

Spatially variable sponge recruitment in seagrass meadows in the southern Gulf of Mexico

José Alberto Aguirre-Téllez

Posgrado de Ecología Marina, CICESE

Enrique Ávila

kike@ola.icmyl.unam.mx

Universidad Nacional Autónoma de México

Lydia B. Ladah

University of California San Diego (UCSD)

Research Article

Keywords: Seagrass meadows, marine sponges, recruitment, spatial distribution, artificial substrates

Posted Date: May 13th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9589752/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

The spatial variability in species composition, richness, and abundance of sponge recruitment within *Thalassia testudinum* seagrass meadows was explored using artificial seagrass units (ASUs), deployed for 85 days at the central, edge, and outer meadow zones of three sites in the southern Gulf of Mexico. Seven sponge species were recorded, matching earlier reports of adult presence in the region. Ranked in order, from highest to lowest relative abundance, species included *Haliclona implexiformis*, *Amorphinopsis atlantica*, *Mycale* cf. *microsigmatosa*, *Haliclona* sp., *Dysidea etheria*, *Chondrilla caribensis*, and *Halichondria melanadocia*. Species richness (1–3 species per ASU) and abundance (1–4 individuals per ASU) did not differ among zones within each meadow, however significant differences were found among sites, attributed to environmental differences. The detection of sponge recruits on ASUs placed at the outer zone of the meadows, where seagrass does not naturally exist, indicates that sponge larvae do disperse beyond the meadow edge, suggesting connectivity between meadows and adjacent mangrove habitats. Conversely, the absence of adult sponges in the areas outside of the meadow appears to be driven by lack of firm substrate for attachment and potentially by no seagrass canopy to shield recruits from environmental stressors, rather than by limited dispersal. These results, among the few to document sponge recruitment in seagrass habitats, contribute essential insight into larval dispersal patterns and habitat connectivity for benthic sponge fauna.

Introduction

Marine sponges (Phylum Porifera) constitute one of the most conspicuous and abundant groups of sessile invertebrates in seagrass meadows (Borowitzka et al. 1990; Sivaleela et al. 2013; Ávila et al. 2015; Setiawan et al. 2021; Campanino et al. 2023). These invertebrates establish a mutually beneficial relationship with seagrasses, as they provide nutrients such as nitrogen and phosphorus to the seagrass, whereas seagrasses provide substrate, refuge and dissolved organic carbon to the sponges, as well as environmental stability (sediment, light and temperature), acting as ecosystem engineers (Fell and Lewandrowski 1981; Wulff 2006; Archer et al. 2015; Setiawan et al. 2021; Archer et al. 2021). The role of sponges as alternative microhabitats for a wide variety of benthic organisms has also been highlighted in these environments (e.g., Ávila and Ortega-Bastida 2015; Ávila and Briceño-Vera 2018; Briceño-Vera et al. 2021, 2024; Campanino et al. 2023).

Despite the recognized ecological importance of sponges in these habitats, their spatial distribution and dispersal remain poorly understood (e.g., Sivaleela et al. 2013; Prabhakaran et al. 2013; Landau et al. 2013; Ávila et al. 2015; Demers et al. 2016; Setiawan et al. 2021; Bachtiar et al. 2022, 2023). Previous research on seagrass-dwelling sponges has revealed patchy distributions, characterized by high variability both within and among sites (Ávila et al. 2015; Demers et al. 2016). Such patterns have been linked to spatial heterogeneity in local environmental conditions and habitat features, including seagrass density and biomass, as well as the availability of alternative hard substrates such as mollusk shells within the meadows (Prabhakaran et al. 2013; Ávila et al. 2015; Demers et al. 2016). In addition, patchiness in sponge distribution across different habitats has been attributed to biological constraints, particularly limited larval dispersal, reliance on asexual propagation, and restricted connectivity between populations (Hooper et al. 2002; Hooper and Kennedy 2002; Fromont et al. 2006). Nevertheless, the spatial distribution of sponge recruits in seagrass meadows remains an unexplored topic.

Extensive seagrass meadows (dominated by *Thalassia testudinum* K.D.Koenig 1805, *Halodule wrightii* Ascherson, 1868, and *Syringodium filiforme* Kützinger 1860) exist in the Bay of Campeche, in the southern Gulf of Mexico (SGoM), where sponges are a common component of the marine biodiversity. Studies on sponges in this region have addressed various aspects of their ecology, such as their distribution, abundance, interactions with other organisms, and reproduction of some of the most common species (Ávila et al. 2015; Ávila-García et al. 2019; Briceño-Vera et al. 2021, 2024). Many of the seagrass-dwelling sponge species in this region are also present in adjacent mangrove root habitats, suggesting high faunal connectivity between these habitats, however the soft bottom areas that separate seagrass meadows from mangroves are generally devoid of sponges. We hypothesized that their absence in these areas is due to the lack of hard substrate for the settlement and growth of recruits, along with reduced refuge against predation and environmental factors (such as sedimentation, light, and hydrodynamics) which can impact survival.

One of the methods currently used to expand knowledge of organisms in seagrass meadows has included the use of artificial seagrass units (ASUs) (Trautman and Borowitzka 1999; Donnarumma et al. 2014). ASUs have been used to compare the richness and density of epifaunal and infaunal species between natural meadows and external areas (Lee et al. 2001) as well as to evaluate predation on seagrass-dwelling organisms (Canion and Heck 2009). They have also helped determine the diversity and distribution of epiphytic communities on seagrass blades along with fish recruitment in seagrass (Trautman and Borowitzka 1999; Upston and Booth 2003; Donnarumma et al. 2014). They have also been useful in evaluating the recruitment of diverse invertebrates (Lee et al. 2001; Canion and Heck 2009; Parfitt 2013) and vertebrates (Bell 1985; García-Sanz 2009; Shahbudin 2011) within meadows.

In this study, Artificial Seagrass Units (ASUs) were utilized to evaluate the distribution of sponge recruits in shallow *T. testudinum* meadows located within an estuarine system of the southern Gulf of Mexico. These structures, designed to replicate the morphology of natural seagrass, were made available as settlement substrates during the warmer months, when the release of larvae by numerous sponge species is typically observed (Mariani et al. 2005; Riesgo and Maldonado 2008). Specifically, spatial variations within and among sites in the composition, richness, and relative abundance of sponge recruits in *T. testudinum* meadows were explored, together with the environmental factors.

Material and Methods

Study Area

This study was conducted within the Laguna de Términos (Campeche, Mexico), which is located in the SGoM. This is the largest coastal lagoon in Mexico (2500 km²), which is connected to the Gulf of Mexico by two major inlets (David and Kjerfve 1998). In this location, three experimental sites (seagrass meadows dominated by *T. testudinum*) were selected along the inner coastline of Isla del Carmen, a barrier island that separates the lagoon from the Gulf of Mexico (Fig. 1). Site 1 was situated on the western side of the island (18°38'24.07"N, 91°47'49.86"W), Site 2 in the central zone (18°42'37.21"N, 91°37'13.72"W), and Site 3 on the eastern side (18°44'31.62"N, 91°32'13.66"W) (Fig. 1). The distance between Sites 1 and 2 was 7.5 km, while Sites 2 and 3 were separated by 23 km. These sites had depths between 0.5 and 1.0 m.

Use of artificial seagrass units (ASUs)

This study used artificial seagrass as a substrate to assess the settlement of sponge recruits in *T. testudinum* meadows. An ASU consisted of a plastic mesh base (20 cm x 20 cm, with a 1 cm opening) to which green plastic straps 1.2 cm wide were attached to simulate *T. testudinum* leaves. The density and length of the straps were set to simulate natural *T. testudinum* meadows in the study area (Hernández-Peña 2018). In this case, 80 straps were attached in each ASU with a length of 30 cm (Fig. 2). A total of 15 ASUs were placed at each study site, with five in the central zone of the meadow, five at the edge zone, and five in the zone outside the meadow (Fig. 2). The ASUs were positioned parallel to the coastline (using 35 cm length steel rod hooks to anchor them to the substrate) with a separation of 2 m between each one. The distance between each zone was 20 m (Fig. 2). These experimental structures were deployed from June 30 to September 23, 2022 (summer season), when the water temperature reaches its yearly maximum, and many sponge species release their larvae (e.g., Maldonado and Young 1996; Mariani et al. 2005; Ávila-García et al. 2019).

