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**SPONGE SPECIES RICHNESS AND ABUNDANCE AS INDICATORS OF
MANGROVE EPIBENTHIC COMMUNITY HEALTH**

BY

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The Caribbean fire sponge (*Tedania ignis*) is a prominent member of the red-mangrove root community at Twin Cays and throughout the region. It contains a toxin that may cause severe skin irritation in humans but does not affect a rich community of invertebrates, such as entoprocts, polychaetes, crustaceans, and ophiuroid brittle stars which populates its surface and interior spaces. (Photo, Chip Clark.)

SPONGE SPECIES RICHNESS AND ABUNDANCE AS INDICATORS OF MANGROVE EPIBENTHIC COMMUNITY HEALTH

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MARIA C. DIAZ^{1,2}, KATHLEEN P. SMITH³, AND KLAUS RÜTZLER¹

ABSTRACT

In the Caribbean Sea, sponges are diverse and common colonizers of subtidal mangrove substrates such as aerial roots and peat banks. On the other hand, few species are widely distributed, whereas the majority is rare. Biodiversity studies should therefore cover appropriately sized survey areas to allow the encounter with species that have low population densities. In the characterization of sponge population structure at specific sites, it is preferable to use a large number of short transects rather than a few long ones. Trials conducted at mangrove islands on the southern Belize barrier reef platform show that surveying multiple transects of 15-20 m length along the fringe of tidal channels (covering 50-70 stilt roots) reveal more than 90% of the epibiont species present at each site. We found that the majority of the widely distributed species are among the most frequent colonizers and their abundance, with the exception of a few, is maintained over at least a six-year period. Sponge species richness can serve as a bioindicator of subtidal community health as long as there are baseline data to determine its variation over time. However, this method is not suitable for comparing geographically distant mangrove systems. Common and widely distributed mangrove species, such as *Haliclona manglaris*, *H. curacaoensis*, *H. implexiformis*, *Mycale magniraphidiphera*, *Clathria venosa*, and *Geodia papyracea*, and other generalist species, notably *Tedania ignis*, *Hyrtios proteus*, *Spongia tubulifera*, *Chondrilla nucula*, *Mycale microsigmatosa*, and *Scopalina ruetzleri*, may best reflect changes in the environmental conditions at particular sites. The families Chalinidae, order Haplosclerida (six *Haliclona* spp. and two *Chalinula* spp.), and Mycalidae, order Poecilosclerida (four *Mycale* spp.), include the most diversified taxa among mangrove sponge populations. Up to 20 percent of mangrove roots at Twin Cays harbored two or three *Haliclona* species each, whereas *Mycale* species were common but rarely two co-occurred on the same root. These families, in particular, are being investigated for their suitability as bio-indicators of mangrove health by evaluating changes in their population dynamics and responses to natural and anthropogenic ecological stress conditions.

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INTRODUCTION

Mangroves are among the most imperiled marine ecosystems since they are subjected to extreme anthropogenic environmental pressures, such as organic run-off from land, disturbances from suspended sediment, and damages from clear-cutting. The rich assemblage of species found associated with subtidal mangrove habitats (aerial roots, peat walls) offer the potential to serve as indicators of the biological and ecological status of this ecosystem. Among the most conspicuous and abundant epibionts of these habitats in the Caribbean we found algae, sponges, ascidians, anemones, and hydroids (Littler et al., 1985; Rützler and Feller, 1987, 1996; Calder, 1991; Ellison and Farnsworth, 1992; Rützler et al., 2000; Goodbody, 2000; Macintyre et al. 2000). In this work we summarize our understanding of the diversity and relative abundance of sponge epibionts on aerial roots of mangrove cays in southern coastal Belize, and we compare it with data generated from other Caribbean mangrove systems.

Until recently, knowledge about the biodiversity of Caribbean mangrove sponges was restricted to a few locations and was dispersed in regional taxonomic monographs, for instance, on the Dry Tortugas, Florida (de Laubenfels, 1936); Bermuda (de Laubenfels, 1950); Port Royal, Jamaica (Hechtel, 1965); Bahamas (Wiedenmayer, 1977); Lesser Antilles (van Soest, 1980, 1984); north-east Colombia (Zea, 1987); and Los Roques, Venezuela (Diaz et al., 1993). The largest research initiative focused on the diversity of mangrove sponges so far has taken place in Belize and was carried out as part of the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program based at the Carrie Bow Marine Field Station on the barrier reef of Belize (Rützler and Feller, 1987; 1996; Rützler, 1995; De Weerdt, et al., 1996; Hadju and Rützler, 1998; Rützler et al., 2000). We have learned that poriferan epibionts in Caribbean mangroves represent an untapped source of biological diversity, with distinct supra-generic composition, and with new species or sub-species to be discovered at every site or geographic locality examined in detail (Rützler et al., 2000).

