

Research Article

Quantification of the non-indigenous ophiuroid *Ophiothela mirabilis* Verrill, 1867 associated with marine sponges with different morphologies

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Abstract

Sponges are normally considered as living hotels and they have been the most common basebionts (45.5%) for the non-indigenous species *Ophiothela mirabilis* Verrill, 1867 in the Brazilian coast. This ophiuroid is native to the Pacific Ocean but is spreading out in the Tropical Western Atlantic since 2000. Regarding this invasion, quantitative data is necessary to understand *O. mirabilis* threat. The aim of this study was to quantify the abundance of *O. mirabilis* on marine sponges along the Brazilian coast, and to evaluate the relationship of the non-indigenous species with sponge phenotypes, to test the hypothesis that this non-indigenous species prefers erect, irregular and yellowish sponges to facilitate attachment and camouflage. Epibiosis of *O. mirabilis* on sponges were photographed in 27 sites from Maranhão to Rio de Janeiro States, Brazil, and the abundance of sponges and ophiuroids on each sponge individual was counted. Only Bahia and Rio de Janeiro States presented an association, which was positively correlated ($R^2 = 0.85$, $F = 36.16$, $p < 0.001$) between sponges and ophiuroid mean abundances. No morphological trait was statistically chosen by *O. mirabilis*, but the null probabilistic model indicates *Mycale (Zygomycale) angulosa* (Duchassaing & Michelotti, 1864) may be a preferred sponge basebiont. This first large-scale quantitative study indicates *O. mirabilis* may become a dangerous invader due to weak host preferences and efficient asexual reproduction strategy. This work can be used as a baseline template for monitoring and eradication programs, especially in Brazilian bays of high diversity and with human impact.

Key words: abundance, bioinvasion, ecological interaction, epibiosis, null model, Porifera

Introduction

Porifera species are benthic organisms able to maintain the health of an ecosystem due to their filtration capability, nutrient delivery, and the provision of heterogeneous, three-dimensional habitats (Bergquist 1978; Diaz and Rützler 2001; Maldonado et al. 2012; de Goeij et al. 2013; Pawlik et al. 2018). The ability of marine sponges to filter dissolved organic matter and microorganisms creates conditions for different organisms to live in association with them, such as detritivores and suspension-feeders, directly

influencing their assemblages of associated fauna and symbionts (Maldonado et al. 2012; de Goeij et al. 2013; Shih et al. 2020).

Marine sponges are involved in several ecological interactions, such as competition (e.g., with corals: Silva et al. 2017) and cooperation with various taxonomic groups (Ribeiro et al. 2003; Rützler 2004; Wulff 2008; Schönberg et al. 2016), which may increase local diversity (Wulff 2012; Beazley et al. 2013; Kazanidis et al. 2016) and drive the epi- and infaunal community structure (Koukouras et al. 1996; Neves and Omena 2003). However, the associated fauna may be also driven by the substrate where sponges attach (Prentiss and Harris 2011; Kazanidis et al. 2016). Sponge-ophiuroid associations are common worldwide and have been suggested as mutualistic (Hendler 1984), commensalistic or parasitic (Henkel and Pawlik 2014). In this association, brittle stars benefit from the acquisition of shelter and food (Clark 1976; Henkel and Pawlik 2014), while evidence of benefit for the sponge hosts is unclear (Mosher and Watling 2009), but may include antifouling (Hendler 1984).

Ophiothela mirabilis Verrill, 1867 was first described from the Pacific Ocean (Clark 1976), and, since 2000, when it was first observed, it is considered a non-indigenous species in the Tropical Western Atlantic Ocean (TWA, Hendler et al. 2012). In the last 20 years, several new occurrence records in the TWA were published enlarging its latitudinal distribution from the Caribbean Sea to Santa Catarina State, Brazil (Hendler et al. 2012; Hendler and Brugneaux 2013; Bumbeer and Rocha 2016; Mantelatto et al. 2016; Moura et al. 2016; Lawley et al. 2018; Thé de Araújo et al. 2018). Most of these studies have recorded the brittle star up to 20 m depth, but it has been also recorded associated to *Leptogorgia miniata* (Milne Edwards & Haime, 1857), in the mesophotic zone (up to 120 m), off the Amazon River mouth (Moura et al. 2016). The species has been recorded associated to species attached in both natural and artificial substrates (Mantelatto et al. 2016; Bumbeer et al. 2016; Lawley et al. 2018; Thé de Araújo et al. 2018), which may amplify its competitiveness in relationship with other restricted ophiuroids.

The natural Pacific lineage of *O. mirabilis* is six-armed with a central disk around 2 mm in diameter and changes color (red, purple, orange, yellow and white) to camouflage (Clark 1976; see Verrill 1867 for color variants). However, the Atlantic lineage possess exclusively yellow color (Hendler et al. 2012), and less than six arms, suggesting that the introduction may have arisen from a single lineage followed by asexual spread. Recent genetic evidence (Alitto et al. 2020) has confirmed the species identity of Brazilian specimens but has not yet traced the origins of the introduction or indeed the species relationships within the *Ophiothela* species complex of 20 putative species.

So far, the limited quantitative data on the reproduction, population structure and growth of *O. mirabilis* in the TWA indicates the species may become an invader due to a high asexual reproduction rate and gregarious

and generalist behaviours (Tavares et al. 2019). These authors described almost 40% of *O. mirabilis* with a central disc regenerating after a split, indicative of fission, while the qualitative study of Mantelatto et al. (2016) mentioned several individuals without six arms, also indicating that asexual reproduction is the primary means of population maintenance and growth.

Ophiothela spp. are known to densely colonize sponges and gorgonian corals on Indo-West Central Pacific reefs, on the Pacific coast of Panama (Clark 1976), and on the Caribbean and Brazilian coasts (Hendler et al. 2012; Hendler and Brugneaux 2013; Mantelatto et al. 2016). Porifera represents 45.5% of the known benthic species hosting the epibiont *O. mirabilis* in the Brazilian littoral zone, while the second most representative group were corals, mainly gorgonians, with 24.2% (Hajdu et al. 2011; Hendler et al. 2012; Mosher and Watling 2009; Hendler and Brugneaux 2013; Mantelatto et al. 2016; Skinner et al. 2016; Ribeiro et al. 2017; Lawley et al. 2018).

