Macrofauna inhabiting the sponge Paraleucilla magna (Porifera: Calcarea) in Rio de Janeiro, Brazil

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Sponges (phylum Porifera) are important components of the benthic marine fauna known for their interactions with vertebrates and a large sort of invertebrates seeking for food, shelter or substrate for attachment. Studies on this subject, however, were restricted only to the macrofauna inhabiting sponges of the class Demospongiae. In the present work, we describe the macrofauna associated with a calcareous sponge in Brazil, Paraleucilla magna. Individuals of this allegedly nonnative species were monthly collected during one year in Rio de Janeiro (Brazil). Fifty taxa representing 10 animal phyla were found associated with P. magna. The most frequent and abundant taxa were Crustacea, Mollusca, Polychaeta and Bryozoa, while echinoderms, cnidarians, ascidians, nemerteans, platyhelminthes and sponges were less frequent or even rare and less abundant. Juveniles of several taxa and pregnant females of Crustacea were found associated with P. magna, but these associations were not exclusive. The macrofauna associated with P. magna did not present a clear seasonality, although it was possible to observe a change in the community composition alongside the year. The volume of the sponges was significantly related to the diversity index (H') and number of taxa, but not with evenness (J') and number of individuals. Our results show that P. magna is used as a substrate for attachment and/or shelter by its associates and that most of these associations are just opportunistic. The data presented here reiterate a previous proposal that sponges are important biodiversity reservoirs and that they should be seriously considered in conservation programmes.

Keywords: macrofauna, sponges, Paraleucilla magna, Rio de Janeiro, Brazil

Submitted 5 July 2011; accepted 10 January 2012; first published online 7 June 2012

INTRODUCTION

Sponges (phylum Porifera) have long been considered 'living hotels' due to the great diversity and abundance of other taxonomic groups that are often found in association with them (Pearse, 1950; Klitgaard, 1995; Ribeiro et al., 2003). These associations represent a wide range of ecological interactions, facultative or obligatory, that range from mutualism to parasitism; however, the exact nature of many associations remains unclear (Wulff, 2006). Because sponges have bodies composed of an intricate network of canals, associated organisms may find substrate and shelter inside them (Çinar et al., 2002; Huang et al., 2008). As sponges are important components of benthic communities and interact with a wide range of organisms (Wulff, 2006; Becerro, 2008), they are considered to be important reservoirs of marine biodiversity (Cerrano et al., 2006).

Previous studies of sponge-associated fauna have been carried out in the North Atlantic Ocean (Frith, 1976; Biernbaum, 1981; Peattie & Hoare, 1981; Klitgaard, 1995; Huang *et al.*, 2008; Fiore & Jutte, 2010), the Caribbean (Pearse, 1950; Villamizar & Laughlin, 1991), the Mediterranean (Rützler, 1976; Koukouras *et al.*, 1985, 1992, 1996; Ilan *et al.*, 1994; Cinar *et al.*, 2002), the Pacific Ocean

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1996; Ilan *et al.*, 1994; Çinar *et al.*, 2002), the Pacif

(Long, 1968; Magnino et al., 1999; Beaulieu, 2001; Skilleter et al., 2005; Cerrano et al., 2006) and the Indian Ocean (Abdo, 2007). Only three studies have been performed in the South Atlantic Ocean: one in Argentina (Cuartas & Excoffon, 1993) and two in Brazil (Duarte & Nalesso, 1996; Ribeiro et al., 2003). Other studies along the Brazilian coast have revealed associations between sponges and particular groups of organisms: gammarids and caprellids (Serejo, 1998), copepods (Bispo et al., 2006) and polychaetes (Neves & Omena, 2003). With the exception of two studies that focus on hexactinellid sponges (Beaulieu, 2001; Fiore & Jutte, 2010), all studies of sponge-associated fauna focus on the class Demospongiae. Only one study, conducted in Hampshire, England, has investigated the associated fauna of a calcareous sponge. This study, however, found no fauna associated with either Sycon ciliatum (Fabricius, 1780) or Grantia compressa (Fabricius, 1780) and did not describe any organisms found with Leucosolenia botryoides (Ellis & Solander, 1786) (Frith, 1976).

Paraleucilla magna Klautau et al., 2004 is a calcareous sponge found along the Brazilian coast (adjacent to the Rio de Janeiro, São Paulo and Santa Catarina States) and in the Mediterranean (along the southern coast of Italy and around Malta). In both regions, it is considered to be a nonnative species, although its origin is still unknown (Klautau et al., 2004; Longo et al., 2007; Zammit et al., 2009; Gravili et al., 2010). It lives attached to hard substrates in photophylous or sciaphylous conditions and in pristine or polluted

waters (Klautau et al., 2004; Longo et al., 2007; Gravili et al., 2010). This species has a leuconoid aquiferous system with a large atrial cavity and many canals that can be easily occupied by other organisms. In the original description of *P. magna*, crustaceans, echinoderms and polychaetes were described as associating with this species (Klautau et al., 2004); however, there has been no subsequent research on its associated fauna. Therefore, to gain knowledge about the associated macrofauna of calcareous sponges, we investigated the composition of macrofauna inhabiting *P. magna* over the course of one year. The objectives of this study were to: (1) describe the species composition of the associated macrofauna of *P. magna*; (2) investigate the influence of sponge volume on these associations; and (3) analyse the influence of seasonality on these associations.

