

Sponge–rhodolith interactions in a subtropical estuarine system

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Abstract The interactions between sponges and red macroalgae have been widely documented in tropical and subtropical environments worldwide, and many of them have been documented as mutualistic associations. Sponges, however, have also been frequently described as part of the associated fauna of rhodolith habitats (aggregations of free-living non-geniculated coralline macroalgae). Nonetheless, the types of interaction they establish as well as the role of sponges in these habitats remain unknown. In this study, the associations between sponges and rhodoliths were investigated in an estuarine ecosystem of the Mexican Pacific based on qualitative and quantitative data. A total of 13 sponge species were identified in five newly discovered rhodolith beds dominated by the non-geniculate coralline macroalga *Lithophyllum margaritae*. The sponge assemblages were strongly restricted to rhodolith habitats. The best predictor of

sponge abundance (from 5.1 to 51.7 ind m⁻²) and species richness (from 2.6 to 6.1 sponge species m⁻²) was the rhodolith density rather than other population descriptors assessed (e.g., average size, branch density and sphericity). The identified sponges included a variety of forms: massive (46 %), encrusting (23 %), excavating (15 %), cushion-shape (8 %) and digitate (8 %). Moreover, more than 50 % of sponge species recorded (mainly massive and encrusting forms) were frequently found overgrowing and binding rhodoliths. *Halichondria* cf. *semitubulosa* and *Mycale cecilia* were the most common binding agents; these species bind an average of 3.1 and 6.6 rhodoliths per sponge individual, respectively. These findings reveal the importance of rhodoliths as habitat forming species, since these seaweed beds notably increased the substrate complexity in soft bottom environments. In addition, the relatively high abundance of sponges and their capability to bind rhodoliths suggest that these associated organisms could have an important contribution to rhodolith bed stability.

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Introduction

Interactions between sponges and macroalgae have been recorded worldwide and are often considered to be mutualistic associations (see review by Wulff 2006). In such interactions, sponges may gain (1) structural support (Vacelet 1981; Rützler 1990; Trautman et al. 2000; Calcinaï et al. 2006; Carballo et al. 2006); (2) organic compounds derived from algal photosynthesis (Grant and Hinde 1999; Davy et al. 2002); (3) protection against predation (Wulff

1997) and (4) enhance its spatial distribution (from wave-protected to wave-exposed sites) (Carballo et al. 2006). In return, the alga may (1) reach bigger size and acquire structural protection against abrasive hydrodynamics (Trautman et al. 2000; Carballo et al. 2006; Calcinai et al. 2006), (2) expand their photosynthetic surfaces in order to reduce self-shading and increase their distribution range with depth (Enríquez et al. 2009), (3) enhance their dispersal capacity through fragmentation (Carballo et al. 2006) and (4) receive nitrogenated compounds provided by the sponge catabolism (Davy et al. 2002).

Typically, in most of these associations, the associated macroalga belongs to the Division Rhodophyta, within which the interactions with geniculate coralline algae are frequent (Ávila et al. 2010). These invertebrates have also been commonly reported as conspicuous inhabitants of rhodolith beds (free-living non-geniculate coralline algae, also known as maerl) (e.g., Solórzano et al. 1991; Steller et al. 2003; Aguilar et al. 2009; Sciberras et al. 2009). However, the types of interaction they can establish as well as the possible role of sponges in these habitats remain unknown. In some instances, it has been suggested that sponges and other fouling organisms (e.g., tunicates and anemones) could reduce the movement of rhodoliths and therefore affect their sphericity (Steller and Foster 1995; Marrack 1999; Foster 2001). It has also been argued that boring sponges may have an important role in the bioerosion process of these calcareous substrata (Leal et al. 2012).

Recent expeditions along the Mexican Pacific coasts have revealed the presence of new rhodolith beds in shallow estuarine systems of the Mexican Pacific (Ávila and Riosmena-Rodríguez 2011). These habitats are characterized by a noticeable diversity and abundance of associated organisms, including sponges. According to preliminary observations, most of the sponge species show encrusting and massive growth forms and were observed overgrowing rhodoliths. The role of sponges as binding organisms in other contexts is better known, as they have been widely documented in coral reefs and in temperate rocky habitats (see review by Bell 2008). In coral reefs, for example, sponges and other organisms participate in regeneration processes through rubble stabilization (Wulff 1984; Scoffin and Hendry 1984; Rasser and Riegl 2002). In rhodolith beds, however, the role of sponges as substrate stabilizers as well as its potential effects (positive or negative) on these algae and the associated biota has not been previously investigated.