The good mobility of *O. mirabilis* indicates it can choose the best host. In order to verify the putative preference of *O. mirabilis* for hosts, the aims of this study were to quantify the abundance of the ophiuroid on marine sponges, and to evaluate the relationship of the non-indigenous species with sponge phenotypes and substrates where they were attached. Based on observations of this species cited above, we anticipate that abundances will be higher on erect, irregular, and yellowish sponges to facilitate attachment and camouflage.

Materials and methods

Study Area

The Brazilian coast is over 8000 km-long, comprising nine coastal biogeographic zones (Spalding et al. 2007). We surveyed 27 sites (21 natural and six artificial) between 1 and 25 m depth, comprising two biogeographic regions and six states (Table 1; Figure 1). In northeastern Brazil, beachrock tide pools (Ferreira Júnior et al. 2018) were surveyed at Maranhão (MA; 2°27'S; 44°11'W), Ceará (CE; 3°43'S; 38°32'W) and Rio Grande do Norte States (RN; 5°74'S; 36°55'W) by freediving. SCUBA diving was used to survey the sandstone reef of the Parque Estadual Marinho da Pedra da Risca do Meio (PEMPRM), off Ceará State (Soares et al. 2016), and rocky shores of Fernando de Noronha Archipelago (FN; 3°51'S; 32°25'W), off Pernambuco (PE) State, and Todos os Santos Bay (TSB; 12°50'S; 38°38'W), Bahia (BA) State. Both diving techniques were used to survey several sites at Ilha Grande Bay and Sun Coast rock shores, Rio de Janeiro State (RJ), southeastern Brazil.

Data collection

Data was collected between April 2013 and November 2017, all interactions between *Ophiothela mirabilis* and marine sponges were photographed *in situ*

Table 1. Sites surveyed. MA: Maranhão, CE: Ceará, RN: Rio Grande do Norte, FN: Fernando de Noronha Archipelago (PE: Pernambuco state), TSB: Todos os Santos Bay (BA: Bahia state), IGB: Ilha Grande Bay, and Sun Coast (RJ: Rio de Janeiro state). See Fig. 1 for map of all sites surveyed. (*) sponge-*Ophiothela mirabilis* Verrill, 1867 association.

State	Site name	Map ID	Longitude (West)	Latitude (South)	Type of Substrate	Depth (m)	Date
Northeast (NE) region							
MA	Araçagi	C1	-44,204167	-2,463055	Natural	up to 1	Nov, 5 2017
	Panaquatira	C2	-44,022778	-2,498611	Natural	up to 1	Nov, 5 2017
CE	Tide pools	C3	-38,800806	-3,546639	Natural	up to 2	Apr, 8–11 2016
	Pedra da Risca do Meio	C4	-38,433333	-3,55	Natural	15–25	Apr, 12 2016
RN	Maracajá	C5	-35,288847	-5,3985	Natural	3–8	Apr, 15 2016
	Pirambúzios	C6	-35,106311	-6,005006	Natural	up to 1	Apr, 17–18 2016
PE	Fernando de Noronha Archip.	C7	-32,410556	-3,840278	Natural	10–30	Apr, 20–24 2016
BA	Frades Island	C8	-38,6429	-12,816817	Natural	3–8	Feb, 17 2016
(TSB)	Barra Port*	Sa	-38,5337	-13,004236	Natural	1–5	Feb, 15–20 2016
	Germânia shipwreck*	Sb	-38,543889	-13,008611	Artificial	4–7	Feb, 16 2016
	Boião*	Sc	-38,533333	-13,016667	Artificial	18–20	Feb, 16 2016
	Deck*	Sd	-38,517542	-12,967542	Artificial	1–3	Feb, 18 2016
	East waterbreak*	Se	-38,520011	-12,970281	Artificial	5–10	Feb, 18 2016
	North waterbreak*	Sf	-38,515219	-12,964194	Artificial	5–10	Feb, 17 2016
Southeast (NE) region							
RJ	Tartaruga, Búzios*	Sg	-41,90155	-22,752806	Natural	1–3	Mar, 16 2013
Sun Coast	Prainha, Arraial do Cabo	C9	-42,020253	-22,959956	Natural	1–3	Jan–Mar, 2013
IGB	Abraãozinho*	Sh	-44,154311	-23,133833	Natural	3–8	Apr, 2013 to Jun, 2015
	Crena*	Si	-44,155269	-23,137528	Natural	1–3	Dec, 2015
	Abraão Island*	Sj	-44,166444	-23,114972	Natural	3–8	Apr, 2013 to Jun, 2015
	Barreto*	Sk	-44,190556	-23,101944	Natural	3–15	Apr, 2013 to Jun, 2015
	Lagoa Azul*	Sl	-44,239703	-23,086033	Natural	3–8	Apr, 2013 to Jun, 2015
	Caxadaço*	Sm	-44,163214	-23,174519	Natural	3–8	Aug–Sep, 2013
	Jorge Grego	C10	-44,156064	-23,172736	Natural	10–20	Sep, 2013
	Parnaióca	C11	-44,254244	-23,188575	Natural	3–15	Feb–Mar, 2014
	Deck*	Sn	-44,494519	-23,023336	Artificial	3–8	Jul, 19 2013
	Sandri Island*	So	-44,48735	-23,042336	Natural	3–15	Jul, 18 2013
	Araraquara Island*	Sp	-44,55585	-23,054631	Natural	3–8	Jul, 19 2013

(Figure 2), using CANON G15 camera, following standard protocols (Álvarez et al. 2008; Beuchel et al. 2010; Van Rein et al. 2011; Mantelatto et al. 2013; Berov et al. 2016; Moreno 2020), used previously with sponges (e.g.: Berman et al. 2013; Cárdenas et al. 2016). The number of individuals (abundance) of *O. mirabilis* on each sponge individual was quantified (photo image analysis software ImageJ version 1.49n, Schneider et al. 2012) in each photo to create a data matrix of sponge species (Nsp) versus ophiuroid (Nom) abundances.

Larger and common sponges were identified *in situ* by expert researchers using field guides, but thin encrusting individuals were collected for spicule and skeleton architecture visualization and identification (Hooper and van Soest 2002) to avoid misidentification. Slides were prepared following protocols of Hajdu et al. (2011). All collected sponge specimens were deposited at Universidade do Estado do Rio de Janeiro and Museu Nacional, Universidade Federal do Rio de Janeiro Porifera collections. The identification of *O. mirabilis* in the photos was based on the external morphology, such as central disc size, color and number of arms (Clark 1976), which are unique in the TWA.

