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PADRÕES ESPACIAIS, ESTRUTURA E DINÂMICA DA COMUNIDADE MEIOFAUNAL DE DIFERENTES SUBSTRATOS NA REGIÃO LITORÂNEA DO GOLFÃO MARANHENSE

MARCOS EDUARDO MIRANDA SANTOS

São Luís – MA

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Tese de doutorado apresentada ao Curso de Doutorado do Programa de Pós-Graduação em Biodiversidade e Biotecnologia – Rede BIONORTE, na Universidade Federal do Maranhão, como requisito parcial para a obtenção do Título de Doutor em Biodiversidade e Biotecnologia.

Orientador: Prof. Dr. Jorge Luiz Silva Nunes

São Luís – MA

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Pedro Demo

SANTOS, Marcos Eduardo Miranda Santos. **Padrões espaciais, estrutura e dinâmica da comunidade meiofaunal de diferentes substratos na região litorânea do Golfão Maranhense**. 2023. 125 f. Tese (Doutorado em Biodiversidade e Biotecnologia) – Universidade Federal do Maranhão, São Luís, 2023.

RESUMO

A zona costeira é um ambiente em constante mudança e que está sob influência direta de processos naturais e ações humanas. É composta por diversos ecossistemas, como lagunas costeiras, praias e restingas, que são essenciais para a biodiversidade e oferecem vários recursos para as populações humanas. No entanto, o rápido crescimento urbano e atividades humanas desordenadas ameaçam a região, tornando-a uma das áreas mais ambientalmente vulneráveis do mundo. A meiofauna bêntica, composta por organismos microscópicos que habitam os sedimentos, desempenha um papel crucial nos ecossistemas costeiros. Ela exerce um papel importante no fluxo de energia nos sistemas bênticos, servindo como alimento para outros organismos, além de ser usada como indicador de qualidade ambiental. Apesar disso, as comunidades meiofaunais são pouco estudadas no Brasil, especialmente na região Nordeste e na Costa Amazônica. Considerando a importância ecológica desse componente do bento, o presente estudo teve como objetivo descrever os padrões espaciais, a estrutura e a dinâmica das comunidades meiofaunais na região litorânea do Maranhão (Brasil). Para isso, foram realizadas coletas de substratos na Ilha do Medo, Laguna da Jansen, Praia do Araçagy, Praia do Calhau e Praia de São Marcos, em áreas de restingas, bancos de areia e poças de maré. Uma análise cientométrica também foi realizada para verificar o interesse científico em estudos acerca da influência da heterogeneidade espacial na colonização de diferentes substratos por organismos meiofaunais (Capítulo 1). A análise revelou que as macroalgas são o substrato mais frequentemente estudado, especialmente a invasora *Sargassum muticum* (Yendo) Fensholt (1955). Os Estados Unidos e o Brasil são os países mais produtivos nessa área de pesquisa. Análises multivariadas, especialmente o Escalonamento Multidimensional Não Métrico (nMDS), são comumente usadas. Nos últimos anos, houve um declínio no número de estudos, possivelmente devido ao surgimento de linhas de pesquisas mais atrativas para os meiobentologos. Também foi analisado o papel da arquitetura do habitat de *Spartina alterniflora* Loisel (1807) e *Ulva lactuca* Linnaeus (1753) na estruturação das comunidades meiofaunais do Golfão Maranhense (Capítulo 2). Os resultados indicaram que a complexidade estrutural afetou a riqueza, mas não a densidade da meiofauna. *S. alterniflora*, o substrato mais complexo, abrigou uma maior abundância e riqueza de táxons meiofaunais do que *U. lactuca*. Por fim, foram avaliados os padrões de distribuição espacial da meiofauna em três áreas com diferentes níveis de perturbação (Capítulo 3). Foram identificadas diferenças significativas na distribuição espacial da meiofauna em função da perturbação antropogênica. A área mais poluída visualmente (Laguna da Jansen) apresentou densidade e riqueza maiores do que o esperado. O estudo sugere que a Praia do Calhau (área classificada como moderadamente impactada) sofre impactos ambientais significativos. Dentre as variáveis ambientais consideradas nesse estudo, a salinidade, matéria orgânica, tamanho do grão do sedimento e concentração de nitrato, foram as que mais influenciaram a estrutura da comunidade meiofaunal. Ainda há pouco conhecimento sobre as dinâmicas das comunidades meiofaunais na região costeira do Maranhão, de modo que estudos futuros são necessários para compreender as relações entre a meiofauna e o substrato, além dos processos estruturantes desta comunidade biológica.

Palavras-chaves: Bentos; Litoral Amazônico Brasileiro; Macromarés; Maranhão.

SANTOS, Marcos Eduardo Miranda Santos. **Spatial patterns, structure and dynamics of the meiofaunal community of different substrates in the coastal region of Golfão Maranhense**. 2023. 125 f. Thesis (PhD in Biodiversity and Biotechnology) – Federal University of Maranhão, São Luís, MA-Brazil, 2023.

ABSTRACT

The coastal zone is a constantly changing environment under the direct influence of natural processes and human actions. It consists of diverse ecosystems, such as coastal lagoons, beaches, and sandbanks, which are essential for biodiversity and provide various resources for human populations. However, rapid urban growth and disorderly human activities threaten the region, making it one of the most environmentally vulnerable areas in the world. Benthic meiofauna, composed of microscopic organisms that inhabit sediments, play a crucial role in coastal ecosystems. It plays an important role in the flow of energy in benthic systems, serving as food for other organisms, as well as being used as an indicator of environmental quality. Despite this, meiofaunal communities are poorly studied in Brazil, especially in the Northeast and along the Amazon coast. Considering the ecological importance of this component of the benthos, this study aimed to describe the spatial patterns, structure, and dynamics of meiofaunal communities in the coastal region of Maranhão (Brazil). To this end, substrates were collected from Ilha do Medo, Laguna da Jansen, Praia do Araçagy, Praia do Calhau, and Praia de São Marcos in areas of restingas, sandbanks, and tide pools. A scientometric analysis was also carried out to verify the scientific interest in studies on the influence of spatial heterogeneity on the colonization of different species (Chapter 1). The analysis revealed that macroalgae are the most frequently studied substrate, especially the invasive Sargassum muticum (Yendo) Fensholt (1955). The United States and Brazil are the most productive countries in this area of research. Multivariate analyses, especially non-metric multidimensional scaling (nMDS), are commonly used. In recent years, there has been a decline in the number of studies, possibly due to the emergence of more attractive lines of research for meiobentologists. We also analyzed the role of the habitat architecture of Spartina alterniflora Loisel (1807) and Ulva lactuca Linnaeus (1753) in structuring the meiofaunal communities of the Golfão Maranhense (Chapter 2). The results indicated that structural complexity affected the richness but not the density of meiofauna. S. alterniflora, the most complex substrate, harbored a greater abundance and richness of meiofaunal taxa than U. lactuca. Finally, the spatial distribution patterns of meiofauna in three areas with different levels of disturbance were assessed (Chapter 3). Significant differences were identified in the spatial distribution of meiofauna as a function of anthropogenic disturbance. The most visually polluted area (Laguna da Jansen) showed higher density and richness than expected. The study suggests that Calhau Beach (an area classified as moderately impacted) is suffering significant environmental impacts. Among the environmental variables considered in this study, salinity, organic matter, sediment grain size, and nitrate concentration influenced meiofaunal community structure. There is still little knowledge about the dynamics of meiofaunal communities in the coastal region of Maranhão, so future studies are needed to understand the relationships between meiofauna and the substrate, as well as the structuring processes of this biological community.

Keywords: Benthos; Brazilian Amazonian Coast; Macrotides; Maranhão.

SUMÁRIO

APRESENTAÇÃO

A tese de doutorado aqui apresentada é o resultado de um estudo sobre a estrutura e dinâmica das comunidades meiofaunais em ecossistemas costeiros do estado do Maranhão, Brasil. Este trabalho se insere em um contexto mais amplo de pesquisa em Ecologia Marinha e Conservação da Biodiversidade Costeira, com o objetivo de compreender as complexas interações entre organismos meiofaunais e os substratos que habitam e, assim, contribuir para a tomada de decisões baseadas em evidências.

Os ecossistemas costeiros são de grande relevância, tanto em termos ecológicos quanto econômicos, devido à sua rica biodiversidade e aos serviços ecossistêmicos que oferecem. No entanto, essas áreas também são altamente vulneráveis às mudanças ambientais, à urbanização e às atividades humanas. Portanto, compreender a ecologia desses ecossistemas e como as comunidades meiofaunais respondem a diferentes fatores é fundamental para sua conservação e manejo sustentável.

Ao longo dos últimos anos, a pesquisa em ecologia costeira tem se aprofundado, buscando elucidar os processos que ocorrem nos ambientes de transição entre o ambiente terrestre e o marinho. Nesse contexto, a meiofauna, um grupo de organismos diminutos que habitam os interstícios dos sedimentos marinhos, emergiu como um importante foco de investigação. Esses organismos desempenham um papel crucial nos ciclos biogeoquímicos e na cadeia alimentar, ligando as atividades do bento às águas sobrejacentes. Portanto, compreender como as comunidades meiofaunais são estruturadas e respondem a diferentes variáveis ambientais é importante para analisar os processos que ocorrem nos ecossistemas costeiros.

Esta tese abrange uma análise cientométrica e dois estudos realizados em diferentes áreas costeiras de São Luís, Maranhão. Os estudos concentraram-se em aspectos específicos da ecologia das comunidades meiofaunais, como a influência da complexidade estrutural de substratos e das perturbações ambientais sobre a estruturação das comunidades.

Um dos principais achados deste trabalho foi a identificação das variáveis ambientais que mais influenciam a estrutura das comunidades meiofaunais em diferentes áreas costeiras do Maranhão. A salinidade mostrou-se um fator significativo na Praia do Calhau e São Marcos, enquanto a matéria orgânica desempenhou um papel central na Laguna da Jansen. Além disso, a pesquisa demonstrou que diferentes grupos da meiofauna respondem de maneira distinta às variações ambientais. Os Nematoda foram mais abundantes na Laguna da Jansen, onde a matéria orgânica é mais elevada, sugerindo uma adaptação a essas condições.

Por outro lado, a Praia do São Marcos apresentou uma alta densidade de Copepoda, o que pode ser indicativo de uma melhor qualidade ambiental nessa área. A Praia do Calhau, por sua vez, destacou-se pela maior densidade de Tardigrada, que são conhecidos por sua capacidade de resistir a condições adversas.

Outro aspecto relevante deste trabalho é a análise cientométrica realizada, que revelou preferências e tendências nos métodos de pesquisa utilizados na colonização de diferentes substratos por organismos meiofaunais. Observou-se um aumento no uso de análises multivariadas nos estudos analisados, bem como um crescimento no uso de modelos matemáticos. A modelação ecológica preditiva emergiu como um tema de investigação promissor na ecologia bêntica de habitats marinhos e costeiros. A análise também oferece recomendações para pesquisas futuras, enfatizando a necessidade de estudar a meiofauna em diferentes morfologias de macroalgas, macroalgas cosmopolitas, animais como substratos e refinar a identificação taxonômica. Dessa forma, a análise cienciométrica realizada serve como guia para pesquisas futuras na compreensão das relações entre a meiofauna e o substrato e sua importância ecológica nos ecossistemas marinhos.

Este estudo é apenas um dos primeiros passos na elucidação da dinâmica das comunidades meiofaunais nos ecossistemas costeiros do estado do Maranhão. Recomenda-se que futuras pesquisas aprofundem a quantificação da complexidade estrutural dos substratos, incluam diferentes componentes faunísticos do bento (meio e macrofauna) para obter um conhecimento mais abrangente dos efeitos ecológicos dos substratos em níveis tróficos superiores e avaliem os efeitos temporais das pressões antrópicas na estrutura da comunidade meiofaunal. Ao fazer isso, haverá mais informações disponíveis para respaldar as estratégias para a conservação dos ecossistemas costeiros maranhenses.

1 INTRODUÇÃO

A zona costeira é um ambiente complexo e em constante mudança devido a processos naturais em amplas escalas temporais e à crescente ação antrópica (Serra; Farias Filho, 2019). Essa região é composta por diversos ecossistemas como manguezais, praias, campos de dunas, estuários, entre outros ambientes, que lhe conferem uma diversidade de habitats e a configuram como um local de importante riqueza natural (Dias; Oliveira, 2013).

Por ser um ambiente provedor de recursos às populações humanas, a zona costeira sofre um intenso processo de ocupação, com a consequente construção de grandes centros urbanos e a expansão desordenada das atividades antrópicas (Rêgo; Soares-Gomes; da Silva, 2018). Atualmente, cerca de 50% da sociedade reside em até 100 quilômetros de distância do mar e a maioria das megacidades do mundo (> 10 milhões povos) são ocupações adjacentes às praias (PNUMA, 2011).

As aglomerações urbanas exercem fortes pressões sobre os ambientes costeiros em todo o mundo e afetam potencialmente os recursos naturais (Marcus, 2004). Por estar exposta a grandes pressões antrópicas e diferentes formas de uso do solo, essa área é mundialmente a região sob maior estresse ambiental, pois 80% das ações antrópicas, como os processos acelerados de intensa urbanização, atividades portuárias e exploração turística, se concentram nela (da Silva; Santos, 2020).

Os vários habitats que compõem a zona costeira são formados por sedimentos de constituição variada, cujos grãos deixam pequenos espaços entre si, chamados de interstícios, ocupados fundamentalmente por água e por uma pequena quantidade de ar (Seibold; Berger, 2017). Esses espaços tornam o habitat altamente especializado, exigindo dos organismos que neles vivem adaptações morfológicas e funcionais como tamanho reduzido, modificação da forma do corpo, proteção mecânica, pigmentação, órgãos estáticos, sistemas de fixação e redução das gônadas (Veras *et al.*, 2017).

Dentre os ambientes costeiros, destacam-se as praias arenosas e os ambientes vegetados. As praias arenosas são caracterizadas pela concentração de sedimentos inconsolidados formados por areia, cascalho, argila e silte carreados pelas ondas e deriva litorânea (Gallop *et al*., 2020). Elas estão sujeitas a processos dinâmicos, como deposição de sedimento e erosão, que constantemente alteram suas configurações (Armenio *et al*., 2019). Além disso, compreendem um dos sistemas mais extensos do mundo, e um dos mais importantes do ponto de vista ecológico, devido à biodiversidade que abriga, com destaque para os organismos bênticos, que perfazem uma parte significativa da biomassa total desses ecossistemas (Santos; Silva; Azevedo-Cutrim, 2018). Os ambientes costeiros vegetados, como manguezais, restingas e dunas, fornecem habitat para uma variedade de organismos, ajudam a proteger as costas dos processos erosivos, e contribuem para a qualidade das águas (Jordan; Fröhle, 2022). Além disso, desempenham um papel importante na mitigação das mudanças climáticas, pois armazenam carbono nas raízes e na vegetação (Scarano; Ceotto, 2020).

Na região entremarés, além da faixa de areia, existem microhabitats biogênicos e abiogênicos que fornecem nichos diversificados aos organismos meiofaunais (Sedano *et al.*, 2020). Dentre esses ambientes, as poças de maré são alguns com maior heterogeneidade de habitat (Veiga; Sousa-Pinto, Rubal, 2016). Definidas como depressões ou cavidades preenchidas pela água do mar represada durante a baixa-mar e sem conexão direta com a água do mar (Zander; Nieder; Martin, 1999; Davis, 2000), estas poças são ambientes altamente estressantes devido às variações espaço-temporais de sua estrutura físico-química (Nunes; Pascoal; Piorski, 2011; Aguiar *et al.*, 2021).

As poças de maré são formadas quando a água do mar inunda uma área costeira durante a maré alta (Mendonça *et al*., 2018). Quando a maré baixa, a água é drenada, deixando para trás uma poça rasa de água salgada. As propriedades físico-químicas das poças de maré são influenciadas por uma série de fatores, incluindo a localização, a profundidade e a extensão da exposição às marés (Carminatto *et al*., 2018). A salinidade das poças de maré é geralmente alta, mas pode variar dependendo da sua localização, extensão da exposição às marés e presença de fontes de água doce (Matthews-Cascon; Lotufo, 2006). As poças de maré localizadas em regiões temperadas podem experimentar temperaturas que variam de acordo com as estações do ano, enquanto àquelas localizadas em regiões tropicais geralmente apresentam temperaturas mais constantes (Carminatto *et al*., 2018). No que se refere ao oxigênio dissolvido, níveis mais altos são registrados em poças bem misturadas pela ação das ondas, enquanto níveis mais baixos são registrados em poças isoladas e que não são bem misturadas (Carminatto *et al*., 2018).

Dentre os organismos que residem na zona costeira, destaca-se a meiofauna bêntica, definidos como animais microscópicos capazes de passar por uma malha de 0,5 mm e serem retidos em uma malha de 44 µm (Mare, 1942; Giere 2009; Worsaae *et al*., 2023). Essa comunidade exerce um importante papel no fluxo de energia nos sistemas aquáticos, servindo como alimento para a própria meiofauna, macrofauna e ictiofauna (Coull, 1969). Além disso, auxilia no processo de remineralização de detritos orgânicos, transferindo-os para o mesmo nível trófico e para níveis tróficos superiores (Pantó *et al*., 2015).

Em razão do seu tamanho, a comunidade meiofaunal apresenta grande diversidade taxonômica em comparação com a macrofauna e com a microfauna (Lage; Coutinho, 2012). A maioria dos metazoários que integra a fauna intersticial são invertebrados encontrados em abundância nos sedimentos marinhos de todo o mundo (Giere, 2009). A meiofauna é classificada em meiofauna permanente, que compreende àqueles organismos que vivem todo o seu ciclo de vida no sedimento, como os Copepoda Harpacticoidea, Mystacocarida, Nematoda, Ostracoda, Rotífera e Turbellaria; e meiofauna temporária, que compreendem estágios iniciais de animais macrofaunais, como Gastropoda, Nemertina, Holothiuroidea e Polychaeta (Giere, 2009).

A meiofauna pode ser encontrada colonizando diversos tipos de substratos. Pode ser encontrada dentro do sedimento, compondo a infauna; ou ainda, sobre substratos biogênicos ou abiogênicos, compondo a epifauna. Nas regiões costeiras, a composição das comunidades meiofaunais varia vertical e horizontalmente devido às diferenças no tamanho dos grãos, a fatores físico-químicos, em especial a temperatura, salinidade e oxigênio dissolvido no sedimento; e a fatores bióticos, como predação e competição interespecífica (da Silva; Albuquerque; Albuquerque, 2018). As migrações nessa comunidade, por sua vez, estão associadas principalmente a mudanças na umidade do sedimento; os animais com frequência movem-se para cima e para baixo quando a maré sobe e os espaços se enchem de água (Mclachlan; Winter; Botha, 1977; Giere, 2009).

Quando se considera a relação entre a meiofauna e o substrato, a maioria dos estudos têm se concentrado em táxons específicos como Amphipoda (Tavares; Grande; Jacobucii, 2013; Machado; Siqueira; Leite, 2017; Bueno; Leite, 2019; Machado et al., 2019; Gabr; Ziena; Hellal, 2020), Copepoda Harpacticoida (Arroyo *et al.*, 2004; Song *et al.*, 2010, Mascart *et al*., 2015; Portianko, 2017), Nematoda (Boaden, 1999; da Rocha *et al.*, 2006; Buys *et al*., 2021) e Ostracoda (Frame; Hunt; Roy, 2007; Mazzini *et al*., 2014). No entanto, estudos quantitativos com dados ecológicos de toda a comunidade meiofaunal ainda são escassos (Veiga *et al*., 2016). Por outro lado, a meiofauna tem sido cada vez mais utilizada em estudos ambientais e de biomonitoramento em função de seu pequeno tamanho e grande densidade, o que facilita a obtenção de amostras quantitativas e transporte ao laboratório; e a rápida resposta à eventos de poluição (Zeppilli *et al*., 2015; Pereira *et al*., 2017; Bertocci *et al*., 2019; Cui; Zhang; Hua, 2021; Ingels *et al*., 2021; Losi *et al*., 2021; Santos *et al*., 2023).

Os primeiros estudos envolvendo a meiofauna como indicadora de qualidade ambiental de ecossistemas aquáticos datam da década de 1970 (Warwick; Price, 1979; Coull; Hicks; Wells, 1981; Warwick, 1981; Raffaelli; Mason, 1982; Amjad; Gray, 1983;

Lambshead, 1986). Após esses estudos, os organismos meiofaunais passaram a ser considerados excelentes indicadores de contaminação. Nos anos seguintes, vários outros estudos relataram os efeitos do enriquecimento orgânico sobre a abundância da meiofauna, corroborando o uso desses organismos no monitoramento ambiental (Tietjen; Alongi, 1990; Coull; Chandler, 1992; Essink; Romeyn, 1994, 1998; Duplisea; Hargrave, 1996; Schratzberger; Warwick, 1998; Netto; Valgas, 2007; Cruz *et al.*, 2018; García-Gomes *et al.*, 2022; Santos *et al*., 2023).

Apesar de sua importância ecológica e econômica, ainda são poucos os estudos publicados sobre a meiofauna no Brasil, em especial na região Nordeste. Os estudos com organismos bênticos encontrados na literatura científica, no geral, estão mais voltados para a macrofauna. Maria, Wandeness e Esteves (2016), avaliando o estado da arte de estudos relacionados à meiofauna de praias arenosas no Brasil, encontraram apenas 37 estudos publicados em revistas indexadas; dos quais apenas oito foram realizados na região Nordeste, sendo todos no estado de Pernambuco (por exemplo, Souza-Santos *et al*., 2003; Santos *et al*., 2009). Apesar de já ter se passado sete anos desde a publicação do estudo de Maria e colaboradores (2016), a literatura científica relacionada à meiofauna no litoral nordestino continua escassa, pois embora novos estudos tenham sido publicados nos últimos sete anos (Cidreira; Venekey; Kelmo, 2020; Pontes *et al*., 2021; da Silva, *et al*., 2022; Cavalcanti *et al*., 2023), ainda são poucos quando comparados ao número de estudos publicados sobre a macrofauna, por exemplo.

