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Diversity of mangrove root-dwelling sponges in a tropical coastal ecosystem in the southern Gulf of Mexico region

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Abstract

Sponges are one of the most conspicuous groups of epibionts in mangrove prop root habitats. However, with the exception of the Caribbean and the Indo-Pacific regions, studies focused on species diversity are lacking in other locations that have high mangrove coverage and are relatively distant from coral reef environments. Because mangrove-root epibiont communities, in general, have been understudied worldwide, this research contributes to filling this knowledge gap. In this study, a total of 30 sponge species (belonging to three subclasses, 14 families and 19 genera) were recorded as epibionts on prop roots of the red mangrove *Rhizophora mangle* in a tropical coastal ecosystem of the Southern Gulf of Mexico. Of these, five were new records for the Gulf of Mexico, 14 were new for the Mexican coasts of the gulf and 25 were new for the study area. Moreover, a similarity analysis based on presence/absence data of mangrove-associated sponges reported throughout the Western Central Atlantic region revealed that the sponge assemblage from the study area was more similar to those documented in most of the Caribbean locations (Jamaica, Cuba, Martinique, Panama, Venezuela, Belize and Colombia) rather than with those of the Northeast of the Gulf of Mexico, Guadeloupe and Trinidad. This relative intra-regional dissimilarity in the structure of mangrove-associated sponge assemblages may be related to differences in environmental conditions as well as taxonomic effort. The study area, unlike most of the Caribbean locations, is characterized by estuarine conditions and high productivity throughout the year. The inter-site variability recorded in the composition of mangrove-associated sponges was influenced by a set of factors such as salinity, dissolved oxygen and hydrodynamism. This study shows the importance of exploring the mangrove-associated sponge assemblages from different regions of the world as it furthers knowledge of the biodiversity and global distribution of this group.

Keywords: Porifera, Biodiversity, Southern Gulf of Mexico, *Rhizophora mangle*, Distribution

Introduction

Mangrove prop roots that extend into the intertidal and subtidal zone constitute a habitat for a wide diversity of sessile invertebrates [1, 2]. In these habitats, sponges (Phylum Porifera) in addition to being one of the most conspicuous groups of epibionts [3–5], can establish mutualistic relationships with mangroves [6] and have been proposed as indicators of environmental change and mangrove epibenthic community health [4, 7]. However, despite the wide distribution of these biogenic habitats in the world, most research on the mangrove-associated sponge communities has been concentrated in two main regions, the Caribbean and the Indo-Pacific [4, 8–11]. In many of these studies, high sponge species richness has been highlighted, and species composition was found to

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differ sometimes significantly from that of adjacent habitats (such as coral reefs and seagrass beds) [3, 12].

In the Gulf of Mexico region (GoM), a recent review documented a total of 339 sponge species from different marine environments (e.g. coral reefs, seagrass meadows, soft and rocky bottoms and mangrove stilt roots) from both shallow and deep waters [13]. Although there have been some records of species associated with mangrove root habitats (*Rhizophora mangle* Linnaeus, 1753) in this region, these are limited to the Northeastern coasts of the gulf [14, 15]. In the Southern/Southwestern coasts of the basin (Mexican coasts of the GoM), despite efforts to understand the regional diversity of sponges, studies conducted there have emphasized coral reef environments [e.g. 16–19, among others]. Sponge assemblages in other coastal environments of this region, such as mangroves, have not been investigated so far.

Therefore, this study aims to contribute to knowledge of the biodiversity and spatial distribution of mangrove root-dwelling sponges in tropical coastal ecosystems of the Southern Gulf of Mexico eco-region (SGM), particularly, in one of the Mexican states (Campeche) with the largest cover of mangrove forests [20]. The similarity of the sponge assemblage recorded in the study area with those reported in locations in the Caribbean and in the Northeast of the Gulf of Mexico is also discussed.

