Symbiotic relationships between sponges and other organisms from the Sea of Cortes (Mexican Pacific coast): same problems, same solutions

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Abstract: This study provides a morphological description of three symbiotic associations between sponges (Haplosclerida) and other macroorganisms from the Sea of Cortes (Mexican Pacific Ocean). These associations include: (1) a two-sponge association (Haliclona sonorensis/Geodia media), (2) a sponge-red macroalga association (Haliclona caerulea/Jania adherens) and (3), a sponge-coral association (Chalinula nematifera/Pocillopora spp.). So far these interactions seem to be obligatory for the sponges (Haliclona spp. and C. nematifera), since we have never found them living in isolation. Interestingly, similar associations have been described from other places around the world. Associations quite similar to (1) have been described from the Caribbean, and associations (2) and (3) are comparable to others described from the Western Pacific. Instead of comparing these associations with their “sibling” associations worldwide, we discussed the ability of haplosclerid sponges to form symbiotic associations with other organisms, since these sponges pertain to the group of which the most associations have been described.

Keywords: Sea of Cortes, sponge-alga, sponge-coral, symbiotic associations, two-sponge

Introduction

Sponges are one of the major phyla found in the hard-substrate marine benthos (Sarà and Vacelet 1973). One of their more interesting characteristics is that they are able to establish a great diversity of relationships (mutualism, commensalism and parasitism) with unicellular and multicellular organisms (Palumbi 1985, Rützler 1990, Magnino and Gaino 1998, Ilan et al. 1999, Wulff 1999, Thakur and Müller 2004). Most of these relationships have been reported in the Caribbean (West 1979, Rützler 1990, Wulff 1997a, 1997b, 1999, Wilcox et al. 2002), Mediterranean Sea (Uriz et al. 1992, Gaino and Sarà 1994), Red Sea (Meroz and Ilan 1995, Ilan et al. 1999), Indo-Pacific region (Steindler et al. 2002, Calcínei et al. 2004) and Western Pacific (Vacelet 1981, Trautman et al. 2000). Surprisingly, in a large number of cases, the same species are involved in similar interactions in different oceans (Ilan et al. 1999, Wulff 2006). For example, the sponges Haliclona caerulea Hechtel, 1965, Haliclona cymaeformis Esper, 1794 and Dysidea janiae (Duchassaing and Michelotti, 1864) are species found to establish similar interactions with red macroalgae (Vacelet 1981, Rützler 1990, Trautman et al. 2000, Carballo and Ávila 2004). However, it is unknown whether this group of “cosmopolitan” associations occurs in the East Pacific Ocean.

The order Haplosclerida (Demospongiae) is the group in which the most of the symbiotic relationships have been registered with the family Chalinidae Gray, 1867 accounting for more than 50% of the associations described in this order (see discussion). Sponges of this order can establish associations with microorganisms such as bacteria (Vacelet et al. 2001), cyanobacteria (Steindler et al. 2002), dinoflagellates (Garson et al. 1998) and zoochlorellae (Frost and Williamson 1980), and with macroorganisms such as polychaetes (Dauer 1974), macroalgae (Vacelet 1981), barnacles (Ilan et al. 1999), hydrozoans (Schuchert 2003), anthozoans (West 1979), ostracods (Henkel and Pawlik 2005), insects (Gaino et al. 2004) and other sponges (Wilcox et al. 2002).

In the present study, we describe three interactions involving haplosclerid sponges from the Sea of Cortes (Mexican Pacific Ocean). They are a two-sponge association (Haliclona sonorensis-Geodia media), a sponge-alga association (Haliclona caerulea-Jania adherens) and a sponge-coral association (Chalinula nematifera-Pocillopora spp.). We discuss the surprising parallelism that exists worldwide, given that very similar interactions occur in different oceans. In addition, we comment on the characteristics that this group – in which more symbiotic relationships have been registered – has in order to establish these symbiotic associations.
Material and methods

Specimens of the three associations were collected by SCUBA diving from 2 to 12 m depth, in four localities from the Sea of Cortes (Eastern Pacific Ocean, Mexico) (Fig. 1). We followed the techniques described by Rützler (1974) for spicule and tissue preparations for light microscopy. Cross-sections of the specimens were washed in distilled water and then dried on a cover glass and coated with gold for scanning electron microscope (SEM) observations. A number of 20 to 50 spicules chosen randomly were measured (length x width) from each of the specimens studied. The number between brackets in each description is the average. After the description, the specimens were fixed in formaldehyde 4% and after 24 h they were transferred to 70% alcohol for their preservation. All the specimens were deposited in the Colección de Esponjas of the Instituto de Ciencias del Mar y Limnología, UNAM (LEB-ICML-UNAM), in Mazatlán (Mexico).

