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Influence of sponge morphology on the composition of the polychaete associated fauna from Rocas Atoll, northeast Brazil

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Abstract The relationships between the morphology of sponges and variables describing their harbored polychaete fauna were analyzed along Rocas, the only known South Atlantic Atoll, together with the location on host and feeding habits. The identification and quantification of all the associated organisms highlighted the dominance of polychaetes. The adults of the symbiotic species *Haplosyllis spongicola* were the most dominant sponge endobionts. However, both juveniles and epitokes (reproductive individuals) of *H. spongicola* were also found, suggesting that this species completes its life cycle inside the host. Polychaete density was significantly greater in lobate sponges than in massive and encrusting forms. Conversely, the highly specific symbiotic mode of life of *H. spongicola* species seems to play a major role in structuring the composition of the polychaete fauna in relation to sponge morphotypes along Rocas Atoll.

Keywords Polychaetes · Morphology · Sponges · Porifera · Rocas Atoll · Brazil

Introduction

Polychaetes commonly establish close associations with sponges, because the presence of holes, grooves, chambers, and channels provides a good shelter and

often food resources as a supply of organic matter to their associates (Cinar and Ergen 1998; Martin and Britayev 1998). Polychaetes may inhabit all sponge available space: they may live attached to the sponge surface (epifauna) or within their canals and choanosome (infauna) (Pérès 1982; Cinar and Ergen 1998). The relationships between polychaetes and sponges can be fortuitous (i.e. the involved organisms may inhabit a variety of substrata and the presence of the “host” is irrelevant), but they may also involve a high degree of specificity, giving rise to either commensalistic or parasitic relationships (Martin and Britayev 1998).

Sponges having a complex gross morphological structure often harbor a more abundant fauna (Frith 1976; Cuartas and Excoffon 1993; Klitgaard 1998), while changes in sponge growth (i.e. linked to environmental factors) seem to play a major role in structuring its composition (Peattie and Hoare 1981; Duarte and Nalesso 1996). No direct relationship between associated fauna and sponge morphology has been previously reported. However, the differences in abundance and number of species appear to be a function of biotic interactions (viz. predation, competition, allelochemical attractants, and defenses) among the fauna within each sponge species (Koukouras et al. 1992) [allelochemical = biologically active metabolite (Muricy et al. 1993)].

Both amphipods and ophiuroids have been previously reported as dominant sponge-associated groups along the Brazilian coast (Duarte and Nalesso 1996; Ribeiro, unpublished data). A recent study on the taxonomy of Rocas Atoll sponge mentioned the existence of close associations between many sponge species and polychaetes (Moraes, personal communication). The aim of the present investigation is thus to compare the species composition, species richness, diversity, and density of the polychaete fauna associated with sponges with different morphological features along Rocas Atoll. Additionally, their location and feeding habits were analyzed.

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Material and methods

Study site

Rocas Atoll ($3^{\circ}51'S$, $33^{\circ}49'W$) is located 266 km off the northeast Brazilian coast (Fig. 1). It is the only known atoll of the South Atlantic and an inhabited biological reserve. The reef rim has an elliptical shape, 3.5 km long (west–east oriented) and 2.5 km wide, which is built by encrusting coralline red algae, vermetid gastropods, and encrusting foraminiferans. A great number of intertidal pools occur along the reef area. They vary greatly in size and shape, ranging from a few centimeters to 4 m deep. A flat surface covered by sediment is located in the central part of the atoll. On the west side, there are two sand cays, Farol and Cemiterio Islands. A semi-enclosed lagoon is located in the northeast area of the atoll (Gherardi 1996; Netto et al. 1999).

