



Distribution patterns and habitat suitability of the non-native brittle star *Ophiothela mirabilis* Verrill, 1867 along the Western Atlantic

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ABSTRACT

The Pacific epizoic brittle star *Ophiothela mirabilis* Verrill, 1867 has successfully established itself along the Southwestern Atlantic. While reports of this species show high densities and an expanding range throughout the Western Atlantic, specific knowledge regarding populations and their potential for distribution is scarce. We assess herein the current distribution and abundance patterns of *O. mirabilis* along the subtropical SW Atlantic coast while simultaneously employing ecological niche models (ENMs) to predict suitable habitats in the future. *Ophiothela mirabilis* is currently distributed in both poly- and euhaline estuarine and inner continental shelf areas. Population densities tend to increase from the inner shelf (≤ 492 individuals.m⁻²) to estuarine habitats (≥ 815 individuals.m⁻²), characterized by a 53.38% mean habitat suitability index, until being limited by unsuitable environmental habitats. Octocoral species are the most densely and frequently colonized hosts (up to 3.6 individuals.cm⁻² of host's area). Currently, occurrence records for *O. mirabilis* encompass disjunct habitats from Santa Catarina (S Brazil) to Southeast Florida (USA). Our ENMs predicted that *O. mirabilis* has the potential to further spread across the warm marine provinces of the Western Atlantic, as they are characterized by $\geq 40.72\%$ of environmentally suitable habitats. The occurrence of the species correlates mainly to mean calcite concentration and mean sea surface temperature, which accounts for 56.97% of the performance of the ENMs. The high spreading capacity and the maintenance of dense abundances on hosts raises questions about its effects on recipient biodiversity and systems.

1. Introduction

The brittle star *Ophiothela mirabilis* Verrill, 1867 is epizoic, colonizing mainly ascidians, bryozoans, octocorals, sponges and zoanthids in both natural and artificial hard-substrates (Bumbeer and da Rocha, 2016; Mantelatto et al., 2016). High population densities are often reported on these hosts in Atlantic communities (Hendler et al., 2012; Lawley et al., 2018; Mantelatto et al., 2016; Tavares et al., 2019), although abundance and distribution patterns in the recipient systems have not been systematically assessed. Individuals of *O. mirabilis* undergoing fission are common, which might be related to a metabolic strategy that opts for asexual reproduction, contributing to the maintenance of dense populations (Tavares et al., 2019). It has been hypothesized that high brittle-star densities can cause negative effects on hosts, such as the obstruction of feeding structures and polyp extension, restriction of water flow or being subjected to increased trailing forces (Mantelatto et al., 2016). In contrast, histological analyses of octocoral host tissue indicated no direct impacts from *O. mirabilis* (Rich et al.,

2020). Recently, the decline in abundance of an epizoic ctenophore species in Southeast Florida, USA was simultaneously followed by the introduction and increasing densities of *O. mirabilis* (Glynn et al., 2019). Unfortunately, experimental studies are still needed to assess negative host responses to the non-native brittle star.

Ophiothela mirabilis is native from the Pacific (Clark, 1976), but has successfully established itself in Atlantic habitats. The first occurrence reported in the Atlantic was in Rio de Janeiro (SE Brazil) in 2000 (Hendler et al., 2012). Since then, *O. mirabilis* has been recorded in Bahia (NE Brazil), São Paulo (SE Brazil), Espírito Santo (SE Brazil) and Paraná (S Brazil) between 2004 and 2009 (Hendler et al., 2012). Distribution records were later expanded between 2011 and 2014 to Santa Catarina (S Brazil; Lawley et al., 2018), Pernambuco (NE Brazil; Mantelatto et al., 2016), Ceará (NE Brazil; Araújo et al., 2018), Amazon reefs (N Brazil; Moura et al., 2016), French Guinea, Tobago (Hendler and Brugneaux, 2013) and St. Vincent (Hendler et al., 2012). Since then, the Atlantic distribution has progressed to St. Kitts (Rich et al., 2020), Martinique (Ferry et al., 2020) and Southeast Florida (USA; Glynn et al., 2019), the

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northernmost record up until now.

Ecological niche models (ENMs), based on the association between occurrence records and environmental variables, have become a relevant tool in identifying the ecological requirements of species (Austin et al., 2019; Hemery et al., 2016), while predicting the potential distribution of non-native species over wide spatial areas (Carlos-Júnior et al., 2015; Laeseke et al., 2020; Lins et al., 2018; Pinochet et al., 2019; Riul et al., 2013). The fundamental niche is the set of environment variables that a species can theoretically survive and reproduce, while the realized niche additionally takes biotic interactions into account (Soberón and Nakamura, 2009). Although the concepts of ENMs and species distribution models (SDMs) are often interchangeable, recent literature has seen them as two distinct approaches (Feng et al., 2019; Melo-Merino et al., 2020). While ENMs often predict the fundamental niches, and is commonly applied to the dispersion potential of invasive species, SDMs attempt to estimate the actual geographic distributions of species. By integrating correlative approaches and the functional traits of biotic interactions, the ENMs may reveal a reliable realized niche (Kearney and Porter, 2009).

One of the many implications of global shipping is the dispersion of non-native species beyond their native range by means of ship hulls or ballast water (Seebens et al., 2013). Estuaries are one of the many types of coastal ecosystems vulnerable to these biological invasions given their proximity to ports, often seen as hotspots for invasion (de Frehse et al., 2016). The Paranaguá Estuary Complex, one of the largest and most preserved estuaries on the Brazilian coast, is also one of the most important port regions of Latin America. At least 19 non-native benthic invertebrate species have been recorded in this subtropical estuarine

system and in nearby areas (Bumbeer and da Rocha, 2016). Their presence is often attributed to local port activities (Bumbeer and da Rocha, 2016). Shipping activity is likely also the vector responsible for introducing *O. mirabilis* along the Western Atlantic based on its disjunct occurrence records (Hendler and Brugneaux, 2013). Local dispersion may also occur along coastal habitats through the rafting of individuals in ocean currents (Hendler and Brugneaux, 2013). However, there is no evidence of recruitment through larval settlement (Tavares et al., 2019).

Considering that *O. mirabilis* may change the appearance of hard-bottom systems (Hendler et al., 2012), our study carries out an *in situ* assessment of its current distribution and abundance patterns, estimating densities on habitats and host species across a range of coastal habitats of a subtropical sector of the Western Atlantic. We additionally identify ecologically suitable habitats on larger spatial scales to predict future spreading events in the Western Atlantic using ENMs. By combining *in situ* surveys and ENMs, we attempt to predict the abundances found in the smaller-scale sampling through the habitat suitability index of our ENMs.

2. Materials and methods

2.1. Distribution and abundance patterns along a subtropical coast (Paraná, S Brazil)

2.1.1. Study area

The inner continental shelf of the Paraná subtropical coast is formed predominantly by unconsolidated bottoms, with rocky shores scattered around islands (Fig. 1). A well-marked seasonal hydrographic regime

