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FEATURE ARTICLE

Sponge host characteristics shape the community structure of their shrimp associates

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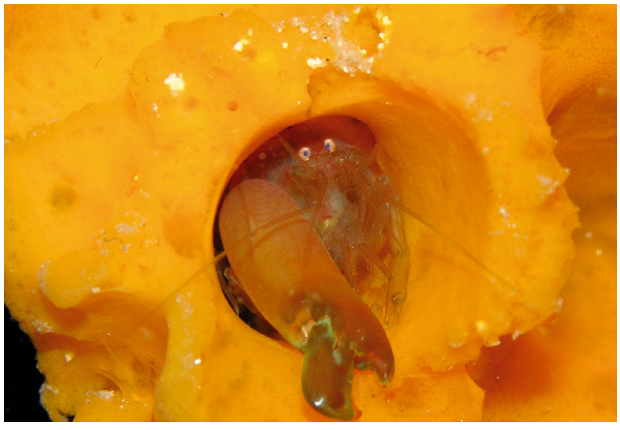
ABSTRACT: Both body size and habitat architecture have pervasive effects on the form, function, and interactions of organisms, and can play especially important roles in structuring intimate associations between host organisms and their obligate associates. In this study, we examined how body size is related to host use in a diverse clade of closely related snapping shrimp species (*Synalpheus*) that live in the interior canals of sponges. Using data from an extensive survey of sponge-dwelling *Synalpheus* from Jamaica, we tested how sponge morphology (interior canal size and individual sponge volume) was related to the identity and diversity of *Synalpheus* inhabitants. In cross-species comparisons, we found a strong positive correlation between *Synalpheus* species body size and sponge host canal size, using both raw species correlations and phylogenetic independent contrasts. Shrimp abundance increased with sponge volume in all sponge hosts tested, and species richness increased with volume in 2 host sponge species. Despite this evidence for a strong constraining influence of habitat architecture on shrimp communities, simulation studies demonstrated that shrimp used only a subset of appropriately sized sponges, indicating that size matching is not the sole determinant of sponge host use. Closely related sponges hosted more similar shrimp communities than unrelated sponges (despite moderate similarity in canal size between unrelated sponges), suggesting that additional genus-specific sponge traits also influence host use. Our study suggests multiple sponge traits likely limit *Synalpheus* host use, and has important implications for understanding how host use influences speciation of this diverse group.

KEY WORDS: *Synalpheus* · Sponge · Coral reef · Host use · Size · Harrison's rule



A snapping shrimp *Synalpheus* sp. defends its host sponge *Lissodendoryx colombiensis*.

Photo: Arthur Anker

INTRODUCTION

Body size fundamentally influences the ecology of organisms, affecting metabolism, reproduction, species interactions, and abundance (Peters 1983, Werner & Gilliam 1984, Labarbera 1989, Martin & Palumbi 1993, Brown 1995, Gillooly et al. 2001, White et al. 2007). Because of the often direct effects of body size on individual fitness, the ecological factors driving the evolution of body size within species' lineages have been well explored (Kirk 1991, Novotny & Basset 1999, Johnson et al. 2005, Hultgren & Stachowicz 2009, Moen et al. 2009, Poulin 2009), though the evolutionary development of community-wide variation in size has been less well studied (but see (Holling 1992, Moen et al. 2009).

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Body size also has profound effects on species interactions and, consequently, on the abundance, co-occurrence, and trophic dynamics of species in communities (Werner & Gilliam 1984, Brose et al. 2006, White et al. 2007). Certain types of species interactions are highly size-structured, including many mutualistic plant–pollinator relationships (Fenster et al. 2004, Borrell 2005, Dalsgaard et al. 2009) and interactions between parasites and their hosts (Kirk 1991, Poulin & Hamilton 1997, Sasal et al. 1999, Johnson et al. 2005). In a broad sense, the body size of any small 'associate' species—here defined as a species that is an obligate associate (e.g. parasite or mutualist) of an often larger host—is often correlated with the size of the host, which also serves as the associate's habitat. In parasite–host systems, the widespread tendency for larger parasite species to live on larger host species is termed Harrison's rule, and has been demonstrated across a taxonomically broad group of parasites (Harrison 1915, Johnson et al. 2005). However, body size can also be influenced by biogeographic factors such as latitude (e.g. Bergmann's rule; see Blackburn et al. 1999) that may mask or weaken host effects on parasite size (Randhawa & Poulin 2009). More recently, studies testing for positive cross-species size correlations between parasites and their hosts have corrected for shared phylogenetic history (Kirk 1991, Poulin & Hamilton 1997, Sasal et al. 1999, Johnson et al. 2005), a particularly important step as body size may be evolutionarily conserved in closely related associate lineages. Examining how size structures interactions between associates and their hosts in a phylogenetic context provides a unique opportunity to test the extent to which phylogenetic conservatism of associate size interacts with selection imposed by host size.

In addition to exerting strong selection on the sizes of individual associate species, host size and architecture can also influence the abundance and richness of associate communities (Abele & Patton 1976, Duarte & Nalesso 1996, Poulin & Rohde 1997). In many cases, positive relationships between host size and associate abundance or diversity are analogous to area–diversity relationships seen in classic island biogeography studies (but see Kuris et al. 1980). However, host–associate interactions differ from community biogeographic systems in that other biotic attributes of the host—such as phylogenetic history, geographic range, and population density—may have strong effects on associate richness, in some cases obscuring relationships between host size and associate diversity (Kuris et al. 1980, Gregory 1990, Morand & Poulin 1998, Nunn et al. 2003, Poulin & Mouillot 2004, Hughes & Page 2007). In addition, evolution of obligate host associations has facilitated adaptive radiations in many systems (Price 1980, Mitter et al. 1988, Malenke et al. 2009); as such, many groups of specialized host associates may be closely related and share similar adaptations to the host, including not only body size (Sotka et al. 1999) but also physiological adaptations such as tolerance of host chemical defenses (Ehrlich & Raven 1964, Mitter et al. 1991, Janz & Nylin 1998). However, few studies have examined how phylogenetic relatedness of hosts and associates may interact with size to influence patterns of host use in a community.