MATERIALS AND METHODS

Sampling

Five specimens of P. magna (Figure 1B) were collected monthly throughout 2005 (except in February, when only four individuals were collected; and in April, when no collection occurred), totalling 54 specimens. All specimens were collected at Vermelha Beach $(22^{\circ}57'18''S-43^{\circ}09'42''W)$, in Rio de Janeiro, Brazil (Figure 1A: Lanna et al., 2007). Specimens were collected by snorkelling at 0-4 m depth and were removed from the substrate with a knife. While underwater, each specimen was bagged individually (to avoid the escape of associated organisms) and then fixed and preserved in 93% ethanol. At the laboratory, the volume of each sponge was calculated by liquid displacement in a graduated cylinder (see Ribeiro et al., 2003; Lanna et al., 2007). Sponge specimens were then carefully fragmented under a stereomicroscope to remove the macrofauna (>1 mm) that remained inside. Associated organisms of each sponge specimen were separated by morphotype within higher taxa and then identified to the lowest possible taxonomic level with the help of specialists.

Data analysis

We counted the total number of associated individuals and the total number of taxa to calculate species richness, frequency, abundance, density, diversity (H'), and Pielou's evenness (J')(Ludwig & Reynolds, 1988). To investigate whether the total volume of P. magna specimens collected each month (i.e. the sum volume of the five analysed individuals) could predict species richness, abundance, diversity and evenness, we performed a linear regression (Sokal & Rohlf, 1995). The values of species richness, frequency, abundance, density, diversity (H') and Pielou's evenness (J') obtained for each month were used as replicates to test whether these attributes of the associated fauna varied between the dry (April to September) and rainy (October to March) seasons. All data were tested for normality and homoscedasticity prior to performing analyses of variance (ANOVAs). Temporal patterns in the community of associated fauna were assessed by means of a principal component analysis (PCA), in which the dimensionality of 21 species (the number of species that occurred in more than one month) was reduced to only two components (latent variables) representing the primary temporal patterns of dominant species. As most species were

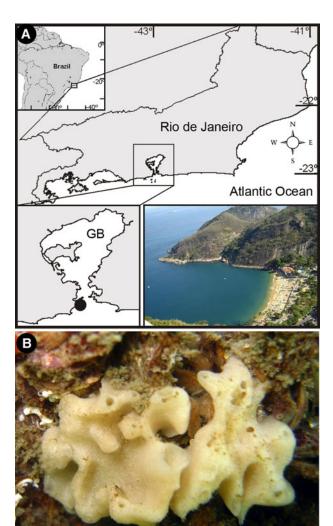


Fig. 1. (A) Map of the study area. Vermelha Beach is located at the entrance of the eutrophic Guanabara Bay (GB) (black dot at inferior left corner). Map source: DIVA-GIS, Vermelha Beach (photograph: F. Azevedo); (B) *in vivo* photograph of *Paraleucilla magna*.

2 cm

rare, and because many zeros were present in the data table (see Table 1), we applied a Hellinger transformation prior to analysis (see Legendre & Gallagher, 2001). PCA scores obtained for each month were used as replicates for the ANOVA to test whether these attributes of the associated fauna varied between the dry and rainy seasons (Jassby & Powell, 1990).

RESULTS

Associated macrofauna

A total of 349 individuals, representing 51 species and 10 phyla, were identified living in association with the 54 analysed specimens of P. magna (Table 1). The mean species richness of associated taxa was 11.9 species/month (± 4.4 : Table 2). Arthropoda (mostly Crustacea) showed the highest species richness (17 species); followed by Annelida, with 11 taxa of polychaetes; and Mollusca, with nine species (Table 1). The

Table 1. Variation of the number of taxa associated with Paraleucilla magna. Colonies of Hydrozoa were not quantified, and their presence is marked with "P". The total number of individuals/colonies for each taxon and month, and the total number of taxa of each phylum (within parentheses), are provided. (Por, Porifera; Cni, Cnidaria; Pla, Plathyhelminthes; Nem, Nematoda; Ann, Annelida; Art, Arthropoda; Mol, Mollusca; Bry, Bryozoa; Ech, Echinodermata; Asc, Ascidiacea). (*) indicates the presence of juveniles.