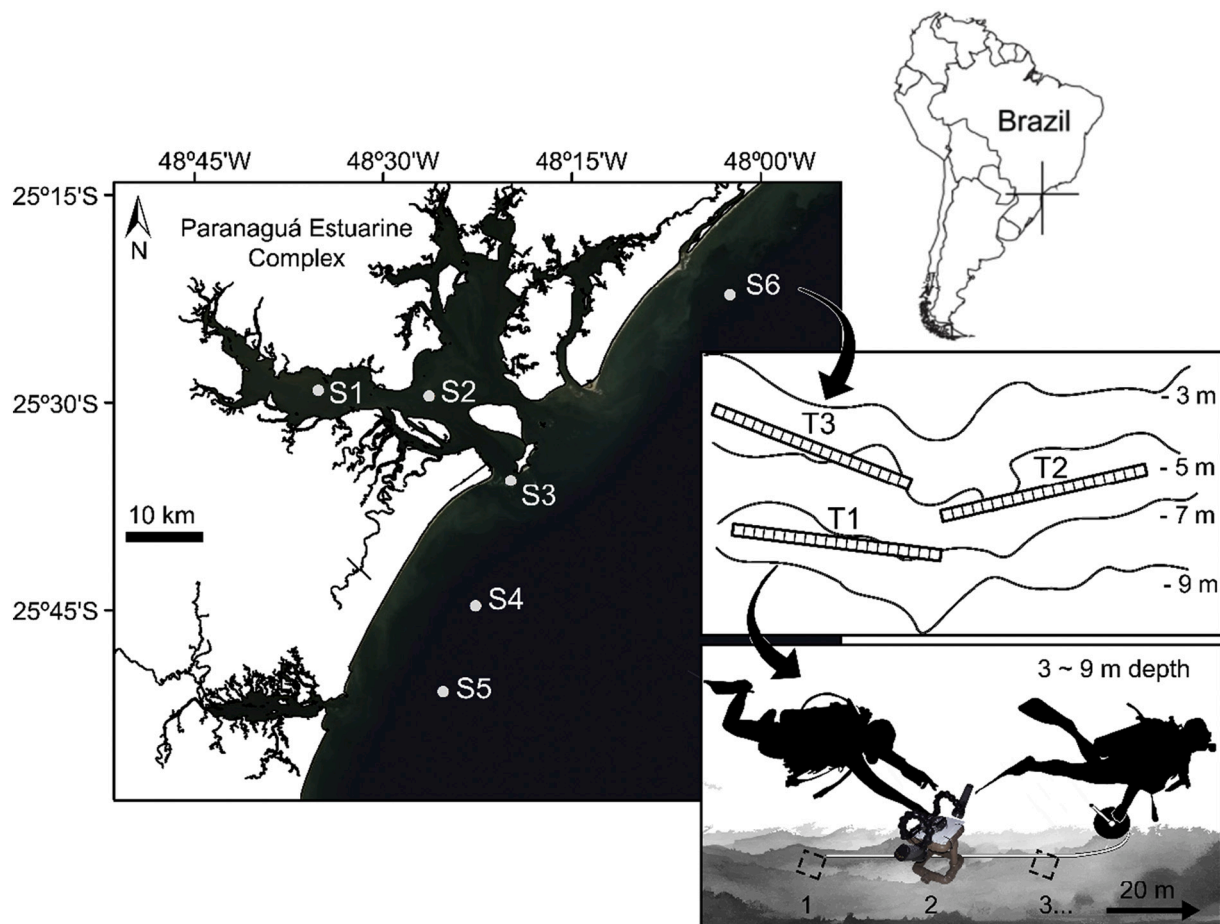


Fig. 1. Map of the Paraná coast, in southern Brazil, showing the six sampling sites; S1, S2, and S3 corresponding to the meso-, poly- and euhaline estuarine sectors, respectively, and S4, S5 and S6 corresponding to the inner shelf sectors. In each site, three randomly 20 m linear transects were set between 3 and 9 m deep in natural rocky substrates. Throughout all transects, photoquadrats (0.01 m²) of the substrate were taken every meter and up to the distance of 1 m on each side of the transect.

characterizes the region. The water column is warm and stratified during November and March, while it is cold and homogeneous for the rest of the year, with temperatures ranging between 17.6 °C to 29.6 °C and salinities from 28.4 to 37.5 (Brandini et al., 2007). The Paranaguá Estuary Complex, the largest estuary on the Paraná coast (Angulo et al., 2016), is surrounded by mangroves, marshes, sandbanks and occasionally rocky shores (Lana et al., 2001). Its water body is categorized into sectors according to salinity: euhaline, with salinity similar to that in the inner shelf; polyhaline, with moderate values; or meso- and oligohaline, having the highest freshwater inputs (Lana et al., 2001).

2.1.2. Sampling design and field procedures

A spatially hierarchical design was used for underwater sampling conducted by SCUBA diving along random transects. Surveys were conducted between January and April 2018. Transects were set up at six sites, distanced in the scale of kilometers, with an average of 15 km apart: S1, S2 and S3 correspond to meso-, poly-, and euhaline estuarine sectors, respectively; while S4, S5 and S6 correspond to the inner continental shelf (Fig. 1). Local names and geographical coordinates are as follows: S1, Gererê Island (25.4809°, -48.5817°); S2, Cobras Island State Park (-25.4803°, -48.4329°); S3, Galheta Island (-25.5853°, -48.3239°); S4, National Marine Park of Currais Islands (-25.7365°, -48.3670°); S5, Itacolomi Island (-25.8412°, -48.4077°); and S6, Figueira Island (-25.3564°, -48.0381°).

At each site, three random 20-m linear transects, 15 m apart on average, were set between 3 and 9 m deep in natural rocky bottoms. The length of the transects was adapted from Bumbeer et al. (2016) and was determined by the features of the regional subtropical shores. Throughout the transects, photoquadrats (10 × 10 cm, corresponding to 0.01 m²) of the substrate were taken at every meter and up to a distance of 1 m on each side of the transect. Thus, in total, 360 photoquadrats were collected and analyzed, covering 18 transects and six sites (Fig. 2). The ideal area of the photoquadrats was previously defined based on the size of *O. mirabilis*, which shows a lobulated disk ranging from 1.3 to 4.3 mm (Granja-Fernández et al., 2014). Horizontal and vertical substrate photographs had a 7 MP resolution, and were taken using a GoPro Hero 3 Black coupled with macro lens and two flashlights. The distance between the lens and substrate was fixed at 15 cm. Once photographed, all observed host species were systematically recorded or collected when their identification *in situ* was not possible. All collected material was stored individually in numbered plastic bags and treated with menthol solution in seawater, then fixed in the field using 4% formaldehyde.

2.1.3. Processing of images and data

Photoquadrats were analyzed using PhotoQuad© software (Trygonis and Sini, 2012) to determine: a) Population density of *O. mirabilis* expressed by the number of individuals per 0.01 m² of substrate; b) Occurrence frequency of *O. mirabilis* estimated by its presence or absence in each sample unit, expressed in percentages; c) Coverage rate

of *O. mirabilis* estimated by the overlap of 40 random pixels in the photoquadrats, expressed in percentage; and d) Density of *O. mirabilis* per host species, estimated by the number of individuals per coverage host area and expressed by the number of individuals per cm² of the host. These four dependent variables were grouped by sites for the subsequent analyses of significance.

2.1.4. Data analysis

The assessment of the significance of dependent variables of population density, occurrence frequency, and coverage rate of *O. mirabilis* was analyzed applying general linear regression models (GLMs; Zuur et al., 2007), adjusting them to the predictor variables of host species and sites. We applied the negative binomial as the probability distribution family and compared the models using the Akaike Information Criterion (AIC). Differences with the *post hoc* test of general linear hypotheses (GLHT) were further identified. The statistical analysis and graphs were generated using the R environment and programming language (R Development Core Team, 2020). To produce an improved visualization of the spatial variability of *O. mirabilis* for the subtropical coast studied, we constructed a bubble chart with the population densities of *O. mirabilis* extrapolated to m².

2.2. Ecological niche models for the Western Atlantic

2.2.1. Species occurrence records

By using all available occurrence records, we can generate a more realistic ENMs of the invasive species (Jiménez-Valverde et al., 2011). We extracted occurrence records for *O. mirabilis* from two databases, Global Biodiversity Information Facility (GBIF – <http://www.gbif.org/>) and Ocean Biogeographic Information System (OBIS – <http://www.iobi.org/>) on May 29, 2020, from peer-reviewed articles and from our study (Table A1). We used 234 occurrence records of *O. mirabilis* from 1950 to the present day, with 134 corresponding to the Indo-Pacific, 63 to the Eastern Pacific and 37 to the Atlantic (Fig. 3). Duplicate occurrence records or coordinates without environmental variable data were eliminated. We used reference WGS-84 for the geographic coordinates of the occurrence records. Recently, a combined integrative taxonomic study provided evidence that *Ophiethela danae* Verrill, 1869 can be considered as a junior synonym of *O. mirabilis* (Alitto et al., 2020), which significantly increased the distribution range we considered for this analysis.

2.2.2. Environmental variables

Environmental variables were extracted from the Bio-ORACLE v2.0 database (Assis et al., 2018). Only influential environmental variables towards species survival and fundamental niche requirements were selected (Jiménez-Valverde et al., 2011). We selected for the range and mean sea surface temperature (SST), mean salinity, mean calcite concentration, mean pH and mean chlorophyll concentration at maximum

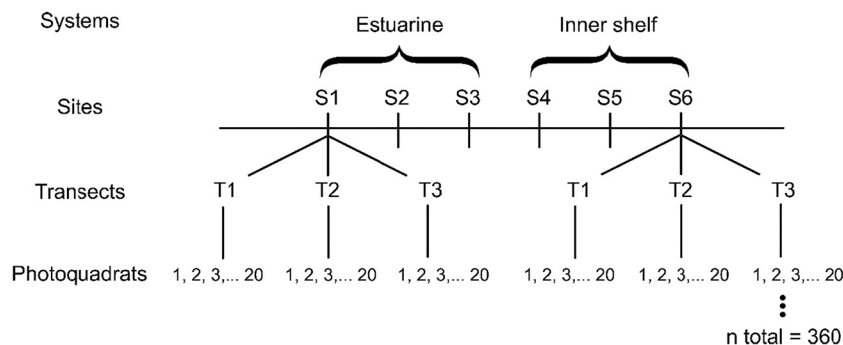


Fig. 2. Spatial hierarchical sampling design adopted in this study. In total, 360 photoquadrats were obtained and analyzed, covering 18 transects distributed in estuarine and inner shelf sites.



