The role of environmental factors and habitat on morphological plasticity of the seagrass-dwelling sponge Haliclona implexiformis in the Southern Gulf of Mexico

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Abstract

This study examined spatial and temporal variation in the morphology of the sponge *Haliclona implexiformis* inhabiting *Thalassia testudinum* meadows in the southern Gulf of Mexico. Environmental parameters and seagrass characteristics were analyzed across three sites and two seasons (dry and rainy) to evaluate their influence on sponge morphology. Results showed significant spatial differences among sites, while no consistent seasonal effects were detected. Monthly variability was significant but without a clear pattern across sites. Sponges from the most hydrodynamic site were smaller and exhibited larger oscular diameters, whereas those from more sheltered sites were larger and more branched. Hydrodynamism, organic matter content, and the proportion of coarse sediment particles (mollusk debris) were the factors most strongly associated with morphological variation. Although seagrass attributes, including leaf density and length, did not exhibit a direct correlation with sponge morphology, they may indirectly influence sponge form by altering sedimentation dynamics and local hydrodynamic conditions. Despite the proximity of the study site to an urban area, no anthropogenic influence was detected. The phenotypic plasticity of *H. implexiformis* appears to facilitate its establishment and persistence in seagrass meadows, conferring resilience to environmental variability and enabling morphological adjustments that optimize survival under changing conditions.

Introduction

Marine sponges (phylum Porifera) are among the most diverse and abundant invertebrates inhabiting benthic ecosystems. Their remarkable adaptability to environmental fluctuations has enabled them to persist through geological eras, with extant species displaying broad latitudinal and bathymetric distributions (van Soest et al. 2012). This ecological success is largely explained by their capacity to adjust to contrasting environmental settings. Indeed, across their wide range of habitats, sponges are influenced by physical, chemical, and biological drivers that modulate key processes such as respiration, feeding, reproduction, and growth (Bell et al. 2023).

One of the most distinctive features of sponges is their high morphological plasticity, expressed as variation in growth form, oscular size and density, skeletal density, or branch development, which is strongly shaped by environmental conditions (Carballo et al. 2006). Environmental drivers such as hydrodynamic regime, sedimentation rate, substrate type and orientation, and predation pressure are particularly relevant, as they induce clear morphological responses (Hill and Hill 2002; Bell et al. 2015; Briceño-Vera et al. 2024). At broader ecological scales, this plasticity also translates into community-level patterns; i.e., sponge assemblages vary not only in species composition but also in dominant morphotypes, thereby reflecting local environmental gradients (de Voogd and Cleary 2007; Schönberg 2021). For instance, compact and robust morphologies tend to dominate high-energy environments due to their resistance to fragmentation, whereas calmer and more sedimentary habitats favor branching forms with larger oscula that minimize burial risks (Carballo et al. 2006; Bell et al. 2015). Moreover, under conditions of extreme nutrient limitation, some deep-water species, particularly carnivorous sponges,

may develop erect, pedunculated, or highly branched morphologies, further illustrating the adaptive versatility of the group (Vacelet 2007; Schönberg 2021).

At the population level, the influence of environmental drivers on sponge morphology, such as growth form, oscular diameter and density, skeletal density, spicule shape and size, and branch development, has been examined through manipulative experiments (Hill and Hill 2002; Carballo et al. 2006; Ávila and Briceño-Vera 2018). Assessing these relationships is particularly relevant because several morphological attributes, including sponge volume, oscular diameter and density, and branch complexity, have been widely used as predictors of the diversity and abundance of associated organisms (Ribeiro et al. 2003; Pérez-Botello et al. 2023). Indeed, the availability of niches for both epi- and endobionts is expected to increase with greater sponge volume, a higher number of internal canals, oscula and branches (Koukouras et al. 1996; Gherardi et al. 2001). Nevertheless, few studies have explicitly quantified how specific environmental drivers shape sponge morphology in seagrass meadows, critical habitats where sponges play a key role in mediating ecosystem functions such as nutrient cycling (Archer et al. 2015; McMurray et al. 2018).

The sponge *Haliclona* (*Reniera*) *implexiformis* (Hechtel 1965) is a common species inhabiting shallow seagrass meadows of the tropical western Atlantic (de Voogd et al. 2025). Although its biology and ecology (Ávila et al. 2015a), reproductive strategies (Ávila-García et al. 2020), and role as a host for associated fauna (Briceño-Vera et al. 2021) have been documented, the environmental drivers underlying its morphological variability remain poorly understood. To address this gap, the present study investigates the spatial (among seagrass meadow sites) and temporal (dry vs. rainy seasons) variation in the morphology of *H. implexiformis* within a tropical coastal lagoon in the southern Gulf of Mexico. For this purpose, we measured a suite of environmental parameters, including seagrass-associated variables (density, biomass, and leaf length) potentially influencing sponge morphology. Furthermore, because the study sites were located at varying distances from an urban area, we also assessed indicators of anthropogenic pressure such as biochemical oxygen demand, fecal coliforms, total nitrogen, and phosphorus.

Materials and methods

Study area

This study was performed in the Laguna de Terminos (LT), a tropical coastal lagoon located in the southern Gulf of Mexico (Fig. 1), which has approximately 2500 km^2 (Kuc-Castilla et al. 2015), an average depth of 3.5 m, and receives freshwater input from three main rivers (Paz-Ríos et al. 2023). In this lagoon-estuarine system, three climatic seasons have been recognized: dry season (March–June), rainy season (June–October), and the winter storms or 'northerns' season (November–February) (Rivera-Monroy and Twilley 1996). The term 'northern' is a local name for the stormy season in the Gulf of Mexico characterized by the presence of north cold air masses (wind speed ranging from 21 to 30 m s^{-}

^{1}) coming from high latitudes, and strong winds (Passalacqua et al. 2016). This research focused on the most contrasting periods, the dry and rainy seasons.

In the north part of the lagoon (where the marine conditions prevail), extensive seagrass meadows, dominated by *T. testudinum*, can be found (Cuevas et al. 2021), which harbor abundant populations of the sponge *H. implexiformis* throughout the year (Ávila et al. 2015a; Ávila-García et al. 2019).

Sampling method

To examine the variations in the morphology of *H. implexiformis* and the possible influence of environmental factors and habitat characteristics, three sampling sites were chosen. These sites were located in the inner side of Isla del Carmen (Site 1: 18°39´32´´N – 91°44´03´´W; Site 2: 18°39´54´´N – 91°40´10´´W, and Site 3: 18°44´31´´N – 91°32´13´´W), at different distances from the main urban area, Ciudad del Carmen, which is one of the fastest-growing municipalities in Mexico (Cuevas et al. 2021): Site 1 at 5 km, Site 2 at 15 km and Site 3 at 30 km (Fig. 1). The three sites were located approximately 30 m from the shoreline and at a depth varying between 0.5 and 0.8 m.