No que se refere à Costa Amazônica, também se observa um crescimento tímido no número de estudos publicados sobre a meiofauna após a publicação do artigo de Maria e colaboradores (2016). Estudos como o de Venekey (2017); Baia; Venekey (2019); Venekey; Melo; Rosa Filho (2019); Baia; Rollnic; Venekey (2021); Santos; Petracco; Venekey (2021) e dos Santos; Baia; Venekey (2023) figuram dentre alguns dos mais recentes. Nesse sentido, os artigos resultantes dessa tese, realizados no Litoral Amazônico Nordestino buscam contribuir com o conhecimento sobre a comunidade meiofaunal na região.

No Brasil, avalia-se que as pressões socioeconômicas na área costeira vêm provocando, no decorrer do tempo, um processo acelerado de urbanização não programada e alta degradação dos recursos naturais, que ameaçam a sustentabilidade econômica, ambiental e a sobrevivência humana (Pereira *et al*., 2017). A Zona Costeira Maranhense possui 640 quilômetros de faixa e apresenta um mosaico de ecossistemas de alta relevância ambiental, com mangues, restingas, campos inundáveis, dunas e outros ecossistemas ecológica e economicamente importantes (Gama *et al*, 2011), que sofrem com as pressões decorrentes do avanço da ocupação urbana (Machado; Rodrigues, 2020). Além disso, principalmente nas praias, existe uma intensa circulação de pessoas, o que gera acúmulo de resíduos (Neres; Neres, 2022). Essas regiões têm sofrido degradação ambiental decorrente do lançamento de efluentes, resíduos sólidos, remoção de dunas litorâneas, construções urbanas dentro e em torno das praias, supressão da vegetação e fauna praiana associada à especulação imobiliária e ao turismo desordenado (Rêgo; Soares-Gomes; da Silva, 2018).

A região costeira norte de São Luís comporta um percentual populacional bastante significativo, o que ocasiona diferentes necessidades e interesses, além de possuir potencialidades econômicas e naturais que devem ser exploradas em concessão com os instrumentos de gestão territorial, pois a junção de todas as atividades relacionadas ao uso e ocupação não planejados da Zona Costeira tem produzido diversos impactos ambientais (Santos; Silva; Azevedo-Cutrim, 2021).

Diante do exposto, esta tese teve como objetivo descrever os padrões espaciais, a estrutura e a dinâmica da comunidade meiofaunal em poças de maré e bancos de areia na região litorânea do Golfão Maranhense; e assim esclarecer os processos estruturantes desta comunidade biológica na região.

1.1 OBJETIVO GERAL

- Descrever os padrões espaciais, a estrutura e a dinâmica da comunidade meiofaunal em diferentes substratos na região litorânea do Golfão Maranhense, Brasil.

1.2 OBJETIVOS ESPECÍFICOS

- Determinar composição, densidade e riqueza das comunidades meiofaunais nas áreas amostradas.
- Verificar o interesse científico em estudos acerca da influência da heterogeneidade espacial na colonização de diferentes substratos por organismos meiofaunais.
- Analisar o papel da complexidade estrutural de dois diferentes substratos fitais na estruturação das comunidades meiofaunais entremarés.
- Testar a existência de um gradiente de perturbação ambiental na região litorânea de São Luís, usando uma abordagem multivariada que incorpore a meiofauna e as variáveis ambientais sedimentares e da água como uma indicação integrada.

2 CAPÍTULO 1: SCIENTOMETRIC ANALYSIS AND TRENDS FOR RESEARCH ON SUBSTRATE COLONIZATION BY MEIOFAUNA

Aceito para publicação no periódico **Ecological Research** (Qualis: A3; Fator de Impacto: 2.056).

Análise cientométrica e tendências para pesquisas sobre colonização de substratos pela meiofauna

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ABSTRACT:

The relationships between meiofaunal communities and substrate are relatively well documented in the scientific literature. However, a comprehensive quantitative review of global research on the colonization of different substrates by meiofauna has never been conducted. In this work, a scientometric analysis pertinent to the subject was conducted, aiming to verify the scientific interest in different substrates in studies dealing with the influence of spatial heterogeneity on meiofaunal colonization. A total of 124 articles published between the years 1967 and 2023 were selected and found in online databases. Macroalgae were the most used substrate in the analyzed studies, and it was the one that harbors the highest abundance and richness values compared to other substrates. Studies predominantly focused on specific taxonomic groups, namely Copepoda Harpacticoida and Ostracoda. Nematoda, Copepoda Harpacticoida, and Amphipoda were the most commonly recorded meiofaunal taxa. The geographical distribution of studies showed that the United States was the most productive country in this field, followed by Brazil. Multivariate analyses were the preferred quantitative method used in the studies, particularly Non-Metric Multidimensional Scaling (nMDS). A decline over the years in the number of studies on the relationship of meiofauna with substrates in the scientific literature has been observed. Since macroalgal colonization is already relatively well documented, diversification in the choice of substrates is recommended in future studies.

KEYWORDS: Habitat architecture. Structural complexity. Spatial heterogeneity. Macroalgae. Literature review.

1 INTRODUCTION

The meiofauna comprises a group of invertebrates whose body size ranges from 0.044 mm to 0.5 mm (Mare 1942; Ptatscheck *et al.* 2020a; Worsaae *et al.*, 2023). This faunal assemblage plays an important role in the energy flow in benthic systems, serving as food for other meiofauna, macrofauna, and ichthyofauna (Coull 1990). It also stands out as one of the most representative biotic components that make up the benthic community, inhabiting from the supralittoral of coastal areas to the deepest regions of the ocean (Giere 2009; Veiga *et al.* 2016).

In coastal zones, the composition of meiofaunal communities varies vertically and horizontally due to differences in grain size and physicochemical factors, in particular temperature, salinity and dissolved oxygen in the sediment (Bouvy and Soyer 1989; Giere 2009; da Silva *et al.* 2018; Santos *et al.* 2023). The high variability in the qualitative-quantitative composition of this assemblage is attributed to various biological factors, including food availability, which leads to the distribution of meiofauna into mosaics (Findlay 1981; Cooke *et al.* 2014); chemotaxis (Moens and Vincx 1997; Gerald *et al.* 2022); predation (Bell and Coull 1978; Hicks 1984; Weber and Traunspurger 2015; Ptatscheck *et al.* 2020b);

life cycle timing (Vranken *et al.* 1981); and bioturbation (Schratzberger and Warwick 1999; Tita *et al.* 2000; Bonaglia *et al.* 2020; Wang *et al.* 2020).

In the field of Meiobenthology, several lines of research have been explored to understand the ecology and dynamics of these small invertebrates in aquatic environments. Some of the main research streams, according to Giere (2009, 2019), include studies on: 1) the colonization of substrates, especially macroalgae, and macrophytes, and their influence on meiofaunal community structure; 2) the distribution and diversity of meiofauna in different habitats and geographic regions; 3) the interaction between meiofauna and other ecosystem components, such as macrofauna and microorganisms; 4) the effects of climate change and environmental factors on meiofauna distribution and abundance; 5) the role of meiofauna in nutrient cycling and energy transfer in benthic ecosystems; and 6) the impacts of human activities, such as pollution and increased microplastics, on meiofauna and their adaptive responses. These researches are fundamental to reveal the ecological importance of meiofauna and their implications for the conservation and management of marine ecosystems.

Meiofauna is known for its ability to colonize new microhabitats (Fleeger and Decho 1987; De Troch *et al.* 2005; Ptatscheck and Traunspurger 2020). Furthermore, animals with epibenthic or epiphytic habits are better colonizers than true interstitials (Pinto *et al.* 2013; Piazzi *et al.* 2016; Balsamo *et al.* 2020). This largely stems from habitat architecture, as substrates with more complex morphology usually offer a greater number of microhabitats for colonization due to the ease of trapping fine sediments (Gibbons 1991; Veiga *et al.* 2016).

"Habitat architecture" refers to the spatial and structural attributes that define a habitat (Hacker and Steneck 1990), specifically how the structures are arranged in space and how they influence biological communities. The study of habitat makes it possible to understand the patterns of distribution, diversity, and abundance of a set of organisms that coexist at a given spatial scale (Resetarits Jr. 2005). Many ecological studies have focused on the colonization strategies of meiofauna, specifically the relationships between the architecture of different substrates and species abundance (Bell *et al.* 1984; Atilla *et al.* 2003; Mirto and Danovaro 2004; Costa *et al.* 2016; Veiga *et al.* 2016; García-Gómez *et al.* 2022). However, a comprehensive quantitative review of global research on the colonization of different substrates by meiofauna has never been conducted.

Thus, this scientometric analysis aims to answer the following questions: i) which substrates are most frequently studied in research on the influence of spatial heterogeneity on meiofauna? ii) which taxa have been the most recorded in these studies? iii) in which countries were the studies carried out? iv) to what extent has the scientific literature on meiofauna-substrate relationships grown in the last decades? v) which journals have the largest number of studies on the subject under investigation? vi) which quantitative analyses have been used in these studies? vii) what are the trends and perspectives for studies on the colonization of substrates by meiofauna?

2 METHODS

The present study was developed through a systematic literature review with a scientometric approach. Scientometrics is a field of study that involves the measurement and analysis of scientific literature, capable of revealing gaps in the overall scientific production (Lima Vieira *et al.* 2021), as well as trends and patterns for new studies (Luiza-Andrade *et al.* 2017).

The literature search process was carried out by subject, in July 2023, in Thomson Reuters' Web of Science Core Collection (WoS), Scopus (Elsevier), Google Scholar (Google), and the Scientific Electronic Library Online (SciELO). In all databases, the same descriptors were used: “meiofauna”, “meiobenthos”, “substrate”, “colonization”, “habitat architecture”, “structural complexity”, “community structure”, “macroalgae”, “macrophyte”, “artificial substrates”, “Amphipoda”, “Copepoda”, and “Nematoda”. To increase the number of papers relevant to the study's objective, the descriptors were combined with the keyword “meiofauna/meiobenthos”, “Amphipoda”, “Copepoda”, and “Nematoda” using the Boolean operator “AND” (“meiofauna” AND “substrate”, “meiofauna” AND “colonization”, “meiofauna” AND “habitat architecture”, “meiofauna” AND “structural complexity”, “meiofauna” AND “community structure”, “meiofauna” AND “macroalgae”, “meiofauna” AND “macrophyte”, “meiofauna” AND “artificial substrates”, “meiobenthos” AND “substrate”, “meiobenthos” AND “colonization”, “meiobenthos” AND “habitat architecture”, “meiobenthos” AND “structural complexity”, “meiobenthos” AND “community structure”, “meiobenthos” AND “macroalgae”, “meiobenthos” AND “macrophyte”, “meiobenthos” AND “artificial substrates”, “Amphipoda” AND “substrate”, “Copepoda” AND “substrate”, “Nematoda” AND “substrate”, “Amphipoda” AND “colonization”, “Copepoda” AND “colonization”, “Nematoda” AND “colonization”, “Amphipoda” AND “habitat architecture”, “Copepoda” AND “habitat architecture”, “Nematoda” AND “habitat architecture”, “Amphipoda” AND “structural complexity”, “Copepoda” AND “structural complexity”, “Nematoda” AND “structural complexity”, “Amphipoda” AND “community structure”, “Copepoda” AND “community structure”, “Nematoda” AND “community structure”, “Amphipoda” AND “macroalgae”, “Copepoda” AND “macroalgae”, “Nematoda” AND “macroalgae”, “Amphipoda” AND “macrophyte”, “Copepoda” AND “macrophyte”, “Nematoda” AND “macrophyte”, “Amphipoda” AND “artificial substrates”, “Copepoda” AND “artificial substrates”, “Nematoda” AND “artificial substrates”).

The inclusion criteria defined for the screening of studies were: a) studies whose main objective was to specifically evaluate the influence of the substrate on the meiofauna; b) original scientific articles; c) only articles available in full text; d) time frame from 1942 (year in which Mare coined the term meiobenthos) to July 2023; e) studies using substrates collected in the intertidal region; f) studies that considered only the epibiotic meiofauna; g) studies encompassing both experimental colonization and natural colonization from any substrate. The exclusion criteria were: a) grey literature; b) literature reviews; c) texts that did not correspond to the research objective; d) that presented duplicates in more than one database; e) studies published in journals cited in predatory journal lists (Prado *et al.* 2017; Beall *et al.* 2020; Predatory Reports 2023); f) studies that did not present information on the density or diversity of meiofaunal communities; g) studies using infaunal meiobenthos. Since the intention was to analyze only the meiofauna and substrate relationship, spatial and regional differences in where the substrates were collected were not considered, nor were spatial heterogeneities related to environmental quality. No restriction was made based on the language of the articles. Organisms recorded as “larvae” were not considered in the taxocenosis analysis because it was not possible to identify to which taxonomic group they belonged. Copepods of the orders Calanoida, and Cyclopoida were grouped into Other Copepods. Collembola and Diptera were grouped into Insects.

The search retrieved articles with the descriptors used in their titles, keywords, or abstracts. For the selection of articles, the title of the study, year, main results, and conclusions were considered. When articles were found that matched the objectives and met the inclusion and exclusion criteria, the texts were read in full for data extraction, according to previously delimited categories: year, the country where the study was carried out, the substrate used, taxocenosis, most representative taxa, quantitative analyses performed, and journal where it was published.

The Impact Factor (IF) of the journals was determined for each paper as reported in the 2022 edition of the Journal Citation Reports (JCR). The number of citations for each paper was retrieved from the Web of Science, Crossref, and Scopus databases.

2.1 Statistical Analysis

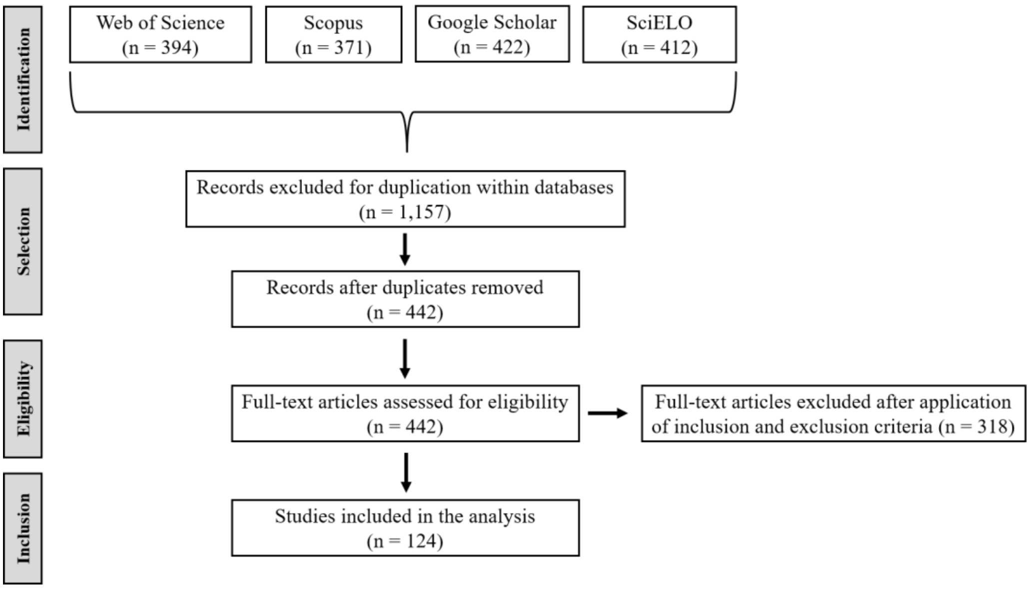
Since the data were non-linear, a Generalized Additive Model (GAM) with Poisson distribution was used to verify significant relationships between the years and the number of publications that focused on the investigated topic. The model was fitted with 12 basis functions (k) and smoothed using restricted maximum likelihood (REML). Chi-square (X^2) tests were performed to identify relationships among some of the variables analyzed: substrates and year of publication, substrates and nationality of the first author, substrates and journal chosen for publication, journal and country where the study was carried out.

The PRISMA flowchart (Figure 1) and the list of taxa on each substrate (Figure 2) was constructed in the Canva Design application. The worldwide geographical distribution of the studies was plotted using QGIS software version 3.22 (QGIS Development Team 2023). To visualize the relationship between substrates and taxa, a weighted bipartite network was constructed. The same method was used to visualize the relationship between the geographical distribution of the studies and the journals in which they were published. The analyses and graphs (except Figure 1 and 2) were performed in R software version 3.5.1 (R Core Team 2023). The packages “bipartite” (Dormann *et al.* 2008), “mgcv” (Wood 2004) and “ggplot2” (Wickham 2016) were used.

3 RESULTS

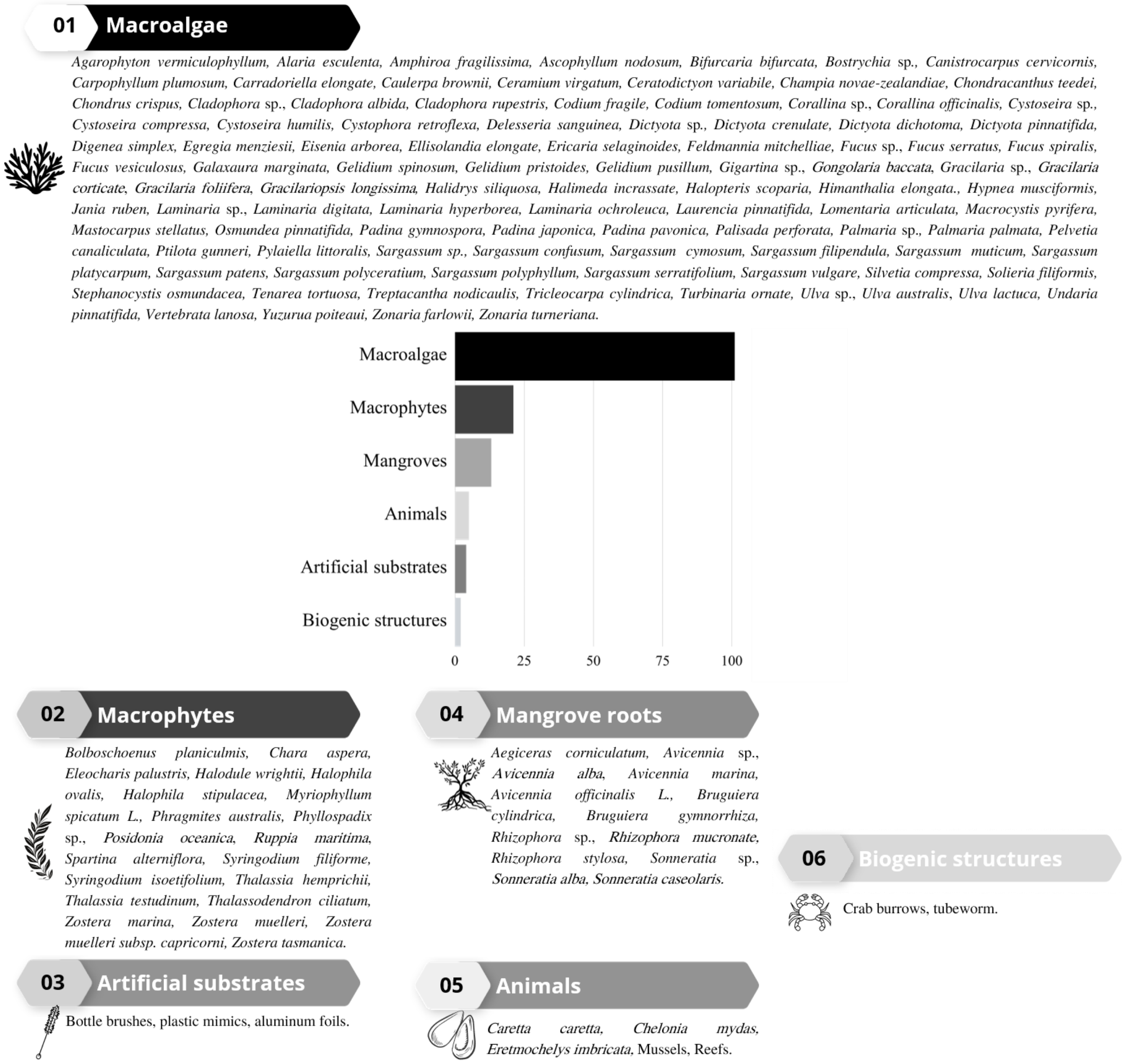
A total of 442 articles were found, and after the application of inclusion and exclusion criteria, 124 were selected for the construction of this study (Fig. 1).

Fig. 1 PRISMA flowchart detailing the number of retrieved articles in each utilized database, the number of excluded articles with justifications, and the articles included in the scientometric analysis.



The main substrates considered in studies on meiofauna colonization were macroalgae (69.17%) and macrophytes (14.38%). Artificial substrates (2.73%) and biogenic structures (1.36%), on the other hand, were the least used (Fig. 2). It is observed that colonization and succession on natural substrates, such as macroalgae and macrophytes, are numerically more documented in the literature compared to other substrates.