After 85 days, the ASUs were covered with a mesh (1 mm opening) to retain any recruits that might detach and placed in a plastic bag with water from the site to prevent desiccation of the recruits during transportation to the laboratory.

Separation, identification, and quantification of sponge recruits

The sponge recruits settled on both sides of the artificial seagrass leaves were separated and identified using standard morphological methods (based on the spicules present and their arrangement in the choanoderm and ectoderm) to the genus or species level, using literature from the region and the World Porifera Database (Rützler 1978; de Voogd et al. 2022), and quantified. Recruits were visible to the naked eye, varying in size from 0.5 cm to 5 cm in length. Species composition per site, average species richness/ASU, average density of each sponge species/ASU, and relative abundance (%) of each species based on the total number of sponge recruits per site and experimental zone were recorded.

Environmental parameters

The environmental factors measured in each experimental zone (center, edge, and outside of the meadow) were water temperature (°C), salinity (UPS), sedimentation/resuspension rate ($\text{Kg dry weight/m}^2/\text{day}^{-1}$), and hydrodynamics ($\% \text{ dissolution/day}^{-1}$). Water temperature and salinity were measured using a YSI-model EXO2 multiparameter probe. To measure the sedimentation/resuspension rate, three PVC sediment traps with an internal opening of 2.5 cm and a height of 15 cm were used in each experimental zone (Ávila et al. 2015; Briceño-Vera et al. 2024). The traps were placed at the beginning of the experiment (vertically and 1 meter apart from each other) and removed at the end. The sediment collected in the traps was washed with distilled water to remove salt and then placed in an oven (at 60°C for 48 hours) to obtain dry weight. The average sedimentation/resuspension rate was expressed in $\text{kg m}^{-2} \text{ day}^{-1}$ for each site and zone.

Hydrodynamics was calculated based on the weight loss (g) of plaster cylinders caused by water movement over a specified period. Three 5 cm diameter plaster cylinders were placed simultaneously in each experimental area, anchored 30 cm from the bottom on vertical PVC supports. After five days, they were removed and dried in an oven at 50°C for 48 hours to obtain dry weight. Based on the weight loss due to material dissolution, the average dissolution rate in the cylinders in each zone was calculated and expressed as the average dissolution rate (% dissolution day⁻¹) (Carballo et al. 1996), per the estimate of the decrease in the mass of each cylinder as linearly related to water velocity (Muus 1968; Komatsu and Kawai 1992; Maldonado and Young 1996).

Data analysis

To determine whether the environmental (temperature, salinity, hydrodynamics, and sedimentation/resuspension rate) and biological variables (species richness and density of sponge recruits) met the assumptions of normality and homoscedasticity, Shapiro-Wilk and Levene tests were performed, respectively. To examine spatial variations (between sites and zones) in temperature, species richness, and abundance of sponge recruits, the nonparametric Kruskal-Wallis (KW) analyses of variance followed by Tukey's test as a post hoc test was performed. For salinity, sedimentation/resuspension rate, and hydrodynamic data, two-way analyses of variance (two-way ANOVAs) were performed (site factor: 3 levels; zone factor: 9 levels) followed by the Student Newman-Keuls post hoc test. Analyses were conducted using SigmaPlot (v 12.1).

To analyze the sponge communities recruited on the ASUs, a Bray-Curtis similarity matrix (Bray and Curtis 1957) was generated from the abundance data of the sponge species after square root transformation. An ANOSIM test was used to detect significant differences between groups (Clarke 1993). The contribution (%) of each of the sponge species to the similarity and/or dissimilarity within and between the groups was also determined using a similarity percentage analysis (SIMPER) (Heaven and Scrosati 2008). A Canonical Correspondence Analysis (CCA) evaluated the multivariate relationship between the abundance of sponge recruits and the environmental variables (hydrodynamics, sedimentation/resuspension rate, salinity, and temperature). The CCA was performed using Past (software v. 4.13).

Results

Species richness, composition, and abundance

Recruits of seven sponge species, belonging to one class, five orders, and five families, were recorded on the ASUs (Table 1). Most recruits were observed near the base of the ASUs (within the first 10 cm) and were smaller than 5 cm (Figs. 3a–d). In addition to sponges, ascidians, barnacles (Figs. 3a–c), and epiphytic seaweeds were also attached to the structures, although these organisms were not quantified.

Table 1
Sponge species found in the ASUs of each experimental zone and site.

Species	Site 1			Site 2			Site 3		
	Center	Edge	Outside	Center	Edge	Outside	Center	Edge	Outside
<i>Amorphinopsis atlantica</i>	*	*							
<i>Haliclona</i> sp.	*	*	*						
<i>Haliclona implexiformis</i>			*		*	*	*		*
<i>Chondrilla caribensis</i>					*				
<i>Halichondria melanadocia</i>					*				
<i>Dysidea etheria</i>					*				
<i>Mycale</i> cf. <i>microsigmatosa</i>							*	*	*

The highest species richness was found at Site 2, with a total of four species and an average of 0.69 ± 0.31 species per ASU. At Site 1 and Site 3, three species (0.91 ± 0.16 species per ASU) and two species (0.83 ± 0.21 species per ASU) were found, respectively (Fig. 4a). Across experimental zones, the greatest richness was found at the edge zone, with seven species (1.10 ± 0.58 species per ASU), followed by the central zone with four species (0.55 ± 0.30 species per ASU) and the outer zone with three species (0.67 ± 0.45 species per ASU) (Fig. 4b). No sponge recruits were found at the central zone of Site 2. The overall average richness was estimated at 0.54 ± 0.14 species/ASU.

The highest abundance of sponge recruits was found at Site 2 (12 individuals, 0.92 ± 0.38 individuals per ASU), followed by Site 1 (11 individuals, 1.0 ± 0.19 individuals per ASU) and Site 3 (11 individuals, 0.92 ± 0.23 individuals per ASU) (Fig. 4c). Across zones, the highest abundance was found at the edge zone (1.45 ± 0.37 individuals per ASU), followed by the outer (0.92 ± 0.29 individuals/ASU) and central zones (0.54 ± 0.14 individuals per ASU) (Fig. 4d). The overall average abundance of sponge recruits was 0.94 ± 0.16 individuals per ASU.

No significant differences in species richness or abundance were detected among sites (species richness: KW, $H = 2.29$, $P = 0.32$; abundance: KW, $H = 0.97$, $P = 0.62$) or among zones (species richness: KW, $H = 4.12$, $P = 0.13$; abundance: KW, $H = 4.1$, $P = 0.13$) (Fig. 4).

Regarding relative abundance (Fig. 5), *Haliclona implexiformis* (Hechtel, 1965) was the most abundant species overall, with 15 individuals (44%). In contrast, *Chondrilla caribensis* Rützler, Duran & Piantoni, 2007 and *Halichondria melanadocia* de Laubenfels, 1936 were the least abundant, with only one individual each (3%). At the site level, *Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004 was the most

abundant species at Site 1 (45.5%), *H. implexiformis* at Site 2 (58.3%), and *Mycale* cf. *microsigmatosa* Arndt, 1927 at Site 3 (54.5%).

Sponge assemblages

The sponge assemblages that settled on the ASUs clustered into four groups at a 35% similarity level. The ANOSIM showed no significant differences between experimental zones, whereas significant differences were observed among sites ($R = 0.52$, significance level = 0.7%, 280 permutations). Group A was composed of species from the exposed site (central and edge zones). Group B was composed of species from the semi-exposed site (edge and outer zones) and the exposed site (outer zone). Group C was composed of species from the protected site (edge, central, and outer zones). Group D included the ASUs from the central zone of the semi-exposed site, where no sponge species were recorded (Fig. 6).

Through the SIMPER analysis, the percentage contribution of each sponge species to the similarity within and between the groups identified by the cluster analysis was determined. In Group A (average similarity = 86.8%), similarity was mainly explained by *A. atlantica* (58.5%). In Group B (average similarity = 48.9%), *H. implexiformis* contributed entirely to the similarity (100%), whereas in Group C (average similarity = 59.1%), *M. cf. microsigmatosa* accounted for the greatest contribution (81.6%) (Table 2).

Table 2
Similarity and dissimilarity percentages within and between groups formed in the cluster and species contributions.