At each site, within a 10 x 10 m seagrass area, 15 individuals of *H. implexiformis* were randomly collected by snorkeling during each dry and rainy season. To ensure the representativeness of the sampled individuals, five sponges were collected in March, April, and May for the dry season, and five in August, September, and October for the rainy season. The specimens were carefully detached from their substrates, placed individually in previously labeled plastic bags, and transported to the laboratory, where they were frozen until further processing. During each sampling month and using a PVC corer (15 cm diameter; 5 cm depth), five seagrass samples were also collected by site (a total of 15 samples for the dry and 15 for the rainy seasons). Seagrass samples were placed in previously labeled plastic bags and transported to the laboratory, where they were frozen until further analysis.

Morphological characterization of H. implexiformis

First, an evaluation of the skeletal elements (type of spicules present and dimensions) of each sponge individual was carried out to confirm its taxonomic identity according to a previous description of *H. implexiformis* in the study area (Ávila et al. 2015a). For each sponge individual, the volume (mL), estimated by the fluid displacement method (Rützler 1978), the length of branches (cm), measured as the distance from the sponge surface to the tips of the oscular elevations, together with the mean oscular diameter (mm) were measured with a Vernier caliper. The number of branches and oscula were recorded for each sponge individual.

Leaf density, leaf length, and biomass of seagrass

The seagrass density was determined by counting all the seagrass leaves per core sample and expressed as the number of leaves m^{-2}. For each leaf, the length (cm) from the top of the sheath to the

tip was measured. The dry biomass of leaves (above-ground biomass) was evaluated by weighing all the leaves after they were dried in an oven at 60°C for 48 h (kg dry weight (DW) m^{-2}).

Environmental parameters

During each sampling date at each site, the temperature (°C), salinity (PSU), and dissolved oxygen (mg L^{-1}) were measured near the bottom. Temperature and salinity were measured with a portable YSI model 63 multiparameter sonde (Yellow Springs Instruments, Yellow Springs, OH, USA), and the dissolved oxygen with a DO9100 digital dissolved oxygen meter.

Two liters of water (samples) were collected at each site to determine the concentration of fecal coliforms (MPN), total nitrogen (mg L^{-1}), total phosphorus (mg L^{-1}), and biochemical oxygen demand (BOD, mg L^{-1}), following the techniques described in the Mexican norms NMX-AA-042-2015, NMX-AA-026-SCFI-2010, NMX-AA-029-SCFI-2001, and NMX-AA-028-SCFI-2001, respectively.

The sedimentation rate (kg DW m^{-2} day^{-1}) was determined at each site during the studied seasons. For this, four sediment traps, consisting of 3 cm diameter x 25 cm length PVC pipes, were placed vertically and were replaced every month. In the laboratory, the trapped material was rinsed with distilled water to remove salts and dried at 60°C for 24 h before weighing (see details of this method in Carballo et al. 2006).

The hydrodynamism at each sampling site was estimated using the plaster dissolution method, which is based on the weight loss of plaster cylinders over a given time (see details of this method in Gambi et al. 1989). At each site, four 5-cm-diameter cylinders were placed 10 cm from the bottom over 5 days. In this case, the mass loss of each cylinder is independent of fluctuations in flow direction and velocity (Denny 1988) but is linearly related to flow velocity and water temperature. It was not necessary to calibrate the effect of water temperature on plaster dissolution, since the temperature at the three sites studied was similar. The hydrodynamism was expressed as the average dissolution rate of plaster cylinders (% dissolution day^{-1}).

The granulometry of the sediments was determined by the wet sieving method (very coarse sand > 2000 µm, coarse sand > 840 µm, fine sand > 420 µm, very fine sand < 420 µm), according to criteria established by Inman (1952) and Folk (1965). For this evaluation, three sediment cores (15 cm diameter x 5 cm depth) were extracted monthly at each site where the sponge and seagrass were collected. After sieving, samples were dried at 60°C for 72 h, and the material retained on each sieve was weighed to obtain the relative percentage of each particle size per core. The percentage of organic matter at each site/season was determined by calcination (particles < 420 µm only), which consisted of calcining the sediment samples at 550°C for 2 hours, and by weight difference (initial weight - final weight), the organic matter was obtained.

Data analysis

Data on environmental parameters and seagrass meadows were grouped and considered as the predictor matrix. As a result of the observed correlations between every pair of variables through the Draftsman plots, showing skewed bivariate distributions among the variables, the fecal coliform, hydrodynamism, percentage of sediment particles > 420 µm, > 840 µm, and biomass (seagrass) data were ln-transformed. After that, all data were normalized, and an association matrix was constructed using Euclidean distance among observations. To test for differences among sites and seasons, a PERMANOVA was performed using a two-factor design: site factor (fixed) with three levels and season factor (fixed) with two levels. For this, 9999 permutations of the residuals were used under a reduced model and the sum of squares Type III. To visualize the pattern of variation in environmental characteristics, a Principal Coordinate Analysis (PCO) was used. In this plot, an overlay trajectory was performed by month and split by sites to show the temporal variations. Given limited permutation possibilities for seasonal comparisons, a Monte-Carlo test was employed (Anderson and Braak 2003).

Regarding morphological data of *H. implexiformis*, the same pre-analytical procedures were followed, and volume data were ln-transformed. Subsequently, all data were normalized, and an association matrix was constructed using Euclidean distance among observations. To determine whether the morphology of *H. implexiformis* differs among sites and seasons, a PERMANOVA was conducted with a three-factor design: site factor (fixed) with three levels, season factor (fixed) with two levels, and month factor (random and nested in season) with six levels. For this, 9999 permutations of the residuals were used under a reduced model and the sum of squares Type III. A Principal Coordinate Analysis (PCO) was used to visualize the sponge morphology variations among sites and seasons. In this plot, an overlay trajectory was performed by month and split by sites to show the temporal variations. We used a Monte-Carlo test to compare seasons due to the few possible permutations in the analysis (Anderson and Braak 2003).

A binary divisive clustering (LINKTREE) was used to determine potential drivers that could explain the sponge characteristics at both the spatial and temporal scales. An Analysis of Similarities (ANOSIM) with 9999 permutations was simultaneously run to identify the statistical significance of the multivariate structure in the groups generated by the LINKTREE. All data analyses were performed according to the non-multiparametric routine suggested by Clarke et al. (2014) using the software PRIMER V.7 (PRIMER-E Ltd, Plymouth, U.K.).

Results

Environmental data

Data on the environmental factors and the seagrass meadow characteristics measured in each site during the dry and rainy seasons are shown in Table 1. The PERMANOVA results revealed that environmental characteristics considered in this study were statistically different among sites (pseudo-F = 5.3613, p = 0.0001) but not between seasons (see Table 2). In this analysis, the SitexSeason interaction was not significant (p = 0.088). Temporal variability (among months) was significant (pseudo-F = 2.062,

p = 0.0143), and a visual inspection of the PCO shows that this might be the case, although there was not a clear pattern among sites (Fig. 2).