Ecologically speaking, sponges in Caribbean mangrove systems are known to be dominant in abundance and species diversity, to offer their mangrove-root substratum direct protection from damaging isopod borings, and to stimulate root development by increasing nutrient availability through microbial symbionts (Rützler, 1969; Sutherland, 1980; Toffart, 1983; Alvarez, 1989; Bingham, 1992; Ellison et al., 1996; Farnsworth and Ellison, 1996; Diaz and Ward, 1997; Diaz et al., in press). Sponge distribution shows a vertical zonation that is determined by the frequency of air exposure (Rützler, 1995). Farnsworth and Ellison (1996) report that massive sponges dominate the fouling community, both in terms of numbers of roots occupied (35%) and percent of space covered (30%) on red mangrove prop-roots which on average have 90% of their subtidal portion covered by epibionts. Competitive abilities, such as growth rates and chemical defenses against predation play an important role in sponge abundances (Wulff, 2000, 2002). Successful colonization of roots appears to be controlled primarily by the supply of larvae (Farnsworth and Ellison, 1996) that are known, among tropical sponges, to have poor dispersal and recruitment ability (Zea, 1993, 1996; Rützler et al., 2000).

We have recently initiated a multi-site monitoring effort to evaluate the status of sponge populations at two Caribbean sites: Bocas del Toro in Panama, and Twin Cays and Manatee Cay in Belize. By studying the structure and dynamics of sponge populations at these sites we expect to extract patterns of distribution and abundance that may serve as an indicator measure of epibiont community health. In the present work, we will analyze data published and new data on the diversity and abundance of sponges on mangroves in southern Belize, and compare them with observations obtained elsewhere in the Caribbean. We will discuss the potential use of sponges in the evaluation of mangrove systems health.

LOCALITIES AND METHODS

Five sites, four at Twin Cays, and one in the Pelican Cays were selected as study locations. Table 1 lists their geographic coordinates, and habitat conditions. At Twin Cays, two sites (Sponge Haven South and Sponge Haven North) were established along the main channel on the leeward side of the West Island, and two sites (Hidden Creek and The Lair) were determined along deep channels that branch off the main channel (see map in Rützler et al., 2004). These latter two channels are less exposed to waves from wind and passing boats, the most common water disturbances in the islands. Hidden Creek and The Lair both are contiguous to internal ponds and lakes and therefore strongly influenced by twice-daily tidal changes that empty and fill these lagoons. The site in the Pelican Cays is located in lagoon C of Manatee Cay, and is characterized by low water turbidity, low wave exposure, and proximity to coral reefs (Macintyre et al., 2000).

Transects (30 m long) were placed along the red-mangrove fringe at each site. On each root within a transect, we counted the presence of all sponge species and nine other

Table 1. Location of sites in mangrove islands on the southern Belize barrier reef surveyed during August 2003, and some of their physical characteristics.

Site	Coordinates	Depth (m)	Wave exposure	Turbidity	No. roots/m	Mangrove habitat
Lair channel ¹	16° 49' 46.3" N 88° 06' 06.1" W	1.5–1.8	Very low	Low	3.5	Internal channel
Sponge Haven South ¹	16° 49' 40.5" N 88° 06' 16.5" W	1–1.8	Low	Mid	3.3	Main channel
Sponge Haven North ¹	16° 49' 43.3" N 88° 06' 17.1" W	1–1.2	Low	Mid	4	Main channel
Hidden Creek ¹	16° 49' 33.7" N 88° 06' 11.3" W	1.8–2	Very low	Mid	2	Internal channel
Manatee Lagoon ²	16° 40' 03.3" N 88° 11' 32.4" W	1–1.5	Very low	Low	4	Pond

¹Twin Cays; ²Pelican Cays

of the most conspicuous functional groups (grouped taxa): filamentous cyanobacteria, fleshy green algae, calcareous green algae, fleshy red algae, calcareous red algae, macroalgal turf (mixture of various algal species), anthozoans, bivalves, and ascidians. The sponge species were photographed, and if their identity was unclear, a small fragment was collected, fixed in a solution of formalin in seawater (10%), and transferred into ethanol 70% within a week. At the field station, a compound microscope was used to examine skeleton structure in dried hand sections cleared in Permout medium (Fisher Scientific). Spicule types were determined after dissolving samples in concentrated household bleach (5% sodium hypochlorite).

