

Habitat preference of Zoantharia genera depends on host sponge morphology

Javier Montenegro-González, Alberto Acosta

Unidad de Ecología Sistemática, Departamento de Biología, Facultad de Ciencias,
Pontificia Universidad Javeriana, Bogotá, D.C. Colombia

montenegroj@javeriana.edu.co; laacosta@javeriana.edu.co

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Abstract

Objective. Studies about sponge-zoanthid symbioses have been focused on understanding the specificity of the association, rather than testing what are the characteristics that make the host suitable to be colonized. For the first time it is investigated whether the Zoantharia *Parazoanthus* and *Epizoanthus* preference is related to the host sponge morphology (shape and mechanical resistance). **Materials and methods.** Sponges were categorized according to their shape and mechanical resistance. The presence/absence of zoanthids was recorded in 1,068 sponges at San Andres Island, and their habitat preference was evaluated using indices and confidence intervals. **Results.** 85 *Parazoanthus* colonies (78% of the total associations) and 24 *Epizoanthus* colonies (22%) were associated to sponges (10.2% in total). *Parazoanthus* uses branched and compressible sponges although prefers encrusting and fragile sponges, while *Epizoanthus* shows the opposite pattern, it can inhabit encrusting and fragile sponges but prefers branched and compressible sponges. **Conclusion.** These results indicated that sponge morphology is an important trait in zoanthid habitat selection. On the other hand, the similarity in the habitat used by zoanthids suggests the possibility of inter-generic competition if common resources are limited in time and space, while the differential habitat preference allows the competitive coexistence of both genera.

Key words: *Epizoanthus*, host, *Parazoanthus*, symbiont, sponge, morphology.

Resumen

La preferencia de hábitat de géneros de Zoantharia depende de la morfología de la esponja. Objetivo. Los estudios sobre la simbiosis entre zoantídeos y esponjas se han centrado en la comprensión de la especificidad de la asociación, en lugar de explorar cuáles son las características que hacen que un huésped sea adecuado para ser colonizado. Por primera vez se investiga si en los Zoantharia *Parazoanthus* y *Epizoanthus* la preferencia está relacionada con la morfología de la esponja hospedera (forma y resistencia mecánica). **Materiales y métodos.** Las esponjas fueron categorizadas según su forma y resistencia mecánica. La presencia/ausencia de zoantídeos se registró en 1.068 esponjas en la Isla de San Andrés y la preferencia de hábitat se evaluó utilizando diferentes índices e intervalos de confianza. **Resultados.** 85 colonias de *Parazoanthus* (78% del total de asociaciones) y 24 colonias de *Epizoanthus* (22%) se encontraron asociadas a esponjas (10,2% en total). *Parazoanthus* usó esponjas ramificadas y compresibles, pero prefirió las incrustantes y frágiles; mientras que *Epizoanthus* demostró el patrón contrario, habitando en las esponjas incrustantes y frágiles, pero prefiriendo las esponjas ramificadas y compresibles. **Conclusión.** Estos resultados indican que la morfología de las esponjas es un aspecto importante para la selección de hábitat por parte del zoantídeo. Por otra parte, la similitud en el hábitat usado por los zoantídea sugiere la posibilidad de competencia entre géneros si los recursos que comparten llegan a ser limitantes en tiempo y espacio; mientras que, la diferencia en la preferencia de hábitat permitiría la coexistencia competitiva de ambos géneros.

Palabras clave: *Epizoanthus*, hospedero, *Parazoanthus*, simbiosis, esponja, morfología.

Resumo

A preferência de habitat de gêneros do Zoantharia depende da morfologia da esponja. Objetivo. O estudo sobre a simbiose entre zoantídeos e esponjas têm-se centrado na compreensão da especificidade da associação, em vez de explorar quais são as características que tornam ao hospedeiro adequado a ser colonizado. Pela primeira vez se pesquisa nos Zoantharia, *Parazoanthus* e *Epizoanthus*, se a preferência está relacionada com a morfologia da esponja hospedeira (forma e resistência mecânica). **Materiais e métodos.** As esponjas foram classificadas de acordo com a sua forma e resistência mecânica. A presença/ausência de zoantídeos foi registrada em 1.068 esponjas na ilha de San Andres e a preferência de habitat foi avaliada através de diferentes índices e intervalos de confiança. **Resultados.** 85 *Parazoanthus* (78% do total das associações) e 24 *Epizoanthus* (22%) foram encontradas associadas com esponjas (10,2% do total). *Parazoanthus* utilizou esponjas ramificadas e compressíveis, mas preferiu as incrustantes e frágeis; enquanto *Epizoanthus* demonstrou o padrão oposto, habitando nas esponjas incrustantes e frágeis, mas preferindo as esponjas ramificadas e compressíveis. **Conclusão.** Estes resultados indicam que a morfologia das esponjas é um aspecto importante na seleção do habitat pelos zoantídeos. Além disso, a semelhança do habitat utilizado pelos zoantídeos sugere a possibilidade de competição inter-gêneros se os recursos compartilhados são limitantes no tempo e no espaço; enquanto que, a diferença na preferência de habitat permitiria a coexistência competitiva de ambos os gêneros.

Palavras-chave: *Epizoanthus*, hospedeiro, *Parazoanthus*, simbioses, esponja, morfologia.