Group A	Similarity (%)	Species	Contribution (%)
	86.83	<i>A. atlantica</i>	58.58
Group B	48.97	<i>H. implexiformis</i>	100
Group C	59.15	<i>M. cf. microsigmatosa</i>	81.66
Dissimilarity (%)			
Groups A & B	87.1	<i>H. implexiformis</i>	34.34
		<i>A. atlantica</i>	32.85
Groups A & D	100	<i>A. atlantica</i>	56.81
Groups B & D	100	<i>H. implexiformis</i>	66.78
Groups A & C	100	<i>A. atlantica</i>	31.8
		<i>M. cf. microsigmatosa</i>	27.06
Groups B & C	71.05	<i>M. cf. microsigmatosa</i>	39.04
Groups D & C	100	<i>M. cf. microsigmatosa</i>	68.27

Environmental parameters

The average data of environmental factors measured in each site and zone are shown in Table 3. The highest average sedimentation/resuspension rate ($1.6 \pm 0.21 \text{ kg m}^{-2} \text{ day}^{-1}$) and the lowest temperature ($30.5 \pm 1.16^\circ\text{C}$) were recorded at Site 1. Site 2 was the most hydrodynamic location ($73.5 \pm 7.21\%$ dissolution), with Site 3 showing the lowest, per plaster ball erosion results ($50.0 \pm 12.9\%$ dissolution). Significant variations among sites were detected for both hydrodynamics and sedimentation/resuspension rate (ANOVA, $F = 9.303$, $P < 0.01$; ANOVA, $F = 16.04$, $P < 0.001$, respectively), while no significant differences detected zones in each meadow. No significant differences in water temperature or salinity were found among zones or among sites (KW, $H = 8.02$, $P > 0.05$; ANOVA, $F = 5.13$, $P > 0.05$, respectively).

Table 3

Average data ($\pm$ standard deviation) of environmental factors measured in the sites and experimental zones. Temperature ($^\circ\text{C}$), salinity (UPS), hydrodynamism (% dissolution), and sedimentation/resuspension rate ($\text{kg/m}^2/\text{day}^{-1}$).

Site	Temperature	Salinity	Zone	Hydrodynamism	Sedimentation/resuspension rate
1	30.4 ± 0.54	28.6 ± 0.90	Central	74.2 ± 5.5	1.57 ± 0.1
			Edge	72.4 ± 1.5	1.41 ± 0.3
			Outside	64.5 ± 11.5	1.84 ± 0.4
2	31.1 ± 0.56	28.1 ± 0.25	Central	65.2 ± 0.4	0.78 ± 0.5
			Edge	77.0 ± 2.5	0.95 ± 0.2
			Outside	78.3 ± 3.0	0.99 ± 0.1
3	31.1 ± 0.58	28.5 ± 0.64	Central	62.4 ± 4.9	0.86 ± 0.3
			Edge	36.5 ± 38.6	0.99 ± 0.3
			Outside	51.3 ± 22.5	0.84 ± 0.3

Discussion

The total species richness recorded in the ASUs (seven sponge species) was relatively low compared to that reported for adjacent habitats such as submerged mangrove roots (30 species; Castellanos-Pérez et al. 2020). However, our results are consistent with the richness reported for seagrass meadows in this region (six species in *T. testudinum* meadows; Hernández-Peña 2018). These findings suggest that the ASUs simulated natural conditions and that the sampling period was appropriately chosen to evaluate sponge recruitment in the study area. It should be noted that all species recorded in this study have been previously reported in both seagrass meadows and mangrove root habitats of the region, which facilitated their identification (Ávila et al. 2015; Hernández-Peña 2018; Ávila-García et al. 2019; Castellanos-Pérez et al. 2020).

Although *H. implexiformis* was recorded as the most common species with the greatest relative abundance in this study, the dominant species varied among sites. Specifically, *A. atlantica* was identified as the most abundant at Site 1, *H. implexiformis* at Site 2, and *M. microsigmatosa* at Site 3. These inter-site differences in

dominant species and, more generally, in species composition may be explained by the environmental requirements of each. According to the CCA results (total inertia = 62.61%, axis 1 = 62.62%, axis 2 = 37.38%), the species found exclusively at Site 1 (*A. atlantica* and *Haliclona* sp.) were associated with higher sedimentation/resuspension rates, those recorded at Site 2 (*H. implexiformis*, *C. caribensis*, *H. melanadocia*, and *Dysidea etheria* de Laubenfels, 1936) with higher water motion, and the species recorded at Site 3 (*M. cf. microsigmatosa*) with higher salinity (see Fig. 7).

Therefore, although the species found are common in the estuarine system, they do seem to exhibit particular environmental preferences. Supporting this hypothesis, the literature shows that *A. atlantica* has been reported as more abundant in turbid and hydrodynamic environments, whereas *H. implexiformis* has been found to be more abundant in sheltered sites (Briceño-Vera et al. 2021, 2024). Therefore, the variations recorded in the sponge assemblages of the ASUs deployed across different experimental sites and zones may be explained by the local distribution patterns of the species in this estuary. Similar spatial variation in sponge assemblages has been documented for mangrove root habitats in the study area and was previously attributed to environmental factors such as salinity, dissolved oxygen, and hydrodynamics (Castellanos-Pérez et al. 2020).

In our study, species richness and abundance showed no significant variation between sites or zones. However, the abundance of adults of the three main sponge species found in this study (*H. implexiformis*, *H. melanadocia*, and *C. caribensis*) has been shown to exhibit small-scale spatial variation within local seagrass meadows, without a clear pattern related to the distance from the shore (Ávila et al. 2015). Ávila et al. (2015) also found a positive correlation between the abundances of *H. melanadocia* and *H. implexiformis* and the amount of mollusk shell debris within the meadow, highlighting the importance of additional hard substrates for sponge larval settlement.

The presence of sponge recruits on ASUs placed outside the meadow shows that larval dispersal extends beyond the seagrass meadow, and their absence in adjacent soft-bottom areas might be explained by the lack of firm substrate suitable for growth. Of course, survival and recruitment to adults may be reduced due to factors such as predation, sedimentation, and solar irradiance (Russ 1980; Kuffner 2001; Maldonado et al. 2008), which are beyond the scope of this study. Yet our results do suggest that larvae do reach outside the meadow and at least some can survive at least the duration of this study.

Light has been highlighted as an important factor in determining the numbers and rates of larval settlement of sponges (Ettinger-Epstein et al. 2008). Previous studies have reported that larvae of many sponge species display positive phototaxis in the first hours after release, shifting to negative phototaxis before settlement, while in other species negative phototaxis is maintained throughout the free-living period (Maldonado and Young 1996). This behavior has generally been associated with the search for substrates that provide refuge from environmental stressors (Ávila and Carballo 2006; Ettinger-Epstein et al. 2008). For instance, in the coral reef sponge *Luffariella variabilis* (Poléjaeff 1884), it was experimentally demonstrated that light levels of $56 \mu\text{mol s}^{-1} \text{m}^{-2}$ reduced settlement rates and inhibited larval settlement by 60% compared to dark controls (Ettinger-Epstein et al. 2008). However, it has also been suggested that in sponges from shallow and clear waters (mainly those inhabiting horizontal substrates), post-settlement mortality may be influenced less by light itself and more by associated factors such as siltation and algal overgrowth (Maldonado and Young

1996), both of which are known to negatively affect sponge survival (Sara and Vacelet 1973; Wilkinson and Vacelet 1979). In the present study, the three-dimensional structure of the ASUs and the vertical arrangement of the strips (leaves) provided not only firm substrates for attachment but also physical protection against solar radiation, predators, and siltation, thereby resembling the conditions of natural seagrass meadows (Canion and Heck 2009). Consequently, the structural complexity provided by ASUs outside seagrass meadows may have contributed to increased species density after their deployment duration.

During this experiment, the ASUs were also colonized by sessile organisms other than sponges, including rapid colonizers of bare substrates, such as colonial ascidians and barnacles (Stanley and Newman 1980; López-Victoria et al. 2006). In the case of ascidians, competition for space with juveniles of *Alcyonium siderium* Verrill, 1922, *Bugula pacifica* (currently *Crisularia pacifica* Robertson, 1905), and other fouling organisms has been documented in Long Island Sound, USA, causing mortality to these species (Osman and Whitlatch 1995b). With an r-type reproductive strategy and rapid growth, barnacles can also occupy available space rapidly, preventing settlement by other sessile organisms. In the present study, this biological factor varied among sites, as ASUs deployed at Site 1 and Site 2 were heavily colonized by barnacles, while those at Site 3 were predominantly colonized by ascidians (Figs. 3a, b). Therefore, in addition to the physical and chemical factors mentioned above, the negative influence of these competitors on sponge recruit survival might be a factor.