	Taxa	January	February	March	May	June	July	August	September	October	November	December	Total
Por (1)	Leucosolenia sp.	1	0	0	0	0	0	0	0	0	0	0	1
Cni (1)	Hydrozoa	О	P	0	0	P	0	P	0	0	P	0	
Pla (1)	Enchiridium evelinae (Marcus, 1949)	1	0	0	0	0	0	0	0	0	0	0	1
Nem (1)	Unidentified Nememtea	1	0	0	0	0	0	0	0	0	0	0	1
Ann (11)	Sabellidae sp.*	1	0	0	0	0	0	О	0	0	0	0	1
	Branchiomma luctuosum (Grube, 1869)	1	0	0	0	0	0	0	0	О	0	0	1
	Phyllodocidae	1	0	0	0	0	0	0	0	О	0	0	1
	Syllidae sp. 1	3	0	0	0	0	0	0	0	О	0	0	3
	Syllidae sp. 2	2	0	0	0	0	0	0	0	1	0	0	3
	Syllidae sp. 3	1	0	1	1	1	0	0	0	О	0	0	4
	Syllidae sp. 4	O	1	0	0	0	0	0	0	О	0	0	1
	Syllidae sp. 5	О	0	0	0	1	0	0	0	О	0	0	1
	Syllidae sp. 6	О	0	0	0	0	1	0	0	О	0	0	1
	Syllidae sp. 7	O	0	0	0	0	0	1	0	О	0	0	1
	Naineris setosa (Verrill, 1900)	О	0	0	0	0	0	0	0	О	0	1	1
Art (17)	Stenothoidae	1	О	0	2	0	16	6	7	3	21	2	58
	Melitidae sp.	O	0	0	0	0	0	2	0	О	1	0	3
	Quadrimaera quadrimana (Dana, 1852)	1	0	0	0	0	0	0	1	0	6	0	8
	Elasmopus pectenicrus (Bate, 1862)	6	0	1	2	1	2	0	0	О	0	3	15
	Dulichiella appendiculata (Say, 1818)	3	0	0	0	0	0	0	0	О	0	0	3
	Podoceridae sp.	O	0	0	0	0	0	О	1	0	0	5	6
	Corophiidae	O	0	0	0	0	0	0	0	О	1	0	1
	Cymadusa filosa (Savigny, 1816)	3	0	0	2	0	4	10	3	10	18	1	51
	Isopoda	O	0	0	0	0	0	О	0	1	0	0	1
	Carpias sp.	O	0	0	0	0	0	0	0	О	3	0	3
	Mithrax sp.*	O	0	0	0	0	0	2	0	О	0	0	2
	Epialtus bituberculatus (Milne Edwards, 1834)	О	0	0	0	0	0	1	0	0	0	0	1
	Micropanope nuttingi (Rathbun, 1898)	O	0	0	1	0	0	1	0	О	0	0	2
	Petrolisthes armatus (Gibbes, 1850)	O	0	0	0	0	0	0	0	О	1	0	1
	Pachycheles monilifer (Dana, 1852)	O	0	0	0	0	0	0	0	О	0	2	2
	Pachycheles laevidactylus (Ortmann, 1892)	O	0	0	0	2	5	10	9	4	3	2	35
	Pycnogonida sp.	2	0	0	0	0	0	О	0	0	0	0	2
Mol (9)	Bivalvia sp. 1	O	0	0	1	25	9	3	1	2	1	0	42
	Bivalvia sp. 2	O	0	0	1	0	0	0	0	О	0	0	1
	Bivalvia sp. 3	O	0	0	0	1	3	О	1	1	1	2	9
	Mytilidae sp.*	О	0	0	3	1	2	0	1	1	2	0	10
	Sphenia fragilis (Adams & Adams, 1854)	0	0	0	1	О	О	0	0	0	0	0	1
	Arca sp.	0	0	0	0	0	О	0	0	0	1	0	1
	Gastropoda sp.	0	0	0	0	0	0	0	0	O	1	0	1
	Calyptraeidae	1	0	1	О	О	1	0	1	0	3	0	7
	Crepidula sp.	0	0	1	1	0	0	0	0	0	0	0	2

November Ophiactis savignyi (Müller & Troschel, 1842) Amphipholis squamata (Delle Chiaje, 1828) Scrupocellaria aff. reptans (Linnaeus, 1758) ytechinus variegatus* (Lamarck, 1816) Ophiactis lymani (Ljungman, 1872) Botrylloides giganteum (Pérès, 1949) Bugula neritina (Linnaeus, 1758) Hippoporina sp. Number of specimens Ech (4) 3 Asc (3) Bry

Fable 1. Continued

species diversity of the total associated macrofauna was high (H' = 3), but the total evenness was low (J' = 0.4) (Table 2).

The most abundant higher taxa were Arthropoda (54%), Mollusca (21%) and Bryozoa (9%) (Figure 2), while the most frequent were Arthropoda, Annelida (Polychaeta), Mollusca and Bryozoa, present in 72.2%, 57.4%, 48.2% and 40.7% of sponges, respectively (Figure 3). Chordata (Ascidiacea), Cnidaria (Hydrozoa) and Echinodermata were found less frequently (present in 22.2%, 14.8% and 12.9% of sponges, respectively), while Platyhelminthes, Nemertea and Porifera were found in only 1.8% of specimens (Figure 3). The density of associated individuals was highest in November and June (3.1 and 2.8 individuals cm⁻³) and lowest in February and January (0.2 and 0.3 individual cm⁻³). This variation was not significantly different between the dry and rainy seasons (Table 3A).

Juvenile representatives of Crustacea (*Mithrax* sp.), Polychaeta (Sabellidae sp. and Syllidae spp.), Mollusca (Mytilidae sp.) and Echinodermata (*Lytechinus variegatus*) were found living associated with *P. magna*. In addition, pregnant crustacean females were also frequently observed.

Volume

Total sponge volume (i.e. the sum volume of sponges collected each month: Table 2) did not differ between seasons (Table 3B) but varied significantly with both species diversity (H') ($R^2 = 0.43$, df = 10, P = 0.027: Figure 4A) and the number of taxa (species richness) ($R^2 = 0.37$, df = 10, P = 0.04: Figure 4B), indicating that larger sponges contained a higher variety of taxa and a higher diversity of species. Nonetheless, regression analyses indicated that the total volume each month varied with neither the Pielou evenness index (J') ($R^2 = 0.04$, df = 10, P = 0.52: Figure 4C) nor the total number of associated individuals (abundance) ($R^2 = 0.03$, df = 10, P = 0.56: Figure 4D).

Seasonality

The periods of lowest and highest richness (February = 4; January = 20, respectively) coincided with the months of lowest and highest diversity (H') (February—H' = 1.4; January—H' = 2.7, respectively) (Table 2). Abundance (i.e. the number of associated individuals) was lowest in February (only three individuals), while the highest was in November (66 individuals) (Table 1; Figure 5). The evenness of associated macrofauna tended to be high, being highest in February and March (J' = 1.0) and lowest in June (J' = 0.6) (Table 2). None of these community descriptors differed significantly between the dry and rainy seasons (Table 3C-F).