Fig. 3. Non-native occurrence records of the brittle star *Ophiothela mirabilis* in the Atlantic are indicated by red circles. All biogeographic provinces (distinct colors) with ecoregion boundaries are outlined according to Spalding et al. (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

depth. We investigated the collinearity and the multicollinearity between the environmental variables by evaluating the Pearson's coefficient and variance inflation factor (VIF), following rule-of-thumb thresholds $|r| > 0.5$ and $|r| > 10$, respectively (Table A2).

To reduce the effects of unequal sampling of a species' distribution, occurrences were limited to one per grid cell of 5 arcmin, that represents 0.08° or 9.2 km at the equator (Assis et al., 2018). Environmental variables represent mean annual estimates from both satellite and *in situ* observations, collected between 2000 and 2014 (Assis et al., 2018). Layers of coastlines, rivers, national boundaries and state boundaries within South and North America were used from Wessel and Smith (1996).

2.2.3. Ecological niche modelling

Values for each of the environmental variables were extracted from the pixels of each occurrence record. We selected 7000 random pixels in geographic space that did not hold a species occurrence record for the geographical background in each model. The number of background records (pseudo-absences) was based on the spatial extent of the study area and our computational capacity (Barbet-Massin et al., 2012; Feng et al., 2019). All models were fitted with maximum entropy (MaxEnt), generalized additive model (GAM) and support vector machine (SVM) using the R package 'sdm' version 1.0–82 (Naimi and Araújo, 2016). GAM is a statistical method, while MaxEnt and SVM are both machine-learning methods. Occurrence records were restricted to 70% for training and 30% for testing. We performed 70 replications per method

using the bootstrapping procedure from training data.

One challenge in ENMs is to choose the appropriate statistical model across all the different methods and assumptions, finding one that most reliably represents niche requirements and consequently the potential dispersion of the species. A good way to do this is by performing an ensemble of predictions from multiple ENMs approaches (Araújo and New, 2007). Therefore, our 210 models were generated and combined by the weighted average ensemble procedure using true skill statistics (TSS) and calculated from training data, which generated continuous result model set maps with combinations of the best predictive performances of the algorithms. Occurrence records intended for testing were used to evaluate model set performance through independent (area under the curve – AUC) and threshold dependent measures (TSS). AUC values close to 1 indicate good adjustments, while values below 0.5 indicate worse than random performance. TSS values close to 1 also indicate good adjustments, while values below 0 indicate worse than random performance.

2.2.4. Predicting the realized niche

Considering that *O. mirabilis* is an epizoic species with a strong interaction with their hosts, the availability of host species is a crucial factor for its potential distribution. The absence of records and information in the literature about predation may indicate that it is not a limiting factor for the brittle star dispersion. As well, interspecific competition in the recipient systems apparently does not constraints its spread. Therefore, we attempt to predict the realized niche of *O. mirabilis* by overlapping the extend of the predicted fundamental niche of the brittle star and the main hosts.

Except for the occurrence records that were extracted only from GBIF and OBIS on November 23, 2020, the same steps above of ENMs of *O. mirabilis* were applied to the main host species. Binary maps of suitable habitats for the main host species were predicted from the average thresholds of maximum specificity and sensitivity. The ENMs of *O. mirabilis* were overlapped on the hosts, and its percentage was calculated. Finally, we calculated the similarity of ENMs of *O. mirabilis* and of the host species by Schoener's metric (*D*), similarity statistic (*H*)

based on Warren et al. (2008), and Spearman's rank correlation (*RC*), using the R package 'ENMTools' version 1.0.2 (Warren et al., 2010). All analyses and models were produced in the R environment and programming language (R Development Core Team, 2020).

3. Results

3.1. Distribution and abundance patterns along the Paraná coast (S Brazil)

The brittle star *O. mirabilis* is distributed in poly- and euhaline estuarine and inner shelf habitats (Fig. 4). The population densities of *O. mirabilis* extrapolated to m^2 were 815 inds. m^{-2} , 848 inds. m^{-2} , 492 inds. m^{-2} and 117 inds. m^{-2} on sites S2, S3, S4 and S5, respectively (Fig. 4). *Ophiothela mirabilis* was not recorded in site S1, located in the mesohaline estuarine sector or in site S6, the area furthest away from port activity (Fig. 4).

The highest population densities and coverage rates were recorded in sites S2, S3 and S4, while the lowest was recorded in site S5 (Fig. 5). The highest frequencies of occurrence were recorded in the estuarine sites S2 and S3, while the lowest was recorded at inner shelf sites S4 and S5 (Fig. 5). The population density, occurrence frequency and coverage rate of *O. mirabilis* varied significantly as to host species and sites (Table 1).

Ophiothela mirabilis was associated with nine different hosts in our study, including sponges *Drumacidon reticulatum* (Ridley & Dendy, 1886), *Mycale (Zygomycale) angulosa* (Duchassaing & Michelotti, 1864), *Polymastia janeirensis* (Boury-Esnault, 1973), *Tedania (Tedania) ignis* (Duchassaing & Michelotti, 1864) and an unidentified species belonging to Demospongiae; cnidarians *Carijoa riisei* (Duchassaing & Michelotti, 1860) and *Leptogorgia punicea* (Milne-Edwards & Haime, 1857); ascidian *Didemnum perlucidum* Monniot F., 1983; and an unidentified bryozoan species *Schizoporella* sp. Until now, 64 host taxa are recorded in the Atlantic for *O. mirabilis* (Table A3).

The octocoral *Leptogorgia punicea* was the most heavily colonized host (3.6 ± 0.896 inds. cm^{-2} ; mean \pm confidence interval) followed by

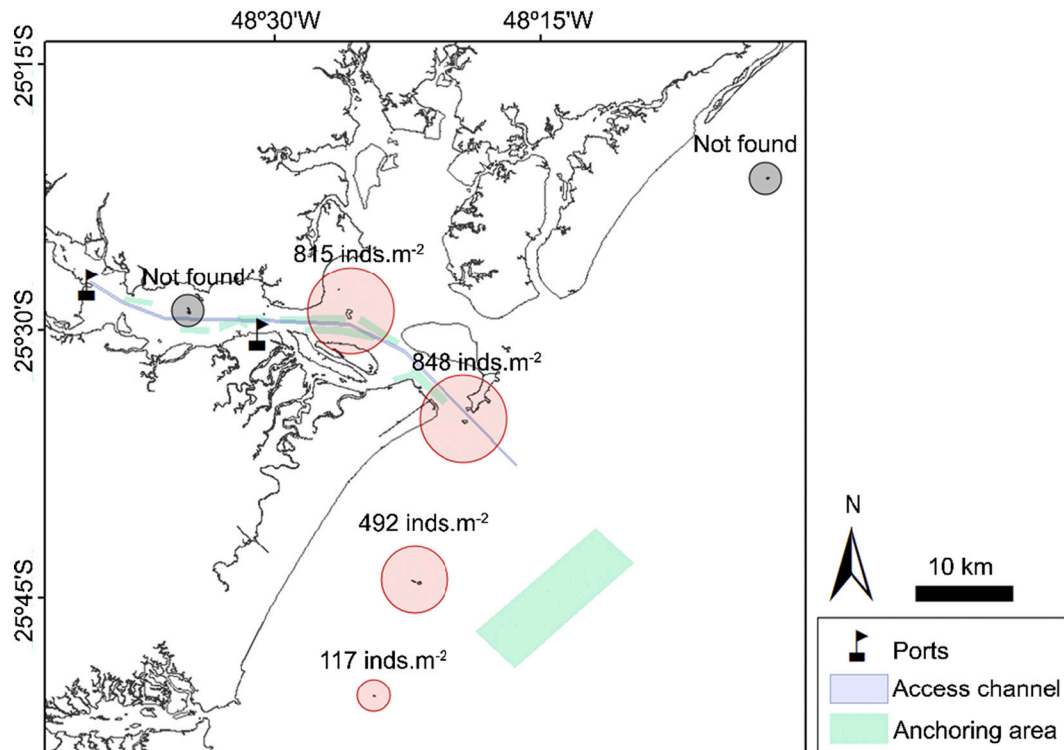


Fig. 4. Population densities of *Ophiothela mirabilis* (individuals. m^{-2}) across the six sampling sites, including the shipping channel, port and anchorage sites.