Introduction

Habitat preference is a subject of great importance that allows researchers to infer the ecological requirements of a given organism, and to explain its abundance and spatial distribution (1). It is also important to understand ecological (competition, local extinction, coexistence) and evolutionary processes (adaptations, niche separation, and speciation) in a changing world. Habitat is defined as the place that has all the resources (biotic and abiotic) and conditions for survival, reproduction and the establishment of local populations (2, 3), or the place (spatially limited) where density or other population parameters are different from those of other localities or contiguous patches (4). For example, in symbiotic (host and guest) relationships, the host will be the space and habitat for the guest, and different host types (patches) will define the symbiont population density. However, the space, as part of the organism's habitat, can be available or not, depending on the presence or absence of limiting factors (physical and biological) that prevent the establishment, survival or reproduction of any given organism (host or symbiont). According to Brinkman *et al.* (5) the use of an available habitat is linked to its abundance in the system, but it does not mean that all the available habitats will be used. On the other hand, habitat preference is understood as a consequence of selection or asymmetrical use of some resources over others by each individual in the population (in a non-random way), from all the available habitats (6, 4), and must be evaluated at the population level (7). According to Litvaitis *et al.* (8) and Matthiopoulos (9) habitat preference can only be inferred, or indirectly evaluated, through the use that the organisms make of physical and biological resources in the available habitats. However, results may be misinterpreted because the preference for some particular resources is commonly extrapolated as the organism's

habitat preference (all of the resources and conditions), when only a part of its ecological requirements has been evaluated (10).

The asymmetric use of any resource depends on the organism's requirements, with criteria that vary in time and space in relation to life cycle stages or even within a particular stage when the resources change. But it also depends on the quality, quantity and availability of resources in a particular patch (6). Some researchers have proposed that habitat preference must be evaluated as the difference between the relative proportions of all used habitat and its availability (potential use). This statement implies selecting a habitat and establishing realistic categories depending on the organisms life history to measure the habitat categories that the organisms use, do not use, select (asymmetric use), and prefer at the population level.

Considering the arduous and complex fieldwork required to assess all the resources used by an animal, and in order to build up new theory, we propose that habitat preference may be easily evaluated by examining symbiotic interactions such as those that involve guest and host (11). In particular, sessile organisms could be used as an example for habitat preference assessment because once the selection for a particular substrate (habitat) has been done by larvae, it will not change through the remaining life cycle of the organism, and the host used as habitat (easily delimited) should provide all or the primary resources required for the symbiont survival, growth, and reproduction. In consequence, symbiont habitat preference could be inferred based on few resources and with less sampling effort.

In the marine environment, sponges (sessile, filter feeding organisms with large morphological plasticity) are an important component of reef ecosystems and are well known for having a large number of symbiotic associations (12).

Chavarró *et al.* (13) explain the benefits that sponges provide to their symbionts, such as substrate, microhabitat, shelter and food, as it happens with the Anthozoa, Gastro-poda, Bivalvia, Polychaeta, Pycnogonida, Maxillopoda, Malacostraca, Ofiuroidea, Zoantharia and Asteroidea (14). The sponge-zoanthid association (Cnidaria, Anthozoa, Zoantharia, suborder Macrocnemina) is widely distributed in tropical and subtropical waters (i.e. Pacific, Mediterranean; 15), from the intertidal zone down to the deep sea. These symbioses are common also in the Caribbean region, where two genera, *Parazoanthus* (4 species) and *Epizoanthus* (2 species), are associated to 14% of the total described sponges (close to 92 species; 16).

Studies related to sponge-zoanthid symbioses have been focused mainly on specificity rather than on preference. Specificity is defined by Lincoln *et al.* (17) as the state of being restricted to a given species. Other definitions indicate that it is the taxonomic range of hosts that can be used by a specific symbiont; the quality of being specific to a particular organism (on which or in which it lives) rather than organisms in general, or the host to symbiont ratios (18). Studies about specificity on sponge-zoanthid associations began with West (19), who quantified the relationship of *Parazoanthus* and *Epizoanthus* with their most common host sponges. Later, Crocker and Reiswig (20) inferred that *Parazoanthus* and *Epizoanthus* substrate specificity was “relatively high” (50% of zoanthids species are restricted to a single or a few host sponges). In a more recent, intensive and extensive study done in the Caribbean, Swain and Wulff (16) did not agree with the last statement after examining the pattern of specificity at multiple taxonomic levels. Most *Parazoanthus* and *Epizoanthus* appeared to have a low degree of specificity and were able to successfully associate themselves with many species of sponges, whereas sponges were highly specific to zoanthids (species accepted as partners); most of the sponge species are exclusively associated with a single zoanthid species and none of the hosts with more than two.

Currently it is known that the sponge-zoanthid association goes from diffuse to specialized. In the Caribbean region zoanthids colonize several different sponge orders and use many sponge species: 46 sponge species are colonized by *Parazoanthus swiftii*, 22 by *P. parasiticus*, 13 by *P. catenularis*, 8 by *P. puertoricense*, and 5 by *Epizoanthus cutressi* (16). *Epizoanthus* sp. nov. *sensu* Crocker and Reiswig (20) is the most specialized species, colonizing a single sponge genus (three *Plakortis* species). It is also known that new species combinations in the sponge-zoanthid symbioses may occur in nature depending on the island, depth, habitat studied and sampling effort (16). This fact may increase the known habitat amplitude for a par-

ticular zoanthid species, affecting the evaluation of any used resource (i.e. substratum) since more categories will have to be considered.

None of the previous authors have objectively evaluated preferences as the difference between the relative proportions of all used resources, and their availability (potential use) has not been measured. Mathematical indices, graphical methods, and statistical procedures (confidence intervals) have not been applied, nor has a particular variable of the host sponge been fully evaluated. In consequence, the following question remains: is there a zoanthid preference for any particular resource provided by the sponges? In our study, by using an approach different to the traditional specificity approach, we tried to test whether sponge morphology is an important trait in zoanthid habitat preference. That is based on Crocker and Reiswig’s (20) hypothesis that sponge morphology and structure (spicules) may be a characteristic favouring zoanthid larvae colonization. We assume that if zoanthid preference really exists in nature, this preference will become evident even working at higher taxonomic levels (genera) as it has happened in other studies on biological patterns.