In the present study, we examined the role of body and habitat size in structuring host–associate interactions in a community of sponge-dwelling snapping shrimps *Synalpheus* spp. in Jamaica. The majority of Caribbean *Synalpheus* species belong to the Gambarelloides species group (Chace 1972, Dardeau 1984, Rios & Duffy 2007) and are obligate sponge-dwellers, residing in the internal canals of their sponge hosts (Duffy 1992, Macdonald et al. 2006, Rios & Duffy 2007) and feeding on sponge tissue and organic matter. In the Caribbean, >40 described Gambarelloides-group *Synalpheus* spp. inhabit ~20 different sponge host species, and data from >20 yr of taxonomic and distributional surveys in Belize and Panama demonstrate that most *Synalpheus* spp. are highly host-specific (Duffy 1992, Macdonald et al. 2006, Rios & Duffy 2007, Macdonald et al. 2009). These surveys have also documented nearly 100% occupancy of appropriate host sponges in the field (Macdonald et al. 2006). Together with behavioral evidence of strong territoriality in *Synalpheus* spp. (Duffy et al. 2002, Toth & Duffy 2005), these data suggest that competition for sponge hosts (and their value as long-term habitat and predator refuges) is high. Several early studies observed that sponge canal size influences host use in *Synalpheus* spp. (Westinga & Hoetjes 1981, Erdman & Blake 1987). Duffy (1992) quantified these observations and demonstrated (using 4 *Synalpheus* species) that larger *Synalpheus* species inhabited sponges with larger canal widths, and preferred larger canal widths in choice assays. However, these studies used only a limited number of host and associate species, and little is known about whether *Synalpheus* spp. size and sponge canal size are correlated over larger taxonomic and spatial scales, e.g. all sponge-dwelling *Synalpheus* spp. living in a certain region.

The size of entire sponges (i.e. volume) also likely affects community structure of *Synalpheus* spp. inhabitants. Worldwide, sponges host an extraordinary diversity of occasional and obligate associate species, and studies on these 'living hotels' (cf. Pearse 1932) have consistently found positive correlations between sponge volume and abundance (Pearse 1932, Duarte & Nalesso 1996, Henkel & Pawlik 2005)—and in some cases species richness (Westinga & Hoetjes 1981, Erdman & Blake 1987)—of associate communities.

The present study specifically capitalized on a recent survey of *Synalpheus* spp. communities in Jamaica (Macdonald et al. 2009), as well as recent advances in *Synalpheus* taxonomy (Rios 2003, Macdonald & Duffy 2006, Rios & Duffy 2007, Anker & Tóth 2008, Macdonald et al. 2009) and phylogenetics (Duffy et al. 2000, Morrison et al. 2004), to examine community-wide correlations between the size and taxonomic relatedness of sponges and the body sizes of their shrimp associates from a phylogenetic perspective. Specifically, we tested: (1) whether sponge host canal size is correlated with shrimp body size, (2) whether the match between shrimp body size and sponge canal size can accurately predict host use in simulation studies, and (3) how sponge volume affects the abundance and diversity of *Synalpheus* spp. communities co-occurring in sponges.

MATERIALS AND METHODS

Field collections. This study capitalized on a recent survey of sponge-dwelling *Synalpheus* spp. (>2500 individual shrimp) from 96 individual sponges collected in Discovery Bay, Jamaica; field sampling, study sites, and taxonomy were described in detail by Macdonald et al. (2009). We measured volume (ml) of individual sponges by displacement; for sponges embedded in rubble, we measured the volume of sponge + rubble, dissected out the sponge from the rubble, and subtracted the volume of rubble to get sponge volume. We sectioned sponges into 1 cm slices (2 to 6 slices total) and photographed slices in seawater under a piece of plexiglass to measure canal size using methods modified from Duffy (1992). Briefly, we traced the diameter of randomly selected canals and measured area and Feret's diameter (maximum diameter) using ImageJ (Abramoff et al. 2004). As the canals used by shrimp were continuous throughout the sponge and approximately cylindrical, this method gave consistent canal diameter values for all sponge species. We measured 10 to 50 canals per individual sponge (mean = 15 per sponge), depending on total sponge volume (5 to >700 ml). To standardize the number of canals used to determine canal size, we randomly selected 10 canals to calculate the mean canal size for an individual, and calculated species means by averaging the mean values of multiple individuals of a sponge species. Species means and SEs calculated using this truncated data set (10 canals ind.$^{-1}$) were not significantly different from means calculated using all canal data available for an individual (2-tailed paired *t*-test, $p > 0.31$). We lacked adequate canal width data on one sponge (*Spheciospongia vesparium*).

Frequency of shrimp occurrence in sponges (Table 1) was quantified from Macdonald et al. (2009). We re-classified 2 sets of *Synalpheus* spp. specimens using DNA sequences (matched against sequences in Morrison et al. 2004) and morphological characters (K. M. Hultgren unpubl. data). *S. yano* (VIMS 08JAM4801-02) was reclassified as *S. ul* (described in Rios & Duffy 2007), and 11 ind. of *S. pandionis* (VIMS 08JAM5902-3, 06-07, 10-15) were reclassified as *S.* '*pandionis* red' (described in Rios 2003). We included one obligate sponge-dwelling species (*S. brevicarpus*) from outside of the Gambarelloides group. We also mapped 4 species from the present study to undescribed species in the Morrison et al. (2004) phylogeny (species have subsequently been described) using morphology and DNA sequencing. These included *S. elizabethae* (=*S.* '*rathbunae* A'; Rios & Duffy 2007), *S. carpenteri* (=*S. bousfieldi* A; Macdonald & Duffy 2006). *S. thele* (=*S. chacei* A; Macdonald et al. 2009). and *S. belizensis* (=*S. paraneptunus* paraBE02; Anker & Tóth 2008). We excluded 3 species (*S. pectiniger*, *S. mcclendoni*, and *S. brevifrons*) that were collected infrequently (<3 ind.).