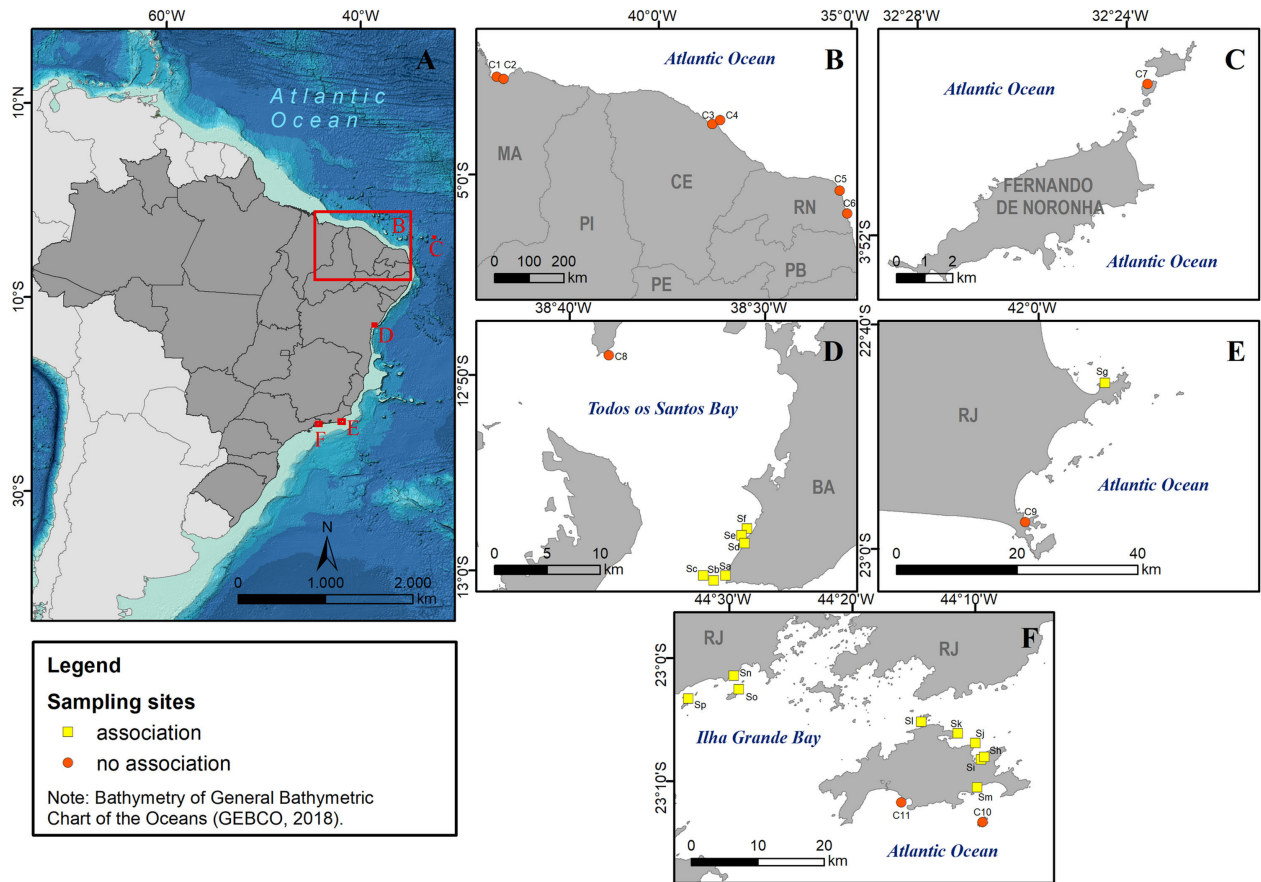


Figure 1. Brazilian states surveyed (hatched). Inset maps show sites where *Ophiothela mirabilis* Verrill, 1867 was recorded in association with sponges (Bahia – BA, and Rio de Janeiro – RJ, states). Refer to Table 1 for geographic names and coordinates.