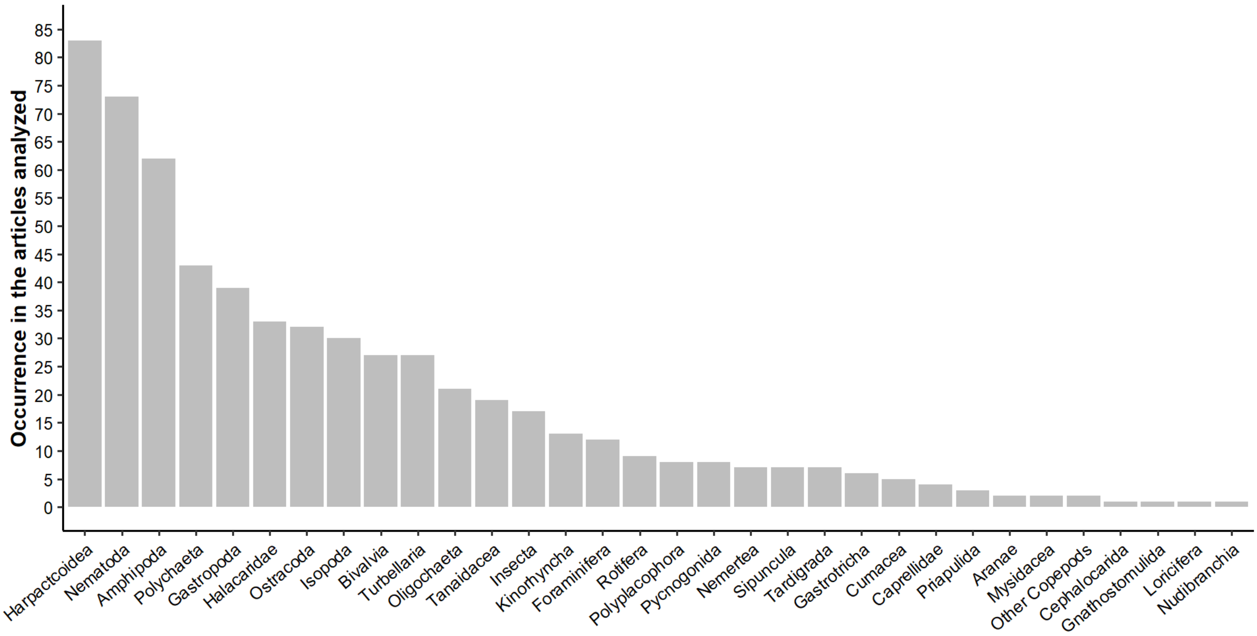
Fig. 2 Main substrates used in studies of meiofaunal colonization.



In all, 101 macroalgae taxa were used in the studies analyzed. Macroalgae of the class Phaeophyceae were the most frequent, highlighting *Sargassum muticum* (Yendo) Fensholt, which was the species with the highest occurrence among the analyzed studies. As for the macrophytes, the highlight was the grass *Spartina alterniflora* Loisel.

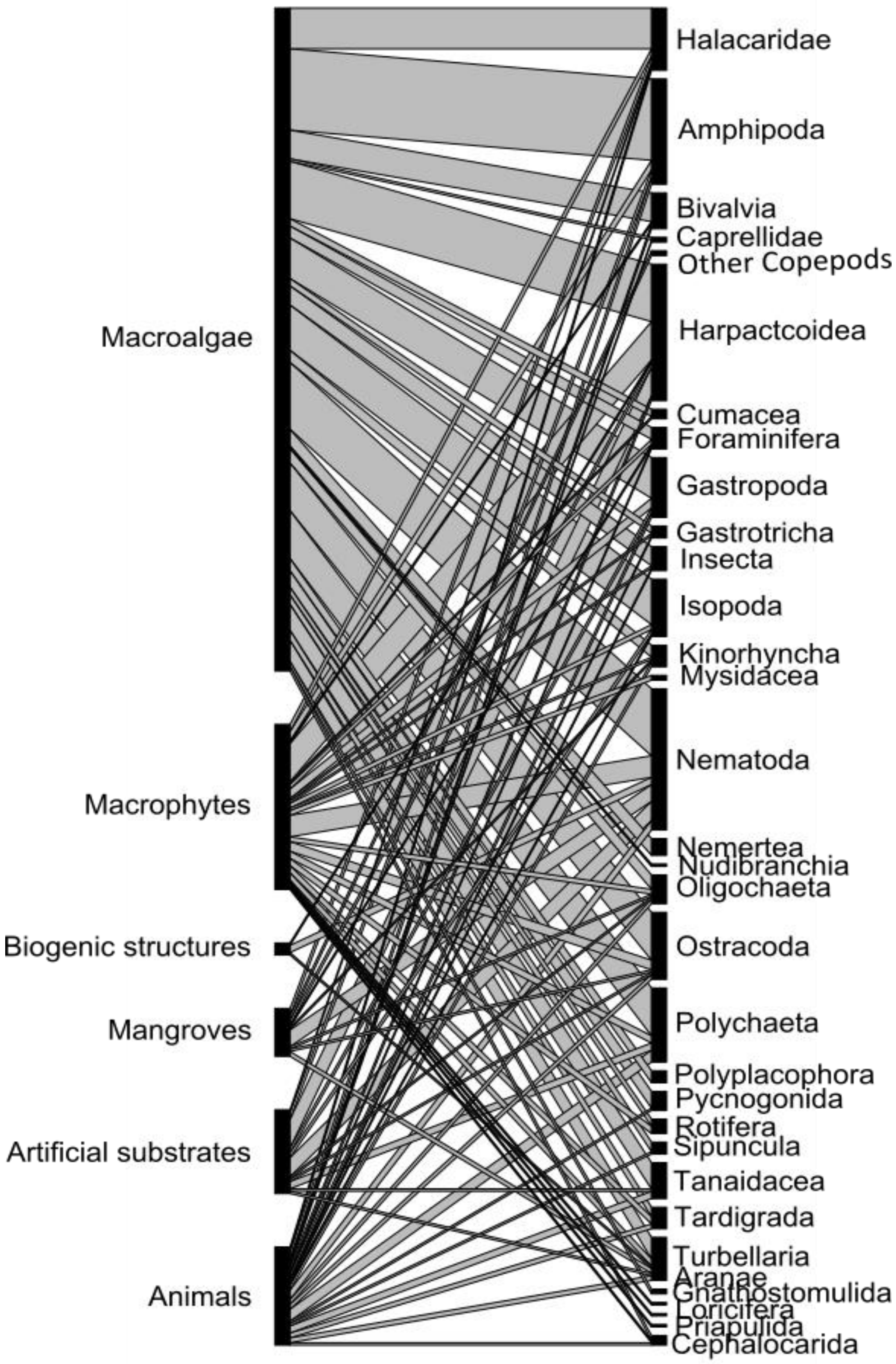
Overall, 32 meiofaunal taxa were recorded in the selected articles (Fig. 3), with 34 studies focusing on only one taxon. Of these, Copepoda Harpacticoida was the most commonly used, followed by Ostracoda, Nematoda, and Amphipoda.

Fig. 3 Taxa recorded in the literature reviewed.



The other studies, which analyzed the whole meiofaunal assemblages, recorded similar taxocenosis. The most frequently recorded taxa were: Copepoda Harpacticoida, Nematoda, Amphipoda, and Polychaeta. Nematoda, Copepoda, and Amphipoda are, in this order, the taxa that stood out most in abundance and density in the studies considered. As a consequence of the greater number of studies using macroalgae as substrates, the bipartite network showed a greater association between taxa and this substrate, so that 84.37% of the taxonomic groups of invertebrates were found colonizing macroalgae (Fig. 4).

Fig. 4 Bipartite network relating invertebrate taxa to the substrates used in the studies analyzed.



The selected articles were published in 49 different journals (Table 1), many of which are considered high-impact journals. Most of the papers were published in Marine Biology

(14.5%), Marine Ecology Progress Series (12%), Journal of the Marine Biological Association of the United Kingdom (8%), Journal of Experimental Marine Biology and Ecology (7.25%), and Hydrobiologia (5.6%).

Table 1. Number of articles published by scientific journal. TP: Total Publications. IF: Impact Factor.

Journal	TP	IF 2022	Category	Rank by IF
Marine Biology	18	2.4	Marine and Freshwater Biology	29/106
Marine Ecology Progress Series	15	2.5	Ecology	88/169
			Marine and Freshwater Biology	27/106
			Oceanography	27/63
Journal of the Marine Biological Association of the United Kingdom	10	1.2	Marine and Freshwater Biology	73/106
Journal of Experimental Marine Biology and Ecology	9	2	Ecology	103/169
			Marine and Freshwater Biology	42/106
Hydrobiologia	7	2.6	Marine and Freshwater Biology	26/106
Marine Biology Research	4	1.1	Ecology	145/169
			Marine and Freshwater Biology	79/106
Journal of Sea Research	4	2	Marine and Freshwater Biology	42/106
			Oceanography	37/63
Aquatic Botany	3	1.8	Marine and Freshwater Biology	46/106

			Plant Sciences	138/238
Ecology	3	4.8	Ecology	36/169
Estuarine, Coastal and Shelf Science	3	2.8	Marine and Freshwater Biology	19/106
			Oceanography	22/63
Marine Ecology	3	1.1	Marine and Freshwater Biology	79/106
Marine Pollution Bulletin	3	5.8	Environmental Sciences	67/274
			Marine and Freshwater Biology	4/106
Oecologia	3	2.7	Ecology	75/169
Cahiers de Biologie Marine	2	0.6	Marine and Freshwater Biology	98/106
Journal of the Faculty of Science*	2			
Journal of Marine Research	2	0.5	Oceanography	60/63
African Journal of Marine Science	1	1.2	Marine and Freshwater Biology	73/106
Aquatic Ecology	1	1.8	Ecology	114/169
			Limnology	21/11
			Marine and Freshwater Biology	46/106
Atlântica**	1			
Austral Ecology	1	1.5	Ecology	131/169
Bioikos*	1			
Biologia Marina Mediterranea*	1			
Biological Invasions	1	2.9	Biodiversity Conservation	19/64

			Ecology	67/169
Biota Neotropica	1	1.2	Biodiversity Conservation	47/64
Bulletin of Marine Science	1	1.5	Marine and Freshwater Biology	60/106
			Oceanography	46/63
Continental Shelf Research	1	2.3	Oceanography	30/63
Coral Reefs	1	3.5	Marine and Freshwater Biology	11/106
Diversity	1	2.4	Biodiversity Conservation	26/64
			Ecology	90/169
Estuaries (Currently Estuaries and Coasts)	1	2.7	Environmental Sciences	170/274
			Marine and Freshwater Biology	22/106
Freshwater Biology	1	2.7	Ecology	75/169
			Marine and Freshwater Biology	22/106
Helgoland Marine Research**	1			
Integrative Biosciences (Currently Animal Cells and Systems)	1	2.9	Cell Biology	137/191
			Zoology	10/176
Invertebrate Biology	1	1.2	Marine and Freshwater Biology	73/106
			Zoology	92/176
Journal of Marine Sciences*	1			
Journal of the North American Benthological Society (Currently Freshwater Science)	1	1.8	Ecology	114/169
			Marine and Freshwater Biology	46/114
Marine and Freshwater	1	1.8	Fisheries	28/54

Research			Limnology	11/21
			Marine and Freshwater Biology	46/106
			Oceanography	40/63
Marine Biodiversity	1	1.6	Biodiversity Conservation	35/64
			Marine and Freshwater Biology	55/106
Marine Biodiversity Records**	1			
Marine Environmental Research	1	3.3	Environmental Sciences	140/274
			Marine and Freshwater Biology	12/106
			Toxicology	36/94
Marine Turtle Newsletter*	1			
Nauplius	1	0.7	Marine and Freshwater Biology	94/106
			Zoology	143/176
New Zealand Journal of Marine and Freshwater Research	1	1.6	Fisheries	32/54
			Marine and Freshwater Biology	55/106
			Oceanography	42/63
Regional Studies in Marine Science	1	2.1	Ecology	100/169
			Marine and Freshwater Biology	39/106
Revista Brasileira de Oceanografia (Currently Ocean and Coastal Research)	1	0.8	Marine and Freshwater Biology	92/106
			Oceanography	54/63
Revista de Biologia Tropical	1	0.6	Biology	83/92
Scientia Marina	1	1.4	Marine and Freshwater Biology	63/106

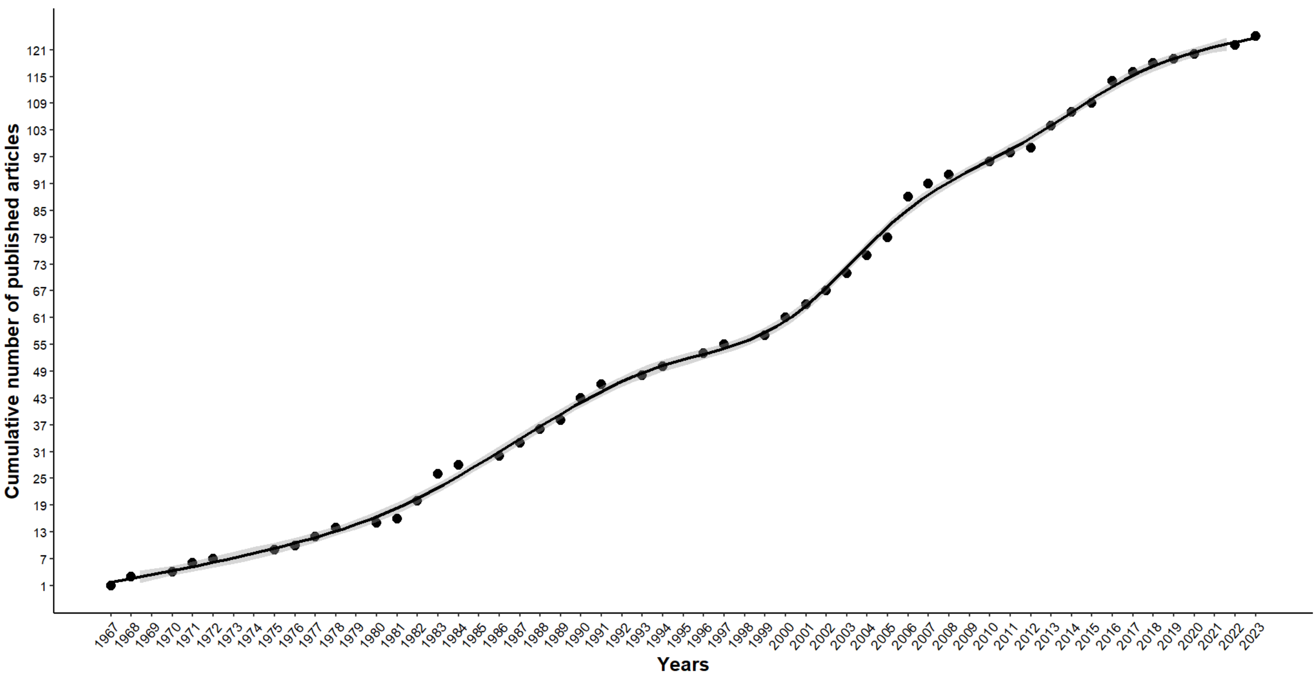
South African Journal of Zoology (Currently African Zoology)	1	1.1	Zoology	103/176
Studies on Neotropical Fauna and Environment	1	0.9	Zoology	124/176
Wetlands	1	2	Ecology	103/169
			Environmental Sciences	212/274

* Not registered in Journal Citation Reports 2022.

** Journal discontinued.

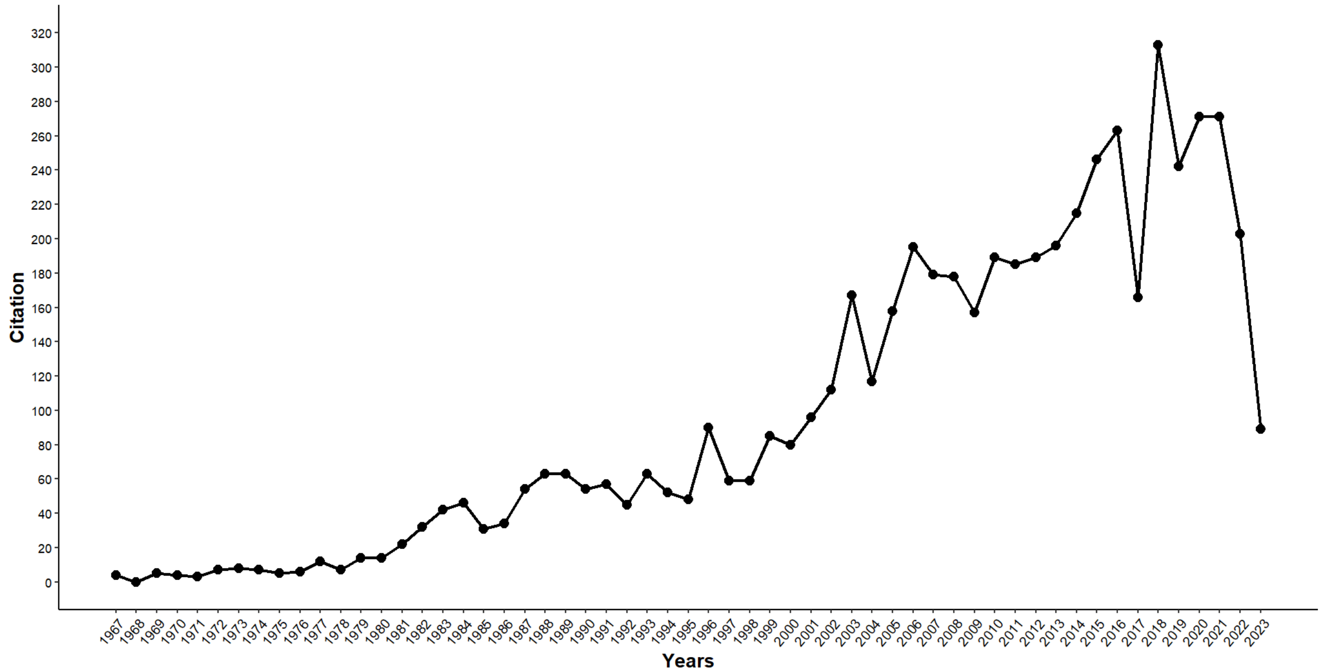
The first study found was published in 1967. In it, Hopper and Meyers analyzed the colonization by nematodes in the turtle grass, *Thalassia testudinum* K.D.Koenig, 1805. In the last 56 years, the frequency of publications ranged from zero to a maximum of nine, in 2006. A decrease in the number of studies with the investigated approach can be noticed in the last decade, since most studies (75%) were published before 2010 (Fig. 5). The Generalized Additive Model (GAM) did not indicate significant variation (p = 0.942; edf = 10.98; explained deviation = 70.6%) in the number of publications as a function of time. The model's explanatory power was substantial (R^2 (adj) = 0.99). The results indicate that there is no trend in the residuals of the model. The model fit is satisfactory, as evidenced by the fit statistics and the significance of the smooth terms.

Fig. 5 Cumulative distribution of articles published between the years 1967 to 2023. The solid line represents the smoothed value while the shaded area represents the 95% confidence interval.



In order to evaluate the impact of publications focusing on substrate colonization by benthic meiofauna, the total number of citations obtained by the 124 publications analyzed was plotted in a graph as a function of time (Fig. 6). In total, the studies received 5,620 citations. It is observed that the citations per publication for all articles peaked in 2018, and decreased thereafter. Although a growth in the number of citations is observed over the past 56 years, it has not occurred in a linear fashion, with periodic oscillations observed over time.

Fig. 6 Total citations of articles focusing on substrate colonization by meiofauna, from the year of publication of the first study (1967) to 2023.



The study by Hacker and Steneck (1990), published in the journal Ecology, is, among the articles found, the one indexed with the highest number of citations (229) from the date of its publication until 2023 (Table 2). The second article with the highest number of citations (Coull and Wells 1983) was also published in the journal Ecology.

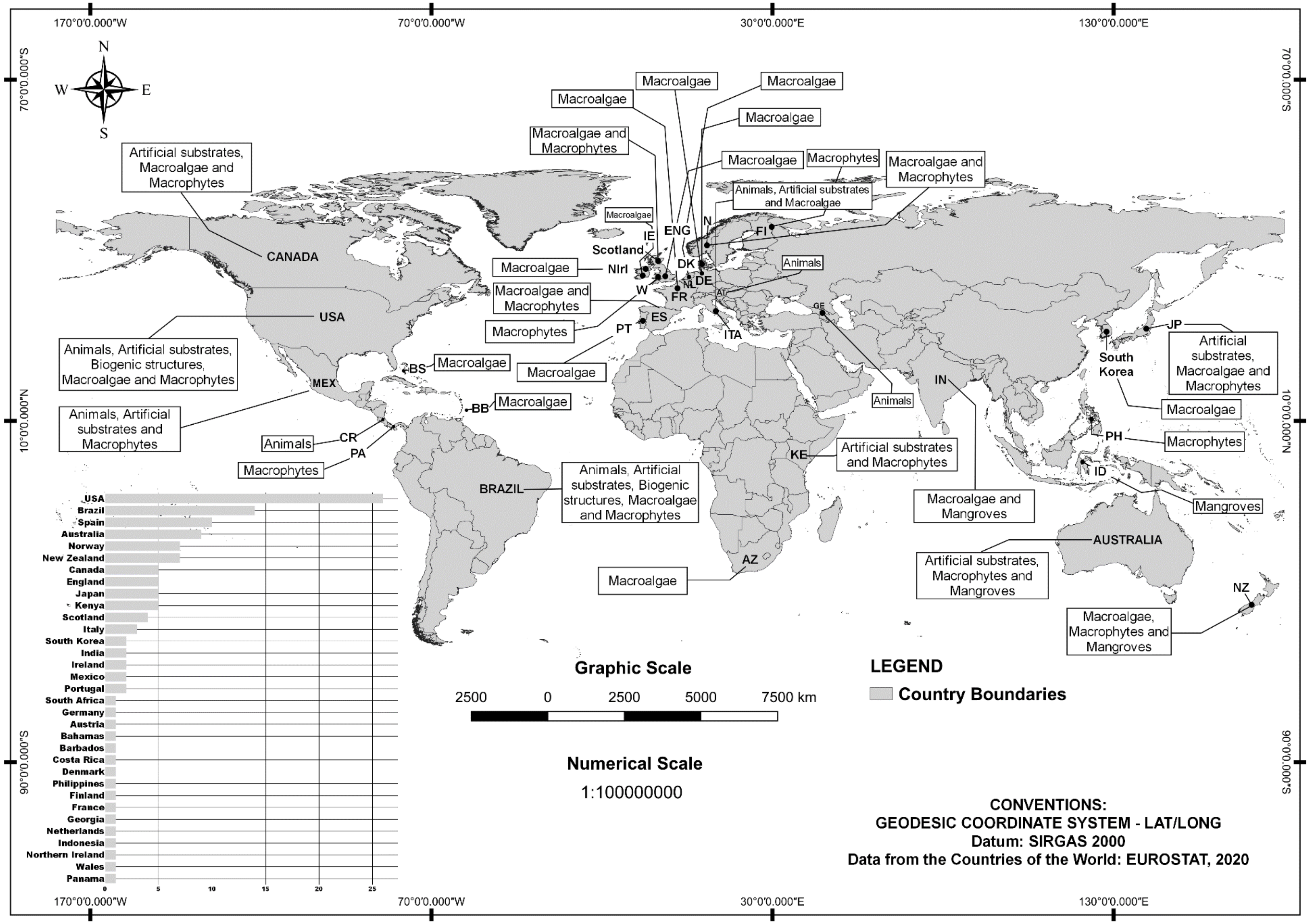
Table 2. Articles focusing on the colonization of substrates by meiofauna with the highest number of citations, from the year of their publication until 2023.