Parazoanthus and *Epizoanthus* differ in a variety of ecological characteristics: 1. The degree of intimacy with the host; while adult colonies of *Parazoanthus* live on or beneath the host sponge surface, in *Epizoanthus* the colony is embedded in the sponge pinacoderm (only tentacles remain exposed). The degree of intimacy has been negatively correlated with the number of host sponge species, being lower for *Epizoanthus* (16). 2. The volume and size of expanded polyps as well as the tentacle number are lower in *Epizoanthus* than in *Parazoanthus*. Those variations in characteristics could be mechanisms to avoid competition via niche differentiation (different host species) as suggested by Swain and Wulff (16). Testing preference by using a particular and important resource such as sponge morphology will give us new clues related to this hypothesis, and can be useful in revealing the underlying ecological and evolutionary factors in the symbiosis.

Materials and methods

The quantification was carried out at the oceanic island of San Andres, which is part of an extensive archipelago in the Colombian Caribbean (13° 19' - 13° 31' N, 81° 20' - 81° 25' W; Zea 1987; Díaz *et al.* 1995). “Blue Wall” and “La Piscinita” sites were selected in order to maximize the chances of finding sponge-zoanthid associations and to cover the highest possible number of habitats (windward

and leeward sides, respectively) and microhabitats within areas containing a high coral reef development based on richness and coverage within a depth range of 5 to 30 m (Figure 1).

The geomorphologic profile of Blue Wall is characterized by a reef flat starting at 5 m in depth and composed of dispersed coral colonies down to 10 m; this terrace ends in a deep slope at 300 m off the SE coast, dominated by corals (*Diploria* sp., *Millepora* sp., and *Porites* sp.) and sponges (21, 22). In contrast “La Piscinita” or “Poxhole” is a well developed fringing reef, with a fossil coral reef terrace at 4 m in depth, and a high coral diversity and cover down to 20 m in depth, where the slope starts (dominated by *Montastraea* sp. and *Agaricia* sp.) (21). In San Andres, 89 sponges (22) and five zoanthids have been reported (23), with the exception of *Epizoanthus* sp. nov.

Data Sampling

In each study area, 12 haphazard transects (50 x 1 m) were set with a rope in the most diverse sites. Two transects per depth were quantified, parallel to the coast, separated 10 m away. The sampling was done every five meters between 5 to 30 m depth. Total diving effort was of approximately 1,968 min (five trained divers). All of the sponges and the presence/absence of *Zoantharia* (*Parazoanthus* and *Epizoanthus*) within transects (50 m²) were recorded. Sponges were recorded and classified according to their shape, following categories described in Bell and Barnes (24) with some minor modifications, shown here in parentheses: cup, tubular, encrusting (0-1 cm in thickness), globular (including massive types), and branching (including arborescent types). Sponge taxonomy was not studied in this project, but some interactions were recorded in a videotape.

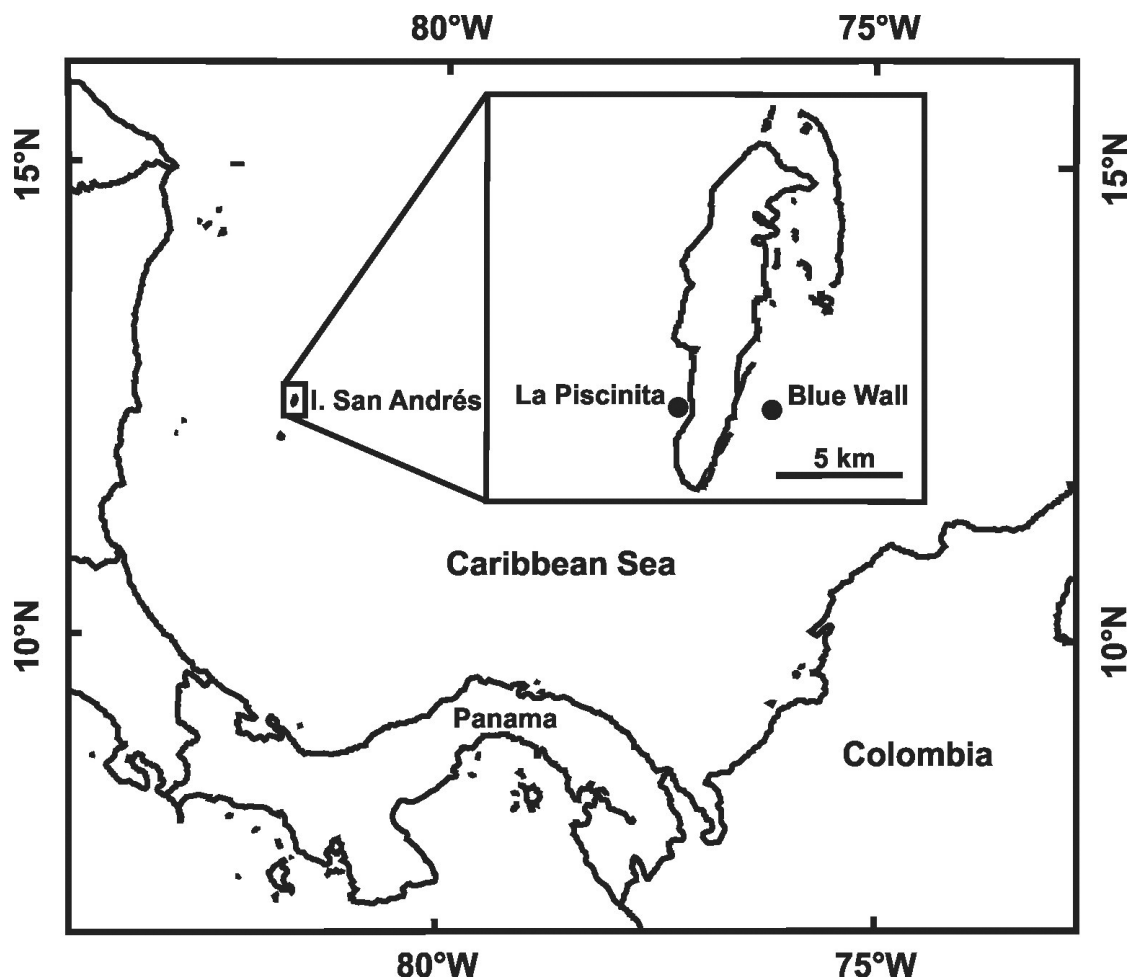


Figure 1. Location of San Andres Island in the Colombian Caribbean and the two study areas: the “Blue Wall” reef slope and “La Piscinita” fringing reef. Modified from López and Zea (54).