Table 1
Data on environmental parameters and seagrass meadows in each site and season.

	Site 1		Site 2		Site 3	
Parameter	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**
Temperature (°C)	29.13 ± 2.32	30.07 ± 0.32	29.60 ± 2.12	30.30 ± 1.71	29.10 ± 2.03	30.27 ± 1.74
Salinity (PSU)	30.33 ± 6.03	30.77 ± 3.91	31.53 ± 4.50	31.73 ± 3.35	34.20 ± 2.03	33.73 ± 2.20
Dissolved oxygen (mg L)	9.73 ± 2.70	10.60 ± 3.82	7.37 ± 0.80	6.17 ± 2.11	9.73 ± 2.35	8.97 ± 1.27
Sedimentation (kg m^{-2} day^{-1})	1.10 ± 0.34	1.21 ± 0.74	0.48 ± 0.09	0.49 ± 0.03	0.70 ± 0.19	0.36 ± 0.19
Fecal coliforms (MPN)	2.00 ± 0.00	14.00 ± 20.78	2.83 ± 1.44	3.93 ± 3.35	2.00 ± 0.00	2.00 ± 0.00
BOD (mg L)	3.80 ± 0.80	1.43 ± 0.21	2.20 ± 1.00	1.67 ± 1.10	2.30 ± 0.90	1.77 ± 0.21
Total Nitrogen (mg L)	33.62 ± 21.88	17.97 ± 3.99	31.75 ± 14.37	16.20 ± 3.80	37.35 ± 26.03	20.77 ± 5.44
Total Phosphorus (mg L)	21.51 ± 9.35	29.74 ± 0.59	21.97 ± 7.56	25.61 ± 7.71	26.03 ± 5.51	26.02 ± 6.62
Hydrodynamism (% of dissolution)	74.32 ± 0.00	36.00 ± 0.00	22.69 ± 0.00	24.10 ± 0.00	21.83 ± 0.00	23.91 ± 0.00
% Organic matter	3.32 ± 0.91	3.52 ± 0.46	9.47 ± 2.97	6.32 ± 0.63	11.53 ± 1.53	14.31 ± 2.38
%<420 µm	81.10 ± 27.12	52.24 ± 4.87	40.09 ± 13.62	53.16 ± 4.94	45.71 ± 13.78	57.01 ± 17.43
%>420 µm	9.81 ± 14.37	21.39 ± 3.67	2.42 ± 0.33	2.32 ± 0.61	4.25 ± 3.17	4.39 ± 1.77
%>840 µm	3.36 ± 5.28	16.55 ± 6.84	3.92 ± 0.21	4.47 ± 0.66	4.08 ± 1.39	4.31 ± 2.40
%>2000 µm	5.73 ± 7.57	9.81 ± 4.21	53.57 ± 13.78	40.06 ± 3.67	45.97 ± 17.63	34.29 ± 13.72
Seagrass biomass (kg m^{-2})	1.27 ± 1.25	0.74 ± 1.00	0.48 ± 0.20	0.53 ± 0.30	0.30 ± 0.07	0.29 ± 0.12
Seagrass density (leaves m^{-2})	3629.30 ± 1413.76	3067.17 ± 1208.85	2863.45 ± 1243.29	2769.13 ± 1006.98	1233.66 ± 438.97	1765.60 ± 767.98
Leaf length (cm)	19.12 ± 6.06	14.35 ± 2.52	11.65 ± 1.89	11.43 ± 2.41	18.42 ± 2.67	11.86 ± 1.35

Table 2
Permutational Analysis of Variance of environmental parameters among sites and seasons.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Site	2	93.676	46.838	5.3613	0.0001*	9941	-
Season	1	25.77	25.77	1.4708	0.2013	10	0.2215
Month(season)	4	70.086	17.521	2.0056	0.0048*	9905	-
SitexSeason	2	29.578	14.789	1.6928	0.0882	9928	-
Residuals	8	69.89	8.7363				
Total	17	289					
Asterisk indicates values less than alpha of < 0.05.							

According to PCO, which explained 50% of the total variation (axis 1: 32%; axis 2: 18%), parameters with greatest correlation (> 70%) were: i) the percentage of organic matter and ii) the percentage of very coarse sediment particles, greater in Sites 2 and 3 than in Site 1, iii) seagrass biomass, iv) sedimentation rate, v) hydrodynamism, vi) percentage of very fine particles and vii) biochemical oxygen demand, greater in Site 1 than in Sites 2 and 3. Temporal variation within Site 1 was related to the percentage of fine and coarse particles (> 420 µm, > 840 µm, respectively), which increased during the rainy season (Fig. 2).

Morphological characteristics of the sponge

Data on the sponge morphological characteristics measured at each site during the dry and rainy seasons are shown in Figs. 3 and 4. When examining the morphological data of *H. implexiformis*, significant differences were found among sites (pseudo-F = 9.3163, p = 0.0001) but not between seasons (p = 0.09) (see Table 3). In the case of the interaction SitexSeason of the PERMANOVA test, it was not significant. On the other hand, temporal variability among months was significant (pseudo-F = 2.062, p = 0.0143), but there was not a similar pattern in each site. A visual inspection of the PCO, which explained 75.46% of the total variation (axis 1: 51.8%; axis 2: 23.7%) shows that this might be the case, as there were clear seasonal differences in site 2 only (Fig. 5). The PCO also showed that parameters that had the greatest correlation (up to 70%) were: i) oscular diameter, greater in Site 1 than in Sites 2 and 3, ii) total volume, and iii) branch length, greater in Sites 2 and 3 than in site 1. Temporal variations within Site 2 were related to the number of branches and oscula present in sponges, which decreased from the dry to the rainy season (Figs. 4B and D).

Table 3
Permutational Analysis of Variance of sponge *H. implexiformis* among sites and seasons.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Site	2	108.15	54.077	9.3163	0.0001*	9959	-
Season	1	14.012	14.012	2.1585	0.0997	10	0.1292
Month(season)	4	25.965	6.4913	2.062	0.0143*	9920	-
SitexSeason	2	23.77	11.885	2.0475	0.1	9949	-
SitexMonth(Season)	8	46.437	5.8046	1.8438	0.0071*	9885	-
Residuals	72	226.66	3.1481				
Total	89	445					
Asterisk indicates values less than alpha of < 0.05.							

Sponge characteristics and environment

The classification analysis (LINKTREE) separated site 1 from sites 2 and 3 (first division: A); on the one hand, sites 2 and 3 were grouped with both seasons (group B), on the other hand, site 1 and both seasons were grouped (group J). This separation of site 1 vs sites 2 and 3 was statistically significant ($R = 0.74$, $p = 0.0002$). The environmental parameters that most contributed to this separation were hydrodynamism (higher at site 1 than at the other two sites), the percentage of organic matter, and the percentage of very coarse sand (> 2000 µm) (both higher at sites 2 and 3 than at site 1). Within subdivisions B and J, there were no significant differences in sponge characteristics that could be explained by any of the environmental parameters (Fig. 6).