In addition to spatial competition, predation is an obvious factor not evaluated in this study which might affect sponge recruit survival, as they may be consumed by spongivorous organisms such as fish and echinoderms (Pawlik 1983; Sheild and Witman 1993). In the seagrass meadows of Laguna de Términos, the Mayan cichlid *Cichlasoma urophthalmus* (Günther 1862) has been reported as one of the most abundant fish species, with sponges included in its omnivorous diet (Guevara et al. 2007). Thus, it is possible that part of the sponge settlement in these habitats is consumed by these fish.

Conclusion

The results of this study demonstrate that sponge recruitment in *T. testudinum* meadows is strongly influenced by habitat complexity and environmental conditions. Although species richness recorded in the ASUs was lower than that reported for adjacent mangrove roots, it was consistent with values previously observed in seagrass habitats, highlighting the suitability of ASUs as experimental tools. The variation in dominant species among sites reflected specific environmental preferences, underscoring the role of local conditions such as hydrodynamics, sedimentation, and salinity in structuring assemblage composition. Moreover, the presence of recruits outside seagrass meadows shows that dispersal can extend beyond the meadow, although survival may be constrained by the absence of firm substrates and by greater predation and sedimentation. Finally, the colonization of ASUs by other sessile organisms suggests competition for space may also determine recruitment success. Together, these findings show that habitat heterogeneity and structural complexity is essential for supporting sponge diversity in estuarine ecosystems.

Declarations

Conflict of 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.

Funding

was provided by the Instituto de Ciencias del Mar y Limnología (Internal Project 618). Hernán Alvarez-Guillén and Andres Reda-Deara provided field assistance. José Alberto Aguirre-Téllez received a scholarship from the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI).

Author Contribution

A.T.J.A. contributed to conceptualization, writing the original draft, investigation, formal analysis, and methodology. Á.E. contributed to conceptualization, writing, review and editing, supervision, project administration, funding acquisition, and investigation. L.L. contributed to writing, review and editing, supervision, and formal analysis.

Acknowledgement

Funding was provided by the Instituto de Ciencias del Mar y Limnología (Internal Project 618). Hernán Alvarez-Guillén and Andres Reda-Deara provided field assistance. José Alberto Aguirre-Téllez received a scholarship from the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI).

Data Availability

All data supporting the findings of this study are available within the paper.

References

1. Archer SK, Stoner EW, Layman CA (2015) A complex interaction between a sponge (*Halichondria melanadocia*) and a seagrass (*Thalassia testudinum*) in a subtropical coastal ecosystem. J Exp Mar Biol Ecol 465:547–552. <https://doi.org/10.1016/j.jembe.2015.01.003>
2. Archer SK, English PA, Campanino FM, Layman CA (2021) Sponges facilitate primary producers in a Bahamas seagrass system. Mar Biol 168:162. <https://doi.org/10.1007/s00227-021-03977-x>
3. Ávila E, Briceño-Vera AE (2018) A reciprocal inter-habitat transplant reveals changes in the assemblage structure of macroinvertebrates associated with the sponge *Halichondria melanadocia*. Estuaries Coasts 41:1397–1409. <https://doi.org/10.1007/s12237-017-0359-2>
4. Ávila E, Ortega-Bastida AL (2015) Influence of habitat and host morphology on macrofaunal assemblages associated with the sponge *Halichondria melanadocia* in an estuarine system of the southern Gulf of Mexico. Mar Ecol 36:1345–1353. <https://doi.org/10.1111/maec.12233>

5. Ávila E, Yáñez B, Vázquez-Maldonado LE (2015) Influence of habitat structure and environmental regime on spatial distribution patterns of macroinvertebrate assemblages associated with seagrass beds in a southern Gulf of Mexico coastal lagoon. *Mar Biol Res* 11:755–764. <https://doi.org/10.1080/17451000.2015.1007875>
6. Ávila-García AK, Ávila E, Gelabert-Fernández R (2019) The reproductive period of the sponge *Haliclona (Reniera) implexiformis* and its relationship with water temperature and salinity. *Cah Biol Mar* 60:547–552.
7. Bachtiar R, Madduppa HH, Bell JJ (2022) Contrasting drivers of sponge and seagrass assemblage composition in an Indo-Pacific seagrass meadow. *J Mar Biol Assoc UK* 102:565–575. <https://doi.org/10.1017/S002531542200087X>
8. Bachtiar R, Madduppa HH, Bell JJ (2023) Variation in autotrophic and heterotrophic sponge abundance in a shallow water seagrass system. *Mar Ecol* 44:e12765. <https://doi.org/10.1111/maec.12765>
9. Bell JD, Steffe AS, Westoby M (1985) Artificial seagrass: how useful is it for field experiments on fish and macroinvertebrates?. *J Exp Mar Biol Ecol* 90:171–177. [https://doi.org/10.1016/0022-0981\(85\)90118-2](https://doi.org/10.1016/0022-0981(85)90118-2)
10. Borowitzka MA, Lethbridge RC, Charlton L (1990) Species richness, spatial distribution and colonization pattern of algal and invertebrate epiphytes on the seagrass *Amphibolis griffithii*. *Mar Ecol Prog Ser* 64:281–291. <https://doi.org/10.3354/meps064281>
11. Briceño-Vera AE, Ávila E, Rodríguez-Santiago MA, Ruiz-Marín A (2021) Macrofaunal assemblages associated with two common seagrass-dwelling demosponges (*Amorphinopsis atlantica* and *Haliclona implexiformis*) in a tropical estuarine system of the southern Gulf of Mexico. *Helgol Mar Res* 75:1. <https://doi.org/10.1186/s10152-021-00546-z>
12. Briceño-Vera AE, Ávila E, Rodríguez-Santiago MA, Nava H (2025) Environmental shifts and their impact on sponge-associated macroinvertebrate communities in seagrass ecosystems. *Hydrobiologia* 852:265–281. <https://doi.org/10.1007/s10750-024-05707-y>
13. Campanino FM, English PA, Layman CA, Archer SK (2023) Sponge presence increases the diversity and abundance of fish and invertebrates in a subtropical seagrass bed. *Estuaries Coasts* 46:1009–1020. <https://doi.org/10.1007/s12237-023-01186-x>
14. Canion CR, Heck Jr KL (2009) Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Mar Ecol Prog Ser* 393:37–46.
15. Carballo JL, Naranjo SA, García-Gómez JC (1996) Use of marine sponges as stress indicators in marine ecosystems at Algeciras Bay (southern Iberian Peninsula). *Mar Ecol Prog Ser* 135:109–122.
16. Castellanos-Pérez PDJ, Vázquez-Maldonado LE, Ávila E, Cruz-Barraza JA, Canales-Delgadillo JC (2020) Diversity of mangrove root-dwelling sponges in a tropical coastal ecosystem in the southern Gulf of Mexico region. *Helgol Mar Res* 74:1–9.
17. David LT, Kjerfve B (1998). Tides and currents in a two-inlet coastal lagoon: Laguna de Términos, Mexico. *Cont Shelf Res* 18: 1057–1079.
18. de Voogd NJ, van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, Alvarez de Glasby B, Hajdu E, Pisera AB, Manconi R, Schoenberg C, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Díaz MC, Cárdenas P, Carballo JL (2018) World Porifera database.