Sampling and sample processing

Twenty six sponge samples were collected by snorkeling from 18 November to 8 December 1999 at ten stations along Rocas Atoll, located in the intertidal pools and lagoon (Fig. 1). The sponges were picked off the reef flat with a knife and quickly placed into plastic bags in order to prevent the loss of associated fauna. In the field, the samples were anesthetized by hypertonic magnesium chloride solution. After 2 h, they were fixed in 4% formalin. In the laboratory, they were transferred to 70% ethanol. The volume of each sponge was determined by water displacement. The sponges were identified to species level. According to taxonomic laboratory observations and the taxonomic description of the species (Moraes 2000), the morphological types of sponges were classified as lobate, encrusting, and massive [definitions: lobate = having rounded projections; massive = large, compact structure without definable shape; encrusting = thin, sheet-like coating of the substrate (Boury-Esnault and Ruetzler 1997)] (Fig. 2). All the associated fauna was sorted and quantified. Polychaete individuals were identified to the lowest taxonomic level and their location on the host was recorded. All polychaete specimens collected were deposited in the National Museum, Rio de Janeiro state (MNRJ).

Data analysis

Biological variables such as density (ind/cm^3), dominance, species richness (total number of species), diversity (Shannon-Weaner), and evenness (Pielou) were calculated for each sample. A Kruskal-Wallis test was applied to analyze the significance of differences in biological variables among morphological types of sponges. The statistical package SYSTAT 7.0 was used for data analysis.

Fig. 1 Location of Rocas Atoll. Sampling stations are identified by numbers: 1 Barreta Falsa pool; 2 Tiny pool; 3 Cemitério pool; 4 Salão pool; 5 Tartarugas pool; 6 Ancoras pool; 7 Rocas pool; 8 Lagoon; 9 Reef Rim Crack; 10 Farol pool. [From Netto et al. (1999) with modifications]

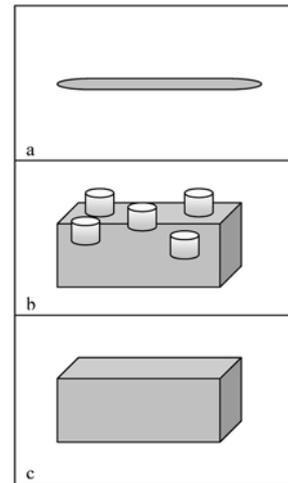
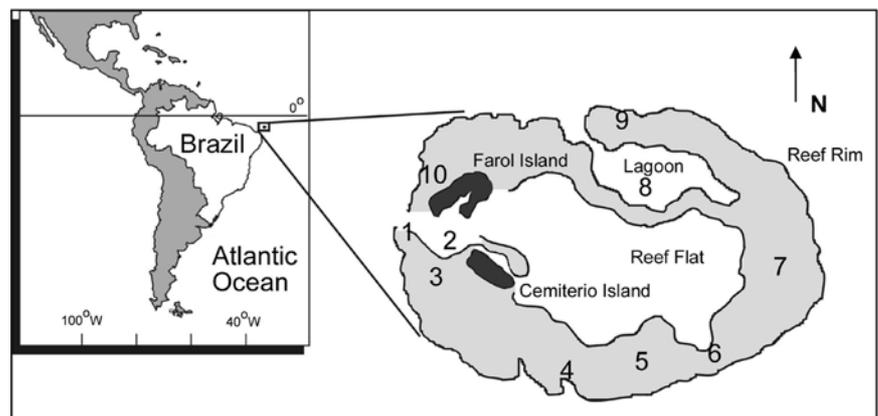


Fig. 2 Sponge morphological types: **a** encrusting; **b** lobate; **c** massive. [From Boury-Esnault and Ruetzler (1997) with modifications]

In order to verify the similarity between the polychaete fauna of different sponge shapes, a Bray Curtis distance index [data transformed to $\log(x+1)$] and a UPGMA cluster analysis were applied. In the analysis of feeding habitats of the polychaetes, trophic guilds proposed by Fauchald and Jumars (1979) were employed with some modifications (the taxa *Syllis* sp. b is a carnivore motile non-jawed).