The cup-shaped sponges were identified by an inverted cone shape, a terminal oscule with a diameter greater than its base, and a single vertical projection. Tubular sponges have one or more cylindrical elongations with a diameter smaller or equal to the oscule located in the apical region, and projected from a common base. The encrusting sponges cover the substrate without a defined shape (25). Globular sponges have wide bases, soft texture, thickness, compact consistence, and can have a defined shape. Branching sponges have elongated forms, a small base, and branch diameter relatively constant (25), (Figure 2).

Sponges were also classified according to their mechanical resistance into compressible, elastic and fragile. We

deduced these categories from the study by Chanas and Pawlik (26) on sponge mechanical strength. Compressible sponges were defined as those that return to their initial state after removing the pressure force applied in opposite directions by finger compression without suffering structural damage (27), (Figure 2). Elastic ones are able to recover their original shape after a tension force has been applied pulling away any of the sponge edges with two fingers (27). Fragile sponges are susceptible to fragmentation when pressure and tension forces are applied simultaneously (27). In this case a small portion at the sponge's edge was compressed and pulled simultaneously to record whether it would fragment easily (Figure 2). External forces were applied using the thumb and index fingers.

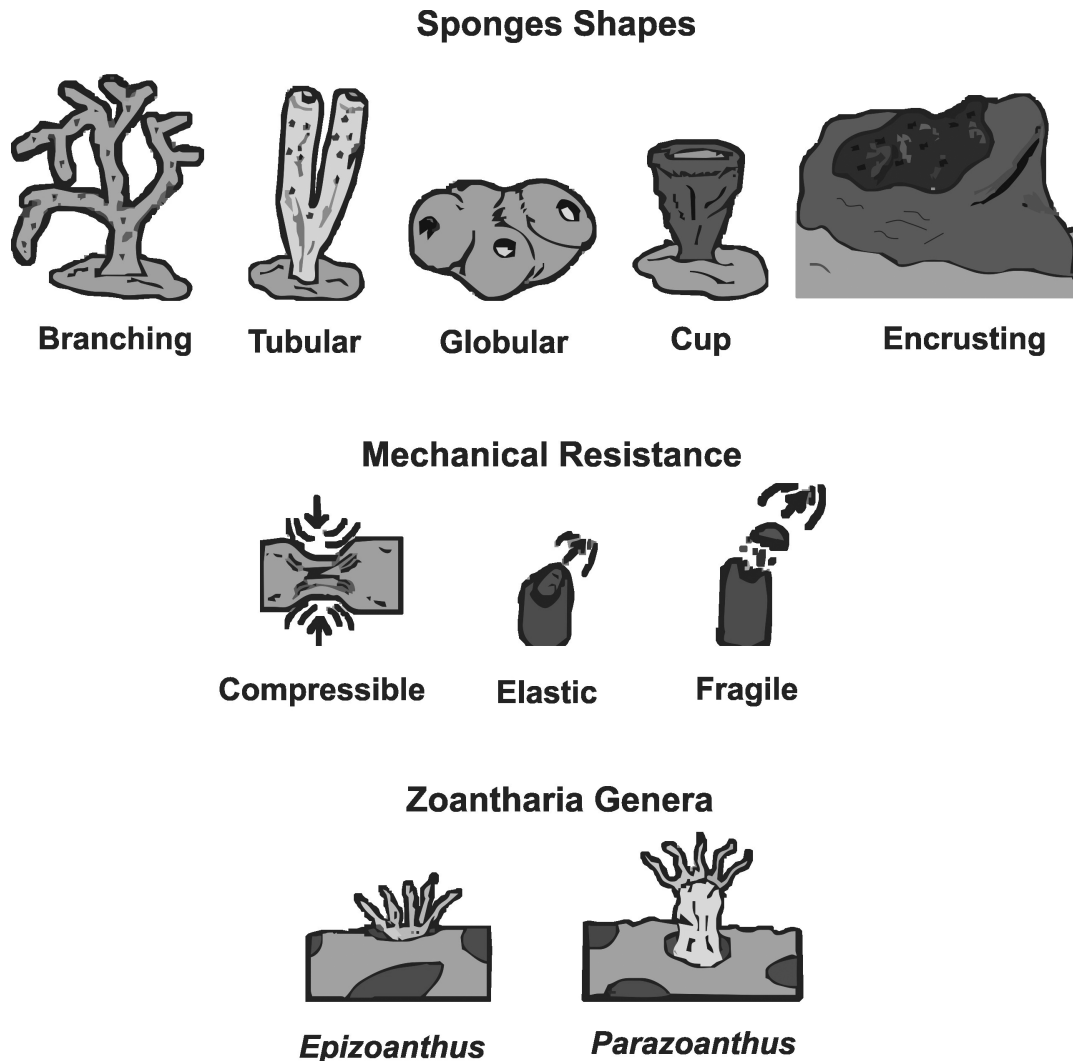


Figure 2. Sponge shape (encrusting, tubular, globular, cup and branching) and mechanical resistance categories (compressible, elastic and fragile) employed to quantify the presence/absence of the zoanthid genera *Epizoanthus* (embedded in sponge pinacoderm) and *Parazoanthus* (on sponge surface).