Seasonal changes in the community of macrofauna associated with *P. magna* were analysed using biplots based on PCA (Figure 6A). The total amount of variation explained by the first two scores (corresponding to the first two principal components) was 56.9%. The PCA biplot did not show a clear seasonal difference between the dry and rainy seasons. Nevertheless, three groups of species were partially distinguished by the analysis:

Group A (formed mainly by the bryozoan *Scrupocellaria* aff. *reptans* (Linnaeus, 1758) and the ascidians *Didemnum* sp. 1 and *Bugula neritina* (Linnaeus, 1758)), which appeared between February and June;

					-							
	January	February	March	May	June	July	August	September	October	November	December	Year
Number of species	20	4	9	14	11	12	12	10	8	18	13	50
Number of specimens	38	3	12	28	42	47	38	26	23	66	26	349
Species diversity (H')	2.7	1.4	2.1	2.4	1.5	2.0	2.1	1.8	1.7	2.1	2.4	3.0
Evenness (J')	0.9	1.0	1.0	0.9	0.6	0.8	0.8	0.8	0.8	0.7	0.9	0.4
Total volume of sponges (cm ³)	115	18	8	11	15	38	52	24	12	21	67	381
Density (ind. cm ⁻³)	0.3	0.2	1.5	2.5	2.8	1.1	0.7	1.1	1.0	3.1	0.4	0.0

Table 2. Summary of the ecological data collected each month.

Group B (formed mainly by the mollusc Bivalvia sp. 1 and the crustaceans *Pachycheles laevidactylus* Ortmann, 1892 and *Cymadusa filosa* Savigny, 1816) that appeared from July to November;

Group C (formed mainly by the ophiuroid *Ophiactis lymani* Ljungman, 1872) comprised only one species and was found exclusively in January and December.

Scores of the first component (PC1), which account for 38.7% of the variation, did not differ significantly between the dry and rainy seasons (Figure 6B; Table 4A). However, the scores of the second component (PC2), which account for 18.2% of the variation, were significantly different between these seasons (Figure 6C; Table 4B).

DISCUSSION

Paraleucilla magna exhibited moderate-to-low richness of associated macrofauna (51 species) relative to all other sponge species investigated to date (48 Demospongiae and two Hexactinellida), the latter of which yielded an average of 95.5 associated taxa (\pm 162.2), with a minimum of two and a maximum of 809 taxa (e.g. Westinga & Hoetjes, 1981; Villamizar & Laughlin, 1991; Cuartas & Excoffon, 1993; Klitgaard, 1995; Koukouras et al., 1996; Betancourt-Lozano et al., 1998; Magnino et al., 1999; Çinar et al., 2002; Neves

Ascidiacea Others
3,%
Echinodermata 4%

Polychaeta 5%

Bryozoa 9%

Arthropoda 54%

Fig. 2. Proportion of higher taxa associated with Paraleucilla magna.

& Omena, 2003; Ribeiro et al., 2003; Abdo, 2007; Huang et al., 2008). In P. magna, Crustacea was the most abundantly represented group of associated organisms (54%), followed by Mollusca (21%) and Bryozoa (9%). In other studied sponges, Crustacea was also one of the two most abundantly represented groups, being present in 80% of the sponge species examined, followed by Polychaeta (60%) and Echinodermata (24%). Molluscs were the second most abundant group in P. magna (21%); however, this is not a common occurrence, as they have been identified as a dominant group in only a few species of sponges (8% of those examined so far: Long, 1968; Peattie & Hoare, 1981; Klitgaard, 1995; Koukouras et al., 1996). The same pattern occurs with Bryozoa, which was the third most abundant taxon in P. magna but is not considered to be among the two most abundant organisms in other studied sponges. However, bryozoans were the second most dominant group (12.8% of the total number of taxa) found in demosponges of the Faroe Islands, north-eastern Atlantic (Klitgaard, 1995) and, as in the present study, Klitgaard (1995) also found that most of the bryozoans were attached to the outer surface of the sponges. Associations between sponges and bryozoans may be related to the fact that sponges may provide suitable substrate to bryozoans in habitats of otherwise limited substrate availability, as noted by Klitgaard (1995).

A study of the associated fauna of the demosponge *Mycale microsigmatosa* Arndt, 1927 was performed at the same location of the present study (Ribeiro *et al.*, 2003). Both *P. magna* and *M. microsigmatosa* exhibit associated

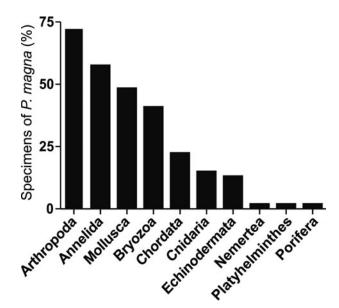


Fig. 3. Percentage of Paraleucilla magna specimens hosting each higher taxon.

Table 3. Summary of the analysis of variance testing the influence of seasonality (dry versus rainy seasons) on community descriptors during the study period.

	df	Sum Sq	Mean Sq	F value	Pr(>F)
(A) Density	of asso	ciated individu	als		
Season	1	0.552	0.5520	0.4402	0.5236
Residuals	9	11.285	1.2539		
(B) Sponge	volume	:			
Season	1	404.600	404.6000	0.3559	0.5655
Residuals	9	10232.800	1137.0000		
(C) Species	richnes	ss			
Season	1	0.109	0.1091	0.0049	0.9455
Residuals	9	198.800	22.0889		
(D) Numbe	r of ass	ociated individ	uals		
Season	1	186.380	186.3800	0.5943	0.4605
Residuals	9	2822.530	313.6200		
(E) Diversit	y (H')				
Season	1	0.032	0.03292	0.1850	0.6773
Residuals	9	1.601	0.17797		
(F) Evennes	ss				
Season	1	0.025	0.02579	2.6065	0.1409
Residuals	9	0.089	0.00989		

macrofauna of similar species richness (51 and 75 species, respectively) and composition. However, the differences observed in taxonomic composition between these two sympatric species can be explained by the different sample sizes of each study: in the present study, we analysed 54 specimens of P. magna, while Ribeiro et al. (2003) analysed 19 specimens of P. magna and P. microsigmatosa. Species diversity was the same between P. magna and P. microsigmatosa (P = 3), while evenness was lower in P. magna (P = 0.4, versus P = 0.7 for P microsigmatosa). The difference in evenness values between both species may be also due to sampling differences: in the

