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Composition, distribution and substrates of the sponge fauna (Porifera: Demospongiae) at the National Park of Anavilhanas

Composição, distribuição e substratos da fauna de esponjas (Porifera: Demospongiae) no Parque Nacional de Anavilhanas

Cecília Volkmer-Ribeiro[1]
cvolkmer1427@gmail.com

Valdir Florêncio da Veiga Júnior[2]
valdirveiga@ufam.br

Demetrio Luis Guadagnin[3]
dlguadagnin@gmail.com

Iuri Bezerra de Barros[2]
iuribb@gmail.com

Camila Castelo Branco Herzog[1]
camila.olympus@gmail.com

Abstract

Freshwater sponges, being sessile animals, heavily depend upon a substrate on which their larvae or their gemmules will settle. It is expected different sponge species to exhibit preferences or adaptations to specific substrates and habitats. Studies targeted to evaluate the role substrates play in the distribution of freshwater sponge communities are rare. Here we evaluate the effect of different substrates and habitats in the distribution of freshwater sponge communities in the igapós of Anavilhanas, the world largest freshwater archipelago. Two surveys aiming to uncover the sponge fauna and corresponding substrates were performed in the Anavilhanas National Park at the low water period, when seasonally flooded surfaces are exposed. Two transects were carried out by boat along the margins of the River Negro and its canals among the islands or inside parts of the yet inundated forest. Also several higher parts of the islands at the time free of the flooding waters were crossed by foot. The sponge crusts were first visually searched for and next sampled, having its GPS taken and its environments and substrates shortly described. The association between the presence of nine sponge species, seven different environments and seven types of substrates detected were used in a Redundancy Analysis (RDA). The first two axes of RDA accounted for 45.9% of variation in the species data. The overall RDA was significant (P = 0.005; Number of permutations = 199). Substrates, especially trunks, branches, leaves and sand, were more important than environments to explain the variability in the distribution of sponge species.

Key words: Continental sponges, substrates, shaded habitats, flooding pulses, Brazilian Amazonia.

Resumo

Sendo animais sésseis, as esponjas de água doce dependem de um substrato sobre o qual suas larvas ou suas gêmulas se fixarão. Espera-se que espécies diferentes mostrem preferências ou adaptações a substratos e habitats específicos. Estudos para avaliar o papel dos substratos na distribuição de comunidades dessas esponjas são raros. Aqui avaliamos o efeito de diferentes substratos e habitats na distribuição de comunidades dessas esponjas, nos igapós de Anavilhanas, o maior arquipélago de águas doces do mundo. Dois levantamentos destinados a detectar a fauna espongológica e os correspondentes substratos foram feitos no Parque Nacional de Anavilhanas, no período de águas baixas, quando as superfícies estacionalmente inundadas estão expostas. Dois transectos foram percorridos de barco, ao longo das margens do rio Negro e seus canais entre as ilhas ou dentro das porções de florestas ainda inundadas. Porções mais elevadas no interior das ilhas, nessas ocasiões, livres da inundação, foram percorridas a pé. As

[1] Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul. Caixa Postal 1188, 90001-970, Porto Alegre, RS, Brasil.
[2] Departamento de Química, Instituto de Ciências Exatas, Universidade Federal do Amazonas. Av. General Rodrigo Octávio Jordão Ramos, 3000, 69077-000, Manaus, AM, Brasil.
[3] Programa de Pós-Graduação em Biodiversidade Animal, Departamento de Engenharia Sanitária e Ambiental, Universidade Federal de Santa Maria. Av. Roraima, 1000, 97105-900, Santa Maria, RS, Brasil.

crostas das esponjas foram inicialmente buscadas a olho nu e, em seguida, amostradas, registrando-se seu posicionamento geográfico (GPS), substrato e ambiente. A associação entre nove espécies de esponjas, sete diferentes ambientes e sete distintos tipos de substratos identificados foi utilizada em Análise de Redundância (RDA). Os dois primeiros eixos da RDA responderam por 45.9% da variação nos dados das especies. O RDA geral foi significativo (P = 0.005; Número de permutas = 199). Substratos, especialmente troncos, galhos, folhas e areia foram mais importantes do que os ambientes para explicar a variabilidade na distribuição das espécies.

Palavras-chave: esponjas continentais, substratos, habitats sombreados, pulsos de inundação, Amazônia Brasileira.

Introduction

Floodplains stand for about 8% of the Amazonian Biome, there included the Brazilian, Peruvian, Bolivian and Colombian Amazônia (Ferreira *et al.*, 2005). According to Prance (1979) igapó is a regional term applied to a type of soil and inundated forest subjected to swampy conditions resulting from seasonal flooding by black or clear Amazonian waters. The igapó forests as well as their other non forest vegetation occur in terrains of Tertiary or even Pre-Cambrian formations and as such poor in nutrients (Fittkau, 1971; Ayres, 1986; Ferreira and Almeida, 2005). The soil poverty takes to waters with very particular characteristics whilst the cover vegetation exhibits notorious adaptations to the flooding, sedimentation, erosion, pH and productivity conditions (Ferreira *et al.*, 2005). The Anavilhanas Archipelago stands for a notorious igapó area flooded by the black waters of River Negro, a contributor to the left lower stretch of the Amazon River.

