**Universidade do Estado do Rio de Janeiro**
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# Preditores ambientais e biológicos da invasão do ofiuroide *Ophiothela mirabilis* no Atlântico Oeste

Rio de Janeiro
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Tese apresentada, como requisito parcial para obtenção do título de Doutora, ao Programa de Pós-Graduação em Ecologia e Evolução, da Universidade do Estado do Rio de Janeiro.

Orientador: Prof. Dr. Luciano Neves dos Santos
Coorientador: Prof. Dr. Carlos Renato Rezende Ventura

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# RESUMO

TAVARES, Marcela Rosa. *Preditores ambientais e biológicos da invasão do ofiuroide* Ophiothela mirabilis *no Atlântico Oeste*. 2023. 130 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

Espécies marinhas invasoras podem causar sérios danos aos ecossistemas costeiros, desde a extinção de espécies nativas a profundas alterações em processos ecossistêmicos. Espécies inconspícuas, cujos efeitos adversos não são facilmente perceptíveis, podem ser denominadas invasoras silenciosas. A presença do ofiuroide *Ophiothela mirabilis* no Atlântico Oeste parece ser um caso de invasão silenciosa. Seus efeitos no ambiente ainda não foram constatados e pouco se sabe sobre os requerimentos ecológicos que permitiram o seu estabelecimento e a expansão da sua distribuição na área não-nativa. Esta Tese apresenta três objetivos principais desenvolvidos em capítulos independentes: I) desvendar os padrões de distribuição e colonização das espécies do gênero *Ophiothela*, destacando informações de áreas nativas e não-nativas colonizadas por *O. mirabilis*, II) prever áreas ecologicamente adequadas para a colonização por *O. mirabilis* através de modelagem de nicho ecológico, e III) investigar como a abundância de *O. mirabilis* está atrelada às condições da água e à disponibilidade de hospedeiros em uma região onde a espécie foi previamente registrada em diversos substratos. Para os capítulos I e II, registros da distribuição do gênero *Ophiothela* foram compilados da literatura, sendo que apenas registros para *O. mirabilis* foram utilizados para modelar áreas suscetíveis à invasão. O objetivo do capítulo III foi alcançado a partir de amostragens realizadas na Baía da Ilha Grande entre 2021 e 2022. Os resultados demonstraram que as espécies de *Ophiothela* estavam distribuídas entre as latitudes 33°S e 38°N, em 75% dos domínios marinhos. A afinidade de colonização das espécies do gênero foi alta para Cnidaria, independentemente da origem da população. *Ophiothela mirabilis* foi a única espécie registrada como invasora e sua distribuição compreendeu mais de 6.700 km no Atlântico Oeste. Maior plasticidade no uso do substrato foi detectada nas áreas não-nativas, o que indica que a disponibilidade de hospedeiro não limita o potencial invasor de *O. mirabilis*. As costas atlânticas dos continentes Americano e Africano são altamente propensas à ocorrência de populações não-nativas de *O. mirabilis*. Populações nativas estão distribuídas por todo Indo-Pacífico. Produtividade primária, salinidade e calcita foram as variáveis da água que mais contribuíram para a definição de áreas adequadas para a ocorrência de *O. mirabilis*. Os dados sugeriram que estes ofiuroides podem expandir a sua distribuição especialmente em águas ricas em nutrientes e calcita, com salinidade de 35 e temperaturas superiores a 22°C. Dados coletados na Baía da Ilha Grande indicaram que *O. mirabilis* coloniza especialmente esponjas e cnidários, entretanto esponjas parecem ser abundantemente colonizadas em condições ambientais favoráveis. Estas condições foram representadas por águas com temperatura entre 28,6 e 30°C, pH variando de 7,8 a 8,1, salinidade entre 33 e 34 e transparência superior a 9 m. Entretanto, octocorais foram os hospedeiros preferencialmente colonizados pelos ofiuroides não-nativos independentemente das condições abióticas presentes. Embora ainda haja muitas lacunas para o entendimento do processo de invasão da espécie no oceano Atlântico, nossos dados contribuíram para o entendimento dos requerimentos ecológicos desta espécie invasora em áreas não-nativas e poderão direcionar a definição de áreas prioritárias para o manejo e controle populacional da espécie.

**Palavras-chave**: Espécies invasoras. Uso de habitat. Epibionte. Distribuição geográfica. Modelagem de nicho ecológico. Abundância. Octocorais.

# ABSTRACT

TAVARES, Marcela Rosa. *Environmental and biological predictors of* Ophiothela mirabilis *invasion in the Western Atlantic*. 2023. 130 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

Invasive marine species may cause serious damage to coastal ecosystems, from extinction of native species to profound changes in ecosystem processes. Inconspicuous species, whose adverse effects are not readily noticeable, may be termed silent invaders. The presence of the brittle star *Ophiothela mirabilis* in the West Atlantic seems to represent a case of silent invasion. Its effects on the environment have not yet been detected and little is known about the ecological requirements that allowed its establishment and the expansion of its distribution in the non-native area. This Thesis presents three main objectives that were developed in independent chapters: I) to reveal the patterns of distribution and colonization of the genus *Ophiothela*, highlighting information from native and non-native areas colonized by *O. mirabilis*, II) to predict ecologically suitable areas for *O. mirabilis* occurrence through ecological niche modeling, and III) to investigate how the abundance of *O. mirabilis* is linked to water conditions and hosts in a region where the species was previously recorded in different substrates. For objectives I and II, distribution records of the genus *Ophiothela* were compiled from the literature, and only records for *O. mirabilis* were used to model areas prone to invasion. The objective III was achieved based on samplings carried out in Ilha Grande Bay between 2021 and 2022. The results showed that *Ophiothela* species were distributed between latitudes 33°S and 38°N, in 75% of the marine domains. The colonization affinity of the species was high for Cnidaria, regardless of population origin. *Ophiothela mirabilis* was the only species recorded as invasive and was distributed over 6,700 km in the Western Atlantic. Greater plasticity in substrate use was detected in non-native areas, which indicates that host availability does not limit the invasive potential of *O. mirabilis*. The Atlantic coasts of the American and African continents were highly prone to the occurrence of *O. mirabilis* in the non-native region. Native populations were distributed throughout the Indo-Pacific. Primary productivity, salinity and calcite were the water variables that most contributed to the definition of suitable areas for the occurrence of *O. mirabilis*. Data suggested that these ophiuroids can expand their distribution especially in nutrient and calcite-rich waters, with salinity of 35 and warmer than 22°C. Data collected in Ilha Grande Bay indicated that *O. mirabilis* colonizes especially sponges and cnidarians, however sponges seem to be abundantly colonized under favorable environmental conditions. These conditions were represented by waters with temperature between 28.6 and 30°C, pH varying from 7.8 to 8.1, salinity between 33 and 34 and transparency greater than 9 m. However, octocorals were the hosts preferentially colonized by non-native ophiuroids regardless of the local abiotic conditions. Although there are still many gaps in understanding the invasion process of the species in the Atlantic Ocean, our data contributed to understand the ecological requirements of this invasive species in the non-native area and may guide the definition of priority areas for management and population control of the species.

**Keywords**: Invasive species. Habitat use. Epibiont. Geographic distribution. Ecological niche modeling. Abundance. Octocorals.

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# INTRODUÇÃO GERAL

Espécies marinhas são constantemente transportadas de um local para outro em todo o mundo por meio de ações antrópicas (BLACKBURN et al., 2014). Esse transporte pode ocorrer de forma intencional ou não intencional. Muitas espécies podem ser introduzidas propositadamente em determinados sistemas para fins de aquacultura, por exemplo (ANIL; KRISHNAMURTHY, 2018). Entretanto, o principal vetor de introdução da maior parte das espécies invasoras marinhas é a navegação, onde as espécies podem ser transportadas, de forma não intencional, através de água de lastro ou mesmo aderidas a cascos de embarcações (MOLNAR et al., 2008).

Muitas das espécies exóticas marinhas não sobrevivem às interações bióticas e abióticas encontradas no novo ambiente ou mesmo às condições de transporte e, portanto, não conseguem se estabelecer (MOLNAR et al., 2008). Entretanto, algumas se estabelecem, se reproduzem e são capazes de formar populações estáveis ao longo do tempo (BLACKBURN et al., 2011). Algumas destas espécies podem se integrar à comunidade local, não causando danos significativos ao ambiente (BLACKBURN et al., 2014), enquanto outras podem causar impactos desastrosos (MOLNAR et al., 2008; ANIL; KRISHNAMURTHY, 2018; e. g., ZENETOS et al., 2005; WALTERS, 2009; BYRNE et al., 2013). Quando impactos negativos são constatados, as espécies são reconhecidas como invasoras. Seus efeitos no ambiente podem ser muito variáveis e ocorrerem de forma direta ou indireta. Podem causar desde a extinção de espécies nativas, até a alteração na ciclagem de nutrientes e estrutura de habitats, interferência em interações ecológicas bem estabelecidas entre a biota local, ou mesmo causar prejuízos à economia e saúde humanas, entre outros impactos (BLACKBURN et al., 2014, MOLNAR et al., 2008).

No ambiente marinho, alguns invertebrados de pequeno porte podem ser reconhecidos como invasores silenciosos, pois além de serem introduzidos de forma não intencional em diversos locais, são difíceis de detectar e causam impactos negativos no ambiente que não são prontamente reconhecidos (MIGLIETTA; LESSIOS, 2009). Assim, podem ser negligenciados pela comunidade científica por longos períodos até que os prejuízos causados aos ecossistemas se tornem evidentes (BAX et al., 2001). Quando isso ocorre, a falta de entendimento sobre os requerimentos ecológicos destas espécies, mesmo em áreas nativas, não permite que sejam delineadas estratégias eficientes de controle da disseminação das mesmas. Além disso, ações mitigadoras dos seus impactos geralmente não são mais viáveis

(MIGLIETTA; LESSIOS, 2009). Portanto, o constante monitoramento de populações de espécies não-nativas é necessário para que se possa entender como interagem com o meio e quais são as necessidades vitais para a sobrevivência e manutenção de suas populações no ambiente não-nativo.

A espécie de ofiuroide *Ophiothela mirabilis* (VERRILL, 1867), originária dos Oceanos Índico e Pacífico, tem sido considerada invasora nas áreas costeiras do Atlântico Oeste e pode representar um caso clássico de invasão silenciosa (TAVARES et al., 2021). Esta espécie foi registrada pela primeira vez na área não-nativa em 2000, na Ilha do Pai, no estado do Rio de Janeiro, Brasil (23°S; HENDLER et al., 2012). Acredita-se que seu transporte transoceânico tenha ocorrido através da sua associação com comunidades incrustantes aderidas ao casco de embarcações (HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013). Ao longo dos anos, a espécie expandiu sua área de ocorrência não-nativa por longas extensões, a qual atualmente compreende quase toda a costa do Brasil, Guiana Francesa, Mar do Caribe e Sul da Flórida (HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013; ARAÚJO et al., 2018; FERRY, et al. 2020; GLYNN, et al. 2020). Após sua detecção na costa brasileira, aspectos ecológicos e biológicos da espécie passaram a ser mais investigados, porém ainda há muitas lacunas com relação ao conhecimento dos seus requerimentos ecológicos e seus efeitos no ambiente. Uma característica marcante não só de *O. mirabilis*, mas de todas as espécies do gênero *Ophiothela*, é seu hábito de vida epibionte (TAVARES et al., 2021). Estes ofiuroides vivem em associação com diversos organismos bentônicos, tanto animais quanto vegetais (e.g. MANTELATTO et al., 2016; FORTUNATO; LÔBO-HAJDU, 2021). Este fato, aliado à ampla expansão da sua área de distribuição em apenas 23 anos após seu primeiro registro, faz com que a espécie seja considerada invasora. Possíveis impactos negativos da sua presença sobre a biota nativa têm sido apontados (MANTELATTO et al., 2016). A densidade elevada de ofiuroides registrada sobre alguns hospedeiros poderia impedir a protração de estruturas alimentares, como a extensão dos pólipos em corais, e afetar significativamente a alimentação de algumas espécies hospedeiras (MANTELATTO et al., 2016). Além disso, abundâncias elevadas de ofiuroides poderiam aumentar o peso dos organismos bentônicos e, consequentemente, sua força de arrasto em regiões com elevado hidrodinamismo (MANTELATTO et al., 2016). Entretanto, nenhum prejuízo aos hospedeiros foi confirmado até o momento. Experimentos recentes com algumas espécies de octocorais hospedeiras não demonstraram efeitos evidentes da densidade de *O. mirabilis* sobre suas taxas de alimentação (GLYNN et al., 2021; DERVICHE; LANA, 2022), apesar da necessidade de mais investigações sobre esta questão, considerando outras espécies bentônicas. É importante considerar que estes ofiuroides podem causar prejuízos ao ambiente de outras formas, como através de competição por recursos com outras espécies epibiontes nativas ou alterando processos ecossistêmicos. Por isso, estudos focados em entender a biologia e ecologia desta espécie, especialmente sobre populações não-nativas, são essenciais para compreender seu processo de invasão.

Desta forma, esta tese foi elaborada com o intuito de preencher parte das lacunas de conhecimento acerca da interação de *O. mirabilis* com os componentes biótico e abiótico nas suas áreas de ocorrência nativa e não-nativa. Avaliar as características ambientais onde a espécie ocorre, assim como as condições que permitem que a espécie prospere no ambiente (i. e. onde mantém populações numerosas) são essenciais para compreender o sucesso da invasão de *O. mirabilis* no Oceano Atlântico. No primeiro capítulo, utilizamos dados disponíveis na literatura científica especializada para desvendarmos os padrões de distribuição e colonização das espécies do gênero *Ophiothela* ao redor do mundo. Especificamente, nosso objetivo foi rastrear a propagação de *O. mirabilis* na região não-nativa e avaliar quais grupos de organismos bentônicos poderiam ser mais afetados pela expansão da sua área de distribuição no oceano Atlântico. No segundo capítulo, nós utilizamos o mesmo banco de dados para prever áreas suscetíveis à invasão por *O. mirabilis* no mundo através de modelagem de nicho ecológico. Seu nicho fundamental foi estimado ao comparar o conjunto de variáveis da água extraídas de acordo com o faixa de ocorrência atual da espécie com a distribuição de gêneros de hospedeiros previamente registrados em associação com *O. mirabilis*. No terceiro capítulo, investigamos como os padrões de abundância de *O. mirabilis* estão atrelados às condições abióticas locais e aos componentes de habitat (i.e. organismos bentônicos que poderiam servir de hospedeiros para a espécie) em uma região onde *O. mirabilis* foi previamente registrado em uma grande variedade de hospedeiros. Com essas informações, poderemos contribuir para a demarcação de áreas prioritárias para aplicação de ações de manejo da espécie, em especial se impactos negativos da sua presença forem detectados.

# 1 GEOGRAPHIC DISTRIBUTION OF THE *OPHIOTHELA* BRITTLE STARS: PLASTICITY IN SUBSTRATE USE AND IMPLICATIONS FOR THE INVASIVE *O. MIRABILIS* IN THE ATLANTIC

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## 1.1 Introduction

The rate of species introduction worldwide has increased significantly following the globalization process (ESPÍNOLA; JUNIOR, 2007; SIMBERLOFF et al., 2013). Some non-native species that thrive in new habitats may become invasive, posing adverse impacts to marine ecosystems on varied scales (MOLNAR et al., 2008; e. g., ZENETOS et al., 2005; WALTERS, 2009; BYRNE et al., 2013). Accordingly, invasive species represent one of the main threats to ecosystem functioning and biodiversity (ALLENDORF; LUNDQUIST, 2003), leading to global commitments and actions to minimize their adverse environmental effects (MCNEELY et al., 2001; BAX et al., 2003). The effectiveness of control actions against invasive species is variable but more promising when invader impacts are detected early. However, most marine system invasion processes are unknown, especially for small-sized organisms and less studied groups, such as plankton and invertebrates.

Several introduced invertebrates have remained untracked in invaded systems, although this process, termed “silent invasion”, represents a severe threat for native species and ecosystem functioning (BAX et al., 2001; MIGLIETTA; LESSIOS, 2008; KARATAYEV et al., 2015). The study of small-sized and inconspicuous invaders is under-represented in the scientific literature, possibly due to difficulties in their detection and assessment. This fact contrasts with the broader knowledge available about larger invasive species, whose impacts are easier to recognize and attract more attention from the scientific community and society (GIRALDES et al., 2016). Moreover, pre-invasion data on the structure, dynamics, and ecological interactions of native populations and environmental requirements of the invader are generally lacking, preventing full evaluations of the effects of non-native species on invaded systems. Therefore, tracking introduction reports, distribution patterns, and habitat requirements of small-sized invertebrate species is crucial to construct scenarios regarding invasion risks and prevent damage caused by silent invaders on native species and ecosystems (DELANEY et al., 2008).

Shipping is the main silent invasion pathway in marine environments, mostly through ballast water and biofouling (MOLNAR et al., 2008; ANIL; KRISHNAMURTHY, 2018). This allows species to cross biogeographic barriers and abiotic filters beyond the limits of their natural occurrence areas (BLACKBURN et al., 2014). These sea travelers can deal with harsh abiotic conditions and increased competition with other “ship passengers”. Consequently, travel survivors are more prone to colonize and establish populations in new environments (ESPÍNOLA; JUNIOR, 2007; BLACKBURN, 2011). Some of the most conspicuous examples of silent invaders are the sun corals *Tubastraea coccinea* LESSON, 1830, and *Tubastraea tagusensis* WELLS, 1982 (SILVA et al., 2014; GIRALDES et al., 2016), which have been widely introduced in the South Atlantic through biofouling. They have greatly impacted native communities, and consequently, the functioning of many marine systems throughout the Brazilian coast (LAGES et al., 2012; SILVA et al., 2014).

The detection of the non-native brittle star *Ophiothela mirabilis* VERRILL, 1867 in Atlantic waters is a possible case of silent invasion of an Echinodermata member, thus drawing increasing researcher attention (HENDLER et al., 2012). The *Ophiothela* genus is still scarcely studied, but all extant six species are known epibionts native to Indo-Pacific waters. In 2000, HENDLER et al. (2012) recorded the presence of *O. mirabilis* in the Atlantic Ocean for the first time. Since then, this brittle star has been detected through ~6,700 km along the Brazilian coast (ARAÚJO et al., 2018), reaching the coastlines of the French Guiana, Antilles, and South Florida (HENDLER; BRUGNEAUX, 2013; GLYNN et al., 2019; FERRY et al., 2020; RICH et al., 2020). The transportation of fouling organisms on human-made structures, such as ship hulls and oil platforms, is considered the main *O. mirabilis* invasion vector and the major steppingstone in assisting its spread throughout Atlantic waters (HENDLER et al., 2012; MANTELATTO et al., 2016; LAWLEY et al., 2018; TAVARES et al., 2019). Furthermore, the successful establishment of *O. mirabilis* in the Atlantic may also be associated with the ability of this invader to colonize a high variety of benthic organisms (MANTELATTO et al., 2016), its continuous clonal reproduction (TAVARES et al., 2019), and the looseness of its ecological interactions (e.g., lack of potential competitors and predators). Although ecological data on most *Ophiothela* species is limited, available information indicates they share similar biological traits and requirements, suggesting an invasive potential in coastal ecosystems worldwide. Therefore, tracking information on the distribution of *Ophiothela* brittle stars is important to identify which species have been introduced into non-native areas and prevent adverse impacts on native species and ecosystems if they do become invasive.

In the present study, an overview of the geographic distribution of *Ophiothela* species and their patterns of substrate colonization in both native and non-native regions were identified in order to evaluate their occurrence range and track the spread of introduced populations. Data on the colonization patterns of natural substrates (i.e., host organisms) of native Indo-Pacific brittle star populations were also considered to unveil the groups of benthic organisms that would be more affected by the invasion progress of *O. mirabilis* in the Atlantic. To this end, we conducted an extensive literature survey to address four main questions: (1) What is the global distribution pattern of the *Ophiothela* genus? (2) Have other species of this genus besides *O. mirabilis* been recorded as introduced or invasive around the globe? (3) Do these epibionts display an affinity for specific host organisms during colonization? (4) Are colonizing patterns different between native and introduced *O. mirabilis* populations?

## 1.2 Methods

An electronic survey was performed to compile all published data on the *Ophiothela* genus up to 2019. We retrieved data from the Web of Science, Scopus, and Google Scholar electronic databases using "*Ophiothela*" as a keyword. The search comprised scientific articles, book chapters, and grey literature (theses and technical reports; see Appendix 1). We also scanned the references of all retained studies for occurrence data not detected in our primary search. Our database included only studies that provided geographic distribution records for the assessed *Ophiothela* species. Information concerning the occurrence site, *Ophiothela* species (according to author identification), geographical coordinates, sampling date, colonized organisms, and complete reference were compiled from each study.

Alitto et al. (2020) suggested that *O. danae* is a junior synonym for *O. mirabilis* due to a high similarity of external morphology, shape measurements, and COI sequences found between some individuals (including syntypes) from both species and specimens from the Brazilian coast. Fatemi & Stöhr (2019) indicated the possible existence of a new fissiparous *Ophiothela* species that shares morphological traits with *O. danae* and *O. venusta*. However, we assumed a conservative position in the present study, considering *O. danae* and *O. mirabilis* as different taxonomic entities and the species indicated by Fatemi & Stöhr (2019) as *Ophiothela* sp. to prevent bias concerning the species distribution accepted so far.

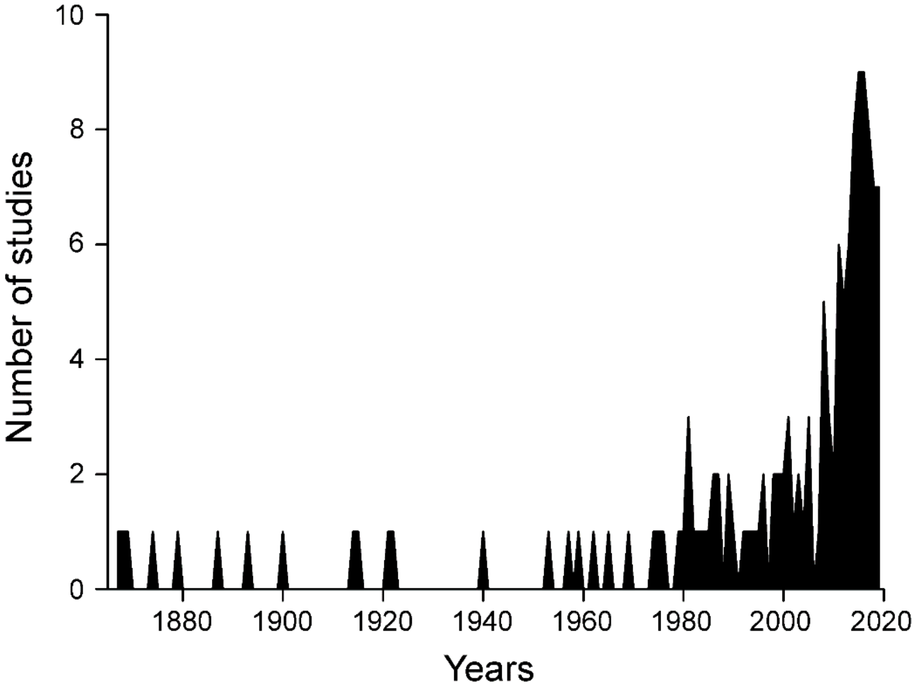
The occurrence sites were assigned to ecoregions, provinces, and realms, following the Marine Ecoregions of the World (MEOW) categories proposed by Spalding et al. (2007). Geographical coordinates were estimated using Google Earth when not provided by the study, using occurrence site names. The midpoint facing the nearest coast was applied whenever coordinates were not available in the retained articles but corresponded to a small-scale region, such as islands, small beaches, or cities. Whenever large-scaled species distribution information indicated a single ecoregion, the midpoint along the coast was used as the occurrence site. We did not consider inexact localities and given areas spread across more than one ecoregion. A given record was assigned to a specific ecoregion by plotting the coordinates in a MEOW shapefile (http://www.marineregions.org/downloads.php) using Google Earth. Maps were plotted using the Quantum GIS 3.2.3 software (QGIS DEVELOPMENT TEAM, 2020) to represent the geographic distribution of *Ophiothela* genus species worldwide.

Occurrence records were defined as each link among a certain *Ophiothela* species, its geographical coordinates, and the study that reported its occurrence. Each connection between an occurrence record and a host organism was considered as an association record. We used the World Register of Marine Species database (WoRMS; http://www.marinespecies.org/index.php, accessed on April 15, 2020) to check current terminology, *Ophiothela* species classification, and hosts identified at the genus or species level. A Principal Coordinates Analysis (PCoA) was applied to evaluate dissimilarities regarding benthic organism patterns colonized by *O. mirabilis* between native and introduced populations. Jaccard distances were calculated for the matrix concerning the presence and absence of *O. mirabilis* in six taxonomic host organism groups. The correction method established by Cailliez & Pages (1976) for negative eigenvalues was used as available in Legendre & Legendre (1998), using the “pcoa” function available in the “ape” package (PARADIS et al., 2019) of the R version 3.4.4 statistical software (R CORE TEAM, 2020). The PCoA plot was generated using the “ggplot2” and “phyloseq” packages in the R statistical software (MCMURDIE; HOLMES, 2013; WICKHAM et al., 2020).

