of coastal waters as well as to nutrient cycling in the water column (e.g., Welsh et al. 2003, Vozzo et al. 2021).

Our data also suggest the importance of morphodynamics for the distribution of species and functional traits across beaches. We noted that coastal armoring impacts on polychaetes depend on the morphodynamic stage since the highest values of abundance for this group are only found in not-armored beaches toward more dissipative states (high BI). This result corroborates recent investigations showing that human stressors impact macrofauna differentially according to sandy beach type (Costa et al. 2022). The BI was also positively related to taxonomic richness in the subtidal zone, indicating that beaches with flat topographic profiles and fine sediments sheltered more species. Although it is a pattern largely recognized in the literature (Defeo and McLachlan 2005; McLachlan and Dorvlo 2005; Lercari and Defeo 2006; Checon et al. 2018), we also found new evidence that many functional traits have modalities related to the BI, such as scavenger species, short-planktonic and non-planktonic larval dispersion, low-marine adult motility, and lifespans greater than 2 years (Fig. 4.5). Furthermore, we found greater abundance and biomass among supratidal arthropod populations on Santa Rita Beach (intermediate beach) than on Dura Beach (dissipative beach), mainly on the vegetated segments, also suggesting a morphodynamic effect. Dissipative beaches are recognized to present less abundant arthropod fauna than intermediate or reflective beaches (Barboza et al. 2012; Degli et al. 2021). These results signal the need for new approaches using a gradient of beaches ranging from dissipative to reflective to investigate and account for the influence of morphodynamics on the functional structure of macrobenthic communities, considering also their possible interactions with human disturbances.

As the effects of coastal armoring are expected to worsen with the predicted climate change impacts, the results presented here suggest some potential future scenarios for armored sandy beaches. Considering the predicted sea-level rise and increase in storm events, communities of armored beaches are not expected to maintain high biomass stock and abundance patterns similar to those of not-armored beaches. This result is expected since coastal armoring reduces beach resilience to climatic events (Lucrezi et al. 2010; Witmer & Roelke, 2014; Machado et al. 2016), indicating a synergistic effect connecting local (coastal armoring) and global (climate change) disturbances. Additionally, armored narrow beaches such as the ones studied here are at serious risk of being fully submerged by the end of the century (Slott et al. 2006; Cooper et al. 2020; Defeo et al. 2021). Although suspension feeders, the most prevalent feeding guild of armored beaches, require submersion to feed, many of them are intertidal organisms (Amaral et al. 2016), and they would suffer negative consequences due to a loss of intertidal habitats. Last, climate change conditions are also changing the morphodynamics of beaches across the world (Schlacher et al. 2008; Scapini et al. 2019), and advances in the recognition of the influence of beach characteristics on the functional and taxonomic structure of assemblages are needed to predict outcomes of this impact on armored beaches.

We conclude that coastal armoring can reduce the abundance and biomass of macrobenthic communities and populations, generating a species-dependent effect that is variable on different types of beaches. With regard to beach functioning, armored and vegetated beaches seem to present a predominance of distinct functional groups, which are responsible for important processes for maintaining beach functioning. Therefore, our results reveal the impacts of man-made structures on beach biodiversity and functional composition, highlighting the potential for coastal armoring to hamper biodiversity services on sandy beaches. Finally, our results draw attention to the urgent need for new conservation strategies that preserve the connection between beaches and dunes/coastal plains to deal with local changes, especially considering the potential for synergistic impacts of global changes.

5. CHAPTER IV: EFFECTS OF NATURAL AND ANTHROPOGENIC STORM-STRANDED DEBRIS IN UPPER-BEACH ARTHROPODS: IS WRACK A PREY HOTSPOT FOR BIRDS?

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Abstract

Allochthonous debris (wrack) that are stranded on sandy beaches are important components for the functioning of these ecosystems. In the current global change context, wrack deposition tends to change as the extreme-storms events increases, and it is needed to understand how different types of debris can affect beach biodiversity. Here, we hypothesized that natural debris (i.e., algae and land-plant debris) optimize the short-term aggregation of benthic arthropods on the beach ecosystem, while anthropogenic debris (i.e., plastics) does not perform this function. We also expected that the potential short-term aggregation of arthropods in the natural debris would create a transient prey hotspot (i.e., points of high prey concentration) for birds on the beach ecosystem. To test these hypotheses, we performed manipulative-field experiments with debris addition and predator exclusion by cages on a short temporal scale (maximum 20 days). We found that natural debris aggregated higher community abundances than anthropic debris and also higher than treatments without debris, while community richness was not affected by wrack. No differences were noted comparing the community aggregation on plastic debris and treatments without debris. The coleopterans were the group responsible for this aggregation, mainly represented by *Phaleria testacea*, which aggregated on natural debris with abundances five times greater than on plastic debris and control sites. However, we did not find any evidence of increased predation by birds on the coleopterans aggregated in the natural debris. We conclude that the arthropod aggregation in the wrack is a phenomenon primarily associated with natural debris, not occurring in plastic debris, although the role of this faunal aggregation as a prey hotspot for birds was not evident in short term. These results showed that the wrack type matters in terms of consequences for beach arthropods, bringing an alert against beach cleaning methods that are adopted indiscriminately, also signaling the need for long-term studies to proceed with investigating the wrack functions for top predators on sandy beaches.

Keywords: Benthic macrofauna**,** algae debris, land-plant debris, plastic pollution, predator exclusion, *Phaleria testacea*.

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* *Unpublished paper*

5.1 Introduction

Sandy beaches are coastal ecosystems largely appreciated by human society. The conservation of beach landscapes for human uses is strongly dependent on a complex web of natural relationships that maintain their ecological balance. For instance, allochthonous debris stranded on sandy beaches, known worldwide as "wrack", are important components for maintaining biodiversity and functioning in these ecosystems (e.g., Dugan et al. 2003; Innocenti et al. 2018; Rodil et al. 2019). Sandy beaches naturally have low primary production, thus wrack, composed mainly of macroalgae debris, plays a key role as an allochthonous carbon source on the base of the trophic web (Lercari et al. 2010; Reyes-Martínez et al. 2015). Despite the need of maintaining this natural process for sandy beaches conservation, the 21st century began oppositely, with fast and intense coastal urbanization, an increase in marine litter, and the growing impacts caused by climate changes (Defeo et al. 2009; 2021). All these threats have great potential to impact beach features including the wrack deposition patterns, which can affect the ecological balance of these ecosystems in a near future (Defeo et al. 2021).

Many benthic species on sandy beaches use the wrack as food or shelter (Colombini et al. 2000; Ruiz-Delgado et al. 2014). Wrack-associated biodiversity is mainly the arthropod macrofauna, including upper-beach insects, such as the coleopterans, and crustaceans such as isopods and amphipods (e.g., Colombini et al. 2000; MacMillan et al. 2016; Lowman et al. 2019). Changes in wrack coverage on the sediment surface can therefore affect the macrofaunal aggregation (MacMillan et al. 2016; Schlacher et al. 2017), the species activity (Fanini et al. 2016), and, consequently, the organic-energy flux on the ecosystem (Gómez et al. 2018; Lowman et al. 2019; Rodil et al. 2019). Moreover, wrack deposition on beaches is strongly associated with the occurrence of extreme climate events (Pattiaratchi & Wijeratne 2019; Defeo et al. 2021), which highlight the importance of understanding the biodiversity-wrack relationship in the current global change context.

The frequency and intensity of extreme-storms events are increasing worldwide due to global changes (Elsner et al. 2008; Lin & Emanuel 2016). In this regard, changes in wrack deposition are also ongoing worldwide (Defeo et al. 2021) and are expected to be different according to the context of each beach. This expectation is supported by the fact that the amount and composition of wrack stranded on each beach after an extreme-storm event are different depending on many factors. The beaches' geographic location (Ruiz-Delgado et al. 2014), their morphodynamic features (Orr et al. 2005; Gómez et al. 2013) and their proximity to anthropogenic structures (Strain et al. 2018; Pattiaratchi & Wijeratne 2019) or estuarine mouths

(Ruiz-Delgado et al. 2015) are examples of factors that can influence the wrack stranded on sandy beaches. Wrack composition can include different macroalgal species (Rodil et al. 2019) but also land-plant debris (Ruiz-Delgado et al. 2014; 2015), seagrass (Colombini et al. 2009), bryozoans (Rörig et al. 2017) or marine litter such as plastic (Esiukova 2017), with possibly different consequences for the beach ecosystem.