The hard selection pressure exercised by the flooding pulses came out to favor freshwater sponges all along Central Amazonia because of their production of gemmules by which means they overcome the dry periods in várzea as well as in the igapó flooded areas (Volkmer-Ribeiro, 1981, 1999; Batista *et al.*, 2003; Volkmer-Ribeiro and Almeida, 2005). Because of their abundant occurrence in such environments the sponges cannot be disregarded in studies devoted to aquatic biocenosis surveys and community structures. River Negro is the largest black water river in the world. Olson *et al.* (1998) remarked that this basin detained good levels of preservation of its natural resources deserving high priority in conservation actions. Those came to take place with the settlement first of the Ecological Station of Anavilhanas (Federal Decret nº 86.061/87) and next with its transformation into the National Park of Anavilhanas (Federal Law nº 6409/05, which received the presidential approval on October, 29, 2008).

Studies targeted to specifically evaluate the role substrates play in the distribution of freshwater sponge communities are rare and none had been performed towards the ones living in a black water igapó. Jewell (1935) reports the most comprehensive observations of ecological factors affecting growth and distribution of freshwater sponges in lentic environments, until now. Her studies were carried on 102 lakes at Vilas County, northern Wisconsin, USA. No statistics were applied to the results and substrates were not specifically considered or related by her to the detected distributions. However, the color and shading of the waters came out as important factors favoring distribution. Most recently, Eggers (2001) and Dröscher and Waringer (2007) studied the relationship between habitat characteristics and freshwater sponges distribution in respectively branch canal Salzgitter, Lower Saxony, Germany and the Danubean floodplain in Austria. Droscher and Waringer (2007) were the sole authors to select substrates (macrophytes, dead wood and mineral surfaces) when searching for sponge specimens and habitat physical and chemical characteristics. In what respects the Amazonian region, Batista (2007) investigated the sponge fauna, its habitats and related ecological characteristics at the protected area of Meandros do Rio Araguaia at the States of Tocantins, Mato Grosso and Goiás, Brazilian Amazonia. This area exhibits an array of Amazonian lentic and lotic habitats seasonally flooded by a river with clear waters. Substrates were not given exclusive attention by the author, but were taken into consideration when composing a habitat, as for instance, the rocky bottoms and banks of the river. Statistics was applied to detect relationships of each sponge community with the surveyed habitats.

The array of different substrates offered by a tropical forest seasonally flooded by black waters and the lack of surveys of the sponge fauna of a large igapó of high priority in conservation led the authors to select the Anavilhanas National Park for this investigation. This paper aims at evaluating the role the substrates in this Amazonian system play in the distribution of freshwater sponge communities. The results are expected to contribute to the Park management projects as well as to the preservation of its sponge fauna.

Material and methods

Study area

The Anavilhanas Archipelago is located in the River Negro, 180 km northwest from Manaus, Amazonas

State, Brazil (02°00’ - 03°02’S and 60°27’ - 61°07’W). It is a complex of islands, ponds, channels, marshes and barrier islands. The Anavilhanas region resulted from a mega fluvial capture of the river bed due to a neo-tectonic process that altered the river course (Filho *et al.*, 2005). The Anavilhanas National Park is formed by the Archipelago itself and by a continental portion at the left margin of River Negro. It covers an area of 342,344 ha and comprises about 400 islands, which during some months of the year are partially submerged in the waters of the River Negro. Dozens of beaches with fine white sand and hundreds more clay-covered areas emerge around these islands during the dry season. These sandy soils are very common in the upper River Negro and occupy large areas. In the lower River Negro they appear in patches of a few hectares interspersed with clay soils (Oliveira *et al.*, 2001) and non-stratified deposits producing elongated islands consisting mainly of silt and clay; the sediment from the river bed has high clay content (Leenheer and Santos, 1980). The chemical characteristics of the River Negro waters, upstream of Manaus, include low ionic content (9-10 µS cm^{-1}), pH values of 4.8-5.1, low content of K, Na, Mg and Ca, with dominance of sodium, low alkalinity, high concentrations of silica among the dissolved solids and the humic acid content is ten times higher than in the Amazon River (Furch and Junk, 1997).

Sampling methodology

We sampled sponges in 36 sites in the Archipelago, on two occasions, in March 2010 (sites 1-28) and November 2010 (sites 29-36), on different sections of the archipelago, in other to capture the full range of habitats, substrates and species (Figure 1). The first survey was carried in the southern part of the park at the beginning of the flood period, and the second in the northern portion at the peak ebb, both providing good exposure of the flooded substrates. The searching and sampling of sponges was carried out by boat along the margins of the River Negro and its canals between the islands or in the inside parts of permanently inundated forest. Also, several higher parts of the islands at the time free of the flooding waters, were crossed by foot. Searching included a wide variety of substrates subjected to the seasonal flooding or permanently submerged, down to one meter from the drought water line. We recorded the geographical location with a standard GPS. We took photographs of specimens *in situ* to facilitate identification

