



Sargassum species as hydrozoans substrates: Key patterns of association or just availability?

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ABSTRACT

The genus *Sargassum* comprises both benthic and holopelagic species, serving as basibionts for numerous marine organisms, including frequent epibiotic occurrences of hydrozoans (Cnidaria). Several aspects of the epibiotic interaction between hydrozoans and *Sargassum* species remain insufficiently explored. This includes patterns such as the hydrozoan community's composition and abundance across sections and structures of *Sargassum*. To address these gaps, we conducted an investigation aiming to uncover potential differences in the species composition and abundance of hydrozoan epibionts on benthic and holopelagic *Sargassum* species (BSS and HSS, respectively) from the Atlantic and Pacific Oceans of Mexico. Additionally, we sought to characterize hydrozoan epibionts preferences for specific sections and structures of *Sargassum*. Our analysis identified 18 hydrozoan epibiont species on *Sargassum*, belonging to Leptothecata (88.9%) and anthoathecata (11.1%), with one new register for *Sargassum* species. Each *Sargassum* species harbored a distinct hydrozoan epibiont species with a marked higher mean total coverage. The total percentage coverage of hydrozoans on BSS exhibited less variability than HSS. The basal section of BSS hosted the highest number of species. Concerning *Sargassum* structures, a greater species richness was found on the axis and the blades. Our study also demonstrates that differences in hydrozoan species primarily depend on the geographical distribution of *Sargassum* species.

1. Introduction

The genus *Sargassum* (Phaeophyceae: Sargassaceae) comprises 360 accepted marine brown algae distributed globally in tropical and temperate waters (Guiry and Guiry, 2023). These algae can form massive benthic and holopelagic populations, creating complex ecosystems that offer substrate, food, and shelter for numerous organisms (Gower et al., 2013; Stiger-Pouvreau et al., 2023). Certain *Sargassum* species have applications in various human sectors such as animal feed, pharmacology, and cosmetics (Stiger-Pouvreau et al., 2023), while others are associated with ecological effects and impacts on human activities and health, such as the introduction of exotic *Sargassum* species, the occurrence of large holopelagic *Sargassum* accumulations in the Caribbean, and the presence of potential pathogens on *Sargassum* (Britton-Simmons, 2004; Van Tussenbroek et al., 2017; Gower and King,

2019; Rodríguez-Martínez et al., 2019; Mincer et al., 2023; Pérez-Posada et al., 2023).

Sargassum is a well-documented basibiont for various marine taxa, including Ascidiacea, Acarina, Cirripedia, Gastropoda, Gymnolaemata, Hydrozoa, Nematoda, and turbellarians (Weis, 1968; Abé et al., 2013; Alleyne et al., 2023). Hydrozoans (phylum Cnidaria) are ubiquitous components of marine food webs, associated with diverse organisms, including quite frequent epibiotic occurrences on *Sargassum* (Nishihira, 1965, 1968; Boero, 1984; Fitridge et al., 2012; Carral-Murrieta et al., 2023a). Furthermore, as the *Sargassum* ages, it tends to host a higher abundance of hydrozoans, which makes it less suitable for human utilization (Alleyne et al., 2023).

A recent global review listed 131 hydrozoan species associated with only 26 *Sargassum* species (Carral-Murrieta et al., 2023a). Hydrozoans are known as substrate generalists, colonizing various surfaces,

Abbreviations: BSS, Benthic *Sargassum* species; HSS, Holopelagic *Sargassum* species.

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including natural and artificial substrates like floating docks, boats, vertebrates, aquatic plants, and macroalgae (Frick et al., 2003; Oliveira and Marques, 2007; Calder et al., 2014). Their colonization typically begins with swimming or drifting larvae, often in the form of a planula, which settles on a substrate and develops into a solitary polyp or a colony (Sommer, 1992). Efficient attachment to different substrates relies on a hydrorhiza, a net-like structure that extends onto the substrate, eventually giving rise to new stems or modules, such as hydranths (Mills et al., 2007).

Previous studies have suggested that the epibiotic interaction between *Sargassum* species and hydrozoans can be influenced by various factors, including morphological, behavioral, developmental, and ecological characteristics. It was found that hydrozoans possessing a chitin exoskeleton around the hydranth (= Leptothecata) are more prevalent than those lacking this morphological structure (i.e., the non-monophyletic anthoathecate), as this structure usually allows

Leptothecata to endure adverse environmental conditions (cf., Mendoza-Becerril et al., 2020a). Additionally, different hydrozoans tend to occupy specific areas on the algal thallus, which relates to larval settlement patterns and space competition (Nishihira, 1973; Ryland, 1974). Other studies have focused on seasonal patterns of hydroid cover (Cunha and Jacobucci, 2010) and their growth on specific sections or morphological structures along *Sargassum* thalli (Mendoza-Becerril et al., 2020a; Niemann, 1986; Nishihira, 1973; Rackley, 1974; Ryland, 1974). Furthermore, *Sargassum*'s morphological complexity and the presence of hydrozoans are directly related to the assemblage of other epibionts, such as bryozoan and caprellids (Ryland, 1974; Jackson, 1977; Carvalho et al., 2022).

Despite the accumulated knowledge, epibiosis patterns between hydrozoans and *Sargassum* species remain insufficiently explored due to the absence of comprehensive and representative sample collections, methodological heterogeneity in prior research, and even the inherent