## 1.3 Results

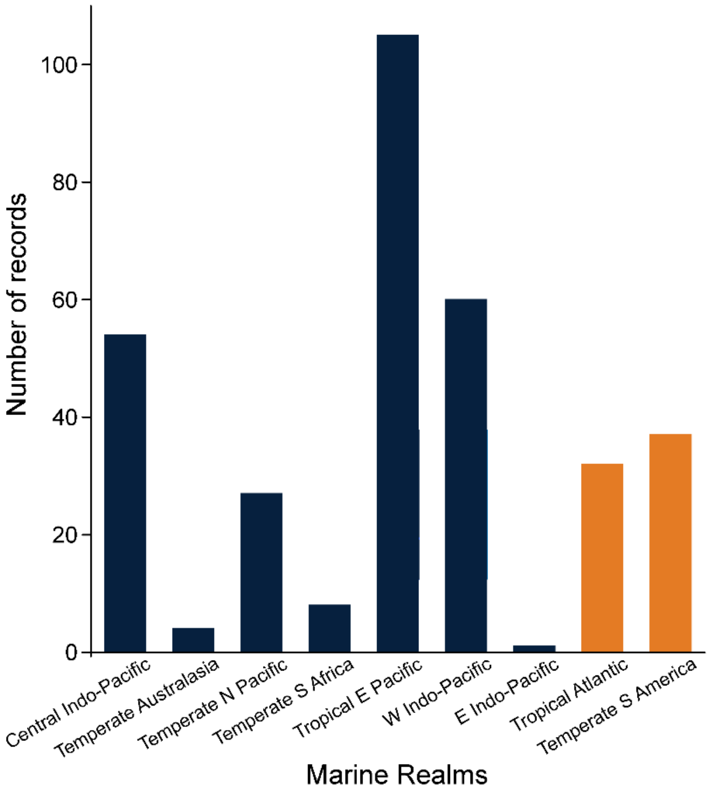
The literature review yielded 240 publications, 137 of which provided occurrence data and were useful for further analyses. Studies ranged from 1867 to 2019, were available in English, Portuguese, Spanish, French and German languages, and covered all six *Ophiothela* species. Only 24 publications were available online between 1867 and 1980. Since then, the number of publications has increased, peaking at nine studies in 2015 and 2016 (Figure 1). Most papers were published in scientific journals (73%), followed by books (14.6%) and grey literature (12.4%).

Figure 1 - Number of studies (N = 137) per year on species belonging to the *Ophiothela* genus according to an electronic survey (see Methods for details).



A total of 328 occurrence records for the six *Ophiothela* species were obtained from the retained studies in 55 marine ecoregions, 29 provinces, and nine realms worldwide, between 33 ºS and 38 ºN. Most occurrence records for this genus were concentrated in three native realms, namely the Tropical Eastern Pacific (32%), Western Indo-Pacific (18.3%), and Central Indo-Pacific (16.5%). *Ophiothela mirabilis* was the only species recognized as introduced or invasive worldwide. Non-native records of this species occurred in two Atlantic realms, the Temperate South America and Tropical Atlantic (represented by 69 records; Figure 2).

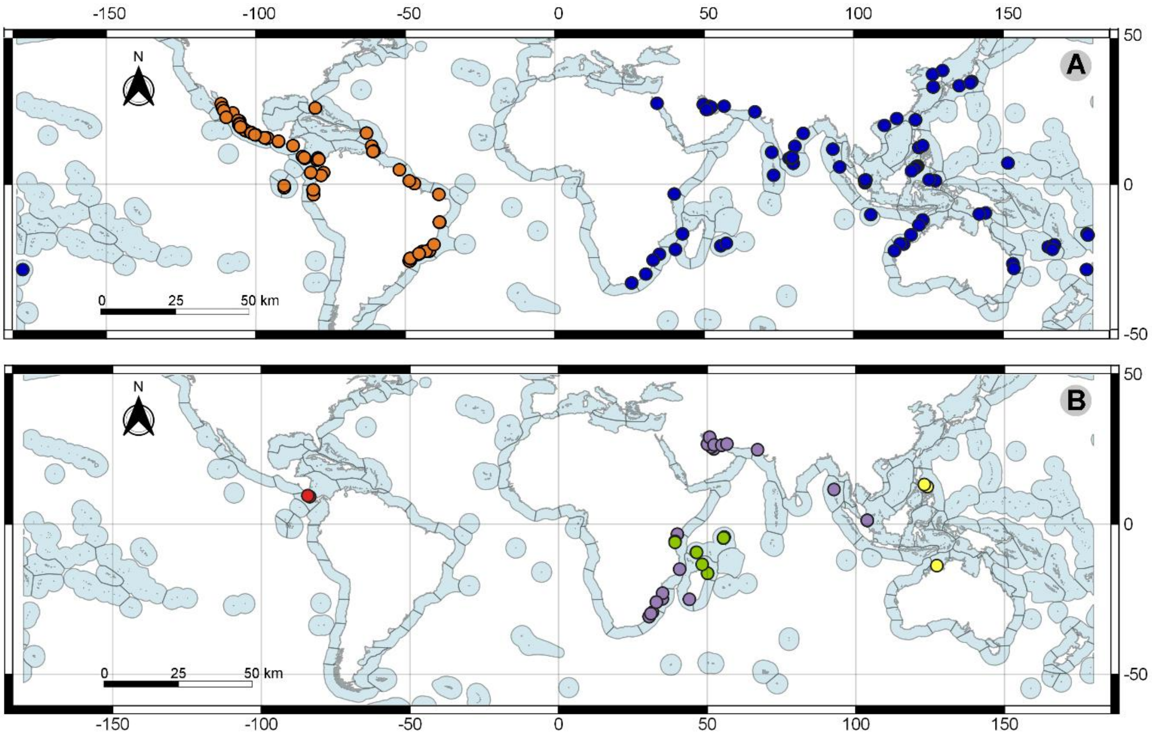
Figure 2 - Number of occurrence records for *Ophiothela* species (N = 328) in native and non-native realms.



Legend: Native realms are represented by dark blue bars and non-native realms by orange bars.

*Ophiothela mirabilis* is the best-documented species (N = 182), although not the most widespread longitudinally. Its distribution includes three marine realms within its native area (Temperate Northern Pacific, Tropical Eastern Pacific, and Eastern Indo-Pacific) and two along its non-native region, as mentioned previously. This species has spread along the coasts of South Florida, the Antilles, French Guiana, and Brazil (Figure 3a). *Ophiothela danae* was the most widespread species (N = 85), recorded in the Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific, Temperate Southern Africa, and Western Indo-Pacific (Figure 3a). The other four species exhibited narrower distribution patterns: *O. venusta* (N=30), *O. tigris* (N = 8), *O. vincula* (N = 3), and *O. gracilis* (N = 2; Figure 3b).

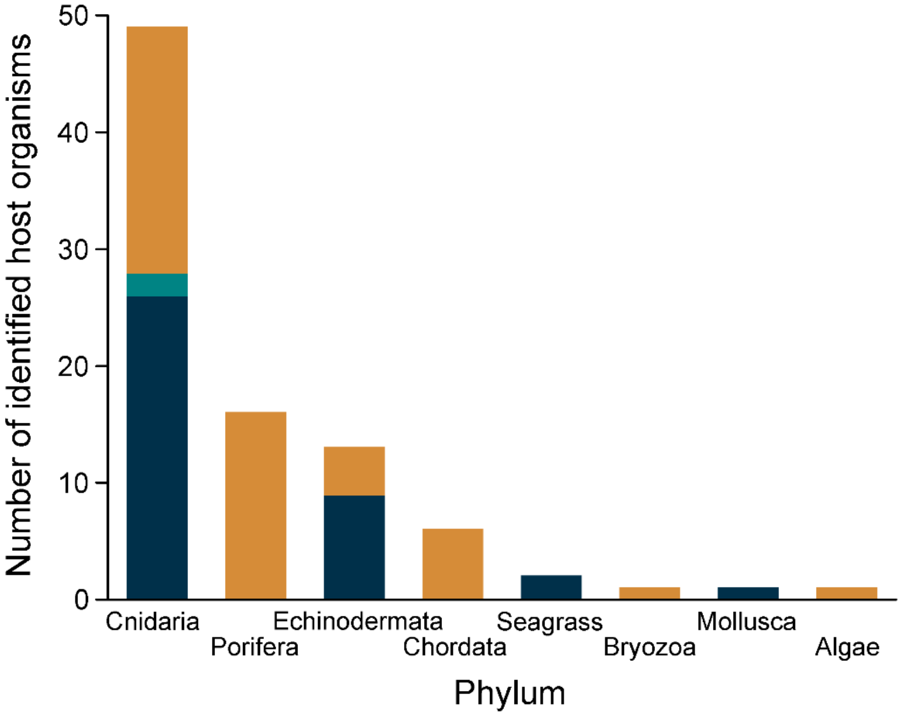
Figure 3 - World map indicating the distributions of *Ophiothela* species.



Legend: (A) *Ophiothela mirabilis* (N = 182, 🟠) and *O. danae* (N = 85, 🔵), and (B) *O. gracilis* (N = 2, 🔴), *O. vincula* (N = 3, 🟡), *O. tigris* (N = 8, 🟢) and *O. venusta* (N = 30, 🟣).

The association of *Ophiothela* with host organisms was cited by 54.7% of the retained studies, accounting for 280 habitat association records. The host organisms were identified at the genus or species level in 60.3% of these records. From those accurately identified records, the authors reported 89 benthic organisms as hosts for *Ophiothela* species, comprising eight phyla: six benthic macroinvertebrates, one seaweed (Ochrophyta), and one seagrass (Tracheophyta) (Figure 4). Records of non-native *O. mirabilis* populations indicate associations with 51 host organisms belonging to several taxonomic groups, i.e., Cnidaria, Porifera, Echinodermata, Chordata, Bryozoa, and algae. In contrast, records for native *O. mirabilis* populations revealed only nine benthic host invertebrates, all belonging to Cnidaria and Echinodermata phyla. Only the cnidarian *Carijoa riisei* (DUCHASSAING; MICHELOTTI, 1860) was colonized by both native and introduced *O. mirabilis*. In native zones, *Ophiothela danae* has been recorded in association with the greatest variety of host organisms (N = 25), comprising the Cnidaria, Echinodermata, and Mollusca phyla. In contrast, the other *Ophiothela* species colonize only nine hosts, including cnidarians, echinoderms, mollusks, and seagrasses.

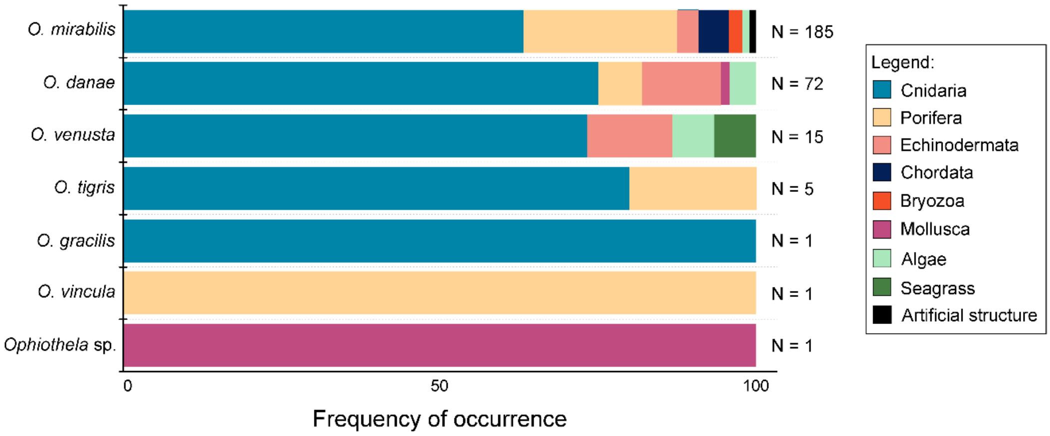
Figure 4 - Number of identified host organisms per phylum in native areas, non-native zones and co-occurring species.



Legend: Native areas are represented by dark blue bars, non-native zones by orange bars and co-occurring species by light blue bar.

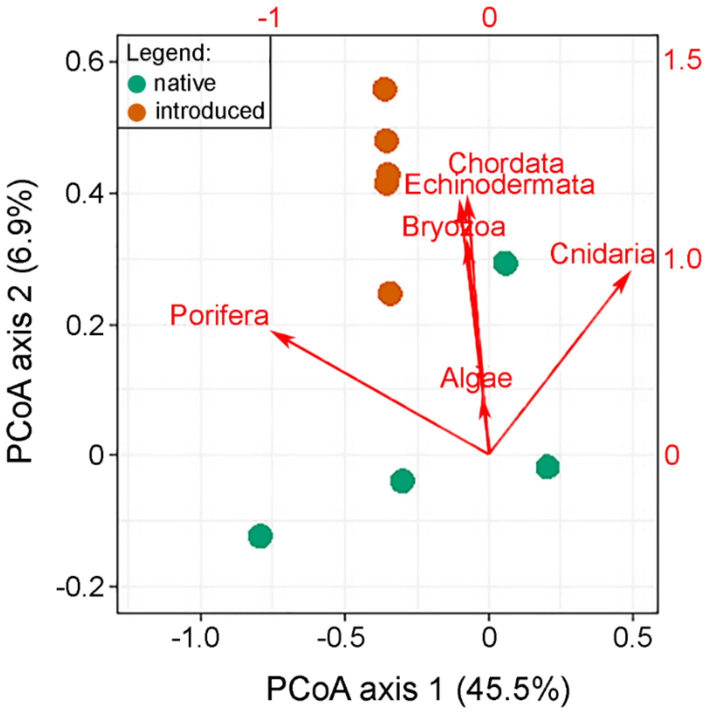
Cnidarians were the most frequent hosts associated with *Ophiothela* species, regardless of the origin of the brittle star populations (i.e., native or non-native) and considering all association records (even those at higher taxonomic levels; Figure 5). A single study reported artificial structures as colonization substrates for introduced *O. mirabilis*. The first two axes of the principal coordinates analysis (PCoA) explained 52.4% (trace = 12.98; Figure 6) of the variability concerning the association of native and introduced *O. mirabilis* populations with host organisms. Introduced *O. mirabilis* was, in general, reported in association with a greater taxa variety of host organisms. Non-native *O. mirabilis* populations colonized benthic organisms that were not occupied by any other *Ophiothela* species in their native region, such as Chordata, Bryozoa, and algae. Still, they were more often associated with Cnidaria and Porifera. In contrast, native *O. mirabilis* populations exhibited associations with fewer groups of host organisms, especially Cnidaria and, at lesser levels, Porifera. Only a single study reported an association between native *O. mirabilis* and Echinodermata.

Figure 5 - Frequency of association of *Ophiothela* species per phylum of host species (N = number of association records).



Legend: N = number of association records.

Figure 6 - Principal coordinates analysis of the presence-absence data of native and introduced *Ophiothela mirabilis* populations on six phyla of host organisms, based on Jaccard distances.



## 1.4 Discussion

This study evaluated the worldwide distribution of all six *Ophiothela* genus species and revealed habitat colonization patterns in native and non-native areas. These species are well-distributed worldwide, with most records concentrated within the intertropical zone of the Indian and Pacific oceans. *Ophiothela danae* is the most widespread species in the Indo-Pacific region, and is associated with the highest variety of host organisms among all native populations. However, non-native populations were recorded for *O. mirabilis* only in two Atlantic Ocean realms. Habitat association records also revealed that these two epibiont brittle stars display a great affinity for cnidarians as colonizing substrates, irrespective of their native or non-native occurrence regions. Our findings highlight the significant plasticity in habitat colonization described for introduced *O. mirabilis* populations in the Atlantic Ocean, indicating that habitat availability may not be a constraint for this species establishment.

Some issues concerning *Ophiothela* species identification are noteworthy. Alitto et al. (2020) raised the hypothesis that *O. danae* is a junior synonym for *O. mirabilis*. However, the authors used only ophiuroids from the Brazilian coast and only few specimens identified as *O. danae* and *O. mirabilis* (including syntypes) for external morphology and COI sequence comparisons. Despite their efforts concerning molecular, morphometric, and morphological comparisons between *O. mirabilis* and *O. danae*, the hypothesis of a single brittle star species should be further investigated through the use of more specimens, gene sequences, and molecular markers before full validation. In addition, the identification of *O. vincula* is unclear since molecular analyses indicate a low genetic divergence between this species and *O. danae*. In this sense, further systematic studies concerning the revision of the *Ophiothela* genus are required to unveil the relationship among brittle star species.

The macro-scale perception on the distribution patterns of *Ophiothela* brittle stars indicates that all the six species comprising the genus are geographically spread across 75% of the world’s marine realms. This wide distribution range suggests that *Ophiothela* brittle stars may share the same adaptive zone (as defined for starfish by BLAKE, 1990). Their lifestyle of living on animals and macroalgae, asexual reproduction (in the case of *O. mirabilis* and *O. danae*), and major morphological features (small disc size, strong hook-shaped spines, streptospondylous arm vertebra articulations, sturdy plates, and radial shields) allow the occupation of a specific niche in the shallow-water marine environment. Only a few other ophiuroid species (e.g., some *Ophiactis* species), which live associated with the seafloor and under rocks, share the same adaptive zone as *Ophiothela* (CLARK, 1976; FUJITA; NAMIKAWA, 2006).

The ability to reproduce by fission, small body size, and epibiont habits combined with their arm morphological structure are key traits that may explain the high invasiveness of *O. mirabilis* in the Atlantic waters. This brittle star can cling tightly to a great variety of benthic species (VERRILL, 1867; CLARK, 1976; TAHERA, 2001), including fouling organisms living on ship hulls and oil platforms, allowing for long distance dispersion (HENDLER et al., 2012; MANTELATTO et al., 2016; LAWLEY et al., 2018; TAVARES et al., 2019). The distribution of introduced populations throughout a broad geographic Brazilian coast range may thus be associated with a high propagule pressure held by the continuous arrival of new individuals through the increased circulation rates of vessels and oil platforms in this region (FERREIRA et al., 2009). Natural dispersal by rafting on algae or animal fragments may also occur (HENDLER; BRUGNEAUX, 2013; ARAÚJO et al., 2018). However, it is quite unlikely that this pathway could carry large numbers of individuals and lead to significant contributions to the high detected densities of *O. mirabilis*. For example, Tavares et al. (2019) registered large aggregations of this brittle star (1.78 ± 0.63 specimens $mL^{-1}$ per sponge) at the Rio de Janeiro coast (22 ºS), Brazil. Ferry et al. (2020) also recorded high densities (2.8 brittle $stars.cm^{-2}$) of *O. mirabilis* on the surface of the cnidarian *Gorgonia ventalina* at Martinique Island. Since *O. mirabilis* exhibits a planktonic larva, it is also possible that dispersal may occur naturally or artificially through ballast water (MANTELATTO et al., 2016; ARAÚJO et al., 2018). Some authors have reported similar dispersal mechanisms for other ophiuroids with similar features, such as *Ophiactis savignyi* (MÜLLER; TROSCHEL, 1842) (HENDLER, 1991; ROY; SPONER, 2002; HENDLER; BRUGNEAUX, 2013). However, gaps in understanding the sexual reproduction of *O. mirabilis* are still noted (HENDLER; BRUGNEAUX, 2013; MANTELATTO et al., 2016). Tavares et al. (2019) reported no trace of gonads or recently settled juveniles in two *O. mirabilis* populations on the Southeastern Brazilian coast. The primary *O. mirabilis* dispersal mechanism seems to be association with fouling communities in vessels. Therefore, the wide distribution range of the *Ophiothela* genus as a whole may be an important supply for the multiple sources of worldwide introduction of *O. mirabilis* and its congeners due to the high circulation of trade and tourism vessels.

Since the presence of suitable colonization substrates is one of the main ecological requirements for *Ophiothela* brittle star survival, this issue seems to be crucial for the transport, introduction, and establishment of *O. mirabilis* in new habitats. Non-native *O.*

*mirabilis* populations exhibit remarkable plasticity concerning habitat colonization. Host taxa in the introduced area were more numerous and distributed across different taxonomic groups than native populations and concerning their congeners in the Indo-Pacific waters. However, this pattern might be an artifact from the level of host identification used by each study. In general, host identification was performed at a higher level than genus and species (mainly, Cnidaria and Porifera) in native *Ophiothela* brittle star regions. Therefore, further studies focusing on substrate colonization by *Ophiothela* species at high host organism taxonomic resolution (at the genus or species level) are necessary. According to our findings, investigations concerning if *O. mirabilis* can colonize non-living substrates, which was mentioned by a single study, are also relevant. Bumbeer & Rocha (2016) reported the association of this brittle star with artificial structures in a port area in Southern Brazil (25 ºS), but whether *O. mirabilis* specifically colonized the artificial structures themselves or benthic organisms living on these structures remains unclear. If *O. mirabilis* does not depend on living organisms to survive, the chance for its establishment in coastal communities is significantly increased.

Most records concerning host-*Ophiothela* associations indicate a greater affinity of these brittle stars for cnidarians during colonization processes, regardless of the occurrence area. *Carijoa riisei* was the single host species identified in both native and non-native regions, and the most frequent host recorded on the Brazilian coast (23 ºS; MANTELATTO et al., 2016). The availability of the same colonizing habitat in both regions may also assist in *O. mirabilis* invasion, due to its presumably evolutionary affinity with this kind of substrate. Furthermore, this cnidarian might carry brittle stars worldwide since it is often found as a fouling species in ship hulls. Although a mutual advantage is one of the possible relationships between *O. mirabilis* and its hosts (CLARK, 1976; MOSHER; WATLING, 2009), some degree of host damage may occur due to the massive colonization found for this invader in non-native areas. Some studies suggest that ophiuroids may impair the protraction of host feeding structures, increase the total weight of the colonized organisms, and even deflect water currents over filter-feeding invertebrates (MANTELATTO et al., 2016; FERRY et al., 2020). Ascertaining host-invader affinity is key to predict which benthic organisms would be most affected by the high densities of *O. mirabilis* in non-native areas. An experimental study also described that chemical substances produced by the gorgonian *Phyllogorgia dilatata* (ESPER, 1806) exert a positive chemotaxis upon *O. mirabilis* (RIBEIRO et al., 2017). Thus, further studies are required to unveil the relationship between *Ophiothela* species and their hosts, especially to validate the hypothesis of adverse brittle star impacts on host organisms in invaded areas.

In addition to depict the global distribution pattern of the *Ophiothela* genus, our literature review also allowed us to highlight specific knowledge gaps concerning the invasiveness potential and host affinity of its six brittle star species. The *Ophiothela* genus is still poorly studied, although the number of publications on these species has increased over time. Most publications merely reported *Ophiothela* brittle stars in a given region, while about half mentioned their association with host species. However, ecological interactions and population attributes, such as ophiuroid density or abundance in their native area are virtually absent from the literature (see JAMES, 1995; KUMAGAI; AOKI, 2003; HERNÁNDEZ, 2014; PURCELL; ERIKSSON, 2015). *Ophiothela* species were not even the main focus in studies performed in native regions. On the other hand, most investigations performed in non-native regions focused only on the biological features of *O. mirabilis* (e.g., MANTELATTO et al., 2016; TAVARES et al., 2019). Our review highlights the lack of information on the geographical distribution, population dynamics, and ecological requirements of *Ophiothela* species. These subjects are essential to unveil the life-history traits of these species, which is especially important considering the possible negative impacts of *O. mirabilis* introduction on the native Atlantic biota.

This study is the first effort to summarize the main *Ophiothela* genus distribution and host organism colonization patterns worldwide. We emphasize the high invasive potential of this genus, even if only *O. mirabilis* colonization in the Atlantic Ocean has been assessed so far. Further information on the *Ophiothela* genus population structure and dynamics, functional role in ecosystems, and ecological requirements are sorely needed to confirm the occurrence of adverse impacts. Therefore, broadening the ecological knowledge on *Ophiothela* brittle stars is crucial to formulate effective strategies for native biota preservation and monitor the spread of non-native *O. mirabilis* populations to other areas, both throughout the Atlantic Ocean and in other regions.

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# 2 BEYOND THE HOSTS: THE ROLE OF WATER VARIABLES IN PREDICTING ECOLOGICALLY SUITABLE AREAS FOR AN INVASIVE BRITTLE STAR

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## 2.1 Introduction

Human activities are promoting the introduction of alien species (AS) in aquatic systems around the world, and those that become invasive lead to harmful effects on local fauna and flora, the economy, or human health (MOLNAR et al.. 2008; e. g., ZENETOS et al., 2005; WALTERS, 2009; BYRNE et al., 2013). The successful introduction and establishment of an AS depend on its ability to overcome biotic and abiotic filters during transportation, arrival and establishment in the recipient area (BLACKBURN et al., 2011). The ecological conditions tolerated by an AS that enable the survival and maintenance of its population in a new range define its niche (HUTCHISON, 1957; PETERSON, 2003).

Ecological niche models (ENMs) have been frequently used to predict areas prone to invasion (BARBOSA et al., 2012; LEIDENBERGER et al., 2015) to prioritize risk assessments and the development of control and eradication policies. This approach predicts the fundamental niche of a focal species, i. e. the subset of the environmental conditions which theoretically allow a positive population growth rate (COWELL; RANGEL, 2009; SOBERÓN; NAKAMURA, 2009). ENMs correlate species occurrence with ecological variables (i. e. realized niche, excluding biotic interactions; SOBERÓN; NAKAMURA, 2009), defining its fundamental niche in the environmental space (GUISAN et al., 2014). The predicted niche is then projected over a geographical area of interest to assess suitability for invasion (PETERSON, 2011).