Results

Thirteen sponge species belonging to Demospongiae were examined. According to shape, *Ectyoplasia ferox* (Duchassaing and Michelotti, 1864), *Plakortis* sp. 1, and *Scopalina ruetzleri* (Wiedenmayer, 1977) were classified as encrusting (Fig. 2a); *Aiolochoxia crassa* (Hyatt, 1875), *Amphimedon compressa* (Duchassaing and Michelotti, 1864), *Amphimedon viridis* Duchassaing and Michelotti, 1864, *Aplysina* sp., and *Ircinia felix* (Duchassaing and Michelotti, 1864) were classified as lobate (Fig. 2b); and *Agelas clathrodes* (Schmidt, 1870), *Agelas dispar* Duchassaing and Michelotti, 1864, *Chondrosia collectrix* Schmidt, 1870, *Plakortis* sp. 2, and *Topsentia ophiraph-*

idites (de Laubenfels, 1954) were classified as massive (Fig. 2c). Associated invertebrates included seven major taxonomic groups (class and above) comprising 7,344 individuals, recorded on and inside a total of 1,465 cm³ of sponge. Polychaetes represented 96% of total individuals of the total associated fauna, showing a clear dominance over crustaceans, ophiuroids, foraminiferans, vermetid gastropods, sipunculans, and sponges. Crustaceans were common by number of individuals on the encrusting sponge *Plakortis* sp. 1, and the massive sponges *A. dispar* and *Plakortis* sp. 1 sheltered a great number of ophiuroids and sipunculans, respectively. The highest density of total associated fauna was recorded on the lobate sponge *Aplysina* sp. (60.3 ind/cm³) whereas the massive form *A. dispar* sheltered the greatest variety of groups (Table 1).

Sixteen polychaete taxa belonging to seven families were determined. Syllids were dominant in terms of both number of taxa and abundance. *Haplosyllis spongicola* (Grube, 1855) showed the highest infestation rate, found in 65% of sponges and representing 98% of the total associated polychaete fauna. This species reached 1,909 individuals per sponge host *A. crassa*. All the other polychaete species occurred in a very low density (i.e. 3 ind/cm³) when compared to *H. spongicola* (137 ind/cm³) in all sponges analyzed (Table 2). *H. spongicola* individuals were far more abundant in lobate than in massive and encrusting forms. All the eunicids (*Eunice* sp. a, *Eunice* sp. b), the nereidid *Nereis trifasciata* (Grube, 1878), the syllid *Syllis* sp. c, and the cirratulids were only found in lobate sponges, whereas the spionid *Aonides* sp. and the sabellid *Myxicola* sp. infested massive forms only. The highest densities found for the taxa Sabellidae and *Syllis* sp. b among the different sponge types were found in encrusting forms. The presence of some other taxa, like the syllid *Branchiosyllis oculata* (Ehlers, 1887) and the serpulid *Filograna* sp., was not related to any specific sponge growth form (Table 2).

Lobate sponges showed a significantly greater density of polychaetes than massive and encrusting ones and they also harbored the richest polychaete fauna. Massive sponges tended to have higher diversity than encrusting and lobate forms and encrusting sponges tended to have higher evenness than the other forms (Fig. 3). Polychaete density varied significantly between sponge morphotypes (Kruskal-Wallis, $H = 13.51$, $p < 0.05$).

Juveniles, males, and female epitokes [adult reproductive worms showing traces of stolon formation (schizogamy)], and adults (nonreproductive) of *H. spongicola* were found inside the sponges. In some cases, this species also exhibited the same coloration as its sponge hosts, being purple when associated with *A. crassa*; red in *Aplysina* sp., *A. viridis*, and *A. compressa*, and white in *T. ophiraphidites*. Many individuals of this species were found with projected pharynges on the sponge hosts.