Most of the previous studies comparing the effect of different types of wrack debris on beaches focused on distinct macroalgal species and their effects on benthic macrofauna. These contributions showed that, while some macroalgal species can improve benthic productivity, such as the kelps (Schlacher et al. 2017), others can negatively affect macrofaunal species, such as the red macroalga (Heery 2018). The properties of the different types of wrack such as morphology (Gómez et al. 2013), water retention capacity (Rodil et al. 2008), and nutritional value (MacMillan & Quijón 2012) are determinants variables that influence the responses of benthic biodiversity. Other common types of wrack such as land-plant debris or plastics are still neglected in these comparisons, with rare exceptions, and their effects on the macrofaunal aggregation and the possible ecosystem consequences are still unknown. As a result, beach cleaning is largely adopted indiscriminately, removing beach debris without concerns about the wrack type and their possible ecological role (Zielinskia et al. 2019).

Wrack deposition could be particularly important for predatory birds that use benthic biodiversity as food on sandy beaches. Shorebirds usually forage in intertidal and supratidal habitats (Hidalgo et al. 2010; Horn et al. 2020; Schlacher et al. 2017), feeding on macrofaunal species that are usually aggregated in wrack deposition zones on sandy beaches (Dugan et al. 2003; Schlacher et al. 2017). Many species of birds, including migratory ones (Leal et al. 2013), are top predators on beaches and feed mainly on amphipods, isopods, and insects available in the sediments (McLachlan et al. 1980; Pinotti et al. 2014; Lercari et al. 2010; Reyes-Martínez et al. 2015). In the current global change context, shorebirds are already strongly threatened, demonstrating a clear reduction in their populations in recent years (Clemens et al. 2016). This scenario is potentially worsened considering that its prey species associated with the beach wrack could be greatly vulnerable to global changes and human interventions (Schooler et al. 2017). Therefore, understanding the patterns of macrofaunal wrack aggregation and prey availability can support birds' conservation strategies in the current scenario (Dugan et al. 2003; Schlacher et al. 2016; 2017).

Based on that, here we aimed to evaluate the effects of different types of storm-stranded wrack (natural and anthropogenic debris) on the benthic macrofauna, focusing on the upper-beach arthropod fauna and investigating the potential short-term consequences of these effects for predatory birds on the beach ecosystem. Considering that different wrack properties, including their nutritional value, can be determinant of their effects on benthic macrofauna (Rodil et al. 2008; MacMillan & Quijón 2012) and that wrack could improve the prey availability for birds (Schlacher et al. 2017), we tested the following hypotheses: (1) That natural organic wrack such as marine macroalgae and land-plants debris optimize the short-term aggregation of benthic arthropods on the beach ecosystem, while anthropogenic artificial debris, such as plastics, does not perform this function; (2) That the potential short-term aggregation of arthropods in the natural-wrack stranded on the beach ecosystem creates transient prey hotspots (i.e., points of high prey concentration) used by birds. Therefore, we expected that the natural-wrack deposition on sandy beaches would momentarily aggregate macrofauna individuals which would be predated by birds on a short temporal scale.

5.2 Materials and methods

5.2.1 Study area

The present study was developed on the north coast of the São Paulo State, located on the southeastern coast of Brazil (Fig. 5.1-A). This subtropical region is characterized by several sandy beaches exposed to different types of wrack, including natural and anthropogenic debris (e.g., Ruiz-Delgado et al. 2015; Moreira et al. 2016;). The diversity of wrack types on the southeastern coast of Brazil occurs because this region simultaneously has preserved rocky shores with abundant macroalgae (e.g., Pardal-Souza et al. 2017), estuaries that bring land-plant debris to the coastal zone (Ruiz-Delgado et al. 2015), and high levels of urbanization, including great waste sources such as ports and touristic cities (Izar et al. 2019; Ribeiro et al. 2021). Additionally, this region is severely submitted to frequent extreme-climate events (e.g., Machado et al. 2016; Corte et al. 2017), which contributes to the wrack deposition on their beaches.

We specifically chose Juréia beach, located in the São Sebastião city, as a model area to design experiments aiming to test our hypotheses (Fig. 5.1-A and 5.1-B). Juréia beach is an exposed intermediate to reflective beach with a preserved and vegetated supratidal zone (authors personal observation), adequate for the maintenance of an abundant benthic and bird fauna. Moreover, previous visits to Juréia beach after storms revealed its wrack composition encompasses a great diversity of debris, mainly mangrove-plant debris (leaves and propagules), macroalgae of the species *Sargassum* sp. and *Ulva* sp., and macroplastic waste (discardable cups, bags, or packing). Due to these features, we considered Juréia beach as a good model to perform our experiments.

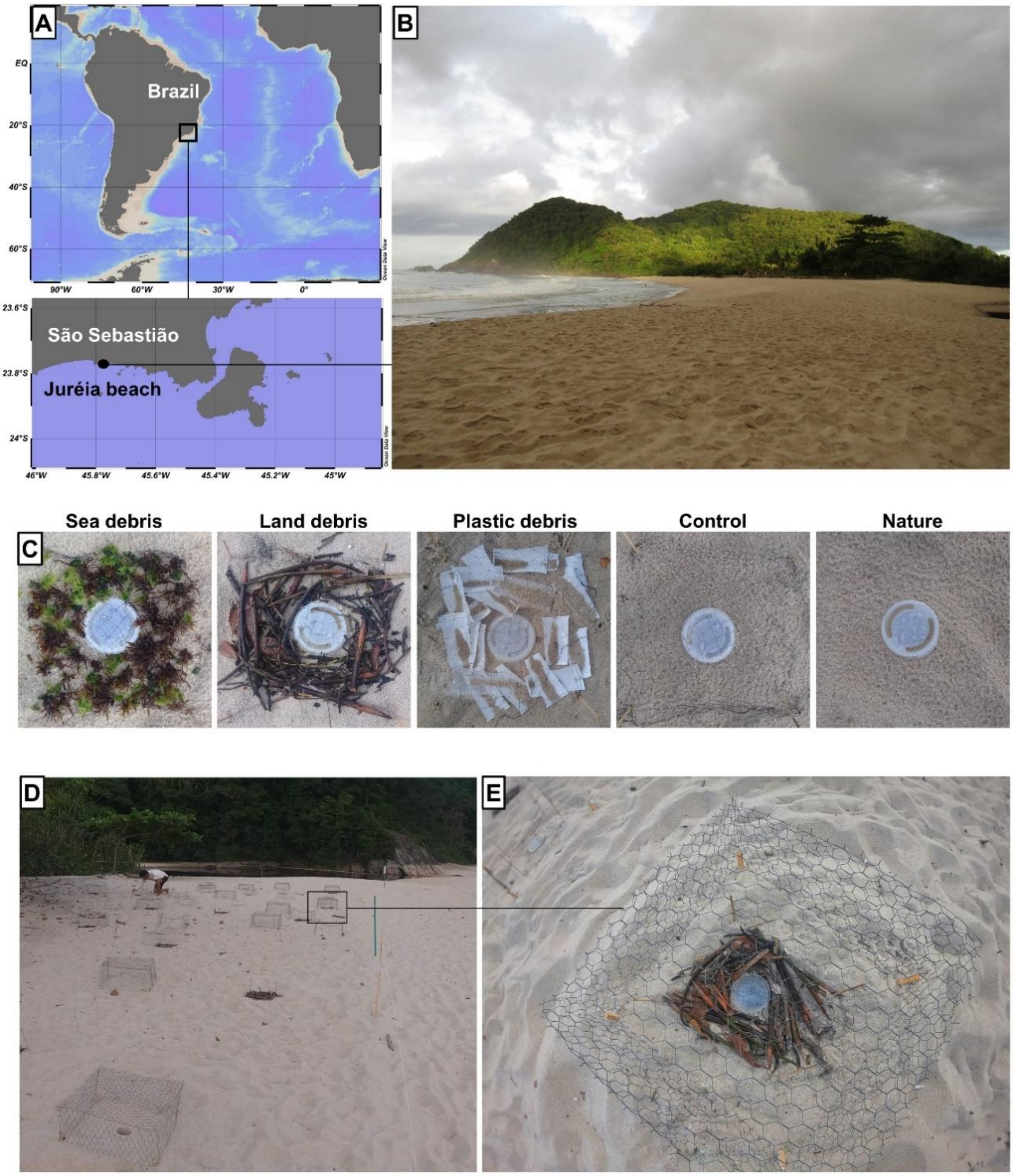

Figure 5.1. (A) Study area, located in São Sebastião city, north coast of the São Paulo State, southeastern coast of Brazil. (B) Photographic record of Juréia beach, where the experiments were carried out. (C) Experimental units (squares) illustrating the five treatments used for the aggregation experiment, with a pitfall trap closed in their middle. (D) Photographic record with an overview of the predation experiment during the installation process. (E) Photographic zoom with an experimental unit of the predation experiment, illustrating the treatment with land debris, pitfall trap, and closed cage for predator exclusion.