We calculated proportional host use of a shrimp species by dividing the number of occurrences in a sponge species by the total number of sponges a shrimp species occurred in (Table 1). To estimate mean size of shrimp species living in a sponge species, we measured the carapace length (CL) in mm (the distance from the rostrum to the posterior edge of the carapace) of all ovigerous females (i.e. females with embryos and/or distinct ovaries) and non-ovigerous individuals inhabiting a sponge using an ocular micrometer. Sex is difficult to determine in *Synalpheus*; for pair-living species, we assumed non-ovigerous individuals to be male (see Macdonald et al. 2009); for social species, non-ovigerous individuals occur in equal sex ratios (Toth & Bauer 2007). For sponges hosting >10 ind., we measured the largest individual and 9 randomly chosen individuals of each sex (ovigerous females and non-ovigerous individuals). For shrimp species that were host specialists, we calculated mean shrimp species size from all individual sponges for which we had canal size data; for shrimp inhabiting >1 sponge species (<80% of occurrences in a single sponge species), we calculated shrimp species means across all sponge hosts a shrimp species was found in.

Correlations between shrimp body size and sponge canal size. If host use were constrained by the match between shrimp size and sponge size, we would expect a positive correlation between the body size of a shrimp species and the canal size of its sponge host(s). We tested this in 2 ways. First, for all individual sponges for which we had canal and shrimp size data, we plotted the correlation between mean canal size of an individual sponge and mean size of each shrimp species in that sponge (unit of replication = shrimp species in an individual sponge). This allowed us to visualize intraspecific variation in both sponge canal

Table 1. Sponge host species, mean ± SE canal diameter (cm), and diversity of associated *Synalpheus* communities. Phylogenetic information is available for underlined shrimp species (codes indicate names used in Morrison et al. 2004); these species were used in independent contrast analyses. n: number of individual sponges measured per species. Data in each cell indicates percentage of total occurrences in that sponge species (parentheses: number of individual sponges from which species were sampled, number of individual *Synalpheus* measured); **bold**: sponge species in which each shrimp species was most numerically abundant

	Sponge host species								
	Hyattella intestinalis	*Auletta* cf. *sycinularia*	*Agelas clathrodes*	*Agelas dispar*	*Xestospongia proxima*	*Xestospongia subtriangularis*	*Aiolochroia crassa*	*Lissoden-doryx* sp.	*Hymeniacidon caerulea*
Host canal size	0.413 ± 0.083	0.7229 ± 0.012	0.55 ± 0.077	0.464 + 0.060	0.465 ± 0.061	–	0.888 ± 0.141	1.035	0.5356 ± 0.0385
n	23	2	6	11	3		8	1	2
***Synalpheus* species**									
S. corallinus	**100 (1, 2)**								
S. irie		**100 (2, 4)**							
S. 'pandionis red', panrPA01								**100 (1, 12)**	
S. plumosetosus		**100 (1, 4)**							
S. thele, chanBE01			**100 (4, 51)**						
S. agelas, agelFL01			50 (4, 13)	**50 (2, 10)**					
S. androsi, andrBE01	**100 (2, 4)**								
S. belizensis, paraBE02					**100 (4, 13)**				
S. bocas					**75 (2, 6)**	25 (1, 3)			
S. brevicarpus, brevPA06							**100 (9, 23)**		
S. carpenteri, bouaBE01			37.5 (6, 23)	**62.5 (9, 56)**					
S. duffyi					**60 (3, 40)**	40 (1, 10)			
S. elizabethae, rataPA01	**100(5, 47)**								
S. pandionis, pandBE02								**100 (2, 6)**	
S. regalis, regaBE01	**100(10, 99)**								
S. sanctithomae, sancBE01	**75(3, 5)**	25							
S. ul	20(1, 1)							20	**60 (2, 3)**
S. williamsi, willBE02									**100 (2, 2)**

size and size of different shrimp species living in that sponge.

Because the previous data do not correct for similarity among sponge or shrimp due to common ancestry (e.g. conspecific sponges might have similarly sized canals) we calculated correlations between mean body size of a shrimp species and mean canal size of the sponges inhabited by that shrimp species (unit of replication = shrimp species). We calculated mean shrimp species size as:

$$k^{-1} \cdot \sum_{i=1}^{k} \mathrm{CL}_i \quad (1)$$

and calculated mean sponge canal size for that shrimp species as:

$$k^{-1} \cdot \sum_{i=1}^{k} \mathrm{CS}_i \quad (2)$$

where k is the number of individual sponges that shrimp species occurred in, CL_i is the mean CL of that shrimp in individual sponge i, and CS_i is the mean canal size of sponge i.

For shrimp that used more than one host sponge, this set of correlations (all interactions) incorporated variability in body size and canal size across multiple sponge hosts. We also calculated sponge–shrimp correlations for the most common interactions (dominant interactions), by using only the mean shrimp CL and sponge canal size from the sponge species in which the focal shrimp species was most numerically abundant (Table 1). We calculated correlations using both sets of data (all interactions and dominant interactions) using raw species values and phylogenetic independent contrasts (Felsenstein 1985). For the latter analyses, we accommodated phylogenetic uncertainty by using 2 recent phylogenetic trees based on 1067 bp of sequence data and 66 morphological characters: (1) a Bayesian consensus tree (Duffy & Macdonald 2010) and (2) a weighted parsimony tree (single most parsimonious tree, Morrison et al. 2004, their Fig. 3). We trimmed each tree to include only species for which we had shrimp body size and canal size data and excluded species not included in either phylogeny (*Synalpheus irie*, *S. corallinus*, *S. ul*, *S. plumosetosus*, *S. bocas*, and *S. duffyi*). We calculated contrasts using the phenotypic diversity analysis program, PDAP (Midford et al. 2003), implemented in the program Mesquite v. 2.6 (Maddison & Maddison 2009). We assigned equal branch lengths for each tree, as inclusion of multiple informative mor-

phological characters in both trees made it difficult to accurately quantify evolutionary change along branches. All trait values used in the analyses were log-transformed, and before calculating correlations we ensured that the absolute value of each contrast was not correlated with the square root of the corrected branch lengths (Garland et al. 1992, Midford et al. 2003). Because significant correlations between these 2 values indicate a violation of assumptions for independent contrasts, we used sign tests to assess significance for any set of contrasts violating these assumptions.