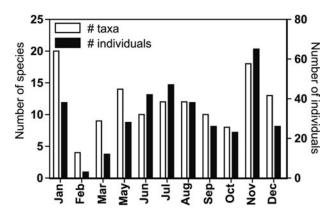


Fig. 4. Monthly variation in the number of species and individuals associated with *Paraleucilla magna*.

present work several collections throughout the year were made, while Ribeiro et al. (2003) made only one collection. The most striking difference between these two species is in the total number of associated individuals (abundance): P. magna was associated with 349 individuals (0.9 individual cm⁻³), while M. microsigmatosa was associated with 2235 (13 individuals cm⁻³). If we consider that both sponges have the same type of aquiferous system (leuconoid), we could expect similar internal canals and, consequently, similar associated macrofauna. Nonetheless, in fact, the atrium of P. magna is larger than that of M. microsigmatosa, and whereas P. magna is massive, M. microsigmatosa is an incrustant sponge. In addition, the external surface of P. magna is full of folds, while M. microsigmatosa has a smoother surface. Despite these morphological characteristics that seem to characterize P. magna as a better host, M. microsigmatosa is host to more associated organisms. A possible explanation for this difference in macrofauna abundance is the presence of chemicals that might reduce predation in

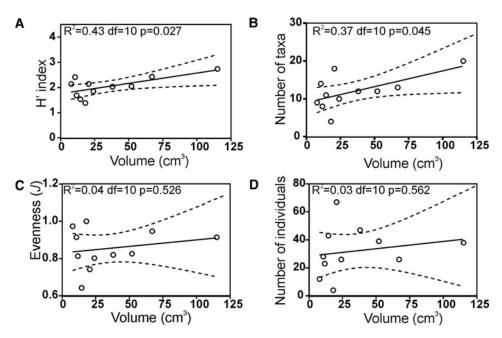


Fig. 5. Quantitative analyses of the macrofauna associated with *Paraleucilla magna*. Linear regression between sponge volume and (A) species diversity (H'); (B) number of taxa; (C) evenness (J'); and (D) number of individuals. The dotted line indicates the 95% confidence intervals.

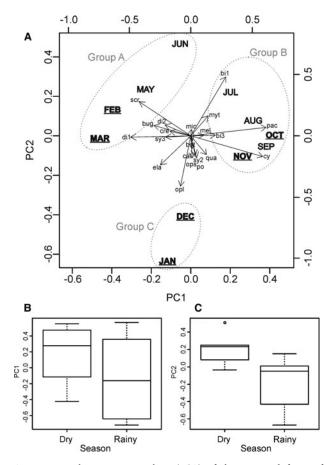


Fig. 6. Principal component analysis (PCA) of the associated fauna of Paraleucilla magna. (A) A biplot representation of the PCA showing both observations (months) and variables (species) in the same graph. The left and bottom axes use the unity for observations, while the top and right axes are graduated according to the first two principal components of the original variables. PC1 accounts for 38.7% of the total variation, while PC2 accounts for 18.2%. Months are represented by upper case letters (those of the rainy season are underlined) and species are represented by small characters (bi1, Bivalvia sp. 1; bi3, Bivalvia sp. 3; bot, Botrylloides giganteum; bug, Bugula neritina; cal, Calyptraeidae; cre, Crepidula sp.; cym, Cymadusa filosa; di1, Didemnum sp. 1; di2, Didemnum sp. 2; ela, Elasmopus ectenicrus; mel, Melitidae sp.; mic, Micropanope nuttingi; myt, Mytilidae sp.; opl, Ophiactis lymani; ops, Ophiactis savignyi; pac, Pachycheles laevidactylus; pod, Podoceridae sp.; qua, Quadrimaera quadrimana; scr, Scrupocellaria aff. reptans; sy2, Syllidae sp. 2; sy3, Syllidae sp.); (B & C) Box plots of the scores of (B) the first principal component (PC1) and (C) the second principal component (PC2) in the dry and rainy seasons. Each box displays the median, upper and lower quartiles of the distribution of sponge volume per month. Box whiskers represent the maximum and minimum range, while empty circles show outliers.

Table 4. Summary of the analysis of variance testing the influence of the two main principal components on the seasonality (dry versus rainy seasons) of the associated fauna during the study period. (Significance codes:* - 0.05).

	df	Sum Sq	Mean Sq	F value	Pr(>F)
(A) PC1					
Spp.*season	1	0.2126	0.2126	0.9401	0.3576
Residuals	9	2.0353	0.2261		
(B) PC2					
Spp.*season	1	0.3972	0.3972	5.4382	0.0446*
Residuals	9	0.6573	0.0730		

M. microsigmatosa and, consequently, provide more protection for its associated macrofauna. Although this hypothesis has not been tested, M. microsigmatosa does produce a series of compounds, some of which inhibit microorganism proliferation (Compagnone et al., 1999). The potential importance of sponge allelochemicals in influencing the composition and abundance of associated fauna has already been pointed out (Koukouras et al., 1992; Skilleter et al., 2005). A good example can be found in the work of Betancourt-Lozano et al. (1998), which describes a significant relationship between inquilinism and the antibiosis activity of Aplysina fistularis (Pallas, 1766) in Mexico.