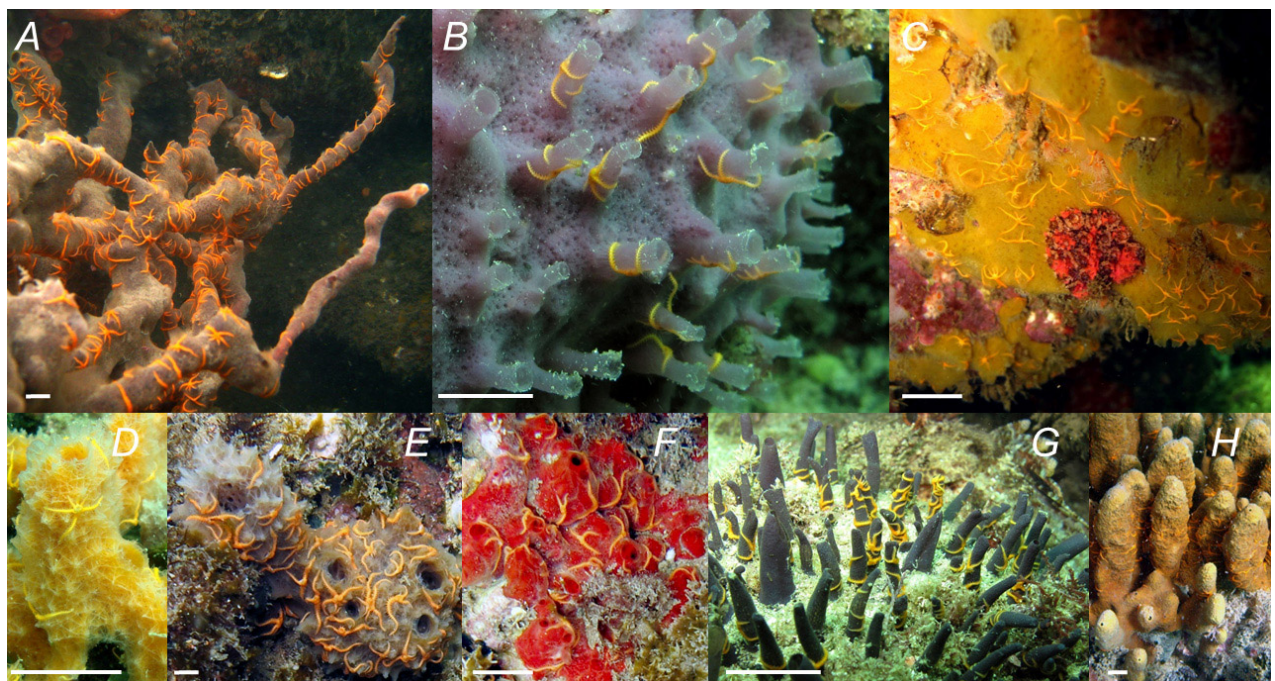


Figure 2. *In situ* photos of the epibiosis of the non-indigenous ophiuroid *Ophiothela mirabilis* Verrill, 1867 on marine sponges with different growth forms, surface types, and colors along the Brazilian coast. A: *Mycale (Zygomycale) angulosa* (Duchassaing & Michelotti, 1864), B: *Siphonochalina* sp., C: *Mycale (Aegogropila) americana* van Soest, 1984, D: *Callyspongia* sp. 1 yellow, E: *Callyspongia* sp. 1 green, F: *Monanchora arbuscula* (Duchassaing & Michelotti, 1864), G: *Polymastia janeirensis* Boury-Esnault, 1973, H: *Aplysina fulva* (Pallas, 1766). Photographs taken at A, B and G: Ilha Grande Bay, C: Angra dos Reis, H: Búzios, Rio de Janeiro State; D, E, and F: Todos os Santos Bay, Bahia State. Scale = 1 cm. Photos by Gisele Lôbo-Hajdu (A–G) and Humberto Fortunato (F).

Data analysis

Abundance of sponges (Nsp) harboring *O. mirabilis* individuals and abundance of the ophiuroid (Nom) were log+1 transformed and mean values were used to apply statistical analyses after verifying data normality (Kolmogorov-Smirnov test) and to reduce variance (Sokal and Rohlf 1981). Linear regression analysis and ANOVA one-way between the mean Nsp and the mean Nom were calculated to see the relationship between these metrics, excluding sponge species with only one individual in association with *O. mirabilis*, because mean and standard deviation values would not be detected.

In order to test putative preference for sponge phenotypes, ANOVA one-way was tested for sponges' morphotype, surface and color. Each of these traits was sorted in two categories: Morphotype – erect and flatten; Surface – irregular and smooth; Color – yellowish and light to dark. Sponge phenotypes are commonly used to discriminate species and morphotype variation may influence the associated biota, including ophiuroids (Neves and Omena 2003; Ávila and Ortega-Bastida 2014; Dahihande and Thakur 2017). The external classification used here was based in the Porifera Thesaurus (Boury-Esnault and Rützler 1997). ANOVA one-way also tested the Nsp and Nom mean values to evaluate our hypothesis that sponges possessing erect (easier to hold and possibly large amount of food), irregular (easier for the brittle star to attach) forms, and yellowish color would be preferred for *O. mirabilis*. Finally, ANOVA one-way was applied to evaluate whether the type of substrate (artificial or natural) where the sponges attach influences the presence of the ophiuroid. Although *O. mirabilis* were recorded on both natural and artificial substrates (Lawley et al. 2018), and large-scale changes in the surrounding ecosystem influence itinerant associated macrofauna (Gallucci et al. 2020), we consider here that invasive species (e.g. *O. mirabilis*) normally prefers artificial substrates (Ruiz et al. 1997; Glasby et al. 2007).

Raw data was used to calculate the Infestation rate (IF%), which is a kind of index used to evaluate pest threats, mostly in veterinarian studies (Isikber et al. 2016; Santos et al. 2017; Gharbi et al. 2020). It was calculated by the formula

$$IF(\%) = \left(\frac{Nom}{Nomt} \right) * 100,$$

where Nom is the abundance of *O. mirabilis* on each sponge species divided by the total number of *O. mirabilis* in the survey (Nomt) and multiplied by 100. Finally, a null probability was also calculated based on 1000 random permutations to evaluate whether the ophiuroid epibiosis is random. Probability data was Napierian log-transformed and plotted as random maximum, median and minimum values according to observed sponge-ophiuroid association data. All statistical analyses were done in Excel.

Table 2. Sponge-ophiuroid association at the Brazilian coast. *represent new species hosting *Ophiothela mirabilis* Verrill, 1867. Nsp = sponge abundance; Nom = *O. mirabilis* abundance on each sponge species; Transformed (log+1) and standardized (mean and standard deviation, St. dev.) for sponge (sp) and *O. mirabilis* (om) abundances; % is related to the infestation rate of *O. mirabilis* on each sponge species. Bold indicates top 10 host species in total ophiuroid abundance.