Materials and methods

Sampling of sponges was conducted by snorkeling (between March and April 2016 and in March 2019) in nine sites distributed along the Isla del Carmen, Campeche, within the Natural Protected Area Laguna de Terminos, at the Southern Gulf of Mexico (Fig. 1; Table 1). These sites corresponded to tidal creeks bordered by the red mangrove *R. mangle* at 0.7–2.0 m depth. This was the only mangrove species included in the study because it is the only one in the region that develops stilt roots, many of which remain fully or partially submerged in the

Table 1 Geographical coordinates of sampling sites at Isla del Carmen, Campeche, Mexico

Sampling site	Geographical coordinates
Estero Pargo 1	18° 40′ 21.40″ N–91° 44′ 11.83″ W
Estero Pargo 2	18° 39′ 40.10″ N–91° 44′ 54.74″ W
Estero Pargo 3	18° 39′ 05.83″ N–91° 45′ 31.93″ W
Estero Pargo 4	18° 38′ 41.28″ N–91° 45′ 56.59″ W
Estero Pargo 5	18° 38′ 21.30″ N–91° 46′ 13.15″ W
Bahamita	18° 40′ 04.08″ N–91° 42′ 01.03″ W
Cases	18° 41′ 24.06″ N–91° 40′ 42.09″ W
Ensenada Grande	18° 43′ 52.58″ N–91° 34′ 39.71″ W
Estero San Julián	18° 45′ 54.42″ N–91° 31′ 34.61″ W

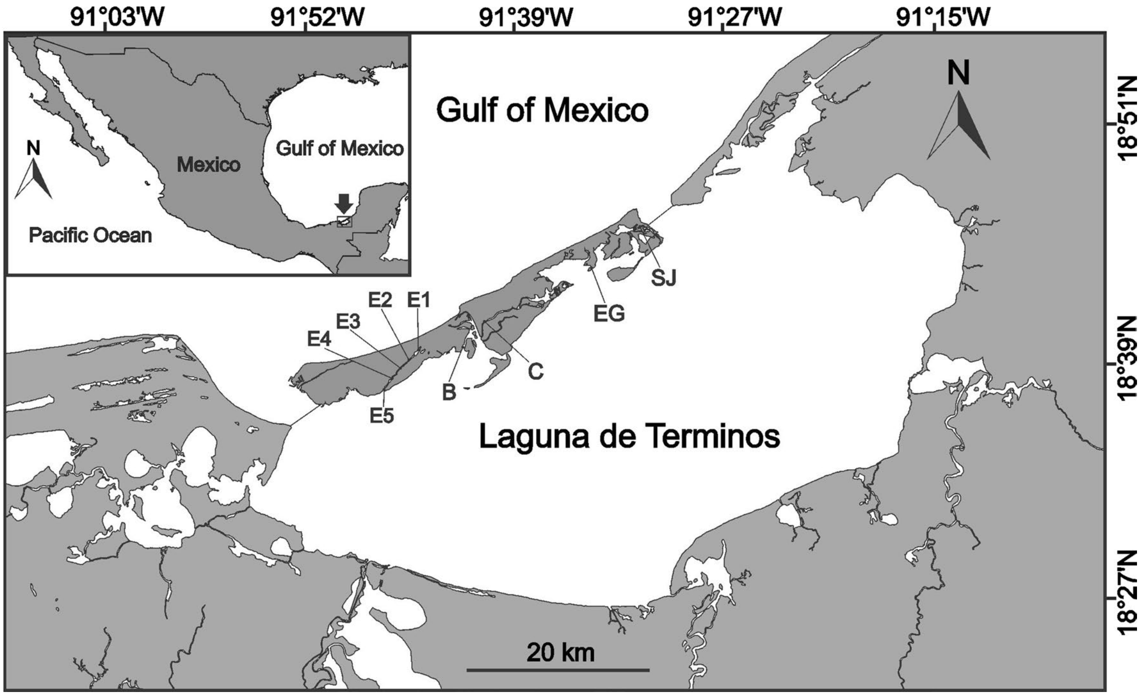

Fig. 1 Location of the study area and sampling sites at the Isla del Carmen in the Southern Gulf of Mexico. *E1* Estero Pargo 1, *E2* Estero Pargo 2, *E3* Estero Pargo 3, *E4* Estero Pargo 4, *E5* Estero Pargo 5, *B* Bahamita, *C* Cases, *EG* Ensenada Grande, *SJ* Estero San Julián