Paraleucilla magna shares with M. microsigmatosa at least four species, two of which (the ophiuroids Amphipholis squamata and Ophiactis savignyi) occur commonly in other sponge species (Table 5). Although echinoderms have been found in only 12.9% of the analysed specimens of P. magna, they (particularly Ophiuroidea) are commonly found in demosponges (Wendt et al., 1985; Duarte & Nalesso, 1996; Betancourt-Lozano et al., 1998; Ribeiro et al., 2003; Abdo, 2007) and other benthic organisms, such as bryozoans (Morgado & Tanaka, 2001). Associations of Ophiactis savigny and O. lymani with marine organisms are apparently common. For example, both species have been described as common epifauna on the tubes of the polychaete Phyllochaetopterus socialis Claparède, 1869 (Nalesso et al., 1995), on the octocoral Carijoa riisei (Duchassaing & Michelotti, 1860) (Neves et al., 2007), and on algae (Mladenov & Emson, 1988). The frequent association of these ophiuroid species with varied taxa (algae, polychaetes, corals and sponges) may indicate that these associations (including with P. magna) are only occasional or opportunistic. These ophiuroids may seek out these organisms only for protection or food (Klitgaard, 1995).

The volume of P. magna was positively related only to species diversity and number of taxa (richness). These relationships have already been observed in other sponge species: S. foetidus (for species diversity) and M. microsigmatosa, M. angulosa, S. foetidus and Spheciospongia vesparium (Lamarck, 1815) (for richness) (Westinga & Hoetjes, 1981; Duarte & Nalesso, 1996; Çinar et al., 2002; Ribeiro et al., 2003). In P. magna, higher volumes can reflect a diverse array of microhabitats inside the sponge, such as more and larger folds, or larger atria and oscula, which could accommodate larger organisms and, consequently, a higher diversity of taxa. On the other hand, no relationship between volume and number of individuals was observed in P. magna, and this relationship has also not been observed in several demosponge species (four from the Aegean Sea: Koukouras et al., 1992; and two from Australia: Skilleter et al., 2005). In P. magna, large volumes might provide habitat for other species that could then compete with the fauna that live in smaller sponges. The fact that we found associated organisms in a great variety of sponge volumes (from 0.3 cm³ to 37 cm³) suggests that this species is rapidly colonized by organisms in the

In the present study, no seasonal variation in community descriptors of the fauna associated with P. magna (species richness, number of individuals, species diversity (H') and evenness index (J')) was detected. This lack of seasonal variation can be explained, in part, by the relationship of some of these descriptors to sponge volume (as described above). As neither sponge volume nor the community descriptors

Table 5. Species associated with Paraleucilla magna that have also been identified in association with other sponge species. 1, Mycale microsigmatosa (Rio de Janeiro — Brazil; Ribeiro et al., 2003); 2, Mycale angulosa (São Paulo — Brazil; Duarte & Nalesso, 1996); 3, Dysidea fragilis (in Rio de Janeiro — Brazil; Serejo, 1998); 4, Topsentia sp. (southeastern United States; Fiore & Jutte, 2010); 5, Ircinia campana (south-eastern United States; Fiore & Jutte, 2010); 6, Sarcotragus foetidus (Turkish Aegean coast; Çinar et al., 2002); 7, Aplysina lacunosa (Venezuelan Caribbean; Villamizar & Laughlin, 1991); 8, Sarcotragus fasciculatus (North Aegean Sea; Koukouras et al., 1985); 9, Sidonops corticostylifera (Rio de Janeiro — Brazil; Clavico et al., 2006); 10, Halichondria panicea (Menai Strait — UK; Peattie & Hoare, 1981); 11, Ircinia strobilina (Bimini — Bahamas; Pearse, 1950); 12, Geodia macandrewii (Faroe Islands; Klitgaard, 1995).

Associated species	1	2	3	4	5	6	7	8	9	10	11	12
Elasmopus pectenicrus	x											
Quadrimaera quadrimana			X									
Dulichiella appendiculata			x	x	x							
Halosydnella brasiliensis	x											
Amphipholis squamata	x	X						x		X		x
Ophiactis lymani		X										
Ophiactis savignyi	x	x				x	x		x		x	

exhibit variation between the dry and rainy seasons (see Table 2), the absence of any seasonal trend could be expected.

Although the PCA biplot (Figure 6A) suggests no seasonal variation between the dry and rainy seasons, the second component (PC2) scores differed significantly between seasons. This latter result indicates that some environmental change (in features such as salinity, temperature or food availability) might influence the composition of the associated fauna community. However, the causes of variation explained by the first component (PC1) are unknown and not likely to be correlated with season. On the other hand, we observed three groups of species that occupied *P. magna* in temporal succession (Groups A, B and C). The establishment of these groups may reflect the life cycle of the associated organisms.

We frequently found pregnant crustacean females and juveniles of several taxa (molluscs, crustaceans, echinoderms and polychaetes) inhabiting *P. magna*, that probably used their host as a temporary shelter during vulnerable periods of their life cycle (i.e. reproductive or juvenile stages). This kind of relationship can be characterized as opportunistic. Ribeiro *et al.* (2003) and Abdo (2007) also found pregnant females, juveniles or reproductively active individuals associated with *M. microsigmatosa* and two *Haliclona* species in Brazil and Australia, respectively.

These findings suggest that sponges may be important shelters during some stages of the life cycle of many invertebrates, enhancing survival. All of these aspects regarding the role of sponges in the community reiterate a previous proposal (Cerrano *et al.*, 2006): namely that sponges are important reservoirs of biodiversity and that the phylum Porifera should be seriously considered in conservation programmes.