In the Haliclona sonorensis/Geodia media association, the surface of G. media covered by H. sonorensis was estimated. First we took photographs of the specimens, then we determined the covered area (%) using the computer program Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006). The frequency of the C. nematifera/Pocillopora spp. association was determined in three transects of 50 m length at a depth between 4 to 6 m. In each one of these transects we chose 20 colonies of coral at random, and determined the percentage of these containing sponge. In the same area, we also checked if the sponge was on another type of substratum. For each sample of the association we determined the species of coral and estimated the percentage of the colony overgrown by the sponge as number of branches with sponge of the total of branches.

Results

Association Haliclona sonorensis/Geodia media Cruz-Barraza and Carballo, 2006 – Geodia media Bowerbank, 1873

Material examined. Eleven specimens of the association were collected between 2 and 5 m depth in two localities from the northern Sea of Cortes: Punta Cazón (Bahía Kino, Sonora, 28°52′20″ N, 112°02′01″ W), and Punta Pinta (La Choya, Puerto Peñasco, Sonora, 31°18′05″ N, 113°59′11″ W) (Fig. 1), from August 2000 to April 2005.

Description of the species involved in the association. The epizoic sponge was identified as Haliclona sonorensis Cruz-Barraza and Carballo, 2006, which is a cushion-shaped sponge from 2 to 5 mm in thickness (Fig. 2A). Consistency is soft, compressible, but fragile and brittle. The surface is smooth and the ectosomal layer is not easily detachable. The color is pinkish violet in life and ocre or light brown in alcohol. The oscules are scarce, and circular or oval-shaped (from 0.5 to 1 mm in diameter), situated at the summits of volcano-shaped elevations. The skeletal material is constituted by oxeas that measure: 77-(112)-150 x 2-(5.6)-10 µm.

The supporting sponge was identified as Geodia media Bowerbank, 1873. This is a massive-incrustating to massive amorphous sponge (from 3.5 to 8 cm thick). The surface is irregular, smooth to the naked eye, but finely rough to the touch. The natural color of the surface is from dark-brown to white. The choanosome is yellowish or beige. Small ostial-pores from 150 to 300 µm are regularly distributed on the surface. The oscules measure from 0.22 to 2.5 mm in diameter. Consistency of the ectosome is very hard due to the cortex of sterrasters. The choanosome is cavernous and very densely spiculated, with a firm and slightly compressible consistency. The skeletal material is constituted by megascleres: oxeas, 620-(1430)-1950 x 10-(31)-42 µm; large styles, 620-(1077)-1260 x 22-(36)-45 µm; strongyloxeas, 150-(197.2)-292 x 2.5-(4.9)-7.5 µm; plagiotriaenes, 550-(1078)-1700 µm rabdome length; and anatriaenes, 1120-(1410)-2040 µm rabdome length, and microscleres: sterrasters, 25-(62.8)-90 µm oxysters, 20-(27.2)-45 µm; oxyospherasters, 6.3-(9.5)-13 µm.

Description of the association. The specimens of the association were found attached to the rocky substrata, covering areas from 8 x 6.5 to 20 x 15 cm, approximately. H. sonorensis forms a thin layer that covers up to 57% of the surface of G. media, while the surface that is not covered by the sponge is occupied by other epibionts (green and red algae, bryozoans, polychaetes and bivalves). Only the oscular areas (from 1 to 4 cm in diameter) are free of these epibionts (Fig. 2A). In some cases, more than one individual of H. sonorensis was observed on a same specimen of Geodia, which was evident by their different tonality of coloration. Despite being interwoven, Haliclona was unattached in some areas, where we observed that the external tissue of Geodia did not seem to be damaged by the epizoic sponge (Fig. 2B, C). The area of G. media lacking epibionts has a rough texture due to the external layer of sterrasters (Fig. 2C, D), but the SEM showed that the megascleres (triaenes and oxeas) of G. media protrude the surface in the areas covered by Haliclona (Fig. 2C, F) penetrating in the Haliclona sonorensis tissue (Fig. 2D, E). There were spicules (oxea) of H. sonorensis inside the ostias and embedded in the choanosome of G. media, and there were also sterrasters of G. media in the choanosome of H. sonorensis.