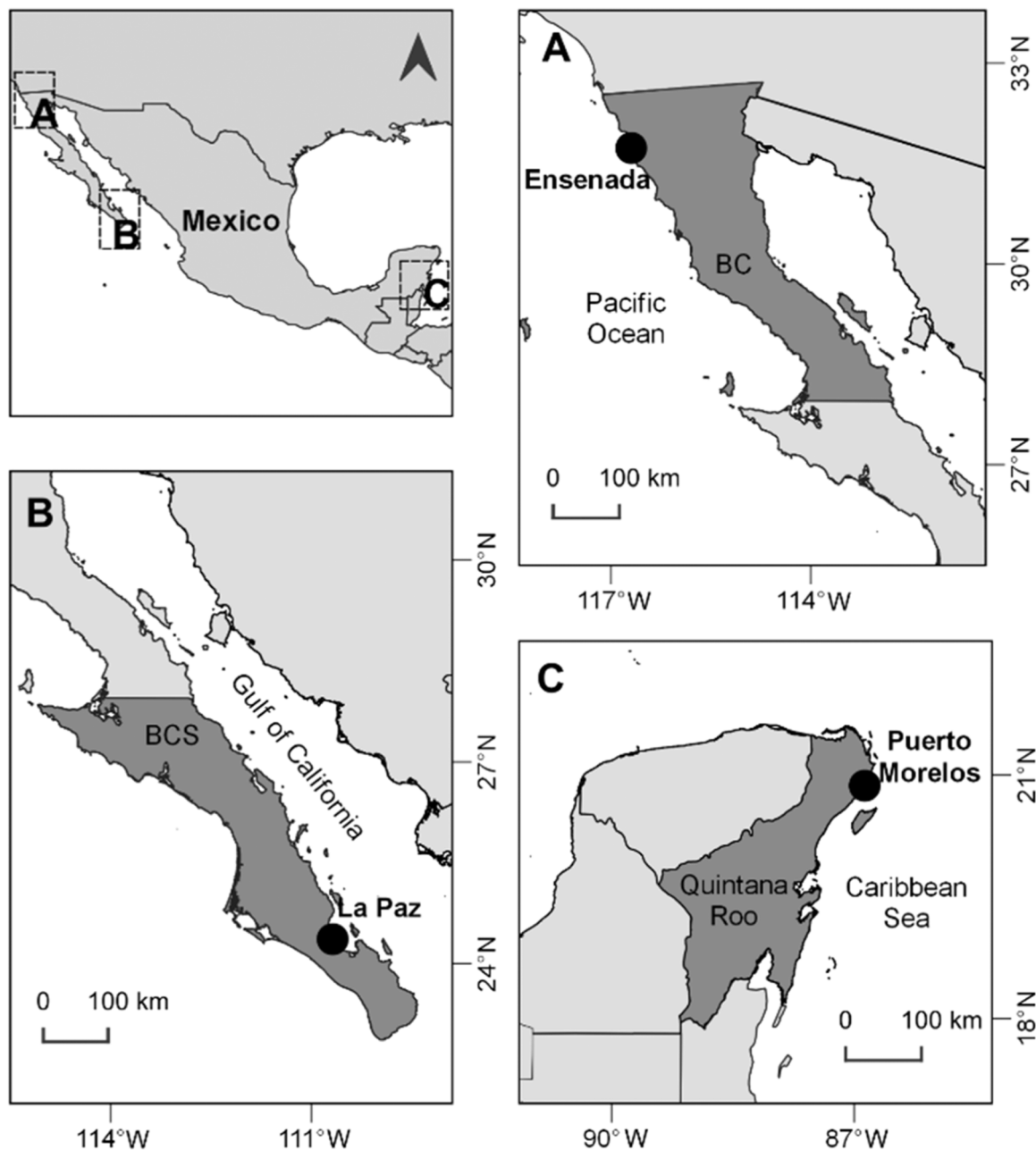


Fig. 1. Collection sites of *Sargassum* thalli. A) Bahía de Todos Santos, Ensenada, Baja California; B) San Juan de La Costa, La Paz, Baja California Sur; C) Puerto Morelos, Quintana Roo.

biological complexity of both the basibionts and epibionts. Therefore, this study pursued two primary objectives aimed at elucidating basic patterns: (1) to investigate potential differences in the species composition and abundance of epibiont hydrozoans on benthic and holopelagic *Sargassum* from the Atlantic and Pacific Oceans of Mexico and (2) to examine whether hydrozoan epibionts exhibit preferences for specific sections and structures of *Sargassum*.

2. Material and methods

2.1. *Sargassum* samples

Sargassum species were selected based on their distribution along Mexican coasts, considering that holopelagic species are restricted to the Atlantic Ocean (Rocha-Ramírez and Siqueiros-Beltrones, 1990; Gower et al., 2013; Aguilar-Rosas et al., 2014). Living thalli of five *Sargassum* species were collected for hydrozoan epibiont analysis between July 2020 and October 2021. Three benthic species were collected in the Pacific Ocean, *Sargassum horneri* (Turner) C. Agardh and *Sargassum muticum* (Yendo) Fensholt in Bahía de Todos Santos (Baja California), and *Sargassum horridum* Setchell & N.L. Gardner in San Juan de la Costa (Baja California Sur, southwest of the Gulf of California). While in the Caribbean, two morphotypes of holopelagic *Sargassum* [*Sargassum fluitans* III (Børgesen) Børgesen; *Sargassum natans* VIII (Linnaeus) Gaillon] were collected in Puerto Morelos (Fig. 1, Fig. 2A, Table 1).

In each site, *Sargassum* collection was conducted following the methods outlined by Carral-Murrieta (2021). For benthic species, twenty thalli of approximately 30 cm long and exhibiting hydrozoan cover were collected by scuba diving and snorkeling approximately

40–50 m from the coast. The holopelagic species were collected by scoop net from floating aggregations approximately 45 m from the coast. The benthic *Sargassum* species (hereafter referred to as BSS) were identified based on the keys and descriptions provided by Aguilar-Rosas and Galindo (1990), Aguilar-Rosas et al. (2007), and Andrade-Sorcía et al. (2014), while the holopelagic *Sargassum* species (HSS) were identified following Parr (1939) and Schell et al. (2015). Each *Sargassum* thallus was examined under a stereomicroscope and a light microscope to separate and identify epibiont hydrozoans in the laboratory. The identification of hydrozoans was carried out to the lowest possible taxonomic level based on faunal and taxonomic review articles (Calder, 1988, 1991, 1997, 2020; Mendoza-Becerril et al., 2020b; Calder et al., 2021).

2.2. Hydrozoan cover on *Sargassum*

On each *Sargassum* thallus, epibiont hydrozoan species cover estimates were determined following the procedures described by Cunha and Jacobucci (2010) and Mendoza-Becerril et al. (2020a). For BSS, each thallus was divided into four equal sections (B = Basal, starting from the holdfast; LM = Lower Middle; UM = Upper Middle; A = Apical) (Fig. 2B). In thalli greater than 30 cm, the first 7.5 cm of section B, the middle 7.5 cm of sections LM and UM, and the last 7.5 cm of section A were analyzed. For HSS, sections were not designated since their morphology does not have a differentiation between basal and apical sections. Additionally, the epibiont hydrozoan species cover in each of the *Sargassum* morphological structures (aerocysts, axis, blades, holdfast, receptacles) was documented.