5.2.2 Experimental design

5.2.2.1 Aggregation experiment

To test our first hypothesis regarding the short-term macrofaunal aggregation in different types of wrack, we performed a manipulative field experiment with debris addition on the sediment surface. First, we established an experimental area 200 m long (parallel to the shoreline) and 5 m wide (perpendicular to the shoreline) in the upper supratidal zone at the west border of Juréia beach. Across this area, we design 120 experimental units (squares with 0.3 m x 0.3 m), separated by at least 1 m, to further addition of debris treatments.

We randomly classified the squares in five experimental treatments (Fig. 5.1-C), resulting in 24 squares per treatment. Three of the five experimental treatments were submitted to the addition of different types of debris (Fig. 5.1-C), as follows: (1) Sea debris, squares with the addition of macroalgae debris composed of a mix of *Sargassum* sp. and *Ulva* sp.; (2) Land debris, squares with the addition of land-plant debris composed by a mix of propagules, branches, and leaves of *Rhizophora mangle* and other mangrove species such as *Avicennia schaueriana* and *Laguncularia racemosa*; (3) Plastic debris, composed only by discardable plastic cups minced. All these types of debris were added to their respective squares, covering the sediment surface within each square. To avoid losing debris to the winds, we installed a contention net (3 cm mesh) over the squares, fixing the net in the sand with small wooden sticks. The squares related to the other two treatments did not have debris addition (Fig. 5.1-C) and were classified as follows: (4) Control, squares with no addition of debris but with the contention net; (5) Nature, squares with no addition of debris and without contention net (bare sand, not manipulated). The use of these two treatments without debris was important to detect the eventual effects of the contention net in the fauna aggregation. They are also important to identify the natural patterns of the macrofauna and their temporal variations in conditions without manipulation.

All the natural debris (sea and land debris) added to the squares were sampled on the beach and were previously washed to remove eventual organisms that possibly were on the debris before the beginning of the experiment. We sampled only fresh debris and, when we did not find fresh macroalgae in enough amount on the beach sand, we sampled them from the adjacent rocky shores using a spatula. The plastic debris added were standardized, taken only from unused/new plastic cups considering that the plastic cups available on the beach sand were not enough and had unknown origin and ages, hampering the standardization.

Before adding the wrack on the squares and aiming to capture the arthropod community that would aggregate there, we installed pitfall traps in the sand within each square of all treatments. Following Schlacher et al. (2017), the pitfall traps had dimensions of 7.5 x 11 cm (opening diameter x height). We buried each trap into the sediment, in the middle of each square, leaving the pitfall opening leveled with the sand surface. To prevent the escape of the organisms that would be captured, we filled 75% of the pitfall's internal volume with a solution of detergent and seawater (Schlacher et al. 2017).

The experiment was performed in March 2021 and we evaluated the macrofaunal aggregation on the squares in three different short-time periods. With this goal, we randomly selected one-third of the squares (40 squares, eight per treatment) to remain installed for 12 hours (between 6 p.m. and 6 a.m. on the first experimental day). Next, another random third of the squares, also with the treatments balanced (eight squares per treatment), remained installed for 84 hours (beginning at 6 p.m. and finishing three days later at 6 a.m.). The last third of the squares remained installed for 156 hours (beginning at 6 p.m. and finishing six days later at 6 a.m.). For all squares, independent of the time period and treatment, the pitfall traps remained closed and were opened to capture the macrofauna only during the last 12 hours (at night, between 6 p.m. and 6 a.m.) before the respective uninstallation of each square. In this sense, although we have different experiment times (12, 84, and 156 hours), the sampling effort of all experimental units was the same (12 hours).

After running the experiment time of each square, we estimated the microclimatic conditions of all of them before removing the pitfall traps. In this regard, we measured the sediment-surface temperature and water content at each square using a digital thermo-hygrometer, totalizing eight squares measured per treatment at each experiment time. Next, we removed the traps from the sand and filtered their content in a mesh of 0.5 mm, retaining the organisms that were captured. The individuals found were preserved in 70% alcohol and, at the lab, they were identified to the lowest possible taxonomic level.

5.2.2.2 Predation experiment

To test our second hypothesis regarding the short-term predation of the arthropods by birds on natural wrack, we perform a manipulative experiment with debris addition and predator exclusion by cages in March 2021 (Fig. 5.1-D). This second experiment focused on the coleopteran *Phaleria testacea* as an arthropod model. This choice is justified by the results of the first experiment, which showed this species as the most abundant and most associated with the natural wrack (see the Results section). Thus, here we tested whether the short-term aggregation of this species on natural wrack could create food hotspots for predatory birds that eventually may feed on *Phaleria testacea*. We expected that, if the birds used the wrack as a prey hotspot, the *P. testacea* abundance would be higher in treatments with predator exclusion than in treatments with predator access.

With this goal, we established an experimental area 150 m long (parallel to the shoreline) and 5 m wide (perpendicular to the shoreline) in the upper supratidal zone at the east border of Juréia beach. Similar to the previous experiment, we design 90 squares with 0.3 m x 0.3 m (experimental units), separated by at least 1 m each, across the experimental area. First, we randomly classified the squares in three experimental wrack-treatments (30 squares per treatment), which were: (1) Land debris, a mix of leaves, branches, and propagules of mangrove plants; (2) Control, without debris and with a contention net; and (3) Nature, without debris and also without a contention net. All these three wrack-treatments were installed as described above for the previous experiment. Moreover, we only used land debris as a model of natural debris for this experiment because they are the most common and most easy to sample on the beach studied, compared to the sea debris.

Secondly, we randomly submitted the 30 squares of each wrack treatment to three predator exclusion treatments (ten squares for each predation treatment at each wrack treatment). The predation treatments were: (1) Closed cages, total exclusion of predators; (2) Opened cages, with the cage structure but with predators' access; (3) Absent cages, without cage and with predators' access. The cages were metallic and cubic, with 0.5 m side and 3 cm grid, fixed on the sandy by wooden stakes (Fig. 5.1-E). The squares remained installed in the middle of the cages, with 0.1 m of distance between the square border and the cage border. The opened cages had all sides (including the upside) with half of the grid removed, allowing the access of the predatory birds. This treatment with opened cages was important to test the eventual effects of the cage structure on *Phaleria testacea*, not related to the predation by birds.

The experiment remained installed for 20 days and, identical to the described for the previous experiment, all squares had a pitfall trap on their middle to capture the prey and further compare their abundance between treatments. The pitfall traps remained closed during the 20 days and were opened to capture the *Phaleria testacea* individuals only during the last 12 hours before the uninstallation of the experiment, at the night (between 6 p.m. and 6 a.m.). Similar to the previous experiment, we also estimated the microclimatic conditions (temperature and water content of the sediment surface) of the squares before sampling the fauna. For this experiment, we also measured the luminosity of the squares, using a digital luximeter, aiming to detect eventual shading effects related to the cages. Next, we removed all pitfall traps, filtering their content and sampling the organisms captured, as described in the previous experiment.

Aiming to test whether the eventual predation effects were not restricted to the abundance of individuals active at the sediment surface, which were captured by the pitfall traps, we also evaluated the abundance of individuals buried in the sediment of all squares. To fill this goal, when the experiment was finished, we collected three sediment sub-samples with a 15 x 5 cm corer (diameter x depth) per square and sieved them to remove the individuals of *Phaleria testacea*. All individuals found (on the pitfalls and corers) were preserved in 70% alcohol. At the lab, we counted the number of individuals per square, registering the abundance of the buried ones (summing the sub-samples) and also of the ones captured by pitfall (the surface-active individuals).

Assuming that the predation effects could be related to the prey body sizes (i.e., large individuals would be easier predation targets), we also measured the total length of all captured individuals using a ruler coupled to a stereo-microscope. After that, we classified the individuals into “small organisms”, the ones with body lengths lower than the local-population mean length (<6,5 mm), and “large organisms”, the ones with body lengths equal to or higher than the local-population mean length (≥6,5 mm).