Discussion

Many of the studies that have evaluated the morphological variability of sponges at the spatial and/or temporal scale have been based solely on the type of sponge shape, using qualitative data (Berman et al. 2013; George et al. 2018; Evans and Montagnes 2019; Broadribb et al. 2021; Schönberg 2021). In Laguna de Terminos, the morphology of the sponge *H. implexiformis* exhibited a clear pattern only at the spatial scale, with individuals from site 1 differing significantly from those at sites 2 and 3. No significant differences were detected between seasons; however, monthly comparisons revealed variations without a consistent pattern at each site, which may be related to the monthly sampling design and/or to differences in environmental conditions of each site. At site 1, they were characterized by being smaller and having larger oscular diameters, and those from sites 2 and 3 were larger and more branched (Figs. 3 and 4B). Temporally, the morphology of individuals from site 2 showed the greatest variation compared with those of sites 1 and 3. In site 2, during the dry season, the individuals presented a greater number of branches and oscula than during the rainy season (Fig. 5). Multivariate analyses revealed that

higher values of hydrodynamism, percentage of organic matter, and proportion of very coarse particles in surface sediments were associated with the sponges having a greater number of branches and oscula.

In general, sponges tend to form thin-branching growth forms under sheltered conditions, while the growth form gradually transforms into a more compact shape when the exposure to water movement increases (Kaandorp and Sloot 2001; Carballo et al. 2006). This type of morphological change in sponges has been studied experimentally, and it has been suggested that they arise as acclimatization tactics to environmental changes (Palumbi 1984; Carballo et al. 2006). For example, in a transplant experiment conducted in Mazatlan Bay (Mexican Pacific), individuals of the sponge *Haliclona caerulea* (in association with red alga *Jania adherens*) were transplanted from 3 m deep to sites with higher and lower hydrodynamic conditions (1 m and 5 m depth, respectively) (Carballo et al. 2006). They found that *H. caerulea* individuals developed flattened forms with smaller oscula at 1 m and branching forms at 5 m. Consistently, in Laguna de Terminos, the individuals of *H. implexiformis* from site with a higher hydrodynamic regime (like site 1) were smaller and with fewer branches, compared with those from sites with less hydrodynamism (like sites 2 and 3), which showed more complex shapes.

At sites 2 and 3, where *H. implexiformis* individuals were larger and more branched, there was also a higher proportion of coarse particles in the surface sediment. These large particles (composed of mollusk shell remains) can provide well-consolidated substrates for sponge growth within seagrass meadows and prevent sponges from being dragged by tidal currents (Duckworth and Wolff 2011). Therefore, the low hydrodynamic conditions, combined with a higher proportion of coarse particles in the sediments, could favor the development of larger sponges. Furthermore, the higher proportion of organic matter in sediments of these sites could indicate a lower sedimentary resuspension and therefore lower hydrodynamic energy (Briceño-Vera et al. 2024).

Regarding the seagrass, the leaf density and length were not directly correlated with *H. implexiformis* morphology. Although Archer et al. (2015) did not find a linear relationship between the abundance of the sponge *Halichondria melanadocia* and leaf density in *T. testudinum* meadows, they argued that the structural complexity of the meadows alters the environment and creates environments that influence the sponge presence. For example, a higher leaf density favors greater settling of suspended particles (Gacia et al. 2003), causing the sponges to restructure their aquifer system by opening their oscula wider or developing more branches (Bell et al. 2015). The higher sedimentation rate found in site 1 was related to denser and longer *T. testudinum* leaves, where the sponges had the largest oscular diameter, which might be a response from the sponge to both seagrass and environmental characteristics.

It is also known that most sponges settled in environments with high sedimentation rates often develop erect and branched forms to avoid becoming buried or having their aquifer system blocked. However, we found that the *H. implexiformis* individuals growing in the site with the highest sedimentation rate were not branching, which could be explained by the fact that this site also has the greatest hydrodynamic regime, which can limit the branching production. Although the study sites were at the same depth, the

greater sedimentation and hydrodynamic regime at site 1 may be because this site is located in an area more exposed to waves generated by the prevailing winds (SE) than sites 2 and 3. These winds can reach speeds of up to 45 km h^{-1} and generate waves and high resuspension of sediments (Vázquez et al. 1999).

On the other hand, it has also been shown that factors such as predation can also affect the branch production in sponges. Hill and Hill (2002) conducted an experimental study on *Anthosigmella varians*, demonstrating that predation had a greater influence on sponge morphology than water movement, mainly in coral reef environments where predation rate is known to be higher (Huston 1985). Although this factor was not examined here, there are no records of spongivorous organisms in this coastal system that could forage on *H. implexiformis*.

In addition to spatial variability, the environmental changes that occurred from one season to another may also affect the abundance and morphology of shallow water sponges (Ávila et al. 2011). In coastal regions of the Pacific and Atlantic of Mexico, for example, seasonal changes in the direction of currents, waves and the pattern of prevailing winds cause fragmentation and/or detachment of the substrate of sponges from the subtidal zone, which in turn results in losses in biomass and population abundance (Ávila et al. 2011; 2022). A previous study conducted in the study area documented a decrease in the abundance of *H. implexiformis* from the dry to the rainy season, which was attributed to fragmentation and/or detachment processes (Ávila et al. 2015a), since the rainy season is characterized by strong winds and higher waves, which constitute a more stressful environment for shallow-water benthic organisms (Hernández-Arana et al. 2003). Significant temporal variation in the morphology of *H. implexiformis* was detected across sites, occurring at a monthly rather than seasonal scale and lacking a clear linear trend. These variations may have been driven by wind intensity and site-specific exposure.

On the other hand, recent studies have shown that urban development in coastal areas together with climate change have caused the loss of seagrass meadows in different regions of the world (van Katwijk et al. 2016; do Amaral Camara Lima et al. 2023), and with this, the ecosystem services they provide (Creed et al. 2023). In fact, over the last decade, the loss of seagrass meadows in Laguna de Terminos has also been more evident, which has been attributed to an increase in wastewater discharges that increase total suspended solids (Cuevas et al. 2021). However, in the present study, no influence of the urban area on the characteristics of the sponge and those of the *T. testudinum* meadows was detected, as parameters such as BOD, fecal coliforms, total nitrogen, and total phosphorus presented values within those established by Mexican standards, even at the closest site. However, it is important to note that these standards are determined in relation to public health and not about their possible ecological effects (SEMARNAT 2022), so it is important to continue monitoring these parameters to assess any anthropogenic influence on the seagrass meadows of this lagoon system in the future.