Permutation tests of sponge host use. We examined whether shrimp size alone predicted sponge host use using permutation tests. We focused on the 4 sponge species (*Agelas clathrodes*, *A. dispar*, *Hyattella intestinalis*, and *Xestospongia proxima*) hosting the most shrimp, and the 6 most abundant shrimp species (*Synalpheus elizabethae*, *S. regalis*, *S. duffyi*, *S. carpenteri*, *S. agelas*, and *S. thele*). These 6 shrimp species, living in these 4 sponge species, composed 95% of the total shrimp abundance in our survey. This simulation randomly reassigned shrimp to appropriately sized individual sponges, but we imposed several constraints to account for the spatial and biological structure of our data. First, we partitioned the survey data by locality (n = 5; see Macdonald et al. 2009) and allowed shrimp at a given locality to only recolonize individual sponges from that locality. We accounted for shrimp social structure by considering each shrimp population (all individuals of a shrimp species living in a single sponge) as a unit, and randomly re-assigned each population as a unit. This preserved the social structure of colony-living eusocial species. For pair-living species in the model, it is unknown whether multiple pairs are related or unrelated, but treating these species as a population unit made our treatment consistent across shrimp species and was a conservative measure that tended to reduce the range of sponge hosts assigned to a unit. For each shrimp population unit, we calculated the range of sponge canal sizes (mean canal size for a given shrimp size ± 5% CI) that each population could inhabit using the equation

$$\text{Mean canal size} = 0.1902 + 0.10736 \times \text{given shrimp size} \quad (3)$$

which describes the relationship between sponge canal size and shrimp species size (see Fig. 1). This allowed us to pinpoint the individual sponges from each location that could accommodate a given shrimp population. We scaled the probability of being assigned to an individual sponge to original shrimp abundance in that sponge (i.e. the number of shrimp niches available). Finally, we randomly reassigned each shrimp population to an individual sponge (within the same locality) based on whether the sponge's mean canal size fell within the range of sizes required by that shrimp population. We performed 100 randomizations using an Excel macro (K. Hultgren unpubl. data), and for both randomized and actual communities we calculated proportional abundance of each shrimp species in different host species, host use richness and diversity (Shannon-Wiener H'), and whether sponge host richness or diversity varied between actual and randomized communities (non-parametric Wilcoxon tests).

Sponge relatedness and shrimp community similarity. We also explored whether related sponge hosts had similar canal sizes and hosted similar *Synalpheus* communities by calculating pairwise community similarity and canal size similarity among different individual sponges using the abundance-based Chao-Jaccard similarity index (Chao et al. 2005), implemented in the program EstimateS (Colwell 2005). For calculations of pairwise canal size similarity, we binned the distribution of measured canal sizes for each individual sponge (n = 10) into 13 equally spaced size categories; for community similarity comparisons, we used the abundance of different *Synalpheus* species in each individual sponge. We used these data to compare mean pairwise similarity of *Synalpheus* communities and canal sizes from: (1) conspecific sponges, (2) congeneric sponges, and (3) unrelated sponges (all other comparisons).

Correlations between sponge volume and shrimp abundance and diversity. Next, we examined the correlation between individual sponge volume (ml) and *Synalpheus* spp. abundance, biomass, species richness, and diversity (Shannon-Wiener H'). We regressed shrimp data on sponge volume for 3 focal sponge species (*Agelas clathrodes*, *A. dispar*, and *Hyattella intestinalis*) for which we had the most complete sampling (n ≥ 9 ind. per species). To estimate shrimp biomass, we used an equation from Duffy & Macdonald (2010):

$$\text{Shrimp body mass (mg)} = 0.5986 \cdot e^{0.4892(\text{shrimp CL in mm})} \quad (4)$$

We estimated interior volume using a subset of individual sponges for which we had ≥20 canals measured (n = 6 to 15 ind. per focal sponge species) by dividing the total area of all canals in a slice by total area of sponge tissue in that slice. All regressions were performed on untransformed data.

RESULTS

Correlations between shrimp body size and sponge canal size

Across individual sponges, shrimp body size increased with increasing sponge canal size ($F_{1,60} = 105.89$, $p < 0.0001$, $r^2 = 0.64$; Fig. 1). Across shrimp species, mean shrimp body size increased significantly with mean sponge canal size for all methodologies and data sets

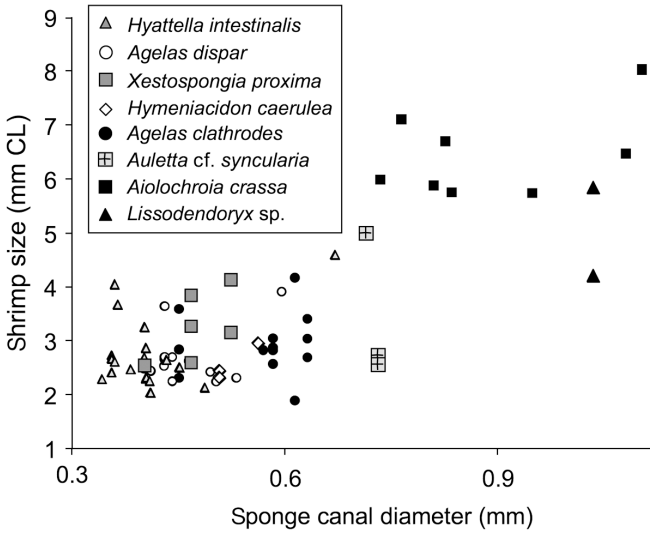

Fig. 1. Relationship between the size of sponge cavities (mean canal size of individual sponges) and *Synalpheus* spp. body size (mean carapace length, CL, of a *Synalpheus* species living in an individual sponge)

(Table 2, Fig. 2a–d). Using raw species means, shrimp body size was positively correlated with sponge canal width both when we considered all interactions ($p = 0.001$; Fig. 2a) and when we considered only dominant interactions ($p = 0.0029$; Fig. 2c). Using phylogenetic independent contrasts, shrimp body size and canal size remained correlated whether using all sponge data (1-tailed sign test, $p = 0.033$; Fig. 2b) or only the dominant shrimp species in the sponge (1-tailed sign test, $p = 0.033$; Fig. 2d). These correlations were still significant when we used the weighted parsimony tree (all interactions, $p = 0.001$; dominant interactions, $p < 0.004$; Table 2).