We also monitored the birdlife on the beach during the experiment, aiming to identify possible predatory species visiting our experimental squares. In this regard, we randomly chose 8 of the 20 experiment days (sampling events) to perform a bird-species survey on the beach and in the experimental area. We performed the bird’s observation using the method "fixed point count" (Bibby et al. 1992) and two people performed the observations at all sampling events. We choose a fixed point that allowed us the entire beach view, located ~100 m off the experimental area, aiming to avoid scaring away the birds. All sampling events lasted three hours in the mornings (between 6 a.m. and 9 a.m.). We also used binoculars and photo cameras (64x digital zoom) to assist the species identification. For all sampling events, we registered the number of occurrences and individuals’ abundance for each bird species, differentiating occurrences inside and outside of the experimental area. Only individuals that were seen foraging on the sand were considered for the register.

5.2.3 Data analysis

5.2.3.1 Aggregation experiment

We performed Generalized Linear Models (GLMs) to evaluate how the microclimatic conditions and the arthropods aggregation on the experimental squares were influenced by the wrack type considering the distinct experiment times. First, regarding the microclimatic parameters measured, a model was applied considering the sediment-surface temperature per square as the response variable while another model was applied considering sediment-surface water content per square as the response variable. With regards to the faunal patterns, one model was applied for the community abundance (response variable: total number of individuals per square) and another for the community richness (response variable: total number of taxa per square). We also calculated the abundance per square of the main taxonomic groups found (i.e., coleopterans, hymenopterans, dermapterans, and arachnids) and applied a model for each one of these groups. All models included two fixed factors as predictors: (1) "Wrack-treatment", five levels (Sea debris, Land debris, Plastic debris, Control, and Nature); (2) "Experiment time", three levels (12, 84, and 156 hours). We also included the interaction between these two factors as a predictor in all models aiming to test whether the wrack effect was dependent on the experiment time applied or whether the temporal variations were different depending on the wrack type.

Each model was adjusted to the family that provided a lower Akaike Information Criterion (AIC), indicating a higher likelihood (Bolker 2008). Accordingly, the model considering sediment temperature was adjusted to the Gamma family (inverse link function) and the model considering sediment water content was adjusted to the Gaussian family (identity link function). The models considering the community abundance and the abundance of the main faunal groups were adjusted to the Negative Binomial family (logarithmic link function), while the model considering community richness was adjusted to the Poisson family (logarithmic link function). Lastly, all models were submitted to the Likelihood Ratio Test (LRT) with the chi-square statistic, in order to identify which predictors provided significant losses of likelihood (considering $\alpha = 0.05$) when excluded from the full models (Bolker 2008). In case of significant effects observed, we applied the pairwise comparisons (z-statistic) between the levels of the factors.

5.2.3.2 Predation experiment

We also applied GLMs to test differences in the microclimatic conditions and in the *Phaleria testacea* parameters comparing the wrack-treatments and the predation-treatments of the experiment. We first applied separated models considering the three parameters measured regarding the microclimatic conditions of the sediment surface (response variables: temperature, water content, and luminosity). Next, we applied four models considering the *P. testacea* abundance per body size class and sampling method as response variables, which were: (1) total abundance of small organisms per pitfall trap; (2) total abundance of large organisms per pitfall trap; (3) total abundance of buried small organisms per square; (4) total abundance of buried large organisms per square. All models included two fixed factors as predictors: (1) "Wrack-treatment", three levels (Land debris, Control, and Nature); (2) "Predation-treatment", three levels (Closed cages, Opened cages, and Absent cages). We also included the interaction between these two factors as a predictor in all models aiming to test whether the predation effects were dependent on the wrack presence or whether the wrack effects changed with or without predation.

For this experiment, each model was also adjusted to the family that provided a lower AIC. Thus, the three models considering the microclimatic conditions were adjusted to the Gamma family (inverse link function) and the four abundance models were adjusted to the Negative Binomial family (logarithmic link function). All models were also submitted to the LRT with the chi-square statistic and, in case of significant effects observed (considering $\alpha = 0.05$), we applied the pairwise comparisons (z-statistic) between the levels of the factors.

5.3 Results

5.3.1 Aggregation experiment

The microclimatic conditions of the experimental squares, considering all experiment times and wrack treatments, presented a sediment-water content with a mean of 60.2 % (minimum = 21 %; maximum = 97 %). Sediment surface temperature, in turn, showed an overall mean of 38.1 ºC (minimum = 27 ºC; maximum = 53 ºC). Both these parameters had greater variations between experiment times than between wrack treatments (Fig. 5.2). In general, the squares sampled after 84 hours presented greater water content and lower temperatures than those sampled after 12 and 156 hours (Fig. 5.2). Despite some specific factors' interactions (Tab. 5.1), wrack effects on the microclimatic parameters within each experiment time were not observed. The unique effect noted was that "Land debris" presented lower temperatures than "Plastic debris" in the shortest experiment time (Fig. 5.2).

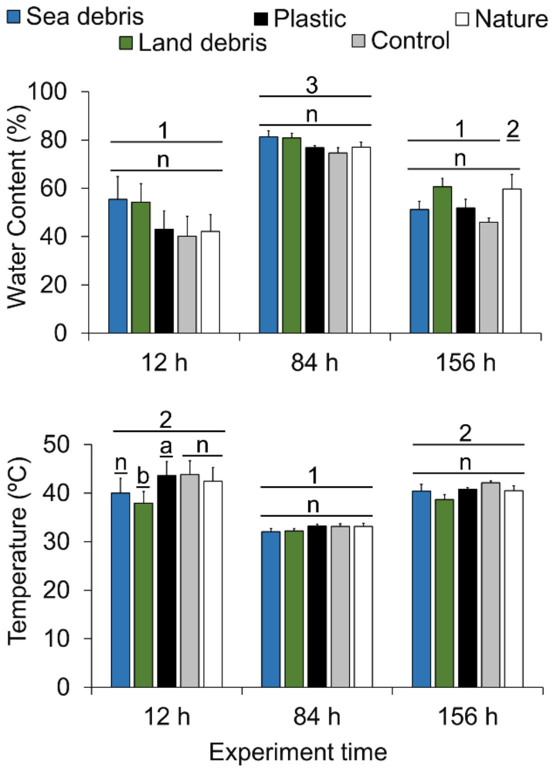

Figure 5.2. Water content and temperature (mean ± standard error) of the sediment surface in the experimental squares that were designed to test the macrofaunal aggregation on different types of wrack. The colored bars indicate the five wrack treatments used while the x-axis presents the three experiment times that were performed. The letters on the top of the bars ("a", "b", and "n") signalize differences or no differences between wrack treatments within each experiment time, that were found on the pairwise comparisons. In this regard, "a" indicates values significantly greater than "b"; "n" indicates values without significant differences. The numbers on the bars ("1", "2", and "3") signalize differences between experiment times considering each wrack treatment, that were found on the pairwise comparisons. In this regard, "2" indicates values significantly greater than "1"; "3" indicates values significantly greater than "2" and "1". The horizontal lines group the bars for which the respective number or letter is valid.

We found a total of 502 individuals of 22 arthropod taxa considering all squares of the experiment. The coleopterans were the most abundant faunal group (173 individuals in total), which were strongly represented by the species *Phaleria testacea* (161 individuals in total). The hymenopterans (i.e., ants) of the genera *Solenopsis* were the second most abundant group (121 individuals in total), followed by the dermapterans (87 individuals in total), the arachnids (49 individuals in total), and by the ants of the genera *Camponotus* (29 individuals in total). Other taxa were most rarely found and had low total abundances (i.e., less than 10 individuals in total), such as the amphipod *Atlantorchestoidea brasiliensis* and the isopods.

Table 5.1. Likelihood Ratio Test (LRT) with the chi-square statistic (Chi) and p-values (in bold when significant) applied from Generalized Linear Models (GLMs) designed considering the microclimatic conditions and the macrofaunal parameters observed in the aggregation experiment. The response variables of each model were sediment water content, sediment temperature, community abundance, community richness, and the abundance of the main arthropod groups found (Coleoptera, Hymenoptera, Dermaptera, and Arachnida). The predictors considered on the models were the wrack-treatment ("Wrack", five levels: Sea debris, Land debris, Plastic debris, Control, and Nature), the experiment time ("Time", three levels: 12, 84, and 156 hours), and the interaction between these two factors (Wrack x Time).