Niche conservatism is a fundamental principle of ENMs (LIU et al., 2020). For a long time, a species' niche was considered evolutionarily stable (PETERSON; VIEGLAIS, 2001; PETERSON, 2003), but there is evidence of niche conservatism and shift during invasions (GUISAN et al., 2014). This issue raised concern about the appropriate use of this tool for predicting AS distribution. However, previous studies show that the most invasive species conserve their climatic niche (i.e., niche predicted using climate-related dimensions), increasing confidence in using this predictive framework (PETERSON, 2011; LIU et al., 2020). Realistic predictions should consider native and non-native records when available (BROENNIMANN; GUISAN, 2008). Using only the information on native occurrences would be insufficient to make a realistic prediction of the species' potential distribution if the niche shifts during the colonization of a new area (BROENNIMANN; GUISAN, 2008). On the other hand, using only non-native records may be problematic since the focal species have not yet colonized all of its potential distribution areas. In both scenarios, the restricted set of environmental conditions experienced by the focal species could underestimate suitable areas for distribution (BROENNIMANN; GUISAN, 2008).

Previous studies have successfully performed ENMs for several marine AS, mainly benthic invertebrates, due to their sessile or sedentary nature (e. g., HERBORG et al., 2007; CHOI et al., 2013; PACK et al., 2022). This modeling tool can be especially relevant for predicting fundamental niches of silent invaders. i. e. invasive species whose impacts remain undetectable for a long time. So, the timing for implementing practical actions to contain their spread and mitigate adverse effects is lost (MIGLIETTA; LESSIOS, 2009). Therefore, efforts can be directed to ecologically suitable areas predicted by the models and not yet occupied by the species to prevent their establishment.

The spread of the silent invader *Ophiothela mirabilis* Verrill, 1867, in the Western Atlantic Ocean has received attention from the scientific community over recent years. This brittle star is native to the Indo-Pacific Ocean and is considered invasive in the Brazilian coast, Caribbean Sea, and Florida littoral (HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013; ARAÚJO et al., 2018; FERRY et al., 2020; GLYNN et al., 2020). Shipping is the most likely pathway of species introduction over oceanic basins due to its association with fouling communities (HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013). Predation or other ecological interactions in the Atlantic Ocean does not seem to restrict the expansion of the invasive brittle star so far, given the high population densities recorded in the non-native area (TAVARES et al., 2019; FERRY et al., 2020), its conspicuous body coloration (usually bright orange, ALITTO et al., 2020), and its low specificity for colonizing the benthic biota (MANTELATTO et al., 2016; TAVARES et al., 2021). Nonetheless, water conditions may be a limiting factor for its distribution. Appropriate abiotic conditions for *O. mirabilis* occurrence were previously assessed for the Western Atlantic (non-native area; DERVICHE et al., 2021) but are lacking for Eastern Atlantic and other native regions of the Indo-Pacific waters. Suitable conditions for the brittle star occurrence should also consider the availability of a wide variety of potential hosts due to its epibiont life habit. Therefore, assessing areas at invasion risk by *O. mirabilis* at a global scale is still a work in progress and should consider the high plasticity in host colonization by this invader.

Monitoring *O. mirabilis* non-native populations in the Atlantic is necessary mainly because it is unknown whether this species negatively affects native biota. A previous study suggested some adverse effects of *O. mirabilis* on hosts: the high abundance of this brittle star could interfere with host feeding activity and increase the weight and, consequently, the drag force sustained by host organisms (MANTELATTO et al., 2016). Although further investigation is still needed, some experimental studies investigated the potential impacts of *O. mirabilis* presence and found no harm to hosts (RICH et al., 2020; DERVICHE; LANA, 2022). Nevertheless, detecting areas at high risk of invasion by this brittle star is crucial to prevent the arrival of propagules and apply efficient control actions in the early stages of the invasion process.

Here, we applied the ENM approach to predict suitable areas for *O. mirabilis* occurrence worldwide using three datasets: (i) native records, (ii) non-native records, and (iii) native and non-native records combined. We also investigated if the predicted fundamental niche overlapped the occurrence of its main hosts and assessed the importance of each water variable for predicting *O. mirabilis* environmental suitability, as well as differences between native and non-native localities. Knowing the species' ecological requirements for its establishment will be essential to predict the next steps of the invasion process of *O. mirabilis* worldwide.

## 2.2 Material and Methods

### 2.2.1 Distribution of *Ophiothela mirabilis*

We performed a literature search on Google Scholar, Scopus, and Web of Science databases, searching for all publications about the *Ophiothela* genus from 2019 to 2021 to update the database used in Tavares et al. (2021). We use the term "*Ophiothela*" as a keyword. Also, we combined data on the distribution records of two species recently accepted as a single taxonomic unit: *O. danae* is synonymous with *O. mirabilis* (according to ALITTO et al. 2020). We compiled information from scientific articles, book chapters, and gray literature (theses and technical reports) (Online Resource). We gathered information on the occurrence site, geographical coordinates, sampling date, colonized organisms (i. e., hosts), and complete references from each study in native and non-native areas into a database. Coordinates were retrieved from each publication or obtained in Google Earth using the occurrence name site when not explicit in the texts, as detailed by Tavares et al. (2021). Links between the geographical coordinates from the species' record and its bibliographic reference define an occurrence record, while those between occurrence records and a host organism define an association record.

### 2.2.2 Data about *Ophiothela mirabilis* hosts

The predicted fundamental niche of *O. mirabilis* must consider the presence of appropriate hosts for colonization. *Ophiothela mirabilis* shows remarkable plasticity in substrate selection for colonization, and species-specific association with benthic organisms is unlikely (TAVARES et al. 2021). However, we chose some Porifera and Cnidaria genera as focal host groups because they comprised most association records of *O. mirabilis* identified at the genus or species level in the literature (40.71% for Porifera and 46.07% for Cnidaria). Furthermore, using genera instead of host species can reduce the lack of accurate host identification in the native region since some studies only described these organisms at higher taxonomic levels (e.g., family, order, class, or phylum). We checked the valid names of all species present in this study on the World Register of Marine Species platform (WoRMS - https://www.marinespecies.org/, accessed on March 5, 2022).

We calculated the percentage of association records for each host genus within Cnidaria and Porifera. There were several host genera with few registrations, so we selected those representing more than 5% of the association records with *O. mirabilis* (Table 1; Online Resource). We downloaded the geographic coordinates for all species of the selected host genera with presence-only occurrence records available on the Global Biodiversity Information Facility (GBIF – http://www.gbif.org/; Online Resource) and the Ocean Biodiversity Information System (OBIS – http://www.iobis.org/) databases on March 5, 2022.

### 2.2.3 Ecological niche modelling (ENM)

We estimated current habitat suitability areas for *O. mirabilis* occurrence using the present-day environmental layers for the surface ocean available on the Bio-ORACLE (v.2.2) database (ASSIS et al., 2018). We considered the abiotic variables that could interfere with the species' fundamental niche (O'HARA; TITTENSOR, 2010; JIMÉNEZ-VALVERDE et al., 2011; KRIGSMAN et al., 2012; PEARMAN et al., 2020). Initially, we chose ten relevant environmental variables for benthic organisms: minimum sea surface temperature (SST), maximum SST, SST range, and the means of the following parameters: SST, salinity, pH, calcite concentration, chlorophyll-a concentration, dissolved molecular oxygen concentration, and primary productivity. We excluded the variables minimum SST, maximum SST, and mean pH after testing for collinearity through Pearson's correlation coefficient (> 0.80). Then, we adjusted the environmental rasters at 0.8º x 0.8º resolution (48 x 48 arcminute, i. e., about 100km² per pixel at the equator). We excluded duplicated geographic coordinates for *O. mirabilis* and its hosts, coordinates in urban areas, invalid coordinates, and those with zero or equal latitude and longitude values.

We predicted the *O. mirabilis* habitat suitability considering: 1) native records, 2) non-native records, and 3) native and non-native occurrence records combined. We performed four widely used algorithms to build an ensemble model of those predictions: BIOCLIM, Mahalanobis distance, Generalized Linear Model (GLM) and Support-Vector Machine (SVM), using the R packages "*dplyr*" (WICKHAM et al. 2022), "*dismo*" (HIJMANS et al. 2021) and "*kernlab*" (KARATZOGLOU et al. 2022). BIOCLIM bases its forecasts on climatic envelopes that correlate the geographic space (i.e., the occurrence records) and the environmental space (i.e., the environmental layers) (HIJMANS; GRAHAM, 2006). The Mahalanobis distance considers the climatic combinations having equal distance to a vector of the average conditions related to the geographic space (FARBER; KADMON, 2003). Bioclim and Mahalanobis algorithms use presence-only data to predict species distribution but require background data (RANGEL; LOYOLA, 2012). The GLM relates the classic linear model to the response variable (i.e., the species distribution), allowing the magnitude of the measurements to be a function of its predicted value (MCCULLAGH; NELDER, 1989). It uses presence-absence data to transform the response variable into distinct distribution patterns (RANGEL; LOYOLA, 2012). Finally, the SVM algorithm computes a binary function that captures regions in the environmental space where the probability density (i.e., the support) lives (SCHÖLKOPF et al., 2001), using only the most informative presence-absence data to predict species distribution. Bioclim, Mahalanobis, and SVM algorithms used an equivalent number of presence and pseudo-absence records randomly calculated, while we established 10000 pseudo-absence records for GLM (BARBET-MASSIN et al., 2012). We adopted ten replicas for each algorithm and randomly subsetted the presence and pseudo-absence data into the train (70%) and test (30%) groups for model evaluation. Then, we evaluated model performance based on the area under the curve (AUC) and the true skill statistic (TSS) metrics. The AUC metric varies from 0.5 (random) to 1.0 (high) performance, while the TSS varies from 0 to 1.0. The results of the TSS evaluation followed the AUC ones (Figure 20; Online Resource). Therefore, we selected replicates with AUC values equal to or greater than 0.8 to build an ensemble model with our forecasts. The ensemble model represents a species' most reliable ecological niche requirements and results from the weighted average of all selected replicas (ARAÚJO; NEW, 2007).

We built binary maps using cut-off thresholds of 25%, 50%, and 75% in habitat suitability (Figure 21 to 23; Online Resource). The 25% threshold was retained for analysis as the predicted suitable area matched all of the *O. mirabilis* occurrence records available. We estimated the potential realized niche of *O. mirabilis* by overlapping the chosen habitat suitability map and the distribution range of host genera. The importance of abiotic variables was extracted from models generated through GLM and SVM algorithms (Table 7; Online Resource), using the R packages “stats” (R CORE TEAM, 2022) and “*rminer*” (CORTEZ, 2010), respectively. We built those models from all available *O. mirabilis* occurrence data and datasets containing only native and non-native records. We performed all modelling predictions and further analysis in the R software v.4.2.0 (R CORE TEAM, 2022).

### 2.2.4 Habitat suitability and environmental variables

We performed a one-way ANOVA to test for differences in *O. mirabilis’* environmental suitability considering (1) only the *O. mirabilis* occurrence records, (2) the host's occurrence records, including areas where *O. mirabilis* has occurred, and (3) only the host's occurrence records (i.e., areas where there were no records of *O. mirabilis*). We used these data to assess whether host availability or suitability of water conditions was the most important factor regulating the distribution of *O. mirabilis* worldwide. The suitability values from the *O. mirabilis* occurrence records were also split into subsets comprising native and non-native records and tested for differences between ranges using Student’s t-test.

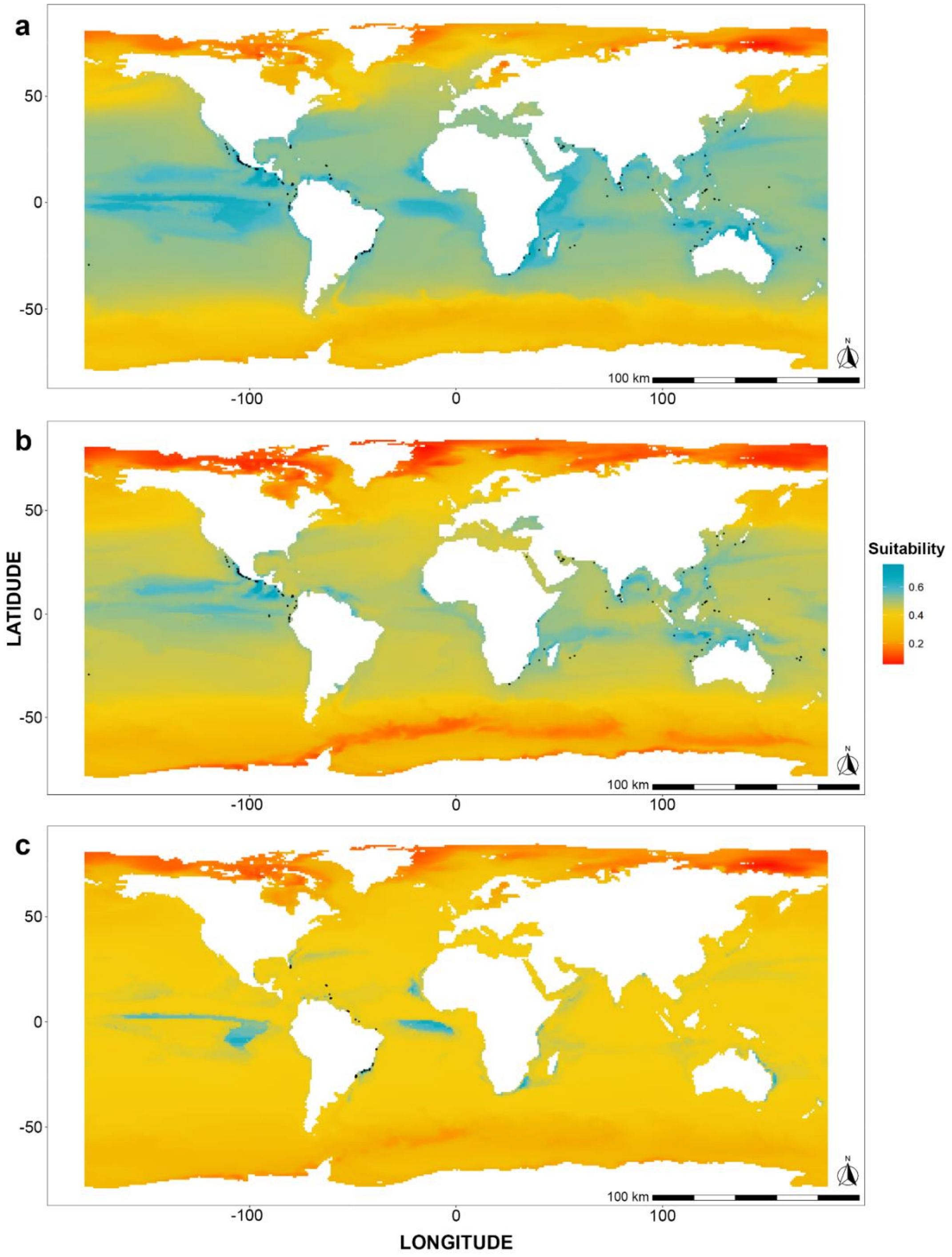
The raw values for each seawater variable were extracted from the ensemble model grid cells using *O. mirabilis* coordinates in the native and invaded areas. We plotted the kernel densities distributions of each variable and compared both areas also using Student's t-test. We also performed the plots and analysis in the R environment (R CORE TEAM, 2022).

## 2.3 Results

### 2.3.1 Review descriptive statistics

The *Ophiothela mirabilis* distribution records database comprised 133 publications between 1867 and 2021. The literature search retrieved 569 occurrence records: 317 in the Indo-Pacific waters (native registrations) and 252 in the Atlantic Ocean (non-native registrations), between latitudes 38ºN and 33ºS (Figure 7). We compiled 77 host-brittle star association records in the native range and 200 in the non-native area. Host genera chosen for overlapping occurrences with *O. mirabilis* fundamental niche were *Aplysina, Callyspongia, Desmapsamma*, *Dysidea*, *Haliclona*, *Monanchora,* and *Mycale*, regarding Porifera; and *Antillogorgia, Carijoa, Eunicea, Gorgonia, Leptogorgia*, *Millepora*, *Muricea,* and *Pacifigorgia*, regarding Cnidaria. The combination of these hosts represented 66.7% and 70.6% of the Porifera and Cnidaria association records, respectively (Table 6; Online Resource).

Figure 7 - Ensemble models of the environmentally suitable areas predicted from the ecological niche modeling of *Ophiothela mirabilis* with occurrence data from native and non-native sites combined, only native sites, and only non-native sites.



Legend: Ensemble models generated with occurrence data from (a) native and non-native sites, (b) only native sites, and (c) only non-native sites.

### 2.3.2 Ecological niche modelling

ENMs predicted suitable areas for *O. mirabilis* occurrence (i. e., its fundamental niche) in tropical and subtropical zones of the world. The selected models based on all available *O. mirabilis* occurrence records presented a mean AUC of 0.868 (Figure 23a; Online Resource). These models predicted more suitable areas in coastal and offshore waters through the Atlantic and Indo-Pacific Oceans (Figure 7a) than those based only on non-combined records (native and non-native ones) (Figures 7b and 7c; Figures 23c and 23e, Online Resource). Observing the 25% cut-off threshold maps, the one built exclusively with native records did not predict areas already invaded by *O. mirabilis*, such as the Brazilian coast (Figure 21b; Online Resource). Also, models based only on non-native records did not predict suitable areas for *O. mirabilis* occurrence in the Indo-Pacific Ocean, representing the species' native range (Figure 21c; Online Resource). Therefore, the suitability layer of the 25% cut-off threshold map based on all available data represented the most plausible set of environmental conditions for predicting the fundamental niche of *O. mirabilis* (Figure 21a; Online Resource).

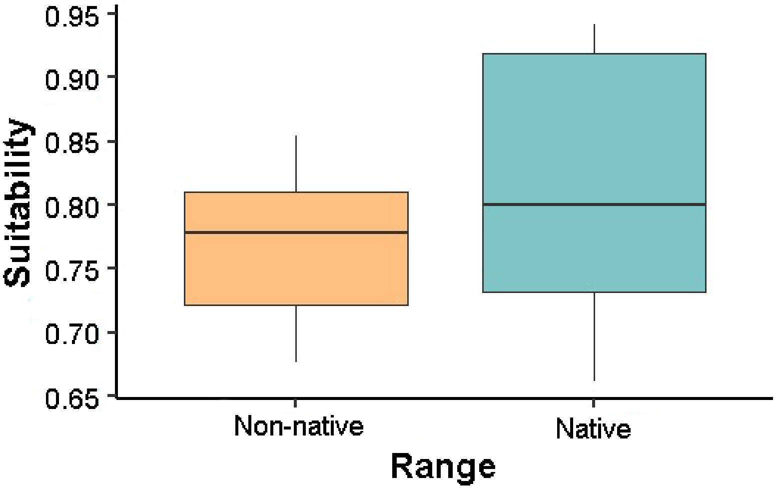
The species' current distribution range (black dots in Figure 7a) comprises areas with minimum and mean environmental suitability of 66.20% and 80.35%, respectively. The mean suitability differs between native and non-native regions, with values of 81.82% in the Indo-Pacific waters and 77.06% in the Atlantic Ocean (Table 1, Figure 8). ENMs found suitable areas in the littoral of South and Eastern Africa, South Asia, and North Australia in the Indo-Pacific waters and in the Pacific coast of Central America. In the Atlantic waters, coastal areas in the South and Southeastern United States, Caribbean Sea, Brazil, and Western Africa were highly suitable for *O. mirabilis* occurrence and thus are at greater invasion risk. The ENMs also predicted appropriate offshore areas for this invader in South Pacific and South Atlantic Oceans (Figure 7a).

Table 1 – Mean values of environmental suitability and seawater variables from native and non-native occurrence sites of *Ophiothela mirabilis* calculated using the present-day environmental layers available on the Bio-ORACLE v.2.2 database. The Student's t-test reveals differences between values from native and non-native regions.

| **Seawater variables** | **Mean ± SD native area** | **Mean ± SD non-native area** | **t statistics** | **d.f.** | **p-value** |
|---|---|---|---|---|---|
| Environmental suitability | 0.7706 ± 0.053 | 0.8182 ± 0.097 | -5.5553 | 295.06 | $6.191x10^{-8}$* |
| Salinity | 33.45 ± 1.5 | 35.36 ± 1.87 | 8.7996 | 152.48 | $2.774x10^{-15}$* |
| Calcite (mol.m$^{-3}$) | 0.550 ± 0.163 | 0.602 ± 0.071 | 3.9172 | 307.87 | 0.0001104* |
| mean SST (ºC) | 27.20 ± 2.27 | 25.28 ± 2.18 | -6.9879 | 190.2 | $4.574x10^{-11}$* |
| Dissolved Oxygen (mol.m$^{-3}$) | 205.739 ± 8.440 | 213.869 ± 9.510 | 7.1167 | 165.52 | $3.189x10^{-11}$* |
| Chlorophyll-a (mg.m$^{-3}$) | 0.282 ± 0.264 | 0.380 ± 0.302 | 2.7116 | 162.83 | 0.007414* |
| SST range (ºC) | 6.58 ± 3.45 | 6.71 ± 2.80 | 0.31356 | 221.5 | 0.7541 |
| Primary productivity (g.m$^{-3}$.day$^{-1}$) | 0.017 ± 0.014 | 0.015 ± 0.012 | -0.81186 | 210.95 | 0.4178 |

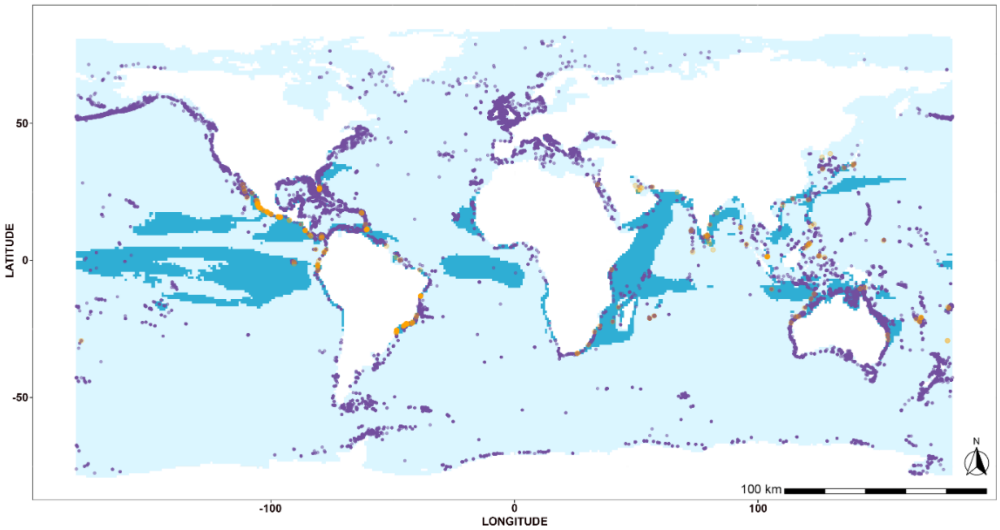
* significant values

Figure 8 - Boxplot of the environmental suitability values for *Ophiothela mirabilis* occurrence in the non-native and native range.



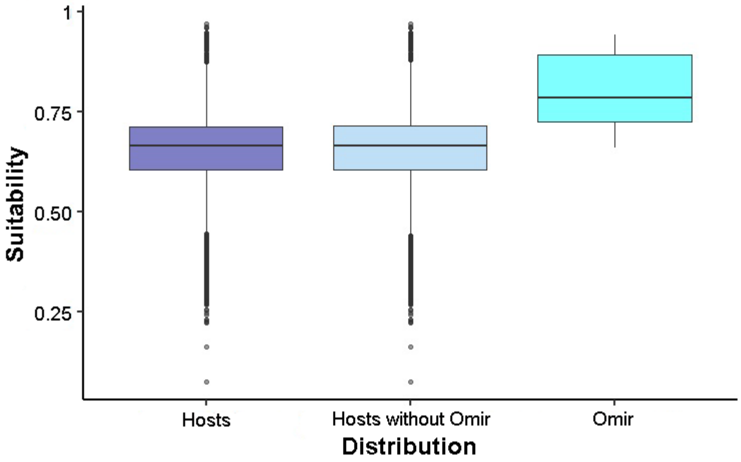
The *O. mirabilis*' fundamental niche overlapped with host distributions (Figure 9) in most environmentally suitable areas, except for Eastern Africa. In addition, sites where the hosts are available for colonization presented mean suitability for *O. mirabilis* occurrence of around 66% and the same where hosts and the brittle star distributions overlapped (0.657±0.097 and 0.659±0.098 - mean±SD, respectively). Estimating environmental properness achieved a mean value of 80.3% in those areas where only brittle star records were considered (0.803±0.088, mean±SD) (ANOVA; F = 339.4; d.f. = 45788; p-value = < 0.001; Figure 10). Primary productivity, salinity, and calcite were the most important abiotic variables for predicting *O. mirabilis* environmental suitability, considering native and non-native occurrence records combined. When analyzing these records separately, primary productivity and salinity were important variables for the predictions in the native range, while only the first one was important for the non-native geographical areas (Table 7; Online Resource).

Figure 9 - Predicted ecological niche of *Ophiothela mirabilis* worldwide due to the overlap of the binary map of 75% environmental suitability in water conditions and the distribution of shared host genera.