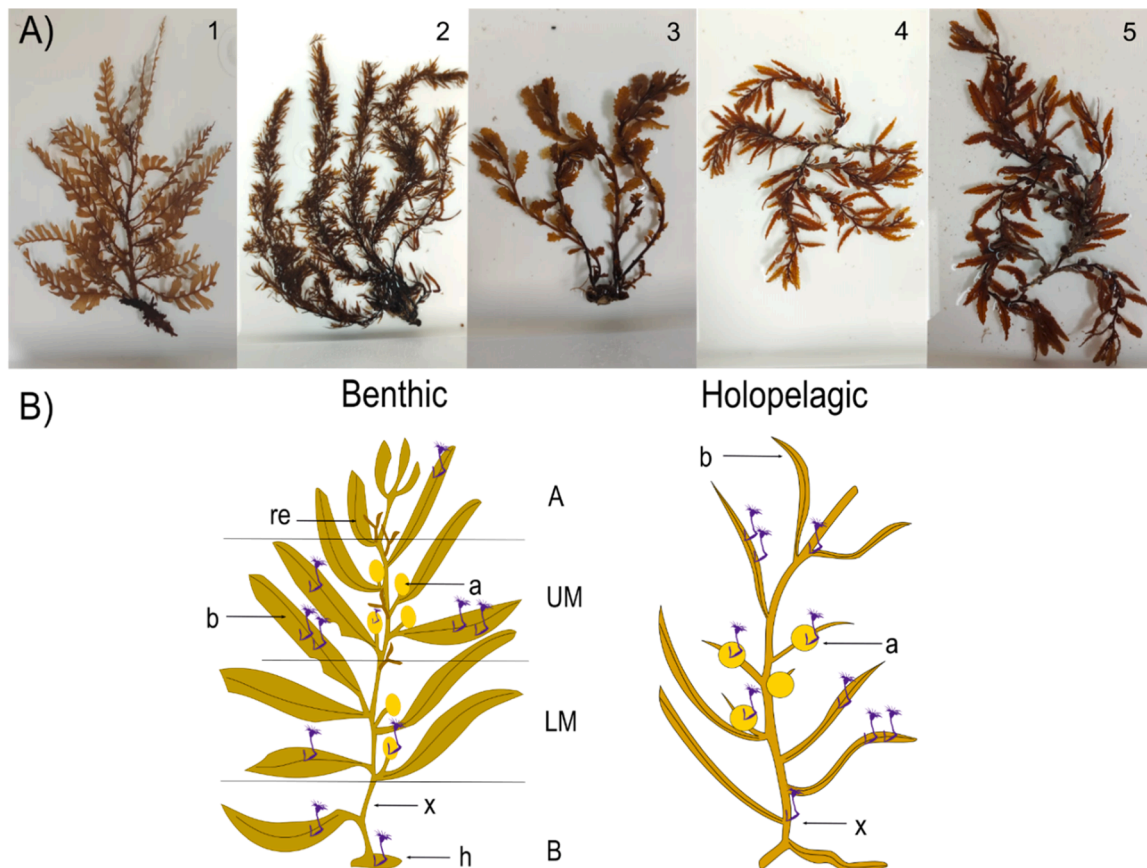


Fig. 2. A) *Sargassum* species sampled in this study. Benthic species: 1. *Sargassum horneri*; 2. *Sargassum muticum*; 3. *Sargassum horridum*. Holopelagic species: 4. *Sargassum fluitans* III; 5. *Sargassum natans* VIII. Scale = 1 cm. B) Hydrozoan cover estimation on both benthic and holopelagic *Sargassum* thalli. Thallus sections: B = Basal, LM = Lower Middle, UM = Upper Middle, A = Apical. Morphological structures: a = aerocysts, b = blade, h = holdfast, r = receptacles, x = axis. Hydrozoans are shown in purple.

Table 1
Sargassum species collected on Mexican coasts.

Sargassum species	Site		State	Climate	Salinity (%)	Water Temperature (°C)	
	Sampling date	Depth					
Benthic							
<i>S. horneri</i>	October 2021	0.5–2 m	Bahía de Todos Santos	Baja California	Temperate and dry ^a	33.3%–33.7% ⁴	11.0–22.5 °C ⁴
<i>S. muticum</i>	October 2021	0.5–2 m	Bahía de Todos Santos	Baja California	Temperate and dry ^a	33.3%–33.7% ⁴	11.0–22.5 °C ⁴
<i>S. horridum</i>	July 2020	1–1.5 m	San Juan de la Costa	Baja California Sur	Hot dessert ²	35.5% ²	22.0–27.0 °C ⁶
Holopelagic							
<i>S. fluitans</i> III	July 2021	Floating	Puerto Morelos	Quintana Roo	Tropical ³	35.7% ⁵	24–32 °C ³
<i>S. natans</i> VIII	July 2021	Floating	Puerto Morelos	Quintana Roo	Tropical ³	35.7% ⁵	24–32 °C ³

^a Simental, Martínez-Urtaza (2008), ²Obeso-Nieblas et al. (2004), ³Coronado et al. (2007), ⁴Mancilla, Martínez (1991), ⁵Merino, Otero (1991), ⁶Monteforte, Cariño (1992).

2.3. Data analysis

Data was analyzed using the R software libraries (R Development Core Team, 2023). A Venn diagram was constructed to identify exclusive hydrozoan species for each *Sargassum* species, employing the EULERR package (Larsson, 2022). Box plots were generated to visualize the percentages of epibiont hydrozoan cover for each *Sargassum* species, categorized under three cover categories: total, sections, and structures. To observe similarities in the community structure of hydrozoans among *Sargassum* species, their structures, sections, and total hydrozoan coverage on *Sargassum* thalli, we performed an nMDS using the Bray-Curtis method (Kruskal and Wish, 1978) with the prior transformation of the fourth root ($\sqrt[4]{}$) to reduce the influence of dominant taxa of the percentage coverages of each hydrozoan species (Clarke, 1993), using the PRIMER program version 7 (Clarke and Gorley, 2015).

To support the previous analyses, a Nonmetric Multidimensional Scaling (nMDS) ordering method was obtained using the Bray-Curtis as a measure of similarity, and vectors of the sections and structures of the *Sargassum* were adjusted with the 'envfit' function with the 'vegan' package (Oksanen et al., 2007).