19. Demers MC, Knott NA, Davis AR (2016) Under the radar: sessile epifaunal invertebrates in the seagrass *Posidonia australis*. J Mar Biol Assoc UK 96:363–377. <https://doi.org/10.1017/S0025315415000612>
20. Donnarumma L, Lombardi C, Cocito S, Gambi MC (2014) Settlement pattern of *Posidonia oceanica* epibionts along a gradient of ocean acidification: an approach with mimics. Mediterr Mar Sci 15:498–509.
21. Fell PE, Lewandrowski KB (1981) Population dynamics of the estuarine sponge *Halichondria* sp. within a New England eelgrass community. J Exp Mar Biol Ecol 55:49–63.
22. Fromont J, Vanderklift MA, Kendrick GA (2006) Marine sponges of the Dampier Archipelago, Western Australia: patterns of species distributions, abundance and diversity. In: Hawksworth DL, Bull AT (eds) Marine, freshwater, and wetlands biodiversity conservation. Topics in Biodiversity and Conservation, vol. 4, Springer, Dordrecht, pp 363–382. https://doi.org/10.1007/978-1-4020-5734-2_24
23. García-Sanz S (2009) Patrones de colonización de peces y macroinvertebrados juveniles en diferentes hábitats submareales. MSc Thesis, Universidad de Las Palmas de Gran Canaria
24. Guevara E, Sánchez AJ, Rosas C, Mascaró M, Brito R (2007) Asociación trófica de peces distribuidos en vegetación acuática sumergida en Laguna de Términos, sur del Golfo de México. Univ Cienc 23:151–166.
25. Hernández-Peña FJ (2018) Patrones de distribución espacial de los ensamblajes de esponjas marinas asociadas con tres especies de pasto marino en el sur del Golfo de México. MSc Thesis, Universidad Nacional Autónoma de México
26. Hooper JNA, Kennedy JA (2002) Small-scale patterns of sponge biodiversity (Porifera) from the Sunshine Coast reefs, eastern Australia. Invertebr Syst 16:637–653.
27. Hooper JNA, van Soest RW (2002) Systema Porifera. A guide to the classification of sponges. Springer, Boston: 1–7.
28. Komatsu T, Kawai H (1992) Measurements of time-averaged intensity of water motion with plaster balls. J Oceanogr 48:353–365.
29. Kuffner IB (2001) Effects of ultraviolet (UV) radiation on larval settlement of the reef coral *Pocillopora damicornis*. Mar Ecol Prog Ser 217:251–261.
30. Landau M, Curtis M, Reiley S (2013) A note on the distribution of some sponges and corals in a seagrass bed, Long Key, Florida. Gulf Mex Sci 31:6.
31. Lee SY, Fong CW, Wu RSS (2001) The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. J Exp Mar Biol Ecol 259:23–50.
32. López-Victoria M, Zea S, Weil E (2006) Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. Mar Ecol Prog Ser 312:113–121.
33. Maldonado M, Young CM (1996) Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. Mar Ecol Prog Ser 138:169–180.
34. Maldonado M, Giraud K, Carmona C (2008) Effects of sediment on the survival of asexually produced sponge recruits. Mar Biol 154:631–641.

35. Mariani S, Uriz MJ, Turon X (2005) The dynamics of sponge larvae assemblages from northwestern Mediterranean nearshore bottoms. *J Plankton Res* 27:249–262.
36. Parfitt C, Whisson G (2013) Artificial habitats deployed on seagrass return lower abundance and diversity of macro-invertebrates than those on sandy substrates in Geographe Bay, Western Australia. *Galaxea, J Coral Reef Stud* 15:60–65.
37. Pawlik JR (1983) A sponge-eating worm from Bermuda: *Branchiosyllis oculata* (Polychaeta, Syllidae). *Mar Ecol* 4:65–79.
38. Prabhakaran MP, Pillai NK, Jayachandran PR, Bijoy Nandan S (2013) Species composition and distribution of sponges (Phylum: Porifera) in the seagrass ecosystem of Minicoy Atoll, Lakshadweep, India. In: Venkataraman, K., C. Sivaperuman & C. Raghunathan (eds) *Ecology and Conservation of Tropical Marine Faunal Communities*. 43–54.
39. Riesgo A, Maldonado M (2008) Differences in reproductive timing among sponges sharing habitat and thermal regime. *Invertebr Biol* 127:357–367.
40. Russ GR (1980) Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *J Exp Mar Biol Ecol* 42:55–69.
41. Rützler K (1978) Sponges in coral reefs. In: *Coral reefs: research methods. Monographs on oceanographic methodology*.
42. Setiawan E, Chodiantoro MR, Insany GF, Subagio IB, Dewi NK, Muzaki FK (2021) Diversity of sponges associated in seagrass meadows at coastal area of Pacitan District, East Java, Indonesia. *Biodiversitas* 22:8.
43. Shahbudin S, Jalal KCA, Kamaruzzam Y, Mohammad Noor N, Dah T, John A (2011) Artificial seagrass: a habitat for marine fishes. *J Fish Aquat Sci* 6:85–92.
44. Sheild CJ, Witman JD (1993) The impact of *Henricia sanguinolenta* (OF Müller) (Echinodermata: Asteroidea) predation on the finger sponges *Isodictya* spp. *J Exp Mar Biol Ecol* 166:107–133.
45. Sivaleela G, Samuel D, Anbalagan T, Shrinivaasu S (2013) Seagrass associated marine sponges in Palk Bay. *Rec Zool Surv India* 113:97–103.
46. Stanley SM, Newman WA (1980) Competitive exclusion in evolutionary time: the case of the acorn barnacles. *Paleobiology* 6:173–183.
47. Trautman DA, Borowitzka MA (1999) Distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphology. *Mar Ecol Prog Ser* 179:215–229.
48. Wulff JL (2006) Ecological interactions of marine sponges. *Can J Zool* 84:146–166.
49. Zea S (1993) Recruitment of demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean. *Mar Ecol* 14:1–21.

Figures

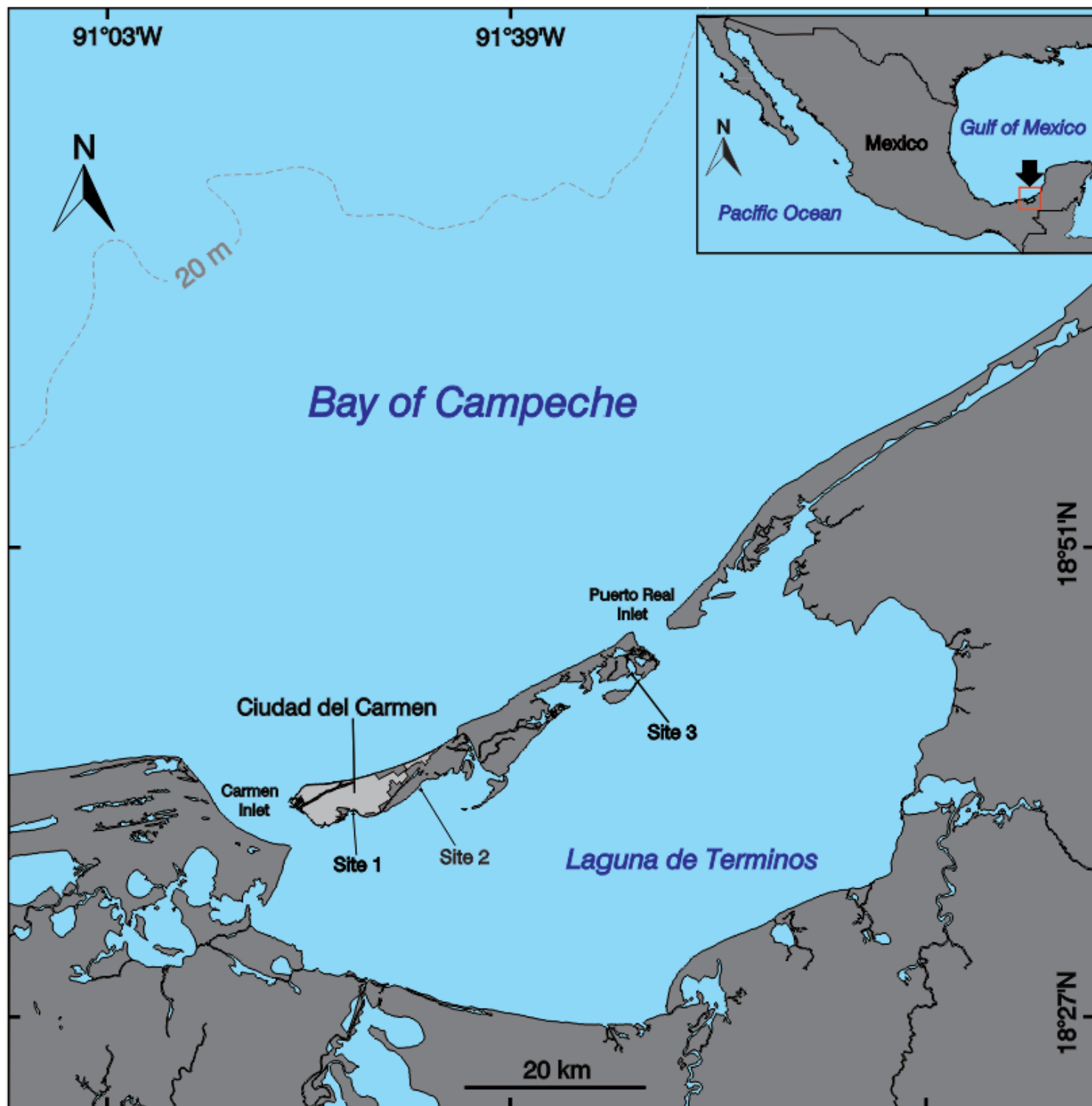


Figure 1

Location of the experimental sites in the northern region of Laguna de Términos, Campeche, Mexico.