Legend: Environmental suitability is represented by dark blue layer, the distribution of shared host genera by purple dots, and the occurrence records of *Ophiothela mirabilis* by orange dots.

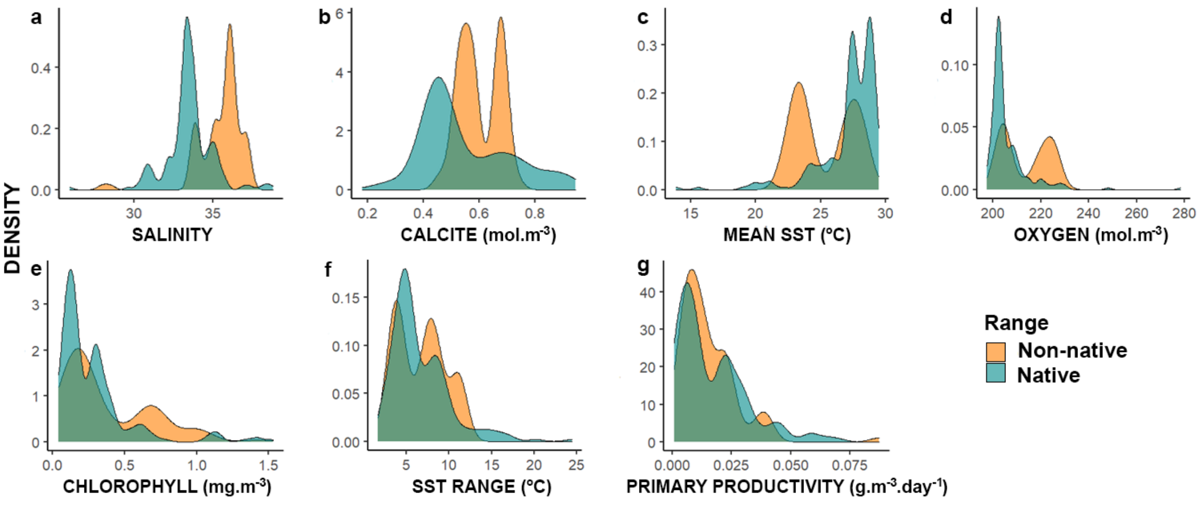
Figure 10 - Boxplot of the environmental suitability values for *Ophiothela mirabilis* occurrence considering its occurrence records and hosts distribution.



Legend: “Hosts” means the distribution of main hosts species; “Hosts without Omir” means the distribution of hosts excluding overlapping brittle star records; and “Omir” means *Ophiothela mirabilis* occurrence records exclusively.

The current global distribution of *O. mirabilis* includes areas with salinity values varying from 24.03 to 38.8, the SST range from 1.66 to 24.43ºC, and variation of the mean concentration of the following environmental variables: calcite from 0.18 to 0.94 mol.m$^{-3}$, the SST from 13.85ºC to 29.44ºC, dissolved molecular oxygen from 197.47 to 278.28 mol.m$^{-3}$, chlorophyll-a from 0.04 to 1.53 mg.m$^{-3}$, and primary productivity from 0.0008 to 0.087 g.m$^{-3}$.day$^{-1}$ (Figure 11). Mean values of salinity, calcite, dissolved molecular oxygen, chlorophyll-a, and mean SST differed significantly between native and non-native areas of *O. mirabilis* occurrence (Figures 11a to 11e; Table 1). Native sites present lower salinity (±33), calcite (0.55 mol.m$^{-3}$), dissolved oxygen (205.74 mol.m$^{-3}$), and chlorophyll-a concentration (0.28 mol.m$^{-3}$), and higher mean SST (±27ºC), in contrast with non-native ones (±35 salinity, 0.602 mol.m$^{-3}$ of calcite, 213.87 mol.m$^{-3}$ of dissolved oxygen, 0.38 mol.m$^{-3}$ of chlorophyll-a, and SST starting at 22ºC). We also did not detect any differences in mean values of the SST range and primary productivity between native and non-native sites (Figure 11f and 11g; Table 1).

Figure 11 - The kernel density of native and non-native occurrence sites of *Ophiothela mirabilis* for the environmental variables used in the ensemble models.



Legend: The kernel density of (a) mean salinity, (b) mean calcite concentration, (c) mean sea surface temperature (SST), (d) mean dissolved molecular oxygen, (e) SST range, (f) mean chlorophyll concentration, and (g) mean primary productivity.

## 2.4 Discussion

Our data indicated the coastal areas of the South and Southeastern United States of America, the Caribbean Sea, the Brazilian coast, the coast of Western Africa, and a middle offshore site in the South Atlantic as environmentally suitable for the spread of *Ophiothela mirabilis*. The vast availability of benthic host species in these areas may contribute to the species dispersion from the currently occupied sites into the predicted fundamental niche. Therefore, these areas are at high invasion risk by *O. mirabilis* and represent monitoring priorities for detecting this silent invader. Our results agree with a previous prediction of *O. mirabilis* fundamental niche in the Western Atlantic, which estimated this area as suitable for its occurrence (DERVICHE et al., 2021). However, we also detected appropriate novel areas for the brittle star occurrence in the Eastern Atlantic and offshore middle South Atlantic and middle South Pacific, drawing attention to the species' dispersal potential. Transportation of the brittle star propagules from Indo-Pacific waters into the Atlantic Ocean probably occurs by shipping due to their association with fouling communities on ship hulls and oil platforms (HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013). Theoretically, such suitable ecological conditions in offshore regions enhance the chances of brittle stars' survival by favoring their transoceanic transport. In addition, the high circulation of vessels in offshore and coastal areas in the Atlantic Ocean may have facilitated the spread of the species over large geographical regions (ARAÚJO et al., 2018; LAWLEY et al., 2018; GLYNN et al., 2020; RICH et al., 2020). The absence of current records of this brittle star in the Eastern Atlantic may result from insufficient sampling efforts in shallow waters in recent years and a lack of specialized taxonomists who can correctly identify the species (GRIFFITHS et al., 2010; POLIDORO et al., 2017). One should also bear in mind that *O. mirabilis* may not be native to all regions in the Indo-Pacific waters, as considered here. The species probably arrived at previously uninhabited areas and established populations, but we could not check this information due to the lack of reports in the literature. Therefore, monitoring *O. mirabilis*' spread in Indo-Pacific waters is also necessary, given that regions such as Eastern Africa and North Australia have been predicted as environmentally suitable but have no record of the brittle star occurrence yet.

Ecological niche models based only on the brittle star non-native records had low predictive power across its entire range of occurrence. They comprised only a subset of abiotic conditions in native sites and, thus, underestimated suitable areas for invasion. Models based only on native records also showed poor quality, as they failed to predict regions currently colonized by *O. mirabilis* in the Western Atlantic, particularly considering the 25% cut-off threshold. The exclusive use of native records to predict areas at high risk of invasion has also produced incorrect suitability estimates in previous studies (BEAUMONT et al., 2009; VERBRUGGEN et al., 2013). Failure in predicting the current distribution of *O. mirabilis* in the non-native area may reveal divergences in the physical and environmental requirements of this species over the geographical space (BROENNIMAN et al., 2007). For instance, we noticed a narrower range of salinity, mean SST, calcite concentration, dissolved oxygen, and chlorophyll-a concentration tolerated by the species in the non-native area when compared with the native one.

Moreover, we detected higher values of these variables in the non-native area, except for mean SST. However, primary productivity did not differ between these zones and was the primary variable contributing to *O. mirabilis'* environmental suitability. Combining ENMs and the Centroid shift, Overlap, Unfilling, and Expansion (COUE) framework could provide further insights into niche expansion or conservatism processes regarding *O. mirabilis* and help understand how this species responds to distinct environmental conditions (GUISAN et al., 2014; PACK et al., 2022). Nonetheless, the three-zone modeling approach (i.e., native, non-native, and combined) adopted in our work represents a simple but valuable strategy for detecting potential shifts or overlaps in species' environmental niches over the geographical space. This approach also enables comparison and the choice for a more realistic ensemble.

Seawater variables are likely the main factors mediating the distribution of *O. mirabilis* worldwide, since potential hosts spread widely beyond the predicted range of suitable areas. These findings contradict our expectations that the host's availability would limit the distribution of *O. mirabilis* because of its epizoic habit. However, this relationship is not species-specific, as *O. mirabilis* occurs on several benthic hosts in the Indo-Pacific range and mainly in the Atlantic waters (TAVARES et al., 2021). Plasticity in host association can boost the silent invasion of this brittle star since we found congeneric host species along coastal areas worldwide. However, these areas had lower environmental suitability for *O. mirabilis* occurrence (66%, i.e., calculated considering all available host records) than we found for the brittle star current distribution (80%). Therefore, tolerance to water conditions likely limits species' survival and establishment in temperate and polar zones. However, shifts in this geographical pattern are expected as high-latitude waters warm, leading to changes in primary productivity and calcite availability (IPCC, 2022) - some of the most important factors for predicting *O. mirabilis* occurrence. Future habitat suitability can be assessed from

ENMs using environmental layers of climate scenarios predicted for the mid and end-century to consider possible poleward expansion and tropical retraction in the brittle star distribution, a pattern expected for species inhabiting low-latitude systems (ANTÃO et al., 2020; PACK et al., 2022).

Environmental data revealed primary productivity as a critical factor in the distribution of *O. mirabilis*. This variable has not been associated with *O. mirabilis* performance by a previous study (DERVICHE et al., 2021). Besides, primary productivity could directly or indirectly affect their currently unknown feeding strategy. Experiments can help better understand this variable's role in the brittle star occurrence. Moreover, the primary productivity may be directly associated with the distribution of its main hosts. Octocorals represented 88.9% of *O. mirabilis* association records within the Cnidaria phylum compiled in our study. Several environmental factors influence the wide distribution of those benthic organisms in all latitudes and their occurrence ranges, such as local hydrodynamics, depth, light incidence, and quantity of particulate organic matter available in the water column (FABRICIUS; ALDERSLADE, 2001; PÉREZ et al., 2016). Most octocorals species are suspension feeders, so the concentration and availability of suspended particulate food influence their growth (FABRICIUS; ALDERSLADE, 2001) and contribute to the highest abundance and diversity in nutrient-rich areas. Although the nature of the brittle star’s relationship with its host is still unknown, this association is crucial for establishing the species in the native and non-native range, since it is not found apart from a host in the natural environment. Salinity was also related to *O. mirabilis* distribution, mainly in the native regions. Most sites where *O. mirabilis’* occurs have mean salinity near 34. Brittle stars cannot regulate internal fluid osmotically and, consequently, are restricted to marine environments (DIEHL, 1986). However, the lower average salinity reported for *O. mirabilis* in the native area reveals that this species can dwell in brackish waters, at least for a short time. Its small body, sealed by strong calcareous plates, limits fluid exchange parts to the tiny tube feet. Therefore, the low osmotic exchange rate could explain brittle star occurrence in areas under 35 salinity on the Indo-Pacific coast and may enable its spread into estuaries and coastal lagoons in the Atlantic.

Calcite, another key variable for *O. mirabilis* distribution, is an essential substance in the body composition of brittle stars (WEBER et al., 1969). These animals constantly lose their arms and spines to evade predators or respond to stress (STANCYK et al., 1994). Some of them can reproduce asexually through the fission of the disc, such as *O. mirabilis* (TAVARES et al., 2019). So, the absorption of environmental calcite to ossicle regeneration is constant (WEBER, 1968; BOWMER; KEEGAN, 1983; DONACHY; WATABE, 1986). The distribution of the species in lower calcite concentration sites in native areas compared with non-native ones can be related to its reproduction modes. Considering that asexual reproduction is predominant in populations at new locations (i.e. non-native populations; TAVARES et al., 2019), we can hypothesize that *O. mirabilis* needs rich-calcite waters to colonize and maintain itself in the new invaded localities. In addition, rich-calcite waters also benefit hosts that need this substance to build the supporting body structures, such as spicules in sponges and sclerites in corals (BRUSCA; BRUSCA, 2003). Sea surface temperature was not one of the main variables predicting *O. mirabilis* distribution. However, analysis of the raw data reveals that 97.4% of the occurrence records are from areas warmer than 22 ºC. Therefore, data suggest that this brittle star thrives in nutrient and calcite-rich waters with salinity above 35 and temperatures higher than 22ºC.

Our work identified areas at risk of invasion by *O. mirabilis* worldwide, providing subsidies for developing early detection, control, and eradication strategies regarding this silent invader. Suitable regions for the brittle star occurrence in the Western Atlantic overall agreed with the early prediction of Derviche et al. (2021). Moreover, the ENMs also revealed the Eastern Atlantic (at tropical and subtropical latitudes) suitable for *O. mirabilis* occurrence. Plasticity in host association and lower average values of most water variables in the native region (in comparison to the non-native one) suggest that there is room for *O. mirabilis* expansion in the Atlantic waters.

We also found suitable areas for *O. mirabilis* spread in the Indo-Pacific Ocean, such as Eastern Africa and North Australia. Still, it is uncertain whether these represent the species' native range or actual sites for the introduction. Nonetheless, we suggest monitoring initiatives should be implemented in each of the mentioned sites, as eradicating invasive species is cheaper and more successful in the early stages of the invasion process (SIMBERLOFF et al., 2013). Furthermore, suitable offshore areas could favor the transportation of this brittle star across oceans. Water conditions likely mediate the spread of *O. mirabilis* rather than host availability, considering the records of several genera outside the suitable areas predicted by ENMs. Instead of registrations of distinct average values of water variables in the native and non-native range, primary productivity is the most relevant factor for predicting *O. mirabilis* environmental suitability. However, further analyses are necessary to reveal whether there is expansion, shift or overlap in *O. mirabilis* ecological niche. Modeling the environmental conditions in which small-sized, hard-to-detect alien species thrive is particularly important to prevent ecological and economic losses. Our work adds to the list of successful ENM studies performed with marine AS and reveals the main sites worldwide at risk of invasion by *O. mirabilis*.

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# 3 OCTOCORAL AVAILABILITY FAVORS ABUNDANCE OF THE INVASIVE *OPHIOTHELA MIRABILIS* DESPITE LESS FAVORABLE WATER CONDITIONS

Manuscrito a ser submetido ao periódico *Coral Reefs* em 2022.

## 3.1 Introduction

Marine alien species (AS) are daily transported and introduced in several coastal regions worldwide (BLACKBURN et al., 2014). The success of biological invasions is linked not only to the survival in transport conditions, but especially to the abiotic and biotic filters inherent to the new environment (COLAUTTI et al., 2016). Adaptation to local conditions allow the AS to reproduce and consequently form viable populations (BLACKBURN et al., 2011). Thus, species can become invasive and cause harmful effects on native biota, environment or human health and economy (MOLNAR et al., 2008, BLACKBURN et al., 2014). However, these negative impacts are not easily noticed sometimes and can remain unrecognizable for a long time. In these cases, the species are known as silent invaders (MIGLIETTA; LESSIOS, 2009). Moreover, an AS can also integrate into the local community and not cause major damage to the environment (BLACKBURN et al., 2014; SAMMARCO et al., 2015). Therefore, understanding their ecological requirements and how environmental conditions, and biotic interactions affect their establishment is a key step towards unraveling the factors that influence the success of these invaders.

The brittle star *Ophiothela mirabilis* VERRILL, 1867 was first reported as non-native in the Western Atlantic Ocean in 2012 (HENDLER et al., 2012). Since then, most of the published studies have showed the expansion of *O. mirabilis* in the non-native occurrence area (e. g. HENDLER et al., 2012; HENDLER; BRUGNEAUX, 2013; ARAÚJO et al., 2018; FERRY et al., 2020; GLYNN et al., 2020). Although it is known that the brittle star’s distribution in the Atlantic waters extends from South Florida to South Brazil (FERRY et al., 2020; DERVICHE et al., 2021), the structure and dynamics of its populations is barely known (but see TAVARES et al., 2019). Few data about abundance or density of *O mirabilis* populations were reported in non-native area (see TAVARES et al. 2019; FERRY et al., 2020; GLYNN et al., 2020; DERVICHE et al., 2021; FORTUNATO; LÔBO-HAJDU, 2021).

Appropriate water conditions and the presence of potential hosts are relevant ecological features that influence not only the occurrence of the species, but also its ability to thrive in the new area (i.e. increase its populations). Recent predictions were made about ecologically suitable areas for *O. mirabilis* occurrence (DERVICHE et al., 2021, TAVARES et al., submitted). However, data relating environmental features with *O. mirabilis* abundance are not provided by scientific databases. In addition, as *O. mirabilis* is an epibiont species, many studies reported the hosts in which the species was found, but none have investigated in depth the ecological relationship between them. Adverse effects of its presence on benthic organisms have already been suggested (MANTELATTO et al., 2016), but nothing in this sense has been confirmed so far. On the contrary, recent studies have not shown any impairment in the feeding activity of some species of octocorals tested (GLYNN et al., 2021, DERVICHE; LANA, 2022). In view of the great plasticity in the use of substrate, more studies need to be carried out in this regard. Similarly, none study focused on investigating if the abundance of the invaders is significantly different among hosts, what could indicate preference in substrate colonization (although clues of preference by cnidarians were raised up by TAVARES et al., 2021).

The success of invasion by an AS can be measured through several factors such as the increase in population size and in the geographic area occupied by the species both latitudinally and bathymetrically, as well as mortality rates and ability to compete for vital resources to the survival and maintenance of populations in the new environment (RIBEIRO et al., 2017; SAMMARCO et al., 2015). Therefore, abundance or density data are proxies to assess the successful performance of an invader in the environment. Dense and stable populations over time provide evidence of successful invasiveness of the species, unlike occurrence data, which do not necessarily reflect whether the species is well established and thriving in a certain site.

Here, we proposed to unravel the environmental features linked to highest abundance of *O. mirabilis* in a region where a great diversity of hosts was previously reported (MANTELATTO et al., 2016). Water conditions and habitat components were evaluated and related to the abundance patterns found for the invader brittle star. We hypothesized that highest *O. mirabilis* abundance would be found in areas with salinity of 35 and warmer than 22°C (as predicted in TAVARES et al., submitted) and associated with arborescent cnidarians. The prioritization of areas for management or population control of the species was discussed based on the characterization of the sites where the species thrives.

## 3.2 Material and Methods

### 3.2.1 Sampling and field procedure

The samples of water variables, habitat components, and *O. mirabilis* specimens were collected once at each season between July 2021 and June 2022. Sampling were performed at three sites in Ilha Grande Bay: Araçatibinha beach (23°9’21.013”S; 44°20’5.305”W), Lagoa Verde (23°8’19.342”S; 44°19’24.892”W) and Abraãozinho beach (23°7’59.909”S; 44°9’5.476”W). Water temperature (°C) and pH were measured at sea surface with a digital multiparameter sensor (ATC model). Salinity was taken with a refractometer, while transparency (m) and depth (m) with a Secchi disc. Habitat features and *O. mirabilis* sampling were recorded through free diving. Searches for colonized organisms (i.e. hosts) by *O. mirabilis* were carried out along 100 m linear transects across one of the rocky shores of each site. When a benthic host colonized by *O. mirabilis* was found, a photoquadrat of 50 cm x 50 cm (= $0.25 m^2$) of the bottom substrate was taken. A total of five photoquadrats were taken at each site and date during the sampling period, totalizing 60 images of bottom habitat composition. The photographs were taken using a GoPro Hero 7. The colonized organisms were collected and stored in identified plastic bags for posterior removal and counting of brittle stars.

### 3.2.2 Image processing and habitat use classification

The photoquadrats were analyzed using the software Coral Point Count with Excel extensions (CPCe) to identify the benthic organisms present at each site and to calculate the area occupied by them in the quadrats. The organisms were identified at species level, and the category shadow was assigned to places where we could not identify the substrate due to shading by other structures or organisms.

The identified benthic organisms were classified according to their body texture (H: hard or S: smooth), body orientation in relation to water column (H: horizontal or V: vertical) and how the ophiuroids could adhere to their surface (S: with the arms stretched, SC: with the arms slightly curved, or E: with the arms entwined to the host). The combination of these three features composed the classification used to characterize the sampling sites according to the pattern of habitat use by *O. mirabilis* during colonization. Therefore, the benthic species were classified as SHS, SVSC, SHSC, HHSC, HVSC, HVE, SVE.

### 3.2.3 Statistical analysis

All statistical analyses were performed in the R software v.4.2.0 (R CORE TEAM, 2022). Water and habitat variables were treated as two distinct groups of predictors. The water variables were composed by values of temperature, salinity, pH, transparency and depth. All those variables were $\log_{10}x$ transformed (except pH) to be considered in the further analysis. The habitat group comprised the percentage area covered by algae, Porifera, Cnidaria, Ascidea, Bryozoa, Echinodermata, shadow and bare substrate. The area values (relative coverage area) were arcsine square root transformed. Both groups of predictors were standardized using the *decostand* function in the *vegan* package (OKSANEN et al., 2022). Analyses carried out with only water variables or combining water and habitat features considered 12 sample units, since water conditions were measured once at each site and field activity. For the combined approach, the mean area of the habitat components was calculated. The same procedure was adopted for brittle star abundance data. On the other hand, analyses performed with only habitat variables or combining abundance values with habitat features considered 60 sample units, as habitat components were evaluated in 60 photoquadrats.

Principal Component Analysis (PCA) was applied to investigate seasonal and spatial patterns in sample ordination of water variables and habitat composition across the sampling sites. We also applied PCA to order the samples according to *O. mirabilis*' habitat use patterns. We performed PCAs using the *princomp* function and extracted the variables importance for each axis using *loadings* function in *stats* package (R CORE TEAM, 2022). The Broken-stick criterion was considered to retain the axes for interpretation. This criterion considers that the interpretable axes have eigenvalues greater than those obtained by a null model (JACKSON, 1993).

Permutational Multivariate Analysis of Variance (PERMANOVA) was applied to investigate differences in water and habitat variables across time and sampling sites. We also examined if *O. mirabilis* abundance shifted over time, across sampling sites, and between the two main categories of habitat use pattern. Comparisons between the dependent and independent matrices were made using the function *adonis2* in the *vegan* package (Oksanen et al., 2022).

Redundancy Analysis (RDA) was applied to investigate the pattern of sample ordination considering water and habitat variables together. We used water conditions as explanatory variables and habitat components (i.e. benthic organisms) as the response matrix on the first RDA to characterize the sampling sites. On the second RDA, we used water and habitat variables together as the predictor matrix of the *O. mirabilis* abundance (response variable). For both analyses, we used the *rda* function in the *vegan* package (OKSANEN et al., 2022).

The PCA and RDA ordination graphs, as well as, the boxplots of abundance data were created using the *ggplot2* package (WICKHAM, 2016).

Generalized Linear Models (GLM), using Poisson distribution and logarithmic link function, were performed to examine the effects of water and habitat predictors on the *O. mirabilis* abundance (response variable). Poisson distribution was chosen after analyzing the distribution of the response variable plotted on a histogram. We ran a global model with water and habitat predictors, using the function *glm* in the *stats* package (R CORE TEAM, 2022). Non-significant variables reported in the model summary were excluded. We ran a novel model and checked for differences from the previous one through an Analysis of Variance (ANOVA). As models were not significatively divergent (p-value >0.05), we chose the simplest. We evaluated the variance inflation factor (VIF) of the final model applying *multicollinearity* function in the *performance* package (LÜDECKE et al., 2021). We also inspected the residuals for heterogeneity of variances through graphs generated by *check_model* function in the same package (LÜDECKE et al., 2021).

### 3.2.4 Electivity index

The Ivlev's electivity index (IVLEV, 1961) was calculated to investigate whether the colonization of benthic organisms by *O. mirabilis* occurs randomly or purposely. The index can be calculated by the following formula:

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)}$$

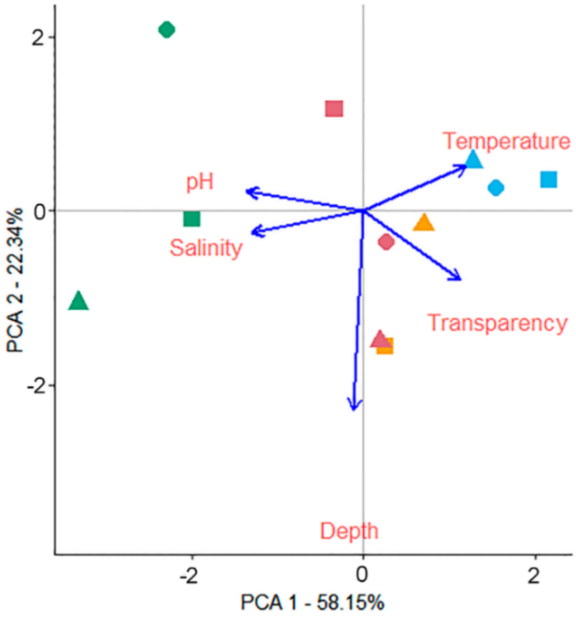
Where E is the selectivity for the host i, $r_i$ is the relative percentage of *O. mirabilis* collected on the host i, and $p_i$ is the relative percentage of area occupied by the host i. The index $E_i$ varies from -1 to 1. Values near to -1 indicate a negative selectivity (i.e. host was avoided for colonization), near to zero indicate randomly occurrence of *O. mirabilis* on a host species (i.e., there is no selection), and values near to 1 indicates a positive selectivity for a certain host (IVLEV, 1961).