Abundance estimates were expressed as a percentage of number of roots that were occupied for each species or group. To allow comparison of abundance of sponge species between this study and Rützler et al. (2000), we distinguished three categories of abundance: 1= rare, for species found in 1-2% of roots; 2= common, for species found in 3-19% of roots; and 3= abundant, for species found in >20% of roots.

RESULTS

Sponge Species Richness at Twin Cays

A total of 35 species were found among the four sites studied at Twin Cays, with 19-23 species detected per site within each transect (Tables 2, 3). Farnsworth and Ellison (1996) reported 20 sponge species at five Twin Cays sites, whereas Rützler et al. (2000) recorded 54 species with approximately 26-42 species per locality (Table 4). In the present study, four species were found only at the Manatee Cay lagoon site: *Chondrilla nucula*, *Placospongia intermedia*, *Mycale "americana"*, and *Amphimedon erina*.

The cumulative number of sponge species per roots surveyed at each study site is expressed in a graph to demonstrate the species area relationship in these communities (Fig. 1). The typical asymptotic curve is obtained for all sites. Overall, the number of species increases until 60-70 roots have been surveyed, stabilizing and changing but slightly after that. This number of roots corresponds to a 15–20 m distance. The number of sponge species per root ranged from 1–8, with a mean species richness value of 1.8–3 (Table 4). Hidden Creek presents the highest species richness per root, despite showing the lowest total number of species.

Table 2. Sponge diversity on mangrove aerial roots at five sites surveyed during August 2003.

Quantitative parameters	Lair channel	Sponge Haven South	Sponge Haven North	Hidden Creek	Manatee Lagoon
Species per root (mean, SD)	2 ± 2	1.8 ± 1.5	2.4 ± 1.6	3 ± 2	1.9 ± 1.4
Species number (range)	1–8	1–6	1–6	1–8	1–5
Species number (total)	22	23	21	19	28

Table 3. Sponge species distribution and frequency of occurrence (%) on roots observed along transect lines at five sites in Central Belize during a survey in August 2003.

Species	The Lair	Sponge Haven South	Sponge Haven North	Hidden Creek	Manatee Lagoon
<i>Oscarella</i> sp.	0	1	0	0	1
<i>Cinachyrella apion</i>	0	0	0	5	0
<i>Geodia papyracea</i>	0	0	1	0	0
<i>Chondrilla nucula</i>	0	0	0	0	19
<i>Placospongia intermedia</i>	0	0	0	0	1
<i>Spiraastrella mollis</i>	0	0	0	0	2
<i>Terpios manglaris</i>	0	0	1	0	0
<i>Tethya</i> aff. <i>actina</i>	1	0	0	0	0
<i>Lissodendoryx</i> aff. <i>isodicyialis</i>	10	10	13	24	0
<i>Biemna caribaea</i>	21	2	13	34	1
<i>Clathria schoenus</i>	0	1	20	0	2
<i>C. microchelus</i>	4	15	7	2	3
<i>C. venosus</i>	2	0	5	5	6
<i>Mycale microsigmatosa</i>	2	6	20	0	2
<i>M. magniraphidifera</i>	5	2	7	2	1
<i>M. carmigropila</i>	0	1	0	0	2
<i>M. "americana"</i>	0	0	0	0	3
<i>Iotrochota birotulata</i>	0	0	0	0	2
<i>Tedania ignis</i>	11	27	33	34	26
<i>Scopalina ruetzleri</i>	0	1	1	3	4
<i>Amorphinopsis</i> sp.	1	0	0	14	0
<i>Halichondria magniconulosa</i>	0	20	17	25	21
<i>Haliclona implexiformis</i>	21	2	20	36	0
<i>H. curacaoensis</i>	27	11	34	44	0
<i>H. manglaris</i>	22	47	39	9	0
<i>H. tubifera</i>	9	3	1	5	0
<i>H. vermeulensis</i>	0	0	0	0	1
<i>Haliclona</i> sp.	0	0	0	0	1
<i>Chalinula pseudomolibta</i>	2	0	0	3	0
<i>Amphimedon erina</i>	0	0	0	0	9
<i>Hyrtios proteus</i>	11	13	6	20	6
<i>Ircinia felix</i>	1	7	0	0	0
<i>Spongia tubulifera</i>	5	6	12	10	6
<i>S. pertusa</i>	3	0	0	0	3
<i>Dysidea etheria</i>	14	0	2	0	0
<i>Chelonaplysilla erecta</i>	0	0	0	0	2
<i>Pleraplysilla</i> sp.	0	0	0	0	3
<i>Halisarca</i> sp.	3	0	0	7	0
<i>Clathrina</i> aff. <i>coriacea</i>	16	1	13	10	16