It is also known that rhodoliths provide a hard substrate that notably increases the substrate complexity and therefore the availability of microhabitats (Foster et al. 1997; Steller et al. 2003). This structural complexity together with the coverage of living rhodoliths appears to be a good predictor of both abundance and species richness of associated organisms (Steller et al. 2003). Most of the studies

have generally been conducted on the entire rhodolith community, including infauna and organisms that inhabit between rhodolith branches (Hinojosa-Arango and Riosmena-Rodríguez 2004; Harvey and Bird 2008). However, it is unknown whether the structural characteristics (e.g., size, branch density and sphericity) and density of rhodoliths can have influence in the diversity and abundance of relatively larger invertebrates such as sponges.

The aims of the present study were therefore: (1) to describe the diversity and abundance of sponges associated with the newly discovered rhodolith beds in the Mexican Pacific coasts, (2) to determine whether the species richness and the abundance of sponges vary as a function of rhodolith structure (size, sphericity and branch density) and abundance and (3) to assess the potential role of sponges as rhodolith bed stabilizers.

Materials and methods

Study area

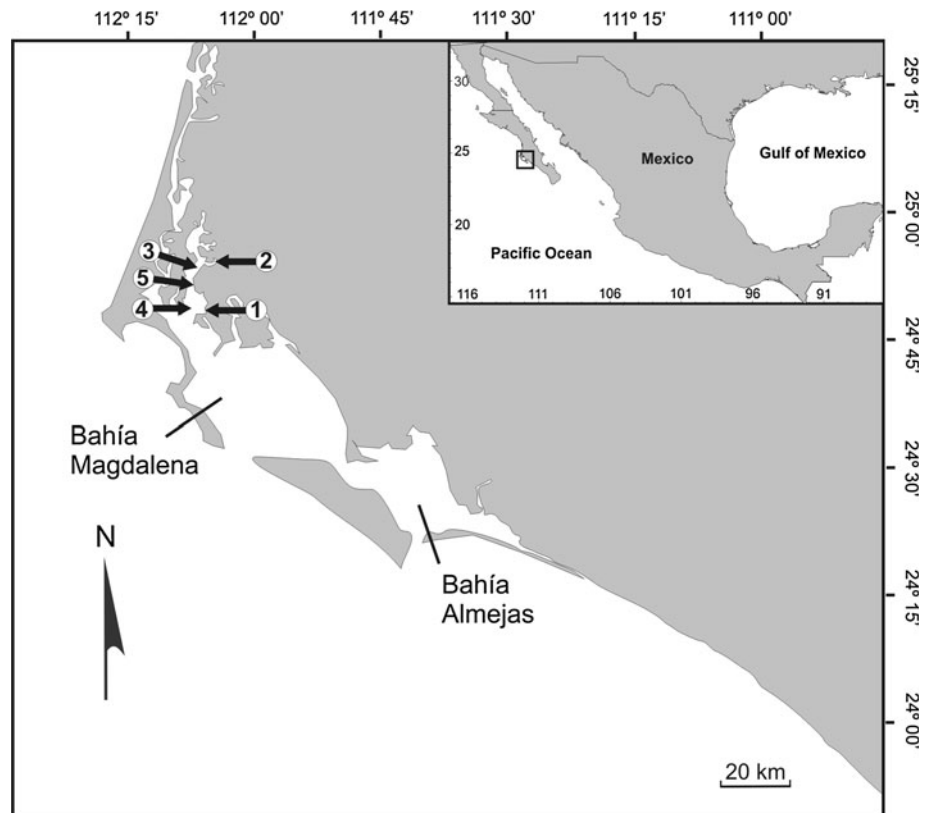
The study area is located in Bahía Magdalena, a coastal lagoon system situated between 24°15'N and 25°20'N and 111°30'W and 112°15'W on the Pacific coast of Mexico (Fig. 1). The lagoon is an irregularly shaped anti-estuarine system (without freshwater influx and high evaporation) composed of intertidal and shallow areas and relatively narrow mangrove channels with an average depth of 3.5 m (Schweers et al. 2006). The sea surface temperatures range from 20 °C during January and February to 27 °C in September (Lluch-Belda et al. 2000). In the shallower zones, salinities reach highs (39.2) in July–August and lows (34.1) in March. The tidal regime (24.8 h) is mixed semidiurnal, with periods of higher high water followed by those of lower low water, a condition that produces greater current velocities during ebb tides (Lankford 1977; Obeso-Nieblas et al. 1999).