Haliclona sonorensis has been invariably found living on the surface of G. media which suggests that this species needs to live in association with G. media.

Association Chalinula nematifera (de Laubenfels, 1954) – Pocillopora spp. Lamarck, 1816

Material examined. A total of ten specimens of this association were collected between 3 and 12 m depth in three sites from Isabel Island (Bahia Tiburones, Playa Las Monas and Playa Iguanas), Nayarit, Mexico (28°52′20″ N, 112°02′01″ W) (Fig. 1), from December 2003 to July 2006.

 Morphological description of the species in the association. The epizoic sponge has been identified as Chalinula nematifera (de Laubenfels, 1954). This is an encrusting sponge of violet color (1-4 mm thickness). This sponge grows only on live corals found in Isabel Island (Fig. 3). The surface is smooth to the naked eye, but it is punctated and shaggy in some places. Oscules are abundant, circular, from 4 to 6 mm
in diameter, and regularly distributed on the surface. They are situated at the summits of volcano-shaped elevations. Consistency is soft and spongy, somewhat elastic and slimy. The skeleton consists of oxeas: 87-(98)-112.5 x 2.5-(4.4)-5 µm. Our specimens also show the characteristic pale threads through the body as described by de Laubenfels (1954), which presumably is a symbiotic fungus (WF Prud’homme van Reine, comments in de Weerdt 2002).

The coral species on which C. nematifera was found were identified as *Pocillopora damicornis* Linnaeus, 1758, *P. meandrina* Dana, 1846, *P. capitata* Verrill, 1864 and *P. verrucosa* Ellis and Solander, 1786. In general, these coral species have characteristic shape because they form densely ramified colonies. They have calices crowded together over regularly-spaced wart-like projections (verrucae) (*P. capitata* and *P. verrucosa*).

**Description of the association.** *C. nematifera* was found always on live ramified corals that live in areas exposed to light, most frequently with *P. verrucosa* (67%), and never on another type of substratum. Nevertheless, it is possible to find these species of coral (mentioned above) without the sponge. Approximately 17% of the *Pocillopora* colonies studied had *C. nematifera* in association. In these sponge/coral interactions, *C. nematifera* can cover branches partially or totally (5±5.12% of the total of branches of the colony), and in all these cases we observed that the surface of the covered coral has no polyps. This sponge adhered firmly to the coral and is not easy to detach it from the substratum without breaking it. In fact, through the SEM images, we observed that the skeletal structure of the sponge seems to be cemented to the coral septa by spongin layers (Fig. 3C).

**Association Haliclona caerulea** Hechtel, 1965 – *Jania adherens* Lamouroux, 1816

**Material examined.** Sixteen specimens of the sponge-alga association were collected from ten sites from the Mazatlán Bay (23°13’49” N, 106°27’43” W), Sinaloa, Mexico (Fig. 1), between 2 to 6 m depth, from November 1997 until October 2003.

**Morphological description of the species in the association.** *Haliclona* (*Gellius*) *caerulea* is a massive sponge (from
3 to 13 cm high), white or beige in life and very brittle. The skeleton is constituted by oxeas (82.5-(177.3)-210 µm) and sigmas (17.5-(21.6)-30 µm). The sponge has an unispicular ectosomal skeleton, formed by an isotropic tangential reticulation of oxeas, and the choanosomal skeleton is a somewhat confused reticulation of uni-multispicular primary and secondary lines that are difficult to appreciate because of their association with the alga (Fig. 4B).

The alga was identified as *Jania adherens* Lamouroux, 1816, which is an articulated erect red macroalga. The alga is pink with white joints, repeatedly branched, with a calcified thallus (from 0.4 to 0.5 mm diameter) except at the genicula.