Three major groups were identified in the cluster analysis, suggesting a gradient of *H. spongicola* dominance within the sponge morphotypes. Group I was mainly composed of lobate sponges, showing the highest dominance values for this symbiont species (100% to 94%). Massive and encrusting forms were more representative in groups II and III, accounting for minimum and also null values of dominance of *H. spongicola* (33% to 0%), respectively (Fig. 4).

The polychaete fauna associated to sponges were grouped into five trophic guilds (Table 3). The carnivores (i.e. syllids, eunicids, and nereidids) were dominant (91%). Syllids, especially *H. spongicola*, were found in all sponge available space whereas nereidids were only found on the surface. The eunicids occurred inside the sponges, with their prostomium protruding from the sponge choanosome. The filter-feeders and surface deposit-feeders (i.e. sabellids, serpulids, spionids, and cirratulids) occupied the same position as eunicids. In general, cirratulids and spionids were found in associa-

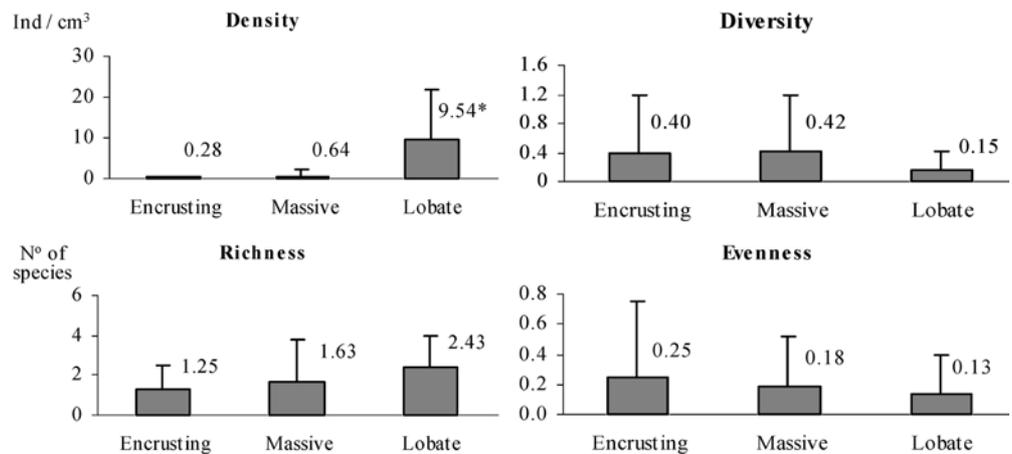
Table 1 List of sponges including (*n*) number of samples, shape and total density (ind/cm³) of the total associated fauna present in sponges from Rocas Atoll (*Cru* Crustacea; *Oph* Ophiuroidea; *For* Foraminifera; *VG* Vermetid gastropoda; *Sip* Sipuncula; *Spo* Sponge; *Poly* Polychaeta)

Sponges	<i>n</i>	Shape	Density								
			(ind/cm ³)								
			<i>Cru</i>	<i>Oph</i>	<i>For</i>	<i>VG</i>	<i>Sip</i>	<i>Spo</i>	<i>Poly</i>	Total	
<i>Agelas clatrodus</i> (Schmidt, 1870)	1	Massive	0.09		0.03						0.12
<i>Agelas dispar</i> Duchassaing and Michelotti, 1864	1	Massive	0.19	0.36	0.07		0.02	0.01	0.22		0.87
<i>Aiolochroia crassa</i> (Hyatt, 1875)	3	Lobate	0.37		1.31	0.03			43.67		45.37
<i>Amphimedon viridis</i> Duchassaing and Michelotti, 1864	3	Lobate	0.05	0.11	0.01			0.01	11.46		11.64
<i>Amphimedon compressa</i> (Duchassaing and Michelotti, 1864)	3	Lobate	0.12				0.01		5.77		5.89
<i>Aplysina</i> sp.	3	Lobate	0.11		0.58	0.02			59.60		60.31
<i>Chondrosia collectrix</i> Schmidt, 1870	1	Massive									-
<i>Ectyoplasia ferox</i> (Duchassaing and Michelotti, 1864)	1	Encrusting									-
<i>Ircinia felix</i> (Duchassaing and Michelotti, 1864)	2	Lobate	0.02		0.10				13.05		13.17
<i>Plakortis</i> sp. 1	2	Encrusting	0.39						0.26		0.65
<i>Plakortis</i> sp. 2	3	Massive	0.35			0.05	0.41		0.02		0.83
<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)	1	Encrusting									-
<i>Topsentia ophiraphidites</i> (de Laubenfels, 1954)	2	Massive		0.09	0.01				4.86		4.95