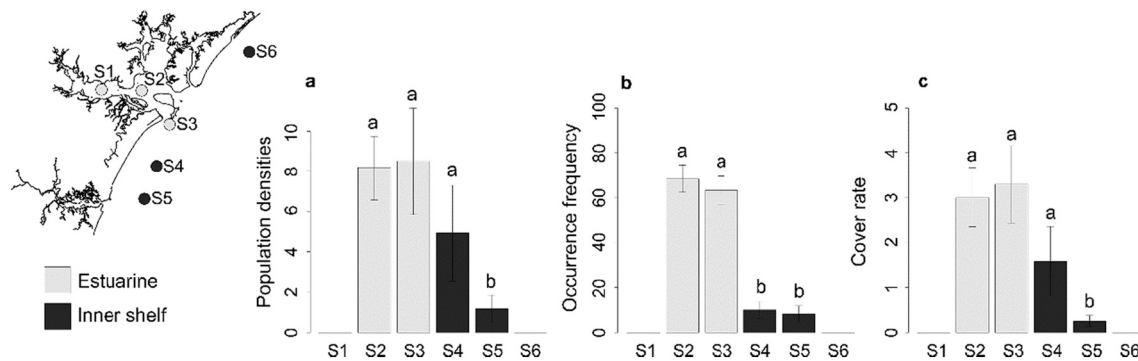


Fig. 5. Variation in (a) population density (individuals.0.01 m⁻²), (b) occurrence frequency (%) and (c) coverage rate (%) of *Ophiothela mirabilis* across the sampled sites. Letters represent significance between the groups adjusted to sites according to the *post hoc* GLHT test. Sites S1, S2 and S3 correspond to the meso-, poly- and euhaline estuarine sectors, respectively; sites S4, S5 and S6 correspond to the inner continental shelf.

Table 1

GLMs of population density, occurrence frequency and coverage rate of *Ophiothela mirabilis* according to sites and host species.

Variables	Predictors	Deviance residuals	AIC	Pr (>Chi)
Population density	sites	300.1	958.0	< 2e-16 ***
	hosts	253.4	873.2	< 2e-16 ***
	sites*hosts	14.7	847.6	0.9023
Occurrence frequency	sites	132.9	313.3	< 2.2e-16 ***
	hosts	55.4	303.5	9.791e-09 ***
	sites*hosts	5.8	315.9	0.9999
Coverage rate	sites	186.2	589.7	< 2e-16 ***
	hosts	150.3	639.2	< 2e-16 ***
	sites*hosts	4.5	591.2	0.9999

*** *p* value < 0.001

the octocoral *Carijoa riisei* (1.3 ± 0.094 inds.cm⁻²). In this sense, these hosts were selected to predict the realized niche of *O. mirabilis* in the ENMs. All remaining host species had a mean density of 0.3 ± 0.043 inds.cm⁻² (Fig. 6). The octocoral *Carijoa riisei* was the most frequently colonized host and the only species with colonization records across all sampled sites. *Ophiothela mirabilis* had only one colonization record for the sponges Demospongiae (unidentified species), *Drumacidon reticulatum* and *Polymastia janeirensis*, and in the bryozoan *Schizoporella* sp., even though they are abundant fouling species. Simultaneous host sharing between brittle stars *O. mirabilis* and *Ophiactis savignyi* (Müller &

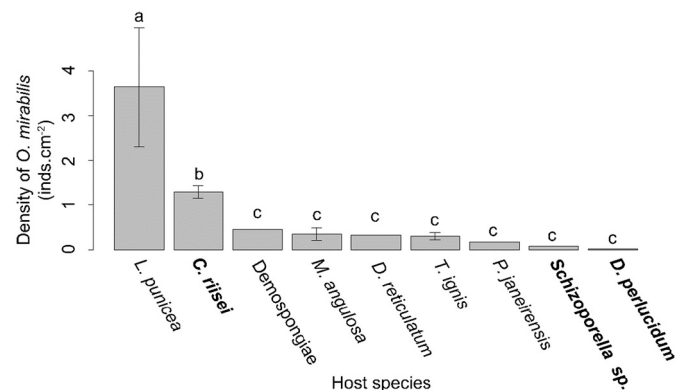


Fig. 6. Density of *Ophiothela mirabilis* per area of host species (individuals. cm⁻²) along the Paraná coast. Species names in bold indicate non-native (*Carijoa riisei*) and cryptogenic taxa (*Didemnum perlucidum*, *Schizoporella* sp.). Letters represent significance between groups adjusted to host species according to the *post hoc* GLHT test.

Troschel, 1842) was also observed on hosts *Leptogorgia punicea*, *Mycale (Zygomycale) angulosa* and *Tedania (Tedania) ignis*.

Outside of our sampling design, rafting by adult individuals of *O. mirabilis* in bryozoan colonies of *Amathia* spp. were recorded during field rounds in Paranaguá Bay. Closer inspection indicated these rafts had broken loose from the substrate. Specimens of *O. mirabilis* were also observed densely colonizing the octocoral *Leptogorgia punicea* at depths of 6 to 16 m in Ponto do Engenho (-27.2930° , -48.3669°) inside Arvoredo Island, Santa Catarina on January 16, 2020 (L. F. Dias, personal observation).

3.2. Ecological niche modelling along the Western Atlantic

The performance of the different models for *Ophiothela mirabilis* was assessed using both AUC (0.949 ± 0.039 ; mean \pm standard deviation) and TSS (0.852 ± 0.059) indexes from the bootstrapping procedure. Our ENMs indicated that areas along the coast of Brazil, the Caribbean Sea and the Gulf of Mexico have ecologically suitable habitats for *O. mirabilis* (Fig. 7; Fig. A1). The current occurrence records for *O. mirabilis* are located in areas with a predicted mean higher than 40.72% habitat suitability index. Considering the subtropical coast of Paraná, only S1 had a habitat suitability index below this value, presenting 34.78% (Fig. 8), while the rest of the sites had $54.65\% \pm 7.99\%$ (mean \pm standard deviation) of habitat suitability index (Fig. 8).

The predicted realized niche of *O. mirabilis* encompasses 80.95% and 71.34% of its suitable habitats in the Southern Atlantic and Northern Atlantic, respectively (Fig. 7). Regarding the niche similarity between *Ophiothela mirabilis* (Fig. A1) and the main host species (Fig. A2), *Carijoa riisei* had the most similar ENMs (Southern Atlantic: $D = 0.777$, $I = 0.793$, and $RC = 0.775$; Northern Atlantic: $D = 0.712$, $I = 0.765$, and $RC = 0.731$), followed by *Leptogorgia punicea* (Southern Atlantic: $D = 0.350$, $I = 0.564$, and $RC = 0.545$; Northern Atlantic: $D = 0.243$, $I = 0.476$, and $RC = 0.445$).

Mean calcite concentration was the most important variable for the total performance of the ENMs of *Ophiothela mirabilis*, contributing 29.54%, followed by mean SST mean (27.43%), mean salinity (22.73%), mean chlorophyll concentration at maximum depth (7.78%), SST range (6.52%) and mean pH (6.01%). The current range of *O. mirabilis* encompasses habitats with mean calcite concentration from 0.53×10^{-4} to 0.051 mol.m⁻³, SST mean higher than 20.23°C , mean salinities values higher than 28.63, mean chlorophyll concentration from 0.004 to 1.64 mg.m⁻³, SST range up to 13.8°C and a mean pH higher than 7.64 (Fig. A3).