Description of environments and substrates

At each point a specimen was collected we recorded the respective environment and substrate, arriving at the final classification of environments in seven categories, as follows:
(i) Open forest, corresponding to the forest in the higher flooded parts of the islands and surveyed dry by foot.
(ii) Igapó forest, corresponding to the close, monotonous, heavily shaded forest, covering the lower levels of the islands, with part of the trunks permanently flooded and surveyed by boat.
(iii) Sandy beaches, corresponding to large river margins covered by sand with sparse bushy vegetation, completely exposed at the peak of ebb and surveyed by foot.
(iv) Hard rocky margins, corresponding to narrow river margins with rock outcrops bordered by the riparian vegetation exposed at the peak of ebb and surveyed by foot.
(v) River sandstone banks corresponding to high soft sandstone outcrops exposed at the peak of ebb usually stuttered with fish holes and surveyed by boat.
(vi) Root curtains of the riparian trees exposed at the low water period at the river banks and surveyed by boat.
(vii) Muddy ponds corresponding to small ponds in the inner parts of some islands, reached along narrow canals and surveyed by foot.
We classified substrates in seven categories, as follows: (i) aerial roots; (ii) twigs; (iii) trunks; (iv) leaves; (v) bottom mud of the inner small ponds; (vi) sand; and (vii) rock or sandstone.

Identifying and cataloging procedures

We prepared spicular dissociation of the sponges accordingly to Volkmer-Ribeiro (1985) and Volkmer-Ribeiro and Turcq (1996) for studies with respectively, light optical and Scanning Electron Microscopy (SEM). The SEM photographs were treated and mounted with the use of computer graphics. Following identification voucher specimens were deposited and cataloged in the Porifera Collection of the Museum of Natural Sciences of the Fundação Zoobotânica do Rio Grande do Sul. (MCN-POR). No specimen was deprived of gemmules so that all the collected material could be identified to the specific level.

Data analysis

We calculated the frequency of occurrence per species as a ratio of the number of sites where each species was present. We explored the association between the presence of sponge species in the different environments and substrates with Redundancy Analysis (RDA), a method of choice for direct gradient analysis in community ecology for short gradients (Legendre and Legendre, 1998). Environmental variables are all binary. We performed the analyses in the package Vegan (Oksanen, 2009) in R statistical program version 2.11.1 (Development Core Team, 2010). We assessed the significance of ordination axes by permutation test (number of permutations = 199) using the mock Anova function for constrained ordinations. We run partial

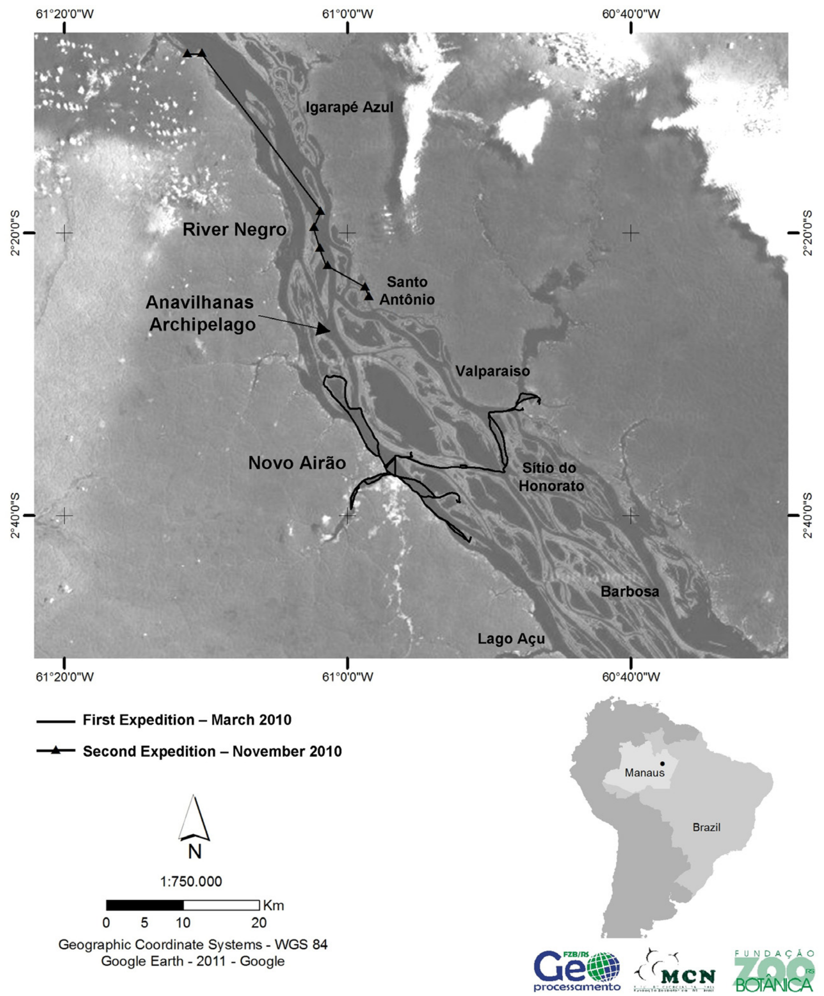

Figure 1. Map of the Anavilhanas Archipelago, Amazonas, Brazil, showing the routes of the two expeditions for sponge sampling carried out in 2010.