water. In each site, a linear transect of 20 m in length was placed along the mangrove border, within which 30 suspended stilt roots of *R. mangle* were randomly selected. On each root, samples of sponges that were morphologically (e.g. form, color, consistency) different were carefully removed from the substrate by hand or using a knife, and promptly placed individually into plastic bags for later taxonomic identification based on external characters, skeletal structure and spicule morphology and size [21]. These sponge samples were of variable size and, when possible, more than one specimen of each species was collected. In each site, the presence/absence of each sponge species was recorded. Environmental parameters such as water temperature (TE), salinity (SA), dissolved oxygen (DO), sedimentation rate (SR), water transparency (TR), depth (DE), hydrodynamism (H), and root length (RL) and circumference (RC) were also recorded in each of the nine sampling sites. Temperature (T°C), salinity and dissolved oxygen (mg/L) were measured by a multi-parameter meter (YSI Model 63, Salinity Conductivity Temperature, Ohio 45,387, USA) at 1 m depth. Sedimentation rate (g dry weight m^{-2} day^{-1}) was measured at each site with a trap system consisting of four sets of plastic bottles (height 23 cm, internal diameter 2.2 cm, and ratio height/diameter 10.4/1) whose opening was vertically positioned at 30 cm from the bottom. Sediment traps remained for 30 days before being taken to the laboratory. The trapped material was repeatedly rinsed with distilled water to remove salts and dried at 70 °C for 48 h before being weighed (dry weight, g) [22]. Water transparency (m) was measured with a Secchi disk and depth (m) with a graduated rule. The hydrodynamism at each site was determined by 'plaster dissolution' [23]. At each site, four pre-weighed (g dry weight) plaster cylinders 6 cm in diameter X 10 cm long were placed 50 cm above the bottom, at a distance of 50 cm from each other, for 6 days. The percentage of plaster dissolution was calculated from the weight loss produced by the water movement during the time they remained exposed. Also, the average length and circumference (cm) of the submerged portion was measured in 10 of the mangrove roots that had been selected to collect sponge samples.

Data about mangrove sponge assemblages documented in the Western Central Atlantic region (Belize [8], Colombia [24, 25], Cuba [26], Guadeloupe [27], Jamaica [28], Panama [29, 30], Martinique [31], Northern Gulf of Mexico (Florida Keys, USA) [14, 15], Trinidad [27] and Venezuela [5, 32–40]) were used for comparison to the assemblage reported in this study. A dendrogram was obtained using the unweighted pair-group method with arithmetic mean (UPGMA) cluster analysis based on Jaccard's similarity coefficient, which was built from a binary matrix (presence/absence) of species distribution. The ANOSIM test was used to detect significant differences between groups [41]. At local scale, a non metric multidimensional scaling (nMDS) analysis was also used (using the UPGMA based on Jaccard's similarity coefficient built from the precence/absence data of species) to visualize the variations in sponge species composition among the nine sampling sites. These analyses were done using PAST program v. 3.25 [42]. In addition to examining the influence of environmental variables on the distribution of mangrove-associated sponges at Isla del Carmen, a redundancy analysis (RDA) was performed using the rda function of the vegan community analysis package [43]. In this analysis, the response variable was the presence/absence of the species at each of the sampling sites. Independent variables included TE, SA, DO, DE, TR, SR, RL, RC and H. After an exploratory analysis, the variables RL and RC were excluded from the analysis because the inflation factor of the variance was > 10. Alpha diversity (α–diversity) was calculated as the mean species richness in each site and the global beta diversity (Whittaker's βw) for all the sampled sites sampled was determined by dividing the total species richness between the mean alpha diversity [44].