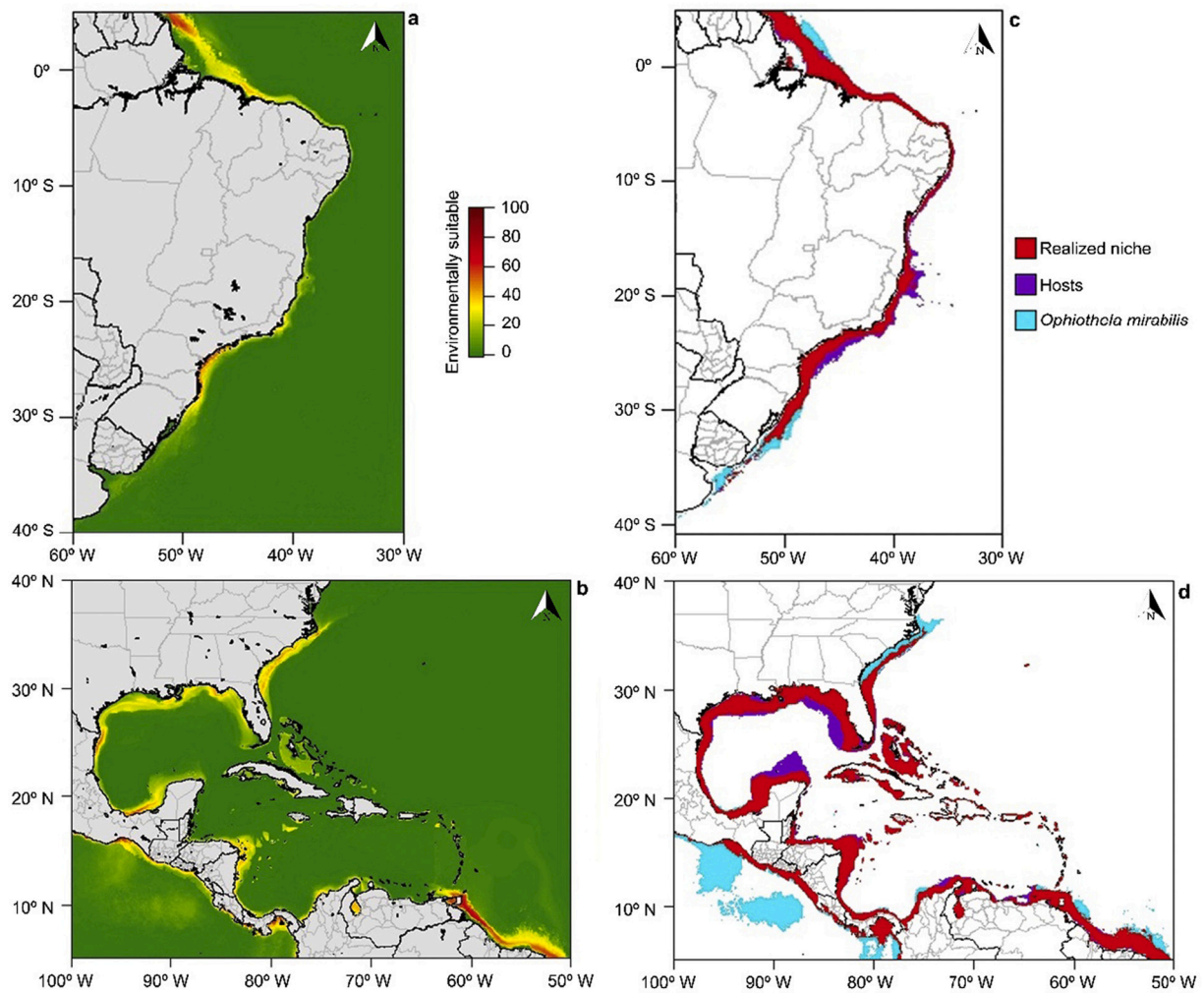


Fig. 7. Suitable habitats predicted for the brittle star *Ophiothela mirabilis* along (a) the Brazilian coast and (b) the Caribbean Sea, including the Gulf of Mexico. Environmental suitability across the habitats range from 0 (not suitable) to 1 (100%) in relation to potential. The predicted realized niche of *Ophiothela mirabilis* (in red), and the binary maps of suitable habitats of *O. mirabilis* (in turquoise) and its main host species (in purple) along (c) the Brazilian coast and (d) the Caribbean Sea, including the Gulf of Mexico. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

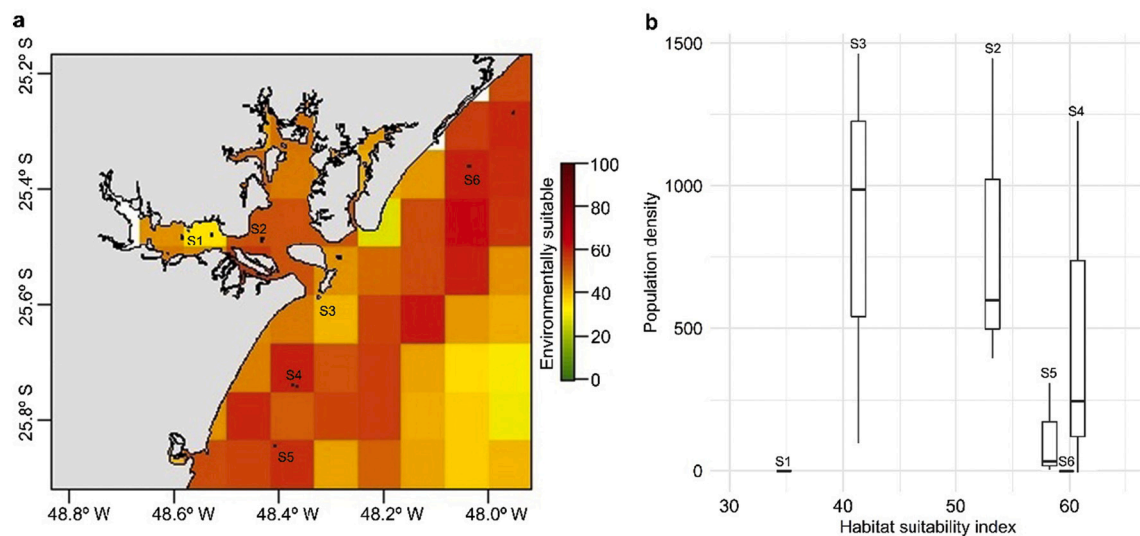


Fig. 8. (a) Suitable habitats predicted for the brittle star *Ophiothela mirabilis* in the sampled study area of Paraná Coast. (b) Variation in population density (individuals.m⁻²) per site according to our habitat suitability index.

4. Discussion

4.1. Distribution and abundance patterns at a regional scale (Paraná coast)

Ophiethela mirabilis is densely populated and widely distributed throughout the inner shelf and high-salinity estuarine habitats. Surprisingly, population densities tended to increase from the inner shelf to estuarine habitats, characterized by a 53.38% mean habitat suitability index, until they decline in the inner estuarine sectors, due to the dominance of low salinity, unsuitable environmental habitats (Fig. 8). Densities of *O. mirabilis* were higher in sites closest to active ports (sites S2 and S3), indicated by the anchoring area and the access channel. These areas also serve regional commercial, tourist and fishing activities. The absence of *O. mirabilis* on the northern inner shelf (site S6) is likely explained by a still ongoing range expansion as it is inserted in the predicted realized niche (Fig. 7). The population densities of *O. mirabilis*, ranging between 117 and 848 inds.m⁻² are comparable to populations found on recruitment plates of fouling species in São Francisco do Sul harbor, Santa Catarina, having extrapolated values for m² ranging between 26 and 798 inds.m⁻² (Lawley et al., 2018). The habitat suitability index of 52.46% of São Francisco do Sul harbor is similar to the Paraná coast. The dense populations of *O. mirabilis* reported in the Atlantic are comparatively higher than that of its native distribution, where maximum densities range between 0.36 and 0.43 inds.m⁻² in the Pacific reefs of Marino Ballena National Park (Costa Rica) and Isla Malpelo (Colombia), respectively (Alvarado and Fernández, 2005; Cohen-Rengifo, 2017).

We also reported on the passive rafting of *O. mirabilis* on hosts that broke loose from the substrate, a strategy that accounts towards increasing the species regional range. Local currents may carry these individuals to nearby habitats, using hard-bottom communities as 'stepping stones'. Since most brittle star hosts are fouling species (Table A3), the lack of hard-substrates would constrain the chances of successful introduction. In this sense, the higher availability of hard-substrates in estuarine habitats compared to inner shelf habitats could also account for the higher population densities and frequencies of *O. mirabilis*. The role that 'stepping stones' play in the spread of non-native species is significant, especially in estuarine environments where the creation of artificial habitats is more frequent than in open waters (Floerl et al., 2009; Glasby et al., 2007). The absence of the species on site S6 may be a consequence of the relative absence of natural or artificial hard-bottoms in the adjacent areas, contrary to what happens in sites (S2, S3, S4, and S5) that are spatially closer and surrounded by artificial reefs (Brandini and da Silva, 2011). Moreover, although site S6 receives recreational and fishing boats, it is the most distant site from the artificial vectors linked to port activity.

Among the host species for *O. mirabilis* in this study, a considerable number are non-native or cryptogenic. The octocoral *Carijoa riisei* is non-native (Concepcion et al., 2010) and the ascidian *Didemnum perlucidum* is cryptogenic to the Southwestern Atlantic (Dias et al., 2016). Some species belonging to *Schizoporella* are also known to be part of a species complex (Tompsett et al., 2009). Regardless, the species recorded in Brazil are considered cryptogenic (Marques et al., 2013; Miranda et al., 2018; Ramalho et al., 2011), at least until studies utilizing molecular techniques can clarify the records (Tompsett et al., 2009). The establishment of invasive species may change the structure and functioning of the recipient systems and consequently facilitate new introductions. For instance, the prevalence of the ascidian *Didemnum psammotodes* over dominant native fouling taxa in an estuary in Espírito Santo (SE Brazil) during a period of drought increased the range of suitable habitat for the introduction of *O. mirabilis* (de Gomes and da Silva, 2020).