RDA to assess the contribution of the one set of the considered environmental variables - environments or substrates, when constrained by the other.

Results

We recorded nine species of sponges representing five genera from the three freshwater sponge families (Figure 2 and Table 1). The Archipelago sponge fauna showed no sign of endemism, the surveyed species being common in the Amazon Basin. Two species, both belonging to the Family Metaniidae, *Metania reticulata* (Bowerbank, 1863) and *Drulia uruguayensis* Bonetto and Ezcurra de Drago (1968) were the most largely distributed in the archipelago (Table 2). *Metania reticulata* was the most frequent species, found in 27 of the 36 sites surveyed. *Drulia uruguayensis* was the second species most frequent, found in 12 sites (33.3%) followed by *Metania fittkaui* Volkmer-Ribeiro (1979), found in 6 sites, with a 16.7% frequency of occurrence. Three species of the genus *Trochospongilla* Vejdowsky, 1883, *Oncosclera navicella* (Carter, 1881), *Drulia browni* (Bowerbank, 1863), and *Acalle recurvata* (Bowerbank, 1863), showed a low frequency of occurrence (2.8 %), all found in only one site (Table 2).

Metania reticulata appeared exclusively constituting remarkable populations that exhibit from thin to thick bulbous crusts on the slender trunks of the arboreal vegetation (Figure 3) characteristic of the most heavily shaded corners of igapós, and occupying levels from the base, near the ground (thus permanently submerged) to those levels of the longer residence of the flooding water (Table 2). *Drulia uruguayensis*, in turn, is a species typical of benthic environments, appearing in the Archipelago embedded in the muddy bottoms of small lakes in flooded areas (Figure 4) or in the sandy bottoms of the rivers margins (Figure 5). These two species also appear but sparsely, in all substrates affected by high floodwater but then in association, in the same substrates, to one or other of the species in the taxonomic list presented here. We did not find crusts of sponges in the dead standing trees fully exposed to light in the arms of the river between the islands, as well as in the riparian vegetation exposed to more intense light.

As a matter of fact, each one of the nine species detected at Anavilhanas exhibits anatomical characteristics which require particular substrates to enhance their seasonal growth. *Metania reticulata* invests in involving growths forming tuberous crusts around the slender trunks which characterize the long, slender trees inside the igapós (Figure 3). The hard closed reticulum of *M. reticulata* retains its gemmules inside inner cameras (Figure 6A). *Drulia uruguayensis* is a benthic dweller which displays hemispherical growths with a large, flat adhesion base and open, hard, hispid reticulum, adapted to stand muddy and sandy bottoms. This species also retains its gemmules inside hard, closed capsules linked to the sustaining skeleton (Figure 6B). *Trochospongilla paulula* (Bowerbank, 1863), *T. pennsylvanica* (Potts, 1882), *T. minuta* (Potts, 1887) and *A. recurvata* all develop slender delicate skeletons, with loosely held gemmules (Figure 6C). The interwoven roots pending at

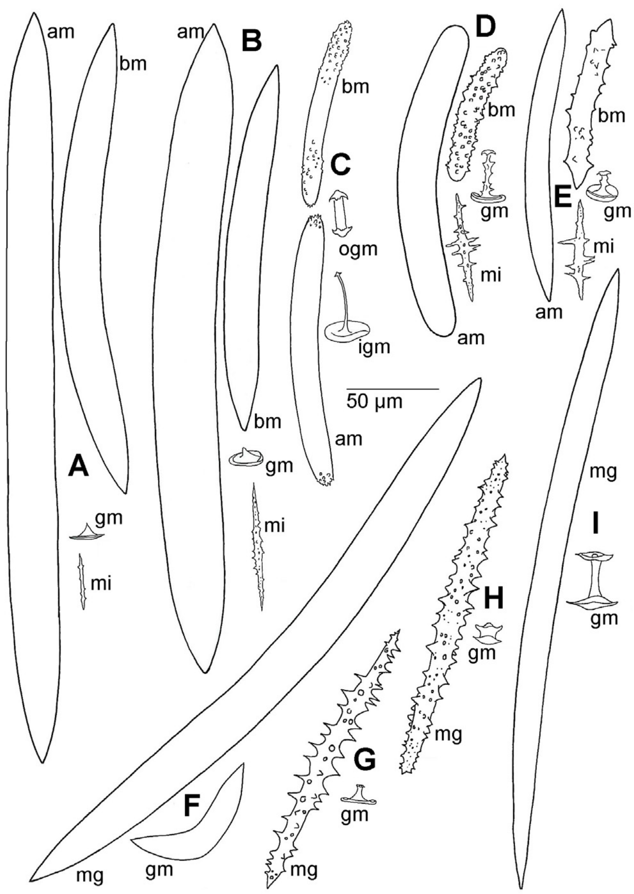

Figure 2. Drawings of the spicular set of the nine freshwater sponge species recorded in the Anavilhanas Archipelago, Amazonas, Brazil: A, *Drulia browni* (Bowerbank, 1863); B, *D. uruguayensis* Bonetto and Ezcurra de Drago (1968); C, *Acalle recurvata* (Bowerbank, 1863); D, *Metania reticulata* (Bowerbank, 1863); E, *M. fittkaui* Volkmer-Ribeiro (1979); F, *Oncosclera navicella* (Carter, 1881); G, *Trochospongilla pennsylvanica* (Potts, 1882); H, *T. minuta* (Potts, 1887); I, *T. paulula* (Bowerbank, 1863) (mg, megasclere; am, alfa megasclere; bm, beta megasclere; gm, gemosclere; agm, alfa gemosclere; bgm, beta gemosclere; mi, microsclere).