ACKNOWLEDGEMENTS

We thank the taxonomy specialists for helping us with identifications of the associated fauna: Luciana Muguet (Bryozoa), Cléo Oliveira (Mollusca), Juliana Bahia (Platyhelminthes), Carlos Renato R. Ventura and Fernanda Viana (Echinodermata), Daniela Barbosa (Ascidiacea), Paulo Paiva (Polychaeta) and Tereza G. Silva (Crustacea). We thank Baslavi Condor and Paulo Paiva for their help in data analysis

and the anonymous referees for their suggestions that improved the quality of the manuscript. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) (E-26/111.541/2008), and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq—480368/2008 2; CNPq/PIBIC—480368/2008 2) for grants and fellowships during this project.

REFERENCES

Abdo D.A. (2007) Endofauna differences between two temperate marine sponges (Demospongiae; Haplosclerida; Chalinidae) from south-west Australia. *Marine Biology* 152, 845–854.

Beaulieu S.E. (2001) Life on glass houses: sponge stalk communities in the deep sea. *Marine Biology* 138, 803–817.

Becerro M.A. (2008) Quantitative trends in sponge ecology research. *Marine Ecology* 29, 167–177.

Betancourt-Lozano M., Gonzalez-Farias F., Gonzalez-Acosta B., Garcia-Gasca A. and Bastida-Zavala J.R. (1998) Variation of antimicrobial activity of the sponge *Aplysina fistularis* (Pallas, 1766) and its relation to associated fauna. *Journal of Experimental Marine Biology and Ecology* 223, 1–18.

Biernbaum C.K. (1981) Seasonal changes in the amphipod fauna of *Microciona prolifera* (Ellis and Solander) (Porifera, Demospongia) and associated sponges in a shallow salt marsh creek. *Estuaries* 4, 85–96.

Bispo R., Johnsson R. and Neves E. (2006) A new species of *Asterocheres* (Copepoda, Siphonostomatoida, Asterocheridae) associated to *Placospongia cristata* Boury-Esnault (Porifera) in Bahia State, Brazil. *Zootaxa* 1351, 23–34.

Cerrano C., Calcinai B., Pinca S. and Bavestrello G. (2006) Reef sponges as host of biodiversity: cases from North Sulawesi. In Suzuki Y., Nakamori T., Hidaka M., Kayanne H., Casareto B.E., Nadao K., Yamano H. and Tsuchiya M. (eds) 10th International Coral Reef Symposium Proceedings, Okinawa, 28 June-2 July 2006. Functional roles of sponges in coral reefs. Tokyo: Japanese Coral Reef Society, pp. 208-213

Çinar M.E., Katagan T., Ergen Z. and Sezgin M. (2002) Zoobenthos inhabiting Sarcotragus muscarum (Porifera: Demospongiae) from the Aegean Sea. Hydrobiologia 482, 107-117.

- Clavico E.E.G., Muricy G., da Gama B. A. P., Batista D., Ventura C.R.R. and Pereira R.C. (2006) Ecological roles of natural products from the marine sponge *Geodia corticostylifera*. *Marine Biology* 148, 479-488.
- Compagnone R.S., Oliveri M.C., Piña I.C., Marques S., Rangel H.R., Dagger F., Suárez A.I. and Gómez M. (1999) 5-Alkylpyrrole-2-Carboxaldehydes from the Caribbean sponges *Mycale microsigmatosa* and *Desmapsamma anchorata*. *Natural Product Letters* 13, 203–211.
- Cuartas E.I. and Excoffon A.C. (1993) La fauna acompañante de *Hymeniacidon sanguinea* (Grant, 1827) (Porifera: Demospongiae). *Neotrópica* 39, 3–10.
- Duarte L.F.L. and Nalesso R.C. (1996) The sponge Zygomycale parishii (Bowerbank) and its endobiotic fauna. Estuarine, Coastal and Shelf Science 42, 139-151.
- **Fiore C.L. and Jutte P.C.** (2010) Characterization of macrofaunal assemblages associated with sponges and tunicates collected off the southeastern United States. *Invertebrate Biology* 129, 105–120.
- Frith D.W. (1976) Animals associated with sponges at North Hayling, Hampshire. *Zoological Journal of the Linnean Society* 58, 353 362.
- Gravili C., Belmontea G., Cecere E., Denitto F., Giangrande A., Guidetti P., Longo C., Mastrototaro F., Moscatello S., Petrocelli A., Piraino S., Terlizzi A. and Boero F. (2010) Nonindigenous species along the Apulian coast, Italy. *Chemistry and Ecology* 26, 121-142.
- Huang J.P., McClintock J.B., Amsler C.D. and Huang Y.M. (2008) Mesofauna associated with the marine sponge *Amphimedon viridis*. Do its physical or chemical attributes provide a prospective refuge from fish predation? *Journal of Experimental Marine Biology and Ecology* 362, 95–100.
- **Ilan M., Ben-Eliahu M.N. and Galil B.S.** (1994) Three deep water sponges from the eastern Mediterranean and their associated fauna. *Ophelia* 39, 45–54.
- **Jassby A.D. and Powell T.M.** (1990) Detecting changes in ecological time series. *Ecology* 71, 2044–2052.
- Klautau M., Monteiro L. and Borojevic R. (2004) First occurrence of the genus *Paraleucilla* (Calcarea, Porifera) in the Atlantic Ocean: *P. magna* sp. nov. *Zootaxa* 710, 1–8.
- Klitgaard A.B. (1995). The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, North-eastern Atlantic. *Sarsia* 80, 1–22.
- Koukouras A., Voultsiadou-Koukouras E., Chintiroglou H. and Dounas C. (1985) Benthic bionomy of the North Aegean Sea. 3. A comparison of the macrobenthic animal assemblages associated with 7 sponge species. Cahiers de Biologie Marine 26, 301–319.
- Koukouras A., Russo A., Voultsiadou-Koukouras E., Dounas C. and Chintiroglou C. (1992) Relationship of sponge macrofauna with the morphology of their hosts in the North Aegean Sea. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 77, 609–619.
- Koukouras A., Russo A., Voultsiadou-Koukouras E., Arvanitidis C. and Stefanidou D. (1996) Macrofauna associated with sponge species of different morphology. Marine Ecology—Publicazioni Della Stazione Zoologica Di Napoli 17, 569–582.
- Lanna E., Monteiro L.C. and Klautau M. (2007) Life cycle of Paraleucilla magna Klautau, Monteiro and Borojevic, 2004 (Porifera, Calcarea). In Custódio M.R., Lôbo-Hajdu G., Hajdu E. and Muricy G. (eds) Porifera research—biodiversity, innovation and sustainability. Rio de Janeiro: Museu Nacional—Série Livros 28, pp. 413–418.
- **Legendre P. and Gallagher E.** (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271 280.
- **Long E.R.** (1968) The associates of four species of marine sponges of Oregon and Washington. *Pacific Science* 22, 347–351.