3. Results

We identified 18 hydrozoan epibiont species on *Sargassum*, with 16 belonging to the superorder Leptothecata (88.9%) and two to anthoathecata (11.1%). *Obelia* cf. *dichotoma* was found on all *Sargassum* species except *S. muticum* (Table 2). Among the BSS, we found 11 hydrozoan species, 10 Leptothecata, and one anthoathecata (Table 2). Six species were detected in *Sargassum horneri* and *S. muticum*, and three in *S. horridum* (Table 2, Fig. 3). The hydrozoans *Hydrodendron* sp. 1, *Dynamena disticha*, and *Orthopyxis* sp. 1 were shared between *S. horneri* and *S. muticum*. Two species were exclusive to *S. horneri*, while three and two species were found exclusively in *S. muticum* and *S. horridum*, respectively (Fig. 3). In HSS, we found eight hydrozoan species, seven Leptothecata, and one anthoathecata. *Sargassum fluitans* III had seven species, while *S. natans* VIII had eight, and all the hydrozoans were found on both *Sargassum* species except for *Clytia* cf. *gracilis* (Table 2, Fig. 3). *Sargassum natans* VIII had one exclusive hydrozoan species (Fig. 3). In contrast, *S. fluitans* III did not host any exclusive hydrozoans.

Some BSS thalli exhibited hydrozoan colonies with gonophores, viz. *Orthopyxis* sp. 1 and *D. disticha* on *S. horneri*, *Orthopyxis* sp. 1 on *S. muticum*, and *O. cf. dichotoma* and *V. halecioides* on *S. horridum*. For HSS, *C. noliformis* and *C. cf. hemisphaerica* with gonophores were found on *S. fluitans* III, and *C. noliformis* and *O. cf. dichotoma* colonies with gonophores were observed on *S. natans* VIII.

The total percentage coverage of hydrozoans on BSS showed less variability than on HSS. For example, *Sargassum natans* VIII exhibited cover values ranging from 0.05% to 100% (Fig. 4A). The hydrozoan with the highest mean percentage coverage of epibiosis for each *Sargassum* species were *Dynamena disticha* for *S. horneri* (0.6%), *Orthopyxis* sp. 1 for *S. muticum* (2.7%), *Ventromma halecioides* for *S. horridum* (11.0%), *Clytia noliformis* for *S. fluitans* III (31.5%), *Aglaophenia latecarinata* for *S. natans*

VIII (41.0%) (Table 2).

Regarding benthic species, *S. horneri* displayed low percentage coverages across all thalli sections. In contrast, *Sargassum muticum* exhibited the most significant variability in the basal area, while *S. horridum* showed the highest variation in the upper-middle section (Fig. 4B). Notably, the variation in hydrozoan cover on thalli structures was lower for BSS than for HSS (Fig. 4C). Within the BSS, the basal section hosted the highest number of hydrozoan species (*S. horneri* = 6; *S. muticum* = 6; *S. horridum* = 3). *Sargassum horneri* did not exhibit hydrozoans in the apical section. On the other hand, *S. muticum* displayed the lowest number of hydrozoan species (1) in the upper-middle section, whereas *S. horridum* had two species in each of the lower-middle, upper-middle, and apical sections (Table 2, SM 1).

The hydrozoans with the highest mean coverage percentages in each section were *D. disticha* in the basal section of *S. horneri* (1.4%), *Orthopyxis* sp. 1 in the basal section of *S. muticum* (9.0%), and *V. halecioides* in the upper-middle section of *S. horridum* (18.1%) (Table 2, SM 1). Regarding structures, the BSS *S. horneri* had the highest number of hydrozoan species on the blades (6 species). In comparison, *S. muticum* had five species on the axis, and *S. horridum* had three species on both the axis and blades. Among the HSS, *S. fluitans* III hosted six species on the blades, and *Sargassum natans* VIII presented eight epibiont species on all its structures (Table 2, SM 1).

The hydrozoans with the highest mean percentages on structures were *D. disticha* on the holdfast (10.0%) of *S. horneri*, *Orthopyxis* sp. 1 on the axis (6.6%) of *S. muticum*, *V. halecioides* on the axis (16.8%) of *S. horridum*, *C. noliformis* on the axis (41.0%) of *S. fluitans* III, and *A. latecarinata* on the axis (41.0%) of *S. natans* VIII (Table 2, SM 1).

The nMDS ordination analyses of the composition of hydrozoan species in the sections and structures of different thalli of *Sargassum* species showed striking similarities, indicating no significant differentiation. However, the cluster for the total hydrozoan cover along *Sargassum* thalli evidenced a separation based on *Sargassum* species and geographic location (Fig. 5).

4. Discussion

Our results demonstrate that differences in hydrozoan species primarily depend on the geographical distribution of the *Sargassum* species. This observation aligns with a global trend where geographical regions exhibit similar hydrozoan-macrophyte associations, with the hydrozoan composition being secondarily influenced by the macrophyte lineages (Oliveira and Marques, 2011). On the other hand, the composition and abundance of epibiont hydrozoans on structures along the thalli of both benthic and holopelagic *Sargassum* species were highly variable without a pattern.

The number of hydrozoan epibionts found on BSS, between 3 and 6 species, was relatively low compared to the number reported for other BSS in previous studies, such as 14 hydrozoan species on Brazilian *Sargassum cymosum* (Cunha and Jacobucci, 2010). In contrast, the number of hydrozoan epibionts on HSS (seven for *S. fluitans* III and eight for *S. natans* VIII) was higher than previously reported for Mexican

Table 2

Mean percentage cover (\pm standard deviation) of hydrozoans according to *Sargassum* species, thalli sections (B=Basal, LM=Lower Middle, UM=Upper Middle, A=Apical), and structures (axis, blades, aerocysts, receptacles, holdfast). *Sargassum* sections and structures not observed or without hydrozoan cover are not included. * anthoathecate species, the rest of the species belong to the superorder Leptothecata. • New records of hydrozoans on *Sargassum* (species category).