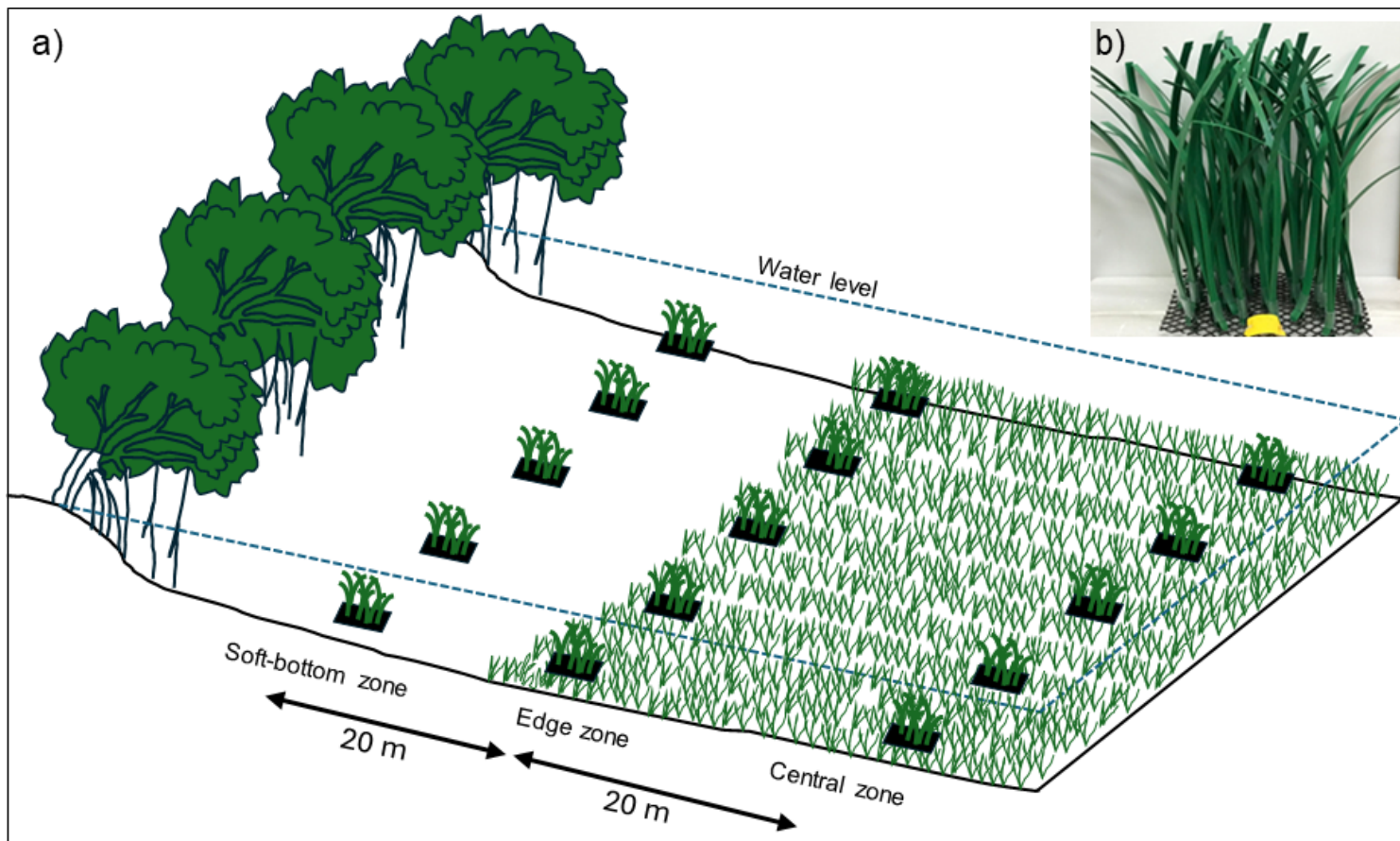


Figure 2

a) Schematic representation of experimental design. b) Artificial seagrass meadow unit (ASU) used in the experiment.

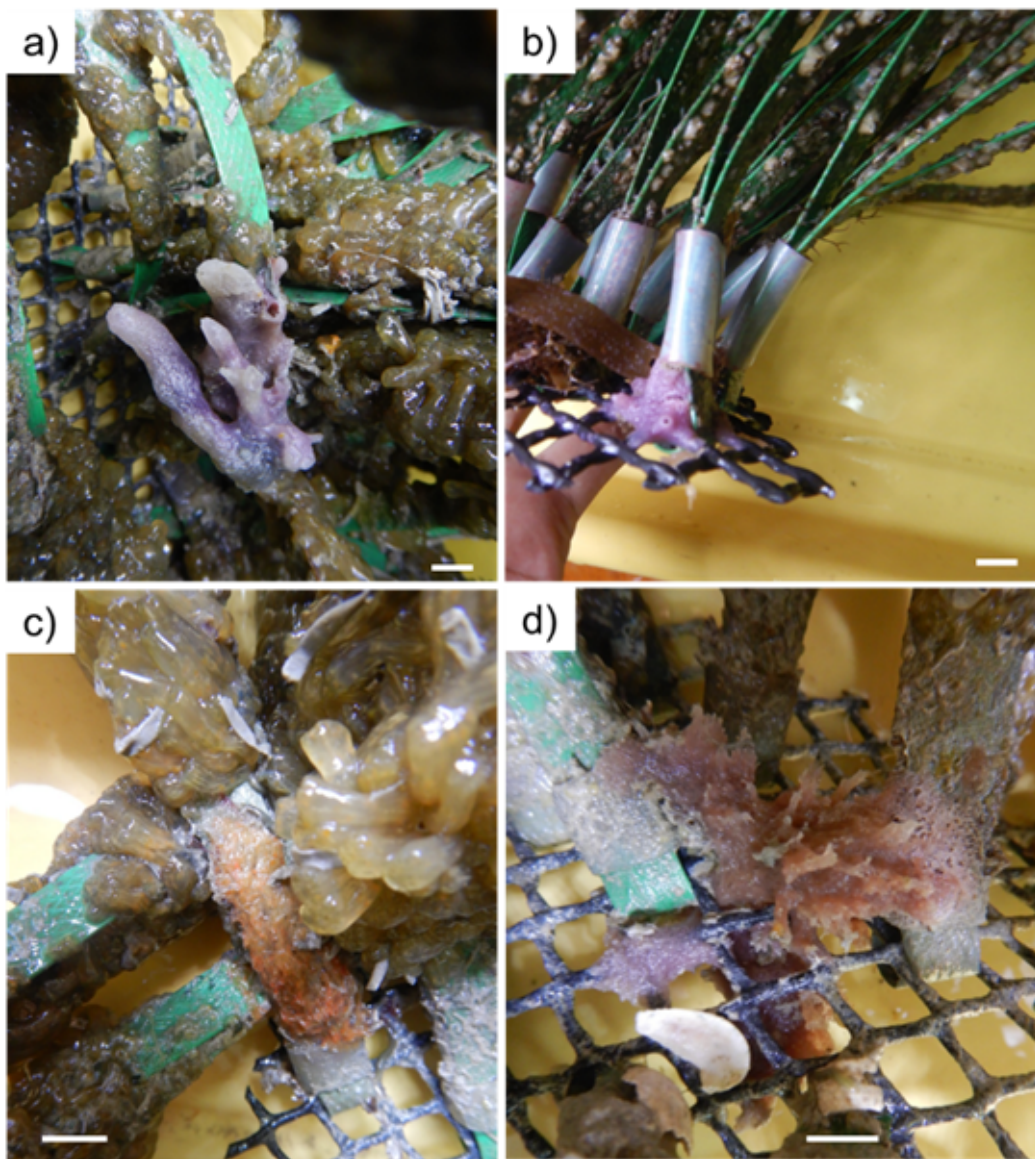


Figure 3

Recruits of sponges and other organisms recorded in the ASUs. a) and b) *Haliclona implexiformis*, c) *Mycale* cf. *microsigmatosa*, and d) *Haliclonasp.*