Predictors	**Sediment water content**		**Sediment temperature**	
	Chi	P	Chi	p
Wrack x Time	64.81	**<0.001**	95.13	**<0.001**
Wrack	77.44	**<0.001**	9.61	0.650
Time	144.10	**<0.001**	72.44	**<0.001**
	Community abundance		**Community richness**	
	Chi	p	Chi	p
Wrack x Time	2.04	0.361	6.39	0.604
Wrack	27.21	**0.007**	18.65	0.097
Time	14.43	0.154	8.05	0.624
	Coleoptera		**Hymenoptera**	
	Chi	p	Chi	p
Wrack x Time	193.30	**<0.001**	3.96	0.138
Wrack	96.97	**<0.001**	7.15	0.712
Time	8.97	0.535	17.40	**0.026**
	Dermaptera		**Arachnida**	
	Chi	p	Chi	p
Wrack x Time	7.10	**0.029**	10.95	0.205
Wrack	16.78	0.158	13.92	0.306
Time	20.96	**0.021**	11.38	0.329

The community abundance was affected by the wrack treatments and the pattern was independent of the experiment time (Tab. 5.1). In general, natural debris presented higher abundance values than anthropic debris and also higher than treatments without debris (Fig. 5.3). Sea debris presented almost double the abundance values compared to the plastic debris and presented about triple the abundance compared to the treatments control and nature. Land debris presented high abundance values, similar to those observed in sea debris, but not significantly higher than the values noted in plastic debris (Fig. 5.3). No differences were detected comparing the treatments control, nature, and plastic debris for the community abundance. We also did not find any effects of the wrack treatments or experiment times on the community richness (Tab. 5.1), although the number of taxa in the natural wrack treatments showed a tendency toward higher values than the other treatments (Fig. 5.3).

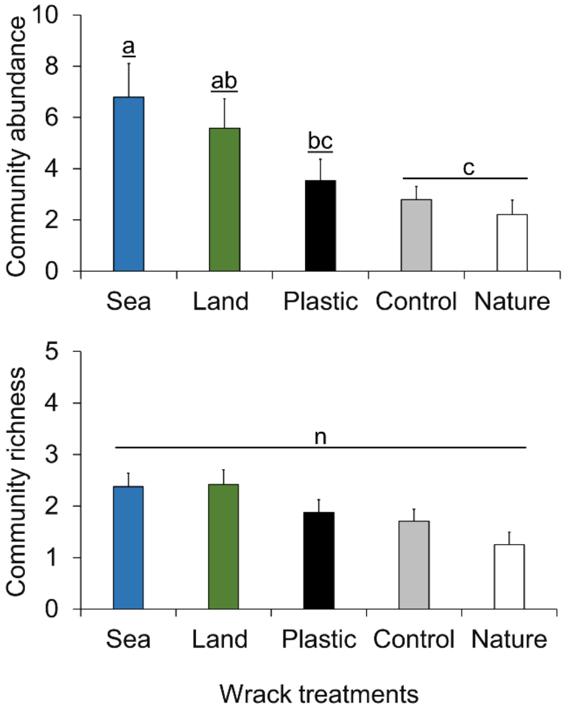

Figure 5.3. Mean ± standard error considering the arthropod community abundance (number of individuals per experimental square) and arthropod community richness (number of taxa per experimental square) in the five wrack treatments used for the aggregation experiment. The letters on each bar ("a", “ab”, “c”, "bc", and “n”) signalize differences or no differences between wrack treatments that were found on the pairwise comparisons. In this regard, "a" indicates values significantly greater than "bc" and "c" but not different from "ab"; "ab" indicates values not different from "bc" but greater than "c"; "bc" indicates values not different from "c". "n" indicates values without significant differences. The horizontal lines group the bars for which the respective letter is valid.

With regards to the principal faunal groups found, the coleopterans were the group most affected by the wrack treatments (Tab. 5.1; Fig. 5.4). For all experiment times, natural wrack aggregated almost five times more coleopterans individuals than the plastic and without-wrack treatments (Fig. 5.4). In general, coleopterans abundance was equal comparing plastic debris and without-wrack treatments, with exception of the 84 hours experiment in which only the treatments with debris, including plastic, presented coleopterans (Fig. 5.4). The hymenopterans, in turn, presented variations between experiment times, with great abundance after 12 hours, but without any effect of the wrack treatments (Tab. 5.1; Fig. 5.4). The dermapterans showed wrack effects dependent on the experiment time, with more abundance at the natural wrack treatments only in the shortest experiment time (Tab. 5.1; Fig. 5.4). Moreover, dermapterans tended to reduce their overall abundance at the natural wrack treatments as the experiment time increases. Lastly, we did not observe any effects of the wrack treatments or experiment times for the arachnids (Tab. 5.1; Fig. 5.4).

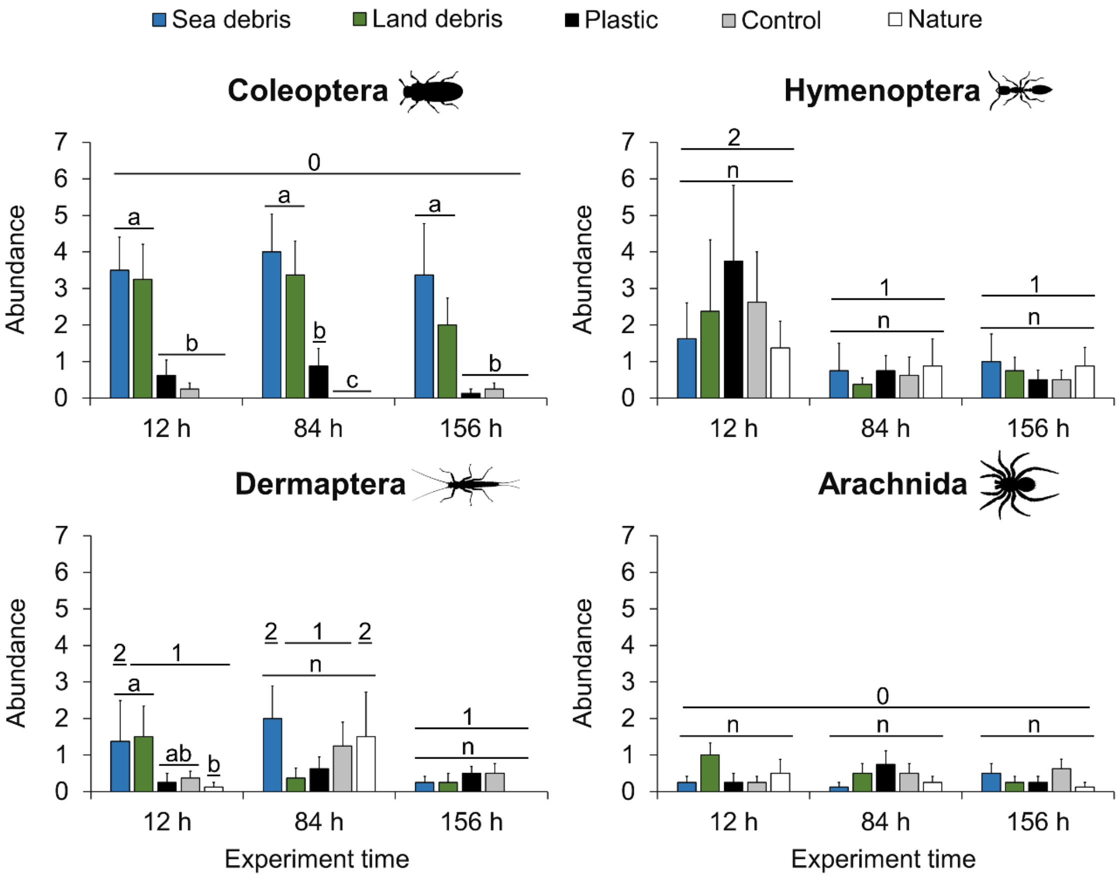

Figure 5.4. Mean ± standard error considering the abundance (number of individuals per experimental square) of the principal arthropod groups found in the five wrack treatments used and the three experiment times performed for the aggregation experiment. The letters on each bar ("a", “b”, “ab”, “c”, and “n”) signalize differences or no differences between wrack treatments within each experiment time, that were found on the pairwise comparisons. In this regard, "a" indicates values significantly greater than "b" and "c" but not different from "ab"; "b" indicates values significantly greater than "c"; "ab" indicates values not different from "b" but greater than "c”. "n" indicates values without significant differences. The numbers on the bars ("1", "2", and "0") signalize differences or no differences between experiment times for each wrack treatment, that were found on the pairwise comparisons. In this regard, "2" indicates values significantly greater than "1"; "0" indicates values without significant differences. The horizontal lines group the bars for which the respective number or letter is valid.