<i>Sargassum</i> species	Hydrozoan species	Thalli sections		Morphology				
		Section	Mean % cover	Structure	Mean % cover	Mean % total		
<i>Sargassum horneri</i>	<i>Aglaophenia pinguis</i> Fraser, 1938•	B	0.19 \pm 0.39	Axis	0.55 \pm 1.46	0.08 \pm 0.2		
		LM	0.04 \pm 0.12	Blades	0.26 \pm 0.68			
	<i>Dynamena disticha</i> (Bosc, 1802)•	B	1.38 \pm 4.13	Axis	2.86 \pm 5.98	0.60 \pm 1.78		
		LM	0.53 \pm 2.05	Blades	0.41 \pm 1.42			
		UM	0.1 \pm 0.36	Holdfast	10 \pm 30.78			
	<i>Hydrodendron</i> sp. 1	B	0.15 \pm 0.53	Axis	0.80 \pm 2.62	0.09 \pm 0.30		
		LM	0.04 \pm 0.20	Blades	0.01 \pm 0.04			
	<i>Obelia</i> cf. <i>dichotoma</i> (Linnaeus, 1758)•	B	0.26 \pm 1.18	Axis	0.72 \pm 03.22	0.15 \pm 0.68		
				Blades	0.07 \pm 0.31			
	<i>Orthopyxis</i> sp. 1	B	0.75 \pm 1.43	Axis	4.23 \pm 8.65	0.30 \pm 0.61		
				LM	0.10 \pm 0.27		Blades	0.12 \pm 0.48
							Holdfast	5 \pm 22.36
<i>Sargassum muticum</i>	<i>Plumularia</i> sp. 1	B	0.01 \pm 0.05	Blades	0.004 \pm 0.02	0.003 \pm 0.02		
		B	0.12 \pm 0.37	Axis	0.21 \pm 0.60			
	<i>Dynamena disticha</i> (Bosc, 1802)•	LM	0.08 \pm 0.34	Blades	0.01 \pm 0.03	0.05 \pm 0.13		
		B	0.51 \pm 1.59	Axis	0.19 \pm 0.61			
	<i>Eudendrium</i> sp. 1 *	LM	0.37 \pm 1.39	Blades	0.09 \pm 0.28	0.15 \pm 0.31		
		B	1.63 \pm 6.31	Axis	0.37 \pm 1.30			
	<i>Haleciidae</i> sp. 1	A	0.04 \pm 0.16	Blades	0.01 \pm 0.04	0.12 \pm 0.39		
		B	0.10 \pm 0.46	Blades	0.02 \pm 0.09			
	<i>Hydrodendron</i> sp. 1	B	9.04 \pm 13.82	Axis	6.56 \pm 10.35	2.71 \pm 4.25		
		<i>Orthopyxis</i> sp.1	LM	4.50 \pm 11.68	Blades		1.17 \pm 2.36	
	UM		1.02 \pm 2.65	Aerocysts	0.01 \pm 0.05			
	A		0.25 \pm 1.10					
<i>Sertulariellidae</i> sp. 1	B	0.79 \pm 3.53	Axis	0.30 \pm 1.36	0.08 \pm 0.37			
	<i>Sargassum horridum</i>	<i>Dynamena quadridentata</i> (Ellis & Solander, 1786)	B	2.63 \pm 11.16		Axis	2.25 \pm 8.86	0.89 \pm 3.82
LM			0.91 \pm 4.05	Blades	0.46 \pm 2.06			
UM			0.14 \pm 0.64					
<i>Obelia</i> cf. <i>dichotoma</i> (Linnaeus, 1758)		B	0.17 \pm 0.76	Axis	0.10 \pm 0.46	0.22 \pm 0.56		
		A	1.13 \pm 3.15	Blades	0.23 \pm 0.72			
<i>Ventromma halecioides</i> (Calder, 1859)		B	6.12 \pm 5.55	Axis	16.78 \pm 11.86	11.01 \pm 7.11		
		LM	8.39 \pm 6.46	Blades	7.85 \pm 4.98			
		UM	18.17 \pm 12.84	Aerocysts	1.96 \pm 5.61			
		A	12.77 \pm 15.56	Receptacles	0.35 \pm 1.14			
				Holdfast	2.5 \pm 11.18			
<i>Sargassum fluitans</i> III		<i>Aglaophenia latecarinata</i> Allman, 1877	NA	NA	Axis	0.04 \pm 0.17	0.1 \pm 0.02	
			<i>Clytia</i> cf. <i>hemisphaerica</i> (Linnaeus, 1767)•	NA	NA	Axis		3.25 \pm 9.71
	NA	NA		Blades	3.96 \pm 9.72			
				Aerocysts	3.75 \pm 8.54			
	<i>Clytia noliformis</i> (McCrary, 1859)	NA	NA	Axis	41.00 \pm 19.15	31.52 \pm 13.17		
				Blades	28.60 \pm 14.97			
				Aerocysts	21.31 \pm 13.22			
	<i>Halopteris</i> sp. 1	NA	NA	Axis	0.05 \pm 0.13	0.04 \pm 0.08		
				Blades	0.02 \pm 0.08			
				Aerocysts	0.01 \pm 0.05			
	<i>Obelia</i> cf. <i>dichotoma</i> (Linnaeus, 1758)	NA	NA	Blades	0.01 \pm 0.03	0.01 \pm 0.03		
		<i>Plumularia strictocarpa</i> Pictet, 1893	NA	NA	Blades		0.02 \pm 0.08	0.03 \pm 0.11
NA	NA		Aerocysts	0.02 \pm 0.09				
NA	NA		Axis	0.32 \pm 0.96				
<i>Zanclaea alba</i> (Meyen, 1834)*•	NA	NA	Blades	0.49 \pm 1.78	2.08 \pm 6.55			
			Aerocysts	0.49 \pm 1.32				
			Axis	40.58 \pm 25.39				
			Blades	34.08 \pm 19.05				
			Aerocysts	29.29 \pm 26.33				
<i>Sargassum natans</i> VIII	<i>Aglaophenia latecarinata</i> Allman, 1877	NA	NA	Axis	0.02 \pm 0.10	0.03 \pm 0.15		
		NA	NA	Blades	0.01 \pm 0.05			
		NA	NA	Aerocysts	0.08 \pm 0.38			
	<i>Clytia</i> cf. <i>gracilis</i> (Sars, 1851)•	NA	NA	Axis	0.35 \pm 1.05	0.33 \pm 0.76		
				Blades	0.19 \pm 0.50			
				Aerocysts	0.46 \pm 1.19			
	<i>Clytia noliformis</i> (McCrary, 1859)	NA	NA	Axis	8.12 \pm 19.15	9.22 \pm 19.91		
				Blades	8.65 \pm 18.76			
				Aerocysts	6.61 \pm 14.13			
	<i>Halopteris diaphana</i> (Heller, 1868)	NA	NA	Axis	11.02 \pm 17.23	0.14 \pm 0.33		
				Blades	0.17 \pm 0.53			
				Aerocysts	0.08 \pm 0.23			
<i>Obelia</i> cf. <i>dichotoma</i> (Linnaeus, 1758)•	NA	NA	Axis	0.88 \pm 1.40	0.49 \pm 1.12			
			Blades	0.26 \pm 0.77				
			Aerocysts	0.56 \pm 1.37				
<i>Plumularia strictocarpa</i> Pictet, 1893•	NA	NA	Axis	0.49 \pm 1.24	0.23 \pm 0.58			
			Blades	0.13 \pm 0.39				