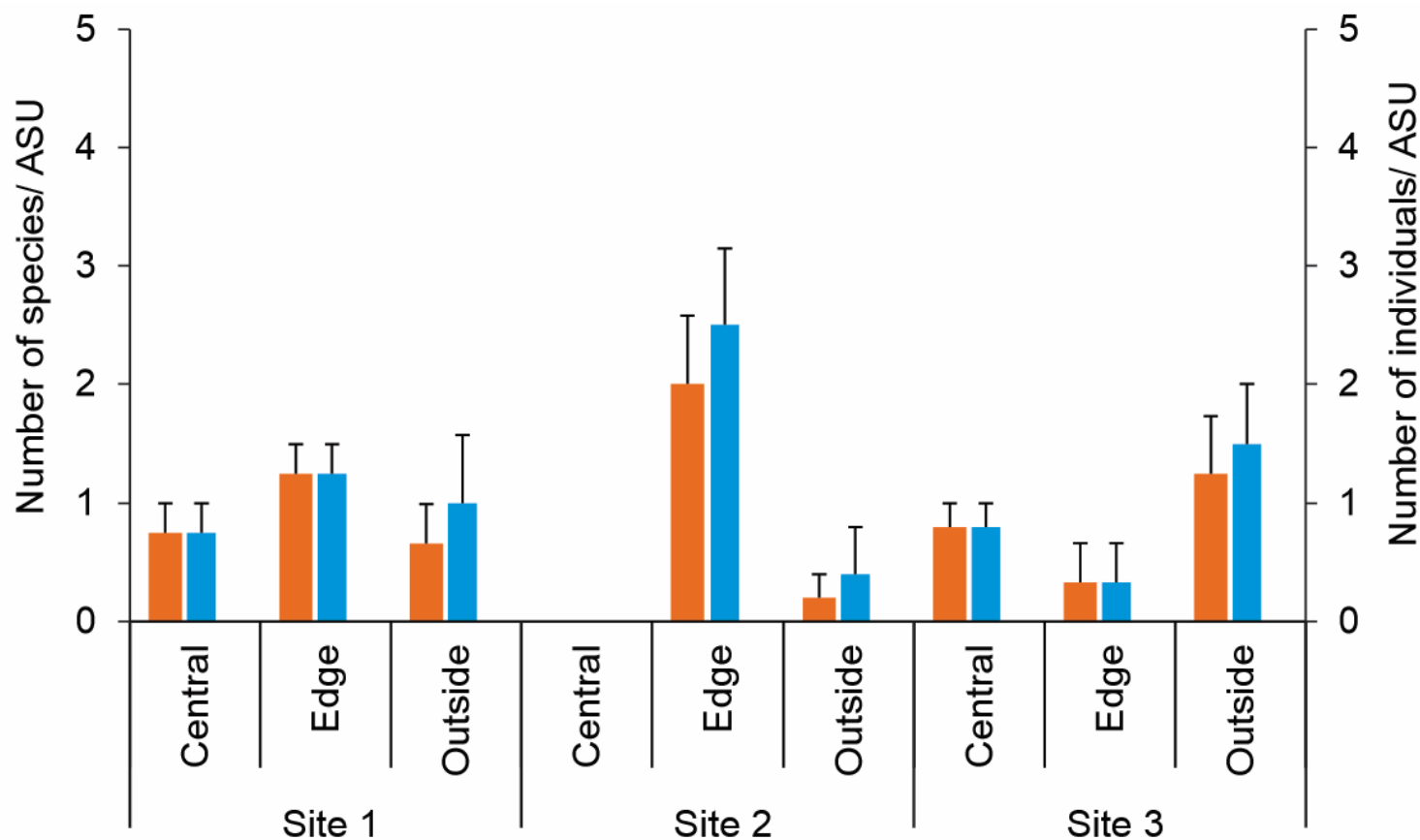


Figure 4

Spatial variation (between sites and zones) in the average ($\pm$ SE) species richness and abundance of sponges recruited in ASUs.

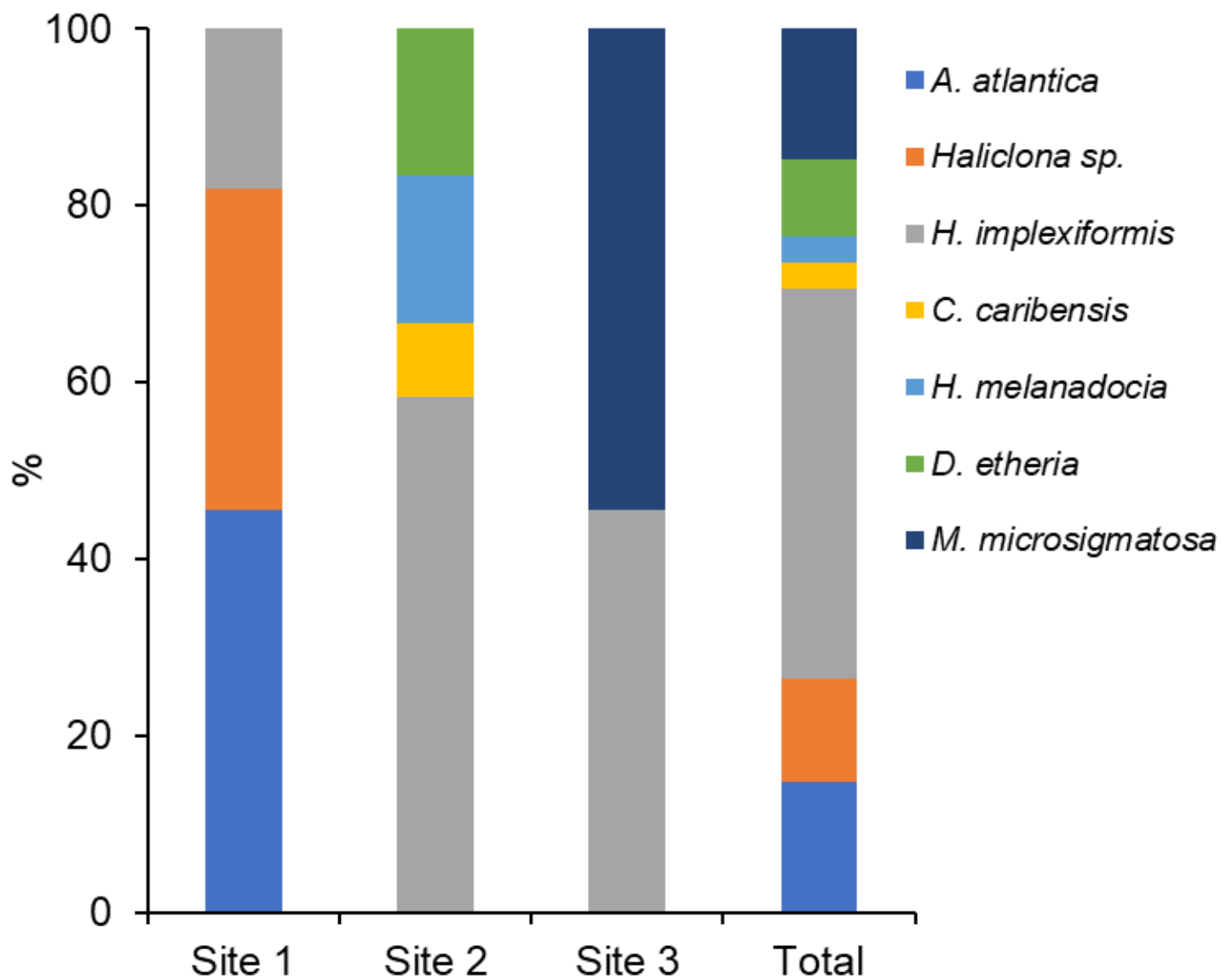


Figure 5

Relative abundance of sponges settled on the ASUs of each study site and total.