5.3.2 Predation experiment

The microclimatic conditions of the experimental squares, considering all wrack and predation treatments, presented a sediment-water content with a mean of 90.5 % (minimum = 79 %; maximum = 99 %). Sediment surface temperature, in turn, showed an overall mean of 24.1 ºC (minimum = 23 ºC; maximum = 25 ºC) while luminosity presented an overall mean of

441 lux (minimum = 237 lux; maximum = 659 lux). Only sediment temperature was affected by the wrack treatments (Tab. 5.2), presenting higher values at the land debris than on treatments without debris (Fig. 5.5). The predation treatments did not affect the microclimatic conditions of the experiment (Tab. 5.2; Fig. 5.5).

Table 5.2. Likelihood Ratio Test (LRT) with the chi-square statistic (Chi) and p-values (in bold when significant) applied from Generalized Linear Models (GLMs) designed considering the microclimatic conditions observed in the predation experiment. The response variables of each model were sediment-surface water content, temperature, and luminosity. The predictors considered in the models were the wrack-treatment ("Wrack", three levels: Land debris, Control, and Nature), the predation-treatment ("Cage", three levels: Closed, Opened, and Absent), and the interaction between these two factors (Wrack x Cage).

	Sediment microclimatic conditions					
Predictors	**Water content**		**Temperature**		**Luminosity**	
	Chi	p	Chi	p	Chi	p
Wrack x Cage	3.06	0.548	1.55	0.818	0.99	0.911
Wrack	3.76	0.709	21.69	**0.001**	1.53	0.957
Cage	6.04	0.419	10.04	0.123	5.40	0.494

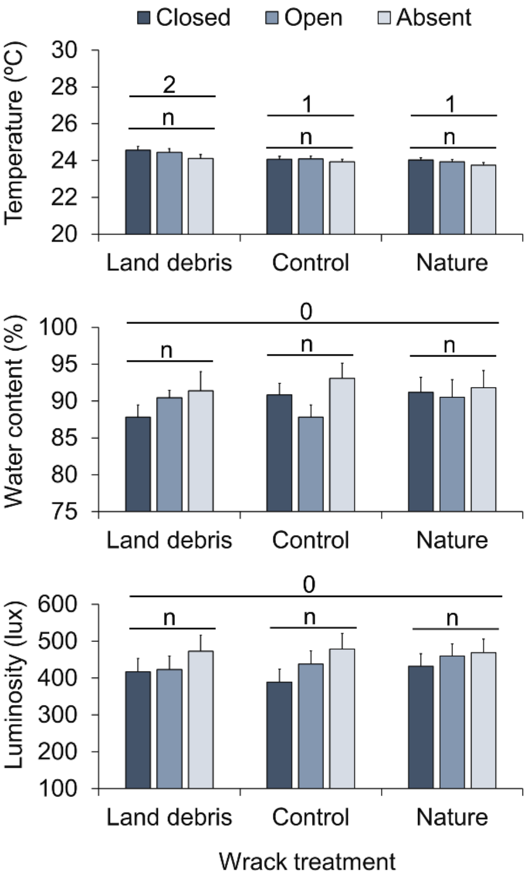

Figure 5.5. Temperature, water content, and luminosity (mean ± standard error) of the sediment surface in the experimental squares that were designed for the predation experiment. The colored bars indicate the three predation treatments (cages) used while the x-axis presents the three wrack treatments that were performed. The letter on the top of the bars ("n") signalizes no differences between predation treatments within each wrack treatment, that were

tested on the pairwise comparisons. The numbers on the bars ("1", "2", and "0") signalize differences or no differences between wrack treatments that were found on the pairwise comparisons. In this regard, "2" indicates values significantly greater than "1"; "0" indicates values without significant differences. The horizontal lines group the bars for which the respective number or letter is valid.

With regards to the *Phaleria testacea* population sampled at the experiment, we found a total of 964 individuals summing all treatments (wrack and predation treatments) and both sampling methods (pitfall and corer). Considering the surface-active individuals, captured by pitfall traps, we found a total of 289 individuals, 116 classified as small organisms and 173 classified as large organisms. Considering the buried individuals, sampled by corer, we found a total of 675 individuals, 388 classified as small organisms and 287 classified as large organisms. Independent of the body size class or the sampling method, we noted that *P. testacea* showed greater abundance values in the treatment with land debris than in the control and nature treatments (Tab. 5.3; Fig. 5.6). The predation treatments, however, did not affect the *P. testacea* abundance, independent of the body size class or sampling method (Tab. 5.3; Fig. 5.6).

Table 5.3. Likelihood Ratio Test (LRT) with the chi-square statistic (Chi) and p-values (in bold when significant) applied from Generalized Linear Models (GLMs) designed considering the *Phaleria testacea* population sampled in the predation experiment. The response variables of each model were the abundance of the body size classes (small organisms: body length < 6.5 mm; large organisms: body length ≥ 6.5 mm) considering the two sampling methods (pitfall: sampling the surface-active individuals; corer: sampling the buried individuals). The predictors considered in the models were the wrack-treatment (“Wrack”, three levels: Land debris, Control, and Nature), the predation-treatment (“Cage”, three levels: Closed, Opened, and Absent), and the interaction between these two factors (Wrack x Cage).

	Surface-active individuals			
Predictors	**Small organisms**		**Large organisms**	
	Chi	p	Chi	p
Wrack x Cage	5.41	0.248	7.00	0.136
Wrack	54.06	**<0.001**	53.90	**<0.001**
Cage	2.05	0.358	3.12	0.210
	Buried individuals			
	Small organisms		**Large organisms**	
	Chi	p	Chi	p
Wrack x Cage	3.46	0.484	1.03	0.905
Wrack	122.07	**<0.001**	105.93	**<0.001**
Cage	3.99	0.136	0.79	0.672