the river margins provide ideal substrates for these four species.

The overall RDA was significant ($P < 0.01$). The first two axes of RDA accounted for 45.9% of variation in the species data (Figure 7). The correlations between environmental characteristics and ordination axes (Table 3) show that substrates, especially trunks, branches, leaves and sand, were more important than environments to explain the variability in the distribution of sponge species. *Metania reticulata* was associated to tree trunks and branches and open and Igapó forests, *M. fittkaui* to rocks and leaves mainly in hard rocky margins of the river, and *D. uruguayensis* to sand, mud and tree roots. No clear pattern of occurrence was found for the other species. In partial RDA, inertia attributed to substrates constrained by environments was 0.22 (30.1 %), while inertia attributed to environments constrained by substrates was 0.12 (16.5 %). Unconstrained inertia was 0.28 (38.7 %).

Discussion

Continental sponges are sessile animals which heavily depend upon a substrate on which their larvae or their gemmules will settle. They generally use roots, stems, branches and even leaves of trees from the flooded banks or permanently submerged bedrock in the rivers (Volkmer-Ribeiro, 1981;

Table 1. Freshwater sponge species (Porifera: Demospongiae) registered in the Anavilhanas National Park, Brazil, the corresponding catalog numbers of the voucher specimens (MCN-POR) deposited in the MCN-FZB Porifera collection and frequencies of occurrence per substrate.

	Species	MCN-POR	Roots	Twiggs	Trunks	Leaves	Mud	Sand	Rocks
Family Spongillidae	*Trochospongilla paulula*	8456	-	-	-	1	-	-	1
	T. pennsylvanica	8472	-	1	-	-	-	-	-
	T. minuta	8512	1	-	-	-	-	-	-
Family Potamolepidae	*Oncosclera navicella*	8455	-	1	1	-	-	-	-
Family Metaniidae	*Metania reticulata*	8461	5	15	19	-	1	-	3
	M. fittkaui	8457	1	-	2	1	-	-	4
	Drulia browni	8474	-	1	1	-	-	-	-
	D. uruguayensis	8460	6	4	2	1	2	1	4
	Acalle recurvata	8469	1	-	1	-	-	-	-

Table 2. Sites where sponges were detected and sampled in the Anavilhanas National Park, Brazil, recorded sponge species, and their substrates and environments.