## 3.3 Results

### 3.3.1 Environmental characterization based on water and habitat variables

The axis 1 of the PCA performed with water variables (eigenvalue = 2.67, retained by Broken-Stick criteria), explained 58.15% of the data variation, and revealed only seasonal patterns of sample separation (Figure 12). These patterns were corroborated by the PERMANOVA results, which indicated that the physical and chemical water variables shifted over time, but did not differ among sampling sites (Tables 2 and 3). Samples were correlated mainly with pH ($r$ = -0.543) and salinity ($r$ = -0.521). Both variables were highest during winter and lowest during summer. Temperature showed an inverse pattern, with highest values during summer and lowest during winter and autumn. Water transparency was full (i.e. Secchi disc reaches the bottom) or near to 80% of the maximum depth at the three sites throughout the sampling period, except at Araçatibinha, where it was near 35% during winter (Table 3).

Figure 12 - Ordination diagram of the sampling units according to a principal component analysis (PCA) of the water variables. All variables, except pH, were log10-transformed.



Legend: Samples were coded by symbols (● – Abraãozinho; ▲- Arçatibinha; ■ – Lagoa Verde) and colors (▬ winter; ▬ spring; ▬ summer; ▬ autumn).

Table 2 – PERMANOVA results. F = pseudo-F value by permutation; d.f. = degrees of freedom; p(perm) = p-values based on 999 permutations. *significant values ($p \leq 0.05$)

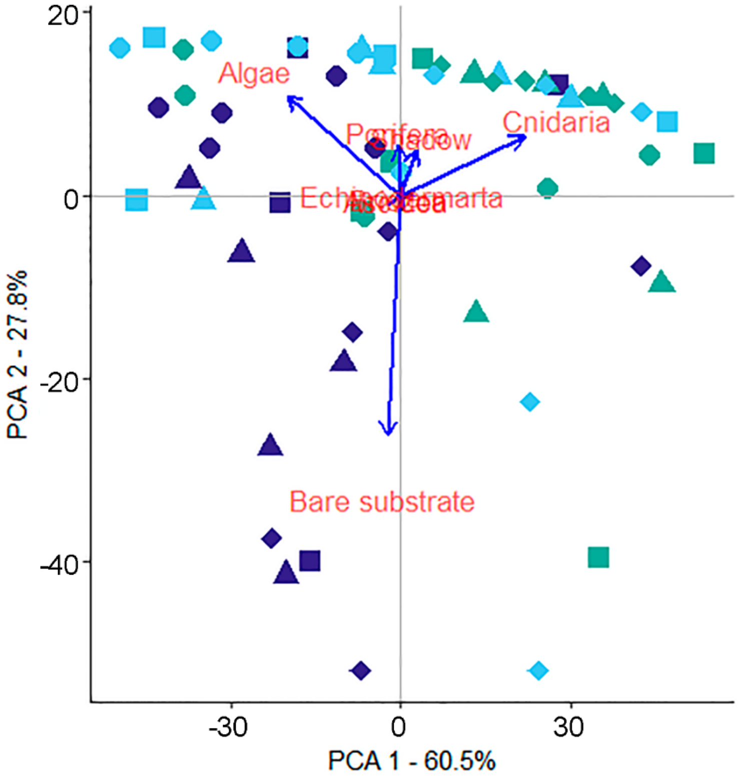
| **Dependent matrix x Independent matrix** | **F** | **d.f.** | **p(perm)** |
|---|---|---|---|
| Abiotic variables x season | 3.2175 | 11 | 0.033* |
| Abiotic variables x site | 0.6119 | 11 | 0.631 |
| Abiotic variables x season x site | 0.6747 | 1 | 0.584 |
| Habitat variables x season | 2.0528 | 59 | 0.056 |
| Habitat variables x site | 5.7343 | 59 | 0.001* |
| Habitat variables x season x site | 0.6211 | 1 | 0.718 |
| Abundance x season | 5.4694 | 59 | 0.02* |
| Abundance x site | 8.3235 | 59 | 0.005* |
| Abundance x season x site | 0.6273 | 59 | 0.462 |
| Abundance x habitat use pattern | 5.1951 | 59 | 0.009* |

Table 3 – Values of abiotic variables and *Ophiothela mirabilis* abundance collected at Araçatibinha, Lagoa Verde and Abraãozinho beaches in Ilha Grande Bay, Brazil at each season. Sampling dates are the same for each season: winter - 22/07/2021, spring - 03/12/2021, summer - 10/03/2022, autumn - 24/06/2022.

| **Sampling sites** | **Water variables** | | | | | ***O. mirabilis* abundance** | | |
|---|---|---|---|---|---|---|---|---|
| | **Temperature (°C)** | **pH** | **Salinity** | **Transparency (m)** | **Maximum depth (m)** | **N° orange morphotype** | **N° purple morphotype** | **Total** |
| **Araçatibinha** | | | | | | | | |
| Winter | 20.9 | 8.7 | 39 | 5.5 | 15.5 | 260 | 59 | 319 |
| Spring | 24.2 | 8.1 | 34 | 10 | 10 | 845 | 0 | 845 |
| Summer | 28.6 | 8 | 34 | 9 | 9 | 536 | 1 | 537 |
| Autumn | 21.5 | 8.4 | 34 | 13 | 13 | 507 | 0 | 507 |
| **Mean** | **23.8** | **8.3** | **35.3** | **9.4** | **11.9** | | | |
| **Lagoa Verde** | | | | | | | | |
| Winter | 21.7 | 8.5 | 39 | 8 | 10 | 528 | 0 | 528 |
| Spring | 24 | 8 | 35 | 8.6 | 15.6 | 950 | 0 | 950 |
| Summer | 30 | 7.8 | 33 | 9.5 | 9.5 | 1124 | 0 | 1124 |
| Autumn | 21.7 | 8.3 | 33 | 7.5 | 7.5 | 613 | 0 | 613 |
| **Mean** | **24.4** | **8.2** | **35** | **8.4** | **10.7** | | | |
| **Abraãozinho** | | | | | | | | |
| Winter | 22.3 | 8.7 | 37 | 6.2 | 6.2 | 237 | 326 | 563 |
| Spring | 29.2 | 8.1 | 33 | 9.8 | 9.8 | 1131 | 56 | 1187 |
| Summer | 29.2 | 8.1 | 33 | 9.8 | 9.8 | 957 | 991 | 1948 |
| Autumn | 22.5 | 8.2 | 33 | 9 | 11 | 1061 | 927 | 1988 |
| **Mean** | **25.8** | **8.3** | **34** | **8.7** | **9.2** | | | |

The PCA performed with habitat data evidenced a spatial ordination of the samples, which was also supported by the PERMANOVA results (Table 2). Samples were more associated with Cnidaria ($r$ = 0.729) and algae ($r$ = -0.673) coverage in the PCA axis 1 (eigenvalue = 762.78, retained by Broken-Stick criteria), which accounted for 60.5% of data variation (Figure 13). Most of Abraãozinho photoquadrats were performed in areas with highest coverage of algae (mainly turf), while Araçatibinha and Lagoa Verde samples were made in areas with greater Cnidaria coverage. PCA axis 2 (eigenvalue = 350.51, also retained by the Broken-Stick criteria) explained 27.8% of variance and evidenced that some photoquadrats were taken close to the rocky shore-sediment threshold during summer and autumn, mainly at Abraãozinho, due to the highest occurrence of bare substrates.

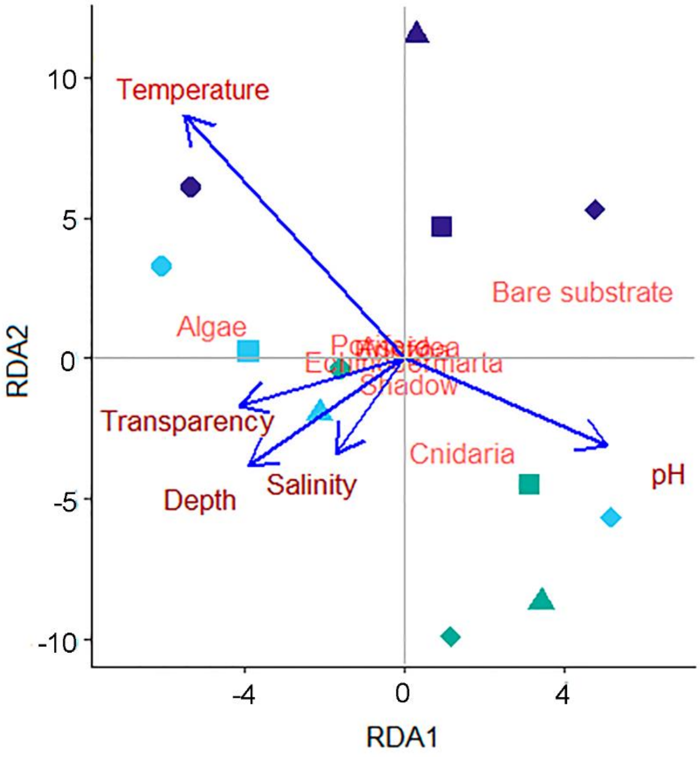
Figure 13 - Ordination diagram of the sampling units according to a principal component analysis (PCA) of the habitat variables. The area values (proportional data) of all variables were arcsine square root transformed.



Legend: Samples were coded by colors (▬ Abraãozinho; ▬ Arçatibinha; ▬ Lagoa Verde) and symbols (■ – winter; ● – spring; ▲- summer; ♦ - autumn).

The RDA analysis performed with water and habitat variables as predictor and response matrices, respectively, summarized 30.85% of data variation (Figure 14). The two first axes explained 93.48% of the total summarized and revealed mainly a spatial pattern of sample scattering. Temperature (*r* = -0.476) and pH (*r* = 0.441) were the main abiotic variables that contributed to this ordination. Highest temperatures were mainly related to the algae coverage, while highest pH were related to the coverage of Cnidaria and bare substrates. Lagoa Verde samples were associated with higher values of salinity, depth, transparency, and algae cover than the other sampling sites. Lagoa Verde and Abraãozinho shared highest temperature samples, while Abraãozinho and Araçatibinha were associated with highest pH values. Araçatibinha presented highest Cnidaria coverage, while Abraãozinho the highest occurrence of bare substrates in the quadrats.

Figure 14 - Ordination diagram of the redundancy analysis (RDA) showing the relationship of the habitat components with water variables. All water variables, except pH, were log10-transformed and the area values (relative percentage cover) of all habitat variables were arcsine square root transformed.



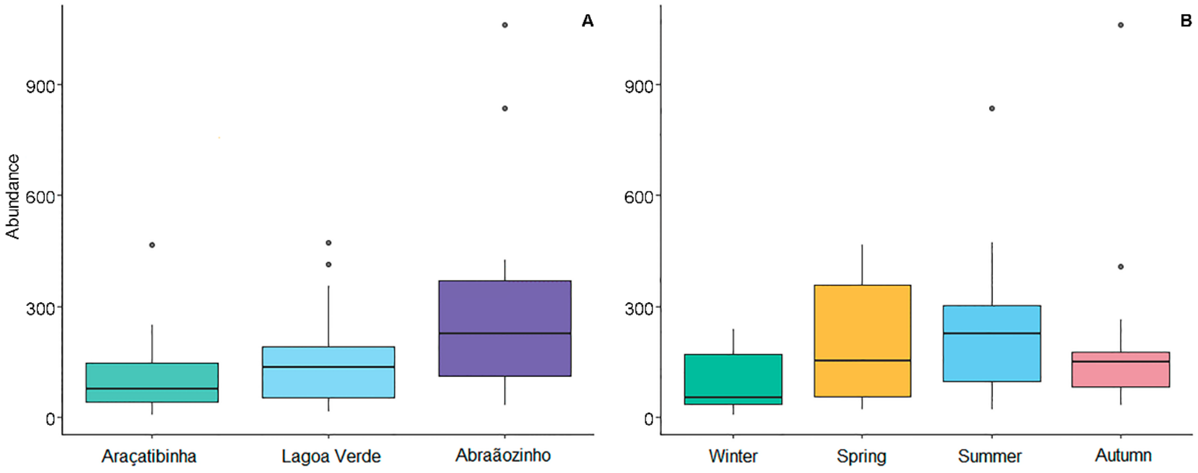
Legend: Samples were coded by colors (▬ Abraãozinho; ▬ Arçatibinha; ▬ Lagoa Verde) and symbols (■ – winter; ● – spring; ▲ - summer; ♦ - autumn).

### 3.3.2 General patterns of *O. mirabilis* abundance

We collected 11,109 *O. mirabilis* specimens during the sampling period: 2,208 at Araçatibinha, 3,215 at Lagoa Verde and 5,686 at Abraãozinho (Table 2). Two body color patterns of *O. mirabilis* (i.e. orange and purple) were found, but both were analyzed as a single species and population, since there was no taxonomical record and systematic evidence in literature that these morphotypes are different species or had ecological differences.

*Ophiothela mirabilis*' abundance varied across beaches and over time (Figure 15A and 15B; Table 2), with highest records at Abraãozinho and during summer and the lowest at Araçatibinha and during winter.

Figure 15 - Boxplots of *Ophiothela mirabilis* abundance for sampling sites and seasons.

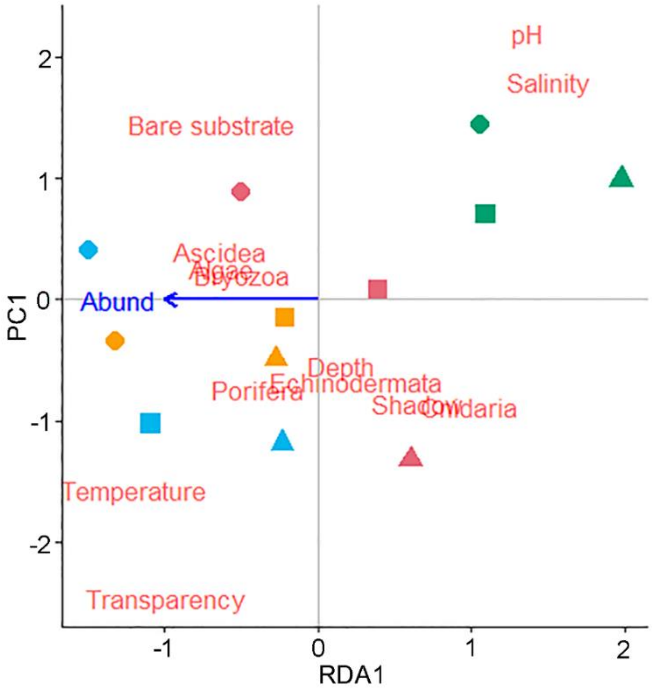


Legend: Boxplots of *Ophiothela mirabilis* abundance were classified by sampling sites (A) and seasons (B). Sites and seasons are coded by colors. A: ▬ Abraãozinho; ▬ Arçatibinha; ▬ Lagoa Verde. B: ▬ winter; ▬ spring; ▬ summer; ▬ autumn.

### 3.3.3 Relationship of *O. mirabilis* abundance with water and habitat characteristics

The RDA analysis performed through combining water and habitat variables as the explanatory matrix and *O. mirabilis* abundance as the response variable, summarized 26.68% of data variation (Figure 16). The samples ordination evidenced that *O. mirabilis* abundance is related to sites with higher temperature and transparency, and greater coverages of Porifera, Bryozoa, Ascidea, algae, and bare substrate.

Figure 16 - Ordination diagram of the redundancy analysis (RDA) showing the relationship of the habitat components and water variables with *Ophiothela mirabilis* abundance. All water variables, except pH, were log10-transformed and the area values (relative percentage cover) of all habitat variables were arcsine square root transformed.



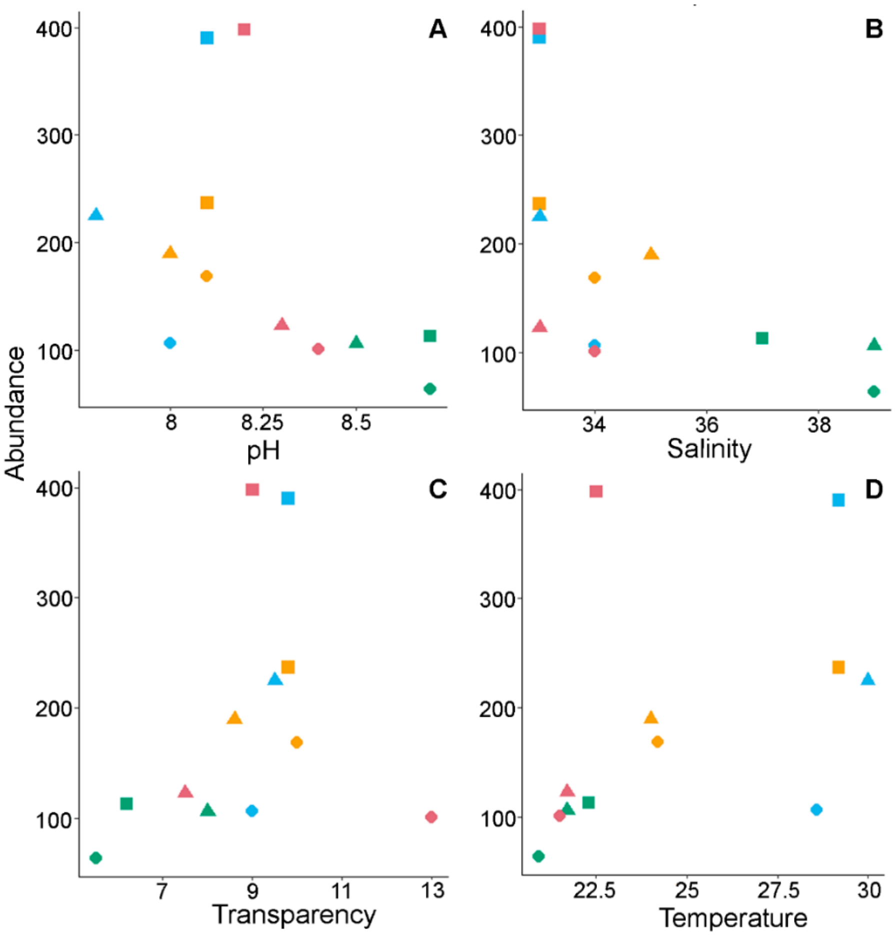
Legend: Samples were coded by symbols (● – Abraãozinho; ▲- Arçatibinha; ■ – Lagoa Verde) and colors (▬ winter; ▬ spring; ▬ summer; ▬ autumn).

Temperature, salinity, transparency, pH, Algae, Cnidaria, Porifera and Ascidea were the variables retained as significant in the final GLM. The variables temperature, pH, Porifera and Cnidaria showed low autocorrelation, while transparency, salinity, algae and Ascidea presented moderate autocorrelation (Table 4). *Ophiothela mirabilis* abundance seems to decrease with higher values of pH (Figure 17A) and salinity (Figure 17B), and to increase with higher transparency (Figure 17C). The relationship of brittle stars with temperature was not clear (Figure 17D). The brittle stars were only recorded on Cnidaria and Porifera hosts. There was no clear trend between *O. mirabilis* abundance and the percentage of area covered by Porifera and Cnidaria hosts (Figures 18A and 18B).

Table 4 - Results of generalized linear model of *Ophiothela mirabilis* abundance with water and habitat variables, and variance inflation factor (VIF). All p-values were significant ($p < 0.001$). The variables temperature, pH, Porifera and Cnidaria showed low correlation, while transparency, salinity, algae and Ascidea presented moderate correlation.

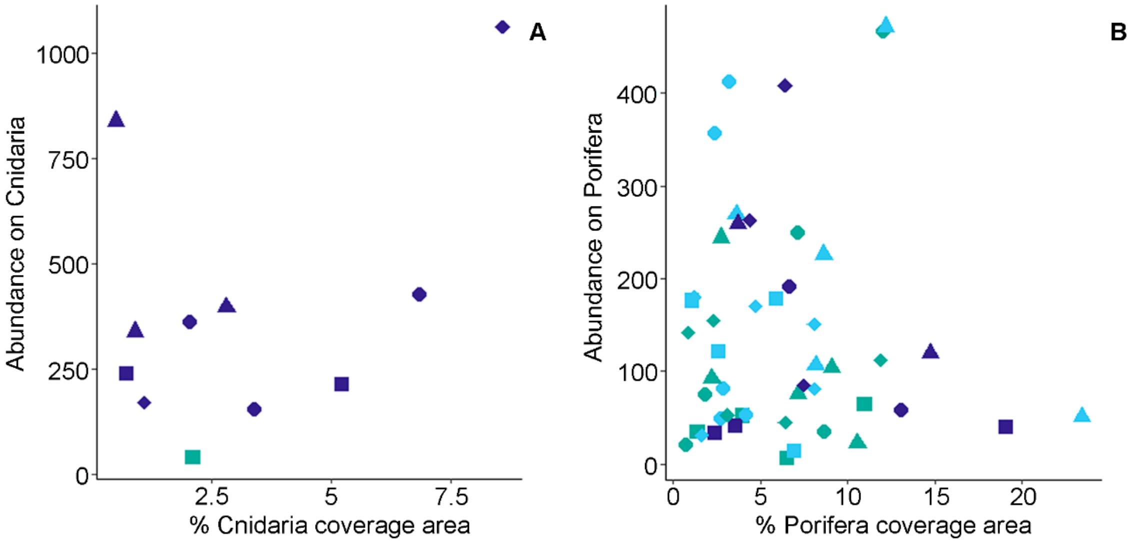
| | **GLM results** | | | | **VIF** | **Autocorrelation** |
|---|---|---|---|---|---|---|
| **Factor** | **Estimate** | **Std. Error** | **z-value** | **p-value** | | |
| Intercept | 5.07343 | 0.02436 | 208.234 | <0.001 | | |
| Temperature | -0.29316 | 0.03858 | -7.598 | <0.001 | 3.00 | Low |
| Salinity | 0.19846 | 0.08353 | 2.376 | <0.001 | 9.07 | Moderate |
| Transparency | 0.11535 | 0.04407 | 2.617 | <0.001 | 2.19 | Moderate |
| pH | -0.57125 | 0.07773 | -7.349 | <0.001 | 8.32 | Low |
| Algae | -0.89724 | 0.09229 | -9.722 | <0.001 | 7.14 | Moderate |
| Porifera | 0.35942 | 0.09093 | 3.953 | <0.001 | 2.52 | Low |
| Cnidaria | -1.30684 | 0.08820 | -14.816 | <0.001 | 6.54 | Low |
| Ascidea | 0.16601 | 0.06328 | 2.623 | <0.001 | 3.31 | Moderate |

Figure 17 - Relationship between *Ophiothela mirabilis* abundance and water variables.



Legend: Water variables - (A) pH, (B) salinity, (C) transparency, and (D) temperature. Samples were coded by symbols (● – Abraãozinho; ▲- Arçatibinha; ■ – Lagoa Verde) and colors (▬ winter; ▬ spring; ▬ summer; ▬ autumn).

Figure 18 - Relationship between *Ophiothela mirabilis* abundance recorded on Cnidaria and Porifera and the percentage of Cnidaria and Porifera coverage area, respectively.

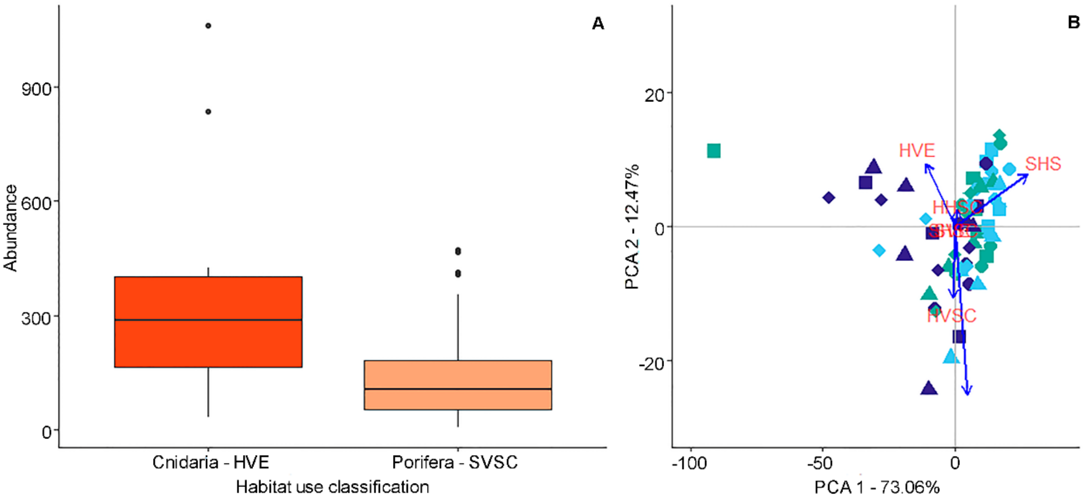


Legend: (A) *Ophiothela mirabilis* abundance recorded on Cnidaria and the percentage of Cnidaria coverage area and (B) *O. mirabilis* abundance recorded on Porifera and the percentage of Porifera coverage area. Samples were coded by colors (▬ Abraãozinho; ▬ Araçatibinha; ▬ Lagoa Verde) and symbols (■ – winter; ● – spring; ▲ - summer; ♦ - autumn).