Rank	Article	Authors	Journal	Year	Citations
1	Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal Amphipod.	Hacker, S. D.; Steneck, R. S.	Ecology	1990	229
2	Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal.	Coull, B. C.; Wells, J. B. J.	Ecology	1983	181
3	Metazoan community structure in relation to the fractal dimensions of marine macroalgae	Gee, J. M.; Warwick R. M.	Marine Ecology Progress Series	1994	176
4	Structure of phytal Harpacticoid Copepod assemblages and the influence of habitat complexity and turbidity.	Hicks, G. R. F.	Journal of Experimental Marine Biology and Ecology	1980	163
5	Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian Coast	Christie *et al.*	Journal of the Marine Biological Association of the United Kingdom	2003	161
6	Colonization of artificial seagrass versus time and distance from source	Virnstein, R. W.; Curran, M. C.	Marine Ecology Progress Series	1986	144
7	Mobile epifauna on subtidal brown seaweeds in	Taylor, R. B.; Cole, R.	Marine Ecology	1994	134

northeastern New Zealand	G.	Progress Series

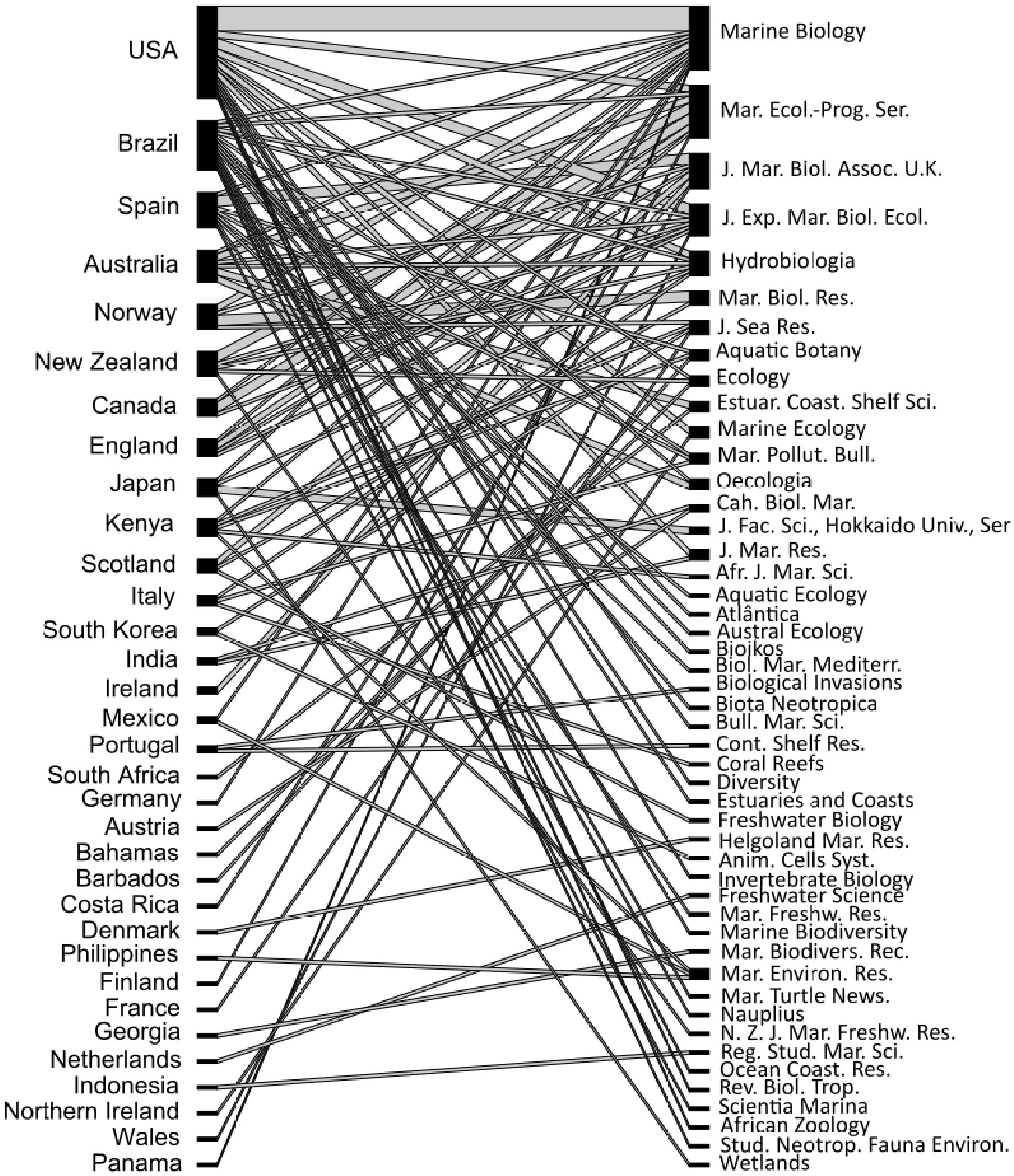
The Fig. 7 shows the geographical distribution of studies, in terms of the number of studies conducted in a specific country. Studies on the colonization of substrates by meiofaunal assemblages have been recorded in 33 countries. The United States (USA) produced the largest number of papers (26 papers, 20.96%), followed by Brazil, where 14 studies (11.29%) were conducted. There is a lack of studies in the polar regions. The first study on the subject was carried out in the USA. In addition, the USA has colonization studies in five of the six substrates found in the literature. Of all the countries registered, 12 have no studies on the colonization of meiofauna in macroalgae. In terms of continent, Europe contributed the largest number of studies (42 articles, 33.87%), followed by North America (37 articles, 29.83%).

Fig. 7 Countries where the analyzed studies were developed and substrates used in each study. "AT" = Austria. "AZ" = South Africa. "BS" = Bahamas. "BB" = Barbados. "CR" = Costa Rica. "DE" = Germany. "DK" = Denmark. "ENG" = England. "ES" = Spain. "FI" = Finland. "FR" = France. "GE" = Georgia. "ID" = Indonesia. "IE" = Ireland. "IN" = India. "ITA" = Italy. "JP" = Japan. "KE" = Kenya. "MEX" = Mexico. "N" = Norway. "NL" = Netherlands. "NIr" = Northern Ireland. "NZ" = New Zealand. "PA" = Panama. "PH" = Philippines. "PT" = Portugal. "USA" = United States. "W" = Wales.



Considering the ten most productive countries (number of articles > 4), it can be observed that eight of them have studies published in Marine Biology, totaling fifteen of the eighteen articles published in this journal (Fig. 8). The USA also published in the journal Marine Ecology Progress Series, which ranked second in the number of publications on the subject.

Fig. 8 Bipartite network linking the country where the study was carried out with the journal where it was published.



Regarding the quantitative analyses used in the different studies, multivariate analyses predominated, used in 41.54% of the studies found (Table 3). Among them, the most used were ordination analyses, in particular, the Non-Metric Multidimensional Scaling (nMDS). In general, this analysis was used to verify the grouping of the different substrate samples as a function of community structure. In second place were the univariate analyses, reported in 33.45% of the articles analyzed. The main tests used were Analysis of Variance (ANOVA) and Kruskal-Wallis tests, to verify significant differences in univariate descriptors (abundance, density and richness) among the different substrates. Ecological indices and mathematical models were sparsely reported, appearing in only 17.64% and 7.35% of the studies, respectively.

Table 3. Quantitative analysis used in studies on the colonization of substrates by benthic meiofauna.

Statistical analysis	**Number of occurrences**
Multivariate analysis	113
Univariate analysis	91
Ecological indices	48
Mathematical models	20

No significant relationships were found between any of the relationships considered (Table 4). The use of the different substrates in the publications analyzed did not differ between years of publication, countries where the study was carried out, or journal. Similarly, the choice of journals did not differ between the countries where the study was carried out.

Table 4. Results of the chi-square test for relationships between different variables analyzed in this study. “df” = degree of freedom.

Relationships	**$\chi 2$**	**df**	***p*-value**
Substrates *x* Year of publication	171	150	0.1155
Substrates *x* Countries where the study was carried out	98.804	90	0.2466
Substrates *x* Journal	100.59	125	0.9468
Journal *x* Countries where the study was carried out	442.34	450	0.5927

4 DISCUSSION

The number of studies on the topic analyzed was low compared to other scientometric analyses (de Carvalho *et al.* 2015; Gao *et al.* 2022; Li *et al.* 2022). It may be due to the absence, in the articles retrieved, of non-indexed studies or studies published in local journals that are not registered in the databases used. In addition, limitations are still observed in the search engines, which result in restrictions in the scientometric methodology when articles do not have the searched terms present in their title, abstract or keywords, where the search engine performs its recruitment (Santos de Moura and Vianna 2020). These documents are not found and are excluded from the searches. Despite this, it is not uncommon to find scientometric analyses in the literature with a low number of retrieved articles due to the specificity of the topic analyzed (Luiza-Andrade *et al.* 2017; Hauser-Davis 2020; Santos de Moura and Vianna 2020; Lima Vieira *et al.* 2021; Sharma *et al.* 2022).

Macroalgae were the most commonly used substrate in studies focusing on colonization by meiofaunal assemblages. Macroalgae are traditionally used in studies of substrate structural complexity because they are microhabitats used by most meiofaunal groups (Frame *et al.* 2007). However, the abundance and diversity of meiofaunal communities differ among different types of macroalgae (Veiga *et al.* 2016), as those with more complex morphology usually offer a greater number of microhabitats for colonization (Gibbons 1991; Veiga *et al.* 2016).

More complex macroalgae provide a greater variety of food resources (Hicks 1980) and better protection from predators (Coull and Wells 1983), desiccation and wave action (Hooper and Davenport 2006, Norderhaug *et al.* 2014); as well as facilitating sediment trapping (Giere 2009). Therefore, meiofauna associated with complex macroalgae generally exhibit higher density and diversity than those associated with less complex macroalgae (Hooper and Davenport 2006, Frame *et al.* 2007). Low densities, on the other hand, are commonly observed in macroalgae with reduced morphological structures (Hicks 1980).

The macroalga *S. muticum* was the most frequently used substrate. It was introduced to Europe in the early 1970s and is now distributed from Norway to Morocco as well as in the Mediterranean Sea (Sabour *et al.* 2013). In general, *S. muticum* was used in studies that compared its associated fauna to that associated with native macroalgae. In these studies, it was found that it indeed harbors a meiofaunal assemblage with a different structure than that found in native macroalgae. The large number of studies with this approach is justified because invasive macroalgae modify the structure and dynamics of native communities

(Levin *et al.* 2002), altering habitat structure, reducing the abundance, richness and primary production of benthic species (Salvaterra *et al.* 2013).

It was observed that studies working with specific taxonomic groups generally used Copepoda and Ostracoda. This may be justified because these crustaceans have appendages that facilitate adhesion to substrates (Gunnill 1982), which prevents them from being easily removed from them by the action of winds or tidal exposure. Thus, these organisms make it easy to assess the effect of structural complexity and identity of the substrates, ignoring, even if not completely, the action of hydrodynamic processes, because once they are able to attach to the substrate, their density and abundance will not decrease drastically due to hydrodynamic processes.

In general, the most abundant meiofaunal groups in most of the studies analyzed were Nematoda, Copepoda Harpacticoida, and Amphipoda. These taxonomic groups are usually the most representative in studies evaluating meiofaunal assemblages, regardless of the focus. However, depending on the environment in which they are inserted, other organisms such as Turbellaria, Oligochaeta, Polychaeta, Tardigrada and Ostracoda can also be found in larger numbers (Warwick and Gee 1984; Giere 2009). This is because there are environmental factors that influence how meiofauna is distributed. In addition, the organisms themselves have adaptations that allow them to live in the interstitial environment, such as their body flexibility, miniaturization, adhesion, special locomotion and reinforcing structures, and specialized organs or even characteristic modes to facilitate locomotion, sometimes in conjunction with adhesion or body elongation (Giere 2009).

Invertebrates occupy a diverse range of microhabitats in macroalgae, such as the algal surface, base of fronds where debris accumulates, and interstices of rhizoids. However, although variation in habitat architecture is associated with an increase in phytal species abundance and richness, there is a difference in the representativeness of phytal community abundance as a function of distinct substrate measures (Schneider and Mann 1984).

Most of the studies analyzed lacked taxonomic refinement. The use of different taxonomic resolutions in the same analysis makes comparisons among biological groups and studies impossible, and may mask important information about individuals, because the more refined the taxonomic resolution the greater the sensitivity of the observed patterns (Heino *et al.* 2013; Luiza-Andrade *et al.* 2017). However, species-level identifications are not always possible, as meiobenthic representatives exist in almost all invertebrate phyla (da Silva *et al.* 1997; Giere 2009), requiring the collaboration of taxonomists for the different groups. The recognized difficulty in identifying meiofaunal organisms is also due to the small body size of individuals, the similar coloration in the early stages of many species, the low detectability, or even the absence of structures important in differentiating species (Orlofske and Baird 2013).

There has been a decrease in the number of studies that investigate the influence of substrate on meiofauna structure. It is possible that this stems from the consensus among meiobentologists that more complex substrates, such as macroalgae and branched macrophytes, are preferred by meiofaunal communities. Thus, new studies with this approach would hardly bring new contributions to the Science. In addition, there are emerging lines of studies with meiofaunal organisms, such as the studies of the impacts caused by microplastics to these assemblages, which although still incipient (Giere 2019), already have some publications with high citation rates (Wright *et al.* 2013; Cole *et al.* 2015; Gusmão *et al.* 2016; Fueser *et al.* 2019). It is also possible that the COVID-19 pandemic and the increase in the number of journals publishing only in open-access mode in recent years have contributed to the reduction in publications on the topic covered in this article.

The analysis showed that from 1967 to 2023, the US was the most productive country in this field. The U.S. has topped the list with the highest scientific production in various areas of knowledge for years (Liao and Huang 2014). The higher number of studies in Europe and North America at the expense of the lower number of articles in Africa, Central America and South America reflects the effect of the economic factor to some degree, especially with regard to the allocation of resources for investments in Science and Technology. In less developed countries, funding is usually insufficient to support studies of (Bozzetti and Schulz 2004). It is noteworthy that in South America, Brazil was the only country with published studies on the subject. This lack of biological knowledge is also true in African, Asian and island countries where the research history is still incipient (Luiza-Andrade *et al.* 2017), as we found only one study per continent.

Our results showed a preference for multivariate analyses by meiobentologists. There is a global trend of increasing use of multivariate statistical methods for marine and coastal benthic ecology (de Carvalho *et al.* 2015). According to James and McCulloch (1990) it is no longer possible to gain a complete understanding of ecology without some knowledge of multivariate analysis. Benthic ecology of marine and coastal habitats has a long tradition of using non-parametric methods (Clarke and Ainsworth 1993; Clarke 1993); this may be the reason why nMDS was the most used multivariate method in the analyzed studies. This observation is in agreement with Clarke *et al.* (2008), who noted that the non-parametric approach to analyze species-by-sample matrices has been widely adopted for marine community ecology in particular. An increase in the use of mathematical models has also been observed. Overall, predictive ecological modeling applied to benthic fauna is an emerging research topic (de Carvalho *et al.* 2015). A lower preference for ecological indices, in turn, may be related to the fact that these metrics mask diversity in large taxonomic groups and generate biased responses to ecological phenomena.

4.1 Perspectives

Based on the information obtained from the scientific literature, some recommendations for future research on the colonization of substrates by meiofauna are presented:

- As shown in the results of the present study, the use of macroalgae as substrates is already well documented in the literature, especially those of the class Phaeophyceae. However, the literature lacks information about the benthic association's resident in macroalgae with morphologies different from those of the aforementioned class.
- How exotic macroalgae are prioritized in meiofauna colonization study, the use of cosmopolitan macroalgae to compare meiofaunal assemblages in macroalgae of the same species, but in different localities, is recommended because it will allow the evaluation of effects of different environments on meiofauna living in macroalgae with the same morphology. Considering the diversity of life strategies adopted by meiofauna, it is possible that there are variations in the way these organisms colonize the same substrate in different regions.
- Studies using animals as substrates are also recommended since this type of study is still scarce. Sessile substrates are efficient for evaluating the structure of the resident meiofaunal assemblage, chemotaxis, and even symbiotic relationships. Mobile substrates, such as animals, on the other hand, can be useful in studies of meiofauna dispersal.
- The identification of meiofaunal taxa at a specific level is still an obstacle to the study of meiofauna, which can be observed by the lack of taxonomic resolution in the articles analyzed. This is due to the lack of taxonomists for meiofaunal groups. In addition, many invertebrate phyla are part of meiofauna, which requires specialized taxonomists for each of these various phyla. Another problem, which particularly affects researchers in underdeveloped and developing countries, is the lack of quality equipment that allows the observation and recording of morphological characters of interstitial animals. However, efforts to identify as many meiofaunal groups as

possible at a specific level should be undertaken in studies that evaluate the entire meiobenthic assemblage, to ensure a better interpretation of the data obtained by using more precise information about the taxa studied.

- Given the increase in marine debris (Bergmann *et al.* 2017; Borrelle *et al.* 2020; Chassignet *et al.* 2021), it is important to consider them as potential substrates to understand how meiofauna colonize different types of debris and whether their presence affects how organisms colonize other substrates.
- Considering that studies on substrate colonization by meiofauna are predominantly carried out *in situ*, laboratory studies (to eliminate the effects of predation and interspecific competition) with specific taxa, especially those that are not highly prioritized by researchers (i.e. Gastrotricha, Kinorhyncha, Tardigrada) also appear as possibilities for future research.

5 CONCLUSION

The scientometric analysis has provided insights into the research on substrate colonization by meiofauna. Macroalgae are the most frequently studied substrate, with *Sargassum muticum* being the most commonly used species. The analysis also showed that the United States was the most productive country in this field, followed by Brazil, reflecting the varying levels of research investments and funding across different regions. Researchers predominantly favored Multivariate analyses, with Non-Metric Multidimensional Scaling (nMDS) being the preferred quantitative method. Additionally, there was a decline in the number of studies focusing on substrate colonization by meiofauna in recent years, possibly due to the consensus that more complex substrates already offer valuable insights into meiofaunal ecology.

For future research, it is recommended to explore meiofaunal colonization in macroalgae with different morphologies, investigate meiofaunal assemblages in cosmopolitan macroalgae across various locations, examine meiofaunal associations with animals as substrates, and address the challenges associated with identifying meiofaunal taxa at a specific level.

This scientometric analysis guides future research directions and emphasizes the importance of understanding meiofauna-substrate relationships to enhance our knowledge of benthic ecosystems and their ecological dynamics. As researchers continue to delve into this field, it is essential to maintain a comprehensive and multidisciplinary approach to advance our understanding of meiofauna colonization and its implications for marine environments.

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3 CAPÍTULO 2: THE INFLUENCE OF THE STRUCTURAL COMPLEXITY OF TWO DIFFERENT BRAZILIAN AMAZON COAST PHYTAL SUBSTRATES ON INTERTIDAL MEIOFAUNAL COMMUNITY STRUCTURE

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Influência da complexidade estrutural de dois diferentes substratos fitais sobre a estrutura da comunidade meiofaunal intertidal no Norte do Brasil

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ABSTRACT:

Phytal environments are settled by meiofaunal communities due a variety of niche options. In this context, this study analyzed the effects of the structural complexity of *Spartina alterniflora* and *Ulva lactuca* from the Maranhão Gulf (Maranhão, Brazil) on meiofauna community aspects. Ten specimens from each species were collected for five months. Eighteen taxa were recorded on the two substrates, 16 associated to *S. alterniflora* and 13 to *U. lactuca*. The mean density of *S. alterniflora* individuals was 3.22 ± 1.17 ind.10 cm^{-2}, and of *U. lactuca*, 2.8 ± 2 ind.10 cm^{-2}. Nematoda, Copepoda, and Amphipoda were present at the highest densities, with the first two the most abundant taxa detected in *S. alterniflora*, while the latter two were the most abundant in *U. lactuca*. The phytal substrate structural complexity did not affect meiofauna density, although it significantly influences taxa richness and community structure.

KEYWORDS: Benthos. Macrotidal. *Spartina alterniflora*. Spatial heterogeneity. Tropical environment. *Ulva lactuca*.

1 INTRODUCTION

The benthic meiofauna is an important food item for both macrofauna and ichthyofauna, comprising part of the total energy required by their consumers (Tito de Morais; Bondiou, 1984). In addition, meiofaunal associations are regularly employed in environmental monitoring studies (Uneputty; Frid, 1998; Esteves; Fonsêca-Genevois, 2006; Gyedu-Ababio; Baird, 2006; de Meira *et al.*, 2013; Semprucci *et al.*, 2015a, 2015b, 2015c; Dezfouli *et al.*, 2016; Allouche *et al.*, 2021; Michelet *et al.*, 2021; Gheller; Corbisier, 2022), due to close associations and dependence on sediment, short life cycle with benthic larval stages and high density, diversity, and sensitivity to environmental changes (Zarghami *et al.*, 2020).