Parazoanthus and *Epizoanthus* genera were identified *in situ* using descriptions made by Crocker (28) and West (19), and a taxonomic key developed for San Andres Island (30). In the Caribbean Region there are four species of *Parazoanthus* reported: *P. parasiticus*, *P. puertoricense*, *P. swiftii*, and *P. catenularis*; and two species of *Epizoanthus*: *E. cutressi* and *Epizoanthus* sp. nov. (16), the latter being the only one not reported previously in the study area.

Data analysis

Data on habitat preference were analyzed for each genus independently using HaviStat© v. 1.0, a computer application designed to carry out all the procedures indicated below (30). The χ^2 and *G* tests were used to test the null hypothesis that resource use (host sponge shape) occurs in accordance to their availability considering all habitats simultaneously (sponges).

The niche amplitude indices of Colwell and Futuyma (31) and Hurlbert (32) were applied to infer whether the sponges were used asymmetrically. To determine which sponge shape is preferred by zoanthids, the indices of Latino and Beltzer (33), Jacob (34), Ivlev (35), Manly *et al.* (36)/Chesson (37) were applied (“/” meaning similar indices). To identify which types of sponges were used by zoanthids and to corroborate preferences, the Bonferroni 95%-confidence intervals were used (38). It is important to clarify that these indices were unable to show habitat use while confidence intervals did. In accordance to Hall *et al.* (39) a resource or habitat is considered unused when the studied organism is not found often or frequently, or when the computed index value falls below an arbitrary criterion established by the author. A graphical analysis to contrast the sponge availability (total sponges sampled) with zoanthid use (category frequency) was done following Yu and Lee (40).

Results

From the total 1,068 sponges investigated, 109 were associated with Zoantharia (10.2 %). Out of those 109 sponges with the association, 85 were associated with *Parazoanthus* (78 % of the total symbioses) and 24 with *Epizoanthus* (22 %).

Parazoanthus and *Epizoanthus* frequencies were dependent on both sponge shape (*Parazoanthus* $\chi^2 = 110.6$, *df* = 4, *p* < 0.001, *n* = 85; *G* = 96.7, *df* = 4, *p* < 0.001, *n* = 85; *Epizoanthus* $\chi^2 = 36.4$, *df* = 4, *p* < 0.001, *n* = 24; *G* = 24.0,

df = 4, *p* < 0.001, *n* = 24) and mechanical resistance (*Parazoanthus* $\chi^2 = 64.8$, *df* = 2, *p* < 0.001, *n* = 48; *G* = 43.4, *df* = 2, *p* < 0.001, *n* = 48; *Epizoanthus* $\chi^2 = 33.3$, *df* = 2, *p* < 0.001, *n* = 38; *G* = 27.6, *df* = 2, *p* < 0.001, *n* = 38). According to the four indices, *Parazoanthus* preferred encrusting and branching sponges, while *Epizoanthus* only preferred branching sponges. Both genera preferred fragile and compressible sponges. However, the Bonferroni confidence intervals indicated that *Parazoanthus* used branching and compressible sponges, but preferred encrusting and fragile ones, while *Epizoanthus* showed an inverse pattern; it used encrusting and fragile sponges but preferred branching and compressible sponges (Table 1).

When the total number of sponges sampled (available or potentially colonised by zoanthids) were independently contrasted with the *Parazoanthus* and *Epizoanthus* colony frequencies by using graphs, *Parazoanthus* showed preference for encrusting and branching shapes, while *Epizoanthus* only for branching; both genera preferred compressible and fragile sponges (Figure 3). The niche breadth indices revealed that both shape and mechanical resistance were not exploited or uniformly used by zoanthids.

Discussion

The results indicate that both zoanthid genera use the sponge shape and mechanical resistance categories asymmetrically; *Parazoanthus* prefers encrusting and fragile sponges and *Epizoanthus* branching and compressible ones.

Shape

The differences between genera in sponge shape preference could be explained by the possible feeding strategies used by each genus according to its location on the host (41) or intimacy level (16). *Parazoanthus* species are passive filter feeders and autotrophic, while *Epizoanthus* could be considered an active filter feeders that take advantage of the host filtration system without generating their own water flow.

Species of the genus *Parazoanthus* live on top or beneath the host sponge surface and prefer encrusting sponges, a sponge shape that allows covering more surface area in comparison with other sponge shapes, and thus maximizing the sponge organic matter uptake through gravitational sedimentation. Rubenstein and Koehl (43) indicated that some zoanthids could be considered as passive filter feeders and consequently *Parazoanthus* may benefit from the

Table 1. Preference for sponge shape and mechanical resistance by each genera, *Epizoanthus* (a) and *Parazoanthus* (b). The results of the Bonferroni 95 %-confidence intervals are presented (c); ranges for each category are omitted. The Latino and Beltzer (33), Jacob (34), Ivlev (35), Manly *et al.* (36)/ Chesson (37) indices are shown. Preference appears in bold font, no use in normal font, and use is underlined and marked with an asterisk (*).