Species	N sp	log+1 sp	Mean (sp)	St. dev. (sp)	N om	log+1 om	Mean (om)	St. dev. (om)	Infestation rate (%)
<i>Amphimedon viridis</i> Duchassaing & Michelotti, 1864*	8	0.95	0.56	0.27	28	1.46	3.50	3.96	0.55
<i>Aplysilla rosea</i> (Barrois, 1876)*	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
<i>Aplysina cauliformis</i> (Carter, 1882)*	8	0.95	0.86	0.42	83	1.92	10.38	13.45	1.62
<i>Aplysina fulva</i> (Pallas, 1766)	1	0.30	0.00	0.00	107	2.03	0.00	0.00	2.09
<i>Aplysina insularis</i> (Duchassaing & Michelotti, 1864)*	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
<i>Callyspongia</i> sp. 1	81	1.91	0.99	0.48	1349	3.13	16.65	23.14	26.34
<i>Callyspongia</i> sp. 2	3	0.60	0.68	0.33	14	1.18	4.67	3.21	0.27
<i>Chelonaphysilla erecta</i> (Row, 1911)	4	0.70	0.72	0.32	22	1.36	5.50	5.20	0.43
<i>Chondrosia</i> sp.*	2	0.48	1.36	0.03	44	1.65	22.00	1.41	0.86
<i>Clathria (Microciona) campecheae</i> Hooper, 1996*	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
<i>Clathria (Thalysias) curacaoensis</i> Arndt, 1927*	1	0.30	0.00	0.00	39	1.60	0.00	0.00	0.76
<i>Clathrina confifera</i> Klautau & Borojevic, 2001*	1	0.30	0.00	0.00	2	0.48	0.00	0.00	0.04
<i>Darwinella</i> sp.*	2	0.48	0.30	0.00	2	0.48	1.00	0.00	0.04
<i>Desmapsamma anchorata</i> (Carter, 1882)	34	1.54	0.91	0.47	528	2.72	15.53	27.83	10.31
<i>Dysidea etheria</i> de Laubenfels, 1936	1	0.30	0.00	0.00	11	1.08	0.00	0.00	0.21
<i>Dysidea janiae</i> (Duchassaing & Michelotti, 1864)*	12	1.11	0.70	0.34	71	1.86	5.92	6.72	1.39
<i>Echinodictyum dendroides</i> Hechtel, 1983*	1	0.30	0.00	0.00	16	1.23	0.00	0.00	0.31
<i>Haliclona (Reniera) chlorilla</i> Bispo, Correia & Hajdu, 2016*	1	0.30	0.00	0.00	2	0.48	0.00	0.00	0.04
<i>Haliclona (Reniera) manglaris</i> Alcolado, 1984	2	0.48	1.28	0.47	48	1.69	24.00	8.30	0.94
<i>Haliclona (Soestella) melana</i> Muricy & Ribeiro, 1999	4	0.70	0.52	0.33	13	1.15	3.25	3.86	0.25
<i>Haliclona</i> sp.*	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
<i>Hymeniacidon</i> sp.*	2	0.48	1.22	0.53	44	1.65	22.00	22.63	0.86
<i>Iotrochota arenosa</i> Rützler, Maldonado, Piantoni & Riesgo, 2007*	3	0.60	0.30	0.00	3	0.60	1.00	1.00	0.06
<i>Iotrochota birotulata</i> (Higgin, 1877)	4	0.70	0.71	0.54	34	1.54	8.50	12.48	0.66
<i>Ircinia felix</i> (Duchassaing & Michelotti, 1864)*	6	0.85	1.05	0.41	99	2.00	16.50	22.04	1.93
<i>Ircinia strobilina</i> (Lamarck, 1816)*	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
<i>Monanchora arbuscula</i> (Duchassaing & Michelotti, 1864)	21	1.34	1.02	0.56	458	2.66	21.81	31.65	8.94
<i>Mycale (Aegogropila) americana</i> van Soest, 1984	1	0.30	0.00	0.00	149	2.18	0.00	0.00	2.91
<i>Mycale (Arenochalina) laxissima</i> (Duchassaing & Michelotti, 1864)	1	0.30	0.00	0.00	13	1.15	0.00	0.00	0.25
<i>Mycale (Carmia) magnirhaphidifera</i> van Soest, 1984*	2	0.48	0.80	0.14	11	1.08	10.00	2.12	0.21
<i>Mycale (Carmia) microsigmatosa</i> Arndt, 1927*	3	0.60	0.67	0.35	14	1.18	5.67	4.04	0.27
<i>Mycale (Zygomycale) angulosa</i> Duchassaing & Michelotti, 1864	31	1.51	1.32	0.59	1641	3.22	35.71	90.41	32.04
<i>Niphates erecta</i> Duchassaing & Michelotti, 1864*	5	0.78	1.11	0.52	111	2.05	22.20	29.97	2.17
<i>Polymastia janeirensis</i> Boury-Esnault, 1973	4	0.70	0.82	0.24	25	1.41	6.25	3.10	0.49
<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)*	5	0.78	0.89	0.67	93	1.97	18.60	28.61	1.82
<i>Siphonochalina</i> sp.*	1	0.30	0.00	0.00	42	1.63	0.00	0.00	0.82
<i>Tedania (Tedania) ignis</i> (Duchassaing & Michelotti, 1864)	1	0.30	0.00	0.00	1	0.30	0.00	0.00	0.02
Total	261				5122				100

Results

From 27 sites surveyed along the Brazilian coast, the association between sponges and *Ophiothela mirabilis* was recorded at 16 sites located in Bahia State (Todos os Santos Bay – TSB) and Rio de Janeiro State (Ilha Grande Bay – IGB, Tartaruga, and Búzios) (see Table 1, Figure 1). A total of 5122 individuals of *O. mirabilis* were associated to 37 sponge species represented by 261 individuals (Figure 2). Of those species, 22 are considered new hosts for the non-indigenous ophiuroid (Table 2, Supplementary material Table S1).

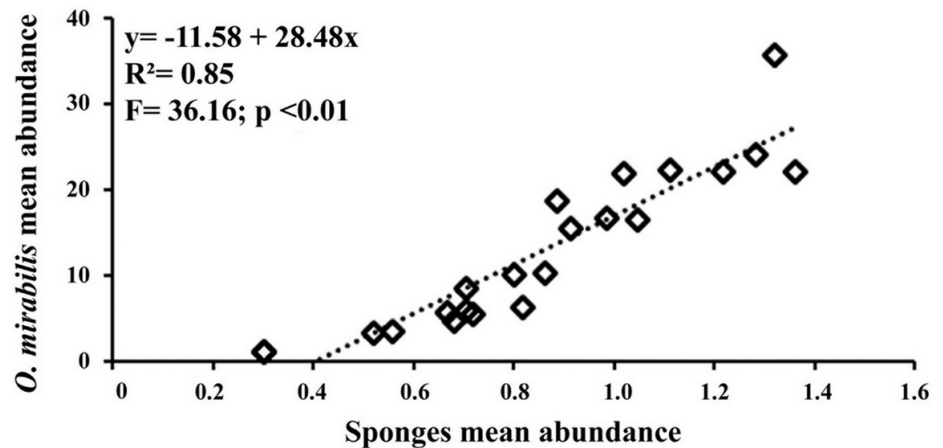


Figure 3. Regression analysis between log+1 mean abundance of *Ophiothela mirabilis* Verrill, 1867 in response to log+1 sponge species mean abundance data.

Even though 65% of the host species are widely distributed along the Brazilian coast and have high depth range, *O. mirabilis* was not found to the north of Bahia State (Maranhão, Ceará, Rio Grande do Norte States and Fernando de Noronha Archipelago).