(continued on next page)

Table 2 (continued)

Sargassum species	Hydrozoan species	Thalli sections		Morphology		
		Section	Mean % cover	Structure	Mean % cover	Mean % total
	<i>Zanclaea alba</i> (Meyen, 1834)*			Aerocysts	0.31 ± 1.00	0.59 ± 0.61
				Axis	1.67 ± 2.75	
				Blades	0.23 ± 0.29	
				Aerocysts	1.09 ± 1.43	

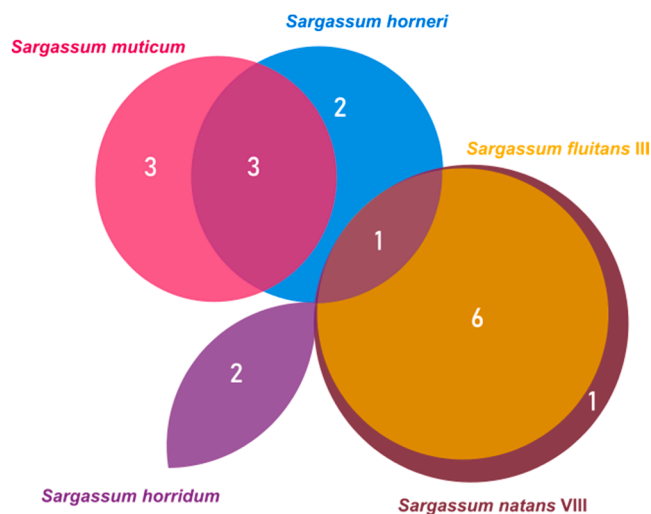


Fig. 3. Venn diagram illustrating shared hydrozoan species among *Sargassum* species.

waters (four on *S. fluitans* III and five on *S. natans* VIII; Mendoza-Becerril et al., 2020a). However, these differences need to be analyzed considering sampling at different times of the year, since temporal variation in hydrozoan species richness and abundance has been observed on *Sargassum* (i.e., Mendoza-Becerril et al., 2020a).

Each *Sargassum* species exhibited one hydrozoan epibiont species with a marked higher mean total coverage, a trend noted in other studies (Cunha and Jacobucci, 2010; Mendoza-Becerril et al., 2020a). For BSS, *D. disticha* on *S. horneri*, *Orthopyxis* sp. 1 on *S. muticum*, and *V. halecioides* on *S. horridum* had the highest mean coverage along the thallus. Among HSS, *C. noliformis* displayed the highest mean coverage on *S. fluitans* III,

while *A. latecarinata* presented that on *S. natans* VIII. The preference of *A. latecarinata* for *S. natans* VIII has been previously documented (Burkenroad in Parr, 1939; Govindarajan et al., 2019). However, *A. latecarinata* has also been found abundantly on *S. fluitans* III in some cases (Burkenroad in Parr, 1939; Govindarajan et al., 2019), a different pattern from our data. Space competition can be severe on algal surfaces (Oswald and Seed, 1986), and most likely, this is the case between *A. latecarinata* and *C. noliformis* in our *S. fluitans* III samples, in which the latter was the dominant species, as observed in previous studies (Mendoza-Becerril et al., 2020a; Alleyne et al., 2023).

Regarding the sections along BSS thalli, the basal section hosted the highest number of species. This is consistent with observations in other phaeophytes, where hydrozoans tend to attach to basal areas and grow upwards, decreasing abundance towards distal sections (Fraschetti et al., 2006). However, hydrozoans exhibited higher coverage in the upper-middle section of *S. horridum*, suggesting that they grew along with new algal growth, similar to other hydrozoan epibionts on *Sargassum* (Ryland, 1974). The number of hydrozoan epibiont species varied among *Sargassum* vegetative structures with more hydrozoan species growing on the axis and blades. In this regard, more hydrozoan species on the axis of *Sargassum* have also been documented by Mendoza-Becerril et al. (2020a). In contrast, other marine organisms like bryozoans prefer aerocysts as settlement substrates (Niermann, 1986).

Regarding the reproductive characteristics of hydrozoans, we observed a prevalence of species with fixed gonophores (cf., Fraschetti et al., 2006; Cunha and Jacobucci, 2010). This suppression of the medusa stage can be considered a strategy to restrict the offspring within the same algal substrate, promoting population stability over dispersal (Ronowicz et al., 2008). Notably, some of the most abundant hydrozoan species bearing gonophores were only found on a few thalli. This pattern might be derived from asexual reproduction, which could efficiently sustain colony growth on brown algae (Gravier-Bonnet, Bourmaud, 2005).