<i>Epizoanthus</i>									
a)	Shape					Mechanical Resistance			Indices Criteria
Preference Index	Cup	Tubular	Encrusting	Globular	Branching	Compressible	Elastic	Fragile	
Latino and Beltzer,1999	0	0.2	0.3	0.1	0.7	0.6	0.2	0.5	> 0.3 = preference
II)Jacob, 1974	-1	-0.4	0	-0.6	0.8	0.6	-0.7	0.4	> 0 = preference
Ivlev, 1961	-1	-0.3	0	-0.5	0.6	0.5	-0.4	0.4	> 0 = preference
a-Manly, 1972 / Chesson, 1978	0	0.1	0.2	0.1	0.7	0.5	0.1	0.4	> 0.5 = preference

<i>Parazoanthus</i>									
b)	Shape					Mechanical Resistance			Indices Criteria
Preference Index	Cup	Tubular	Encrusting	Globular	Branching	Compressible	Elastic	Fragile	
Latino and Beltzer,1999	0	0.1	0.6	0.2	0.5	0.4	0.2	0.8	> 0.3 = preference
II)Jacob, 1974	-1	-0.8	0.7	-0.3	0.4	0.4	-0.7	0.7	> 0 = preference
Ivlev, 1961	-1	-0.8	0.5	-0.3	0.3	0.3	-0.4	0.7	> 0 = preference
a-Manly, 1972 / Chesson, 1978	0	0	0.6	0.1	0.3	0.3	0.1	0.7	> 0.5 = preference

Bonferroni Confidence Intervals									
c)	Shape					Mechanical Resistance			Intervals Criteria
Dependent Variable	Cup	Tubular	Encrusting	Globular	Branching	Compressible	Elastic	Fragile	
<i>Epizoanthus</i>	0.01	<u>0.36*</u>	<u>0.15*</u>	0.35	0.12	0.18	0.75	<u>0.07*</u>	Within intervals = use > superior interval = preference < inferior interval = no use
<i>Parazoanthus</i>	0.01	0.36	0.15	0.35	<u>0.12*</u>	<u>0.18*</u>	0.75	0.07	

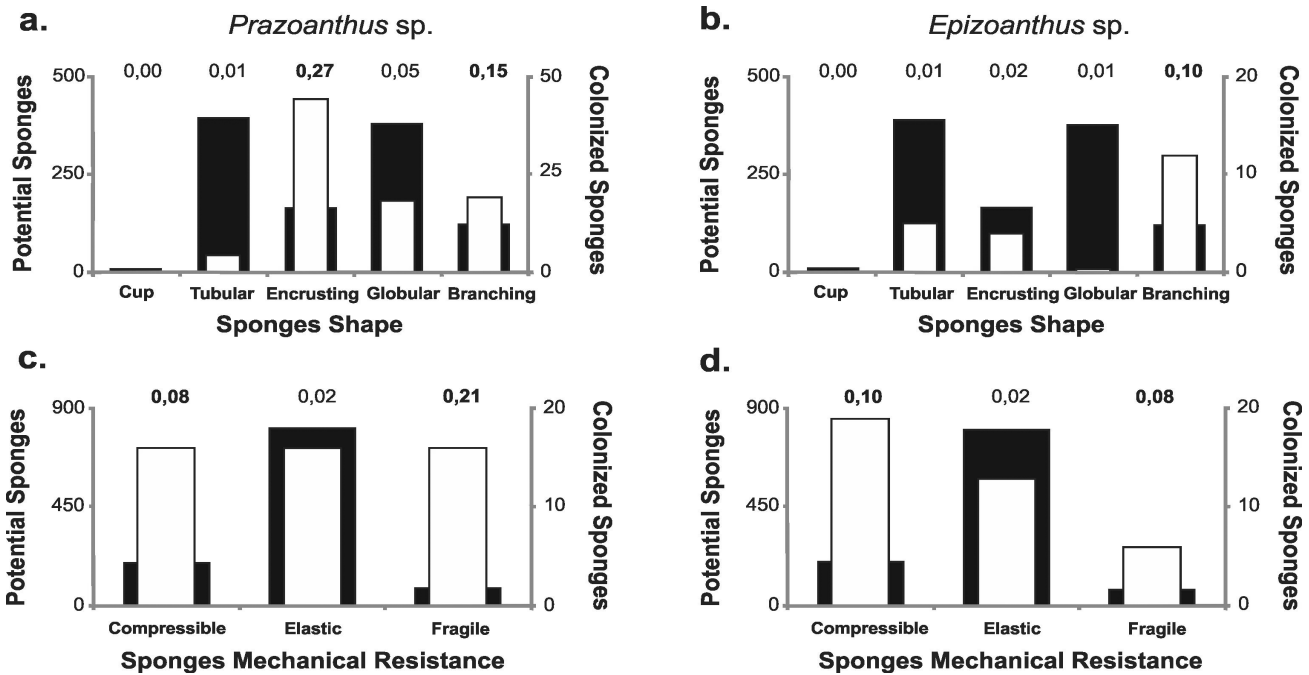


Figure 3. Total sponges sampled (potentially colonised sponges) contrasted with the number of sponges actually colonized by the genera *Parazoanthus* (a,c) and *Epizoanthus* (b,d) according to each shape and mechanical resistance category. Number of sponges not colonized are in black and effectively colonized sponges are in white. The ratio between potential and effective use is indicated above the bars. We consider that there is preference when: the proportions of use are > 0.10 in histograms “a” and “c”; > 0.03 in “b” and 0.06 in “d”.

sponge shape. They are unable to generate water flow by themselves as it has been observed in other marine species, depending largely on the natural water currents to bring exogenous food within the range of their tentacles. It is possible that large polyps and higher tentacle numbers in *Parazoanthus* (16) besides the strategy of covering 75% to 100% of the host sponge surface (*P. swiftii*, 16) are adaptations to maximize rainfall capture, predation, and at the same time light uptake.

It is also well documented that encrusting shapes of benthic organisms maximize the obtainment of light. *Parazoanthus parasiticus*, *Parazoanthus catenularis* and *Epizoanthus cutressi* have zooxanthellae (*Symbiodinium* spp., 19) but it is unknown if they are obtained from the parental colony (incorporated via the gametes or larvae formation) or from the water column. Swain and Wulff (16) found that sponges that host zooxanthellae are nearly exclusively associated with zoanthids species that host endosymbiont zooxanthellae too, suggesting a shared strategy for maximizing exposure to sunlight (16). As a consequence, the encrusting shape (maximum superficial area covered) of host sponges will improve the photosynthetic activity of the zoanthid symbiotic algae and the capture of organic matter. Although most encrusting sponge species are often

overtopped and shaded, the most abundant genus in the study area - *Cliona* (**Table 2**) is frequently found under high light exposure conditions and associated to *P. parasiticus*. In the sea anemones *Bunodeopsis globulifera* and *Bunodeopsis antilliensis* the superficial area and accessory structures are good examples of how to maximize the uptake of both precipitated organic matter and light (44, 45).