Table 2 Density (ind/cm³) of polychaete taxa associated to encrusting, massive, and lobate sponge morphotypes from Rocas Atoll

	Encrusting	Massive	Lobate
SYLLIDAE			
<i>Haplosyllis spongicola</i> (Grube, 1855)	0.29	4.70	132.35
<i>Syllis</i> sp. a		0.04	0.05
<i>Syllis</i> sp. b	0.29	0.01	
<i>Syllis</i> sp. c			0.05
<i>Branchosyllis oculata</i> (Elhers, 1887)	0.29	0.16	0.40
Syllidae		0.01	0.07
EUNICIDAE			
<i>Eunice</i> sp. a			0.35
<i>Eunice</i> sp. b			0.06
Eunicidae			0.03
CIRRATULIDAE			
Cirratulidae			0.01
SABELLIDAE			
Sabellidae	0.13	0.02	0.06
<i>Myxicola</i> sp.		0.02	
SERPULIDAE			
<i>Filograna</i> sp.	0.14	0.11	0.01
Serpulidae			0.02
SPIONIDAE			
<i>Aonides</i> sp.		0.03	
NEREIDIDAE			
<i>Nereis trifasciata</i> (Grube, 1878)			0.09

Fig. 3 Biological variables of polychaete fauna plus standard error in encrusting, massive, and lobate sponges (*asterisk* indicates significant difference)



tion with sponge species that produced great quantities of mucus, such as *A. viridis* and *A. dispar*.

Discussion

The dominance of polychaetes in sponge assemblages throughout Rocas Atoll was an expected scenario. Many previous studies reported on the great abundance of this group within sponges (Frith 1976; Koukouras et al. 1985; Cuartas and Excoffon 1993; Duarte and Nalesso 1996; Klitgaard 1998). Polychaetes are often very abundant in coral reefs, as in many types of marine and estuarine habitats, largely due to their ability to adapt morphologically and reproductively to exploit these

environments (Glasby 2000). High densities of polychaetes in carbonate sediments from Rocas Atoll have also been recently reported (Netto 1999). However, this dominance mainly resulted from the occurrence of one species, *Haplosyllis spongicola*, which is a common and widespread sponge symbiont. This species presents an aggregate pattern of distribution (Martin and Britayev 1998), reaching 1,909 individuals per sponge host (present study data), and several evidences pointed to a probable parasitic relationship with its host sponges. Among them, its location inside the canals of the sponge aquiferous system and in the sponge tissues, and its feeding activity, in which it projects its pharynges to take sponge tissue, which it probably ingests. The fact that the worms exhibited the same coloration as their sponge