Results and discussion

A total of 29 sponge species belonging to three subclasses, eight orders, 14 families, and 20 genera were identified (Table 2; Fig. 2). The most representative subclass was Heteroscleromorpha with 23 species, and just as has been documented in some Caribbean locations, the orders Poecilosclerida and Haplosclerida were dominant in terms of species diversity [45]. Seven species (included six as 'cf.' and one as 'sp.') did not have enough morphological diagnostic characters (small and incomplete specimens), and although we complete the identification, they need to be confirmed. After a minucious taxonomic evaluation, three species were recognized as 'potentially new to science', and they will be described together with other sponges in the region. For the aims of this study, we used the species name with the highest affinity to our species (included as 'aff.'). These species were *Haliclona* (*Gellius*) aff. *tenerrima*, *Scalarispongia* aff. *Linteiformis* and *Spongosorites* aff. *siliquaria*.

The total number of species recorded here was comparable with that of other studies conducted in submerged mangrove root habitats from both the Atlantic and the Indo-Pacific (Table 3). The greatest number of studies have been carried out in Belize and Venezuela for the Caribbean and Indonesia for the Indo-Pacific (Table 3). It is also important to note that of the species recorded in this study only *Halichondria* (*Halichondria*) *melanadocia* Laubenfels, 1936, *Haliclona* (*Reniera*) *implexiformis* (Hechtel, 1965), *Chondrilla caribensis* form

Table 2 Sponge species found associated to mangrove prop roots of *Rhizophora mangle* at Isla del Carmen, Campeche

	Study sites								
Species	**E1**	**E2**	**E3**	**E4**	**E5**	**B**	**C**	**EG**	**SJ**
Myrmekioderma cf. *rea* **									x
Echinodictyum cf. *dendroides* *									x
Cliona celata ***		x	x						
Pione lampa **		x		x	x	x	x	x	x
Coelosphera (*Coelosphera*) *fistula* **						x	x		
Lissodendoryx (*Lissodendoryx*) *carolinensis* **				x			x		
Lissodendoryx (*Lissodendoryx*) *isodictyalis* ***						x		x	
Lissodendoryx (*Lissodendoryx*) *spinulosa* **						x			
Mycale (*Carmia*) *magnirhaphidifera* ***				x	x	x		x	x
Mycale (*Carmia*) *microsigmatosa* **									x
Clathria (*Microciona*) sp. **		x	x	x			x		
Tedania (*Tedania*) *ignis* **					x			x	x
Suberites aurantiacus **						x			x
Terpios cf. *fugax* **	x	x	x	x			x		x
Amorphinopsisatlantica ***					x				x
Spongosorites aff. *siliquaria* **				x	x	x	x	x	x
Halichondria (*Halichondria*) *melanadocia*							x	x	
Haliclona (*Halichoclona*) cf. *magnifica* **				x	x	x			
Haliclona (*Gellius*) aff. *tenerrima* *						x	x	x	
Haliclona (*Reniera*) *implexiformis*					x	x		x	x
Haliclona (*Reniera*) *tubifera* **						x			
Haliclona (*Soestella*) cf. *luciensis* *		x	x	x	x	x	x		
Haliclona (*Soestella*) *piscaderaensis* *						x			
Dysidea variabilis ***					x	x		x	x
Dysidea etheria					x	x		x	
Hyrtios cf. *violaceus* ***						x		x	
Scalarispongia aff. *linteiformis* *								x	
Chondrosia collectrix **						x	x		x
Chondrilla caribensis f. *caribensis*						x			
Alpha diversity (*α*)	1	5	4	8	10	13	10	12	13

E1 Estero Pargo 1, *E2* Estero Pargo 2, *E3* Estero Pargo 3, *E4* Estero Pargo 4, *E5* Estero Pargo 5, *B* Bahamita, *C* Cases, *EG* Ensenada Grande, *SJ* Estero San Julián. New records of species or genus to: GoM (*), SGM (**), Isla del Carmen (***). Alpha diversity for each site is included at the end of the table