Permutation tests of sponge host use

Simulations that randomly assigned shrimp populations to sponge hosts resulted on average in a much higher host range for each shrimp species than observed, even when we limited shrimp to appropriately sized sponges in each locality (Fig. 3). Richness of host species used was significantly higher for simulated relative to observed communities for 5 of 6 shrimp species (Wilcoxon tests against a mean, $p < 0.0001$). Species diversity of hosts was significantly higher in simulated communities for all shrimp species ($p < 0.0001$).

Sponge relatedness and shrimp community similarity

Taxonomically related sponge host species had similarly sized canals and hosted similar *Synalpheus* communities (Fig. 4). Shrimp community similarity (Chao-Jaccard index) was high for both conspecific and congeneric comparisons of shrimp communities (0.40 to 0.71), but community similarity was low for all comparisons between unrelated sponges (<0.01; Fig. 4a). Pairwise individual sponge canal size similarity showed slightly different trends (Fig. 4b): mean canal size overlap between conspecific and congeneric sponges was high (0.64 to 0.81), and size overlap between unrelated sponges was also moderately high (0.14 to 0.46). Thus, despite moderate similarity in sponge canal size distributions (Fig. 4b), *Synalpheus* community similarity in unrelated sponges was very low (Fig. 4a).

Correlations between sponge volume and shrimp abundance and diversity

Volume of individual sponges strongly influenced the abundance and biomass of associated shrimp (Fig. 5). Total shrimp abundance increased with whole sponge volume (i.e. sponge tissue and internal spaces) for all 3 sponge species tested: *Agelas clathrodes* ($p < 0.0001$, $r^2 = 0.954$), *A. dispar* ($p < 0.0001$, $r^2 = 0.953$), and *Hyattella intestinalis* ($p < 0.0001$, $r^2 = 0.843$; Fig. 5a, Table 3). When we combined data from all these host species into a single analysis, the full model was signif-

Table 2. Analyses of the correlation between *Synalpheus* body size and sponge canal size using raw correlations and phylogenetic independent contrasts

Sponge hosts examined	Analysis type and tree	No. correlations or contrasts	*F*	p	R^2
Synalpheus in all sponge hosts	Raw correlation	18	16.299	0.001	0.505
	Contrasts-Bayes tree	11	13.920	0.033[a]	0.518
	Contrasts-weighted parsimony tree	11	15.420	0.001	0.607
Synalpheus in dominant sponge hosts only	Raw correlation	18	12.284	0.003	0.434
	Contrasts-Bayes tree	11	8.385	0.033[a]	0.456
	Contrasts-weighted parsimony tree	11	10.496	0.004	0.512

[a]1-tailed sign test

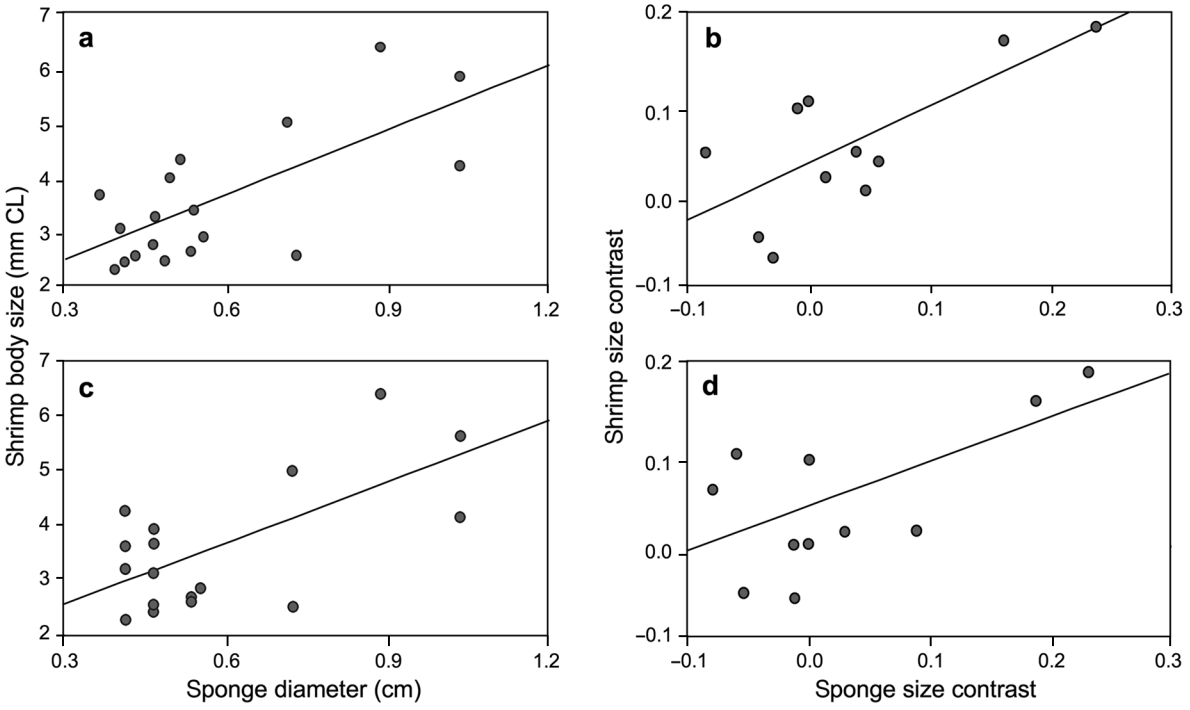

Fig. 2. Correlations between mean sponge canal size and mean *Synalpheus* spp. body size using (a,c) raw species contrasts and (b,d) phylogenetic independent contrasts. Correlations were calculated using (a,b) all shrimp–sponge interactions for a particular shrimp species or (c,d) only the dominant shrimp–sponge interactions