Within this estuarine system, five rhodolith beds were found between August 2008 and February 2009 (Bed 1: 24°48'45"N–112°05'59"W; Bed 2: 24°54'12"N–112°05'24"W; Bed 3: 24°53'47"N–112°06'29"W; Bed 4: 24°48'42"N–112°06'32"W; Bed 5: 24°51'47"N–112°07'14"W). These seaweed habitats were found at depths between 1 and 3 m in relatively narrow areas bordered by mangrove. The bottom in adjacent areas of beds 1, 3, 4 and 5 was sandy with small sea grass patches, whereas in the bed 2, the bottom was constituted by consolidated calcareous rocks with small sections of sand.

Abundance of sponges and rhodoliths

At each rhodolith bed, three interrupted (with intervals of 5 m) line transects of 20 m were placed perpendicular to

Fig. 1 Study area at Bahía Magdalena, Mexico. Numbers indicate the location of the five rhodolith beds



the shore (between 1 and 2 m depth). Then, one meter square quadrant was placed every five meters along each transect, and the total number of sponges and live rhodoliths present on the surface area of bed were visually quantified. In this study, an individual of sponge was defined as being any sponge growing independently (without contact) (Carballo et al. 2008). In some instances, rhodoliths were collected to determine the number of sponges growing on them. Also the number of sponge species within each quadrat was recorded. The total sampled area in each site was 15 m². The abundance of sponges and live rhodoliths was expressed as individuals/m² and the sponge species richness as the number of sponge species/m² (Fig. 2).

In addition, to compare the sponge abundance in and out the rhodolith bed, another three transects (20 m length) were placed (at the same depth and perpendicular to the shore) at a distance of 10 m from the bed. This procedure was done on the adjacent zone of beds 1 and 2. In these sites, the substrate was sandy. The particle size of the surface sediment (first 10 cm) in both sites was generally fine sand, with approximately 50 % of the sediment composed of material finer than <0.5 mm.

Rhodolith size and shape

In order to determine whether the abundance and richness of sponges vary among rhodolith beds according to the rhodolith size and shape, the average size (cm), sphericity and branch density (branches/cm²) of rhodoliths was determined. Rhodolith samples were collected in 0.25 × 0.25 m quadrats placed in the left superior corner of each 1 m² quadrat used for abundance determinations (15 samples per site). Individuals were placed into plastic bags separately and transported to the laboratory.

For each individual, its sphericity was calculated by measuring the longest, shortest and intermediate axes (see detailed method in Bosence and Pedley 1982; Graham and Midgley 2000). The average size was measured considering the longest dimension (Steller and Foster 1995). Branch density of each individual was estimated as the mean number of apical tips counted in three haphazardly placed 1 cm² quadrats (Steller and Foster 1995). The percent live surface area of rhodoliths was estimated based on pigmentation analysis of the coralline algae thallus surface (Bahia et al. 2010).