caribensis Rützler, Duran & Piantoni, 2007 and *Dysidea etheria* Laubenfels, 1936 were previously reported in the study area, but were found in other habitats such as seagrass beds and muddy-sandy bottoms [46, 47]. Of the remaining 25 species, five were new records for the entire GoM (*Echinodictyum* cf. *dendroides*, *Haliclona* [*Soestella*] cf. *luciensis*, *Haliclona* [*Soestella*] *piscaderaensis*, *Haliclona* [*Gellius*] aff. *tenerrima* and *Scalarispongia* aff. *linteiformis*), 14 were new for the SGM and 25 were new for the study area (Isla del Carmen) (Table 2). Among the 29 species were typical mangrove-associated species such as *H.* (*R.*) *implexiformis*, *Mycale* (*Carmia*) *magnirhaphidifera* van Soest, 1984 and *H.* (*H.*) *melanadocia* (widely reported in the Caribbean region) as well as habitat generalist species such as *Tedania* (*Tedania*) *ignis* (Duchassaing & Michelotti, 1864), *Mycale* (*Carmia*) *microsigmatosa* Arndt, 1927 and *Suberites aurantiacus* (Duchassaing & Michelotti, 1864), which have also been reported in other habitats [7, 24].

According to the cluster analysis, the mangrove sponge assemblages reported from the Western Central Atlantic region were separated into two main groups (Fig. 3) that differ significantly (One-way ANOSIM, permutation N = 9999, $R = 0.828$, $p = 0.0064$). Group A includes most of the Caribbean locations (mainly of the Central Caribbean) such as Belize, Colombia, Cuba, Martinique, Jamaica, Panama, Venezuela and one from the Gulf of Mexico, the SGM (this study). Group B includes two Caribbean locations of the Lesser Antilles (Guadeloupe and Trinidad) and one of the Gulf of Mexico, the NGM. These

Fig. 2 Pictures of some of the most typical mangrove-associated sponge species at Isla del Carmen, Campeche, Mexico. **a** *Tedania* (*T.*) *ignis*, **b** *Halichondria* (*H.*) *melanadocia*, **c** *Dysidea variabilis*, **d** *Hyrtios* cf. *violaceus*, **e** *Haliclona* (*R.*) *implexiformis*, **f** *Lissodendoryx* (*L.*) *carolinensis*, **g** *Dysidea etheria*, **h** *Cliona celata*, **i** *Lissodendoryx* (*L.*) *isodictyalis*, **j** *Mycale* (*C.*) *microsigmatosa*, **k** *Suberites auratiacus*, **l** *Echinodictyum* cf. *dendroides*, **m** *Mycale* (*C.*) *magnirhaphidifera*, **n** *Terpios* cf. *fugax*. Scale bar in all pictures = 2 cm

Table 3 Number of sponge species reported in different locations in the Western Central Atlantic and Indo-Pacific regions

Region	Country	Number of species	References
Northeastern Gulf of Mexico	USA	3	[59]
		10	[14]
		9	[15]
Caribbean Sea	Bahamas	13	[60]
	Guadeloupe	4–10	[26]
	Martinique	49	[31]
	Mexico	12	[61]
	Belize	147	[8]
		35	[7]
	Panama	65	[28]
	Cuba	48	[25]
	Curacao and Aruba	22	[3]
	Venezuela	16	[31]
		23	[32]
		18	[33]
		26	[34]
		10	[35]
		40	[36]
		45	[5]
		57	[38]
	Colombia	14	[24]
Indo-Pacific region	Indonesia	30	[10]
		19	[11]

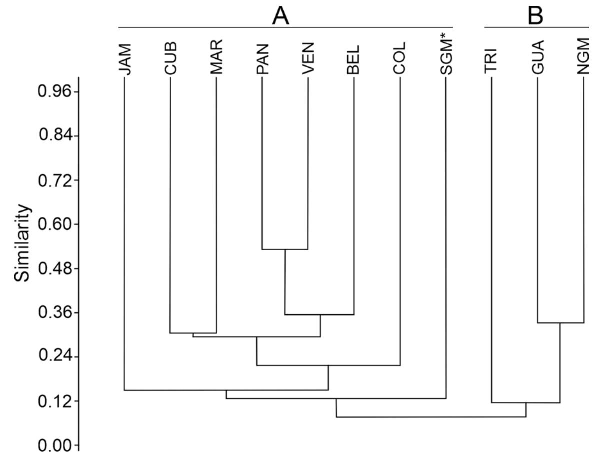

Fig. 3 UPGMA analysis using Jaccard similarity index (Cophenetic correlation = 0.92) for the mangrove sponge fauna reported in the Western Central Atlantic region. *BEL* Belize, *COL* Colombia, *CUB* Cuba, *MAR* Martinique, *GUA* Guadeloupe, *JAM* Jamaica, *NGM* Florida Keys (USA), *PAN* Panama, *SGM* Campeche (Mexico), *TRI* Trinidad, *VEN* Venezuela. The asterisk indicates the sampling location of this study