**Description of the association.** This sponge lives in intimate association with the red calcareous alga *Jania adherens*. The association consists of a massive and compact form where the sponge completely fills the spaces between the algal branches (Fig. 4A). The sponge generally covers the alga, and the algal branches very rarely protrude beyond the association surface. The morphology of the association is derived from the growth form of both organisms. Specimens of this association are lo-
cally abundant in rocky substrate environments (2-6 m depth), in areas of strong wave force. However, in these places, it is not possible to find the two species living in isolation, even though *J. adherens* lives in isolation in the intertidal zone. *Jania adherens* forms compact turfs approximately 2 cm high in the intertidal zone. However, in the subtidal zone (in association with *H. caerulea*) it reaches up to 13 cm in height. In the images obtained by SEM, we observed that the spicules of *H. caerulea* adhere firmly to the stalks of *J. adherens* by means of a fine spongin layer (Fig. 4C). We also observed that the primary lines of the sponge are partially replaced by the macroalgal thallus.

**Discussion**

**Two-sponge association**

Interactions among two or more sponges of different species, including cases of mutualism (Wilcox *et al.* 2002), parasitism (Wulff 1999) or space competition (Rützler 1970, Wulff 2006) have been previously recorded. 

A two-sponge association quite similar to ours was described recently from the Florida Keys (Wilcox *et al.* 2002). In both cases, as it has also been documented for other two-sponge associations (Sim 1998, Wilcox *et al.* 2002),
Haliclona sp. seems to be anchored on the protruding spicules of Geodia spp.

There are studies that suggest that growth and survival increases when certain sponges of different species live in association, because they have different susceptibility to factors such as burial by sediment, fragmentation, predation and pathogens (Wulff 1997a, 1999, Engel and Pawlik 2005, Wulff 2006). However, in the association from the Florida Keys, it was suggested that it could be a mutualistic and obligatory symbiosis, where the external sponge protects its host from the predation, while Geodia sp. offers it a sure substratum for its survival (Wilcox et al. 2002).

However, it is interesting to comment that the Caribbean sponge Geodia gibberosa is chemically undefended against turtle and fish predation (Dunlap and Pawlik 1996, 1998), and uses its chemical products to attract fouling organisms. This could resemble Geodia sp. in association with Haliclona sp. (Wilcox et al. 2002), since one of the benefits acquired by the sponge Geodia cydonium fouled by the red alga Rytyphlöea tinctoria is the protection against the adverse effects of ultraviolet radiation, allowing the specimens to live under illuminated habitats (Mercurio et al. 2006).

It is possible that an obligatory relationship also exists between H. sonorensis and G. media, at least for H. sonorensis, since it has not been found in isolation within the environment where the associations are encountered. In fact, the high specificity of Haliclona to live with Geodia is very interesting because this association does not originate in a highly space-competitive environment like reef ecosystems, and therefore it could not be a simple case of epizoism due to space limitation (Rützler 1970). In addition, it is important to mention that there is no evidence of tissue damage on the surface of G. media covered by H. sonorensis, as it has been documented in other two-sponge interactions (Thacker et al. 1998). Although we did not make experiments to test whether a benefit exists between G. media and H. sonorensis, bioactive natural products have been described in G. media from the Sea of Cortes (Pettit et al. 1981, Pettit et al. 1990), that could attract fouling organisms, similar to Geodia gibberosa (Engel and Pawlik 2000, Engel and Pawlik 2005).

In the association described here, one or more specimens of H. sonorensis are found attached to the same G. media specimen, establishing contact but without fusing. These observations support the idea that this sponge most likely colonizes G. media through larval settlement, in order to obtain an appropriate substratum for its survival (Wulff 1997b, Wilcox et al. 2002).

**Sponge-coral association**

Sponge-coral interactions are common in coral reefs where strong competition for space exists and where it is frequent that aggressive sponges overgrow the coral (Aerts 1998).