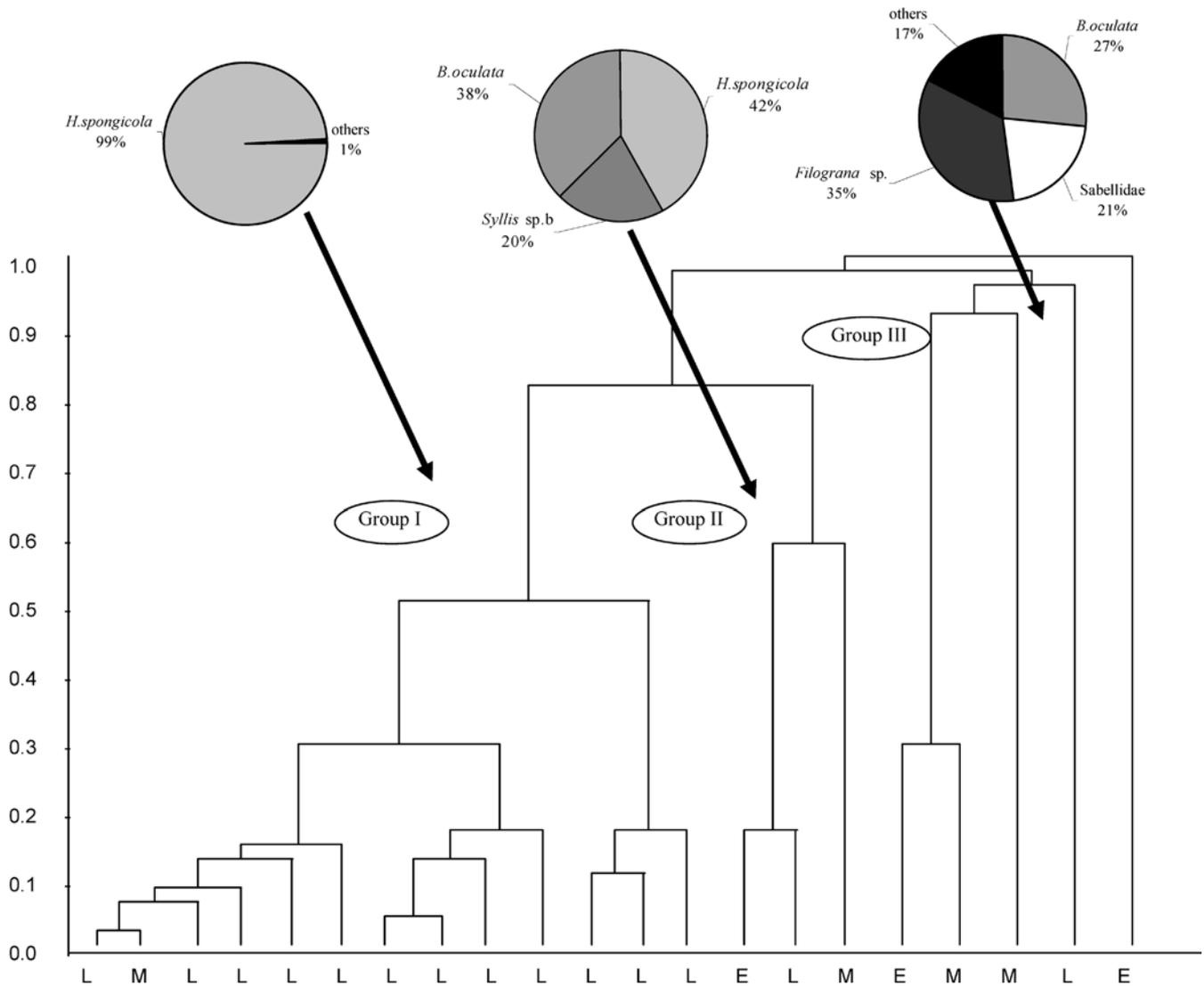


Fig. 4 Cluster analysis evidencing three main groups of polychaete fauna present in (*E*) encrusting, (*M*) massive, and (*L*) lobate sponges

hosts can also be an evidence of this feeding activity. These behavioral adaptations to the parasitic way of life of *H. spongicola* have been previously reported (Cuartas and Excoffon 1993; Klitgaard 1998; Martin and Britayev 1998; López et al. 2001).