The listed associations are based on: the sponge morphologies reported and described by Zea (22) for San Andres Island, the relative cover of sponges recorded in 56 sampling stations during 1992-1997 (Zea S., Pers. Com.), unpublished sponge frequency data (sponge presence/location; Zea S., Pers. Com.), the zoanthids reported by Acosta *et al.* (23) in San Andres Island (Colombian Caribbean), and the sponge-zoanthid association reported in the Caribbean by Swain and Wulff (16).

On the other hand, *Epizoanthus* polyps which are embedded in the sponge pinacoderm (19) may take advantage of the water flow generated by the sponge (13), by intercepting transported organic matter (by direct impact of particles; 43, 41), as has been proposed for some symbiotic filter feeding polychaetes (*Sabellidae* sp.).

Table 2. Potential sponge-zoanthid associations within the study area.

Sponge species	Cover	Frequency	Shape	Mechanical Resistance	Associated Zoantharia species
<i>Cliona varians</i>	9.6	11	Encrusting	Fragile	<i>Parazoanthus parasiticus</i>
<i>Cliona aprica</i>	5.1	5	Encrusting	Compressible	<i>Parazoanthus parasiticus</i>
<i>Cliona delitrix</i>	1.2	9	Encrusting	Compressible, elastic	<i>Parazoanthus parasiticus</i>
<i>Niphates digitalis</i>	1.0	8	Tubular, cup	Compressible, elastic	<i>Parazoanthus parasiticus</i>
<i>Callyspongia vaginalis</i>	0.7	7	Tubular, cup	Compressible, elastic	<i>Parazoanthus parasiticus</i>
<i>Spirastrella coccinea</i>	0.3	3	Encrusting	Compressible, elastic	<i>Parazoanthus parasiticus</i>
<i>Niphates erecta</i>	0.1	1	Branching, encrusting	Compressible, elastic	<i>Parazoanthus parasiticus</i>
<i>Neopetrosia rosariensis</i>	0.5	14	Encrusting, tubular	Compressible	<i>Parazoanthus parasiticus</i>
<i>Parazoanthus catenularis</i>					
<i>Svenzea zeai</i>	1.1	8	Encrusting, globular, tubular	Fragile	<i>Parazoanthus puertoricense</i>
<i>Agelas conifera</i>	0.7	11	Branching, globular, tubular	Compressible, elastic	<i>Parazoanthus puertoricense</i>
<i>Agelas sceptrum</i>	0.1	1	Branching	Compressible, elastic	<i>Parazoanthus puertoricense</i>
<i>Agelas dispar</i>	1.5	18	Branching, globular, cup	Compressible, elastic	<i>Parazoanthus puertoricense</i>
<i>Parazoanthus swiftii</i>					
<i>Ectyoplasia ferox</i>	0.6	10	Branching, globular, tubular	Fragile	<i>Parazoanthus swiftii</i>
<i>Agelas clathrodes</i>	0.4	4	Globular	Compressible, elastic	<i>Parazoanthus swiftii</i>
<i>Iotrochota birotulata</i>	0.1	1	Branching, globular, tubular	Compressible, elastic	<i>Parazoanthus swiftii</i>
<i>Topsentia ophiraphidites</i>	0.1	1	Branching, globular, tubular	Fragile	<i>Parazoanthus swiftii</i>
<i>Xestospongia muta</i>	1.1	7	Tubular, cup	Fragile	<i>Parazoanthus catenularis</i> <i>Epizoanthus cutressi</i>
<i>Cribrochalina vasculum</i>	0.5	5	Branching, cup	Compressible, elastic	<i>Parazoanthus catenularis</i>
<i>Epizoanthus cutressi</i>					
<i>Petrosia pellasarca</i>	0.2	2	Encrusting (fan)	Fragile	<i>Parazoanthus catenularis</i>
<i>Neopetrosia subtriangularis</i>	0.1	1	Branching	Compressible	<i>Parazoanthus catenularis</i>

Kaandorp (46) suggested that the branching shape in any organism will increase the surface area in contact with the water column, partly explaining the relative higher nutrient uptake. In consequence for branching sponges, a higher number of incurrent channels in relation with their environment will maximize the filtration rate, particularly if the nutrient diffusion coefficient is dependent on water flow (47). The hypothesis that *Epizoanthus* may benefit from the host flow due to its higher degree of intimacy could also help to explain the low number of host sponge species associated to this genus, found by Swain and Wulff (16).

Mechanical resistance

Mechanical resistance, as well as other physical characteristics of sponges (shape and color) result from the influence of several environmental conditions (48) such as current, turbidity (organic matter and light), and settlement substrate type. Resistance is also provided by spicules and proteins, which depending on their composition and concentration determine the sponge matrix structure and its tensile strength.

The preference for fragile and compressible sponges is difficult to explain due to the lack of studies quantifying mechanical resistance and explaining how a particular matrix structure can be modified due to the presence of a symbiont. For example, histological studies have shown the building up of a thick network of spongin (by lophocytes) when cirripedes settled in the osculum of *Ircinia fasciculata*, as well as a massive proliferation of microscleres and an increase of fibrogenesis in *Geodia cydonium* colonized by polychaetes (49, 50). In the sponge-zoanthid associations, the sponge *Calcifibrospongia actinostromarioides* is able to physically react to zoanthids by reorganizing its own skeletal elements to form a cyst (50).