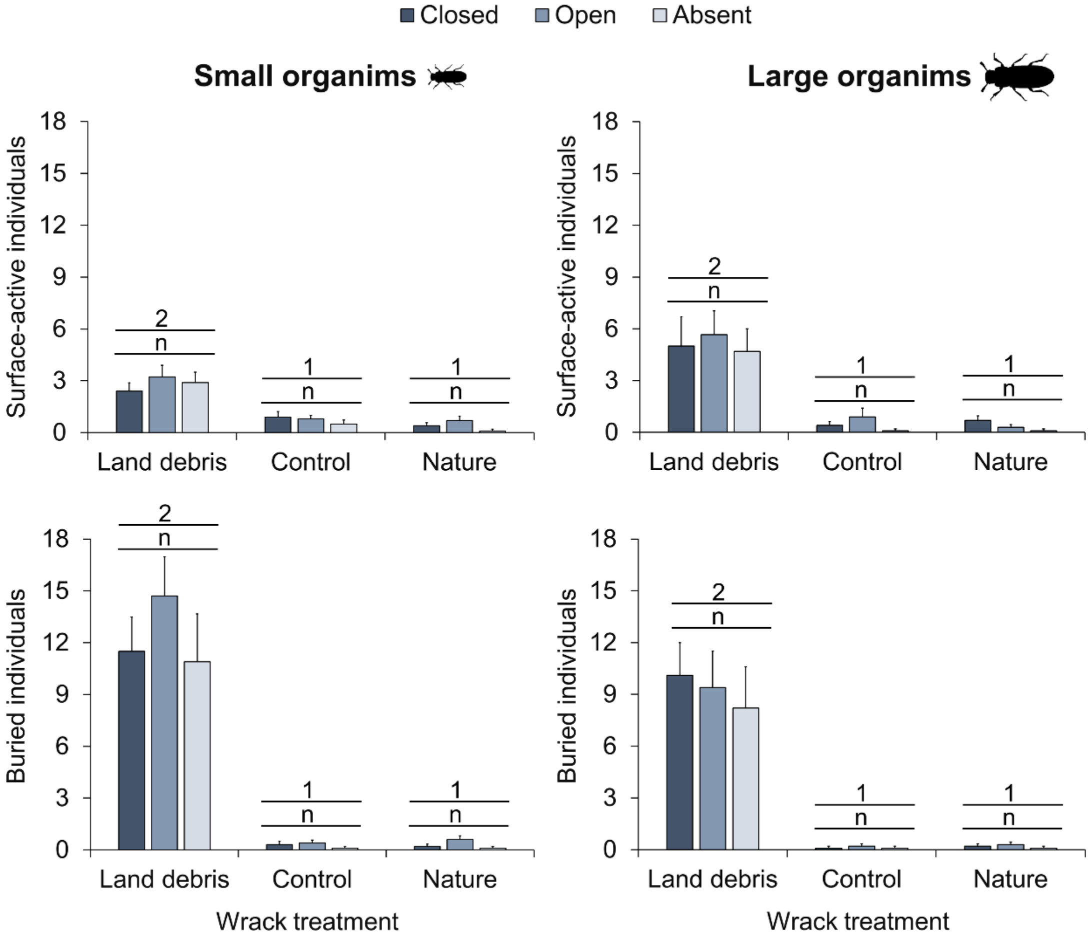

Figure 5.6. Mean ± standard error considering the abundance (number of individuals per experimental square) of the *Phaleria testacea* population found in the predation experiment, considering the two body size classes (small organisms: body length < 6.5 mm; large organisms: body length ≥ 6.5 mm) and the two sampling methods (pitfall: sampling the surface-active individuals; corer: sampling the buried individuals). The colored bars indicate the three predation treatments (cages) used while the x-axis presents the three wrack treatments that were performed. The letter on the top of the bars ("n") signalizes no differences between predation treatments within each wrack treatment, that were tested on the pairwise comparisons. The numbers on the bars ("1" and "2") signalize differences between wrack treatments that were found on the pairwise comparisons. In this regard, "2" indicates values significantly greater than "1”. The horizontal lines group the bars for which the respective number or letter is valid.

A total of 11 species were observed for the birdlife on the beach during the experiment (Tab. 5.4). Considering the entire beach, we observed a total of 105 bird individuals foraging on the sand, of which a total of 25 bird individuals were observed foraging inside the experimental area. The species *Vanellus chilensis* and *Pitangus sulphuratus* were the most frequent considering the entire beach, and, despite these species being seen in all sampling events, they were never seen inside the experimental area (Tab. 5.4). Conversely, the species *Aramides cajaneus* and *Caracara plancus* were the most frequently birds observed foraging inside the experimental area, followed by *Patagioenas picazuro* and *Fluvicola nengeta* (Tab. 5.4).

Table 5.4. List of the birdlife that was observed foraging at the Juréia beach, southeastern Brazil, during the predation experiment designed. (B): values considering the entire beach. (E): values considering only the experimental area.

Bird species	Frequency of occurrence (%)		Maximum abundance (individuals/day)		Mean abundance (individuals/day)	
	B	E	B	E	B	E
Vanellus chilensis	100.0	0.0	5	0	4.38	0.00
Pitangus sulphuratus	100.0	0.0	2	0	1.63	0.00
Aramides cajaneus	87.5	87.5	3	3	1.38	1.38
Caracara plancus	87.5	62.5	2	2	1.63	1.00
Machetornis rixosa	87.5	0.0	2	0	1.50	0.00
Patagioenas picazuro	50.0	25.0	3	3	1.13	0.50
Fluvicola nengeta	37.5	25.0	1	1	0.38	0.25
Ramphocelus bresilius	37.5	0.0	1	0	0.38	0.00
Myiozetetes similis	25.0	0.0	2	0	0.50	0.00
Milvago chimachima	12.5	0.0	1	0	0.13	0.00
Coragyps atratus	12.5	0.0	1	0	0.13	0.00

5.4 Discussion

In this work, we hypothesized that natural organic wrack stranded on the beach ecosystem would promote a short-term aggregation of benthic upper-beach arthropods while plastic debris would not cause this effect. We corroborated this hypothesis by showing that coleopterans, mainly the species *Phaleria testacea*, aggregated on natural-wrack debris with abundances five times greater than on plastic debris. No differences were noted comparing the community aggregation on plastic debris and treatments without debris, signalizing that plastic debris have no role in the arthropod's aggregation. We also hypothesized that this faunal aggregation on natural wrack would create transient prey hotspots for birds and, consequently, *P. testacea* would be predated by birds on a short temporal scale. We cannot corroborate this hypothesis since there is no evidence of predation by birds on the *P. testacea* population here studied. Therefore, we conclude that the upper arthropods aggregation in the wrack stranded on the beach is a phenomenon primarily associated with natural debris, not occurring in plastic debris. Despite this, the role of this faunal aggregation as a prey hotspot for birds was not evident on a short temporal scale in the study area.

The faunal aggregation on natural debris and not on plastic debris could be explained by their different properties. Algae and plants are organic debris that, besides providing shelter for benthic species, they can be used as food (Lastra et al. 2008; MacMillan & Quijón 2012; Suárez-Jiménez et al. 2017; Michaud et al. 2019). Coleopterans tenebrionid of the genus *Phaleria* are deposit-scavenger insects that can feed on a diversity of organic debris (Colombini et al. 2002; Olabarria et al. 2007). As a result, *Phaleria* could be found as the dominant wrack-associated taxa on the supratidal zone in different locations, such as beaches in southern Brazil (Ruiz-Delgado et al. 2014), in Italy (Colombini et al. 2009) and in the present study. Probably due to its diversified feeding mode, this coleopteran was equally abundant comparing algae and plant debris, as we noted here. Previous evidence suggests that *Phaleria testacea* is attracted by the organic decomposition of the natural wrack (Ruiz-Delgado et al. 2015), a process which is quickly performed by bacteria after the wrack deposition on the beach (Mews et al. 2006). Plastic debris, in turn, has no nutritional value and also is not quickly decomposed as the natural debris. Moreover, plastics may also not be a good shelter for benthic fauna as they can release contaminants into the sediment due to chemical additives which are previously incorporated into these products during the manufacturing process (Lambert et al. 2014). All these properties could turn the plastic debris less attractive to *P. testacea*, in comparison with natural debris.

Conversely, other abundant taxa here found such as the ants and spiders were not affected by the wrack presence. Ants of the genera *Solenopsis*, the most abundant hymenopteran of the present study, are opportunists and usually attracted by disturbances on the beach sand, which is common during the turtle nesting, for instance (Allen et al. 2001; Wetterer et al. 2014). It can explain the great abundance of ants at the beginning of our experiment since the sand disturbance promoted by the experiment installation could be attracted them, although without any specific affinity with the different debris deposited. The spiders, in turn, are carnivores and could be present on the wrack when the debris shelter a great abundance of potential preys, such as larvae of insects (Rodil et al. 2008). It was not the case in the present experiment and can justify the equal abundance of spiders between wrack treatments. Our results also showed that dermapterans tended to be attracted by the natural debris in the first hours of the experiment, but it not sustained these patterns as the experiment time increases. Considering that the aggregation experiment was carried out on hot days (38.1 ºC of mean sediment temperature), the debris possibly started to degrade quickly and not remained fresh enough to attract these organisms for more than 12 hours. For *Phaleria testacea*, these hot conditions are not harmful because, in addition to these species being attracted by the fast decomposition, it is also adapted to live in aged and dry wrack and hot sediments (Ruiz-Delgado et al. 2014; Vieira et al. 2016), which justifies its dominance here observed across all experiment times.

During the predation experiment, we observed great aggregations of *Phaleria testacea* in the natural wrack and also noted bird species foraging in the experimental area. *Aramides cajaneus* and *Caracara plancus* were the most frequent birds registered foraging inside the experimental area. *A. cajaneus* are omnivorous, eating grass, seeds, fruits, insect larvae, small reptiles, crustaceans, and gastropods, but mainly eggs of other species (Sick 2001; Marini & Melo 1998; Silva e Silva & Olmos 2015). *C. plancus* is also omnivorous, eating mainly orthopterans and coleopterans (Rodrigues-Estrella & Rodríguez 1997), including tenebrionids (Travaini et al. 2001), which is the family of *P. testacea*. However, this bird also eats fruit, detritus, and dead animals (Sick 2001), as well as other arthropods such as ants and crabs (Sazima 2007), and ectoparasites such as ticks (Tomazzoni et al. 2005). The generalist feeding mode of these species could mean that, although they may have preyed on some individuals of *P. testacea* on the experimental squares, their diet not specialized in arthropods can make the agglomeration of coleopterans less attractive to these birds.