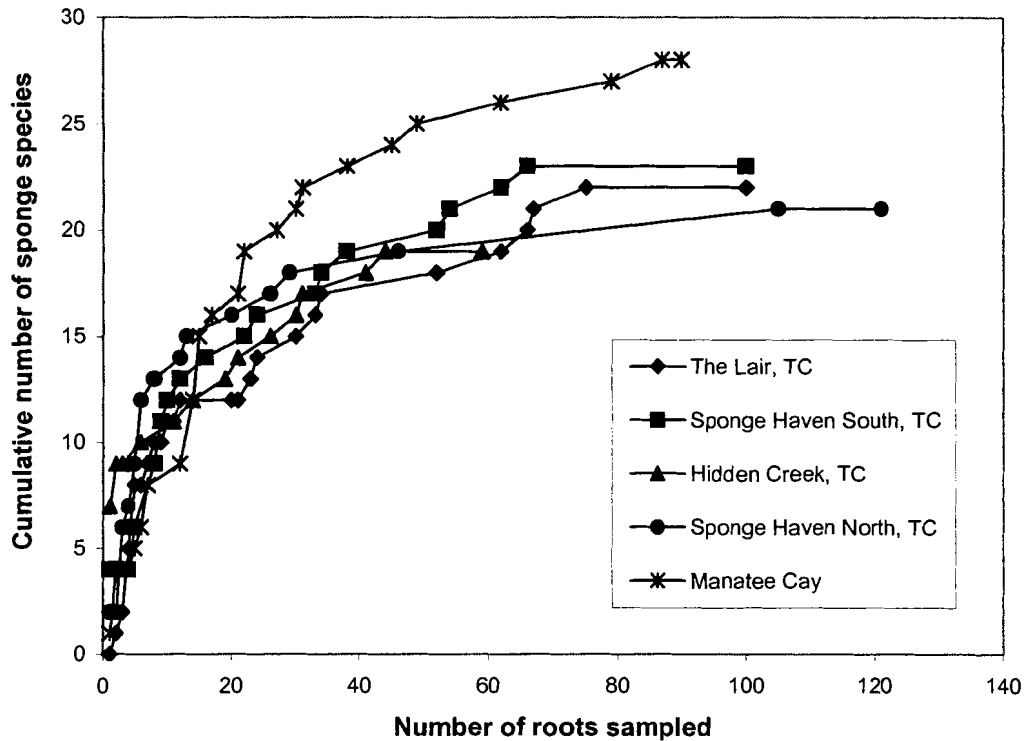


Figure 1. Cumulative number of sponge species on roots surveyed along fringe transects at four Twin Cays (TC) sites and one Pelican Cays site (Manatee Cay); survey of August 2003.

Trends in Sponge Species Richness in Caribbean Mangroves

The data on sponge diversity at geographically distant Caribbean sites (Table 4) shows that sponges can represent a moderate (8–15%) to high (>50%) portion of mangrove-root epifaunal diversity. An extremely diverse mangrove epibiont community was found at the Pelican Cays in southern Belize, with a sponge richness that equaled the taxonomic diversity of macroalgae, 147 species versus 148 species for each group, respectively (Littler et al., 2000; Rützler et al., 2000). The highest diversity occurs in mangrove channels, or lagoons, with depths >1m, and water of low turbidity (Alcolado, in prep; Rützler et al., 2000). The best studied area in the Caribbean, in terms of the biodiversity of marine sponges associated with mangroves, includes several Cays spread over a 50 km section behind the barrier reef of southern Belize (Rützler et al., 2000). The authors found that mangrove sponge species richness may be highly variable within a relatively small geographic scale, such as the difference between low-diversity Twin Cays and Blue Ground Range (54 and 57 species) and rich Pelicans Cays (147 species), located 12–24 km away. Various studies have shown that the Pelican Cays present particular biological and physical conditions that promote epibiont diversity (Table 5). Farnsworth and Ellison (1996) found that this high variability of species composition and richness may also occur between contiguous roots, channels, and lagoons at any one mangrove island.

Table 4. Numbers of sponge and mangrove epifaunal species reported from various Caribbean localities. (NA= not available.)