Conclusions

This study demonstrates that the morphology of the seagrass-dwelling sponge *H. implexiformis* is mainly shaped by site-specific environmental conditions and, to a lesser extent, by temporal factors, without a consistent seasonal trend. Exposure to winds, hydrodynamics, sediment composition, and seagrass structure largely explained the observed differences, with more exposed sites favoring smaller sponges with larger oscula, and sheltered sites supporting larger, branching forms. Although no urban impact was detected, the proximity of Laguna de Términos to a rapidly growing municipality highlights the need for long-term monitoring, given the ecological importance of sponge-seagrass interactions for coastal biodiversity.

Declarations

Ethics declarations

Ethics approval

Not applicable.

Conflict of interest

The authors have no competing interests to disclose.

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Author contributions

Briceño-Vera AE contributed to conceptualization, writing the original draft, investigation, formal analysis, and methodology. Ávila E contributed to conceptualization, writing, review and editing, supervision, project administration, funding acquisition, and investigation. Hernández-Alcántara P contributed to writing, review and editing, supervision, and formal analysis. Cruz-Motta JJ contributed to supervision, investigation, methodology, and formal analysis. Ruiz-Marin A contributed to supervision, investigation, methodology, and formal analysis. Nava H contributed to supervision, investigation, methodology, and formal analysis. Cruz- Barraza JA contributed to supervision, investigation, and methodology. Celis-Hernández O contributed to writing, review and editing, and supervision.

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Data Availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