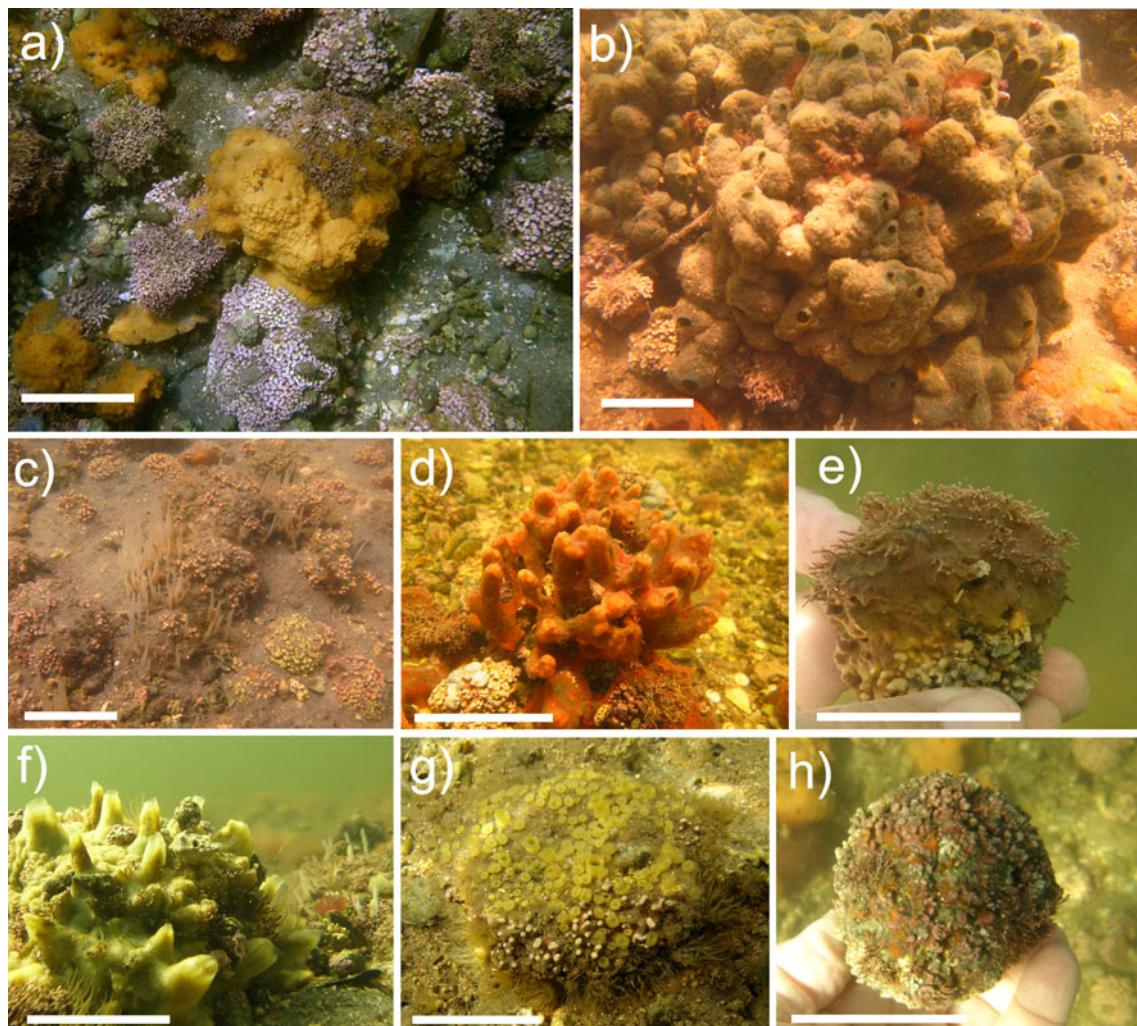


Fig. 2 The most common sponge species associated with rhodolith beds from Bahia Magdalena: **a** *Scopalina* sp., **b** *Suberites aurantiaca*, **c** *Halichondria semitubulosa*, **d** *Mycale cecilia*, **e** *Mycale* cf.

magnirhapidifera, **f** *Halichondria panicea*, **g** *Cliona californiana* and **h** *Cliona euryphylla*. The species from **a–f** were the most common sponges binding rhodoliths in Bahia Magdalena. Scale = 5 cm

Rhodolith collections were carried out in November 2008 in beds 1 and 2, and between January and February 2009 for beds 3, 4 and 5. The coverage area of beds was estimated by taking a series of geographical coordinates around the margins of each bed. The Garmin MapSource program was used to calculate the area (km²).

Rhodolith stabilization by sponges

In order to examine the potential role of sponges as rhodolith stabilizers, the abundance of sponges that bind two or more rhodoliths together was determined. The abundance (individuals/m²) of these sponge species was quantified in three 10 × 1.0 m transects (replicates) randomly placed within beds 1 and 2. Also, the total number of rhodoliths that every sponge attached to was recorded in each transect. A total area of 30 m² was sampled in each site.

Data analysis

One-way analyses of variance (ANOVA) followed by the Student–Newman–Keuls tests were used to assess significant differences in the mean density and structure of rhodoliths (size and branch density), and differences in the mean density and richness of sponges between sites (site was a random factor: 5 levels). For these cases, the average value of each transect was used as replicate (3 replicates/site). To determine whether the abundance of sponges that binds rhodoliths together varied between rhodolith beds (2 sites), one-way ANOVA was performed. Spearman rank correlations were used to assess relationships between the abundance and richness of sponges and abundance, size and branch density of rhodoliths. The average value of each quadrat was used as replicate in these analyses (15/site). The assumptions of normality and homocedasticity in each variable were previously tested by

Table 1 Summary of the rhodolith shape analysis (size, branch density and sphericity)

	Bed 1	Bed 2	Bed 3	Bed 4	Bed 5
Size (cm)	5.6 ± 0.1	5.9 ± 0.2	5.9 ± 0.2	5.5 ± 0.1	6.2 ± 0.3
Branches cm ⁻²	11.2 ± 0.2	9.4 ± 0.3	6.9 ± 0.2	5.5 ± 0.2	7.2 ± 0.3
Spherical forms (%)	99.0	80.8	87.6	81.4	75.0
Discoidal forms (%)	0.0	5.0	2.1	9.3	9.0
Ellipsoidal forms (%)	1.0	14.2	10.3	9.3	17.0
Individuals measured	100	87	100	100	35

The table shows the average (±SE) dimensions of rhodolith samples collected from five beds in Bahia Magdalena in September and November 2008

Kolmogorov–Smirnov’s and Bartlett’s tests, respectively (Sokal and Rohlf 1995).