- Longo C., Mastrototaro F. and Corriero G. (2007) Occurrence of Paraleucilla magna (Porifera: Calcarea) in the Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom 87, 1749–1755.
- **Ludwig J.A. and Reynolds J.F.** (1988) Statistical ecology: a primer on methods and computing. New York: Wiley-Interscience.
- Magnino G., Pronzato R., Sarà A. and Gaino E. (1999) Fauna associated with the horny sponge *Anomoianthella lamella* Pulitzer-Finali & Pronzato, 1999 (Ianthellidae, Demospongiae) from Papua-New Guinea. *Italian Journal of Zoology* 66, 175–181.
- Mladenov P.V. and Emson R.H. (1988) Density, size structure and reproductive characteristics of fissiparous brittle stars in algae and sponges: evidence for interpopulational variation in levels of sexual and asexual reproduction. *Marine Ecology Progress Series* 42, 181–194.
- Morgado E.H. and Tanaka M.O. (2001) The macrofauna associated with the bryozoan *Schizoporella errata* (Walters) in south-eastern Brazil. *Scientia Marina* 65, 173–181.
- Nalesso R.C., Duarte L.F.L., Pierozzi I. and Enumo E.F. (1995) Tube epifauna of the polychaete *Phyllochaetopterus socialis* Claparède. *Estuarine, Coastal and Shelf Science* 41, 91–100.
- Neves B.M., Lima E.J.B. and Pérez C.D. (2007) Brittle stars (Echinodermata: Ophiuroidea) associated with the octocoral *Carijoa riisei* (Cnidaria: Anthozoa) from the littoral of Pernambuco, Brazil. *Journal of the Marine Biological Association of the United Kingdom* 87, 1263–1267.
- Neves G. and Omena E. (2003) Influence of sponge morphology on the composition of the polychaete associated fauna from Rocas Atoll, northeast Brazil. *Coral Reefs* 22, 123–129.
- **Pearse A.S.** (1950) Notes on the inhabitants of certain sponges at Bimini. *Ecology* 31, 149–151.
- Peattie M.E. and Hoare R. (1981) The sublittoral ecology of the Menai Strait. 2. The sponge *Halichondria panicea* (Pallas) and its associated fauna. *Estuarine, Coastal and Shelf Science* 13, 621-635.
- Ribeiro S.M., Omena E.P. and Muricy G. (2003) Macrofauna associated to *Mycale microsigmatosa* (Porifera, Demospongiae) in Rio de Janeiro State, SE Brazil. *Estuarine, Coastal and Shelf Science* 57, 951–959.
- **Rützler K.** (1976) Ecology of Tunisian commercial sponges. *Tèthys* 7, 249–264.
- Serejo C.S. (1998) Gammaridean and caprellidean fauna (Crustacea) associated with the sponge *Dysidea fragilis* Johnston at Arraial do Cabo, Rio de Janeiro, Brazil. *Bulletin of Marine Science* 63, 363–385.
- Skilleter G.A., Russell B.D., Degnan B.M. and Garson M.J. (2005) Living in a potentially toxic environment: comparisons of endofauna in two congeneric sponges from the Great Barrier Reef. *Marine Ecology Progress Series* 304, 67–75.
- Sokal R.R. and Rohlf F.J. (1995) Biometry: the principles and practice of statistics in biological research. 3rd edition. San Francisco, CA: W.H. Freeman & Co.
- Villamizar E. and Laughlin R.A. (1991) Fauna associated with the sponges *Aplysina archeri* and *Aplysina lacunosa* in a coral reef of the Archipiélago de Los Roques, National Park, Venezuela. In Reitner J. and Keupp H. (eds) *Fossil and recent sponges*. Berlin: Springer Verlag, pp. 522–542.
- Wendt P.H., van Dolah R.F. and O'Rourke C.B. (1985) A comparative study of the invertebrate macrofauna associated with seven sponge and coral species collected from the South Atlantic Bight. *Journal of the Elisha Mitchell Scientific Society* 101, 187–203.
- Westinga E. and Hoetjes P.C. (1981) The intrasponge fauna of *Spheciospongia vesparia* (Porifera, Demospongiae) at Curação and Bonaire. *Marine Biology* 62, 139–150.

Wulff J.L. (2006) Ecological interactions of marine sponges. *Canadian Journal of Zoology* 84, 146–166.

and

Zammit P.P., Longo C. and. Schembri P.J. (2009) Occurrence of Paraleucilla magna Klautau et al., 2004 (Porifera: Calcarea) in Malta. Mediterranean Marine Science 10, 135–138.

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