Although *O. mirabilis* is recognized as a generalist that opportunistically chooses its hosts (Table A3; Mantelatto et al., 2016), octocorals are in fact the most populated animals by the brittle star (Fig. 6; Table 1), a similar trend to what happens in its native area (Granja-Fernández

et al., 2014). The densities of *O. mirabilis* on *Leptogorgia punicea* (3.6 ± 0.896 inds.cm⁻²) and *Carijoa riisei* (1.3 ± 0.094 inds.cm⁻²) were at least four times higher than that of any other species (0.3 ± 0.043 inds.cm⁻²). Our findings are remarkably comparable to densities seen in the octocoral *Gorgonia ventalina* Linnaeus, 1758 (2.8 inds.cm⁻²) in Martinique (Ferry et al., 2020), as well as to the mean densities (2.7 inds.cm⁻²) found in the octocorals *Eunicea clavigera* Bayer, 1961, *E. succinea* (Pallas, 1766), *E. tourneforti* Milne Edwards & Haime, 1857 and *Muricea elongata* Lamouroux, 1821 in Southeast Florida (Glynn et al., 2019). The diversity of host octocorals is also higher when compared to the other taxonomic groups, with 37.5% ($n = 24$) belonging to Subclass Octocorallia (Table A3). The chemical sign also given off by the host species may assist *O. mirabilis* in their search for suitable habitats, as evidenced in experiments using crude extract of octocoral *Phyllogorgia dilatata* (Esper, 1806) (Ribeiro et al., 2017). Octocorals also contain feeding deterrent chemicals against predation, making them a good refuge for the brittle stars (Sammarco and Coll, 1992). Furthermore, the branching structures of the octocorals provide support for attachment, thus facilitating colonization (Ferry et al., 2020).

4.2. The suitable habitats of *O. mirabilis* along the Western Atlantic

Our ENMs predicted connectivity of ecologically suitable habitats for *O. mirabilis* along the Brazilian coast, the Caribbean Sea and the Gulf of Mexico. These regions exhibited $\geq 40.72\%$ of environmentally suitable habitats and are located within the predicted realized niche (Fig. 7), highlighting the potential for *O. mirabilis* to increase its range throughout the Western Atlantic. Regions inserted in the predicted realized niche may achieve similar abundances as observed in the surveys of the study area (Figs. 7 and 8).

According to the biogeographic classification of Spalding et al. (2007), the predicted suitable habitats encompass benthic communities in warm marine provinces, including the Warm Temperate Southwestern Atlantic, Tropical Southwestern Atlantic, North Brazil Shelf, Tropical Northwestern Atlantic and Warm Temperate Northwest Atlantic (Fig. 3). With the exception of Warm Temperate Northwest Atlantic, these provinces all display current records of *O. mirabilis* (Fig. 3). However, several ecoregions inside the province's polygons do not have records of the species, especially in the Tropical Northwestern Atlantic, suggesting inadequate sampling efforts or an ongoing range expansion. The absence of the brittle star in suitable habitats may be a consequence of the lack of artificial vectors, and may also indicate potential sites for future establishment. The sampling effort and monitoring in areas with a high habitat suitability index may guide coastal management strategies regarding the potential spread of *O. mirabilis*.

Along the Brazilian coast, ENMs indicated environmentally suitable habitats for *O. mirabilis* where there are already occurrence records, while additionally indicating potential sites further south (Fig. 7). Rio Grande is the southern limit of suitable habitats, with Southeastern Brazil likely being the initial foci for the introduction of *O. mirabilis*, as this is where the first occurrence records of the species are located (Hendler et al., 2012). The introduction of offspring individuals in areas that are adjacent to an initial foci of introduction is defined as propagule rain (Lockwood et al., 2009). Specifically, the number of non-native records is higher across Southeastern Brazil, a pattern that is possibly related to the proximity of propagule rain from the initial foci of introduction, which is likely driven by artificial vectors and passive rafting. There are no records of *O. mirabilis* outside the coastal ecoregions within the Tropical Southwestern Atlantic, such as Trindade and Martin Vaz Islands, Fernando de Noronha, Rocas Atoll or São Pedro and São Paulo Islands (Fig. 3).

Unlike several species for which the freshwater discharge of the Amazon River acts as a biogeographic barrier (Briggs and Bowen, 2013; Miloslavich et al., 2011), our ENMs indicated that the reef communities of the Amazon mouth and surrounding areas is an environmental suitable habitat for *O. mirabilis* (Fig. 7). The occurrence records of

O. mirabilis in association with the octocoral *Leptogorgia miniata* (Milne Edwards & Haime, 1857) (Moura et al., 2016) indicates that it is already established in these reef systems. This pattern highlights the ability of *O. mirabilis* to colonize coastal areas, even those with heavy freshwater inputs, as in the Amazon.

The ENMs also indicated environmental suitable habitats for *O. mirabilis* along the Caribbean Sea and the Gulf of Mexico (Fig. 7). The prevalence of octocorals in most coral reef communities (Johnson and Hallock, 2020) and the higher diversity of octocoral hosts for *O. mirabilis* in the Caribbean Sea (Fanovich et al., 2019; Ferry et al., 2020) could aid the successful introduction of the brittle star. The propagule rain from established populations in Southern and Eastern Caribbean may enable the spread of *O. mirabilis* to ecoregions not yet colonized in the Tropical Northwestern Atlantic (Fig. 3). Similarly, the populations in the Floridian ecoregion may aid the spread of the species towards the Warm Temperate Northwest Atlantic. Vessel traffic may also further contribute towards the introduction of the species in suitable disjunct habitats across the Western Atlantic.

The occurrence of *O. mirabilis* is mainly correlated to mean calcite concentration and mean SST, which account for 56.97% of our ENMs. Environmental suitable habitats increase with values of calcite concentration (Fig. A3), thus indicating regions most susceptible for new introductions. Calcite is important for skeleton building in brittle stars (Brusca and Brusca, 2003). As well, fission reproduction requires a high concentration of calcite to regenerate all lost skeletal structures for body reconstruction. However, calcite concentration may also be related to requirements of the host, such as the formation of sclerites in octocorals, spicules in some sponges and skeletal structures in scleractinian corals (Brusca and Brusca, 2003). Nevertheless, the effects of local calcite concentrations towards the presence of *O. mirabilis* still needs to be defined. SST is the major predictor of marine species' distribution, especially in the case of benthic species (Molinos et al., 2016). The suitable habitats of *O. mirabilis* are significantly constrained by cold waters with mean values less than 21.75 °C (Fig. A3). Even in the cold waters near the Cabo Frio upwelling area, the annual mean SST (1981–2009) ranging from 22.0 to 23.8 °C (Cordeiro et al., 2014) may not constrain the local distribution of *O. mirabilis*. Besides that, the SST range showed a relatively low influence in the brittle star suitable habitats. For instance, the distribution of the invasive cup coral *Tubastraea coccinea* encompasses the Cabo Frio upwelling area, although in significantly lower densities than in higher water temperatures within the same area (Batista et al., 2017). Experimental studies are still needed to assess the physiological responses of *O. mirabilis* to cold waters.

Environmental suitable habitats of *O. mirabilis* were negatively correlated with salinity (Fig. A3). Mean salinity lower than 28 significantly constrain suitable habitats, and is generally considered to be an osmotic stressor in brittle stars (Brusca and Brusca, 2003). Chlorophyll concentration, SST range and pH were comparatively less important to the performance of the ENMs, accounting for only 20.31%. Chlorophyll concentration can be used as a proxy for phytoplankton (Lins et al., 2018), a major feeding item for benthic suspension feeders, which comprise most hosts of *O. mirabilis*. Suitable habitats of *O. mirabilis* were indeed positively correlated to chlorophyll (Fig. A3), potentially indicating slightly higher suitability towards eutrophic and high-nutrient waters conditions. Although SST range represents a climatic extreme that often constrains species distribution, the suitable habitats of *O. mirabilis* remain relatively constant up to 13.68 °C (Fig. A3). The pH showed a similar pattern, remaining constant (Fig. A3).

5. Conclusion

Ours is the first systematic assessment of spatial abundances and distribution patterns in populations of *O. mirabilis* along a subtropical sector of the Western Atlantic. Higher population densities and frequencies of *O. mirabilis* were found to occur in high-salinity estuarine areas, a pattern that may be correlated with port activities. Although

O. mirabilis colonizes a wide spectrum of host species, octocorals are most densely and frequently colonized. Overall, population densities in the Atlantic are considerably higher than those in the native Pacific.

Currently, the non-native occurrence records of *O. mirabilis* encompasses disjunct habitats from Santa Catarina (S Brazil) to Southeast Florida (USA). Our ENMs predicted connectivity of ecologically suitable habitats along the Brazilian coast, the Caribbean Sea and the Gulf of Mexico. Therefore, *O. mirabilis* has the capacity to spread to new habitats across the warm marine provinces of the Western Atlantic, and establish population densities as high as those reported in Southern Brazil. Occurrences are correlated mainly with mean calcite concentration and mean SST. Considering the high spreading capacity and the maintenance of high population densities on hosts, future studies are needed to test explicit hypotheses about the impacts of *O. mirabilis* on the recipient biodiversity and systems.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2020.101994>.