Results

Rhodolith bed structure

Rhodolith beds ranged from 7,000 to 20,000 m² approximately, and the dominant rhodolith forming species was *Lithophyllum margaritae* Hariot. This seaweed showed fruticose and foliose growth forms. The structural characteristics (shape, size and branch density) of rhodoliths from each bed are summarized in Table 1.

The percent live surface area of rhodoliths was of 100 %, as all individuals collected showed a characteristic pinkish pigmentation. Only a few individuals showed bleached portions. Spherical forms were the most common morphology in all rhodolith beds, representing more than 75 % of the total samples for all 5 beds (Table 1). The average size of rhodoliths ranged from 5.5 ± 0.1 to 6.2 ± 0.3 cm with predominant size classes of 40–60 mm. The average size and branch density showed significant differences (ANOVA, size: $p < 0.05$; branch density: $p < 0.05$) between sites. Rhodoliths from bed 1 showed larger sizes ($p < 0.05$) and had higher branch densities than those of the other four sites (Table 1). The average (±SE) density of rhodoliths ranged from 31.8 ± 5.2 ind m⁻² (bed 5) to 215.9 ± 3.02 ind m⁻² (bed 1) (Table 1), and there were not significant differences among the five sites.

Sponge richness and abundance

Thirteen sponge species belonging to 6 Orders and 8 Families were recorded in association with rhodolith beds from Bahia Magdalena (Table 2). These assemblages were characterized by a variety of growth forms: massive (46 %), encrusting (23 %), excavating (15 %), cushion-shape (8 %) and digitate (8 %). The sponge species richness varied significantly (ANOVA, $p < 0.01$) between sites. Richness was significantly higher (SNK test,

$p < 0.01$) in bed 1 (6.1 ± 0.8 species m⁻²) than in bed 2 (2.7 ± 0.6 species m⁻²), bed 3 (2.6 ± 0.2 species m⁻²) and bed 5 (3.6 ± 0.4 species m⁻²). However, richness was not significantly different (SNK test, $p > 0.05$) than those recorded in bed 4 (5.1 ± 0.5 species m⁻²).

The overall sponge abundance ranged from 5.1 to 51.7 ind m⁻² and showed significant (ANOVA, $p < 0.01$) variations between sites. Abundance was significantly (SNK test, $p < 0.01$) higher in bed 1 (total average density = 51.7 ± 6.9 ind m⁻²) than in the other four beds. The most abundant species in all sites were: *Scopalina* sp., *Halichondria* cf. *semitubulosa*, *Haliclona* sp., *Mycale cecilia* and *Halichondria panicea* (Table 2).

Spearman rank correlation analyses indicated that the sponge species richness and sponge density were positively correlated (species richness: $r = 0.59$, $p < 0.01$; abundance: $r = 0.86$, $p < 0.01$) with the rhodolith density (Fig. 3a, b), that is, the number of sponges species and their abundance increased as a function of rhodolith density.

Moreover, when comparing the abundance of sponges outside versus inside these algal beds, sponges were not present in adjacent sandy areas.

Sponges as rhodolith stabilizers

Seven sponge species were identified as binding agents in the rhodolith beds of Bahia Magdalena: *H.* cf. *semitubulosa*, *M. cecilia*, *H. panicea*, *Suberites aurantiaca*, *Scopalina* sp., *Cliona euryphylla* and *Haliclona* sp. (Fig. 4). Six of them were present in bed 1 and three in bed 2. The mean abundance of these species was significantly (ANOVA, $p < 0.01$) higher in bed 1 (4.3 ± 0.14 ind m⁻²) than in bed 2 (1.5 ± 0.07 ind m⁻²).

The most abundant species in bed 1 was *H.* cf. *semitubulosa* (3.2 ± 0.2 ind m⁻²). This species was found binding an average of 3.1 ± 0.2 rhodoliths per sponge individual. In bed 2, the most abundant species was *M. cecilia* (0.6 ± 0.4 ind m⁻²), which bound an average of 6.6 ± 2.0 rhodoliths/individual (Fig. 4). Twenty-one rhodoliths was the maximum number of rhodoliths attached by a single sponge (*M. cecilia* in bed 1). Although the

Table 2 Composition and average density (individuals $m^{-2} \pm SE$) of the sponges surveyed from five rhodolith beds in Bahia Magdalena