Besides inhabiting sediments, meiofauna organisms can also occupy other substrates, such as plants or animals that make up the macrofauna (Attrill *et al.*, 2000; Arroyo *et al.*, 2004; Buschbaum *et al.*, 2006; Norderhaug *et al.*, 2007; Cerrano *et al.*, 2015, Vieira *et al.*, 2018). Some more mobile groups may alternate part of their life cycle between plant substrates and sediments (Bell *et al.*, 1984; Gan *et al.*, 2019). However, for the meiofauna to colonize a certain type of substrate, both colonizable space and the accumulation of degradable organic matter for feeding are required, as well as favorable microorganism growth conditions (Fonsêca-Genevois *et al.*, 2006).

Complex phytal substrates provide a greater variety of food resources (Hicks, 1980) and better protection from predators (Coull; Wells, 1983), desiccation, and wave action (Hooper; Davenport, 2006, Norderhaug *et al.*, 2014), facilitating sediment trapping (Giere, 2009). Therefore, meiofauna associated with complex substrates generally exhibit greater abundance and diversity than those associated with less complex ones (Hooper; Davenport, 2006, Frame *et al.*, 2007; Veiga *et al.*, 2016; Ape *et al.*, 2018a).

The architecture of phytal substrates plays a fundamental role in the structure of meiofaunal communities, as it provides a variety of microhabitats and niches for these organisms (Duarte *et al.*, 2020). In macroalgae, where colonization by meiofauna is better documented (Santos *et al.*, 2023, in press), the organisms stay at the base of the fronds and in the interstices between the rhizoids, where detritus generally accumulates and food resources are more limited (Da Rocha *et al.*, 2006).

Among the various taxa of invertebrates that occur in the meiofauna, Copepoda, Halacaridae, Nematoda, and Ostracoda are the principal representatives of the so-called "phytal meiofauna" (Hicks, 1985). The presence of these groups in phytal substrates is well reported in the literature, given their occurrence and representativeness in studies that analyze the colonization of substrates by meiofauna (Santos *et al.*, 2023, in press).

Most quantitative phytal meiofauna studies focus on specific taxa, such as Copepoda Harpacticoida, Nematoda, Turbellaria, and Ostracoda (Veiga *et al.*, 2016), and few consider the entire community structure (Ape *et al.*, 2018a, 2018b; Gan *et al.*, 2019). In this regard, studies regarding meiofauna associated with plant or animal substrates for the Brazilian coast are scarce, especially compared to macrofauna or even meiofauna assessments in sedimentary environments (Vieira *et al.*, 2018). This is especially true for the state of Maranhão (Brazil), with still insufficient studies concerning this community available.

The state of Maranhão has the second longest coastline in Brazil (El-Robrini *et al.*, 2006). This coastal region is divided between two coastlines, divided by the Bay of São Marcos. The western portion of the state belongs to the Amazon coast and the eastern portion to the northern northeastern coast (Villwock *et al.*, 2005). Maranhão Island is located in the transition region between these two distinct types of coastlines (Silveira, 1964). The coast of Maranhão is characterized by a variety of vegetated coastal environments, including wetlands, dune fields, mangroves, beaches, and sandbanks (Gama *et al.*, 2011; Santos *et al.*, 2023). Despite the diversity of environments and vegetated substrates found there, there are no published studies on the colonization of these substrates by meiofauna in Maranhão or other regions of the Amazon Coast.

To analyze the influence of phytal substrate complexity on meiofaunal community structuring, the present study considered two native plant species, the salt marsh plant *Spartina alterniflora* Loisel 1807 and the algae *Ulva lactuca* Linnaeus 1753. *Spartina alterniflora* is a facultative pioneer halophyte, dominant in saline sites that serves as a substrate for many epiphytic organisms (Gleason, 1986; Lin *et al.*, 2015). Differences in the shape and spatial dispersal of its stalks can lead to structural changes of associated fauna, due to the reduced foraging efficiency of large predators (Macy *et al.*, 2019). *Ulva lactuca* (considered to be a synonym of *U. fasciata* Delile, 1813 by Guiry; Guiry, 2022) is exposed during low tides for long periods of time, resisting desiccation due to the shape of its thallus, allowing it to maintain inter-fold moisture, serving as food, refuge, and protection against desiccation for numerous microinvertebrates (Vieira *et al.*, 2018; Liu *et al.*, 2020).

Banks of *S. alterniflora* are common environments in the coastal-estuarine zone off the coast of the island of Maranhão (Brazil). They are usually found in the upper mediolittoral in front of mangrove bangs and tidal flats, forming homogeneous and/or mixed fields, with the presence of mangrove seedlings growing alongside them (Rebelo, 2000, Ferreira *et al.*, 2012). *U. fasciata* is also a fairly common species on the coast of Maranhão. They are commonly found on rocky shores and tidal pools, in the surf zone. In certain months of the year, this macroalga quickly colonizes large stretches of rock, adding color to the landscape (Correia; Brandão, 1974).

In this sense, this study analyzed the effect of the structural complexity of these two phytal substrates on the structures of intertidal meiofaunal communities in two Maranhão Gulf regions located on Brazilian Amazon Coast. We hypothesize that density, taxa richness, and community structure differ between phytal substrates as a function of their structural complexity, with higher density and richness values found in more complex substrates.

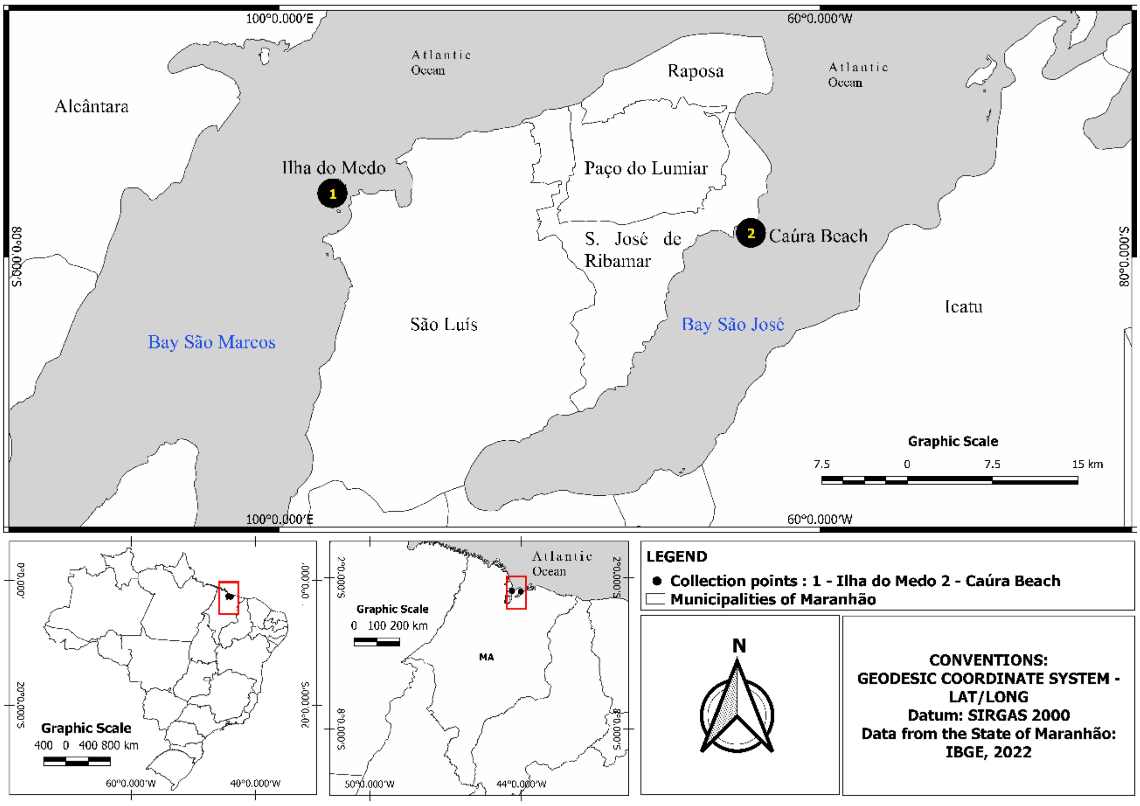
2 MATERIAL AND METHODS

2.1 Study area

The coastal vegetation of the Maranhão Gulf is composed of mangroves, beach vegetation, and leafy trees (dos Santos *et al.*, 2014) (Figure 1). *Spartina alterniflora* specimens were sampled from Caúra Beach (2°33'25"S; 4°2'19"W), in São José Bay, municipality of São José de Ribamar, in the northeast of Maranhão Island (Brazil). This beach is about 1 km long and undergoes intense wind, sea and riverine activity, generating waves and currents that shape local cliffs, mangroves, and local islands (Medeiros, 1988). It has a flat surface, with no elevated sandy deposits. The area has a dry period from August to December, and a rainy period that begins in January and continues until June (Amorim *et al.*, 2023). The climate in the region is Aw (tropical) (Alvares *et al.*, 2013), with average rainfall of around 2000 mm/year and an average temperature of 28°C, with a minimum of 25°C and a maximum of 33°C (INMET, 2023).

Ulva lactuca specimens were sampled at Medo Island (01°27'S; 44°12'W), in São Marcos Bay. The island lies in the portion of the bay with an active estuary, with a well-developed central channel dominated by ebb currents (Muehe, 2006; Castro *et al.*, 2014). Its geomorphological structure includes cliffs, streambeds, beaches, dunes, talus deposits, and tidal flats. The island's vegetation is made up of mangroves, beach vegetation, and leafy trees and its soil varies from clayey to sandy (dos Santos *et al.*, 2014).

Figure 1. Location of the *Ulva lactuca* and *Spartina alterniflora* sampling areas, Maranhão Gulf, Maranhão, Brazil.



2.2 Phytal morphology

Spartina alterniflora Loisel (1807) is a cespitose herb with thick rhizomes and stout, erect aerial stems, ranging from 100 to 150 cm in length (Caetano *et al.*, 2017). This species exhibits alternate, glabrous linear-lanceolate leaves, 10-30 cm long and 4.5 mm wide (Soriano-Sierra *et al.*, 2014). Its flowers consist of 5 to 14 cm long white inflorescences ending in spikes and exhibiting two to three spikelets, some oval and aristate (Bortolus; Schwindt, 2018). It is found near igarapés (streams), forming dense spots bordering mangroves (Bortolus; Schwindt, 2018).

Ulva lactuca Linnaeus (1753) exhibits a rigid membranous consistency, reaching 2 to 10 cm in height with a foliaceous, irregular, and lobed thallus (Aguilar-Rosas *et al.*, 2005). The most frequent form is a 1 to 4 cm wideband attached to the substrate by a tiny holdfast and fronds consisting of two cell layers 0.065 to 0.096 mm thick and thick cuticles ranging from 0.004 to 0.009 mm (Kazi *et al.*, 2016).

2.3 Sampling and sample processing

Ten specimens from each phytal substrate were collected during low tide for five months (May, June, August, September, and October 2014), totaling 50 samples of each substrate. *S. alterniflora* specimens were collected manually from the same bank in the supralittoral zone each month. The samples were extracted from the base and wrapped in plastic bags, while *U. lactuca* specimens were collected manually of tide pools and packaged in 500 mL plastic bottles for transport. To ensure independence of the samples, replicates of *S. alterniflora* were sampled in different areas of the bank and each replicate of *U. lactuca* was collected in different pools.

At the laboratory, the samples were washed under running water over superimposed 0.5 mm and 0.053 mm mesh sieves, according to Boisseau (1975). The material retained in the 0.053 mm sieve was conserved in a 4% formalin saline solution in plastic recipients and elutriated manually in a beaker. The supernatant was then transferred to a Dollfus plate. All meiobenthic organisms were counted and categorized into major groups employing a stereomicroscope.

2.4 Structural complexity of phytal substrates

Structural complexity was measured using biomass and fractal dimensions of substrates as proxies for habitat size and architecture, respectively (Gee; Warwick, 1994; Hooper; Davenport, 2006; Veiga *et al.*, 2014, 2016; Torres *et al.*, 2015; Ape *et al.*, 2018a). The substrates were dried for 48h at 60 °C and then weighed to determine the biomass in grams (Veiga *et al.*, 2014, 2016; Torres *et al.*, 2015; Ape *et al.*, 2018a).

Each substrate replica was lightly crushed and photographed with a digital camera Canon EOS Rebel T7 EF-S 18-55 f/3.5-5.6 IS II BR, to obtain the fractal dimensions. Fractal dimensions were calculated according to McAbendroth *et al.* (2005). Each photograph was converted to TIFF format and transferred to grayscale. A threshold was set to produce a binary image used to quantify the fractal dimensions of area (Da) and perimeter (Dp) for each image, using ImageJ software (Rasband 1997-2012). Da is a measure of the spaces between the branches, so higher values indicate a higher degree of branching (McAbendroth *et al.* 2005; Torres *et al.*, 2015). Dp is a measure of the contour of the macroalgae or the degree of convolutions of its edges, so larger values indicate more divisions at smaller scales (McAbendroth *et al.* 2005; Torres *et al.*, 2015).

2.5 Data analysis

The normality of the biomass, fractal area (Da), and fractal perimeter (Dp) data transformed log(x) was tested by the Shapiro-Wilk test. Statistical differences on these descriptors were determined by a Student's t-test performed for each data set.

The relative abundance, density, richness, and occurrence frequency of each taxon were calculated. To determine the influence of structural complexity (i.e. biomass, Da, and Dp) on density, taxa richness, and community structure, a mixed linear model using 9999 permutations with a Type I (sequential) sum of squares was used to calculate p-values from a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2014). In the analysis, the sampling areas were considered random effects and substrate identity was a fixed factor with two levels (*S. alterniflora* and *U. lactuca*), and biomass, Da and Dp were covariates. Interactions between categorical variables (identity of phytal substrates) and continuous predictor variables (biomass, Da, and Dp) were included in the analyses (Veiga *et al.*, 2014). The analyses were done on the basis of Euclidean similarity matrices for abundance and richness and Bray-Curtis similarity matrices for multivariate data (Veiga *et al.*, 2014).

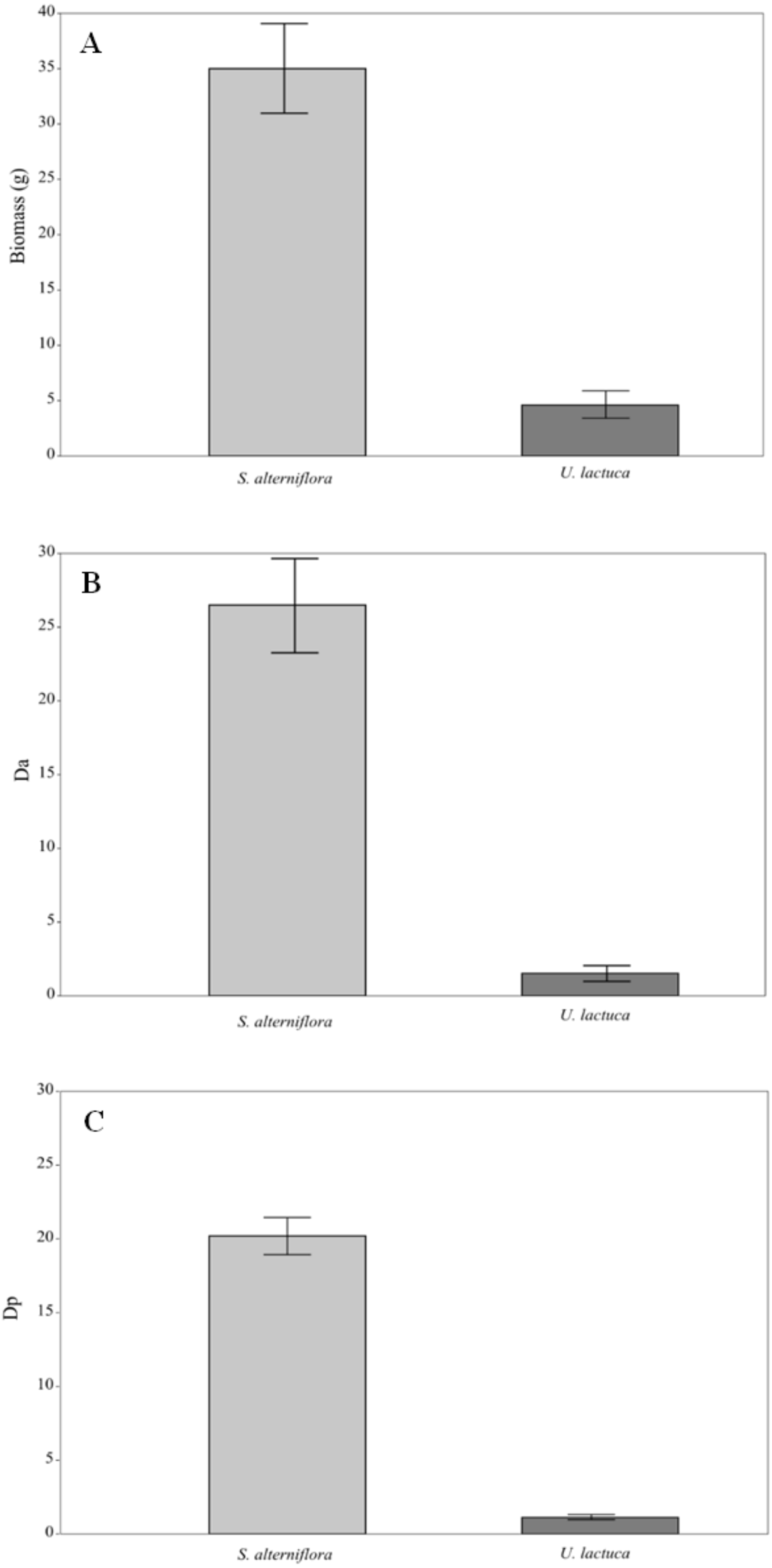
A non-metric multi-dimensional scaling (nMDS) plot was constructed to better visualize inter-group relationships (Clark, 1993). A Similarity Percentages (SIMPER) test was then performed to identify the groups that most contributed to significant effects (Clark, 1993). All analyses were performed using the R software (R Core Team, 2022) packages car (Fox; Weisberg, 2019), ggplot2 (Wickham, 2016), lattice (Sarkar, 2008), permute (Simpson, 2022), and vegan (Oksanen *et al.*, 2022).

3 RESULTS

3.1 Structural complexity of phytal substrates

Biomass values and fractal measurements varied considerably among the studied phytal substrates, with the highest values found in *S. alterniflora* for all three variables (Figure 2). Student's t-test revealed the two substrates studied differed significantly for biomass (t_{91} = 6.233; p = 7^{-12}), fractal area (t_{91} = 4.025; p = 0.0002), and fractal perimeter (t_{91} = 1.105; p = 0.003).

Figure 2. Means (± standard deviation) of biomass (A), fractal dimensions based on area (Da) (B), and fractal dimensions based on perimeter (Dp) (C) of *S. alterniflora* and *U. lactuca*.



3.2 Taxonomic composition

A total of 27.502 organisms and 18 taxa were identified in both substrates, of which 14.852 organisms and 16 taxa were associated with *S. alterniflora*, and 12.650 organisms and 13 taxa with *U. lactuca*. The mean density of *S. alterniflora* individuals was 3.22 ± 1.17 ind.10 cm^{-2}, and of *U. lactuca*, 2.8 ± 2 ind.10 cm^{-2}. Nematoda, Copepoda, and Amphipoda were the most abundant and frequent groups, with the first two more representative in *S. alterniflora* and the latter two more representative in *U. lactuca*. Copepoda occurred in all the samples in both substrates. (Table 1).

Table 1. Relative abundance (Rel.ab) and occurrence frequency (OF) for each taxa detected in each phytal substrate.

Taxa	***Spartina alterniflora***		***Ulva lactuca***	
	Rel.ab(%)	**OF(%)**	**Rel.ab(%)**	**OF(%)**
Acari	4.75	85	3.25	30
Amphipoda	0.6	30	16.65	95
Bivalve	3.4	90	0	0
Cnidaria	0	0	3.09	10
Copepoda	18.8	100	39.43	100
Echinodermata	0.41	10	0	0
Gastropoda	0.93	70	3.25	20
Gastrotricha	2.52	45	4.2	20
Insecta	0.6	45	0	0
Isopoda	0.6	10	4.09	60
Nematoda	62.87	100	6.39	70
Oligochaeta	0.74	20	4.23	50
Ostracoda	0.91	50	3.29	70
Polychaeta	0.7	60	5.2	65
Pycnogonida	0.56	5	0	0
Rotifera	0.8	25	2.99	10

Tardigrada	0.8	5	0	0
Turbellaria	0	0	3.93	40

The structural complexity of the phytal substrates did not affect meiofauna density during the study period. Richness, on the other hand, was significantly affected, with pairwise comparisons indicating that taxa richness in *S. alterniflora* was significantly higher than in *U. lactuca* (Figure 2, Table 2). Meiofaunal communities also differed among the substrates according to the PERMANOVA results (Table 2).

In addition, both richness and community structure showed significant interactions with Da, Dp, and Bi. These results indicate that the effect of structural complexity descriptors differed among the substrates studied, regardless of their identity (Table 2). The observed multivariate pattern indicates a clear separation between substrates in the nMDS ordering (Figure 3). The groups that contributed most to substrate type differences were Nematoda, Copepoda, Amphipoda, and Polychaeta (Table 3). Nematoda was the taxonomic group that contributed most to the dissimilarity between the two substrates, with a significant difference in average abundance between *S. alterniflora* and *U. lactuca*. Therefore, the presence or absence of nematodes explains almost half of the difference between the two substrates.

Figure 3. Means (± standard deviation) of A) richness and B) density of the meiofaunal community associated with *S. alterniflora* and *U. lactuca*.