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Figures

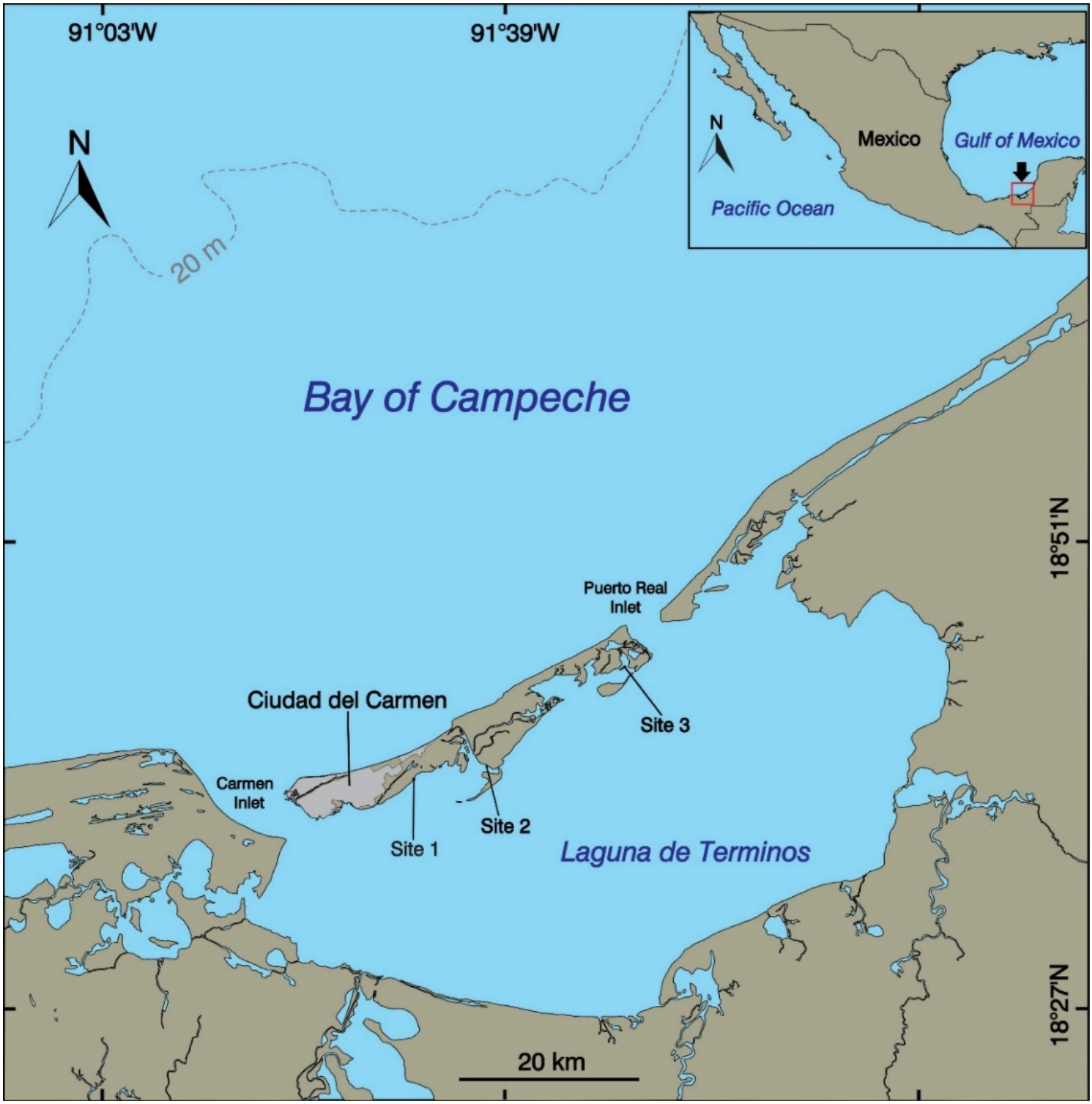

Figure 1

Study area within Laguna de Terminos and the three sampling sites

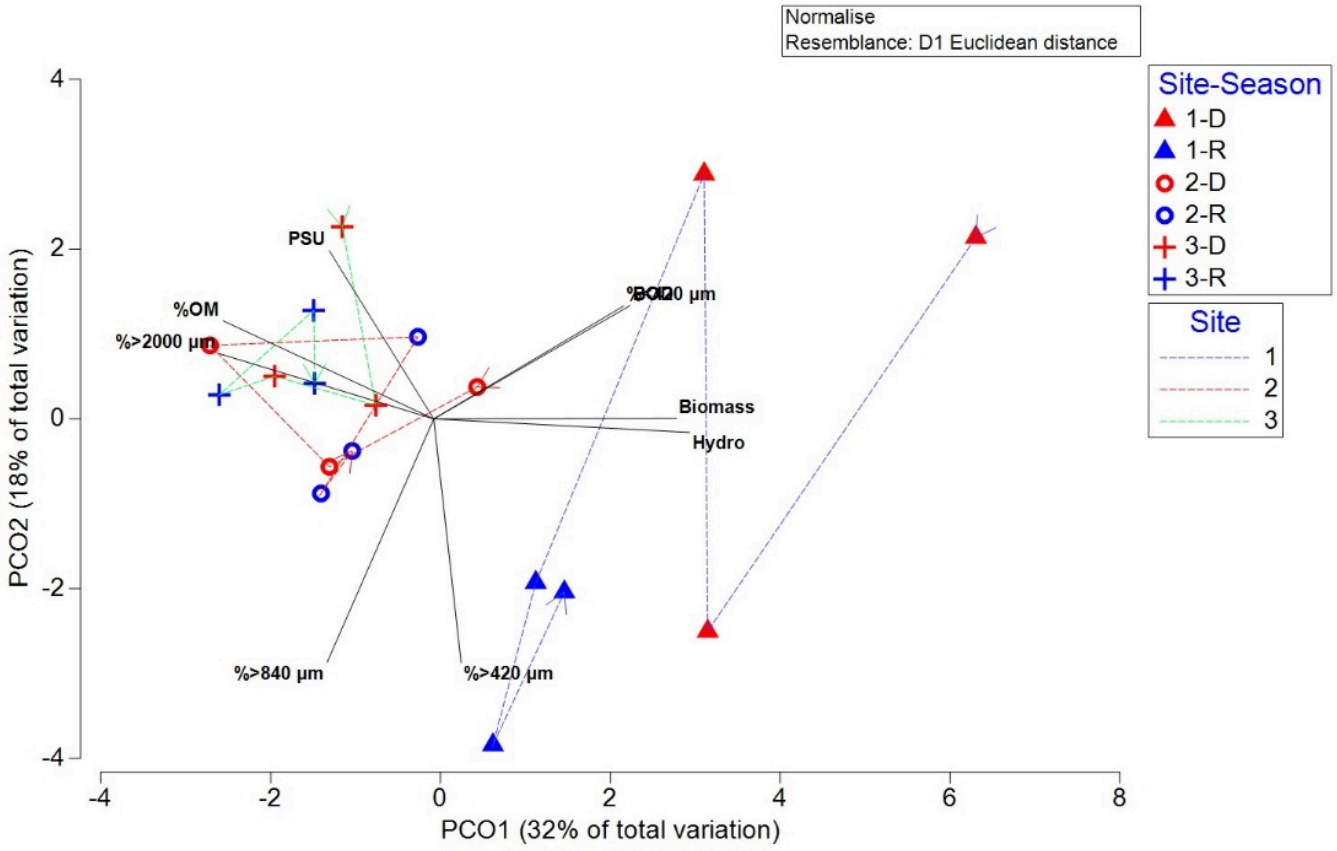

Figure 2

Principal Coordinates Analysis (PCO) of environmental parameters measured in each site during each sampling month and season (D= dry season, R= rainy season). SR: sedimentation rate, BOD: biochemical oxygen demand, Hydro: Hydrodynamism, %OM: percentage of organic matter in surface sediment, and percentage of particle size in surface sediment (<420 µm, >420 µm, >840 µm, and >2000 µm). Trajectories show the temporal variation in each site. Parameters with a correlation >70% are shown in black vectors

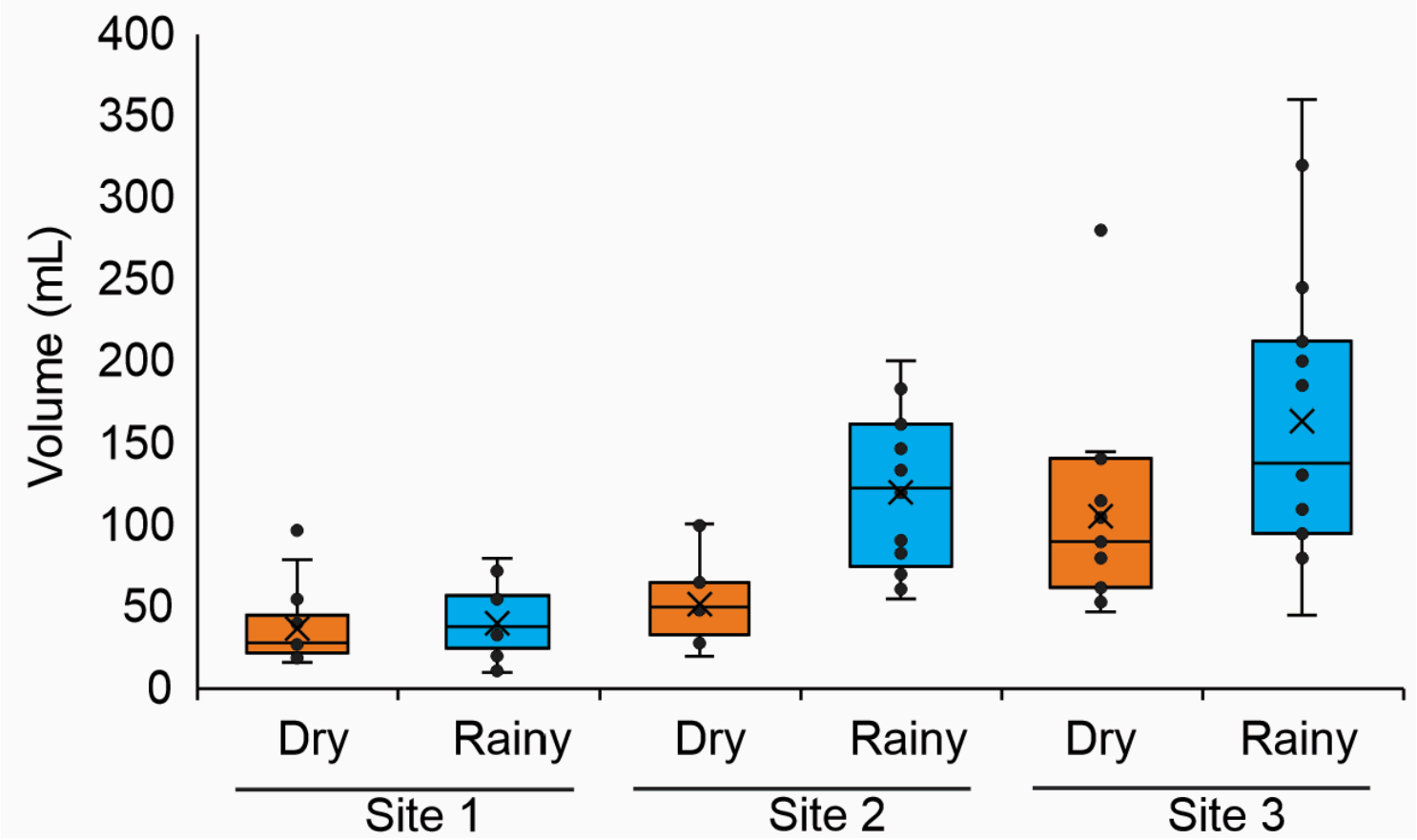

Figure 3

Volume of individuals of *H. implexiformis*collected from three sites of Laguna de Terminos during dry and rainy seasons