findings indicate that the sponge assemblage reported in this study (SGM) is more similar to those documented in most of the Caribbean locations (Jamaica, Cuba, Martinique, Panama, Venezuela, Belice and Colombia) than with those of the NGM, Guadeloupe and Trinidad. As has been documented in other studies, the high spatial heterogeneity (at small and large scale) of mangrove-associated sponge assemblages can be explained by several factors, including the presence of unique species, local colonization events (recruitment) and succession, competition for space, predation, local environmental conditions (including physicochemical parameters and the site exposure to wind-generated waves), and the presence of other habitats (such as coral reefs and seagrass meadows) in surrounding areas [4, 7, 10, 41, 48–51]. Despite the link between the GoM and the Caribbean Sea through the Loop Current [52] and evidence of faunistic connectivity (e.g. corals) between these regions [53], the relative dissimilarity detected between the sponge assemblage of the SGM and those of the Caribbean could be attributed to differences in environmental conditions.

Unlike many of the Caribbean locations, where mangrove-associated sponge assemblages were reported, the region of this study is influenced by three permanent rivers that maintain high productivity (up to 285 g C m^{-2} yr^{-1} in tidal creeks) and turbidity in the coastal zone during the year round [54]. In the study area, the environmental conditions were as follows: TE = 28.5–29.6 °C, SA = 33.9–41.1, TR = 1.05–2.0 m, SR = 78–243 g m^{-2} day^{-1}, DO = 1.3–5.8 mg/L, DE = 0.7–2.0 m, RL = 34.4–77.2 cm, RC = 7.4–10.5 cm, H = 25.1–69.1% and muddy bottom in all sites. Although this study was carried out during the same season of year (dry season), there is also documented evidence that some of these parameters present a wide intra-annual variability in the study area (TE: 25–31.2 °C, SA: 25–36.6 [55], TR: 0.48–2.40 m [54] and SR: 48.3–220.1 g m^{-2} day^{-1} [56]), reflecting the wide range in environmental conditions to which these sponge assemblages are exposed. Conditions such as transparency and sedimentation rate seem to contrast with that described in some study locations of the Caribbean [4], which are relatively near to oligotrophic environments such as coral reefs. Moreover, the locations NGM, Trinidad and Guadeloupe may have been separated from the rest due to the lower number of records (data on sponge species from mangrove habitats) as has been highlighted in previous studies [57] and could be related to a low taxonomic effort [58]. Of the studies conducted in the Caribbean, only the one in Martinique mentions that most of sampling sites were relatively exposed to various sources of anthropogenic pressures (agricultural, domestic, urban and industrial wastes) and some of them were also near a river mouth [31]. Although sampling sites in this study were also exposed to anthropogenic pressures (urban, industrial and agricultural wastes), the sponge assemblages recorded here were little similar to that of Martinique.

At the local scale, a wide inter-site variability in species composition was also detected and a global beta diversity of 1.96 was recorded (Table 2). According to species composition, the nMDS analysis resulted in three groups for the nine sampling sites (Fig. 4). In group A (E5, B, EG and SJ), the sites had the greatest α-diversity (10–13) and were relatively more exposed to wind-generated waves and had greater marine influence (SJ). Those in group B (E2, E3, E4 and C) had intermediate values of α-diversity (4–10) and were located in relatively narrow tidal channels. Group C (E1) had the site with the lowest α-diversity (only one species, *Terpios* cf. *fugax*) and was located at the end of a tidal channel (Fig. 1). In fact, sites E1, E2, E3, E4 and E5 were located within the same tidal channel and a gradient from higher to lower α-diversity from the entrance to the end of this channel was notable. According to RDA analysis, the variables used explained about 61% of the variance of the species distribution at the sampling sites (constrained/uncosntrained variance = 0.60 v. 0.01, $R^2_{adj} = 0.61$). Most of the recorded species were found in areas where values of salinity, dissolved oxygen and root circumference were relatively high, while only two species (*Terpios* cf. *fugax* and *Haliclona* [*Soestella*] cf. *luciensis*) showed a strong relationship with water temperature and transparency (Fig. 5). This result is consistent with that of previous studies, where spatial distribution patterns of mangrove-associated sponges could not be explained by a single factor, but was multifactorial (e.g. including sedimentation rate, turbidity, degree of exposure to waves and desiccation during low tides, spatial competition, root density and/or length, nutrients availability and predation) [4, 7, 49–52].