Sponge species	Growth form	Bed 1	Bed 2	Bed 3	Bed 4	Bed 5
<i>Scopalina</i> sp.	E, M	21.5 \pm 1.8	1.3 \pm 0.8	0.3 \pm 0.2	1.9 \pm 0.7	2.0 \pm 0.7
<i>Halichondria panicea</i>	M	2.1 \pm 0.6	1.9 \pm 1.9	0.1 \pm 0.0	0.8 \pm 0.1	1.3 \pm 0.8
<i>Halichondria</i> cf. <i>semitubulosa</i>	D	20.0 \pm 3.6	2.8 \pm 1.0	1.9 \pm 0.3	6.9 \pm 1.3	2.2 \pm 0.4
<i>Mycale</i> cf. <i>magnirhapidifera</i>	E	2.1 \pm 1.0	0.3 \pm 0.0	0.1 \pm 0.0	0.7 \pm 0.2	0.3 \pm 0.4
<i>Mycale cecilia</i>	E, M	3.3 \pm 1.0	–	–	2.4 \pm 1.3	2.2 \pm 0.5
<i>Suberites aurantiaca</i>	M	0.1 \pm 0.2	0.3 \pm 0.2	–	0.3 \pm 0.1	–
<i>Dysidea cachui</i>	M	0.9 \pm 0.3	–	0.1 \pm 0.0	0.1 \pm 0.1	–
<i>Cliona euryphylla</i>	Ex	0.1 \pm 0.1	0.1 \pm 0.1	0.4 \pm 0.0	0.1 \pm 0.1	0.8 \pm 0.5
<i>Cliona californiana</i>	Ex	0.1 \pm 0.2	–	0.1 \pm 0.0	0.2 \pm 0.1	1.7 \pm 0.4
<i>Haliclona</i> sp.	Cu	0.8 \pm 0.4	–	2.3 \pm 0.5	0.9 \pm 0.7	1.0 \pm 0.0
<i>Haplosclerida</i> sp. 1	M	0.7 \pm 0.6	–	–	0.2 \pm 0.1	0.5 \pm 0.6
<i>Haplosclerida</i> sp. 2	M	–	0.2 \pm 0.1	–	–	–
<i>Clathrinida</i> sp.	M	–	0.1 \pm 0.1	0.1 \pm 0.0	1.1 \pm 0.2	0.3 \pm 0.4

Growth form *E* encrusting, *M* massive, *D* digitate, *Ex* excavating, *Cu* cushion-shape

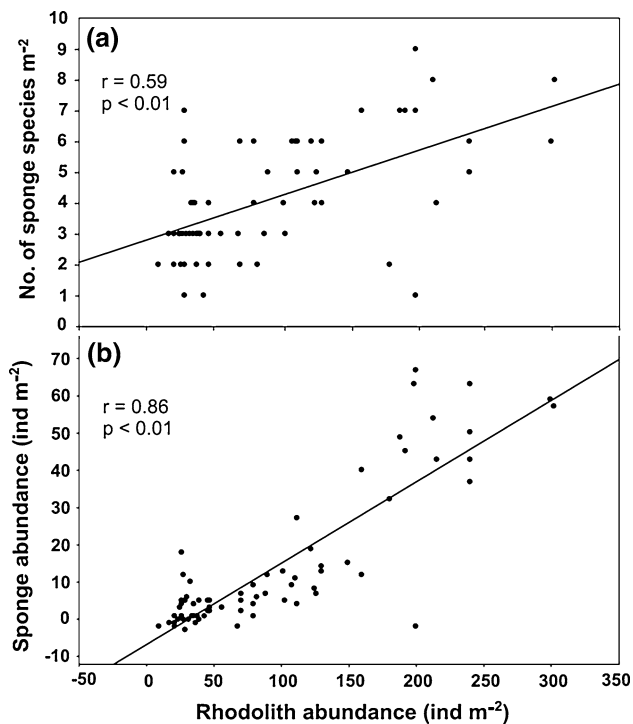


Fig. 3 **a** Relationships between rhodolith density and the number of sponge species m^{-2} and **b** between rhodolith density and sponge abundance

abundance of *M. cecilia* was relatively lower than those of *H. semitubulosa*, individuals of *M. cecilia* generally showed a larger coverage area and therefore bound more rhodoliths. Moreover, *H. semitubulosa* live almost completely buried and was usually binding rhodoliths of the beds surface and those about 5 cm below the surface of sediment. Other sponge species such as *Dysidea cachui* and