The structure of the population of *H. spongicola* found in sponges from Rocas Atoll was composed of individuals of all life stages, including sexually mature adults (epitokes) and many juveniles. This observation suggests that the life cycle of *H. spongicola* occurs inside the host. In spite of this, we could not discard the existence of a phase outside (e.g. swimming stolons producing planktonic larvae), which may occur in a synchronized releasing of both male and female stolons, leading to gamete fertilization in the water column. Its

Table 3 Trophic guilds and location of polychaete taxa on sponges. *Sur* Surface; *Cha* channels. [After Fauchald and Jumars (1979)]

Taxa	Trophic guilds	Sur	Cha
<i>H. spongicola</i> , <i>B. oculata</i> and other Syllidae	Carnivore motile jawed	x	x
Eunicidae	Carnivore motile jawed		x
Nereididae	Carnivore motile jawed	x	
<i>Syllis</i> sp. b ^a	Carnivore motile non-jawed		x
Sabellidae, Serpulidae	Filter-feeding sessile tentaculate		x
Cirratulidae	Surface deposit-feeding motile tentaculate		x
Spionidae	Surface deposit-feeding discretely motile tentaculate		x

^a*Syllis* sp. b does not have a tooth in the muscular pharynge, so it is not a carnivore motile jawed, but a carnivore motile non-jawed)

strategy could be connected to a highly specific symbiotic mode of life. In the light of these data, there is something enabling *H. spongicola* to become competitively superior to other endobiotic species. López et al. (2001) mentioned the long-lasting taxonomic controversy of this species and supported the existence of a sibling or pseudo-sibling species complex being hidden under the name of *H. spongicola*. This statement could suggest the possible relationship between the presence of the species inside many different hosts and the existence of different *H. spongicola* morphotypes.

The population of *H. spongicola* seemed to play a major role in structuring the composition and abundance of the polychaete fauna. Lower densities of this parasitic species in massive and encrusting sponges can give place to a well-distributed polychaete assemblage, resulting in higher diversity and evenness indices. However, the differences in the sponges' growth form can also affect the structure of the polychaete community. The presence of *H. spongicola* apparently did not affect the sponges' growth rate nor did the sponges show abnormal morphologic structures in reaction to the massive presence of these worms. This same observation was also viewed by López et al. (2001) in the coral reef sponge *Cliona* sp. This sponge supported extremely high

densities of *H. spongicola* individuals without apparently causing a decrease in its growth rate or in its sexual and asexual reproductive activities. This same author also reported high infestation rates of *H. spongicola* in tropical aplysiniid sponges (*Aplysina corrugata*, *Aplysina fistularis*, and *Aplysina* sp.) and in the sponge *Ircinia felix* which are both considered here as lobate sponges. Although we could not record the growth rate of the sponges in the present work, we could not discard the possibility that these lobate sponges are able to grow faster than massive and encrusting, allowing them to better support higher densities of *H. spongicola* which is probably feeding on its host. The relationship between the other polychaete species that apparently occurs in a single sponge morphotype may be accidental as we could not determine how frequent these associations between the given species and the sponge form are.

Feeding guilds and location of polychaetes within sponges are other factors that can further define the nature of the interrelationships between the organisms (Martin and Britayev 1998). In this study, the presence of the carnivorous species *H. spongicola* in all sponges' space can also point to its parasitic way of life. The location and specific behavior of the taxa allowed us to suggest that the sponges probably provide habitat and

Table 4 Review of seven works about fauna assemblages from sponges, indicating the sponge species, sponge morphotypes data from references (*Morphotype*¹), sponge morphotypes considered in this study (*Morphotype*²), and density recorded from references