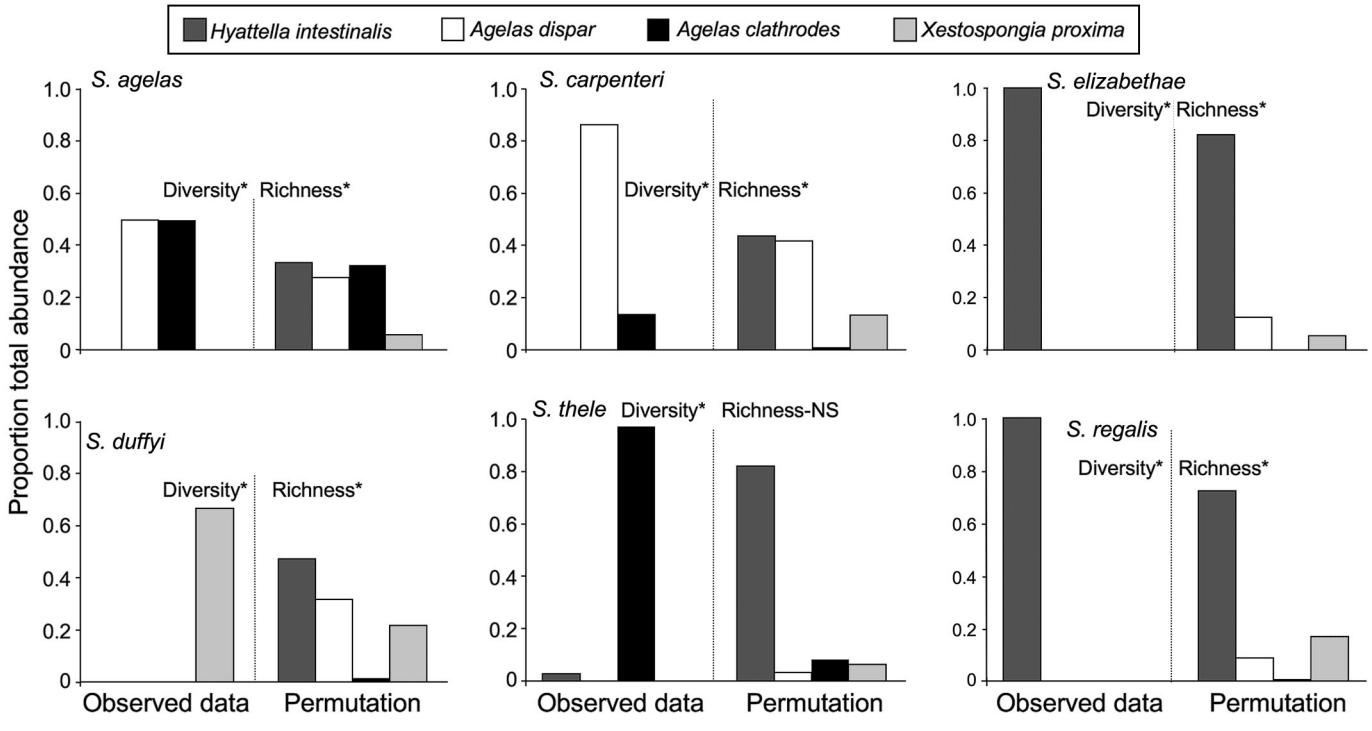

Fig. 3. Observed host use (observed data) and simulated host use (permutation) for the 6 most common *Synalpheus* species in the 4 most common sponge host species. Bars: proportion of total shrimp abundance in that sponge host; *: significant differences in host species richness or diversity (Shannon-Wiener H') between actual and simulated host use (2-tailed Wilcoxon test, $p < 0.0001$); NS: not significant

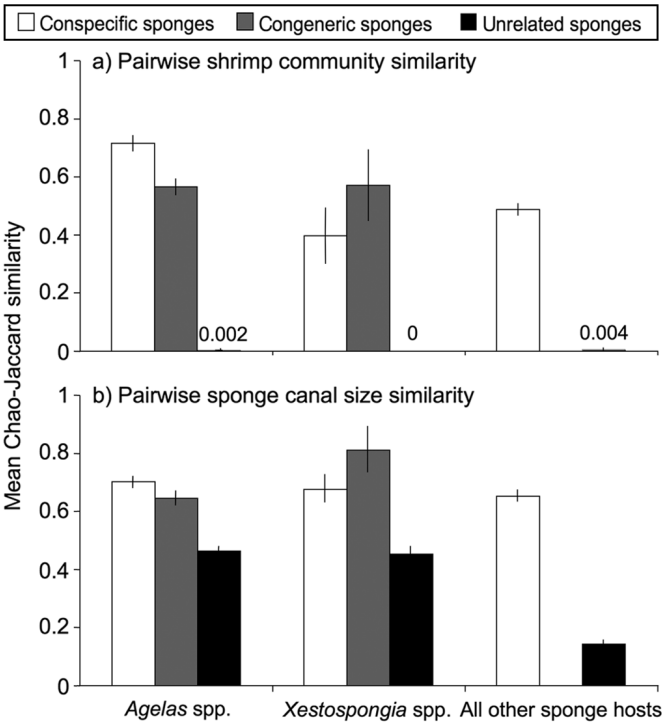

Fig. 4. Mean (a) pairwise community similarity and (b) pairwise canal size similarity of *Synalpheus* spp. communities inhabiting conspecific sponges, congeneric sponges, and unrelated sponges (comparisons across the whole range of sponge species in the data set). Similarity calculations (Chao-Jaccard similarity, weighed by abundance) used communities inhabiting *Agelas* spp. (*A. clathrodes* and *A. dispar*), *Xestospongia* spp. (*X. proxima* and *X. subtriangularis*), and all other sponge hosts. (a) Numbers above unrelated comparisons indicate mean values