Callypongia sp. 1 (Nsp = 81; Nom = 1349), *Desmapsamma anchorata* (Carter, 1882) (Nsp = 34; Nom = 528) and *Mycale* (*Zygomycale*) *angulosa* (Duchassaing & Michelotti, 1864) (Nsp = 31; Nom = 1641) were responsible for almost 70% of the sponge-ophiuroid associations, and 10 species represented 90% of hosting (Table 2). In order to avoid chance associations, 15 sponge species with only one individual hosting *O. mirabilis* were excluded, such as *Aplysina fulva* (Pallas, 1766) (Nom = 107) and *Mycale* (*Aegogropila*) *americana* van Soest, 1984 (Nom = 149). This approach evidenced a positive correlation (Figure 3) between the mean abundance of 22 species of sponge hosts and the mean abundance of epibionts on each sponge host ($R^2 = 0.85$, $F = 36.16$, $p < 0.001$). After 1000 random permutations, *A. fulva*, *M. (Z.) angulosa* and *M. (A.) americana* were observed above the 95% confidence level, but, only *M. (Z.) angulosa* should be considered as preferentially used as host by *O. mirabilis*, following the approach mentioned above (Figure 4).

Ophiothela mirabilis lived on sponges attached on both artificial and natural substrates, without statistical difference, and were recorded here in a totality of seven different growth forms, six surface types and 18 colors (Table 3, Figure 5). The highest mean values of each sponge trait were related to massive growth form (27.8), smooth and velvety surface (30.9) and yellow color (43.5). Surface was the only sponge morphological trait to show statistical significance ($F = 3.76$, $p < 0.001$). Our hypothesis of preference for erect, irregular, and yellowish sponges hosting *O. mirabilis* was statistically refused ($p = 0.78$; Table S2).

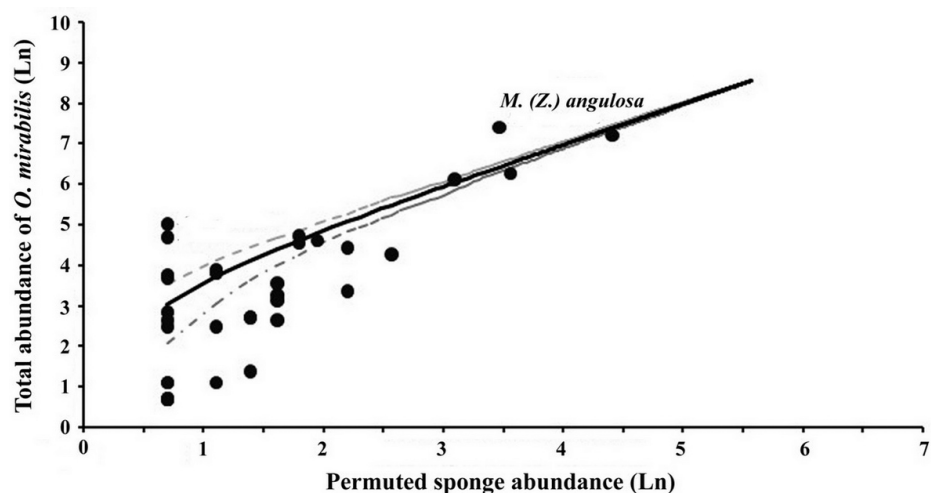


Figure 4. Probability representation of the total number of *Ophiothela mirabilis* Verrill, 1867 on each individual sponge based on 1000 permutations of the data. Abundance of sponge species were Napierian log transformed and represented as black circles, while the median is represented by a solid black line, the maximum possible random values after permutations by a dashed upper line, and the minimum possible random values by a dot-dashed bottom line (confidence level in between dashed lines).

Discussion

Epibiosis of the non-indigenous ophiuroid *Ophiothela mirabilis* on marine sponges was quantitatively evaluated along the Brazilian coast. Since 2000, this species is spreading at the TWA Ocean (Hendler et al. 2012; Hendler and Brugneaux 2013; Lawley et al. 2018), on both natural and artificial substrates, mostly in association with sponges and gorgonian corals (Hajdu et al. 2011; Mantelatto et al. 2016). We recorded *O. mirabilis* being hosted by several sponge species with a wide variety of morphotypes, indicating its generalist behavior and rejecting the hypothesis that *O. mirabilis* prefer erect, irregular, and yellowish hosts.

Although several sponge species hosting *O. mirabilis* in this survey can be found from Maranhão to Rio de Janeiro states (see Muricy et al. 2011), the non-indigenous ophiuroid was only observed in Bahia and Rio de Janeiro states, approximately 1200 km apart in a straight line. In Rio, the Ilha Grande Bay and one beach of the Sun Coast presented the sponge-ophiuroid association, and in Bahia several sites at the Todos os Santos Bay were infested by the non-indigenous species. This finding contrasts with previous data that also indicate its distribution for the coastline of Ceará and Pernambuco at the Northeast region of Brazil (Mantelatto et al. 2016; Thé de Araújo et al. 2018), and off Amazon River (Moura et al. 2016). Most likely the absence of *O. mirabilis* in the north coast of Northeastern region in comparison to Bahia (NE region) and Rio de Janeiro states (SE region) is related to the low effort at this area, which is composed by hugely neglected, in terms of benthic diversity, sandstone reefs and beach-rock formation (Rabelo et al. 2015; Soares et al. 2016; Fortunato et al. 2020b) instead of rocky shores and coral reefs.

Table 3. Comparison within sponge morphological traits and between subgroups with general abundance for both sponges (Nsp) and *Ophiothela mirabilis* Verrill, 1867 (Nom), percentage values for both abundances and mean (with standard deviation, St. dev.) for the ophiuroid associated to each sponge external trait. Higher abundances and mean values are in bold.