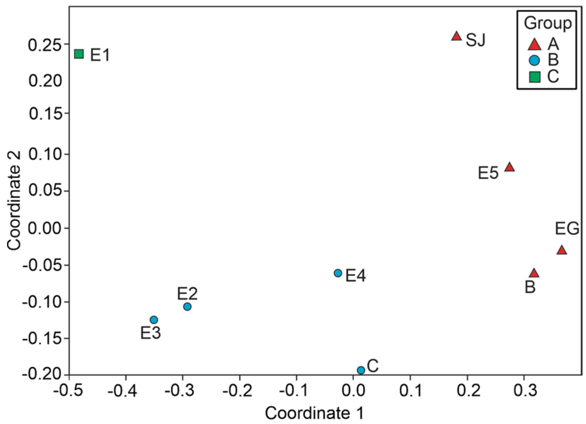

Fig. 4 nMDS ordination plot (using Jaccard similarity index, Cophenetic correlation = 0.88) for nine compared mangrove-associated sponge assemblages at Isla del Carmen, Mexico. *E1* Estero Pargo 1, *E2* Estero Pargo 2, *E3* Estero Pargo 3, *E4* Estero Pargo 4, *E5* Estero Pargo 5, *B* Bahamita, *C* Cases, *EG* Ensenada Grande, *SJ* Estero San Julián

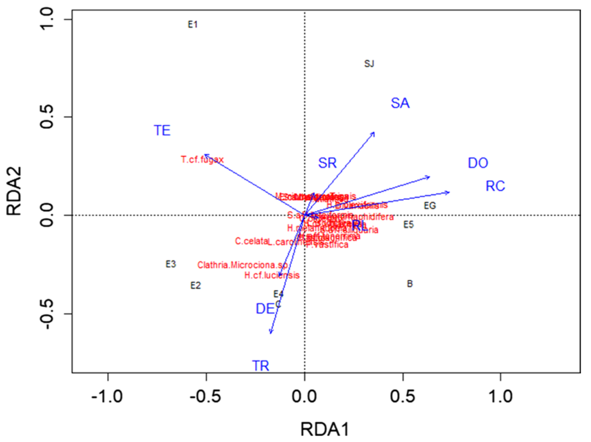

Fig. 5 Redundancy analysis (RDA). The species (red) and their relationship with environmental variables (blue) at the sampling sites (*E1* Estero Pargo 1, *E2* Estero Pargo 2, *E3* Estero Pargo 3, *E4* Estero Pargo 4, *E5* Estero Pargo 5, *B* Bahamita, *C* Cases, *EG* Ensenada Grande, *SJ* Estero San Julián)

In summary, this is the first work where a mangrove-associated sponge assemblage is reported for the Mexican coasts of the Gulf of Mexico. This study contributes to knowledge of marine biodiversity in the coastal region with the greatest mangrove coverage in Mexico, which during the last decades has been threatened by anthropic activities (urban development, agriculture, and oil industry). The data generated in this study will serve as baseline for further studies focused on mangrove-associated sponge communities, which in turn, will contribute to conservation of these important habitats.

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Authors' contributions

EA and LEVM designed the research; EA, LEVM, PJCP and JACB collected and identified the species; EA and PJCP wrote the manuscript and performed part of the analysis; JCCD performed multivariate analyses. All authors read and approved the final manuscript.

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Availability of data and materials

Our manuscript has no associated data.

Ethics approval and consent to participate

Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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