The sponge Chalinula nematifera has been described previously overgrowing hard corals in reefs from the West-Central Pacific (de Laubenfels 1954). Surprisingly, this species also seems to be specifically attracted to pocilloporid corals from the Sea of Cortes, since it has not been found colonizing other types of substratum. Nevertheless, the species of coral associated with this sponge can be found in an isolated form. This suggests that it could be an obligatory relationship for the sponge, and facultative for the host (Pocillopora spp.). We also suggest that this relationship can have negative outcome for the coral, since the sponge seems to be killing the coral tissue, similar to what has been documented for several sponge/coral interactions (Jackson and Buss 1975, Plucer-Rosario 1987, Macintyre et al. 2000, Aerts 2000, Rützler 2002, de Voogd et al. 2004, Coles and Bolick 2006, Gochfeld
et al. 2006). However, we do not know if C. nematifera uses chemical products to kill the coral polyps (Nishiyama and Bakus 1999) or if it simply smothers them (Wulff 1999). Some authors have suggested that the ability of sponges to overgrow corals appears to depend on their growth rate and form (Aerts 2000). For example, in the sponge Terpios hoshinota, it was suggested that its success to overgrow large extensions of live corals is due to a fast spreading rate, aided by fast asexual propagation (fragmentation) (Placer-Rosario 1987, Rützler and Muzik 1993).

Chalinula nematifera possibly finds a substratum that offers multiple protected microhabitats in pocilloporid corals, since they are densely ramified species which are often used as microhabitats by several organisms (Patton 1974). Thus, C. nematifera could likely benefit by finding an appropriate substratum that offers protection against environmental factors (e.g. UV radiation, sedimentation and/or predation). This is an advantage that it could not find with the other non-branched coral species (Porites, Psammocora, Pavona and Fungia) that inhabit the same site as the C. nematifera/ Pocillopora spp. association, most likely because they do not offer this kind of physical protection.

Although in most of the sponge-coral interactions that have been described, it has been found that these relationships seem to be negative for the coral (de Voogd et al. 2004, Coles and Bolick 2006, Gochfeld et al. 2006, López-Victoria et al. 2006), there are also documented cases of mutualisms; for example, the sponge Mycale laevis Carter 1882 which is found encrusting on the lower surfaces of flattened reef corals (mainly on Montastrea annularis) in the Caribbean Sea. M. laevis benefits by colonizing a substrate that is free from other sessile organisms. In turn, the coral benefits from an increased feeding efficiency as a result of water currents produced by the sponge and it is protected from invasion by boring sponges (Goreau and Hartman 1966). In the case of sponge/octocoral associations, the sponge generally obtains structural support from its partner and the octocoral obtains protection against predation (van Soest 1987, Calcinai et al. 2004). In addition, it has been documented that both organisms also benefit by increasing their dispersal capacity (Calcinai et al. 2004).

Sponge-alga association

Associations between sponges and photosynthetic organisms are important not only for the partners, but also for the ecosystem they inhabit, because they can contribute significantly to the primary productivity, mainly in oligotrophic ecosystems (Wilkinson 1983, Steindler et al. 2002). One of the most-studied sponge/macroalga symbioses is the Haliclona cymaeformis/Ceratodictyon spongiosum association (from the Great Barrier Reef, Australia) (Trautman et al. 2000, Trautman and Hinde 2002, Davy et al. 2002), which we could consider as a “sibling” association of the H. caerulea/J. adherens association described here. In both cases the mutualistic association derives similar benefits for the partners (such as protection against physical disturbances, structural support, high dispersal capacity through fragmentation), and in both cases the sponge is a species of Haliclona that lives associated with a red macroalga (Trautman et al. 2000, Trautman and Hinde 2002, Carballo and Ávila 2004, Carballo et al. 2006). However, in spite of the similarities of these two interactions, the H. caerulea/J. adherens association does not live in an oligotrophic environment in the Bay of Mazatlán (see Carballo 2006).

Our investigations into the H. caerulea-J. J. adherens association suggests that this is an obligatory and mutualistic association, where both organisms benefit by increased growth, widespread their distribution area toward an environment where none can inhabit by itself, and by the acquisition of a structural support that gives them bigger rigidity than their free-living form (Ávila and Carballo 2004, Carballo and Ávila 2004, Carballo et al. 2006). H. caerulea can also substitute part of its skeletal structure (mainly primary lines) with the branches of J. adherens, reducing the investment in spicule production (Carballo et al. 2006), as it has been documented in other sponge symbioses (de Laubenfels 1950, Vacelet 1981, Rützler 1990, Uriz et al. 1992). In addition, it has been demonstrated that H. caerulea in association with J. adherens (from the Pacific coast of Panama) acquires the benefit of being protected against fish predation (Wulff 1997a).