Sites	Location	Sponge Species	Substrates	Environments
1	02°37.156'S-60°57.471'W	*M. reticulata*	twiggs, trunks	open Forest
2	02°37.468'S-60°57.940'W	*M. reticulata*	twiggs, trunks	open Forest
3	02°37.593'S-60°59.029'W	*M. reticulata*	twiggs, trunks	open Forest
4	02°37.619'S-60°59.050'W	*M. reticulata*	twiggs, trunks	open Forest
5	02°37.825'S-60°59.242'W	*M. reticulata*	twiggs, trunks	open Forest
6	02°38.115'S-60°59.284'W	*M. reticulata*	trunks	open Forest
6	02°38.115'S-60°59.284'W	*O. navicella*	twiggs	open Forest
7	02°38.257'S-60°59.360'W	*M. fittkaui*, *D. uruguayensis*	rock/sandstone	river sandstone Banks
7	02°38.257'S-60°59.360'W	*T. paulula*	leaves	open Forest
8	02°39.556'S-60°59.790'W	*M. reticulata*	twiggs	sandy beaches
9	02°37.357'S-60°58.648'W	*M. reticulata, M. fittkaui*, *D. browni*	rock/sandstone	river sandstone Banks
10	02°35.783'S-60°55.403'W	*M. reticulata*	trunks	open Forest
11	02°36.425'S-60°52.066'W	*M. reticulata*	twiggs	open Forest
12	02°35.940'S-60°48.723'W	*T. minuta*, *D. uruguayensis*	root curtains	root of the riparian trees
13	02°32.445'S-60°47.661'W	*M. reticulata*, *A. recurvata*	root curtains	root of the riparian trees
13	02°32.445'S-60°47.661'W	*M. fittkaui*	trunks	open Forest
14	02°32.307'S-60°48.213'W	*T. pennsylvanica*, *M. reticulata*, *D. uruguayensis*	twiggs	open Forest
15	02°31.903'S-60°46.492'W	*D. browni*	twiggs	open Forest
15	02°31.903'S-60°46.492'W	*M. reticulata*	trunks	open Forest
16	02°31.588'S-60°47.888'W	*M. reticulata*	trunks	open Forest
17	02°39.001'S-60°52.250'W	*D. uruguayensis*	root curtains	open Forest
17	02°39.001'S-60°52.250'W	*M. reticulata*	trunks	open Forest
18	02°38.963'S-60°52.307'W	*M. reticulata*	trunks	open Forest
19	02°38.940'S-60°52.311'W	*M. reticulata*	trunks	igapó Forest
20	02°38.912'S-60°52.269'W	*M. reticulata*	trunks	igapó Forest
21	02°38.857'S-60°52.280'W	*M. reticulata*	trunks	igapó Forest
22	02°41.447'S-60°51.314'W	*M. reticulata*	twiggs, trunks	open Forest
23	02°40.006'S-60°53.699'W	*M. fittkaui*	bottom mud	hard rocky margins
24	02°39.963'S-60°53.830'W	*M. reticulata*	bottom mud	hard rocky margins
24	02°39.963'S-60°53.830'W	*M. reticulata*	root curtains	root of the riparian trees
25	02°32.663'S-61°00.021'W	*D. uruguayensis*	root curtains	root of the riparian trees
26	02°30.226'S-61°00.069'W	*M. reticulata*	trunks	igapó Forest
27	02°32.939'S-60°58.825'W	*M. reticulata*	trunks	igapó Forest
28	02°36.633'S-60°57.364'W	*M. fittkaui*	bottom mud	hard rocky margins
29	02°22.239'S-61°00.898'W	*D. uruguayensis*	root curtains, rock/ sandstone	hard rocky margins
30	02°20.991'S-61°01.935'W	*D. uruguayensis*	root curtains, twiggs	sandy beaches
30	02°20.991'S-61°01.935'W	*M. reticulata*	twiggs	sandy beaches
31	02°19.521'S-61°02.352'W	*M. reticulata*	twiggs	sandy beaches
32	02°18.371'S-61°01.894'W	*M. fittkaui*	trunks	open Forest
33	02°07.217'S-61°10.629'W	*D. uruguayensis*	rock/sandstone	hard rocky margins
33	02°07.217'S-61°10.629'W	*M. reticulata*	rock/sandstone	hard rocky margins
33	02°07.217'S-61°10.629'W	*M. reticulata*	twiggs, trunks	open Forest
34	02°07.252'S-61°11.297'W	*D. uruguayensis*	sand	sandy beaches
35	02°23.730'S-60°58.749'W	*M. reticulata*	root curtains, twiggs	rock/sandstone
35	02°23.730'S-60°58.749'W	*D. uruguayensis*	bottom mud	muddy ponds
36	02°24.436'S-60°58.480'W	*D. uruguayensis*	bottom mud	muddy ponds

Figure 3. Specimens of *Metania reticulata* (Bowerbank, 1863) (arrows) incrusting the slender trunks of trees at the inner part of an igapó in the Anavilhanas Archipelago, Amazonas, Brazil. The green crusts also belong to sponges, invested by a layer of green musky, due to their reserve of wet organic matter held inside the silicious skeleton. Photo: C. Volkmer Ribeiro.

Figure 4. Population of *Drulia uruguayensis* Bonetto and Ezcurra de Drago (1968) settled at the sandy beach of an island at the low water period. Photo: I.B. de Barros.

Figure 5. Population of *Drulia uruguayensis* Bonetto and Ezcurra de Drago (1968) settled at the muddy bottom of a small pond at the low water period. One specimen is shown in detail at the magnified right upper part of the photograph. Photo: I. B. de Barros.