Other bird species such as *Patagioenas picazuro* and *Fluvicola nengeta* also foraged in the experimental area, but less frequently. *P. picazuro* is not carnivorous but granivores and frugivores that descend to the ground to eat, turning over dead leaves to discover fallen seeds and fruits (Sick 2001, Pascotto & Oliveira 2012). This may mean that this species was attracted to the wrack, but not to the coleopterans present there. *F. nengeta*, in turn, eats mainly insects (Sick 2001, Gabriel & Pizo 2005, Straube et al. 2007) and may have preyed on some individuals of *P. testasea* during the experiment, although not in enough numbers for we noticed differences in the prey abundance comparing the treatments. Thus, we can affirm that, considering the study area, the wrack is visited by predatory birds similar to reported by previous studies on other beaches (Dugan et al. 2003; Schlacher et al. 2017). However, even if the birds feed on the macrofauna aggregated there, we suggest that such predation does not occur in sufficient intensity to generate changes in the prey abundance in the short term (20 days). The low density and richness of birds here found also could contribute to this low predation pressure. Therefore, long-term studies are needed to proceed with this investigation, which also may be replicated on other regions and beaches.

Despite the aggregation of coleopterans in the natural wrack not creating an evident prey hotspot for birds in the short term, this phenomenon may have other important implications for the beach functioning in the study area. The fast and intense aggregation of *Phaleria* *testacea* on the natural wrack and the ability of this genera to feed upon a diversity of organic debris (Colombini et al. 2002; Olabarria et al. 2007; Ruiz-Delgado et al. 2015; Gómez et al. 2018) could indicate that this coleopteran proceeds the wrack degradation and decomposition process in short-term. This wrack processing by the macrofauna is fundamental for the organic matter flux on the beach (e.g., Lastra et al. 2008), for the nutrient cycling (Orr et al. 2005; Dugan et al. 2011; Gómez et al. 2018), and can assist the dissolution of ammonium and nitrate in the sediment interstitial water, which can be later consumed by the beach microbiota or even exported offshore (Lowman et al. 2019). Our results regarding the microclimatic conditions of the predation experiment showed higher temperatures on the land debris than on treatments without debris after the 20 days of the experiment, with could be a consequence and an indicator of this wrack processing and decomposition occurring there. In this sense, the short-term aggregation of *P. testacea* on the natural wrack may assist some key ecosystem services associated with the organic and nutrient flux on the beach studied, although new approaches focused on testing these implications are still needed.

In summary, the present study brought new evidence that the short-term aggregation of arthropods on upper-beach wrack, especially coleopterans, occurs exclusively associated with natural organic debris (i.e., algae and plants), not occurring on plastic debris. On a short temporal scale (20 days), this faunal aggregation does not seem to be used as a prey hotspot for birds in the study area, which signal the need for new investigations using large temporal scales (i.e., months) and other beaches to improve our understanding about the trophic function of this faunal patches. In the current climate change context, the increase of wrack deposition with the increase of the extreme-storm events is expected and, consequently, management actions such as beach cleaning tends to intensify. In this regard, our results showed that the wrack type matters in terms of consequences for the benthic biodiversity, bringing an alert against beach cleaning methods that are adopted indiscriminately across the world (Zielinskia et al. 2019). Thus, the present study could be a step to elaborate and discuss selective methods of beach cleaning, searching to encompass the potentialities of natural debris and the damages of anthropogenic debris, looking forward to properly dealing with challenges such as climate changes and marine litter.

6. FINAL CONSIDERATIONS: WHAT DID WE LEARN HERE?

In the present contribution, we designed a series of small-scale field experiments aiming to test the effects of environmental changes in patterns and processes of sandy beach biodiversity. The conclusions of our different works showed that the macrobenthic biodiversity of the sandy beaches studied is very sensitive to multiple environmental changes. Such conclusions have brought lessons that can advance our understanding of how current global and local changes can affect the sandy beach ecosystem. Moreover, we showed that small-scale approaches are pivotal to evaluate specific environmental changes, isolating specific drivers, to understand their effects on the fauna. Therefore, we argue in favor of the application of small-scale approaches as a conservation tool, useful to generate biological proxies to improve forecast models and monitoring programs, aiming to deal with the multiple environmental changes of the 21st century.

From a perspective of the global threats, our conclusions can contribute to understanding the impacts of flooding and salinity changes, related to sea-level rise and rainfall increase, on early sublethal indicators and patterns of macrobenthic communities and populations. In summary, we showed that flooding can induce the downward displacement (i.e., to deeper layers of the sediment column) of intertidal polychaetes (i.e., *Scolelepis*) and isopods (i.e., *Excirolana armata*), changing the macrofauna vertical distribution on the beach. We also showed a weaker downward displacement with freshwater floods than with saltwater floods for *E. armata*, suggesting a salinity influence on the behavior of this isopod. Salinity reductions also can decrease the community richness and the probability of polychaetes forming high-abundance patches (mainly *Scolelepis* patches) on dissipative beaches. Based on that, we suggest that these species could be important proxies for monitoring programs that aim to detect climate change effects across dissipative beaches of the southeastern coast of Brazil. Specifically, the vertical distribution of both species could be monitored across the coast to detect possible flooding effects related to the sea level rise. The richness and abundance of polychaetes, specially *Scolelepis,* and the vertical distribution of *E. armata*, also seem to be promising indicators to detect possible freshwater-flooding impacts related to the rainfall increase.

From a perspective of the local threats, most related to the human pressures on the coastal zone, our conclusions can contribute to understanding the impacts of increasing urbanization on the sandy beach fauna. In summary, we showed that coastal armoring can reduce the abundance and biomass of beach macrofaunal assemblages and can influence their composition and functional structure, with integrated effects of urbanization and morphodynamic. Particularly, the abundance of polychaetes, the abundance and biomass of the coleopteran *Phaleria testacea*, and the occurrence of large body size species seem to be the patterns most affected by coastal armoring. Based on that and considering the potential synergism between increasing urbanization and increasing sea level and storminess, we suggest that *P. testacea* (for the supratidal zone) and the polychaetes assemblages (for the intertidal and subtidal zone) could be interesting ecological-disturbance proxies for monitoring eventual effects of the coastal squeeze on armored beaches of the southeastern coast of Brazil. For the polychaetes, we call special attention to the occurrence and abundance of *Scoloplos treadwelli*, a species abundant in the region, with large body size, and negatively associated with coastal armoring. Additionally, the coleopteran *P. testacea* is also the main species distinctly affected by beached debris, considering that their aggregation in high abundances on upper beach wrack is a phenomenon strongly associated with natural debris (i.e., algae and leaves), not occurring in plastic debris. Therefore, this coleopteran may be also an indicator to detect ecological effects of changes in beached debris (in amount and composition), especially considering the rising plastic pollution, the storminess increases and, consequently, the increase of beached debris.

Despite achieving interesting conclusions with our small-scale approaches, we understand that some of their inherent limitations must be highlighted. This includes the further need of upscaling the experimental results to understand whether the observed patterns are also valid on greater spatial and temporal scales. An interesting strategy to fill this goal is to apply experimental macroecology studies, supported by global researchers' webs, performing simultaneous experiments on different sandy beaches across the world. It is also necessary novel studies to expand the conclusions to other communities, with different species compositions, and other beach types. In this sense, we suggest that future studies replicate our experiments in other locations, expanding their scales and using different model species, to proceed with our investigations and improve our findings.

Nevertheless, even with these limitations, our approaches were useful to reveal potential proxies to be used in large-scale monitoring programs, as discussed above. More importantly, our approaches could reveal patterns and processes affected by environmental changes that may have consequences for the functioning of beaches and their provision of ecosystem services. The patterns and processes here evaluated, such as faunal vertical displacement and arthropods aggregation on wrack are connected to the sediment bioturbation, the nutrient cycling, and the organic and energy flux in the ecosystem. Thus, the changes in these patterns and processes here evidenced can signalize possible consequences for the beach's functioning, as the assessed threats increase. Additionally, the majority of our results point out the decrease in macrofaunal abundance (and biomass decrease, in some cases) as the main effect of the environmental changes here tested. These insights suggest that, in the long term, losses in benthic biological production and biomass stock are a strong possibility for the beaches on the southeastern coast of Brazil.

Finally, despite such ecosystem consequences were not tested here, we consider that our results are an indispensable first step that can guide further studies with a focus on conserving beach functions and services. Therefore, as a final message, we suggest that monitoring programs must be alert aiming to detect this potential biological loss and potential change in the nutrient/organic flux on the beach ecosystem on the southeastern coast of Brazil. Such task could be helped by the biological proxies here highlighted and should be a priority to conserve sandy beaches functioning, their biodiversity, and ecosystem services for the next changing years.

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APPENDIX A – Scripts of the data analysis (Chapter II)

(Available as digital supplementary material)

APPENDIX B – Species by trait matrix (Chapter III)

(Available as digital supplementary material)