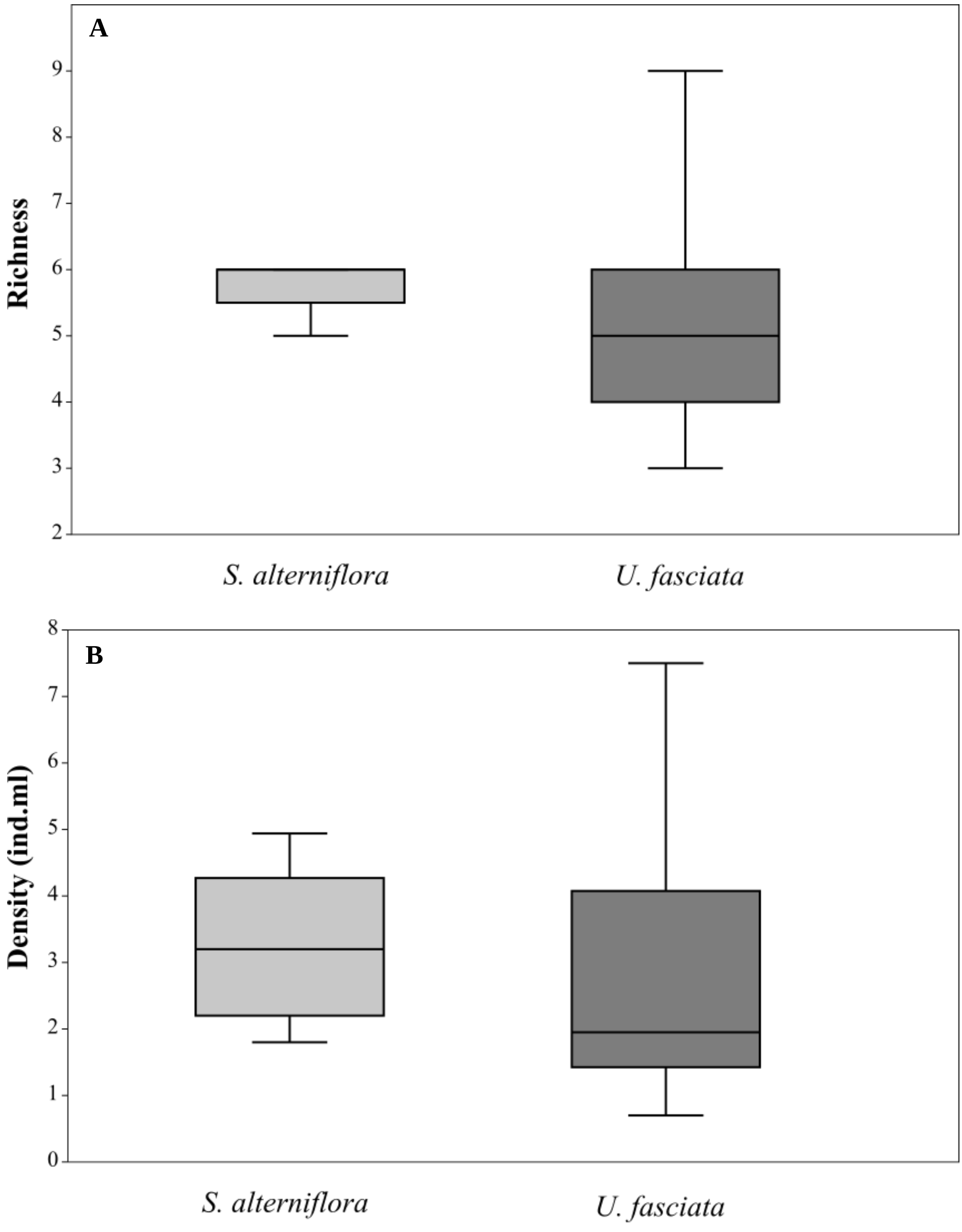


Table 2. PERMANOVA results concerning taxa richness and density and meiofaunal community structure associated with *S. alterniflora* and *U. lactuca*, respectively. Da = dimensions of area. Dp = dimensions of perimeter. Bi = Biomass. Pi = Phytal identity.
'*' - p <0.05; '**' - p <0.01; '***' - p <0.001.

		Richness		**Density**		**Community Structure**	
	df	**MS**	**Pseudo-F**	**MS**	**Pseudo-F**	**MS**	**Pseudo-F**
Da	1	0.341	2.979*	0.07	0.95	1.43	31.51***
Dp	1	0.138	1.209**	0.33	0.44	2.97	9.102***
Bi	1	0.065	0.567**	0.025	0.223	1.376	33.341*
Pi	1	0.249	2.178***	0.02	0.176	2.739	24.76***
Da x Pi	1	0.006	0.056*	0.042	0.367	0.124	20.511**
Dp x Pi	1	0.141	1.231	0.033	0.289	0.05	12.639
Bi X Pi	1	0.137	1.202**	0.092	0.810	0.023	6.61
Residual	91	0.05		0.018		0.091	

Figure 4. nMDS ordination based on the abundances of all taxonomic groups detected in the sampled meiofaunal communities and Bray-Curtis similarity associated with *S. alterniflora* and *U. lactuca* (triangles and squares, respectively). 3D Stress: 0.04533.

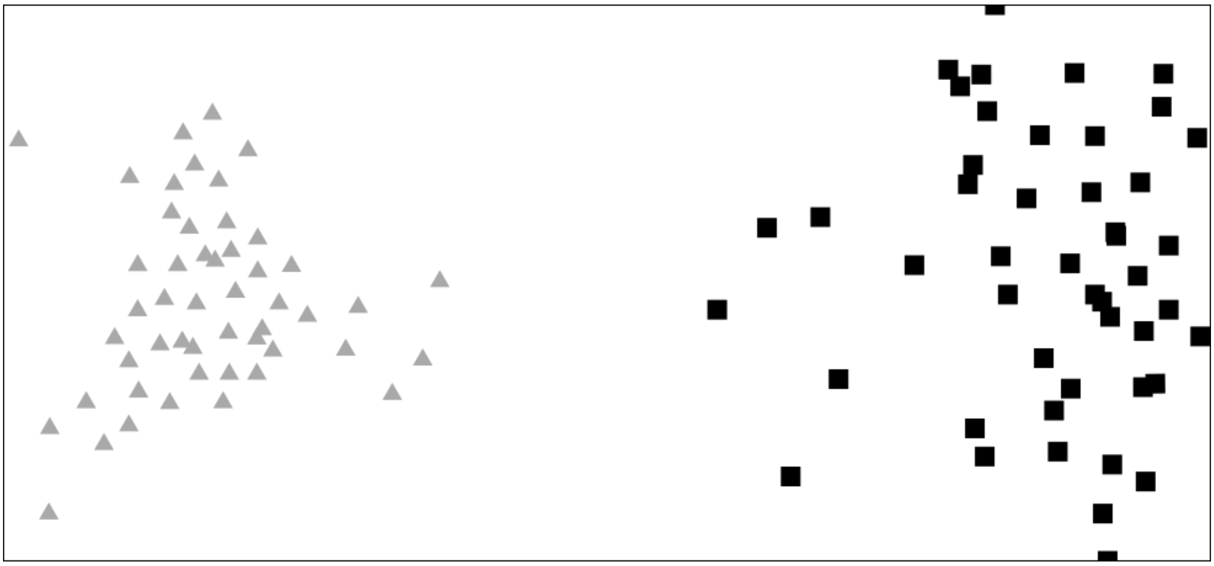


Table 3. SIMPER results indicatings the relative contribution (%) of the four taxonomic groups that contributed the most to significant differences between the faunas associated with *S. alterniflora* (S) and *U. lactuca* (U). The abbreviations in front of each taxa represent the substrate in which the group was the most abundant.

Taxa	Dissimilarity	Contribution (%)	Mean abundance of *S. alterniflora*	Mean abundance of *U. lactuca*
Nematoda (S)	28.32	41.8	62,9	6,38
Copepoda (U)	12.17	17.95	18,8	39,4
Amphipoda (U)	8.024	11.84	0,6	16,6
Polychaeta (U)	2.251	3.321	0,7	5,19

4 DISCUSSION

The findings indicate that phytal substrate complexity plays a significant role in meiofauna community diversity and structure, partially supporting the hypothesis of this study. Considering biomass, fractal area, and fractal perimeter as structural complexity descriptors, *S. alterniflora* presented a higher complexity, when compared to *U. lactuca*. Community richness and structure differed among substrates as a function of structural complexity, but this was not observed for density. Despite this, the most complex substrate (*i.e., S. alterniflora*) harbored the highest meiofaunal abundance and density.

Our results differ from most previous studies, which have identified effects of complexity on abundance but not on richness (Gee; Warwick, 1994; Hacker; Steneck, 1990; Hull, 1997; Norderhaug, 2004; McAbendroth *et al.*, 2005; Hooper; Davenport, 2006; Veiga *et al.*, 2016, Ape *et al.*, 2018a; Vieira *et al.*, 2018). Although no structural complexity effect was observed concerning meiofaunal density, which differs from most studies on the colonization of substrates by meiofauna, organism abundance and community structure were noted as particular to each substrate.

Habitat complexity is of great importance in characterizing the spatial distribution of intertidal species (Beck, 1998, 2000; Veiga *et al.* 2014, 2016; Ape *et al.*, 2018a). Complex substrates are expected to provide multiple resources, allowing for the maintenance of more abundant and diverse communities with different survival requirements (Hicks, 1977, Gibbons, 1991). Branched substrates such as *Spartina* spp. can support higher faunal abundances by providing additional surface area for attachment or offering greater interstitial volume (Bueno *et al.*, 2017).

It is worth noting that Attrill *et al.* (2000, although they worked only with macrofauna) and Christie *et al.* (2009) suggest that fauna composition depends mainly on habitat architecture, while fauna abundance depends on habitat size. In this study, habitat size was used as one of the descriptors of structural complexity, and although the biomass was significantly higher in *S. alterniflora*, there were no significant interactions between density and biomass.

The difference in invertebrate abundance and richness associated with *Ulva lactuca* can be explained, among other factors, by its foliaceous morphotype, with relatively little space available for colonization (Dubiaski-Silva; Masunari, 1995). Thus, the lower number of individuals in *U. lactuca*, compared to *S. alterniflora* may be due to an effect of reduced surface roughness, with animal requiring higher efforts to anchoring themselves (Hacker; Steneck 1990).

Among the four major groups that make up the phytal meiofauna (Hicks, 1985), two were the most representative herein, namely Nematoda and Copepoda. Acari and Ostracoda, which complete the above category, were also present, albeit at lower densities. Tuberllaria and Polychaeta, which also comprise important phytal meiofauna taxa (da Rocha *et al.*, 2006), contributed to data dissimilarity, along with Amphipoda, Copepoda, and Nematoda.

The dominance of Amphipoda and Copepoda has been reported in several meiofauna studies (Mukai, 1971; Kito, 1975; Hicks, 1977; Coull; Wells, 1983; Johnson; Scheibling, 1987; Preston; Moore, 1988; Curvêlo; Corbisier, 2000; Venekey *et al.*, 2008; Pérez-García *et al.* 2015; Veiga *et al.*, 2016), and its higher abundance in *U. lactuca* can be explained by easy adhesion to this substrate conferred by appendages (Fenwick, 1976; Hicks, 1977; 1980; Hacker; Steneck, 1990; Ayala; Martin, 2003; Lacerda; Masunari, 2011). Nematoda dominance in *S. alterniflora* can be associated with the accumulation of fine sediments on this substrate, favoring colonization through a high availability of microhabitat conditions (Warwick, 1981; Curvêlo; Corbisier, 2000, da Rocha *et al.*, 2006). High Da and Dp values in *S. alterniflora* indicate higher divisions in the total substrate space, and additional divisions of space at smaller scales, respectively (McAbendroth *et al.*, 2005). These divisions facilitate sediment trapping.

The effect of beach hydrodynamics was not tested in the present study, but it is important to point out that the area where *U. lactuca* was collected is highly exposed to wave action, making organism adhesion difficult. In addition, this macroalgae was sampled from tide pools, which harbor a variety of meiofauna predators, such as fish and crabs (Dethier, 1980), confined in relatively high densities for a long time (Gibbons, 1991). Thus, the low abundance and richness of *U. lactuca* meiofauna may have been influenced by the sampling area, although it is possible that the amount of microflora, microorganisms, and detritus associated with phytal substrates may differ naturally, leading to a substant significantial effect on the associated meiofauna (Frame *et al.*, 2007; Veiga *et al.*, 2016).

Although it was not possible to increase taxonomic refinement, the data presented corroborates both the conclusion of studies on the colonization of substrates by meiofauna that used specific taxonomic levels (Hull, 1997; da Rocha *et al.*, 2006; Hooper; Davenport, 2006; Lacerda; Masunari, 2011; Tavares *et al.*, 2013) and studies that used higher taxonomic categories (Logan *et al.*, 2008; Bohórquez *et al.*, 2013; Veiga *et al.*, 2016; Ape *et al.*; 2018a; Vieira *et al.*, 2018; Lutz *et al.*, 2019). This finding suggests that different taxonomic levels show the same results under the influence of complexity measures. The taxonomic sufficiency of the upper groups was observed by Rodrigues (2019) when he analyzed the epifaunal community in large groups and the amphipod community at the species level in the macroalga *Sargassum filipendula*.

In summary, the results suggest that phytal structural complexity affects the composition of benthic communities. Although our results are a first step in elucidating the dynamics of meiofaunal communities in coastal Maranhão ecosystems in Brazil, we recognize the need to adopt further measures tailored to the target organisms. In contrast to previous studies, which generally test the effect of structural complexity on different species of macroalgae, in this study, we tested this effect on more taxonomically distant substrates. And although no significant differences in density were identified, numerically the more complex substrate harbored the greatest number of individuals, corroborating previous studies carried out with macroalgae (Buschbaum *et al.*, 2006; Veiga *et al.*, 2016; Ape *et al.*, 2018a; Gan *et al.*, 2019) and macrophytes (Rutledge; Fleeger, 1993; Atrill, 2000; McAbendroth *et al.*, 2005; Mascart *et al.*, 2015; Daudi *et al.*, 2023).

The interaction between macroalgae, macrophytes, and meiofauna is complex and not yet fully understood. However, it is clear that phytal substrates play important roles in supporting meiofauna. The results of this study suggest that substrate identity is less important than complexity in structuring meiofaunal associations. Future studies should aim to quantify substrate identity to further assess potential correlations between substrate structure and meiofauna composition.

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4 CAPÍTULO 3: SPATIAL MARINE MEIOFAUNA VARIATIONS IN AREAS UNDERGOING DIFFERENT DISTURBANCE LEVELS ON THE AMAZON COAST

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Variação espacial da meiofauna marinha em áreas com diferentes níveis de perturbação no litoral Amazônico

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ABSTRACT:

The Brazilian coastal zone comprises several types of environments, including lagoons and beaches, chosen for this study, which evaluate benthic meiofauna spatial distribution patterns in three areas, suffering different disturbance levels, throughout the Brazilian Amazon coast. Sediments from three areas (São Marcos Beach – Low level of disturbance; Calhau Beach – Medium level of disturbance; and Jansen Lagoon – High level of disturbance), in São Luís city (Maranhão, Brazil), were sampled for meiofauna assessments, granulometry and organic matter analyses. A total of 7,254 meiofaunal organisms were identified, 4,371 at São Marcos Beach, 1,856 at Jansen Lagoon, and 1,027 at Calhau Beach. The findings indicate that richness, density, and community structures differed significantly among the sampled areas. Nematoda and Copepoda were the most abundant groups. Copepoda stood out in São Marcos Beach compared to other taxa. Nematoda dominated in Jansen Lagoon. Calhau Beach presented the lowest density and richness values, with Tardigrada as the predominant meiofaunal group. Additionally, the composition of meiofauna was influenced by environmental variables, such as salinity, OM, sediment grain size and nitrate concentration, as well as anthropogenic activities taking place in the sampled areas. Considering the lack of studies in the region with this focus, it is expected that the results presented will contribute to public policies development aimed to conservation of the coastal zone in São Luís.

KEYWORDS: Bioindicators; Coastal lagoon; Nematoda; Organic contamination; Sandy beaches.

1 INTRODUCTION

The coastal zone is a complex and ever-changing environment, due to natural processes on wide time scales and increasing human activities (Danovaro and Pusceddu 2007; Defeo *et al.* 2009; Zho *et al.* 2018). Lately, there has been growing concern about the environmental impacts in this region (Paoli *et al.* 2015) as well as the search for solutions to reduce the effects of anthropogenic actions (Pilouk and Koottatep 2017). However, socioeconomic pressures in coastal areas accelerate unplanned urbanization and natural resource degradation, threatening environmental and economic sustainability (Schlacher *et al.* 2006, 2007; Ariza *et al.* 2010; McLachlan and Defeo 2017; Bertocci *et al.* 2019).

In this context, monitoring studies in coastal regions have aided the management of these areas (Ariza *et al.* 2010; Schlacher and Thompson 2012; Sun *et al.* 2014; Semprucci *et al.* 2015a, 2015b; Peña-Alonso *et al.* 2018), through the use of ecological indicators, such as abundance, density, richness and diversity descriptors, employed to evaluate the status quo of coastal environments and plan public policies (Balsamo *et al.*, 2012; Alves *et al.* 2013). Regularly, the structure of benthic communities is used in environmental studies in order to use the composition of the community as a parameter for environmental quality classification (Weisberg *et al.* 2008; Ranasinghe *et al.* 2009).

Because they live in the interstitium, benthic meiofauna have been used as marine ecosystems quality bioindicators and are routinely analyzed in environmental stress assessments (Gheskiere *et al.* 2005; Moreno *et al.* 2008; 2011; Alves *et al.* 2013; Zeppilli *et al.* 2015). Furthermore, due to their short life cycles, the responses of these organisms to the consequences generated by polluting agents are faster, as benthic meiofauna density and diversity are lower in affected environments, with the most sensitive species disappearing and only the most tolerant resisting (Giere, 2009; Moreno *et al.* 2011; Balsamo *et al.* 2012; Mirto *et al.* 2012; Alves *et al.* 2013; Sun *et al.* 2014; Semprucci *et al.* 2015b; Zeppilli *et al.* 2015a; Bertocci *et al.* 2019).

The coastal zone of Maranhão, in Brazil, presents a mosaic of high environmental relevance ecosystems (Gama *et al.* 2011). However, the advancing local urban occupation has imposed strong pressures on this area (da Silva *et al.* 2013; Rêgo *et al.* 2018; Machado and Rodrigues 2020). Many areas of the state, including the northern coastal region of São Luís city presents significant human population densities, resulting in different needs and interests, and presenting economic and natural potentialities that have been extensively explored, ignoring local environmental laws (Serra and Farias Filho, 2019).

With regard to São Luís coastal region, this area has suffered significant environmental degradation due to effluent discharges, solid waste inputs, the removal of coastal dunes, urban constructions in and around the beaches, beach vegetation suppression, real estate speculation, and tourism (Rêgo *et al.* 2018; Rodrigues *et al.* 2020; Santos *et al.* 2021; Guayanaz *et al.* 2022). And despite all that, coastal management initiatives are practically non-existent (da Silva *et al.* 2013).

Given this scenario, the present study aimed to evaluate meiofauna spatial distribution patterns between three areas suffering different disturbance levels throughout the Brazilian Amazon coast. A perturbation gradient was postulated in the studied environments and hypothesized that meiofaunal diversity and density decreases as the postulated perturbation gradient increases.

2 MATERIAL AND METHODS

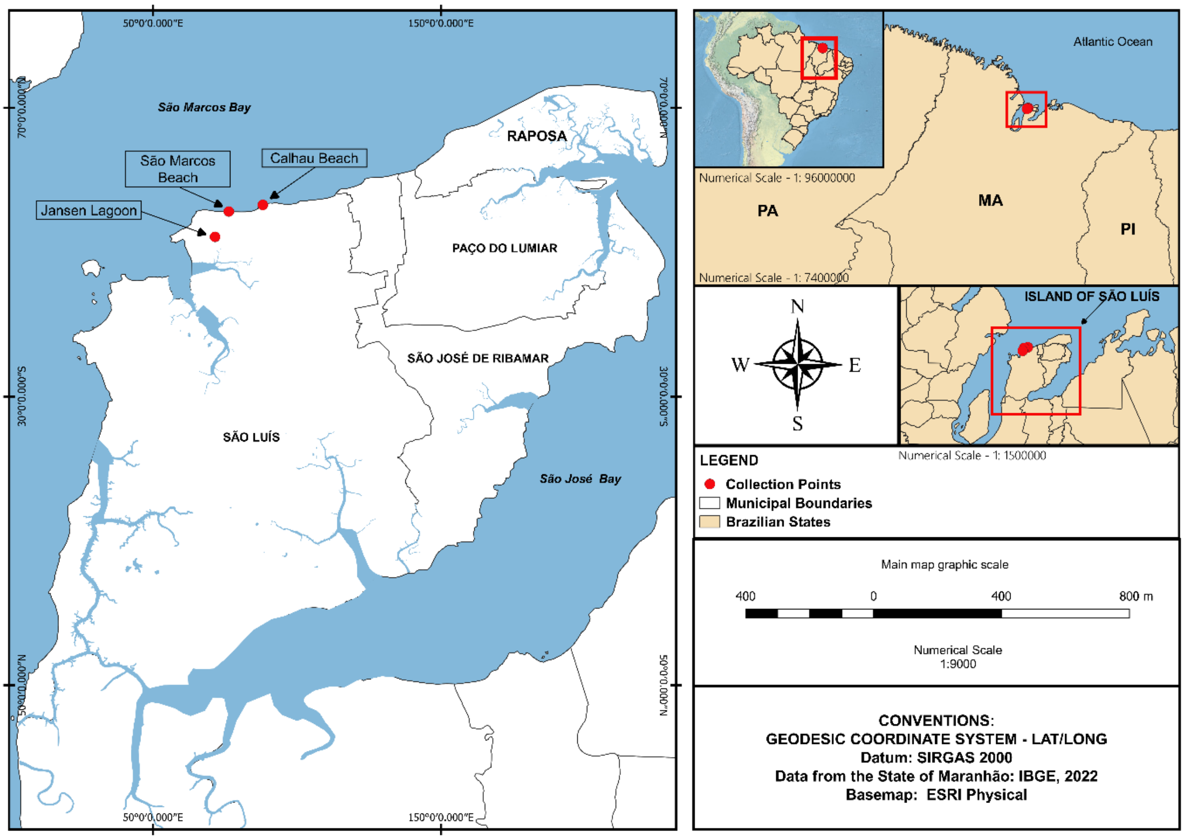
2.1 Study areas

Samples were collected in São Luís city (Maranhão, Brazil), at Calhau (02º28’49.03”S; 44º14’25.79”W) and São Marcos (02º29’11.00”S; 44º18’07.20”W) beaches and Jansen Lagoon (02°29’07’’S; 44°18’02’’W) (Fig. 1). This municipality is one of the four that belong to Maranhão Island, which is inserted in the center of Maranhense Gulf, separating São José Bay to the east and São Marcos Bay to the west (Fernandes *et al.* 2022). This area is characterized by a macrotidal regime (tidal range up to 6.5 m), with strong currents (up to 1.2 m s-1) and moderate wave heights (Hb) up to 1.1 m, with a period of 3 to 8 s (da Silva *et al.* 2013; Masullo 2016).