### 3.3.4 Habitat use patterns of *O. mirabilis*

*Ophiothela mirabilis* was only recorded on Cnidaria and Porifera hosts with vertical body orientation in relation to the water column. All Cnidaria hosts were classified as HVE due to their hard body texture, where *O. mirabilis* can tied its arms. The HVE cnidarians were the octocorals *Carijoa riisei*, *Heterogorgia uatumani*, *Leptogorgia punicea*, and *L. setacea*. Meanwhile, all Porifera hosts was classified as SVSC because of the smooth texture of their bodies, where *O. mirabilis* stands with his arms slightly curved. The hosts classified as SVSC comprised the sponges *Aplysina fulva*, *Desmapsamma acnhorata*, *Mycale angulosa*, and a white Demospongiae. Higher brittle star abundances were recorded on HVE Cnidaria than on SVSC Porifera (Figure 19A; Table 2). The HVE Cnidaria hosts were more related to Abraãozinho beach than to the other sampling sites, as shown in the PCA axis 1 (eigenvalue = 249.53, retained by the Broken-Stick criterion) (Figure 19B).

Figure 19 - *Ophiothela mirabilis* abundance by host group and ordination diagram of the sampling units according to a principal component analysis (PCA) of hosts' classification in relation to the habitat use pattern of *Ophiothela mirabilis*.



Legend: Boxplot of *Ophiothela mirabilis* abundance (A) and ordination diagram of the sampling units according to a PCA of hosts' classification in relation to the habitat use pattern of *Ophiothela mirabilis*. A: boxplots are coded by colors (▬ HVE; ▬ SVSC). HVE means hosts with hard body texture, vertical oriented in relation to water column and where *O. mirabilis* specimens can tie their arms. SVSC means hosts with smooth body texture, vertical oriented in relation to water column and where *O. mirabilis* specimens stands their arms slightly curved. B: samples were coded by colors (▬ Abraãozinho; ▬ Arçatibinha; ▬ Lagoa Verde) and symbols (■ – winter; ● – spring; ▲- summer; ♦ - autumn).

Based on Ivlev's electivity index, the cnidarians *H. uatumani*, *L. punicea* and *L. setacea* were preferably colonized by *O. mirabilis* at the sampling beaches (Table 5). The sponges *A. fulva*, *D. anchorata* and *M. angulosa* were often colonized, but apparently at random. On the other hand, the white Demospongiae and the cnidarian *C. riisei* were negatively selected by the brittle stars, probably because of the few invaders recorded on these hosts.

Table 5 – Results of the Ivlev's electivity index for each host species, total *O. mirabilis* abundance and percentage of coverage area of its hosts during all sampling period.

| **Host species** | **Ivlev's electivity index** | ***O. mirabilis* total abundance** | **% coverage area** |
|---|---|---|---|
| **Porifera** | | | |
| *Aplysina fulva* | 0.0616022 | 792 | 0.45 |
| *Desmapsamma anchorata* | -0.166132897 | 5150 | 4.63 |
| *Mycale angulosa* | 0.106933363 | 909 | 0.39 |
| White Demospongiae | -0.480005167 | 31 | 0.06 |
| **Cnidaria** | | | |
| *Carijoa riisei* | -0.356927995 | 789 | 1.29 |
| *Heterogorgia uatumani* | 0.812428522 | 506 | 0.03 |
| *Leptogorgia punicea* | 0.768091217 | 2497 | 0.21 |
| *Leptogorgia setacea* | 0.54513489 | 435 | 0.08 |

### 3.4 Discussion

Our findings indicated that *O. mirabilis* abundance varied across time and sampling sites. Water conditions and habitat composition may influence directly or indirectly the abundance of the invasive brittle star, since the first set of predictors shifted over time and habitat components were different across sampling sites. The water conditions linked to the highest values of abundance were recorded during summer and comprised water temperature between 28.6 and 30°C, pH values varying from 7.8 up to 8.1, salinity around 33 and 34, and transparency ranging from 9 to 9.8m. Although further studies are still needed to confirm abundance patterns, these water features may indicate the set of suitable abiotic conditions to *O. mirabilis* thrive in non-native areas. This research represents the first step in investigating the relationship of *O. mirabilis* abundance with abiotic conditions, since recent studies have made predictions about water characteristics suitable for the *O. mirabilis* occurrence, without consider where populations could be larger or smaller (DERVICHE et al., 2021; TAVARES et al., submitted). Furthermore, data on the abundance of these invasive brittle stars has been tangentially reported, especially in the non-native area (e. g. FORTUNATO; LÔBO-HAJDU, 2021, ALITTO et al., 2020, TAVARES et al., 2019, GALVÁN-VILLA; RÍOS-JARA, 2018, PURCELL; ERIKSSON, 2014, KUMAGAI; AOKI, 2003). Environmental conditions can directly affect brittle stars abundance, mainly in species capable of asexually reproduce through fission (MLADENOV, 1996), as *O. mirabilis* (ALITTO et al., 2020, TAVARES et al., 2019). Harsh abiotic conditions can trigger fission in echinoderms (MLADENOV, 1996). However, the suitable water features that allow natural reproduction of *O. mirabilis* specimens are not yet recognized, neither if the species reproduces also sexually or only by asexually means (TAVARES et al., 2019, HENDLER; BRUGNEAUX, 2013). Our field data suggested that abundance is greatest in waters with pH around 8.1 and salinity around 33, but our database is not sufficient to extrapolate how ideal these conditions are in locations where other non-native populations have been recorded. Experimental studies should test if those environmental features may represent harsh conditions that could act as triggers to initiate fission and contribute to the increase in the number of specimens in the population.

Abundance of *O. mirabilis* were related to abiotic summer conditions, and also to greater habitat diversity, including representants of the phyla Porifera, Bryozoa, Ascidea, and algae. Although *O. mirabilis* has been reported in association with specimens of all these phyla (and others) in a previous assessment at the same region (MANTELATTO et al., 2016), the brittle stars were only recorded on Porifera and Cnidaria hosts. Some other possible hosts were present not only in the transects carried out, but also in the photoquadrats taken, i. e. very close to the sponges and cnidarians hosts colonized by *O. mirabilis*, but never found associated with the brittle stars. This reinforces the evidence of preference for these organisms during colonization reported by Tavares et al. (2021), who compiled most of *O. mirabilis*' association records on these organisms published to date. However, the invasive brittle star did not colonize all corals and sponges species recorded during the field activities. *Ophiothela mirabilis* was only found associated with benthic organisms vertically orientated in relation to water column and where it could tie its arms on hosts branches or stand with its arms slightly curved. Apparently, being in an elevated position away from the substrate, as well as being able to firmly anchor themselves to the hosts, is important for *O. mirabilis* specimens in some way.

Although *O. mirabilis* can profusely and frequently colonize some Porifera species on all sampled beaches, our data suggested that this association is opportunistic and linked to suitable abiotic conditions, rather than directional as the relationship of the brittle stars with octocorals. The abundance of brittle stars is linked to the presence of Porifera in warmer, clearer waters with lower salinity and pH among the sampled sites. However, *O. mirabilis* preferentially colonizes octocoral cnidarians than other available hosts, regardless of existing abiotic conditions. Highest *O. mirabilis* abundances were found on octocorals, even their area corresponding to only 1.62% of the total area of benthic organisms (i.e. habitat) sampled. *Ophiothela mirabilis* relationship with these benthic organisms is frequently reported in the scientific literature (TAVARES et al., 2021; e. g. GLYNN et al., 2021, GLYNN et al., 2020, RICH et al., 2020; FANOVICH et al., 2019). This close association may be related to intrinsic biological features of octocorals species, their body architecture, or a combination of both. It is already known that *Phyllogorgia dilatata* (ESPER, 1806) produces a secondary metabolite capable of attracting specimens of *O. mirabilis* (RIBEIRO et al., 2017). There is no more information available on this issue so far, but if chemical attraction of these brittle stars by other benthic organisms exists, it may be important for the successful invasion of this species in non-native areas. The body architecture of arborescent cnidarians can also be advantageous for *O. mirabilis* in some ways. The brittle stars can tightly attach to the octocorals by entwining their arms around the host's branches, and thus be less subject to drag forces. This feature can also facilitate the asexual reproduction process, which has been suggested as the main reproductive strategy of the species in non-native areas (TAVARES et al., 2019). An experiment with *Ophiocomella ophiactoides* (another fissiparous brittle star with body dimensions similar to *O. mirabilis*), suggested that specimens could exert force in opposite directions and speed up the fission process, since they tied their arms on the *Amphiroa* filaments (MLADENOV et al., 1983). The same can occur with *O. mirabilis* specimens colonizing octocoral hard branches, and so, contribute to increase the number of individuals presents on a certain host. Therefore, a combination of both features on a host may contribute to the successful establishment of populations of *O. mirabilis* in non-native sites. Experimental studies should be conducted not only to confirm the preference for arborescent cnidarians, but also to understand whether this relationship is based on the production of attracting substances, on the host's body architecture, or on the synergistic effect of both.

The nature of the brittle stars' relationship with their hosts is barely known, but it seems to be essential for the survival of *O. mirabilis* in the natural environment. Some harmful effects of its presence on hosts have been suggested (MANTELATTO et al., 2016), but experimental studies conducted with the octocoral species *Leptogorgia punicea* (DERVICHE; LANA, 2022), and *Muricea elongata* and *Eunicea flexuosa* (GLYNN et al., 2021) found no significant harm on the host feeding. Therefore, although the species is considered invasive in the Atlantic Ocean, none negative impact of its presence was reported so far. Experiments *in situ* and microcosms regarding not only possible harms to hosts, but also to deeply investigating the combination of attractive substances production and body architecture of cnidarians and sponges may be the key to understanding the mechanisms for *O. mirabilis* invasion in the Atlantic waters. Nonetheless, non-native *O. mirabilis* populations should be constantly monitored to prevent its expansion in the invaded area. In view of our findings, non-native areas with water temperature between 28.6 and 30°C, pH values varying from 7.8 up to 8.1, salinity around 33 and 34, and transparency above 9m that harbors octocorals and sponges should be priority in implementing management actions of *O. mirabilis* populations.

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# DISCUSSÃO GERAL

Os resultados gerais da Tese demonstraram que as espécies do gênero *Ophiothela* estão distribuídas em grande parte das áreas costeiras dos Oceanos Pacífico, Índico e Atlântico entre as latitudes 33°S e 38°N, exceto na costa oeste da África (Capítulo 1; TAVARES et al., 2021). A maior parte dos registros de ocorrência destes ofiuroides, especialmente no Indo-Pacífico, é proveniente de listas de espécies realizadas em ambientes costeiros (e. g. JAMES et al., 1969; GRANJA-FERNÁNDEZ; LÓPEZ-PÉREZ, 2012; KEESING et al., 2014; SUPONO et al., 2014; ALITTO et al., 2016; CÁRDENAS-CALLE et al., 2018). Embora o hábito de vida epibionte seja crucial para a sobrevivência destes ofiuroides no ambiente, seus hospedeiros não foram acuradamente identificados ou mesmo reportados em muitos destes trabalhos (TAVARES et al., 2021), o que dificultou a avaliação dos padrões de colonização das espécies nestes oceanos. De forma geral, foi possível evidenciar que a maior parte das espécies de *Ophiothela* foram registradas em associação com corais e esponjas (e.g. MORTENSEN, 1914; CLARK,1940; GOH; CHOU, 1994; PRICE; ROWE, 1996; TAHERA, 2001; MARSH; MORRISON, 2004; MAHARAVO, 2011; GRANJA-FERNÁNDEZ et al., 2014; MANTELATTO et al., 2016; FORTUNATO; LÔBO-HAJDU, 2021). Todos os registros do gênero para o oceano Atlântico referem-se à invasão da espécie *O. mirabilis* (única espécie de *Ophiothela* registrada como invasora no mundo) e englobam uma área de ocorrência de cerca de 6700 km de extensão (HENDLER et al., 2012; HENDLER, BRUGNEAUX, 2013; ARAÚJO et al., 2018; FERRY et al., 2020; GLYNN et al., 2020; TAVARES et al., 2021). A comparação entre os hospedeiros de *O. mirabilis* (= *O. danae* após sinonimização por ALITTO et al., 2020), espécie com maior número de registros, demonstrou uma maior plasticidade na colonização do substrato para as populações de áreas não-nativas, onde seus hospedeiros foram reportados com maior acurácia na identificação (TAVARES et al., 2021). *Ophiothela mirabilis* foi registrado em associação com 51 espécies de organismos bentônicos, pertencentes aos filos Cnidaria, Porifera, Echinodermata, Chordata, Bryozoa, além de espécies de algas (TAVARES et al., 2021; e. g. MANTELATTO et al., 2016, FORTUNATO; LÔBO-HAJDU, 2021). Isso chama a atenção para o potencial de dispersão da espécie em águas costeiras do Oceano Atlântico, uma vez que a disponibilidade de hospedeiros potenciais não parece ser um obstáculo. Estressores biológicos, como predadores ou competidores potenciais ainda não foram identificados. Portanto, a invasão de sistemas próximos é provável e fatores abióticos parecem ser os principais responsáveis por limitar a dispersão da espécie na área não-nativa.

Diante disso, prever áreas suscetíveis a novas invasões (Capítulo 2), i. e. com condições abióticas adequadas e com disponibilidade de potenciais hospedeiros, permitirá a alocação de esforços e recursos para aplicação de medidas preventivas contra a disseminação da espécie  para áreas ainda não habitadas. Nossos resultados indicaram que águas ricas em nutrientes e calcita, com salinidade de 35 e temperaturas superiores a 22°C são mais suscetíveis à invasão da espécie. Assim, evidenciamos que há áreas ecologicamente adequadas para a ocorrência de *O. mirabilis* dentro da faixa latitudinal de distribuição das espécies do gênero, com disponibilidade de potenciais hospedeiros, onde ainda não há registro da espécie, como na costa oeste do continente Africano. Áreas offshore com condições abióticas adequadas para *O. mirabilis* também foram previstas no meio do Atlântico Sul e do Pacífico Sul, o que pode facilitar seu transporte transoceânico em associação com comunidades incrustantes de cascos de embarcações, como vem sendo sugerido (HENDLER et al., 2012; HENDLER, BRUGNEAUX, 2013; LAWLEY et al., 2018). Portanto, sugerimos que projetos de monitoramento sejam desenvolvidos em locais ainda não habitados pela espécie, próximos de áreas de ocorrência conhecidas e/ou que tenham condições ecologicamente adequadas para a sobrevivência de *O. mirabilis*. Medidas de manejo ou controle populacional de espécies invasoras são mais efetivas e baratas se aplicadas nos estágios iniciais do processo de invasão (CUTHBERT et al., 2022). Além disso, embora impactos negativos da presença de *O. mirabilis* sobre a biota nativa do Atlântico ainda não sejam reconhecidos, a espécie pode representar um caso clássico de invasora silenciosa (TAVARES et al., 2021). Portanto, o monitoramento de populações já estabelecidas também é importante para avaliar se efeitos negativos ao ambiente estão acontecendo. A aplicação de qualquer tipo de ação que vise a mitigação desses impactos ou a erradicação da espécie em determinados locais pode não ser efetiva e será certamente mais custosa, se a detecção do invasor não ocorrer rapidamente (CUTHBERT et al., 2022).

Entretanto, apenas a ocorrência da espécie em determinada região não é sinônimo de sucesso de estabelecimento de populações (BLACKBURN et al., 2011). Além de entender onde a espécie ocorre e para onde pode expandir sua área de distribuição, desvendar as condições locais tanto de habitat quanto da água que permitem que *O. mirabilis* prospere (i.e. onde os ofiuroides podem ser encontrados em altas densidades), é crucial para compreender parte dos requerimentos ecológicos da espécie que permitem o crescimento e a manutenção de suas populações em áreas não-nativas. Assim, foi importante investigar como os padrões de abundância de *O. mirabilis* estão atrelados às condições da água e disponibilidade de potenciais hospedeiros em populações já estabelecidas (Capítulo 3). Verificamos que, de fato, *O. mirabilis* coloniza especialmente esponjas e cnidários, entretanto esponjas parecem ser abundantemente colonizadas em condições ambientais favoráveis. Estas condições foram representadas por águas com temperatura entre 28,6 e 30°C, valores de pH variando de 7,8 a 8,1, salinidade em torno de 33 e 34 e transparência entre 9 e 9,8m. Entretanto, octocorais são os hospedeiros preferencialmente colonizados pelos ofiuroides não-nativos independentemente das condições abióticas dos locais amostrados e mesmo quando outros hospedeiros potenciais (que já foram identificados em associação com *O. mirabilis* em outros estudos; e. g. MANTELATTO et al., 2016, FORTUNATO; LÔBO-HAJDU, 2021) estão presentes. Assim, a presença de hospedeiros preferenciais parece ser mais importante para a ocorrência de *O. mirabilis* em grande abundância do que as características abióticas dos locais amostrados, embora ainda não esteja claro como estas variáveis podem afetar o número de indivíduos da população. Acreditamos que a colonização dos organismos bentônicos pode ser mediada por substâncias atratoras produzidas pelos hospedeiros (como é o caso de *Phyllogrogia dilatata*; RIBEIRO et al., 2017), arquitetura dos seus corpos ou um efeito sinérgico das duas condições. Neste estudo, somente coletamos espécimes de *O. mirabilis* associados a organismos verticalmente orientados em relação à coluna d’água e onde puderam se fixar ao hospedeiro com firmeza (i.e. com braços entrelaçados ou ligeiramente curvados sobre a superfície dos organismos colonizados). Isto indica que a arquitetura corporal do hospedeiro parece ter um papel importante para o estabelecimento bem sucedido de populações não-nativas.

Os dados reunidos através do desenvolvimento desta tese, nos permitiram revelar os padrões de distribuição das espécies do gênero *Ophiothela* e reunir evidências da expansão da área de ocorrência da única espécie do gênero considerada invasora: *O. mirabilis*. Através da comparação dos padrões de colonização que ocorrem em áreas nativas e não-nativas, também foi possível constatar quais organismos bentônicos podem ser mais colonizados por densas populações dos ofiuroides invasores em áreas não-nativas. Como *O. mirabilis* aumentou sua área de distribuição por quase toda costa atlântica do continente Americano em apenas 23 anos após o seu primeiro registro, a previsão de regiões com condições abióticas adequadas para a ocorrência de *O. mirabilis* se torna essencial para revelar áreas suscetíveis a novas invasões. Além disso, dados de campo revelaram características ambientais de água e de habitat que permitem a ocorrência de espécie em abundância elevada. Embora ainda haja muitas lacunas no conhecimento de características cruciais para o entendimento do processo de invasão da espécie no oceano Atlântico, nossos dados representam um material de referência para novos estudos e experimentos que visem entender onde populações de *O. mirabilis* podem prosperar. Os artigos científicos derivados desta tese contribuem, portanto, para o entendimento dos requerimentos ecológicos desta espécie invasora em áreas não-nativas e poderão direcionar a definição de áreas prioritárias para o manejo e controle populacional da espécie.

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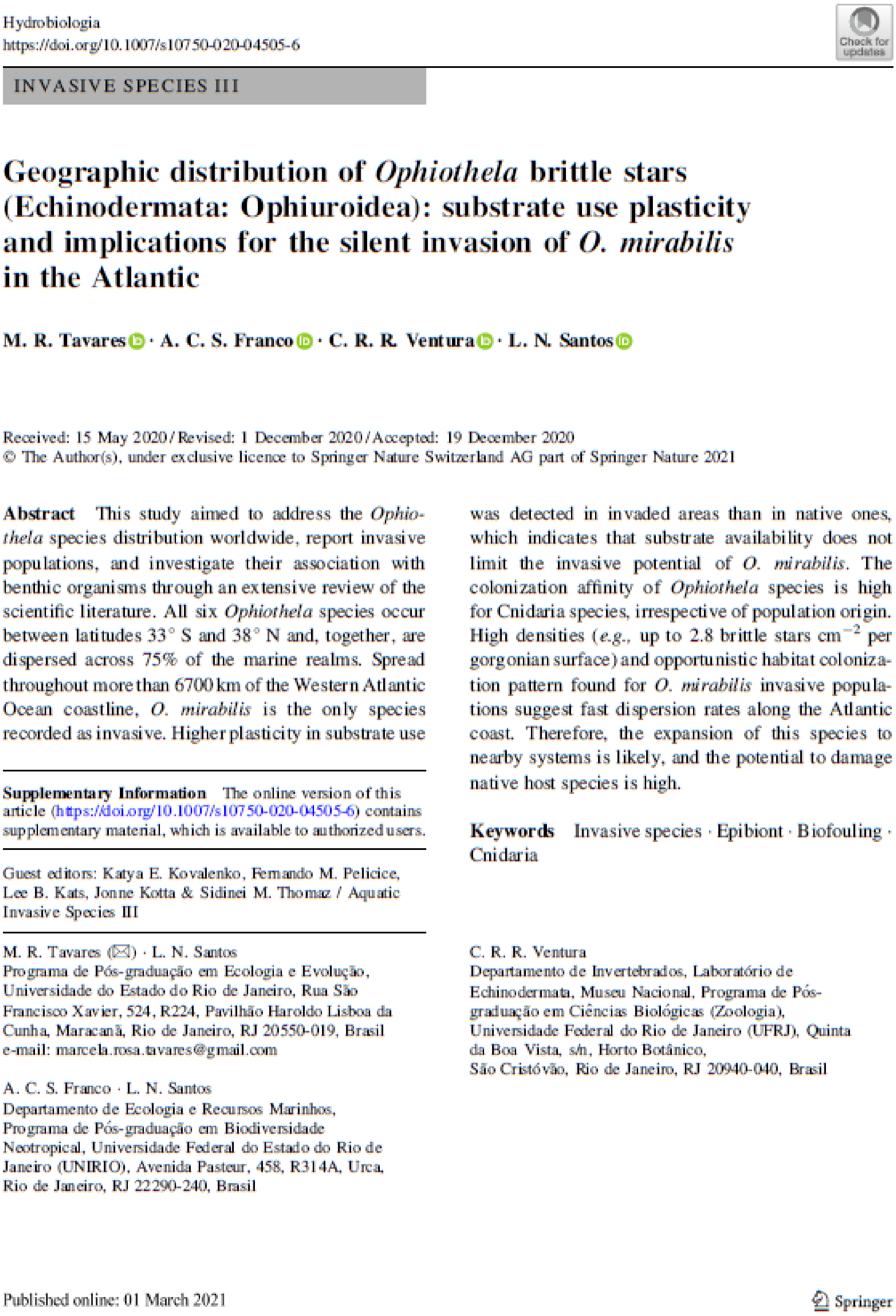
**APÊNDICE A** - Artigo científico publicado no periódico *Hydrobiologia*, volume 848, páginas 2093 a 2103, no ano de 2021.



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INVASIVE SPECIES III

# Geographic distribution of *Ophiothela* brittle stars (Echinodermata: Ophiuroidea): substrate use plasticity and implications for the silent invasion of *O. mirabilis* in the Atlantic

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**Abstract** This study aimed to address the *Ophiothela* species distribution worldwide, report invasive populations, and investigate their association with benthic organisms through an extensive review of the scientific literature. All six *Ophiothela* species occur between latitudes 33° S and 38° N and, together, are dispersed across 75% of the marine realms. Spread throughout more than 6700 km of the Western Atlantic Ocean coastline, *O. mirabilis* is the only species recorded as invasive. Higher plasticity in substrate use was detected in invaded areas than in native ones, which indicates that substrate availability does not limit the invasive potential of *O. mirabilis*. The colonization affinity of *Ophiothela* species is high for Cnidaria species, irrespective of population origin. High densities (*e.g.*, up to 2.8 brittle stars $cm^{-2}$ per gorgonian surface) and opportunistic habitat colonization pattern found for *O. mirabilis* invasive populations suggest fast dispersion rates along the Atlantic coast. Therefore, the expansion of this species to nearby systems is likely, and the potential to damage native host species is high.

**Keywords** Invasive species · Epibiont · Biofouling · Cnidaria

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## Introduction

The rate of species introduction worldwide has increased significantly following the globalization process (Espínola & Junior, 2007; Simberloff et al., 2013). Some non-native species that thrive in new habitats may become invasive, posing adverse impacts to marine ecosystems on varied scales (Molnar et al., 2008; e. g., Zenetos et al., 2005; Walters, 2009; Byrne et al., 2013). Accordingly, invasive species represent one of the main threats to ecosystem functioning and biodiversity (Allendorf & Lundquist, 2003), leading to global commitments and actions to minimize their adverse environmental effects (McNeely et al., 2001; Bax et al., 2003). The effectiveness of control actions against invasive species is variable but more promising when invader impacts are detected early. However, most marine system invasion processes are unknown, especially for small-sized organisms and less studied groups, such as plankton and invertebrates.

Several introduced invertebrates have remained untracked in invaded systems, although this process, termed "silent invasion", represents a severe threat for native species and ecosystem functioning (Bax et al., 2001; Miglietta & Lessios, 2009; Karatayev et al., 2015). The study of small-sized and inconspicuous invaders is under-represented in the scientific literature, possibly due to difficulties in their detection and assessment. This fact contrasts with the broader knowledge available about larger invasive species, whose impacts are easier to recognize and attract more attention from the scientific community and society (Giraldes et al., 2016). Moreover, pre-invasion data on the structure, dynamics, and ecological interactions of native populations and environmental requirements of the invader are generally lacking, preventing full evaluations of the effects of non-native species on invaded systems. Therefore, tracking introduction reports, distribution patterns, and habitat requirements of small-sized invertebrate species is crucial to construct scenarios regarding invasion risks and prevent damage caused by silent invaders on native species and ecosystems (Delaney et al., 2008).