According to the last revision of Carral-Murrieta et al. (2023a) about

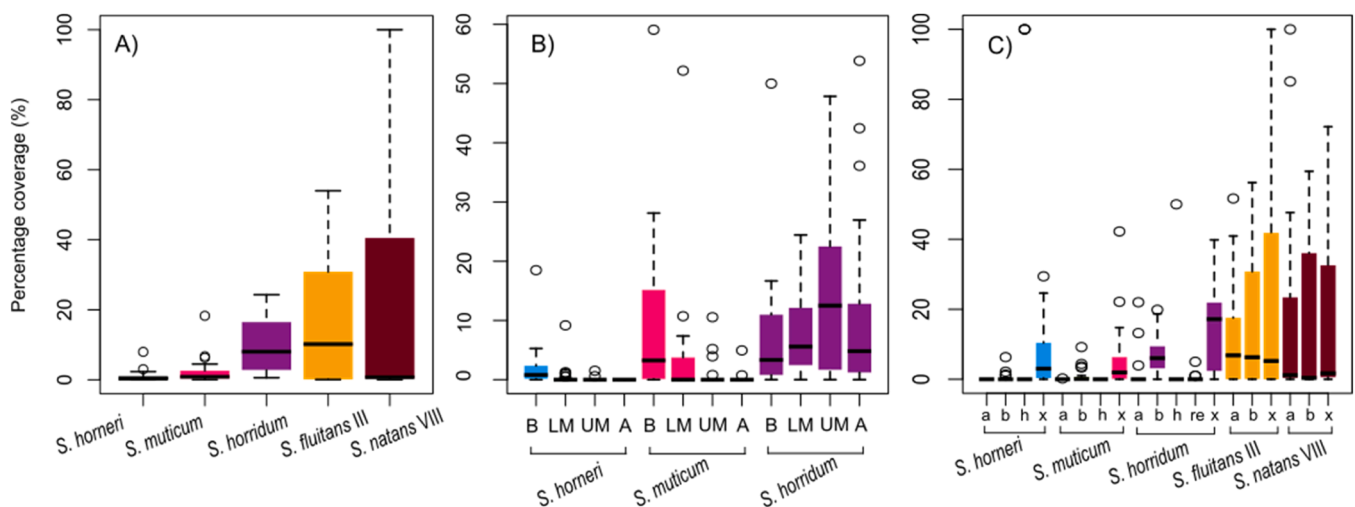


Fig. 4. Percentage coverage (%) of hydrozoans on *Sargassum* species. A) Total percentage coverage. B) Percentage coverage of hydrozoans on different sections of benthic *Sargassum* (B = Basal, LM = Lower Middle, UM = Upper Middle, A = Apical). C) Percentage coverage of hydrozoans on different structures of *Sargassum* (a = aerocysts, b = blades, h = holdfast, r = receptacles, x = axis).

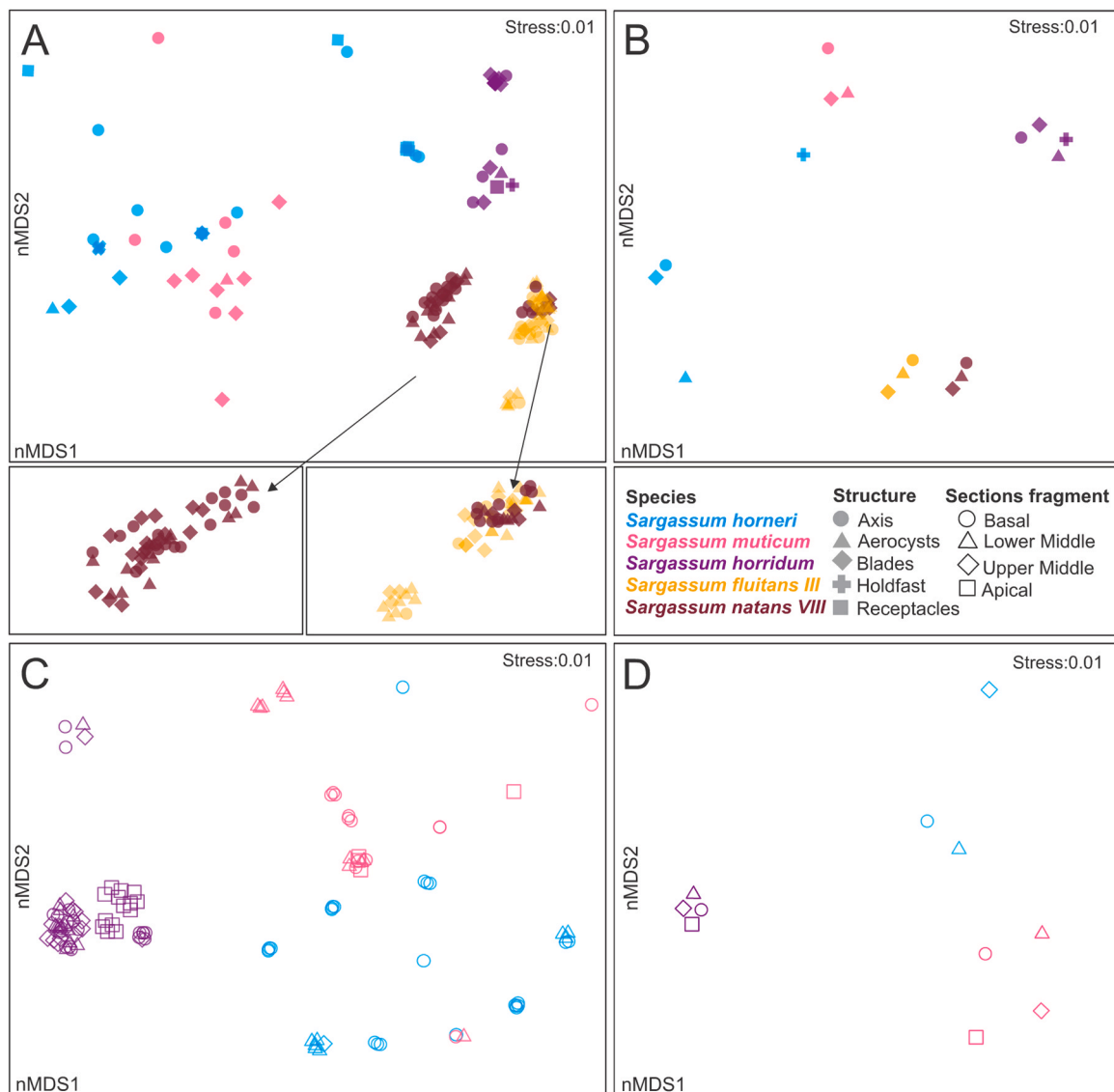


Fig. 5. Nonmetric Multidimensional Scaling showing the similarities in the community structure of hydrozoans among *Sargassum* species. A) Hydrozoan coverage per structure on *Sargassum* thalli, B) Total hydrozoan coverage per structure on *Sargassum*, C) Hydrozoan coverage per section on *Sargassum* thalli, D) Total hydrozoan coverage per section on *Sargassum*.

the number of epibiont species of *Sargassum* in the world, only one species (*Clytia* cf. *gracilis*) is recorded for the first time as epibiont for HSS, growing on *S. natans* VIII. In addition, six species of hydroids are reported for the first time for *S. horneri*, four for *S. muticum*, two for *S. fluitans* III, and three for *S. natans* VIII. Additionally, we report species of *Hydrodendron* and *Eudendrium* for the first time on *Sargassum* in the Pacific Ocean (see Carral-Murrieta et al., 2023b).