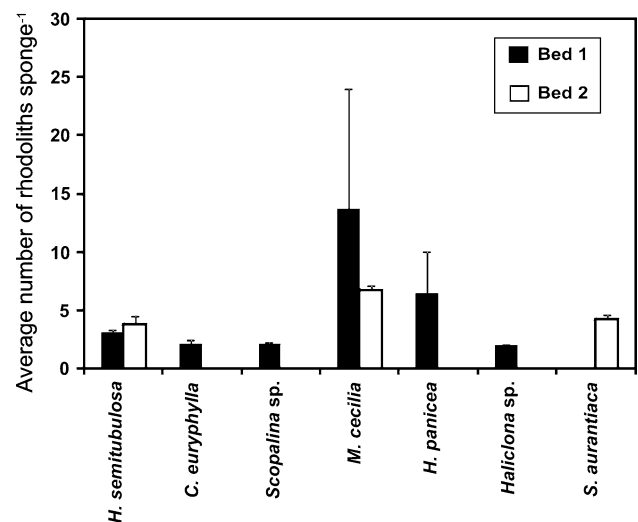


Fig. 4 Mean ($\pm SE$) number of rhodoliths bind per sponge individual in two rhodolith beds of Bahia Magdalena

Mycale cf. *magnirhapidifera* usually attached and grew on a single rhodolith, which could also contribute to rhodolith stabilization by affecting their sphericity.

Brief description of the sponge–rhodolith interactions

Most of sponge species were of encrusting to massive growth form. They overgrew (partially or totally) and filled the space between the rhodolith branches (Fig. 2e, g, h). There was no apparent damage on the tissue of these algae as a result of this interaction. When sponges were detached from rhodoliths, a stronger pigmentation was observed on this area. Individuals of *H. semitubulosa* were often found almost totally covered by sediment, and only the growth

projections and chimney-like siphons protruded from the sediment surface (Fig. 2c). This species developed a wide basal area and finger-like branches. *H. semitubulosa* and *M. cecilia* seem to be the main binding agents, as they were often found to glue together many rhodoliths.

Papillae of the boring species *Cliona californiana* and *C. euryphylla* were commonly observed protruding among rhodolith branches (Fig. 2g, h). In many cases, the rhodolith nuclei (gastropod or bivalve shells) was also infested by these species. Rhodoliths containing boring sponges were relatively more brittle than individuals without these sponges.

Discussion

The five rhodolith beds studied were dominated by *L. margaritae*, a common coralline alga in the region (Riosmena-Rodríguez et al. 1999), whose structural characteristics (average size, rhodolith density and branch density) were within the range of other previously recorded *L. margaritae* beds (Steller et al. 2003; Hinojosa-Arango and Riosmena-Rodríguez 2004). Likewise, the morphological characteristics of these seaweeds indicated that these populations were subject to high hydrodynamic conditions (tidal currents) (Steller et al. 2003). According to the previous studies, the spatial differences in size and branch density could be related to differences in the hydrodynamic conditions and to the intensity of light and its penetration into the water (Marrack 1999).

Our results revealed that areas adjacent to rhodolith beds almost always lacked sponges. These findings confirm the importance of these macroalgae as available hard substrate (Rocha et al. 2006) for associated sponges in estuarine environments, where sandy bottoms are predominant. It is important to mention that most of the sponge species found in this study have also been recorded in other environments of the Mexican Pacific such as rocky shores and associated with *Sargassum* beds (Carballo et al. 2008; Ávila et al. 2010). However, at Bahia Magdalena, these sponges were rarely observed in other hard substrates such as mangrove roots, rocky platforms or sandy flats. The low presence of sponges in these other substrates could be due to the large tidal range observed within this system (up to 2.3 m during spring tide) (Zaitsev et al. 2010). Only *Mycale* cf. *parishi* and *Craniella* sp. were occasionally found on soft bottoms, although their abundance was not quantified.

The species richness and abundance of associated sponges was positively related to rhodolith density, suggesting that the density of rhodoliths appears to be a good predictor of abundance and species richness of associated sponges. Similarly, Steller et al. (2003) documented that *L. margaritae* beds contribute significantly to the benthic

biodiversity at Bahia Concepcion, within the Gulf of California, as richness and abundance of associated faunal species were significantly higher inside rhodolith beds than outside. Our results are in agreement with the suggestion that rhodoliths serve as substrate, refuge or recruitment areas to many organisms (e.g., Barbera et al. 2003; Peña and Bárbara 2007).

Along with substrate availability and complexity, differences in the physical environment (e.g., hydrodynamics and sedimentation rate) also play an important role in spatial variability in abundance and richness of sponges (Carballo et al. 2008). Although these environmental variables were not examined in this study, differences in sponge assemblages detected between sites could be partially related to different degrees of exposure within the bay.