Shipping is the main silent invasion pathway in marine environments, mostly through ballast water and biofouling (Molnar et al., 2008; Anil & Krishnamurthy, 2018). This allows species to cross biogeographic barriers and abiotic filters beyond the limits of their natural occurrence areas (Blackburn et al., 2014). These sea travelers can deal with harsh abiotic conditions and increased competition with other "ship passengers". Consequently, travel survivors are more prone to colonize and establish populations in new environments (Espínola & Junior, 2007; Blackburn et al., 2011). Some of the most conspicuous examples of silent invaders are the sun corals *Tubastraea coccinea* Lesson, 1830, and *Tubastraea tagusensis* Wells, 1982 (Silva et al., 2014; Giraldes et al., 2016), which have been widely introduced in the South Atlantic through biofouling. They have greatly impacted native communities, and consequently, the functioning of many marine systems throughout the Brazilian coast (Lages et al., 2012; Silva et al., 2014).

The detection of the non-native brittle star *Ophiothela mirabilis* Verrill, 1867 in Atlantic waters is a possible case of silent invasion of an Echinodermata member, thus drawing increasing researcher attention (Hendler et al., 2012). The *Ophiothela* genus is still scarcely studied, but all extant six species are known epibionts native to Indo-Pacific waters. In 2000, Hendler et al. (2012) recorded the presence of *O. mirabilis* in the Atlantic Ocean for the first time. Since then, this brittle star has been detected through ~ 6700 km along the Brazilian coast (Araújo et al., 2018), reaching the coastlines of the French Guiana, Antilles, and South Florida (Hendler & Brugneaux, 2013; Glyn et al., 2019; Ferry et al., 2020; Rich et al., 2020). The transportation of fouling organisms on human-made structures, such as ship hulls and oil platforms, is considered the main *O. mirabilis* invasion vector and the major steppingstone in assisting its spread throughout Atlantic waters (Hendler et al., 2012; Mantelatto et al., 2016; Lawley et al., 2018; Tavares et al., 2019). Furthermore, the successful establishment of *O. mirabilis* in the Atlantic may also be associated with the ability of this invader to colonize a high variety of benthic organisms (Mantelatto et al., 2016), its continuous clonal reproduction (Tavares et al., 2019), and the looseness of its ecological interactions (e.g., lack of potential competitors and predators). Although ecological data on most *Ophiothela* species are limited, available information indicates they share similar biological traits and requirements, suggesting an invasive potential in coastal ecosystems worldwide. Therefore, tracking information on the distribution of *Ophiothela* brittle stars is important to identify which species have been introduced into non-native areas and prevent adverse impacts on native species and ecosystems if they do become invasive.

In the present study, an overview of the geographic distribution of *Ophiothela* species and their patterns of substrate colonization in both native and non-native regions were identified in order to evaluate their occurrence range and track the spread of introduced populations. Data on the colonization patterns of natural substrates (i.e., host organisms) of native Indo-Pacific brittle star populations were also considered to unveil the groups of benthic organisms that would be more affected by the invasion progress of *O. mirabilis* in the Atlantic. To this end, we conducted an extensive literature survey to address four main questions: (1) What is the global distribution pattern of the *Ophiothela* genus? (2) Have other species of this genus besides *O. mirabilis* been recorded as introduced or invasive around the globe? (3) Do these epibionts display an affinity for specific host organisms during colonization? (4) Are colonizing patterns different between native and introduced *O. mirabilis* populations?

## Methods

An electronic survey was performed to compile all published data on the *Ophiothela* genus up to 2019. We retrieved data from the Web of Science, Scopus, and Google Scholar electronic databases using "*Ophiothela*" as a keyword. The search comprised scientific articles, book chapters, and grey literature (theses and technical reports; see Appendix 1). We also scanned the references of all retained studies for occurrence data not detected in our primary search. Our database included only studies that provided geographic distribution records for the assessed *Ophiothela* species. Information concerning the occurrence site, *Ophiothela* species (according to author identification), geographical coordinates, sampling date, colonized organisms, and complete reference was compiled from each study.

Alitto et al. (2020) suggested that *O. danae* is a junior synonym for *O. mirabilis* due to a high similarity of external morphology, shape measurements, and COI sequences found between some individuals (including syntypes) from both species and specimens from the Brazilian coast. Fatemi & Stöhr (2019) indicated the possible existence of a new fissiparous *Ophiothela* species that shares morphological traits with *O. danae* and *O. venusta*. However, we assumed a conservative position in the present study, considering *O. danae* and *O. mirabilis* as different taxonomic entities and the species indicated by Fatemi & Stöhr (2019) as *Ophiothela* sp. to prevent bias concerning the species distribution accepted so far.

The occurrence sites were assigned to ecoregions, provinces, and realms, following the Marine Ecoregions of the World (MEOW) categories proposed by Spalding et al. (2007). Geographical coordinates were estimated using Google Earth when not provided by the study, using occurrence site names. The midpoint facing the nearest coast was applied whenever coordinates were not available in the retained articles but corresponded to a small-scale region, such as islands, small beaches, or cities. Whenever large-scaled species distribution information indicated a single ecoregion, the midpoint along the coast was used as the occurrence site. We did not consider inexact localities and given areas spread across more than one ecoregion. A given record was assigned to a specific ecoregion by plotting the coordinates in a MEOW shapefile (http://www.marineregions.org/downloads.php) using Google Earth. Maps were plotted using the Quantum GIS 3.2.3 software (QGIS Development Team, 2020) to represent the geographic distribution of *Ophiothela* genus species worldwide.

Occurrence records were defined as each link among a certain *Ophiothela* species, its geographical coordinates, and the study that reported its occurrence. Each connection between an occurrence record and a host organism was considered as an association record. We used the World Register of Marine Species database (WoRMS; http://www.marinespecies.org/index.php, accessed on April 15, 2020) to check current terminology, *Ophiothela* species classification, and hosts identified at the genus or species level. A Principal Coordinates Analysis (PCoA) was applied to evaluate dissimilarities regarding benthic organism patterns colonized by *O. mirabilis* between native and introduced populations. Jaccard distances were calculated for the matrix concerning the presence and absence of *O. mirabilis* in six taxonomic host organism groups. The correction method established by Cailliez & Pagès (1976) for negative eigenvalues was used as available in Legendre & Legendre (1998), using the "pcoa" function available in the "ape" package (Paradis et al., 2019) of the R version 3.4.4 statistical software (R Core Team, 2016). The PCoA plot was generated using the "ggplot2" and "phyloseq" packages in the R statistical software (McMurdie & Holmes, 2013; Wickham et al., 2020).

## Results

The literature review yielded 240 publications, 137 of which provided occurrence data and were useful for further analyses. Studies ranged from 1867 to 2019 were available in English, Portuguese, Spanish, French, and German languages and covered all six *Ophiothela* species. Only 24 publications were available online between 1867 and 1980. Since then, the number of publications has increased, peaking at nine studies in 2015 and 2016 (Fig. 1). Most papers were published in scientific journals (73%), followed by books (14.6%) and grey literature (12.4%).

A total of 328 occurrence records for the six *Ophiothela* species were obtained from the retained studies in 55 marine ecoregions, 29 provinces, and nine realms worldwide, between 33° S and 38° N. Most occurrence records for this genus were concentrated in three native realms, namely the Tropical Eastern Pacific (32%), Western Indo-Pacific (18.3%), and Central Indo-Pacific (16.5%). *Ophiothela mirabilis* was the only species recognized as introduced or invasive worldwide. Non-native records of this species occurred in two Atlantic realms, the Temperate South America and Tropical Atlantic (represented by 69 records; Fig. 2).

*Ophiothela mirabilis* is the best-documented species ($N$ = 182), although not the most widespread longitudinally. Its distribution includes three marine realms within its native area (Temperate Northern Pacific, Tropical Eastern Pacific, and Eastern Indo-Pacific) and two along its non-native region, as mentioned previously. This species has spread along the coasts of South Florida, the Antilles, French Guiana, and Brazil (Fig. 3a). *Ophiothela danae* was the most widespread species ($N$ = 85), recorded in the Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific, Temperate Southern Africa, and Western Indo-Pacific (Fig. 3a). The other four species exhibited narrower distribution patterns: *O. venusta* ($N$ = 30), *O. tigris* ($N$ = 8), *O. vincula* ($N$ = 3), and *O. gracilis* ($N$ = 2; Fig. 3b).

The association of *Ophiothela* with host organisms was cited by 54.7% of the retained studies, accounting for 280 habitat association records. The host organisms were identified at the genus or species level in 60.3% of these records. From those accurately identified records, the authors reported 89 benthic organisms as hosts for *Ophiothela* species, comprising eight phyla: six benthic macroinvertebrates, one seaweed

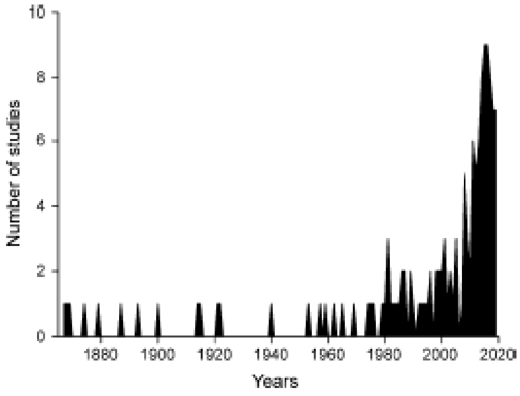

**Fig. 1** Number of studies ($N$ = 137) per year on species belonging to the *Ophiothela* genus according to an electronic survey (see "Methods" section for details)

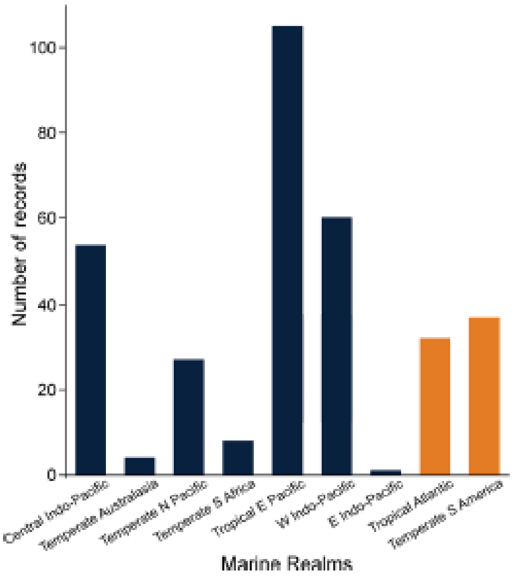

**Fig. 2** Number of occurrence records for *Ophiothela* species ($N$ = 328) in native (dark blue) and non-native (orange) realms

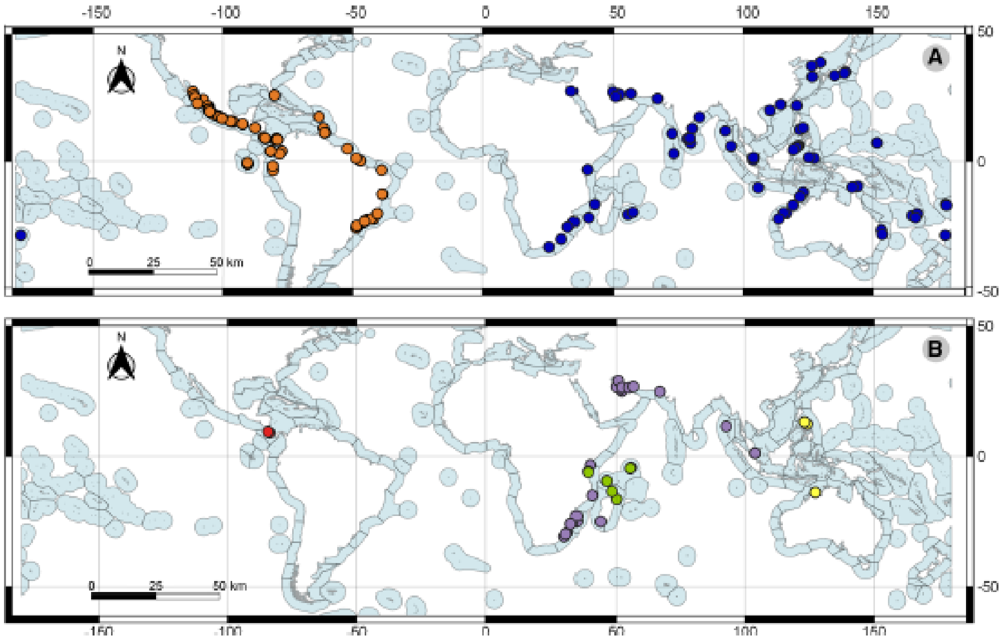

**Fig. 3** World map indicating the distributions of (A) *Ophiothela mirabilis* (*N* = 182, orange circle) and *O. danae* (*N* = 85, blue circle), and (B) *O. gracilis* (*N* = 2, red circle), *O. vincula* (*N* = 3, yellow circle), *O. tigris* (*N* = 8, light green circle) and *O. venusta* (*N* = 30, purple circle)

(Ochrophyta), and one seagrass (Tracheophyta) (Fig. 4). Records of non-native *O. mirabilis* populations indicate associations with 51 host organisms belonging to several taxonomic groups, i.e., Cnidaria, Porifera, Echinodermata, Chordata, Bryozoa, and algae. In contrast, records for native *O. mirabilis* populations revealed only nine benthic host invertebrates, all belonging to Cnidaria and Echinodermata phyla. Only the cnidarian *Carijoa riisei* (Duchassaing & Michelotti, 1860) was colonized by both native and introduced *O. mirabilis*. In native zones, *O. danae* has been recorded in association with the greatest variety of host organisms (*N* = 25), comprising the Cnidaria, Echinodermata, and Mollusca phyla. In contrast, the other *Ophiothela* species colonize only nine hosts, including cnidarians, echinoderms, mollusks, and seagrasses.

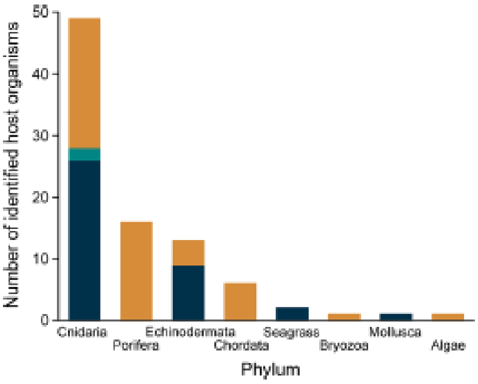

**Fig. 4** Number of identified host organisms per phylum in native areas (dark blue), non-native zones (orange), and both (light blue)

Cnidarians were the most frequent hosts associated with *Ophiothela* species, regardless of the origin of the brittle star populations (i.e., native or non-native) and considering all association records (even those at higher taxonomic levels; Fig. 5). A single study reported artificial structures as colonization substrates for introduced *O. mirabilis*. The first two axes of the

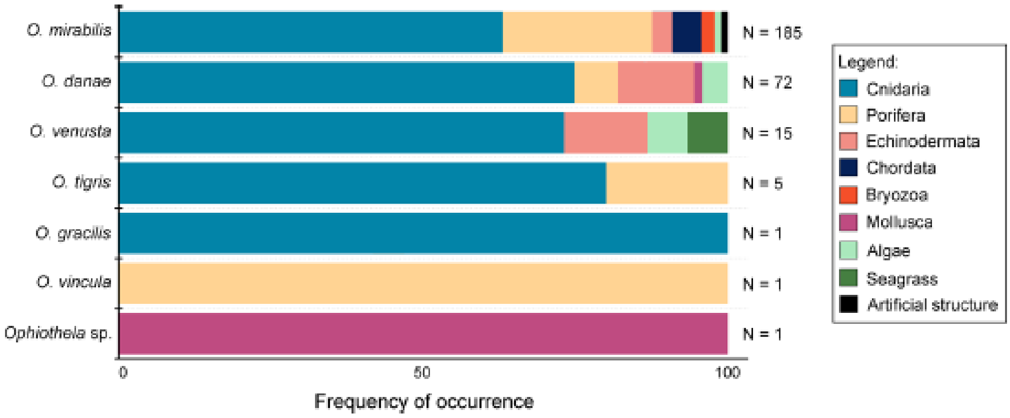

**Fig. 5** Frequency of association of *Ophiothela* species per phylum of host species (*N* = number of association records)

principal coordinates analysis (PCoA) explained 52.4% (trace = 12.98; Fig. 6) of the variability concerning the association of native and introduced *O. mirabilis* populations with host organisms. Introduced *O. mirabilis* was, in general, reported in association with a greater taxa variety of host organisms. Non-native *O. mirabilis* populations colonized benthic organisms that were not occupied by any other *Ophiothela* species in their native region, such as Chordata, Bryozoa, and algae. Still, they were more often associated with Cnidaria and Porifera. In contrast, native *O. mirabilis* populations exhibited associations with fewer groups of host organisms, especially Cnidaria and, at lesser levels, Porifera. Only a single study reported an association between native *O. mirabilis* and Echinodermata.

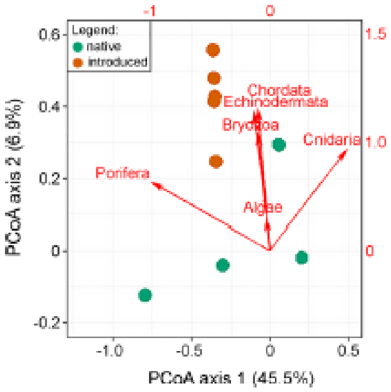

**Fig. 6** Principal coordinates analysis of the presence–absence data of native and introduced *Ophiothela mirabilis* populations on six phyla of host organisms, based on Jaccard distances

## Discussion

This study evaluated the worldwide distribution of all six *Ophiothela* genus species and revealed habitat colonization patterns in native and non-native areas. These species are well-distributed worldwide, with most records concentrated within the intertropical zone of the Indian and Pacific oceans. *Ophiothela danae* is the most widespread species in the Indo-Pacific region, and is associated with the highest variety of host organisms among all native populations. However, non-native populations were recorded for *O. mirabilis* only in two Atlantic Ocean realms. Habitat association records also revealed that these two epibiont brittle stars display a great affinity for cnidarians as colonizing substrates, irrespective of their native or non-native occurrence regions. Our findings highlight the significant plasticity in habitat colonization described for introduced *O. mirabilis* populations in the Atlantic Ocean, indicating that habitat availability may not be a constraint for this species establishment.

Some issues concerning *Ophiothela* species identification are noteworthy. Alitto et al. (2020) raised the hypothesis that *O. danae* is a junior synonym for *O. mirabilis*. However, the authors used only ophiuroids from the Brazilian coast and only few specimens identified as *O. danae* and *O. mirabilis* (including syntypes) for external morphology and COI sequence comparisons. Despite their efforts concerning molecular, morphometric, and morphological comparisons between *O. mirabilis* and *O. danae*, the hypothesis of a single brittle star species should be further investigated through the use of more specimens, gene sequences, and molecular markers before full validation. In addition, the identification of *O. vincula* is unclear since molecular analyses indicate a low genetic divergence between this species and *O. danae*. In this sense, further systematic studies concerning the revision of the *Ophiothela* genus are required to unveil the relationship among brittle star species.

The macro-scale perception on the distribution patterns of *Ophiothela* brittle stars indicates that all the six species comprising the genus are geographically spread across 75% of the world's marine realms. This wide distribution range suggests that *Ophiothela* brittle stars may share the same adaptive zone (as defined for starfish by Blake, 1990). Their lifestyle of living on animals and macroalgae, asexual reproduction (in the case of *O. mirabilis* and *O. danae*), and major morphological features (small disk size, strong hook-shaped spines, streptospondylous arm vertebra articulations, sturdy plates, and radial shields) allow the occupation of a specific niche in the shallow-water marine environment. Only a few other ophiuroid species (e.g., some *Ophiactis* species), which do not live associated with the seafloor and under rocks, share the same adaptive zone as *Ophiothela* (Clark, 1976; Fujita & Namikawa, 2006).

The ability to reproduce by fission, small body size, and epibiont habits combined with their arm morphological structure are key traits that may explain the high invasiveness of *O. mirabilis* in the Atlantic waters. This brittle star can cling tightly to a great variety of benthic species (Verrill, 1867; Clark, 1976; Tahera, 2001), including fouling organisms living on ship hulls and oil platforms, allowing for long distance dispersion (Hendler et al., 2012; Mantelatto et al., 2016; Lawley et al., 2018; Tavares et al., 2019). The distribution of introduced populations throughout a broad geographic Brazilian coast range may thus be associated with a high propagule pressure held by the continuous arrival of new individuals through the increased circulation rates of vessels and oil platforms in this region (Ferreira et al., 2009). Natural dispersal by rafting on algae or animal fragments may also occur (Hendler & Brugneaux, 2013; Araújo et al., 2018). However, it is quite unlikely that this pathway could carry large numbers of individuals and lead to significant contributions to the high detected densities of *O. mirabilis*. For example, Tavares et al. (2019) registered large aggregations of this brittle star (1.78 ± 0.63 specimens $mL^{-1}$ per sponge) at the Rio de Janeiro coast (22° S), Brazil. Ferry et al. (2020) also recorded high densities (2.8 brittle stars.$cm^{-2}$) of *O. mirabilis* on the surface of the cnidarian *Gorgonia ventalina* at Martinique Island. Since *O. mirabilis* exhibits a planktonic larva, it is also possible that dispersal may occur naturally or artificially through ballast water (Mantelatto et al., 2016; Araújo et al., 2018). Some authors have reported similar dispersal mechanisms for other ophiuroids with similar features, such as *Ophiactis savignyi* (Müller & Troschel, 1842) (Hendler, 1991; Roy & Sponer, 2002; Hendler & Brugneaux, 2013). However, gaps in understanding the sexual reproduction of *O. mirabilis* are still noted (Hendler & Brugneaux, 2013; Mantelatto et al., 2016). Tavares et al. (2019) reported no trace of gonads or recently settled juveniles in two *O. mirabilis* populations on the Southeastern Brazilian coast. The primary *O. mirabilis* dispersal mechanism seems to be associated with fouling communities in vessels. Therefore, the wide distribution range of the *Ophiothela* genus as a whole may be an important supply for the multiple sources of worldwide introduction of *O. mirabilis* and its congeners due to the high circulation of trade and tourism vessels.

Since the presence of suitable colonization substrates is one of the main ecological requirements for *Ophiothela* brittle star survival, this issue seems to be crucial for the transport, introduction, and establishment of *O. mirabilis* in new habitats. Non-native *O. mirabilis* populations exhibit remarkable plasticity concerning habitat colonization. Host taxa in the introduced area were more numerous and distributed across different taxonomic groups than native populations and concerning their congeners in the Indo-Pacific waters. However, this pattern might be an artifact from the level of host identification used by each study. In general, host identification was performed at a higher level than genus and species (mainly, Cnidaria, and Porifera) in native *Ophiothela* brittle star regions. Therefore, further studies focusing on substrate colonization by *Ophiothela* species at high host organism taxonomic resolution (at the genus or species level) are necessary. According to our findings, investigations concerning if *O. mirabilis* can colonize non-living substrates, which was mentioned by a single study, are also relevant. Bumbeer & Rocha (2016) reported the association of this brittle star with artificial structures in a port area in Southern Brazil (25° S), but whether *O. mirabilis* specifically colonized the artificial structures themselves or benthic organisms living on these structures remains unclear. If *O. mirabilis* does not depend on living organisms to survive, the chance for its establishment in coastal communities is significantly increased.

Most records concerning host–*Ophiothela* associations indicate a greater affinity of these brittle stars for cnidarians during colonization processes, regardless of the occurrence area. *Carijoa riisei* was the single host species identified in both native and non-native regions, and the most frequent host recorded on the Brazilian coast (23° S; Mantelatto et al., 2016). The availability of the same colonizing habitat in both regions may also assist in *O. mirabilis* invasion, due to its presumably evolutionary affinity with this kind of substrate. Furthermore, this cnidarian might carry brittle stars worldwide since it is often found as a fouling species in ship hulls. Although a mutual advantage is one of the possible relationships between *O. mirabilis* and its hosts (Clark, 1976; Mosher & Watling, 2009), some degree of host damage may occur due to the massive colonization found for this invader in non-native areas. Some studies suggest that ophiuroids may impair the protraction of host feeding structures, increase the total weight of the colonized organisms, and even deflect water currents over filter-feeding invertebrates (Mantelatto et al., 2016; Ferry et al., 2020). Ascertaining host-invader affinity is key to predict which benthic organisms would be most affected by the high densities of *O. mirabilis* in non-native areas. An experimental study also described that chemical substances produced by the gorgonian *Phyllogorgia dilatata* (Esper, 1806) exert a positive chemotaxis upon *O. mirabilis* (Ribeiro et al., 2017). Thus, further studies are required to unveil the relationship between *Ophiothela* species and their hosts, especially to validate the hypothesis of adverse brittle star impacts on host organisms in invaded areas.

In addition to depict the global distribution pattern of the *Ophiothela* genus, our literature review also allowed us to highlight specific knowledge gaps concerning the invasiveness potential and host affinity of its six brittle star species. The *Ophiothela* genus is still poorly studied, although the number of publications on these species has increased over time. Most publications merely reported *Ophiothela* brittle stars in a given region, while about half mentioned their association with host species. However, ecological interactions and population attributes, such as ophiuroid density or abundance in their native area, are virtually absent from the literature (see James, 1995; Kumagai & Aoki, 2003; Hernández, 2014; Purcell & Eriksson, 2015). *Ophiothela* species were not even the main focus in studies performed in native regions. On the other hand, most investigations performed in non-native regions focused only on the biological features of *O. mirabilis* (e.g., Mantelatto et al., 2016; Tavares et al., 2019). Our review highlights the lack of information on the geographical distribution, population dynamics, and ecological requirements of *Ophiothela* species. These subjects are essential to unveil the life-history traits of these species, which is especially important considering the possible negative impacts of *O. mirabilis* introduction on the native Atlantic biota.