References

- Alitto, R.A.S., Granadier, G., Christensen, A.B., O'Hara, T., Di Domenico, M., Borges, M., 2020. Unravelling the taxonomic identity of *Ophiophila* Verrill, 1867 (Ophiuroidea) along the Brazilian coast. *J. Mar. Biol. Assoc. United Kingdom* 1–14. <https://doi.org/10.1017/s002531542000034x>.
- Alvarado, J.J., Fernández, C., 2005. Equinodermos del Parque Nacional Marino Ballena, Pacífico. *Costa Rica. Rev. Biol. Trop.* 53, 275–284. <https://doi.org/10.15517/RBT.V53I3.26785>.
- Angulo, R.J., Borzone, C.A., Noernberg, M.A., da Rosa, L.C., 2016. The state of Paraná beaches. In: Short, A.D., da Klein, A.H.F. (Eds.), *Brazilian Beach Systems*. Springer International Publishing, pp. 419–464. https://doi.org/10.1007/978-3-319-30394-9_16.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.
- Araújo, J.T., Oliveira, M.O., Matthews-Cascon, H., Correia, F.A.C., 2018. The invasive brittle star *Ophiophila mirabilis* Verrill, 1867 (Echinodermata, Ophiuroidea) in the southwestern Atlantic: filling gaps of distribution, with comments on an octocoral host. *Lat. Am. J. Aquat. Res.* 46, 1123–1127. <https://doi.org/10.3856/vol46-issue5-fulltext-25>.
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* 27, 277–284. <https://doi.org/10.1111/geb.12693>.
- Austin, R.A., Hawkes, L.A., Doherty, P.D., Henderson, S.M., Inger, R., Johnson, L., Pikesley, S.K., Solandt, J.L., Speedie, C., Witt, M.J., 2019. Predicting habitat suitability for basking sharks (*Cetorhinus maximus*) in UK waters using ensemble ecological niche modelling. *J. Sea Res.* 153, 101767. <https://doi.org/10.1016/j.seares.2019.101767>.

- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.* 3, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.
- Batista, D., Eduardo, J., Gonçalves, A., Messano, H.F., Altwater, L., Candella, R., Machado, L., Elias, C., Vicente, L., Messano, R. De, 2017. Distribution of the invasive orange cup coral *Tubastraea coccinea* Lesson, 1829 in an upwelling area in the South Atlantic Ocean fifteen years after its first record. *Aquat. Invasions* 12, 23–32.
- Brandini, F., da Silva, A.S., 2011. Epilithic community development on artificial reefs deployed along a cross-shelf environmental gradient off Paraná State, Southern Brazil. *Braz. J. Oceanogr.* 59, 43–53. <https://doi.org/10.1590/S1679-87592011000500007>.
- Brandini, F.P., da Silva, A.S., da Silva, E.T., Kolm, H., 2007. Sources of nutrients and seasonal dynamics of chlorophyll in the inner shelf off Paraná State - South Brazil bight. *J. Coast. Res.* 23, 1131–1140. <https://doi.org/10.2112/04-0360.1>.
- Briggs, J.C., Bowen, B.W., 2013. Marine shelf habitat: biogeography and evolution. *J. Biogeogr.* 40, 1023–1035. <https://doi.org/10.1111/jbi.12082>.
- Brusca, R.C., Brusca, G.J., 2003. *Invertebrates*. Sinauer Associates, Sunderland, Massachusetts.
- Bumber, J., da Rocha, R.M., 2016. Invading the natural marine substrates: a case study with invertebrates in South Brazil. *Soc. Bras. Zool.* 33, e20150211 <https://doi.org/10.1590/S1984-4689zool-20150211>.
- Bumber, J., Cattani, A.P., Chierigatti, N.B., da Rocha, R.M., 2016. Biodiversity of benthic macroinvertebrates on hard substrates in the Currais marine protected area, in southern Brazil. *Biota Neotrop.* 16, e20160246 <https://doi.org/10.1590/1676-0611-BN-2016-0246>.
- Carlos-Júnior, L.A., Barbosa, N.P.U., Moulton, T.P., Creed, J.C., 2015. Ecological niche model used to examine the distribution of an invasive, non-indigenous coral. *Mar. Environ. Res.* 103, 115–124. <https://doi.org/10.1016/j.marenvres.2014.10.004>.
- Clark, A.M., 1976. Tropical epizoic echinoderms and their distribution. *Micronesica* 12, 111–117.
- Cohen-Rengifo, M., 2017. *Equinodermos del Santuario de Flora y Fauna Malpelo*. Universidad Jorge Tadeo Lozano, Pacífico Colombiano.
- Concepcion, G.T., Kahng, S.E., Crepeau, M.W., Franklin, E.C., Coles, S.L., Toonen, R.J., 2010. Resolving natural ranges and marine invasions in a globally distributed octocoral (genus *Carijoa*). *Mar. Ecol. Prog. Ser.* 401, 113–127. <https://doi.org/10.3354/meps08364>.
- Cordeiro, L.G.M.S., Belem, A.L., Bouloubassi, I., Rangel, B., Sifeddine, A., Capilla, R., Albuquerque, A.L.S., 2014. Reconstruction of southwestern Atlantic Sea surface temperatures during the last century: Cabo Frio continental shelf (Brazil). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 415, 225–232. <https://doi.org/10.1016/j.palaeo.2014.01.020>.
- de Frehse, F.A., Braga, R.R., Nocera, G.A., Vitule, J.R.S., 2016. Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. *Biol. Invasions* 18, 3713–3725. <https://doi.org/10.1007/s10530-016-1260-9>.
- de Gomes, L.E.O., da Silva, E.C., 2020. Drought periods driving bioinvasion on hard substrates at a tropical estuary, eastern Brazil. *Mar. Pollut. Bull.* 160, 111563. <https://doi.org/10.1016/j.marpolbul.2020.111563>.
- Dias, P.J., Rocha, R., Godwin, S., Tovar-Hernández, M.A., Delahoz, M.V., McKirdy, S., De Lestang, P., McDonald, J.I., Snow, M., 2016. Investigating the cryptogenic status of the sea squirt *Didemnum perulicidum* (Tunicata, Ascidiacea) in Australia based on a molecular study of its global distribution. *Aquat. Invasions* 11, 239–245. <https://doi.org/10.3391/ai.2016.11.3.02>.
- Fanovich, L., Wothke, A., Mohammed, R.S., 2019. Report on sightings of the potential invasive species *Ophiothela mirabilis* (Echinodermata, Ophiuroidea) in Tobago, W.I. *Living World*. J. Trinidad Tobago F. Nat. Club 29–31.
- Feng, X., Park, D.S., Walker, C., Peterson, A.T., Merow, C., Papeš, M., 2019. A checklist for maximizing reproducibility of ecological niche models. *Nat. Ecol. Evol.* 3, 1382–1395. <https://doi.org/10.1038/s41559-019-0972-5>.
- Ferry, R., Hubert, L., Philippot, V., Priam, F., Smith, J., 2020. First record of the non-indigenous brittle star species *Ophiothela mirabilis* Verrill, 1867 (Echinodermata: Ophiuroidea), off Martinique Island, French Lesser Antilles. *Biol. Invasions Rec.* 9, 228–238. <https://doi.org/10.3391/bir.2020.9.2.08>.
- Floerl, O., Inglis, G.J., Dey, K., Smith, A., 2009. The importance of transport hubs in stepping-stone invasions. *J. Appl. Ecol.* 46, 37–45. <https://doi.org/10.1111/j.1365-2664.2008.01540.x>.
- Glasby, T.M., Connell, S.D., Holloway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Mar. Biol.* 151, 887–895. <https://doi.org/10.1007/s00227-006-0552-5>.
- Glynn, P.W., Coffman, B., Primov, K., Renegar, D.A., Gross, J., Blackwelder, P., Martinez, N., Dominguez, J., Vanderwoude, J., Riegl, B.M., 2019. Benthic ctenophore (order Platyctenida) reproduction, recruitment, and seasonality in South Florida. *Invertebr. Biol.* 138, e12256 <https://doi.org/10.1111/ivb.12256>.
- Granja-Fernández, R., Herrero-Pérezrul, M.D., López-Pérez, R.A., Hernández, L., Rodríguez-Zaragoza, F.A., Jones, R.W., 2014. Ophiuroidea (Echinodermata) from coral reefs in the Mexican Pacific. *Zookeys* 406, 101–145. <https://doi.org/10.3897/zookeys.406.6306>.
- Hemery, L.G., Marion, S.R., Romsos, C.G., Kurapov, A.L., Henkel, S.K., 2016. Ecological niche and species distribution modelling of sea stars along the Pacific northwest continental shelf. *Divers. Distrib.* 22, 1314–1327. <https://doi.org/10.1111/ddi.12490>.
- Hendler, G., Brugneaux, S.J., 2013. New records of brittle stars from French Guiana: *Ophiactis savignyi* and the alien species *Ophiothela mirabilis* (Echinodermata: Ophiuroidea). *Mar. Biodivers. Rec.* 6, e113 <https://doi.org/10.1017/S1755267213000845>.
- Hendler, G., Migotto, A.E., Ventura, C.R.R., Wilk, L., 2012. Epizoic *Ophiothela brittle* stars have invaded the Atlantic. *Coral Reefs* 31, 1005. <https://doi.org/10.1007/s00338-012-0936-6>.
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. *Biol. Invasions* 13, 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>.
- Johnson, S.K., Hallock, P., 2020. A review of symbiotic gorgonian research in the western Atlantic and Caribbean with recommendations for future work. *Coral Reefs* 39, 239–258. <https://doi.org/10.1007/s00338-020-01891-0>.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>.
- Laeske, P., Martínez, B., Mansilla, A., Bischof, K., 2020. Future range dynamics of the red alga *Capreolia implexa* in native and invaded regions: contrasting predictions from species distribution models versus physiological knowledge. *Biol. Invasions* 22, 1339–1352. <https://doi.org/10.1007/s10530-019-02186-4>.
- Lana, P.C., Marone, E., Lopes, R.M., Machado, E.C., 2001. The subtropical estuarine complex of Paranaguá Bay, Brazil. In: Seeliger, U., Kjerfve, B. (Eds.), *Coastal Marine Ecosystem of Latin America*. Springer, Berlin, Heidelberg, pp. 131–145. https://doi.org/10.1007/978-3-662-04482-7_11.
- Lawley, J.W., Fonseca, A.C., Faria Júnior, E., Lindner, A., 2018. Occurrence of the non-indigenous brittle star *Ophiothela cf. mirabilis* Verrill, 1867 (Echinodermata, Ophiuroidea) in natural and anthropogenic habitats off Santa Catarina, Brazil. *Check List* 14, 453–459. <https://doi.org/10.15560/14.2.453>.
- Lins, D.M., de Marco, P., Andrade, A.F.A., Rocha, R.M., 2018. Predicting global ascidian invasions. *Divers. Distrib.* 24, 692–704. <https://doi.org/10.1111/ddi.12711>.
- Lockwood, J.L., Cassey, P., Blackburn, T.M., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers. Distrib.* 15, 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>.
- Mantelatto, M.C., Vidon, L.F., Silveira, R.B., Menegola, C., da Rocha, R.M., Creed, J.C., 2016. Host species of the non-indigenous brittle star *Ophiothela mirabilis* (Echinodermata: Ophiuroidea): an invasive generalist in Brazil? *Mar. Biodivers. Rec.* 9, 8. <https://doi.org/10.1186/s41200-016-0013-x>.
- Marques, A.C., dos Klöh, A.S., Migotto, A.E., Cabral, A.C., Ravedutti Rigo, A.P., Lima Bettim, A., Razzolini, E.L., Matthews Cascon, H., Bardi, J., Kremer, L.P., Vieira, L.M., Arruda Bezerra, L.E., Haddad, M.A., de Oliveira Filho, R.R., Millan Gutierrez, S.M., Pires Miranda, T., Franklin, W., da Rocha, R.M., 2013. Rapid assessment survey for exotic benthic species in the São Sebastião Channel, Brazil. *Lat. Am. J. Aquat. Res.* 41, 265–285. <https://doi.org/10.3856/vol41-issue2-fulltext-6>.
- Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: a literature review and spatial analysis of evidence. *Ecol. Model.* 415, 108837. <https://doi.org/10.1016/j.ecolmodel.2019.108837>.
- Miloslavich, P., Klein, E., Díaz, J.M., Hernández, C.E., Bigatti, G., Campos, F., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M.V., Díaz de Astarloa, J.M., Lewis, M., Yorio, P., Piriz, M.L., Rodríguez, D., Valentin, Y.Y., Gamboa, L., Martín, A., 2011. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PLoS One*. <https://doi.org/10.1371/journal.pone.0014631>.
- Miranda, A.A., Almeida, A.C.S., Vieira, L.M., 2018. Non-native marine bryozoans (Bryozoa: Gymnolaemata) in Brazilian waters: assessment, dispersal and impacts. *Mar. Pollut. Bull.* 130, 184–191. <https://doi.org/10.1016/j.marpolbul.2018.03.023>.
- Molinos, J.G., Halpern, B.S., Schoeman, D.S., Brown, C.J., Kiessling, W., Moore, P.J., Pandolfi, J.M., Poloczanska, E.S., Richardson, A.J., Burrows, M.T., 2016. Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Chang.* 6, 83–88. <https://doi.org/10.1038/nclimate2769>.
- Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva, J.M., Araújo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V., Bahia, R.G., Paranhos, R.P., Dias, R.J.S., Siegle, E., Figueiredo, A.G., Pereira, R.C., Leal, C.V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitão, S., Yager, P.L., Francini-Filho, R.B., Fróes, A., Campeão, M., Silva, B.S., Moreira, A.P.B., Oliveira, L., Soares, A.C., Araújo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A.B., Thompson, C.C., Rezende, C.E., Thompson, F.L., 2016. An extensive reef system at the Amazon River mouth. *Sci. Adv.* 2, e1501252 <https://doi.org/10.1126/sciadv.1501252>.
- Naimi, B., Araújo, M.B., 2016. Sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography (Cop.)* 39, 368–375. <https://doi.org/10.1111/ecog.01881>.
- Pinochet, J., Rivera, R., Neill, P.E., Brante, A., Hernández, C.E., 2019. Spread of the non-native anemone *Anemonia alicemartinae* Häussermann & Försterra, 2001 along the Humboldt-current large marine ecosystem: an ecological niche model approach. *PeerJ* 7, e1756. <https://doi.org/10.7717/peerj.1756>.
- R Development Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org/>.
- Ramallo, L.V., Muricy, G., Taylor, P.D., 2011. Taxonomic revision of some lepraliomorph cheilostome bryozoans (Bryozoa: Lepraliomorpha) from Rio de Janeiro State, Brazil. *J. Nat. Hist.* 45, 767–798. <https://doi.org/10.1080/00222933.2010.535917>.
- Ribeiro, F.V., da Gama, B.A.P., Pereira, R.C., 2017. Structuring effects of chemicals from the sea fan *Phyllogorgia dilatata* on benthic communities. *PeerJ* 5, e3186. <https://doi.org/10.7717/peerj.3186>.
- Rich, L.-P., Dennis, M.M., Freeman, M.A., 2020. New record of the non-native *Ophiothela mirabilis* (Verrill 1867) in St. Kitts, West Indies. *Adv. Oceanogr. Mar. Biol.* 2, 2–6. <https://doi.org/10.33552/AOMB.2020.02.000526>.