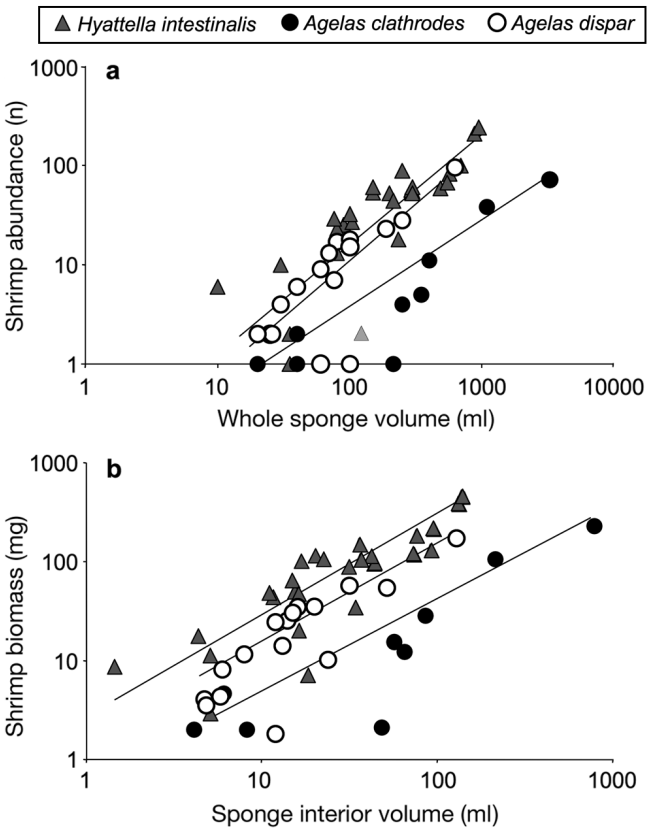

Fig. 5. Effects of individual sponge volume on *Synalpheus* spp. community abundance (all axes in log scale). (a) Number of individual shrimp as a function of whole sponge volume. (b) Estimated biomass of shrimp community as a function of estimated interior sponge volume

icant (ANOVA, $F_{5,47} = 67.858$, $p < 0.0001$; Table 4), and there were significant effects of sponge volume ($p < 0.0001$), sponge species ($p < 0.0001$), and a sponge volume × sponge species interaction ($p < 0.0001$; Fig. 5a), indicating that the relationship between abundance and volume (i.e. shrimp density) differed among sponge species. Results were similar if we regressed shrimp biomass (mg) against estimated interior volume (ml empty space); there were significant positive correlations for *A. clathrodes* ($p < 0.0001$, $r^2 = 0.937$), *A. dispar* ($p < 0.0001$, $r^2 = 0.873$), and *H. intestinalis* ($p < 0.0001$, $r^2 = 0.957$; Fig. 5b). The full model was significant in a combined ANOVA ($F_{5,47} = 86.68$, $p < 0.0001$; Table 4), and there were significant effects of sponge interior volume, sponge species, and an interior volume × sponge species interaction ($p < 0.0001$; Fig. 5b). In contrast to results for shrimp abundance and biomass, there were fewer significant correlations between sponge volume and shrimp richness or diversity (Table 3). Shrimp diversity was not significantly correlated with sponge volume for any of the sponges tested ($p > 0.186$; Table 3), and sponge volume was correlated with shrimp species richness only for *A. clathrodes* (log-linear relationship, $p = 0.0265$, $r^2 = 0.529$) and *A. dispar* (linear relationship, $p = 0.005$, $r^2 = 0.435$).

DISCUSSION

In the present study, we demonstrate strong links between morphological attributes of sponge hosts—both the size of interior canals and individual sponge volume—and the species composition and abundance of symbiotic shrimp inhabitants. Sponge habitat architecture and the size and community structure of shrimp communities were strongly correlated: across a species pool of 18 shrimp species inhabiting 9 sponge species in Jamaica, shrimp body size increased with sponge interior canal size, and these relationships were robust to correction for the close phylogenetic relationships among shrimp species. However, even with these strong size correlations, permutation tests demonstrated that most *Synalpheus* species used only a subset of appropriately sized sponges. Simulated and observed host

Table 3. Regression equations for 3 sponge host species, describing the relationship between shrimp numerical abundance as a function of whole sponge volume (ml), estimated shrimp biomass (mg) as a function of estimated interior volume, and shrimp diversity (Shannon-Wiener H') and richness as a function of whole sponge volume. NS: not significant

Sponge host	F	p	R^2	Equation
Shrimp abundance–whole sponge volume				
Hyattella intestinalis	139.5121	<0.0001	0.954	$y = 0.0224x + 0.6705$
Agelas clathrodes	145.4506	<0.0001	0.953	$y = 0.1488x - 2.0597$
Agelas dispar	285.5576	<0.0001	0.843	$y = 0.217x - 2.948$
Shrimp biomass–estimated interior volume				
Hyattella intestinalis	178.5397	<0.0001	0.957	$y = 0.313x + 2.30$
Agelas clathrodes	154.3152	<0.0001	0.937	$y = 1.395x + 0.600$
Agelas dispar	207.2182	<0.0001	0.873	$y = 2.783x - 0.3195$
Shrimp diversity–whole sponge volume				
Hyattella intestinalis	0.28	0.605	NS	
Agelas clathrodes	2.15	0.186	NS	
Agelas dispar	1.57	0.231	NS	
Shrimp richness–whole sponge volume				
Hyattella intestinalis	0.24	0.631	NS	
Agelas clathrodes	7.85	0.027	0.529	$y = 0.6485(\ln(x)) - 1.2522$
Agelas dispar	10.78	0.005	0.435	$y = 0.0020x + 1.0223$

ranges were the most similar in the 2 eusocial species (*S. elizabethae* and *S. regalis*), possibly because these were the smallest shrimp and may have been limited to the host sponge with the smallest canals (*Hyattella intestinalis*). Utilization of relatively narrow host ranges for most *Synalpheus* species in the present study, even given strong competition for sponge hosts in the field (which we might expect to drive increased host breadth), strongly suggests that size matching is not the sole determinant of sponge host use. Instead, genus-specific factors such as sponge chemistry—supported indirectly by our data indicating closely related shrimp used closely related sponge hosts—may additionally influence host use. Finally, sponge host size also influenced shrimp communities: individual sponge volume was strongly correlated with the total abundance, biomass, and, in some cases, the richness of co-occurring shrimp communities in a sponge.