Worldwide, there are a few studies documenting the sponge diversity on rhodolith beds. For example, in maerl beds from the Ria de Arousa (Galicia, Spain), a total of 39 sponge species were recorded (Solórzano et al. 1991). In deeper rhodolith beds from the western Mediterranean seamounts (up to 100 m depth), Aguilar et al. (2009) identified more than 30 species, and in Ningaloo Reef (Western Australia, between 18 and 102 m depth), Heyward et al. (2010) reported 155 sponge species associated with rhodolith beds. In this study, the total sponge richness was much lower (13 species); however, this is the first study documenting the diversity and abundance of sponges on rhodoliths beds in the Eastern Pacific. Both the density (max. 52 ind m⁻²) and richness (max. 6.1 species m⁻²) of sponges were comparable with those reported in rocky habitats (17.5 ind m⁻² and 4.3 species m⁻², Bell and Carballo 2008; Carballo et al. 2008) and *Sargassum* beds (23.9 ind m⁻² and 4.8 species m⁻², Ávila et al. 2010) of the region.

Although abundance and richness of sponges were not significantly related to size and branch density of rhodoliths, the highest values were found in bed 1. This site presents more closely branched rhodoliths and a higher percentage of spherical forms. Similar findings were documented in rhodolith beds from Maltese Islands (Mediterranean), where the high epifaunal species richness was related to closely branched rhodoliths (Sciberras et al. 2009).

According to the previous studies on these algae, high branch density and a predominance of spherical shapes are indicative of sites exposed to high water motion (Marrack 1999; Steller and Foster 1995). High water activity could also explain in part the relatively higher abundance of sponges, as these organisms require a constant renewal of large water volume to their filter-feeding activities. It is important to mention that bed 1 is positioned at the entrance of a relatively narrow channel closer to the mouth of the bay, which may improve the water flow and could

make it different in sponge abundance and rhodolith shape compared to the other beds. In accordance with a previous study conducted in four of these beds, a non-metric multidimensional scaling (MDS) analysis using presence/absence sponge species data revealed variability in the distribution of sponge assemblages among and within sites, which is likely the result of differences in environmental conditions (Ávila and Riosmena-Rodríguez 2011).

In this study, more than 50 % of sponge species (with lateral growth) were found to bind rhodoliths (3.7 ± 0.2 rhodoliths per sponge individual in average). This indicates that sponges could contribute to immobilization of these unstable biogenic substrata, just as they do in coral reefs and rocky habitats (see review in Bell 2008). In coral reefs, for example, sponges may increase the survival of live coral on Caribbean reefs by binding fragments together, which is expected to increase rates of carbonate accretion (Wulff and Buss 1979). The substrate stability may also enhance the chance of larval settlement of associated organisms (Rasser and Riegl 2002). In rocky habitats, it has been suggested that the stabilization of boulders by sponges and other organisms could potentially reduce disturbance levels (Bell and Barnes 2003). In the rhodolith beds of Bahia Magdalena, sponges could minimize the effects of hydrodynamic conditions, such as tidal currents and storm disturbances, although it is not known to what degree this occurs or its actual effect.

The immobilization of rhodoliths by epibionts could also have potential negative effects. The lower portions of the seaweeds that are in contact with the sediment may be affected, as this area can become anoxic. Our observations of rhodoliths from the Magdalena region point to a distinctive growth pattern for long-term stabilized rhodoliths. They tend to develop thalli with a mushroom-like shape where the sand covered section is dead and the exposed part is still alive. On the other hand, it has also been demonstrated that rhodoliths can survive without movement as they can translocate metabolites to lower surfaces of the thalli or have some heterotrophic utilization of a dissolved energy source, allowing them to grow spherically (Littler et al. 1991). Also, Scoffin et al. (1985) reported that spherical rhodoliths can continue to live under sandy substrata because water flushing through the sand and gravel may move sediment grains. Moreover, some stabilization experiments have resulted in the softening of rhodoliths and breakage of thalli after 6 months of permanent stabilization as a result of overgrowth by tube building amphipod species (Hinojosa-Arango personal comments).

In summary, the results of the present study indicated that shallow-water *L. margaritae* beds constitute an important solid substrate for sponge assemblages in soft bottoms from Bahia Magdalena, since sponges were largely confined to these biogenic substrates as occur in other

macroalgal habitats (Ávila et al. 2010). The significant positive relationships between sponge density and rhodolith density and between sponge species richness and rhodolith density support this fact. Moreover, many of the sponge species recorded here were identified as binding agents of rhodoliths, suggesting an important role in rhodolith stabilization by minimizing effects of hydrodynamic conditions. Further studies are needed for a better understanding of the dynamics of these sponge–rhodolith interactions and their role in estuarine ecosystems.

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