Reference	Sponge species	Morphotype ¹	Morphotype ²	No. ind/cm ³
Frith (1976)	<i>Hymeniacidon perleve</i>	Fistulose	Lobate	0.3
	<i>Mycale macilenta</i>	Fistulose	Lobate	0.2
	<i>Halichondria panicea</i>	Flatter, unbranched	Encrusting	0.2
	<i>Halichondria panicea</i>	Fistulose	Lobate	0.3
	<i>Halichondria panicea</i>	Widely spaced, branched	Lobate	0.2
	<i>Halichondria panicea</i>	Fragile, thinly branched	Encrusting	0.2
Peattie and Hoare (1981)	<i>Halichondria panicea</i>	Small, lobose	Lobate	19
	<i>Halichondria panicea</i>	Amorphous	Massive	15.5
	<i>Halichondria panicea</i>	Lamellar, ramifying	Lobate	15.3
	<i>Halichondria panicea</i>	Encrusting	Encrusting	2.1
	<i>Halichondria panicea</i>	Great, massive	Massive	1.8
Westinga and Hoetjes (1981)	<i>Spherospongia vesparia</i>	Solid, hemispherical to barrel shaped	Lobate	92.1
Koukouras et al. (1992)	<i>Agelas oroides</i>	Lobate	Lobate	16.7
	<i>Petrosia ficiformis</i>	Massive, lobate	Massive/Lobate	16.9
	<i>Ircinia variabilis</i>	Flattened or with long branches	Lobate	96.4
	<i>Aplysina aerophoba</i>	Lobate, massive	Massive/Lobate	91.5
Duarte and Nalesso (1996)	<i>Zygomycale parishii</i>	Globose	Massive	0.5
	<i>Zygomycale parishii</i>	Fistulose	Lobate	0.4
Cinar and Ergen (1998) ^a	<i>Sargotragus muscarum</i>	Complex and massive	Lobate	30.1
Klitgaard (1998)	<i>Geodia barreti</i>	Large, massive	Massive	0.3
	<i>Geodia macandrewii</i>	Large, massive	Massive	4.3
	<i>Geodia</i> sp.	Large, massive	Massive	1.2
	<i>Isops phlegraei</i>	Large, massive	Massive	4.4
	<i>Stryphnus ponderosus</i>	Large, massive	Massive	7.9
	<i>Thenea levis</i>	Sphere shaped or lump formed	Lobate	12.0
	<i>Thenea valdiviae</i>	Sphere shaped or lump formed	Lobate	9.7
	<i>Phakellia robusta</i>	Foliaceous or funnel shaped or ramified	Lobate	2.5
	<i>Phakellia rugosa</i>	Foliaceous or Funnel shaped or ramified	Lobate	1.6
	<i>Phakellia ventilabrum</i>	Foliaceous or funnel shaped or ramified	Lobate	1.1
	<i>Tragosia infundibiliformis</i>	Foliaceous or funnel shaped or ramified	Lobate	1.3

^aData of polychaete fauna only

enhance food supply. The position of filter feeders in the canals close to the sponge openings probably aids them in obtaining food from the waterflow created by the sponge (Ilan et al. 1994). Surface deposit-feeders might obtain food from the organic detritus accumulated on sponge canals and/or microorganisms that also live within the host. Klitgaard (1998) also pointed out the importance of sponge complexity enhancing food supply for the associates.

A clear relationship between faunal densities and sponge morphology was recorded. Lobate morphotypes, which have a more complex structure, showed significantly higher faunal densities. By comparing seven studies about fauna assemblage from sponges (Table 4), we could also demonstrate a direct relationship between sponge morphology and faunal densities. Fistulose, lamellar ramifying, lobate, or sphere-shaped morphotypes, which can be considered as complex-growth sponge forms (here as lobate), sheltered a denser fauna than flatter, unbranched, encrusting, and massive forms. The accumulation of organic detritus and sediment on the sponges seems to explain the abundance of associates on sponges with a complex gross morphological structure (Frith 1976). Although some authors have found that complex sponges supported the most individuals (per unit volume), it has been difficult to establish a clear relationship between density and complexity (Koukouras et al. 1992).

These present results show that although a more abundant polychaete fauna were present in complex gross morphological sponges, the highly specific symbiotic mode of life of *H. spongicola* species seems to play a major role in structuring the composition of the polychaete fauna in relation to sponge morphotypes along Rocas Atoll.

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