Table 4. Summary of ANOVA results on the effects of sponge size and individual sponge host on *Synalpheus* spp. abundance

Factor	SS	df	F	p
Whole sponge volume (WV)	42777.36	1	100.43	<0.0001
Sponge host species (SP)	18993.60	2	22.30	<0.0001
WV × SP	69622.62	2	81.73	<0.0001
Error	20018.98	47		
Interior sponge volume (IV)	198225.24	1	166.69	<0.0001
Sponge host species (SP)	107765.24	2	45.31	<0.0001
IV × SP	265798.35	2	111.75	<0.0001
Error	55893.2	47		

The positive correlations we observed between sponge canal size and shrimp size extend earlier findings on *Synalpheus* in Panama (Duffy 1992), and mirror patterns observed in some plant–pollinator networks (Borrell 2005, Dalsgaard et al. 2009, Stang et al. 2009) and host–parasite systems (Price 1980, Poulin & Hamilton 1997, Johnson et al. 2005). In host–parasite systems, size correlations between parasites and their hosts highlight the often tightly linked coevolutionary trajectories of hosts and parasites, as evidenced by multiple examples of cospeciation in such systems (Price 1980, Hafner & Nadler 1990, Weiblen & Bush 2002). Although strong shrimp–sponge size correlations makes it reasonable to assume that *Synalpheus* have undergone 1-way evolutionary adaptations to the size of their sponge hosts, there is less evidence for clear coevolutionary linkages (e.g. 2-way evolutionary arms races between sponges and their shrimp associates). First, unlike some host–parasite systems—in which parasites specialize on, and often cospeciate with, a single host species (Price 1980, Hafner & Nadler 1990, Weiblen & Bush 2002)—*Synalpheus* spp. rarely showed reciprocally specialized interactions (i.e. a single *Synalpheus* spp. utilizing a sponge host species not used by other *Synalpheus* spp.). Although many shrimp species were specialists on a single sponge host species, those sponge host species were often inhabited by a number of different *Synalpheus* species (Table 1). Second, it is difficult to determine whether shrimp presence modifies host sponge morphology. *Synalpheus* colonize sponges as larval recruits or subadults (E. Tóth unpubl. data), and if the first shrimp to colonize a sponge was a larger species, it is possible that sponges canal diameter could increase as the shrimp grows larger. For example, the largest canal diameters we recorded in *Hyattella intestinalis* (Fig. 1) occurred in a small individual (volume ~35 ml) hosting a single pair of the medium-sized species *S. androsi*. All *H. intestinalis* above a certain size threshold (volume > 125 ml) hosted eusocial colonies of small-bodied species *S. regalis* or *S. elizabethae* within a network of small canals. These data suggest a causal link between presence of large or small *Synalpheus* spp. and intraspecific variability in sponge canal size, although it is difficult to determine whether this is due to ontogenetic changes in sponge shape or presence of different *Synalpheus* species. Furthermore, there is some observational evidence suggesting that certain *Synalpheus* species may

actively excavate canals: members of the *S. paraneptunus* species complex (*S. belizensis*, *S. bocas*, and *S. duffyi*) possess a hollowed-out minor chela that they use to scrape the sides of the canals of their host (E. Tóth pers. comm.), and are often found with sponge tissue in their mouthparts (Anker & Tóth 2008). However, many of the sponges used by shrimp, such as *Agelas* spp., are extremely tough and difficult to cut (Lehnert & van Soest 1998), and the few small individuals of *A. clathrodes* found without *Synalpheus* inhabitants in the present study (n = 3, volume < 25 ml) had canals of similar diameter to occupied individuals, suggesting canal engineering may be unlikely for these sponge hosts.

Within the subset of commonly used sponge hosts (*Agelas clathrodes*, *A. dispar*, and *Hyattella intestinalis*), shrimp community abundance and biomass was tightly linked to individual sponge volume (r^2 = 0.84 to 0.96; Fig. 5a,b), suggesting that shrimp communities were using all available canal space within a sponge. This within-sponge habitat saturation is consistent with observations from the present study and previous work indicating that the majority of appropriate sponge habitat is occupied in the field. Macdonald et al. (2006), summarizing >15 yr of collections in Belize, found >95% occupancy of all appropriate sponge species (i.e. species typically hosting shrimp), and in the present study the only empty sponges we found (*A. clathrodes*, n = 3) were very small (whole sponge volume < 25 ml), suggesting sponge habitats are at a similar premium in Jamaica. Given this habitat saturation, variation in the relationship between *Synalpheus* community abundance and sponge volume among the 3 species of sponges is interesting. In particular, the sponge host *A. clathrodes* supported a lower abundance and biomass of *Synalpheus* inhabitants per unit sponge volume than the other sponge host species (Fig. 5). Additional surveys examining variation in shrimp density and shrimp diversity in sponges across the Caribbean are necessary to examine potential mechanisms for this pattern.

Closely related (conspecific and congeneric) sponges tended to host similar *Synalpheus* communities, but this was not due strictly to similarity in canal size (Fig. 4), as unrelated sponges hosted strongly dissimilar communities despite moderate similarity in canal size. This suggests additional genus-specific host attributes, such as chemistry, may also limit which sponges *Synalpheus* spp. are adapted to live in host use; for example, hypotaurocyamines are sesquiterpene-derived compounds unique to the genus *Agelas* (Duarte & Nalesso 1996, Erpenbeck & van Soest 2007). This idea is supported by trends suggesting phylogenetic conservatism of host use in *Synalpheus*; in many cases, closely related shrimp were limited to closely related sponge hosts. For example, *S. duffyi*, *S. belizensis*, and *S. bocas* (all members of the *paraneptunus* species complex) inhabited only sponges in the genus *Xestospongia.* These patterns highlight the need to develop correlation methods that can correct for the phylogenetic relationships of not only *Synalpheus*, but also their sponge hosts, although the latter analyses await a more accurate resolution of sponge phylogeny. Examining the full range of morphological and physiological adaptations of *Synalpheus* to the sponges they inhabit, as well as the geographic distribution of *Synalpheus*–sponge interactions, are essential to understanding how sponge host use has contributed to the spectacular biodiversity of this diverse shrimp genus throughout the Caribbean.

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