The urban development of São Luís northern coastal area is characterized by building constructions on the dune systems that run parallel to the coastline and cliffs (da Silva *et al.*

2013). These buildings were constructed without permits or environmental agency controls. Until the 1960s, the coastal zone of São Luís was sparsely inhabited, but from the beginning of the 1970s, the city underwent a rapid and unregulated territorial expansion, resulting in several impacts (Espírito Santo 2006).

Figure 1: Map indicating the study areas analyzed in the present study, namely São Marcos Beach, Calhau Beach and Jansen Lagoon.



2.2 Disturbance level classification

The choice of sampling areas and disturbance level classification considered the bathing quality reports issued by the State Secretary for Environment and Natural Resources of Maranhão (Secretaria de Estado de Meio Ambiente e Recursos Naturais do Maranhão – SEMA) from January 2017 to July 2021. These reports were used to identify areas with the highest and lowest incidence of bathing notices. Additionally, other criteria were considered in the selection, as previous studies conducted in the same area and observations, concerning the following parameters, during the sampling campaigns: urbanization/coastal development intensity, domestic effluent discharge, the presence of domestic animals and vehicles, and the intensity of tourism (Adapted from Pereira *et al.* 2017) (Table 1).

Table 1: Areas sampled on the coast of the state of Maranhão (Brazil). Environmental conditions were established based on beach bathing reports, observations during sampling campaigns, and literature data.

Area	Location	Disturbance level	% of improper reports between Jan/2018 and Jul/2021	Observed impacts	Impacts described in the literature
São Marcos Beach	02º29’11.00”S 44º18’07.20”O	Low	19%	Intense coastal development. Intense recreational visitation. Domestic effluent discharges from adjacent bars.	Intense and irregular urbanization resulting from real estate speculation (Silva *et al.* 2009; da Silva *et al.* 2013; Masullo 2016). Domestic effluent discharges (Silva *et al.* 2009; da Silva *et al.* 2013; Masullo 2016; Rêgo *et al.* 2018; Rodrigues *et al.* 2020; Santos *et al.* 2021). Presence of waste in the dunes (da Silva *et al.* 2013; Rodrigues *et al.* 2020).
Calhau Beach	02º28’49.03”S 44º14’25.79”O	Medium	84%	Moderate urbanization. Domestic effluent discharges. Presence of vehicles on the beach.	Domestic effluent discharges (Silva *et al.* 2009; Santos *et al.* 2021). Sediment compactation (Santos *et al.* 2021). High concentration of *Enterococcus* (da Silva *et al.* 2008). Presence of debris on the beach sand

					(Guayanaz *et al.* 2022) Recurrent presence of black tongue* (G1 MA 2018, 2019; O Estado 2016, 2017, 2020, 2021).
Jansen Lagoon	02°29’07’’S 44°18’02’’O	High	Not applicable	Intense urbanization. Domestic effluent discharges. Presence of solid waste and animals. Intense foul odor. Chemical products thrown in the water by adjacent residences aiming at reducing the odor.	High total and thermotolerant coliform indices (Pereira *et al.* 2014; Santos *et al.* 2014). In natura sewage discharges (Ibañez Rojas *et al.* 2013; Pereira *et al.* 2014; Cutrim *et al.* 2019; Silva 2021). High phosphate values (Ibañez Rojas *et al.* 2013). Intense fetid odor (Silva 2021). Presence of solid waste (Silva 2021).

*Term used to describe a black residue caused by direct sewage discharge on the beach from a neighboring Sewage Treatment Plant which malfunctioned, resulting in the pollution of the Calhau River and consequent spillover at Calhau Beach.

2.3 Sampling procedure

Sampling was carried out in November 2021 during low tide. A transect perpendicular to the waterline was drawn in all three areas, from which ten equidistant replicas (10 m) of sediment were collected for meiofauna analyses, totaling 30 samples, using a cylindrical corer with an internal diameter of 2.4 cm to the depth of 20 cm of sediment. Sediment replicas were also collected from each area for particle size and organic matter content analysis. The meiofauna samples were fixed in a 4% formaldehyde solution, still in the field, and physicochemical water variables (pH, salinity, dissolved oxygen, ammonium, and nitrate) were determined in loco with the aid of a multiparameter HI9829 HANNA probe.

2.4 Laboratory procedures

2.4.1 Meiofauna extraction and identification

The samples were elutriated manually into a 100 mL beaker and poured onto overlapping sieves presenting 0.5 mm and 0.045 mm of apertures. This procedure was repeated three times for each sample to maximize organism extraction. The material retained on the 0.045 mm sieve was washed with the aid of a beaker and transferred to a Dollfus plate. The meiofauna was then counted and identified to the level of the main taxonomic groups according to Giere (2009) under a stereomicroscope and microscope, and their density was standardized to individuals per 10 cm-2. All extracted organisms were placed in Eppendorfs containing 70% alcohol.

2.4.2 Sediment analysis

The granulometric analysis was performed according to Suguio (1973). The samples were dried in an oven at 60º C and characterized in particle size, combining the wet sieving technique (sieve > 62 µm) and pipetting. The processing was determined according to the Wentworth scale (1922), with nominal sample classifications carried out according to Folk and Ward (1957). Organic matter content was determined following the muffle ignition of 50 g of dry sediment stored in porcelain crucibles and muffled for 12 hours at 45 ºC (Walkley and Black 1934). After being removed from the muffle, the sediment was weighed again and the difference in weight meant the amount of organic matter (OM) of each sample volatilized during the ignition process.

2.5 Numerical and statistical analysis

The Shapiro-Wilk test (Shapiro and Wilk 1965) and Levene's test (Levene, 1960) were used to verify data normality and homogeneity, transformed in log (x + 1). To analyze community structure, density (N), expressed as number of individuals per 10 cm-2, and richness, expressed as number of taxa (S), were calculated. An Analysis of Variance (ANOVA) One-Way was used to verify significant variations in ecological descriptors between sampled areas. Significant variations were compared using Tukey's *a posteriori* test.

Community structure was compared between studied areas using Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations, based on a Bray-Curtis similarity matrix (Anderson 2014). An nMDS graph was constructed to visualize associations between groups. Relationships between taxa abundance and water and sediment environmental variables were analyzed through a Canonical Correspondence Analysis (CCA) (ter Braak 1986). The Variance Inflation Factor (VIF) was tested to reduce collinearity between variables, but none had to be removed. Finally, CCA significance was tested by an ANOVA test. A significance level of 0.05 was established for all analyses. All multivariate analyses were performed using log (x + 1) transformed data to adjust for the contribution of dominant and rare species (Clarke 1993).

All analyses were performed using the R software (R Core Team 2022) packages car (Fox and Weisberg 2019), ggplot2 (Wickham 2016), lattice (Sarkar 2008), permute (Simpson 2022), and vegan (Oksanen *et al.* 2022).

3 RESULTS

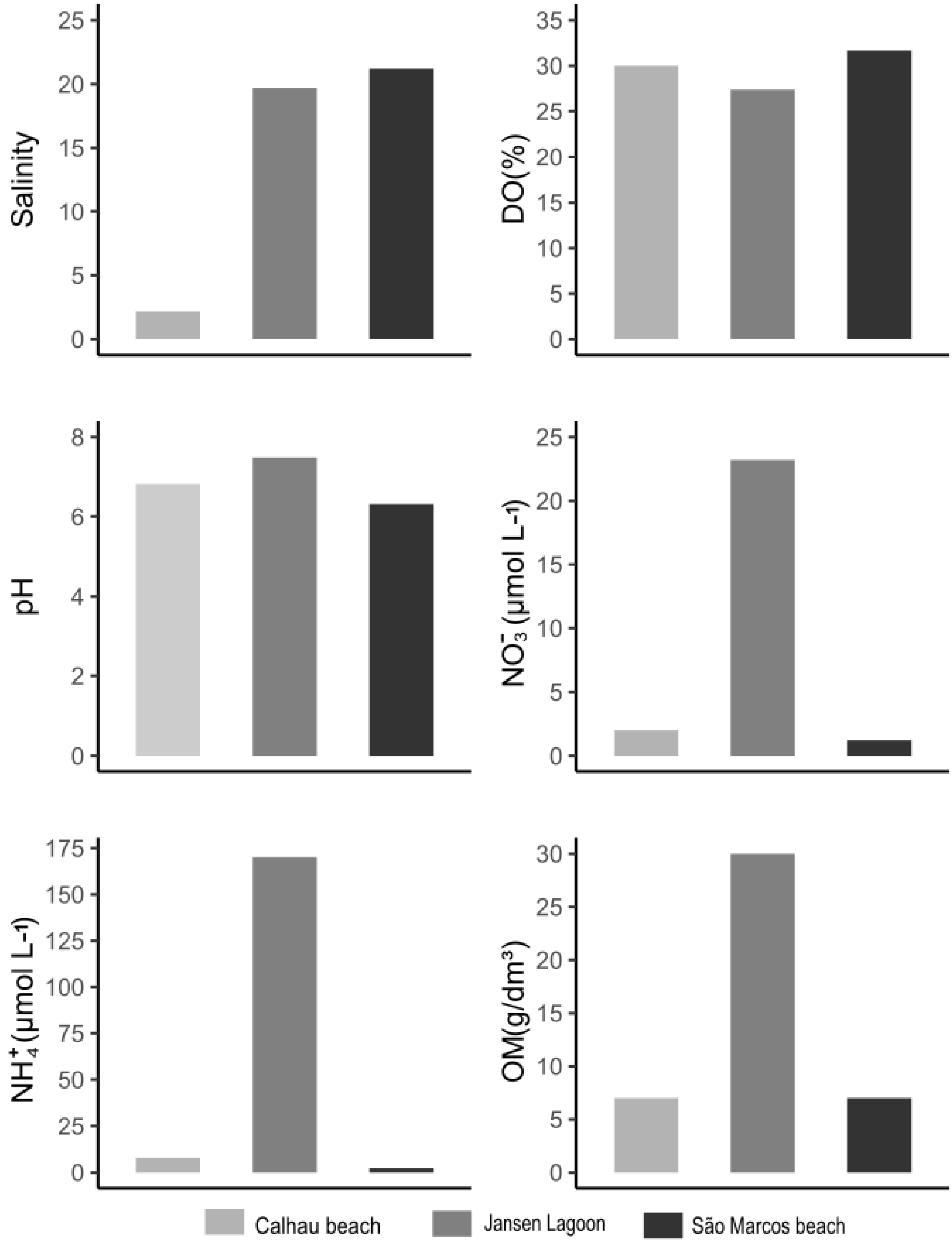
3.1 Environmental variables

The average salinity was $\overline{X}$ = 14.35 (±10.58) among the three study areas, with the lowest and highest values registered at Calhau Beach (2.16) and São Marcos Beach (21.2), respectively. Dissolved oxygen (DO) values ranged from 27.40% at the lagoon to 31.70% at São Marcos Beach ($\overline{X}$ = 29.7±2.16). As for pH, values of 6.32, 6.82 and 7.49 were observed for São Marcos Beach, Calhau Beach and Jansen Lagoon, respectively ($\overline{X}$ = 6.87±0.58) (Fig. 2).

Regarding ammonium (NH4+), nitrate (NO3-), and organic matter (OM) concentrations, the average values for the study areas were 60.13 (±9.35), 8.8 (±2.48), 14.6

(±13.27), respectively, with Jansen Lagoon presenting the highest absolute values for each variable (NH4+ = 170.2 µmol L-1; NO3- = 23.22 µmol L-1; OM = 30 g dm-3) (Fig. 2).

Figure 2: Environmental variables determined in the three study areas.

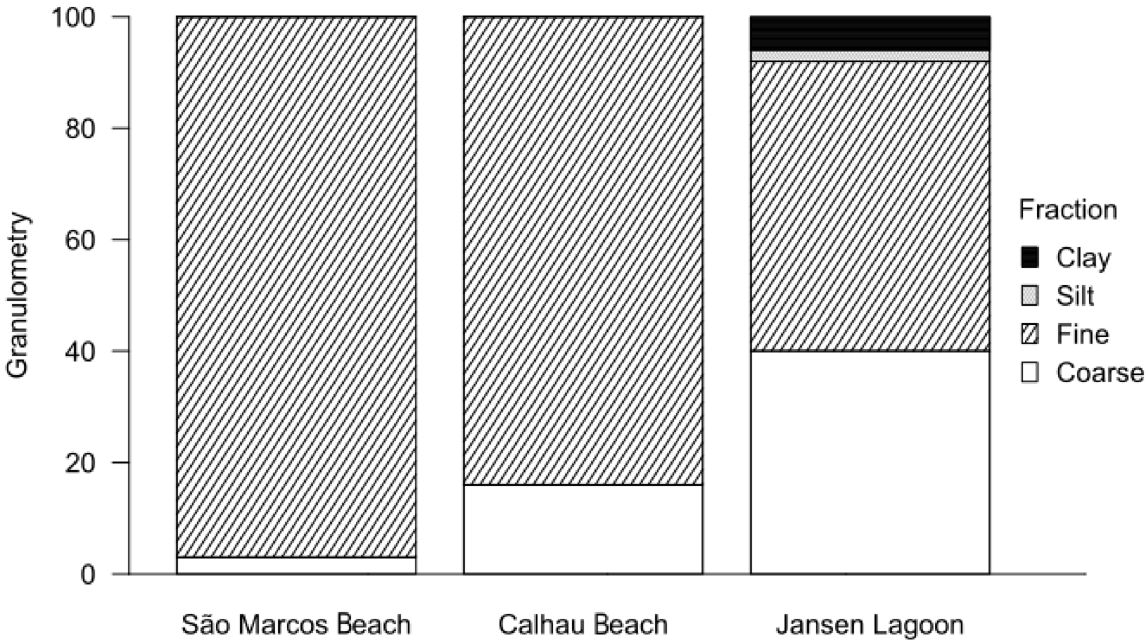


3.2 Granulometry

The sediment in the three study areas was characterized as fine, well sorted or very well sorted sand, corresponding to 97%, 84% and 52% of total sediment at São Marcos and

Calhau beaches and Jansen Lagoon, respectively. The second most abundant fraction was coarse sand. Silt and clay fractions were detected only at Jansen Lagoon (Fig. 3).

Figure 3: Sediment sample granulometry at the São Marcos and Calhau beaches and Jansen Lagoon.



3.3 Meiofauna community

A total of 7,254 meiofaunal organisms were identified, distributed in 10 taxa in the three study areas, 4,371 at São Marcos Beach, 1,856 at Jansen Lagoon and 1,027 at Calhau Beach. The richness detected at São Marcos Beach (10) and Jansen Lagoon (8) were similar, although the faunal composition varied between them, while Calhau Beach presented the lowest value (5) for this descriptor (Table 2).

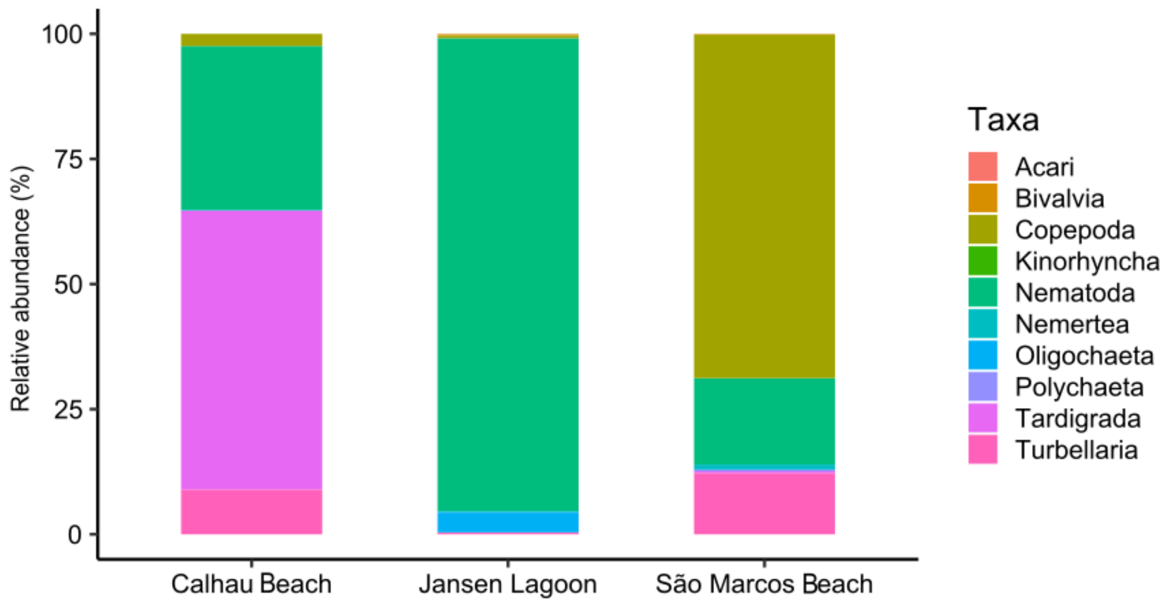
The total density of individuals was 301.7 ind.10 cm^{-2}, ranging from 125.04 ind.10cm^{-2} (Copepoda) to 0.04 ind.10 cm^{-2} (Kinorhyncha). Copepod was the taxon with the highest density, at São Marcos Beach (125.04 ind.10 cm2), meanwhile at Jansen Lagoon, the highest density taxon was Nematoda (73.08 ind.10 cm^{-2}) and at Calhau Beach, Tardigrada (23.83 ind.10cm^{-2}) (Table 2).

Table 2: Taxa density in ind.cm^{-2} (D), frequency of occurrence in percentage (Fo) and richness (S) at each stduy area.

Taxa	São Marcos Beach		Lagoon Jansen		Calhau Beach	
	D	**Fo**	**D**	**Fo**	**D**	**Fo**
Nematoda	31.41	100	73.08	100	14.04	100
Copepoda Harpacticoida	125.04	100	0.41	50	1.04	80
Turbellaria	22.29	100	0.29	40	3.83	60
Nemertea	1.87	50	0.20	20	0	0
Tardigrada	0.62	50	0	0	23.83	100
Oligochaeta	0	0	3.08	40	0.04	10
Polychaeta	0.58	50	0	0	0	0
Acari	0.08	20	0.04	10	0	0
Bivalvia	0.16	30	0.20	20	0	0
Kinorhyncha	0.04	10	0	0	0	0
Overall density	**182.09**		**77.3**		**42.78**	
Overall S	**10**		**8**		**5**	

Copepoda was the most abundant group (41.85%), followed by Nematoda (39.21%), representing 81% of all identified organisms. Copepoda Harpacticoida were noteworthy among the other identified taxa at São Marcos Beach, accounting 69% of the relative organismal abundance. Jansen Lagoon was almost totally dominated by Nematoda, which contributed with 95% of the relative abundance in this area. At Calhau Beach, the predominant meiofaunal group was Tardigrada, which made up 56% of the relative organismal abundance (Fig. 4).

Figure 4: Relative abundance of each meiofaunal taxa identified at Calhau Beach, São Marcos Beach and Jansen Lagoon.

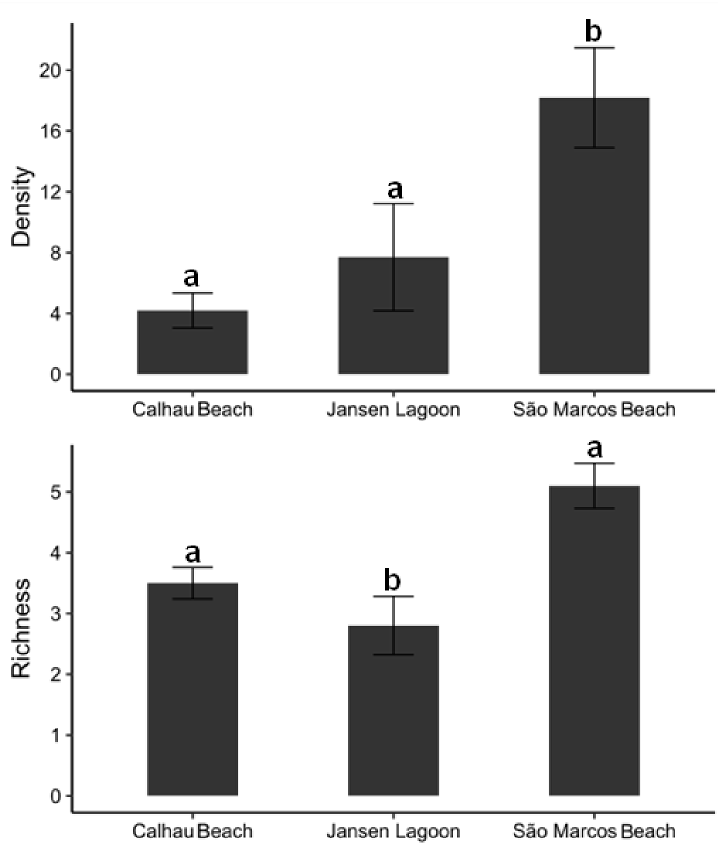


The ANOVA results indicate that density and taxa richness differed significantly among the study areas. The PERMANOVA result indicated a dissimilarity in meiofaunal community structure (Table 3). Paired comparisons indicated that density was significantly higher at São Marcos Beach compared to Calhau Beach and Jansen Lagoon, with no significant difference detected between the last two. Richness was significantly lower at Jansen Lagoon compared to São Marcos and Calhau beaches (Fig. 5).