- Riul, P., Targino, C.H., Júnior, L.A.C., Creed, J.C., Horta, P.A., Costa, G.C., 2013. Invasive potential of the coral *Tubastraea coccinea* in the Southwest Atlantic. *Mar. Ecol. Prog. Ser.* 480, 73–81. <https://doi.org/10.3354/meps10200>.
- Sammarco, P.W., Coll, J.C., 1992. Chemical adaptations in the Octocorallia: evolutionary considerations. *Mar. Ecol. Prog. Ser.* 88, 93–104. <https://doi.org/10.3354/meps088093>.
- Seebens, H., Gastner, M.T., Blasius, B., 2013. The risk of marine bioinvasion caused by global shipping. *Ecol. Lett.* 16, 782–790. <https://doi.org/10.1111/ele.12111>.
- Soberón, J., Nakamura, M., 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19644–19650. <https://doi.org/10.1073/pnas.0901637106>.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573–583. <https://doi.org/10.1641/B570707>.
- Tavares, M.R., Costa, P.A.S., Ventura, C.R.R., 2019. Population size structure, asexual reproduction, and somatic growth estimates of the non-indigenous brittle star *Ophiothela mirabilis* (Echinodermata: Ophiuroidea) on the southeastern coast of Brazil. *Mar. Biodivers.* 49, 1713–1725. <https://doi.org/10.1007/s12526-019-00938-y>.
- Tompsett, S., Porter, J.S., Taylor, P.D., 2009. Taxonomy of the fouling cheilostome bryozoans *Schizoporella unicornis* (Johnston) and *Schizoporella errata* (waters). *J. Nat. Hist.* 43, 2227–2243. <https://doi.org/10.1080/00222930903090140>.
- Trygonis, V., Sini, M., 2012. PhotoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *J. Exp. Mar. Biol. Ecol.* 424–425, 99–108. <https://doi.org/10.1016/j.jembe.2012.04.018>.
- Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62, 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>.
- Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33, 607–611. <https://doi.org/10.1111/j.1600-0587.2009.06142.x>.
- Wessel, P., Smith, W.H.F., 1996. A global, self-consistent, hierarchical, high-resolution shoreline database. *J. Geophys. Res. Solid Earth* 101, 8741–8743. <https://doi.org/10.1029/96JB00104>.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer, New York. <https://doi.org/10.1007/978-0-387-45972-1>.