On the other hand, H. caerulea has never been found in isolated form at the depth range where the sponge-alga association lives in the Bay of Mazatlán, because it has a very fragile structure, and it is unable to live in that environment, which is characterized by strong water movement (Carballo et al. 2006). Although this association reproduces mainly by fragmentation, larval settlements of H. caerulea have been registered in the intertidal zone where J. adherens inhabits in isolated form (Ávila and Carballo 2006). In fact, laboratory experiments demonstrated that the larvae of H. caerulea can select J. adherens as substratum while rejecting others (Ávila and Carballo 2006), probably because the alga fronds offer a shady and tangled microrefuge, which could increase the post-settlement survival (Buss 1979, Maldonado and Uriz 1998).

On the other hand, it is important to add that this association has also been found in other localities in Mexico, such as Tuxpan, Veracruz (in the Gulf of Mexico) and Manzanillo, Colima and Huatulco, Oaxaca (in the Mexican Pacific) (personal observations).

The diversity of associations among the haplosclerid sponges

The three symbiotic sponges (H. sonorensis, C. nematifera and H. caerulea) described in this study belong to the order Haplosclerida, which is one of the most diverse groups of the phylum Porifera (Hooper and van Soest 2002). Upon revising the literature, we have found that most of the sponges (21% of 248 cases) that have been previously recorded establishing associations with other taxa (see introduction), belong to the order Haplosclerida, and mostly to the family Chalinidae (50% of 51 registrations) (Fig. 5) (Dauer 1974, Vacelet 1981, Ellison et al. 1996, Garson et al. 1998, Ilan et al. 1999, Vacelet et al. 2001, Steindler et al. 2002, Wilcox et al. 2002, among others). These associations have been recorded mainly in shallow tropical and subtropical environments (such as coral reefs), which are characterized by a high competition for space and food by the organisms that inhabit there. It seems that some sponges have probably “learned” to associate with
other organisms that offer them some kind of protection against environmental factors (such as fish predation, sedimentation, UV radiation, tissue resistance). For example, in the Geodia sp./Haliclona sp. association, it has been suggested that Geodia sp. is chemically defended against fish predation and protected from sedimentation by the sponge partner (Wilcox et al. 2002). In another haploclerid species such as Haliclona cymaeformis and Haliclona implexiformis that live associated with photosynthetic organisms (macroalga and mangrove respectively), it has been demonstrated that nutrient translocation also exists between the sponge and its host (Ellison et al. 1996, Davy et al. 2002). In the case of species that shelter cyanobacteria (e.g. Adocia atra and Haliclona debilis) in their tissue, it has been suggested that they can benefit by protecting their surface from UV-radiation and/or obtain an alternative source of food (Rützler 1990, Steindler et al. 2002). It has also been suggested that they reinforce their skeletal structure using their partner to avoid being broken into fragments by the current, as is the case of H. caerulea (Carballo et al. 2006) and H. cymaeformis (Trautman and Hinde 2002).

On the other hand, there are many bioactive compounds known in haplosclerid sponges (Frincke and Faulkner 1982, Isaacs and Kashman 1992, van Soest and Braekman 1999), which can also be used for different purposes such as antifoulants (Sera et al. 2002), as antimicrobial compounds (Xue et al. 2004, Ely et al. 2004) or in competition for space (Nishiyama and Bakus 1999).

Conclusions

In general, it seems that in the sponge/sponge and sponge/macroalga associations the relationships are usually mutualistic, or at least no type of damage has been evidenced among the associated organisms. In contrast, in most of the non-boring sponges associated to ramified corals that have been described (including C. nematifera/Pocillopora spp. association), the relationship seems to be negative for the coral species. Nevertheless, it is necessary to do more experimental and population dynamics studies of these associations in order to understand more about the complexity of their life history and their ecological importance in the ecosystem they inhabit.

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References