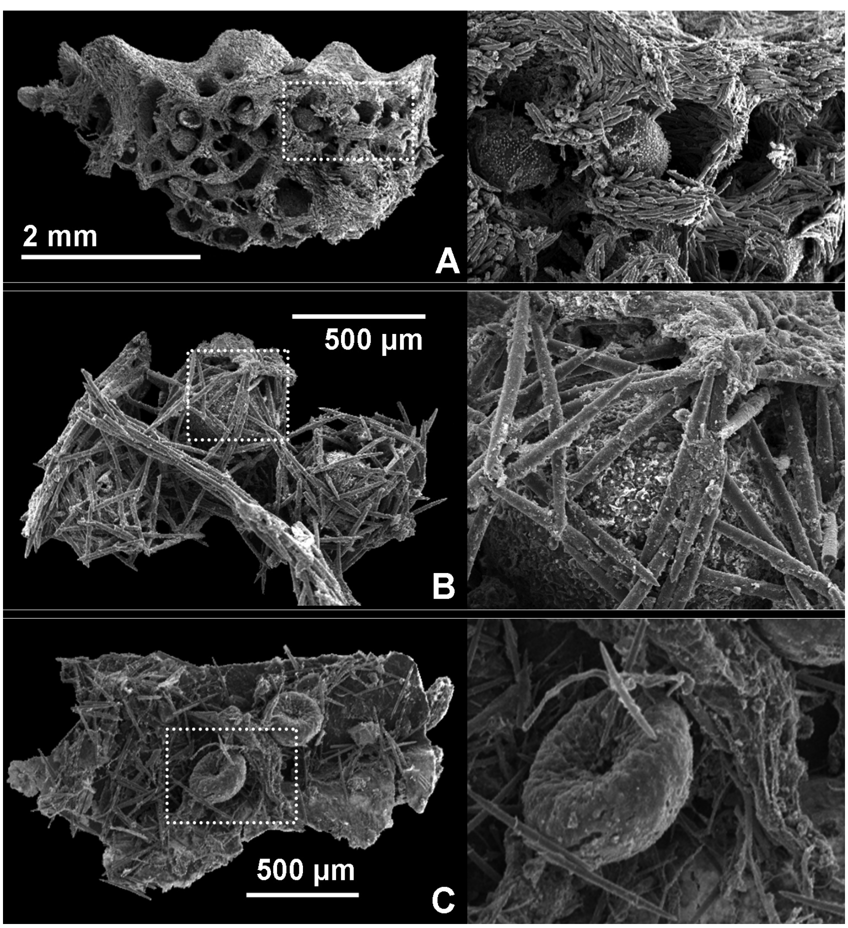

Figure 6. SEM illustrations of the skeletal structure and gemmular fixation in A, *Metania reticulata* (Bowerbank, 1863); B, *Drulia uruguayensis* Bonetto and Ezcurra de Drago (1968); C, *Trochospongilla paulula* (Bowerbank, 1863).

Frost, 1991) not to speak of iron, concrete and wood submerged structures (Jones and Rützler, 1975; Volkmer-Ribeiro *et al.*, 2010). Thus, the Anavilhanas Archipelago proved to be an area that greatly favored the establishment of a sponge fauna due to the seasonal offer of wide variety of substrates affected by high water. These consist of cylindrical stems of arboreal vegetation in the interior of the igapós; trunks, branches and leaves of flooded riparian vegetation; aerial/suspended roots along the river bank, branches and bushes along the white sand beaches, the sandy river shore, fish holes made by the banks of the river, stones/rocks along the banks in lotic environments; and the muddy bottoms of seasonal ponds.

The results reported by Dröscher and Waringuer (2007) for the five sponge species found at the Danube floodplain in Austria also emphasized the importance of hard substrates in the occupation of the environment, with a clear cut preference of different species for wood substrates or rocky substrates. Batista (2007) registered *Trochospongilla repens* (Hinde, 1881) as a species found only on the rocky bottoms of lotic environments at the APA Meandros do Rio Araguai, whereas *Trochospongilla paulula* restrained itself to encrust twigs and leaves of the seasonally flooded vegetation in the area. The present study comes, however, to enlighten a new fact in what respects the preference for substrates among species, whenever structure of the spicular reticula and growth forms are taken into consideration, as here reported for each one of the detected species. Thus, the shape and structure of these species seems to confirm the results obtained with the RDA analysis.

Based on the conducted sampling, two other findings of particular note were that all the observed specimens were some tone of brown in color and they were all situated in well shaded areas provided by the vegetation as well as by the river black waters at the flooding period. An observation, long re-

Table 3. Results of Redundancy Analysis (RDA) for the sponge communities at the National Park of Anavilhanas. Values are correlations between environmental characteristics and ordination axes.

Environmental characteristics	Axis 1	Axis 2
Roots	0.370	0.471
Branches	-0.488	0.372
Trunks	-0.728	-0.194
Leaves	0.479	-0.109
Mud	0.267	0.342
Sand	0.308	0.095
Rocks	0.532	-0.194
Open forest	-0.346	-0.029
Igapó forest	-0.364	-0.099
Sandy beaches	0.035	0.206
Hard rocky margins	0.298	-0.269
River sandstone	0.228	-0.025
Total inertia	0.237	0.099
Explained variation (%)	32.4	13.5