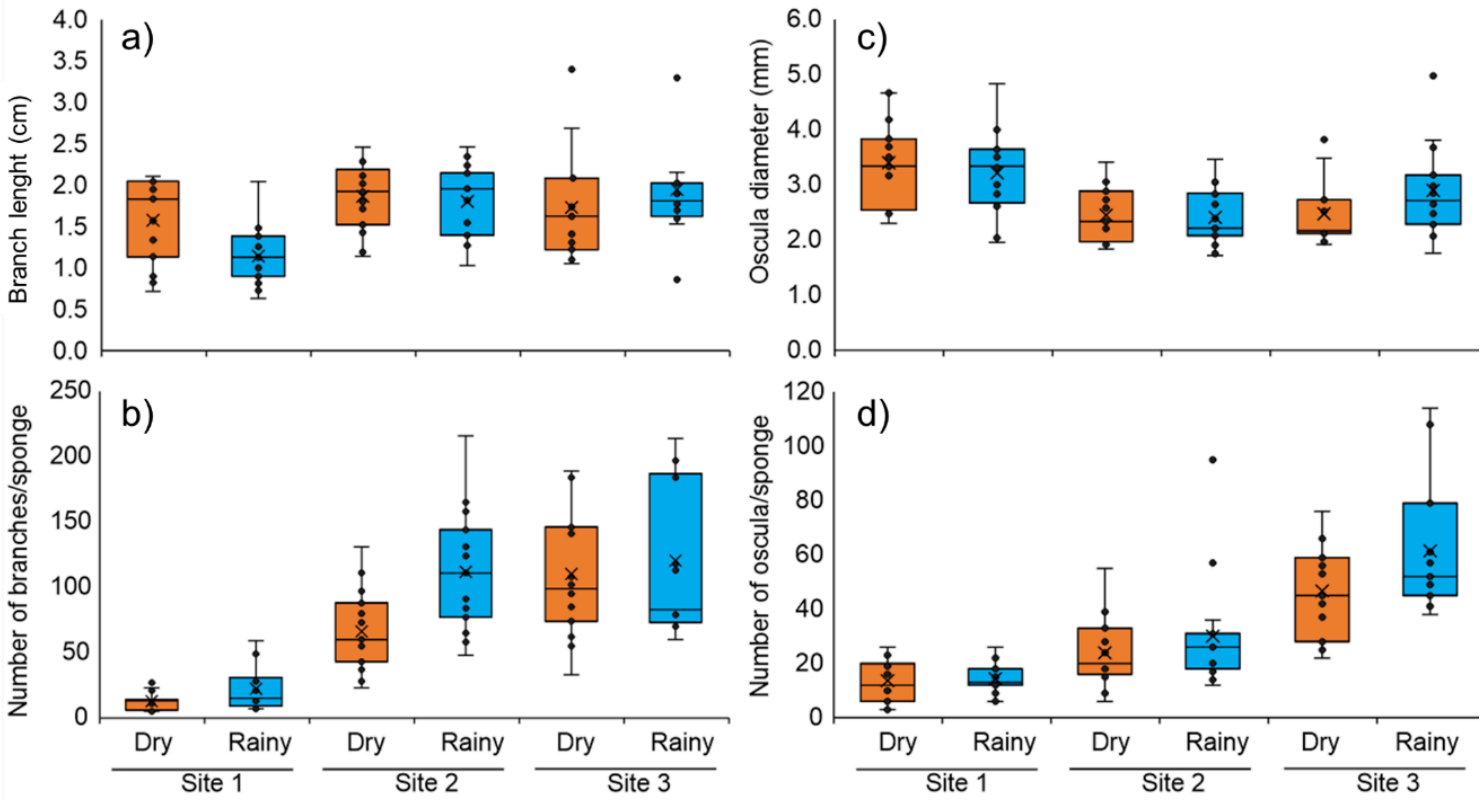

Figure 4

Morphological characteristics measured in *H. implexiformis* individuals: (a) branch length, (b) number of branches per sponge individual, (c) oscular diameter, and (d) number of oscula per sponge individual

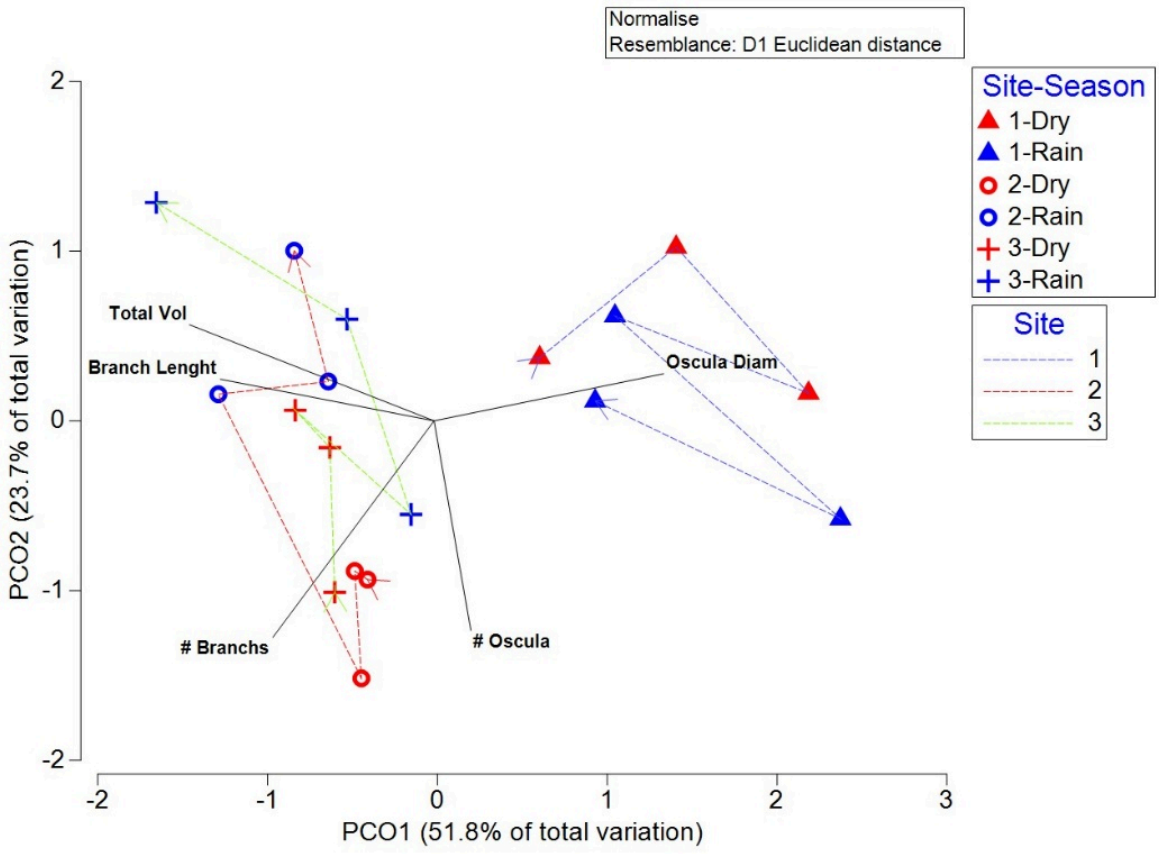

Figure 5

Principal Coordinate Analysis (PCO) showing the centroids of combined factors: Site, Season and Month of *H. implexiformis* characteristics. Trajectories show the temporal variation in each site. Sponge characteristics with a correlation >70% are showed in black vectors