Table 3: Summary of the density and richness ANOVA results and meiofaunal community structure PERMANOVA results for Calhau Beach, São Marcos Beach and Jansen Lagoon (df= degrees of freedom; MS= means square; F= F-statistic; p=p value).

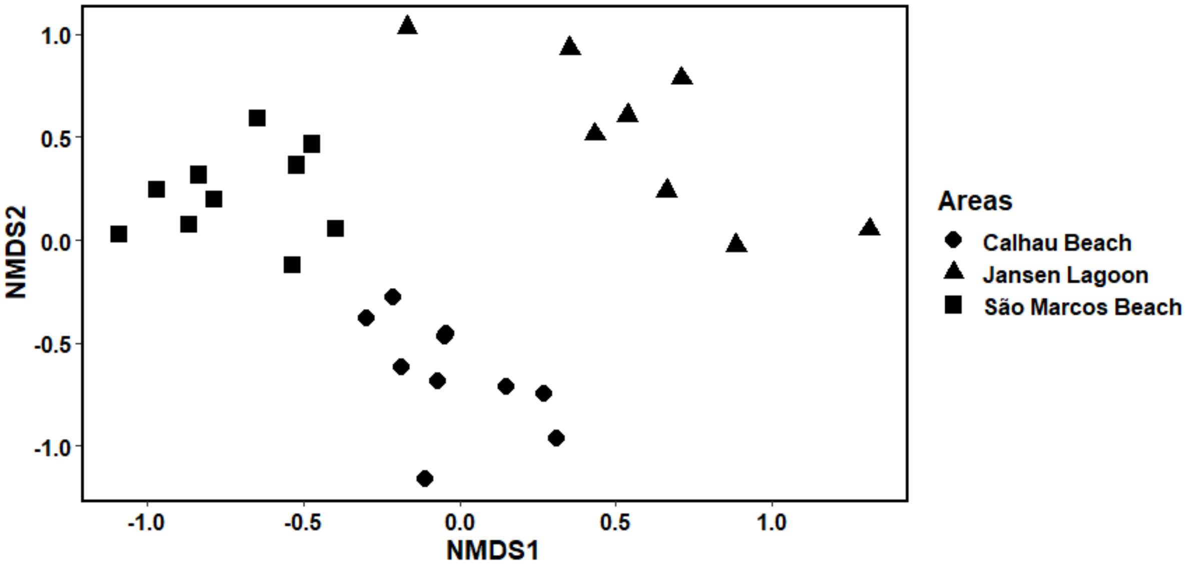
		Density			**Richness**			**Community structure**		
Factor	*Df*	*MS*	*F*	*p*	*MS*	*F*	*p*	*MS*	*Pseudo-F*	*p*
Areas	2	524,68	6,39	0,005	13,9	9,15	0,0009	0,4	12,17	0,0004
Residuals	27	82,01			1,51			0,52		

Figure 5: Average and standard deviations of the analyzed samples density and richness. Different letters indicate statistically significant differences detected by Tukey's test.



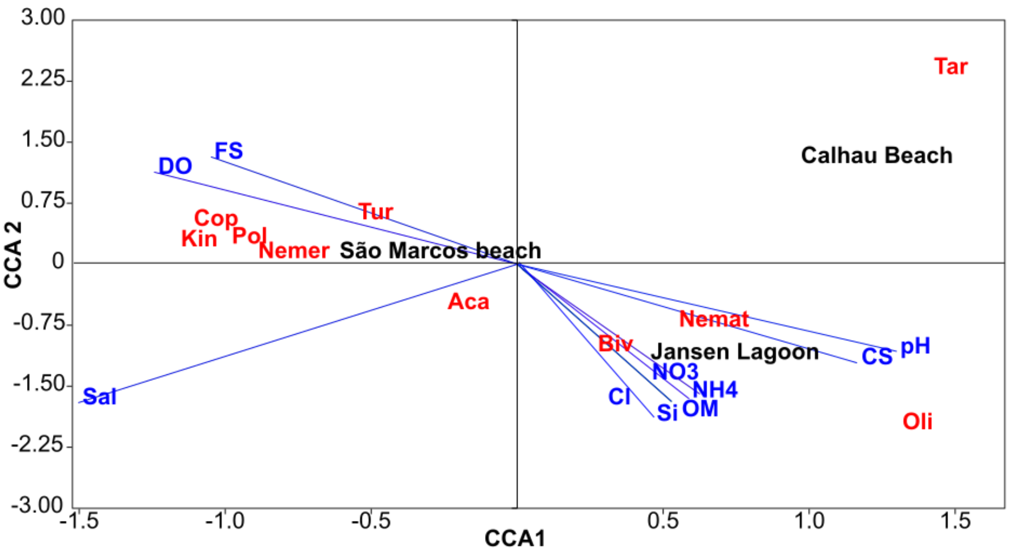
The nMDS analysis demonstrated a clear separation between studied areas in terms of community structure, forming three distinct groups, corroborating PERMANOVA results (Fig. 6).

Figure 6: Similarities between the community structure of the study areas according to the nMDS analysis.



The CCA was significant (p= 0.03) and indicated that 90% of explained data variance associated species density and environmental variables (Axis I: 55.64%; Axis II: 34.36%). Nematoda, Oligochaeta and Bivalvia were positively influenced by OM, pH, NO3-, NH4+ and fine sand at Jansen Lagoon. At São Marcos Beach, Copepoda, Polychaeta, Nemertea, Kinorhyncha and Turbellaria were positively influenced by DO, while Tardigrada were negatively influenced by salinity, at Calhau Beach (Fig. 7).

Figure 7: CCA results concerning meiofauna composition and environmental variables. FS: fine sand. CS: coarse sand. Cl: clay. Si: silt. DO: dissolved oxygen. Sal: salinity. pH: hydrogenic potential. NO3: nitrate. NH4: ammonium. OM: organic matter. Tur: Turbellaria. Cop: Copepoda. Pol: Polychaeta. Kin: Kinorchyncha. Nemer: Nemertea. Aca: Acari. Biv: Bivalvia. Nemat: Nematoda. Oli: Oligochaeta. Tar: Tardigrada.



4 DISCUSSION

Although meiofaunal communities varied among areas suffering different disturbance degrees, forming three distinct groups according to the nMDS analysis, meiofaunal diversity and density did not decrease according to the postulated disturbance gradient. It was expected that Jansen Lagoon would present the lowest values for the analyzed descriptors, which was, instead, observed for Calhau Beach. São Marcos Beach presented the expected pattern for a less impacted environment, displaying the highest density and richness values. Despite the results, we assume that the richness in the present study is being underestimated due to the low taxonomic resolution used.

Jansen Lagoon exhibited a high density of Nematoda, which tend to increase in contaminated environments (Bouwman *et al.* 1984; Ferraz *et al.* 2022), as in this lagoon's case, which receives large loads of surface runoff and pollutants. The overlap of this taxa is explained by its high resistance to osmotic stress (Forster 1998; di Montanara *et al.* 2022; Jonathan 2022) and ability to use enriched sediment organic content as a potential food source (Bongers and Ferris 1999; Losi *et al.* 2021; Jonathan 2022; Xu *et al.* 2022). Furthermore, these worms exhibit a strong relationship with fine sediments (Vanaverbeke *et al.* 2002; Semprucci *et al.* 2010; 2015a; Baia and Venekey 2019), such as those found in the lagoon.

Among the three study areas, Jansen Lagoon presented the second highest taxa density and richness, which may be associated to the higher OM in this area compared to others, explaining the correlation between this parameter to this area in the CCA. Meiofauna composition can increase according to sediment OM, and higher OM concentrations are usually associated to higher amounts of organisms (Mouawad *et al.* 2012). However, although OM from domestic sewage benefits marine meiofauna as a potential food source, negative effects may arise when OM is present in excess, causing anoxic conditions or generating hydrogen sulfide (H2S) when degraded by anaerobic bacteria (de Oliveira and Soares-Gomes 2003).

Despite the concentration of ammonium and nitrate, in three study areas, being within the parameters allowed by Brazilian Environmental Legislation for saline and brackish waters (Brasil 2005), the concentration of these parameters was significantly higher in Jansen Lagoon, when compared to the other areas. Ammonium and nitrate occurs in water as a final product of organic nitrogen biological degradation and is generally used as a poor water quality indicator (Mouawad *et al.* 2012). Moreover, high concentrations of this nitrogenous compound can lead to an excessive microalgae proliferation, with consequent increases in the amount of chlorophyll-a and intense eutrophication events (Penna *et al.* 2004; Bertocci *et al.* 2019). Eutrophication can make sediment hypoxic or anoxic (Penna *et al.* 2004) and benefit opportunistic species (Rabalais *et al.* 2001; Vanaverbeke *et al.* 2004a, b; Carriço *et al.* 2013; Semprucci *et al.* 2015a). When not associated with oxygen limitation, eutrophic conditions can increase microbial activity and, eventually, meiofauna abundance and diversity (Giere 2009).

Copepoda also presented high density. The CCA correlated the abundance of this taxon at São Marcos Beach to sediment DO. Copepods are more representative in well-oxygenated environments (Coull 1999; Moreno *et al.* 2006; De Troch *et al.* 2013; Hure *et al.* 2020; Medellín-Mora *et al.* 2021) and exhibit a relatively larger presence compared to Nematoda at tropical beaches (Giere, 2009), as observed at São Marcos Beach.

Copepoda stood out in terms of density and relative abundance at São Marcos Beach. This group is considered more sensitive to environmental disturbances than other meiofaunal groups (Raffaelli and Mason 1981; Hicks and Coull 1983; Van Damme *et al.* 1984; Raffaelli 1987; Gheskiere *et al.* 2005; Pereira *et al.* 2017). The dominance of these organisms at São

Marcos Beach may be indicative of good environmental quality of this beach, while its near absence at Jansen Lagoon and Calhau Beach may indicate serious disturbances in both areas.

Tardigrada displayed the highest density at Calhau Beach, which is not common, as its density is rarely very high, even in favorable locations (Giere 2009). This result may be related to the low salinity of the study site (Kinchin 1994), corroborating Tilbert *et al.* (2019), who reported that the highest density values of this group coincided with the low salinity gradient. It is likely that these animals have a wide distribution in brackish water, probably alternating between metabolic activity and inactivity (osmobiosis), according to salinity concentration variations (Kinchin 1994).

Calhau Beach exhibited the lowest richness among the three studied areas, potentially due to OM excess and low salinity, as benthic species usually occur in high salinity and low variability areas (Barroso and Matthews-Cascon 2009; Hourston *et al.* 2009; La Valle *et al.* 2021; Laurino and Turra, 2021). These factors, in turn, may be related to the presence of Calhau River tributary and nearby a Sewage Pumping Station (SPW). This SPW contributed to the occurrence of the phenomenon known as "Black Tongue" from 2016 to 2021 (G1 MA 2018, 2019, O Estado 2016, 2017, 2020, 2021), involving in natura SPW sewage releases which, due to malfunctioning, resulted in Calhau River pollution and consequent spillover at Calhau Beach (G1 MA, 2018). Based on these results, it is possible to infer that the conditions on this beach are so adverse that only organisms displaying extreme resilience, such as Tardigrada, are able to survive.

Calhau Beach also suffers from sediment compaction by motor vehicles, some belonging to the municipal government, responsible for waste management (in loco observation). Sediment compaction reduces the space between sediment grains and increases resistance to fluid (gas and liquid) displacement, creating a physical barrier that affects air exchanges and hydraulic conductivity between interstices (Schlacher *et al.* 2008; Giere, 2009), affecting benthic fauna severely.

Nematoda and Copepoda are generally considered the most suitable taxa to assess meiofaunal community ecological conditions (Moore and Bett 1989; Cifoni *et al.* 2021; Cui *et al.* 2021). However, although other studies have also reported significant meiofauna responses to environmental disturbances when employing higher taxonomic categories (Moreno *et al.* 2006; Bianchelli *et al.* 2016a, 2016b; Pereira *et al.* 2017; Losi *et al.* 2021), as in the present study, many authors recognize that increased taxonomic resolution is necessary to better understand ecological patterns (Moore and Bett 1989; Balsamo *et al.* 2012; Zeppilli *et al.* 2015). Identification at a specific level allows for more accurate assessments regarding community structures and sentinel species ecology assessments, which may be employed to detect anthropogenic impacts (Moreno *et al.* 2011, Losi *et al.* 2013, Sahraeian *et al.* 2020).Jansen Lagoon exhibited a high density of Nematoda, which tend towards higher amounts in contaminated environments (Bouwman *et al.* 1984; Ferraz *et al.* 2022), as in the case of this lagoon, which receives high runoff and pollutant inputs. The overlap of this taxa is explained by their high resistance to osmotic stress (Forster 1998; di Montanara *et al.* 2022; Jonathan 2022) and their ability to use enriched sediment organic content as a potential food source (Bongers and Ferris 1999; Losi *et al.* 2021; Jonathan 2022; Xu *et al.* 2022). Furthermore, these worms exhibit a strong relationship with fine sediments (Vanaverbeke *et al.* 2002; Semprucci *et al.* 2010; 2015a; Baia and Venekey 2019), such as those found at the lagoon.

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Despite the concentration of ammonium and nitrate in the three study areas being within the parameters allowed by the Brazilian environmental legislation for saline and brackish waters (Brasil 2005), the concentration of these parameters was significantly higher in Laguna da Jansen compared to the other areas. This ion occurs in water as a final product of the biological degradation of organic nitrogen and is generally applied as a poor water quality indicator (Mouawad *et al.* 2012). Moreover, high concentrations of this nitrogenous compound can lead to excessive microalgae proliferation, with consequent increases in the amount of chlorophyll-a and intense eutrophication events (Penna *et al.* 2004; Bertocci *et al.* 2019). Eutrophication can render the sediment hypoxic or anoxic (Penna *et al.* 2004) and benefit opportunistic species (Rabalais *et al.* 2001; Vanaverbeke *et al.* 2004a, b; Carriço *et al.* 2013; Semprucci *et al.* 2015a). When not associated with oxygen limitation, eutrophic conditions can increase microbial activity and, eventually, meiofauna abundance and diversity (Giere 2009).

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5 CONCLUSION

Data reported herein indicated decreased density and richness at different patterns than expected, as the most visually polluted area in this study, and considered the most disturbed one, exhibited higher density and richness than the one initially categorized as moderately disturbed. Therefore, the results indicate that Calhau Beach suffers much more significant impact compared to Jansen Lagoon, which exhibited high density of Nematoda, benefited from high OM content. São Marcos Beach showed a high density of Copepoda, indicating a higher environmental quality. In contrast, Calhau Beach presented a high density of Tardigrada, organisms known for their remarkable ability to withstand adverse situations.

Meiofaunal community varied significantly in studied areas and meiofaunal composition was significantly affected by environmental variables such as salinity, OM, sediment grain size and nitrate concentration, corroborating literature data regarding the influence of organic enrichment and sediment contamination on meiobenthic nematodes.

This is the first study to compare spatial meiofauna distribution in areas under marine influence on the Island of Maranhão and suffering environmental disturbances. These findings will contribute to coastal management programs and to the development of public policies aimed at the conservation of São Luís coastal zone, taking into account that this municipality is an important tourist hub in Maranhão state. Future studies are recommended to assess the temporal effects of anthropogenic pressures on the meiofaunal community structure of these areas and increase taxonomic resolution, at least for dominant taxa.

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5 CONCLUSÃO

Este estudo investigou a dinâmica das comunidades meiofaunais em ecossistemas costeiros do estado do Maranhão, Brasil. Os resultados mostraram variações significativas na composição da meiofauna entre as áreas de estudo. Na Praia do Calhau e São Marcos a estrutura da comunidade foi influenciada pela salinidade, enquanto que na Laguna da Jansen, a matéria orgânica foi a principal variável estruturante. e tamanho do grão do sedimento.

A Laguna da Jansen apresentou maior abundância de Nematoda, que são beneficiados pelo aumento de matéria orgânica. A praia do São Marcos apresentou alta densidade de Copepoda, padrão que é indica uma maior qualidade ambiental, enquanto a praia do Calhau apresentou maior densidade de Tardigrada que é um grupo que se destaca por sua capacidade de resistir a situações adversas.

A complexidade estrutural dos substratos fitais não afetou a densidade da meiofauna, mas influenciou a riqueza dos taxa e estrutura da comunidade durante o período de estudo. Nematoda, Copepoda e Amphipoda foram os grupos com maior densidade, sendo os dois primeiros mais abundantes em *S. alterniflora*, enquanto os dois últimos foram mais abundantes em *U. fasciata*. Embora estes resultados sejam um primeiro passo na elucidação da dinâmica das comunidades meiofaunais nos ecossistemas costeiros do estado do Maranhão (Brasil), é necessária a adoção de medidas de complexidade adaptadas aos organismos-alvo. Nesse contexto, o uso de dimensões fractais tridimensionais tem se revelado uma metodologia eficiente para estimar a complexidade de substratos com as mais diversas morfologias. Para futuros estudos mais aprofundados, recomenda-se quantificar a complexidade estrutural, a fim de obter conclusões mais precisas sobre a correlação entre a estrutura dos substratos e a composição da meiofauna. Além disso, sugere-se incluir, nos próximos estudos, diferentes componentes faunísticos (meio e macrofauna) para obter um melhor conhecimento sobre os efeitos ecológicos dos substratos em níveis tróficos superiores.

A análise cientométrica evidenciou uma preferência pelas análises multivariadas nos estudos sobre colonização de diferentes substratos por organismos meiofaunais. A ecologia bêntica de habitats marinhos e costeiros tem uma longa tradição no uso de métodos não paramétricos, o que pode ser a razão pela qual o nMDS foi o método multivariado mais utilizado nos estudos analisados. Também foi observado um aumento crescente no uso de modelos matemáticos. Globalmente, a modelação ecológica preditiva aplicada à fauna bêntica é um tema de investigação emergente.

Os resultados apresentados indicam a insuficiência da metodologia utilizada por órgãos governamentais para análise da balneabilidade, a qual baseia-se apenas no uso de descritores microbiológicos das águas (Resolução CONAMA 274, de 29 de novembro de 2000). O uso de abordagens integradas, que considerem as variáveis ambientais da água e do sedimento, e a estrutura das comunidades bênticas residentes, revelou-se uma metodologia mais precisa e satisfatória para a representação da realidade ambiental local. Sugere-se também que sejam realizados estudos que avaliem os efeitos temporais das pressões antrópicas na estrutura da comunidade meiofaunal da região costeira do Maranhão, especialmente considerando a variação sazonal do estado, e que aumentem a resolução taxonômica, pelo menos dos taxa dominante.

Ao chegar ao final deste longo e desafiador percurso de doutoramento, é impossível não refletir sobre as dificuldades enfrentadas ao longo dessa jornada de pesquisa e descoberta. Essa é a oportunidade de compartilhar algumas das experiências pessoais que moldaram essa jornada, na esperança de que essas reflexões possam ressoar com outros doutorandos e pesquisadores que trilham caminhos semelhantes.

A pesquisa científica, apesar de sua beleza e promessa de descoberta, muitas vezes é um terreno instável e incerto. Além disso, ela é também um empreendimento solitário. Passar horas a fio diante do computador ou no laboratório, trabalhando em um projeto que parece ser apenas seu, pode ser desafiador para a saúde mental e emocional. Por outro lado, a pressão de produzir resultados significativos e publicáveis é constante, além, claro, da dificuldade recorrente de conciliação entre trabalho e vida pessoal.

No entanto, à medida que enfrentei essas dificuldades, também encontrei forças. Compartilhar nossas lutas e sucessos com outros pesquisadores criou uma sensação de comunidade e pertencimento que mitigou a solidão do trabalho acadêmico. Além disso, aprendi que o processo de pesquisa é tão importante quanto os resultados. As dúvidas, os tropeços e os momentos de frustração são, na verdade, oportunidades para crescimento e aprendizado. Aprendi a abraçar a incerteza e a aceitar que nem todos os projetos de pesquisa seguem um caminho linear e previsível. Cada revés me ensinou algo valioso e moldou a minha abordagem à pesquisa.

Em retrospectiva, essas dificuldades não são apenas obstáculos, mas partes fundamentais da jornada do doutorado. Elas testaram minha resiliência, minha paixão pela pesquisa e minha determinação em superar desafios. O doutorado não é apenas sobre a obtenção de um título; é sobre o crescimento pessoal e a jornada intelectual que nos transforma.

Portanto, ao concluir este doutorado, quero encorajar todos os estudantes e pesquisadores a abraçar suas próprias dificuldades e incertezas. Elas são uma parte inerente do processo de pesquisa e crescimento acadêmico. Acreditem em si mesmos, busquem apoio quando necessário e lembrem-se de que as maiores conquistas muitas vezes surgem das batalhas mais difíceis.

Enfim, esta tese é o resultado de anos de trabalho árduo, dedicação e perseverança. As dificuldades enfrentadas ao longo do caminho foram desafiadoras, mas também enriquecedoras. Espero que o conhecimento gerado por esta pesquisa contribua para o avanço do nosso entendimento sobre a meiofauna e inspire futuros pesquisadores a explorar as complexidades dessa comunidade faunística. A jornada de pesquisa é uma aventura única e valiosa, e estou ansioso para continuar explorando novos horizontes no futuro.

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