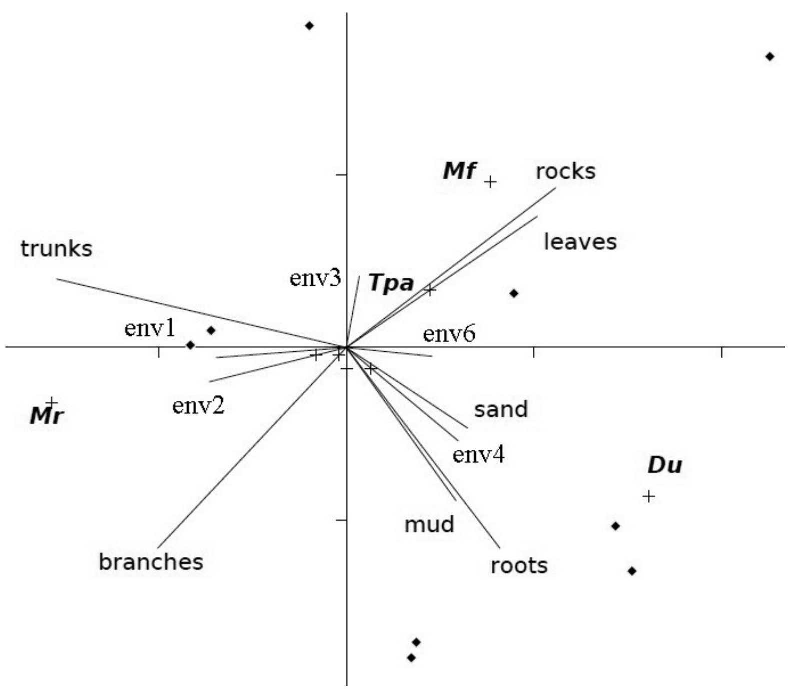

Figure 7. Biplot of the Redundancy analysis (RDA) of the sponge fauna. Env1, Open forest; Env2, Igapó forest; Env3, Sandy beaches; Env4, Hard rocky margins; Env6, root of the riparian trees (crosses: the sponge species; Diamonds: the samplings sites; Mf, *Metania fittkaui* Volkmer-Ribeiro (1979); Mr, *M. reticulata* (Bowerbank, 1863); Tpa, *Trochospongilla paulula* (Bowerbank, 1863); Du, *Drulia uruguayensis* Bonetto and Ezcurra de Drago (1968).

ported by Jewell (1935); Frost (1991) and also detected by the senior author when sampling for freshwater sponges, is confirmed here, which is the preference of most species for shaded habitats. An identical situation has been experimentally proved by Maldonado and Uriz (1998), in the selection of habitats by larvae of marine sponges.

The occurrence of encaged gemmules in *M. reticulata* and *D. uruguayensis* induce to consider that their dispersion in flooded areas must depend largely upon the free-swimming parenchymela larvae resulting from the sexual reproduction. There are no studies on the life span or behavior of these larvae in the freshwater sponges. Some enlightening in this respect may arise from data showing that marine sponges that also produce such larvae (Maldonado and Uriz, 1998) exhibited a preference for the settling in the shaded portions of micro-refuges. This photoreceptive ability, already reported by Frost and Williamson (1980) and Frost (1991), is supported in findings that indicate the presence in sponges of proteins involved in the process of photoreception and vision in other animal groups (Krasco *et al.*, 1997). It is therefore not unreasonable to suggest that the shaded environment of the flooded igapó summed to the brown color of the River Negro waters, provides an important condition in favor of the occupation of an array of particular substrates by the nine detected species of sponges.

All the sampled sponges at Anavilhanas contained gemmules and were totally exposed to the air at the time of the sampling. In the Amazon floodplain environments, subject to the flood pulse, the occurrence of sponges is due to their ability to produce gemmules, resistant bodies, by which means the diverse species are able to survive the periods of exposure to air in the varzea and igapó lakes (Volkmer-Ribeiro, 1981; 1999; Volkmer-Ribeiro and Almeida, 2005; Batista *et al.*, 2003). However, in the case of the two predominant species in the archipelago, a different situation is found regarding the dispersal function, because the gemmules of *M. reticulata* and *D. uruguayensis* are firmly welded to the original skeleton, and have reduced pneumatic layers. For the sponges attached to hanging roots particularly those of the genus *Trochospongilla*, dispersion may be mainly occurring through the displacement of their gemmules which are weakly retained in the fragile skeletons. The moving waters of the river in the flood seasons break them easily, releasing the gemmules for dispersion in both horizontal and vertical gradients.

Clearly, the sponges that permanently occupy the benthos of the river in all the arms between the islands were not sampled. However, at least one species, *D. uruguayensis*, registered here at the bottom of seasonal ponds is likely to be present in such environments, given its primary condition as a benthic species common to deep rocky bottoms of South American rivers (Volkmer-Ribeiro and Pauls, 2000).

The composition of the sponge fauna of Anavilhanas was very similar to that of Lake Tupé (Volkmer-Ribeiro and Almeida, 2005), which is a Ria lake, located on the left bank of the River Negro, 30 km northwest of Manaus. However, a slightly greater wealth of species was detected in Lake Tupé (11 species) in comparison to Anavilhanas (9 species). In Tupé, the most abundant species was also *M. reticulata*, which occupies the entire high floodwater level on the arboreal vegetation along the edge of the lake. However, the lake does not offer environmental features similar to those found at Anavilhanas, given the different situation in relation to the river channel. Tupé is a lake situated on the banks of the River Negro, which only receives water from the river in the rainy season, therefore, during the dry season, only the waters from the streams feed the lake (Scudeller *et al.*, 2005).

The archipelago of Anavilhanas, occupying the entire river channel, favors the formation of habitats with longer periods of flooding and which are multiplied by numerous islands. In this context, the occurrence of ponds where *D. uruguayensis* intensely occupies the muddy bottom substrate represents an unprecedented finding. Equally unprecedented is the occupation of sandy beaches where *D. uruguayensis* sets directly on the sand. On the other hand, the heavily shaded areas within the interior of the islands are occupied by monotonous shrubs of slender, straight individuals, with tuberous incrustations of *M. reticulata* below the low water mark up to the highest floodwater mark. Thus, more exclusive and seasonally drastically submerged environments are established at Anavilhanas, possibly taking the sponge fauna to a though selection, in which the pattern is the abundance of a few species at the expense of specific richness.

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