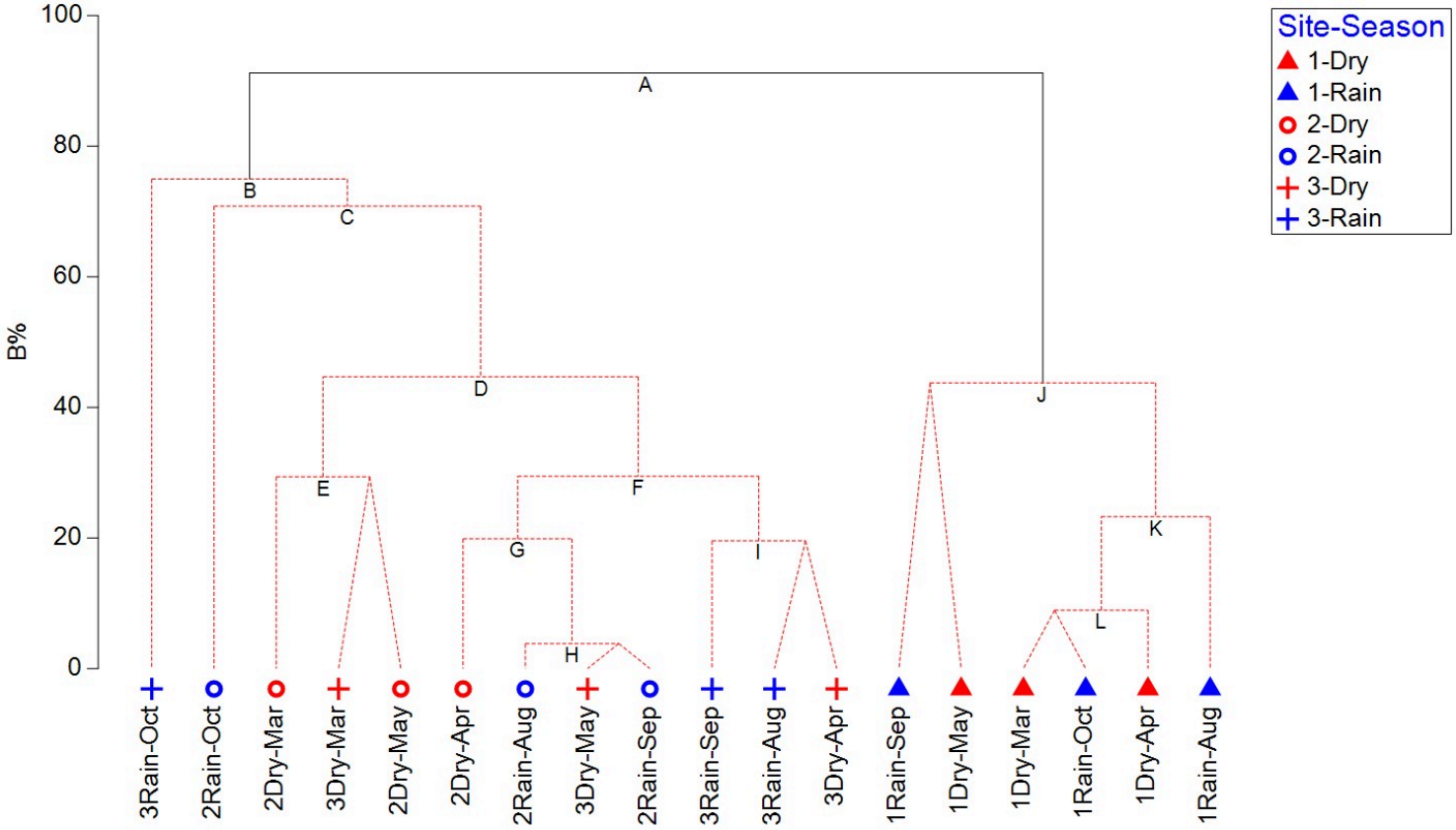

Figure 6

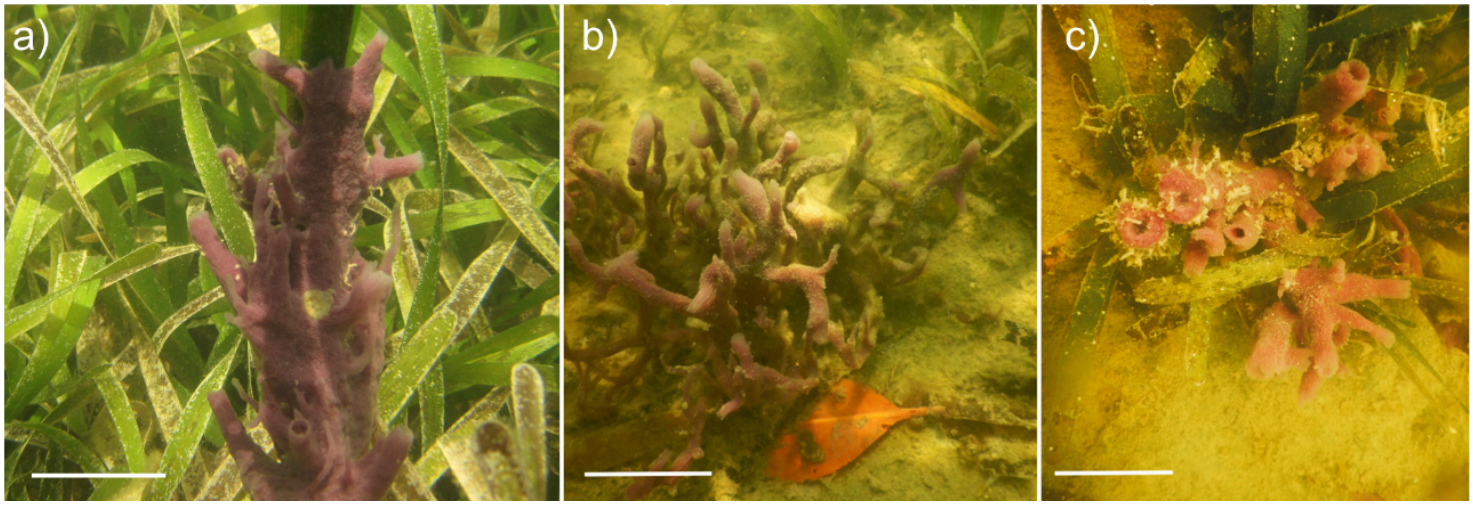

Figure 7

Typical morphology of *Haliclona implexiformis* inhabiting Sites 1 (A), 2 (B), and 3 (C). Scale bar = 5 cm