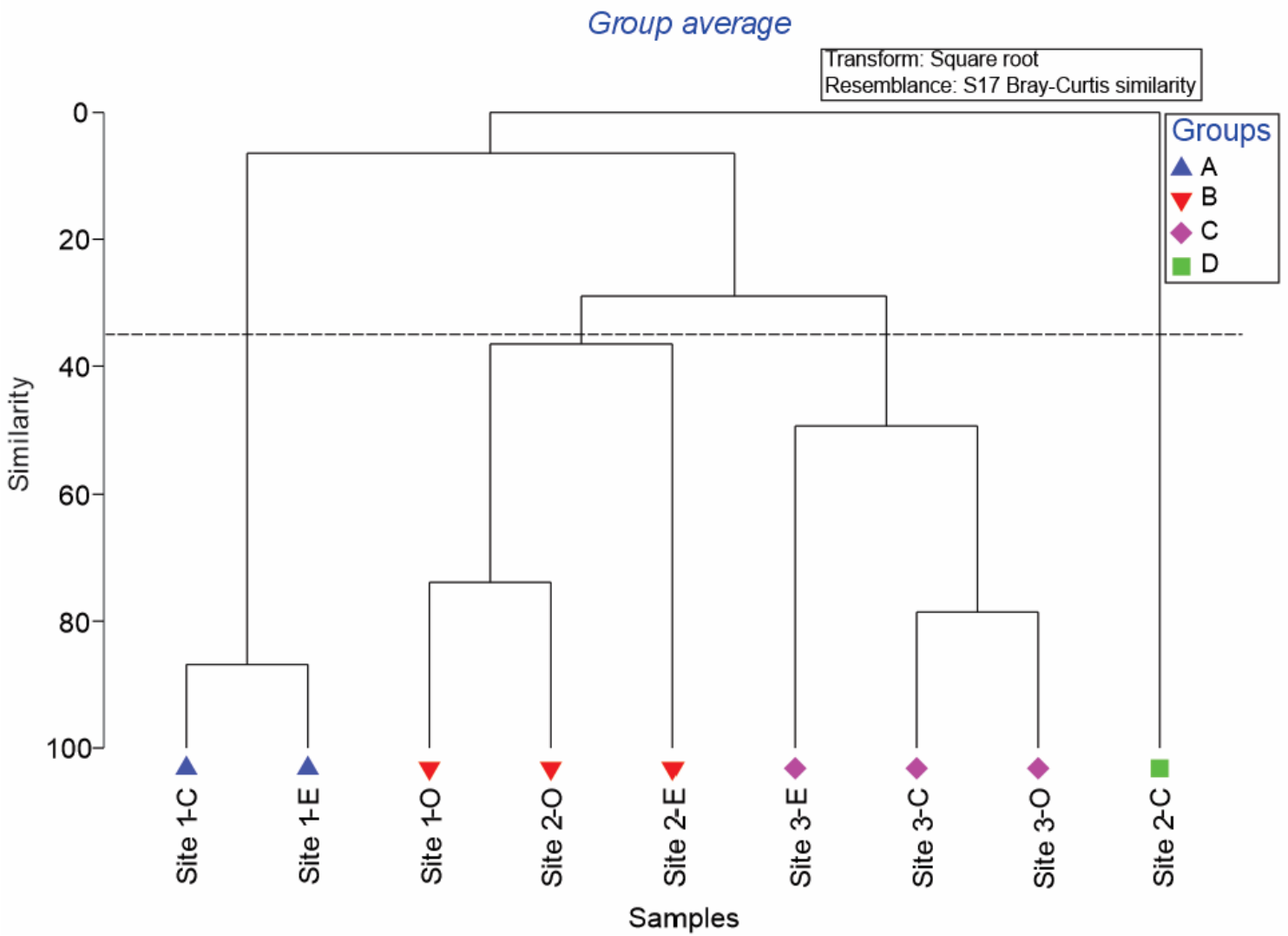


Figure 6

Cluster dendrogram based on Bray-Curtis similarity matrix of abundance data of sponge species settled on the ASUs in each site and experimental zone. The groups of samples formed were indicated with different symbols and colors (A = blue triangle, B = red inverted triangle, C = pink rhombus, D = green square).

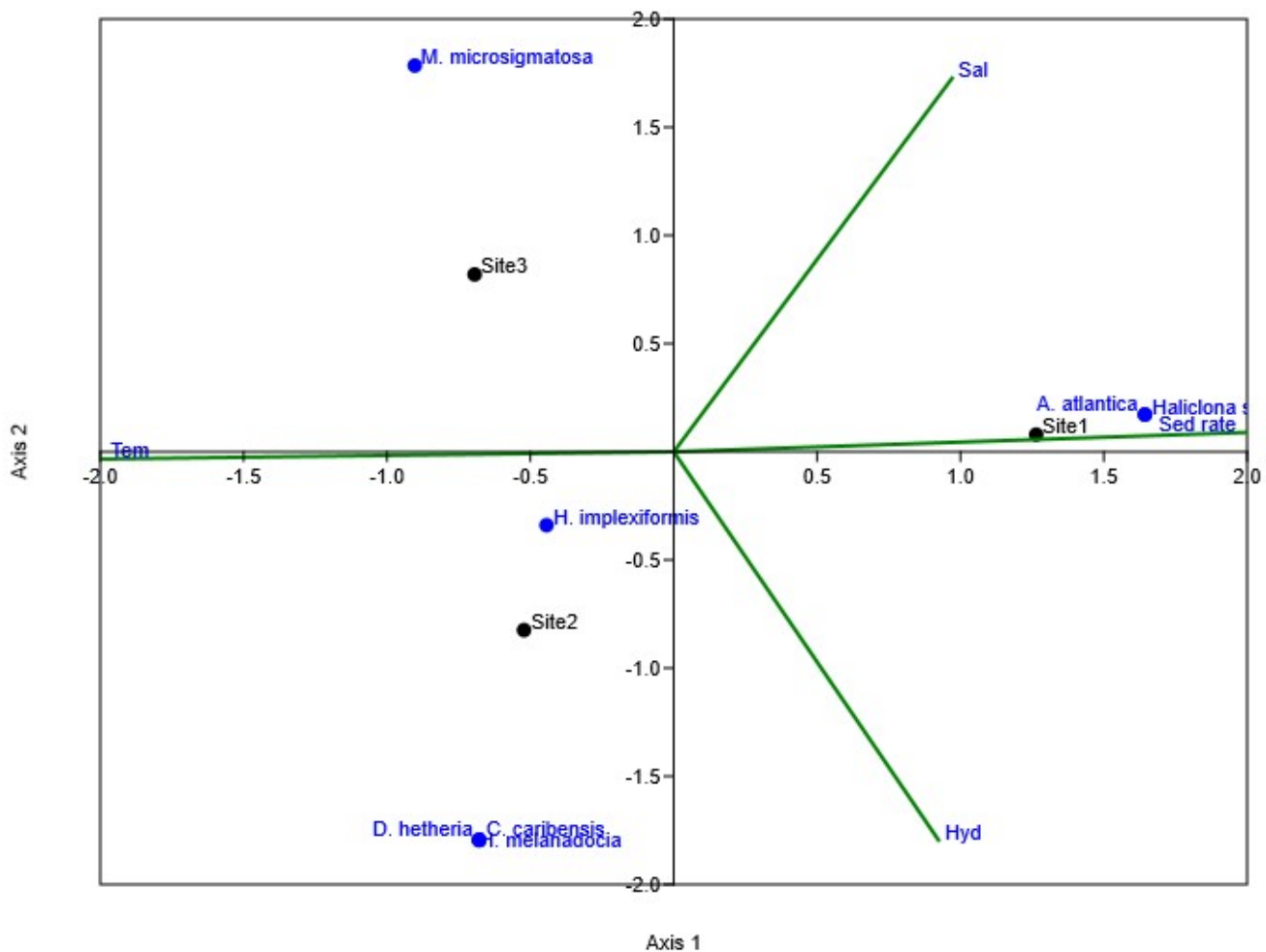


Figure 7

Distribution of sponge species settled on the ASUs at the three experimental sites in relation to hydrodynamism (Hyd), sedimentation/resuspension rate (Sed rate), salinity (Sal), and temperature (Tem). CCA: Vector length and proximity of a sponge species indicate the relative strength of the environmental parameter in influencing its distribution.