Phenotype traits	Nsp	%	Nom	%	Mean (St.dev.)	Subgroup (%)	Mean (St.dev.)
Hypothesis test							
Erect, irregular, yellow	28	10.7	501	9.8	17.9 (0.52)		
Flatten, smooth, light to dark	25	9.6	718	14.0	28.7 (0.56)		
Morphotype							
Digitate	114	43.7	2340	45.7	20.5 (41.9)	Erect (58.5)	748.7 (1080.0)
Ramose	8	3.1	83	1.6	10.4 (12.6)		
Papillate	5	1.9	67	1.3	13.4 (14.5)		
Lobate	41	15.7	505	9.9	12.3 (16.4)	Flatten (41.5)	709.0 (482.9)
Massive	40	15.3	1110	21.7	27.8 (61.9)		
Repent	10	3.8	173	3.4	17.3 (21.9)		
Encrusting	43	16.5	844	16.5	19.6 (32.2)		
Surface							
Conulose	109	41.8	1719	33.6	15.8 (22.3)	Irregular (38.9)	497.5 (819.7)
Corrugate	1	0.4	1	0.0	0		
Microspinate	3	1.1	50	1.0	16.7 (16.7)		
Slightly rough	24	9.2	220	4.3	9.2 (21.1)	Smooth (61.1)	1566.0 (792.0)
Smooth and velvety	58	22.2	2126	41.5	15.2 (26.5)		
Smooth	66	25.3	1006	19.6	39.0 (75.8)		
Color							
White	16	6.1	204	4.0	12.8 (19.4)	Light to dark (63.2)	294.1 (377.0)
White and gray	2	0.8	44	0.9	22.0 (1.4)		
Gray	1	0.4	5	0.1	0		
Beige-pinkish	1	0.4	1	0.0	0		
White-purplish	3	1.1	22	0.4	7.3 (5.0)		
Pinkish	34	13.0	528	10.3	15.5 (27.4)		
Pink	1	0.4	1	0.0	0		
Purple	26	10.0	916	17.9	35.2 (71.7)		
Green	26	10.0	425	8.3	16.3 (20.3)		
Blue	43	16.5	1012	19.8	23.5 (54.0)		
Black	16	6.1	77	1.5	4.8 (6.4)	Yellowish (36.8)	269.6 (215.8)
Red	32	12.3	578	11.3	18.1 (26.5)		
Orange	27	10.3	374	7.3	13.9 (16.2)		
Yellow	6	2.3	261	5.1	43.5 (61.0)		
Brown	7	2.7	112	2.2	16.0 (18.9)		
Brownish	12	4.6	479	9.4	39.9 (58.9)		
Brown-yellowish	5	1.9	58	1.1	11.6 (15.4)		
Brown-purplish	3	1.1	25	0.5	8.3 (4.2)		
Sponge Substrate							
Artificial	80	30.7	997	19.5	12.5 (14.3)		
Natural	181	69.3	4125	80.5	22.8 (47.1)		

Brittle stars were recorded associated to sponges in 16 out of the 27 sites surveyed, including all locations with artificial substrates (buoys, breakwaters, shipwrecks, decks), where sponges attach, in both Bahia and Rio de Janeiro states. Ruiz et al. (1997) and Bumber et al. (2016) reported the use of artificial substrates as steppingstones for the expansion of non-indigenous species. Rhodolith beds, coral and sponge gardens in the mesophotic zone off Amazon River, can probably be used by *O. mirabilis* to spread, in the natural environment, from the Caribbean to Brazil, and the other way around (Hendler and Brugneaux 2013; Cordeiro et al. 2015; Moura et al. 2016; Vale et al. 2018). It could become much more problematic, not only for *O. mirabilis*, but also for a worse threat with a

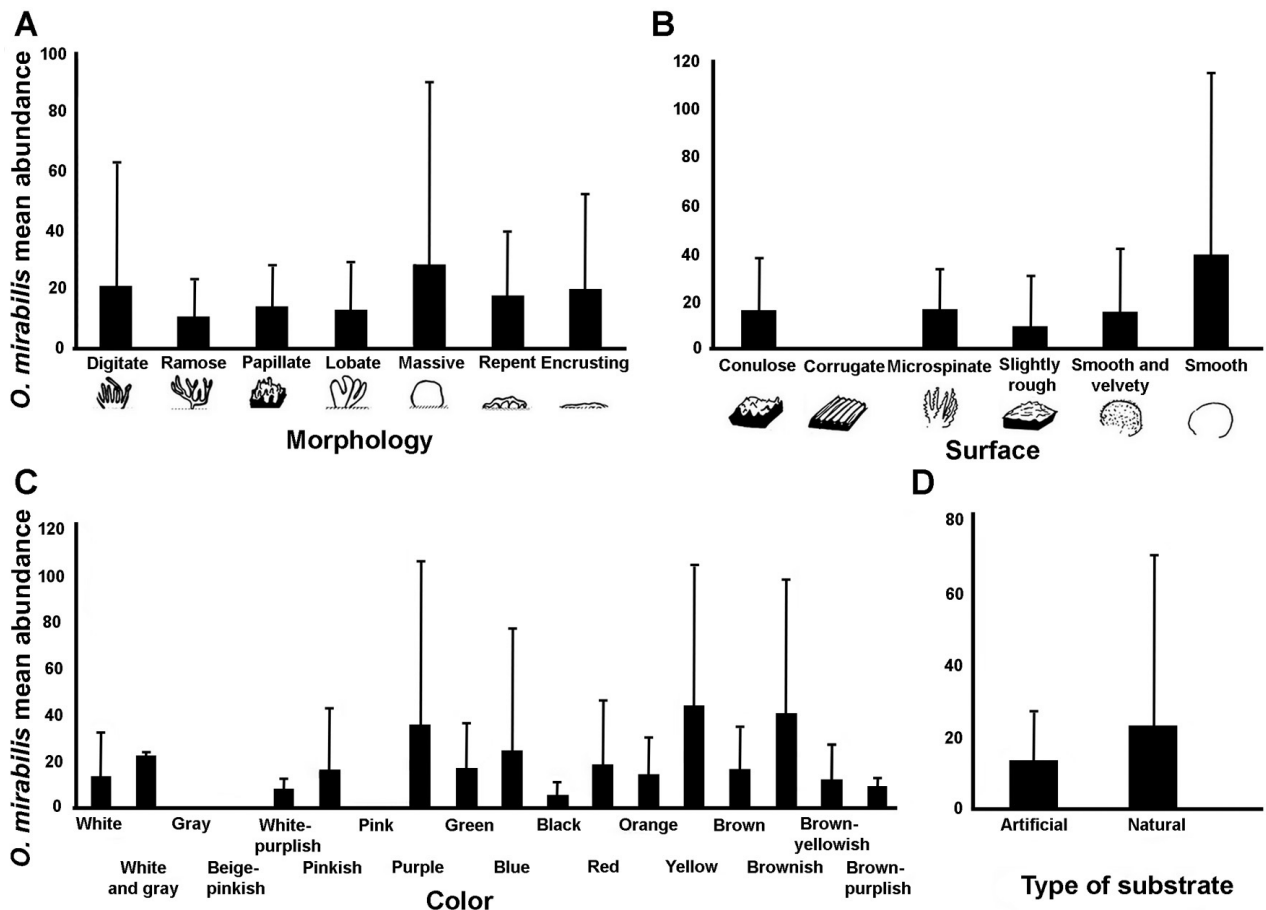


Figure 5. Mean abundance (with standard errors) of *Ophiothela mirabilis* Verrill, 1867 in response to sponge phenotype traits and sponge habitat. A: growth form (erect or flattened), B: surface type (irregular or smooth), C: color (light to dark or yellowish), and D: sponge habitat (artificial or natural substrates).

new invader, if the Brazilian policy to sink scrapped ships, trains, and airplanes to promote tourism diving get to be approved (Miranda et al. 2020).