This study is the first effort to summarize the main *Ophiothela* genus distribution and host organism colonization patterns worldwide. We emphasize the high invasive potential of this genus, even if only *O. mirabilis* colonization in the Atlantic Ocean has been assessed so far. Further information on the *Ophiothela* genus population structure and dynamics, functional role in ecosystems, and ecological requirements is sorely needed to confirm the occurrence of adverse impacts. Therefore, broadening the ecological knowledge on *Ophiothela* brittle stars is crucial to formulate effective strategies for native biota preservation and monitor the spread of non-native *O. mirabilis* populations to other areas, both throughout the Atlantic Ocean and in other regions.

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**Authors' contributions** MRT, ACSF, and LNS contributed to the study conception. The literature search and data analysis were performed by MRT and ACSF. The first draft of the manuscript was written by MRT and ACSF, CRRV, and LNS

commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data Availability** The dataset analyzed during the current study was built with data retrieved from the Web of Science, Scopus, and Google Scholar electronic databases. All publications analyzed are listed in the Appendix in Supplementary Material. Further information will be made available from the corresponding author upon reasonable request.

## Compliance with ethical standards

**Conflict of interest** The authors declare they do not have any conflict of interest.

**Informed Consent** All authors consent to participate of this publication.

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**APÊNDICE B - **Material suplementar do artigo “Geographic distribution of *Ophiothela* brittle stars (Echinodermata: Ophiuroidea): substrate use plasticity and implications for the silent invasion of *O. mirabilis* in the Atlantic” publicado no periódico *Hydrobiologia* em 2021.

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**APÊNDICE C -** Material suplementar submetido com o manuscrito “Beyond the hosts: the role of water variables in predicting ecologically suitable areas for an invasive brittle star” ao periódico *Biological Invasions* em 2022.

Table 6 – Number of association records of *Ophiothela mirabilis* with Porifera and Cnidaria hosts in the native (Indo-Pacific Ocean) and in the non-native (Atlantic ocean) occurrence areas. The host genera with more than 5% of association records are highlighted in bold.

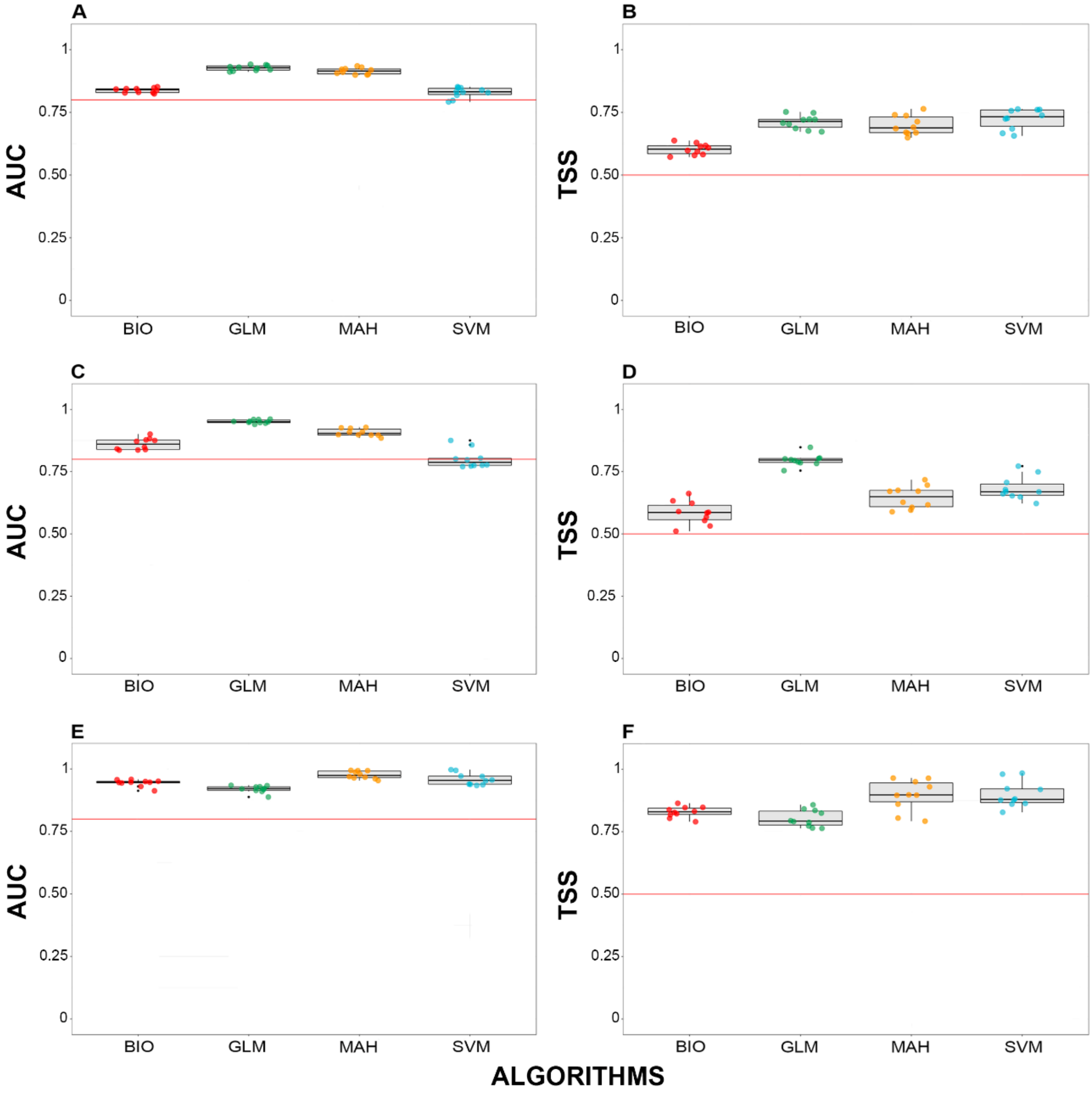
| Host genus | Nº records in the native area | Nº records in the invaded area | Nº total records | Relative frequency (%) |
|---|---|---|---|---|
| **Porifera** | | | | |
| *Amphimedon* | 0 | 3 | 3 | 2.6 |
| *Aplysilla* | 0 | 1 | 1 | 0.9 |
| ***Aplysina*** | 0 | 6 | 6 | **5.3** |
| ***Callyspongia*** | 0 | 10 | 10 | **8.8** |
| *Chelonaplysilla* | 0 | 3 | 3 | 2.6 |
| *Chondrosia* | 0 | 2 | 2 | 1.8 |
| *Clathria* | 0 | 2 | 2 | 1.8 |
| ***Clathrina*** | 0 | 11 | 11 | **9.6** |
| *Darwinella* | 0 | 2 | 2 | 1.8 |
| ***Desmapsamma*** | 0 | 12 | 12 | **10.5** |
| *Dysidea* | 0 | 8 | 8 | **7** |
| *Echinodictyum* | 0 | 1 | 1 | 0.9 |
| *Haliclona* | 0 | 1 | 1 | 0.9 |
| *Hymeniacidon* | 0 | 2 | 2 | 1.8 |
| *Iotrochota* | 0 | 4 | 4 | 3.5 |
| *Ircinia* | 0 | 3 | 3 | 2.6 |
| ***Monanchora*** | 0 | 6 | 6 | **5.3** |
| ***Mycale*** | 0 | 23 | 23 | **20.2** |
| *Niphates* | 0 | 3 | 3 | 2.6 |
| *Polymastia* | 0 | 3 | 3 | 2.6 |
| *Scopalina* | 0 | 4 | 4 | 3.5 |
| *Siphonochalina* | 0 | 1 | 1 | 0.9 |
| *Tedania* | 0 | 3 | 3 | 2.6 |
| **Total** | **0** | **114** | **114** | |
| | | | | |
| **Cnidaria** | | | | |
| *Annella* | 1 | 0 | 1 | 0.8 |
| *Anthoplexaura* | 1 | 0 | 1 | 0.8 |
| ***Antillogorgia*** | 0 | 8 | 8 | **6.3** |
| *Astrogorgia* | 2 | 0 | 2 | 1.6 |
| ***Carijoa*** | 1 | 8 | 9 | **7.**1 |
| *Ctenocella* | 1 | 0 | 1 | 0.8 |
| *Dendronephthya* | 1 | 0 | 1 | 0.8 |
| *Dentitheca* | 0 | 1 | 1 | 1 |
| *Echinogorgia* | 1 | 0 | 1 | 0.8 |
| *Echinomuricea* | 1 | 0 | 1 | 0.8 |
| ***Eunicea*** | 0 | 10 | 10 | **7.9** |
| *Euplexaura* | 1 | 0 | 1 | 0.8 |
| ***Gorgonia*** | 4 | 10 | 14 | **11.1** |
| *Heterogorgia* | 0 | 2 | 2 | 1.6 |
| ***Leptogorgia*** | 11 | 12 | 23 | **18.3** |
| *Melithaea* | 4 | 0 | 4 | 3.2 |
| ***Millepora*** | 3 | 6 | 9 | **7.1** |

| | | | | |
|---|---|---|---|---|
| ***Muricea*** | 6 | 2 | 8 | **6.3** |
| *Muriceopsis* | 0 | 1 | 1 | 0.8 |
| ***Pacifigorgia*** | 8 | 0 | 8 | **6.3** |
| *Palythoa* | 0 | 2 | 2 | 1.6 |
| *Parazoanthus* | 0 | 1 | 1 | 0.8 |
| *Phyllogorgia* | 0 | 1 | 1 | 0.8 |
| *Plexaura* | 0 | 1 | 1 | 0.8 |
| *Plexaurella* | 0 | 1 | 1 | 0.8 |
| *Pocillopora* | 1 | 0 | 1 | 0.8 |
| *Pseudoplexaura* | 0 | 1 | 1 | 0.8 |
| *Pteroeides* | 1 | 0 | 1 | 0.8 |
| *Pterogorgia* | 0 | 2 | 2 | 1.6 |
| *Samogorgia* | 1 | 0 | 1 | 0.8 |
| *Solenocaulon* | 3 | 0 | 3 | 2.4 |
| *Subergorgia* | 3 | 0 | 3 | 2.4 |
| *Verrucella* | 2 | 0 | 2 | 1.6 |
| **Total** | **57** | **69** | **126** | |

Table 7 - Importance coefficient of the abiotic variables extracted from the models generated by the GLM and SVM algorithms from all available *Ophiothela mirabilis'* occurrence records (native and non-native), and for native and non-native occurrence data apart. SST = Sea Surface Temperature.

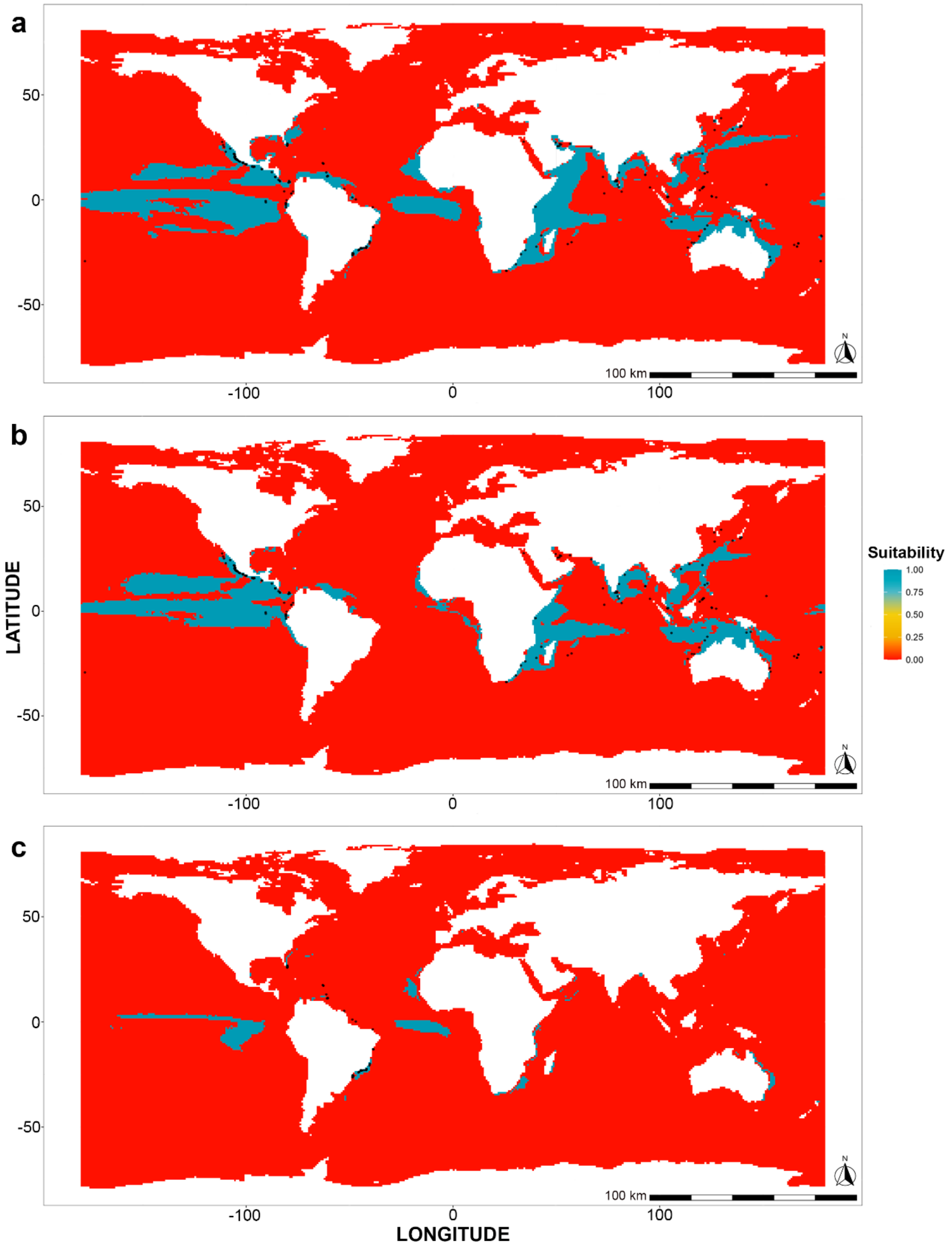
| **Seawater variables** | **Importance coefficient** | | |
|---|---|---|---|
| | All data | Native records | Non-native records |
| GLM | | | |
| Salinity | -0.12727507 | 1.3081532 | 1.3249254 |
| Calcite (mol.m$^{-3}$) | -5.36175444 | -0.3708364 | 0.4564727 |
| Mean SST (ºC) | 0.03498477 | 1.4528479 | 1.9683374 |
| Dissolved oxygen (mol.m$^{-3}$) | -0.07866044 | 0.2365243 | 0.3595088 |
| Chlorophyll-a (mg.m$^{-3}$) | 1.82465649 | -8.1122402 | -13.3190170 |
| SST range (ºC) | 0.16384463 | 0.5144381 | 0.5766670 |
| Primary productivity (g.m$^{-3}$.day$^{-1}$) | 63.80400287 | 428.1071628 | 447.4433439 |
| SVM | | | |
| Salinity | 0.29799254 | 0.21115312 | 0.13797967 |
| Calcite (mol.m$^{-3}$) | 0.21037770 | 0.09377883 | 0.08908023 |
| Mean SST (ºC) | 0.11534603 | 0.06166126 | 0.04304689 |
| Dissolved oxygen (mol.m$^{-3}$) | 0.10269346 | 0.13144612 | 0.18395539 |
| Chlorophyll-a (mg.m$^{-3}$) | -0.03801708 | 0.07478338 | 0.09732678 |
| SST range (ºC) | 0.08490503 | 0.05828249 | 0.06401953 |
| Primary productivity (g.m$^{-3}$.day$^{-1}$) | 0.15066817 | 0.36889481 | 0.38459152 |

Figure 20 – The area under the curve (AUC) and the true skill statistic (TSS) values for models predicted from *Ophiothela mirabilis* occurrence data.



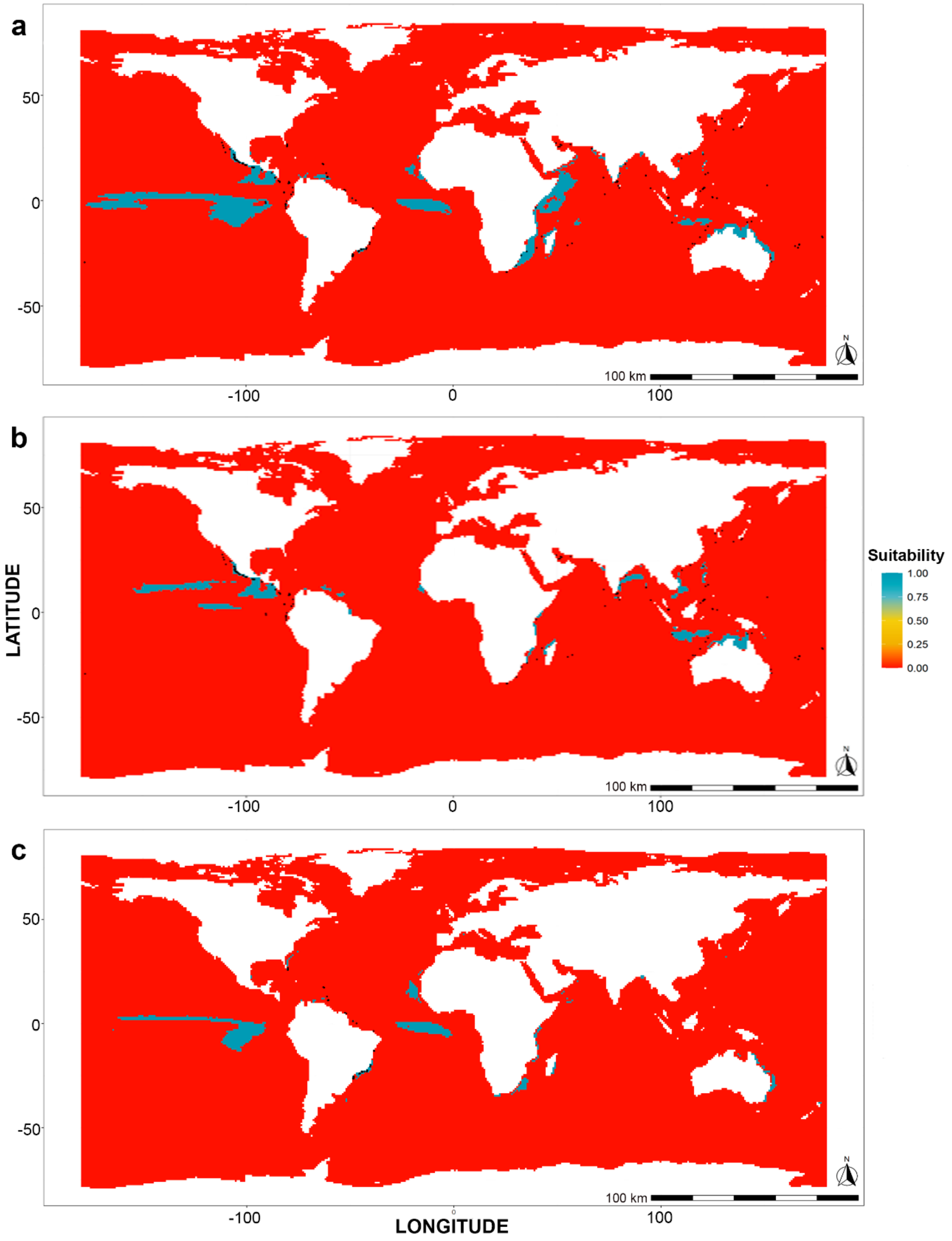
Legend: (A and B) Performance indexes for all *Ophiothela mirabilis* available data, (C and D) for only native records, and (E and F) for only non-native records.

Figure 21 - Binary maps of ensemble models of areas with 75% environmental suitability predicted from the ecological niche modeling of *Ophiothela mirabilis* with occurrence data from native and non-native range, only native records and only non-native records. The ensemble models are based on the BIOCLIM, Mahalanobis distance, GLM and SVM predictions.



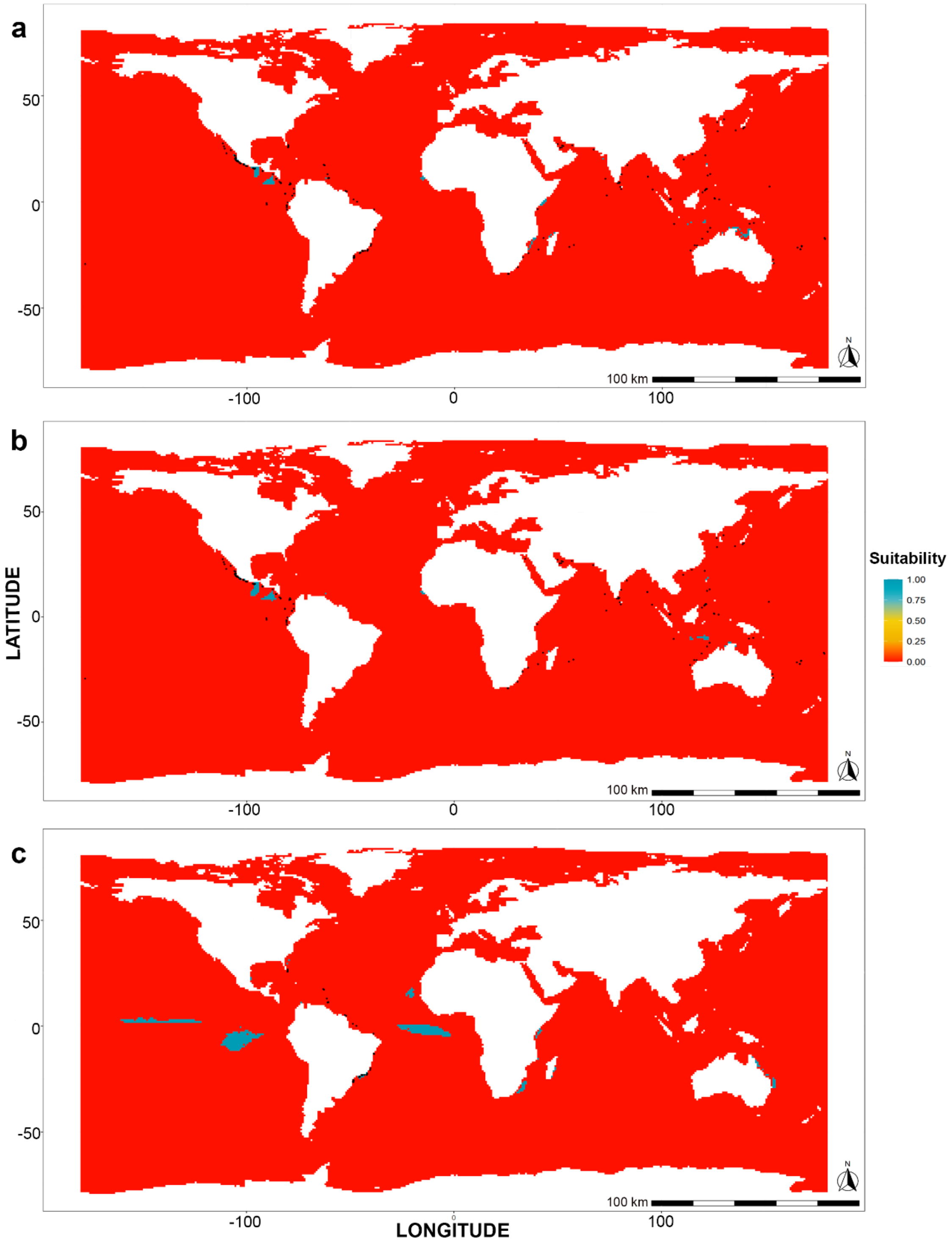
Legend: Binary maps were generated using (a) *Ophiothela mirabilis* occurrence data from native and non-native range, (b) only native records and (c) only non-native records.

Figure 22 - Binary maps of ensemble models of areas with 50% environmental suitability predicted from the ecological niche modeling of *Ophiothela mirabilis* with occurrence data from native and non-native range, only native records and only non-native records. The ensemble models are based on the BIOCLIM, Mahalanobis distance, GLM and SVM predictions.



Legend: Binary maps were generated using (a) *Ophiothela mirabilis* occurrence data from native and non-native range, (b) only native records and (c) only non-native records.

Figure 23 - Binary maps of ensemble models of areas with 25% environmental suitability predicted from the ecological niche modeling of *Ophiothela mirabilis* with occurrence data from native and non-native range, only native records and only non-native records. The ensemble models are based on the BIOCLIM, Mahalanobis distance, GLM and SVM predictions.



Legend: Binary maps were generated using (a) *Ophiothela mirabilis* occurrence data from native and non-native range, (b) only native records and (c) only non-native records.

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**Occurrence records of the Cnidaria and Porifera host genera were downloaded from the following references available in the Global Biodiversity Information Facility (GBIF) database:**

Porifera:

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https://doi.org/10.15468/dl.wyg4er

*Callyspongia* - GBIF.org (04 March 2022) GBIF Occurrence Download

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*Haliclona* - GBIF.org (21 February 2022) GBIF Occurrence Download

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Cnidaria:

*Antillogorgia* - GBIF.org (04 March 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.36hq7k

*Carijoa* - GBIF.org (05 March 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.qmtxmu

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