The sponge matrix structure could be an important factor for the selective settlement (larvae chemotaxis) and the development of the zoanthids. Two mechanisms explain the actual establishment of zoanthid-sponge associations, through larval settlement and direct contact (grafting), where portions of a zoanthid colony already infesting a sponge migrate between adjacent hosts, as in the case of *P. swiftii* (28). It has been assumed that sponge-zoanthid interactions could start, as in other benthic cnidarians, with: 1. the planktonic larvae guided to potential substrates by chemical signals (51), 2. the selection and establishment on an adequate substrate (in the case of zoanthids with

obligate symbiosis with sponges) (16), 3. the metamorphosis to polyp stage (52), and finally, 4. the colony growth through asexual reproduction (budding; 51, 50). However, these processes have never been observed (53), or even worse, the planktonic larvae which have not been well described for *Parazoanthus* and *Epizoanthus* might not be identical.

According to Crocker and Reiswig (20) the megascleras silica spicules that project on the surface of *Iotrochota birotulata* penetrate the polyp mesoglea of *Parazoanthus swiftii* and could be used as anchoring structures in the colonization process. After reviewing the work of Zea (22) who described 89 Colombian Caribbean sponges in detail, we conclude that the higher megascleras spicule frequency is found on fragile sponges (28 %; including also most encrusting shapes), followed by compressible (26 %) species, and finally in elastic (19 %) sponges. This trait besides the three-dimensional spicule organization could explain the selective colonization of *Parazoanthus* on fragile sponges and of *Epizoanthus* on compressible sponges. The importance of the sponge matrix structure (spicule composition, concentration, and organization) for zoanthid larvae colonization is an open research field that deserves further investigation in order to understand the underlying mechanism of the symbioses and the co-evolutionary race of both groups (finding a suitable sponge to colonize vs. avoiding or facilitating colonization).

Considering indirect evidence as the general sponge dominance (habitat availability) in San Andres Island (**Table 2**) and the sponge-zoanthid associations known for the Caribbean, it is possible to infer that *P. parasiticus* and *E. cutressi* are the most common zoanthids in the study area. This hypothesis was validated recently (November 2009) at the same study sites (San Andres) where sampling of both genera revealed relative frequencies of 86.6% and 75% of *P. parasiticus* and *E. cutressi*, respectively. The dominant sponge, *Cliona varians*, is one of the few having the shape and mechanical resistance (encrusting and fragile, respectively) appropriate for *P. parasiticus* (**Table 2**), and consequently *Cliona* should be preferentially colonized by this zoanthid that uses a wide range of sponges with different morphologies (**Table 2**). Also, according to Crocker and Reiswig (20), *Cliona* was one of the sponges most frequently colonized by *P. parasiticus* in Barbados.

On the other hand, the cover of *Cribrochalina vasculum* in the study area is small, although this small cover could offer the morphological characteristic required by *E. cutressi* (branching and compressible). As claimed by Crocker and Reiswig (20), this zoanthid is apparently re-

stricted to a few primary host sponge species as an acceptable settling surface. *Epizoanthus* sp. nov., however, had not been reported previously in San Andres, and its three single hosts (*Plakortis* spp.; 20) seem to be rare within the study area.

Given that *Parazoanthus* and *Epizoanthus* are using similar resources (encrusting and branching sponges, with fragile and compressible mechanical resistance), and recognizing that these taxa as other sessile organisms are substrate-limited, there is the possibility of past inter-specific competition under limiting host sponges conditions. The first evidence of competition was presented by West (19) for *Parazoanthus catenularis* and *Epizoanthus cutressi*, which colonize and compete for space on the same host sponge, *Xestospongia muta*. Later, Swain and Wulff (16) showed that these two species can also colonize *Cribrochalina dura* and *C. vasculatum*, that *P. catenularis* and *P. parasiticus* colonize *Neopetrosia proxima* and *Xestospongia rosariensis*, and *P. puertoricense* and *P. swiftii* colonize *Agelas dispar* and *A. sventres*, respectively. Only in *Xestospongia muta*, a simultaneous colonization of both genera has been reported. The current consequences of such past competition could be the divergence on host selection, settlement location and growth of the two zoanthid genera, and the differential strategies of food and energy obtainment. Our findings suggest that the preferences observed in shape and mechanical resistance could be a possible outcome of competition processes in the past. The persistence of their differences until present would allow the coexistence of both genera. According to Crocker and Reiswig (20) the difference in substrate preference could be an adaptation that contributes to the coexistences of both genera.

Further research to test habitat preference and to infer that sponge morphology influences the 'choice' of the zoanthids larvae will imply: 1. taxonomic information at the species level for sponges and zoanthids (difficult to achieve since at least 700 named sponge species are known), in order to distinguish patterns resulting from shared evolutionary history from those resulting from morphology per se; 2. to measure sponge cover instead of abundance (real habitat available to be colonized by larvae); 3. to quantify zoanthid larvae mortality (pre and post settlement); 4. to test the assumptions of potential sponge-zoanthids associations within the study area; 5. to verify the symbiotic associations; and 6. to analyze the relationships between shape, mechanical resistance and the sponge skeletal properties (matrix structure) to find out which is the factor that most influences the association patterns.

Conclusions

In conclusion, results suggest that sponge morphology, that is shape and mechanical resistance, is an important factor in habitat selection by *Parazoanthus* and *Epizoanthus*. The use of similar resources by both genera raises the possibility of an inter-generic competition occurring in the past (niche differentiation and evolution); while differential habitat preference may be allowing the coexistence of both genera in the present. These results are a general approach to explain the nature and functionality of the sponge-zoanthid association and the first step to clarify which are the resources that drive the association. Future studies must investigate these patterns of morphological preferences at the species level for both sponges and zoanthids.

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Conflict of interest

The authors state that results presented in this article do not involve conflict of interests.

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