The species *O. cf. dichotoma* exhibits a circumglobal distribution and was found on both BSS and HSS in the Caribbean and the Mexican Pacific (Lindner and Migotto, 2002). Also, it has been documented in the Atlantic, Indian, and Pacific Oceans (Millard, 1975). However, it is important to consider that this species exhibits recognized morphological variability and cryptic lineages (Cunha et al., 2017; Penney and Rawlings, 2021). Moreover, many hydrozoan species considered cosmopolitan may fall into a pseudo-cosmopolitan category, explained as a taxon comprised of more than one lineage but with a single binomial name with a false cosmopolitan status (Darling and Carlton, 2018; Calder, 2021).

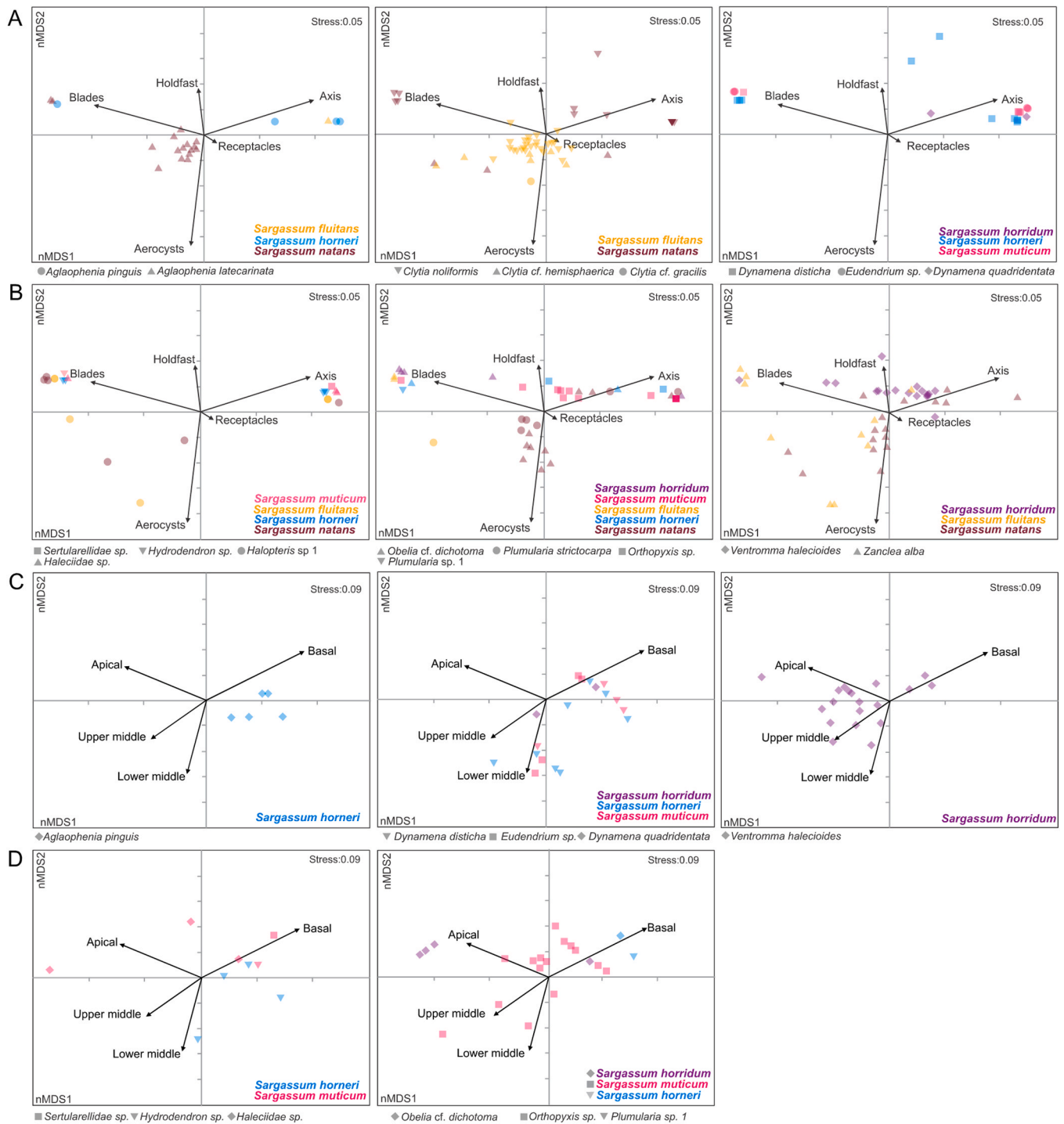
Interestingly, the BSS *S. horneri* and *S. muticum*, collected in the same locality (Ensenada) simultaneously, only shared three hydrozoan

species, which can be attributed to differences in structural complexity, seasonal reproductive growth patterns, and life cycles of these two seaweeds (Cunha and Jacobucci, 2010). Conversely, the HSS shared all hydrozoan species except *C. cf. gracilis*, which has been reported on other BSS (e.g. Cunha and Jacobucci, 2010). This could be due to the opportunistic nature and low substrate selectivity typically exhibited by most hydrozoans (Oliveira and Marques, 2011), as well as the shared origin of *S. fluitans* III and *S. natans* VIII (Godínez-Ortega et al., 2021).

In conclusion, our findings suggest that differences in hydrozoan species primarily depend on geographical distribution of the *Sargassum* species. *Sargassum* species from different locations exhibit unique hydrozoan compositions and there is no pattern of epibiosis concerning the algal morphology (structures and sections) for each *Sargassum* species.

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SM 1. Nonmetric Multidimensional Scaling (nMDS) of sections and structures of hydrozoan epibionts on *Sargassum*. A-B) Hydrozoan cover per structure on *Sargassum* thalli, C-D) Hydrozoan cover per section on *Sargassum* thalli.

capacidad de remoción de arsénico en agua, utilizando el alga café *Sargassum sinicola*; and Medusozoa México (<https://medusozoaamexico.com.mx/>). ACM was supported by CNPq (316095/2021-4). This is a partial contribution of NP-BioMar USP (ACM).

CRedit authorship contribution statement

COCM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft; Writing - review & editing. **ESZ:** Conceptualization, Data curation,

Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing - original draft; Writing - review & editing. **FRCR:** Formal analysis, Methodology, Supervision, Visualization. **ACM:** Supervision, Validation, Writing - original draft; Writing - review & editing. **MAMB:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing - original draft; Writing - review & editing.

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.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.aquabot.2023.103738](https://doi.org/10.1016/j.aquabot.2023.103738).

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