As recorded in Ceará, Rio de Janeiro, Paraná and Santa Catarina states (Mantelatto et al. 2016; Bumbeer et al. 2016; Lawley et al. 2018; Thé de Araújo et al. 2018), *O. mirabilis* is closely related to artificial habitats, especially those used as supporting areas for offshore gas and oil prospecting, shipyard, platforms parking, frequently receiving ballast water, besides the use for recreational activities, with a large transit of boats (Creed et al. 2007; Hatje and de Andrade 2009; Melo et al. 2009; Oigman-Pszczol and Creed 2011; Johnsson and Ikemoto 2015). These maritime activities are the major vectors for the introduction of non-indigenous species (Carlton and Geller 1993; Ferreira et al. 2009; Zanella 2015), which is one of the most powerful threats to marine habitats today. Specifically, at Todos os Santos and Ilha Grande Bays the increase in the maritime traffic has caused an upgrade in the number of alien species in the last two decades (De Paula and Creed 2004; Silva et al. 2011; Almeida et al. 2015; Mantelatto et al. 2016; Miranda et al. 2016; Skinner et al. 2016; Teixeira and Creed 2020). For instance, 16% of the benthic community of Ilha Grande Bay (IGB) was represented by non-native species (Ignacio et al.

2010), some of those with the possibility of changing the local ecosystem (Lages et al. 2011). In turn, invasive species monitoring programs have been conducted (Creed et al. 2017; Teixeira and Creed 2020), especially in respect to the sun coral species *Tubastraea* spp., but without success in the species eradication, due to the slow recognition of the problem, and the rapid expansion of the infestation with high level of reproduction (Leão et al. 2011; Silva et al. 2011; Creed et al. 2017; Teixeira and Creed 2020). To avoid this problem, a management, and perhaps eradication, national project for *O. mirabilis* must be created as soon as possible.

Our data increases the number of benthic hosts of *O. mirabilis* to more than 50 sponge species in the TWA Ocean, emphasizing that this non-indigenous ophiuroid is an extreme generalist (Mantelatto et al. 2016, Lawley et al. 2018). Brittle stars and sponges' associations are widely known and possibly sponges are the most preferable hosts for them (Hendler 1984; Clavico et al. 2006; Henkel and Pawlik 2014). From 37 sponge species analyzed, *Aplysina fulva*, *Mycale* (A.) *americana* and *M. (Z.) angulosa* stand out for hosting more *O. mirabilis* than they could/should probabilistically. The association of *O. mirabilis* with *A. fulva* and *M. (A.) americana* must be considered random because these sponge species are very common in Rio de Janeiro and Bahia states (Muricy and Hajdu 2006; Hajdu et al. 2011; Fortunato et al. 2020a), but only one individual of each was registered hosting the ophiuroid herein. In turn, 31 individuals of *M. (Z.) angulosa* hosted 1641 ophiuroids (mean 35.71), indicating a preference for this species. It has erected and digitated growth form, smooth and velvety surface, which may facilitate ophiuroids attaching, and is probably the preferred sponge species to locally host *O. mirabilis*. The blue or purple color of the sponge did not prevent the yellow ophiuroid epibiosis, which indicates it does not need camouflage in the invaded region. Probably, more important is the chemical defense promoted by *M. (Z.) angulosa*, which avoids crabs and reef fishes (Reppso et al. 2016) and have been recorded as a living hotel for several epi- and endobionts (Duarte and Nalesso 1996; Costa et al. 2015).

Callyspongia sp. 1, *D. anchorata* and *M. (Z.) angulosa* represented 70% of association with *O. mirabilis*. They have erect morphology, but only the former has irregular surface, all possess quite different colors. This morphological variability and absence of preference for a certain trait proves once more the generalist strategy of *O. mirabilis*. This result partially differs from the work of Dahihande and Thakur (2017), who clearly reported a preference of the brittle star *Ophiactis modesta* (Brock, 1888) for the massive over partially buried growth form of the sponge *Biemna fortis* (Topsent, 1897), under high suspended particulate matter (SPM), in Indian Ocean. Itinerant benthic macrofauna can choose the best habitat, and sponges give a combination of diverse morphology and chemical defense for ophiuroids, which promote refuge from competitors

and predators (Majer et al. 2009), and high food availability (Henkel and Pawlik 2014). Some authors have experimentally shown by choice assays that ophiuroids, including *O. mirabilis*, can choose their preferred sponge morphotype (Dahihande and Thakur 2017), and choose for physical or chemical treatments in relation to the Brazilian gorgonian *Phyllogorgia dilatata* (Esper, 1806) (Ribeiro et al. 2017). Based on physical and chemical aspects, further experimental studies must be applied to understand what makes *O. mirabilis* prefers the bluish *M. (Z.) angulosa* instead of other yellow, erect, and smooth or irregular sponges.

A strong positive correlation between the abundance of sponges and the abundance of ophiuroids on each sponge individual was found, but no morphological preference was statistically proved. *Ophiothela mirabilis* was not affected by artificial or natural substrate. In this sense, monitoring programs at Todos os Santos Bay and Ilha Grande Bay are highly recommended to further study the ophiuroid biology, genetic diversity and potential ecological instability that may cause damage to these local hotspots of marine biodiversity.

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Ethics and permits

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All necessary permits for animals sampling in the current study have been obtained from: SISBIO permits Nrs. 52968-1 and 10357-1, NUC-IDEMA permit No. 013/2016, “Instituto Estadual do Ambiente” (INEA) permit # 030/2012, and “Instituto Chico Mendes de Conservação da Biodiversidade” (ICMBio) permit #33745-1.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Raw data of sponges-*Ophiothela mirabilis* associations.

Table S2. ANOVA one-way analyses for hypothesis evaluation.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Fortunato_Lobo-Hajdu_SupplementaryTables.xlsx