Reference	Locality	Number of sponge species	Number of Epifauna Species
Rützler, 1969	Bahamas	13	NA
Sutherland, 1980	Morrocoy, Venezuela	16	32
Toffart, 1981 ¹	Guadalupe	10	70
Toffart, 1981 ¹	Puerto Rico	8	75
Toffart, 1981 ¹	Trinidad	4	50
Toffart, 1981 ¹	Florida	4	32
Diaz et al., 1985	Morrocoy, Venezuela	25	NA
Orihuela et al., 1991	La Restinga, Venezuela	18	35
Bingham and Young, 1992	Indian River, Florida	3	25
Farnsworth and Ellison, 1996	Wee Wee, Spruce, Peter Douglas, and Twin Cays	24	59
Rützler et al., 2000	Twin Cays, Belize	54	NA
Rützler et al., 2000	Pelican Cays, Belize	147	217 ²
Alcolado (unpubl.)	North & S.W. Cuba	48	NA
Diaz et al. 2003	La Restinga, Venezuela	42	NA
Diaz (in prep)	Bocas del Toro, Panamá	60–70	NA

¹See Toffart (1981) for sources of data from each site; ²Number of sponge and ascidian species

Table 5. Comparison of sponge species richness, biological traits, and turbidity level of the subtidal environment at three geographically contiguous sets of mangrove islands behind the barrier reef in southern Belize.

Biological and physical traits	Twin Cays	Blue Ground	Pelican Cays
Sponge species richness (Rützler et al., 2000)	57	54	147
Open-reef taxa (Rützler et al., 2000)	None	Low	High
Spongivorous predators (Wulff, 2000)	Low	NA	High
Roots/ m	2.2	3.6	4-6
Turbidity	Mid	High	Low

Sponge Species Distribution

Figure 2 depicts the diversity of sponge epibionts on mangrove substrates at seven sites in five southern Belize cays from a survey in 1997 (Rützler et al., 2000). Forty four percent of the species (80 spp.) were present only at one site, Cat Cay, whereas less than 4% (7 spp.) were found to be common to all seven localities studied; these were,

Chondrilla nucula, *Clathria venosa*, *Tedania ignis*, *Scopalina ruetzleri*, *Haliclona manglaris*, *Hyrtios proteus*, and *Spongia tubifera*. We should note that *C. nucula*, *T. ignis*, *S. ruetzleri*, and *H. proteus* are species that can also be found inhabiting seagrass beds and shallow reefs habitats nearby. *C. venosa*, *H. manglaris*, and *S. tubifera* seem to be the only mangrove-specific species that are found across the mangrove cays of southern Belize.

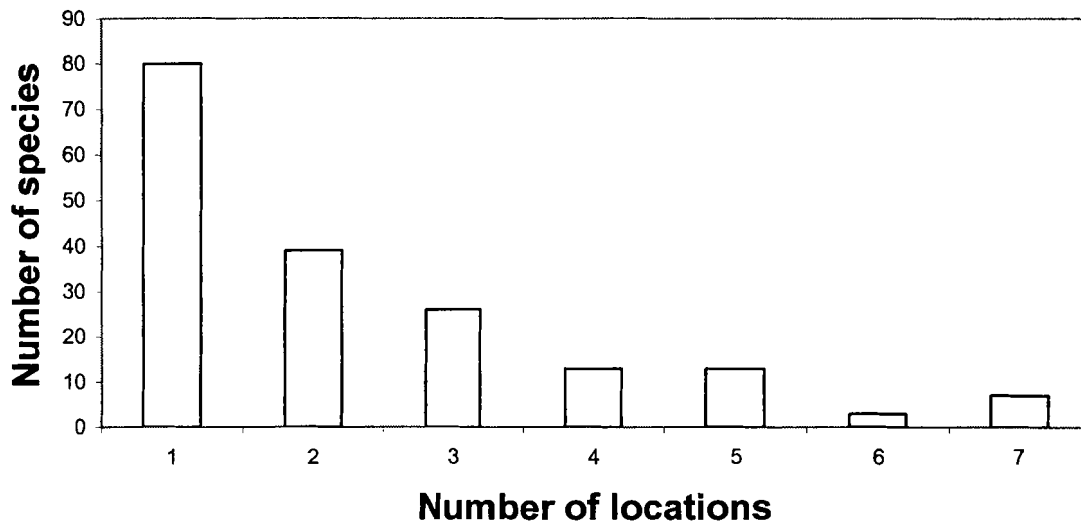


Figure 2. Frequency of sponge species shared between seven locations at five mangrove cays in southern Belize during a survey in 1997 (data from Rützler et al., 2000).

The presence and frequency of occurrence of sponge species on stilt roots determined during the present study are shown in Table 3. Seven species were present at all five study sites: *Biemna caribaea*, *Clathria microchelus*, *Mycale magniraphidifera*, *Tedania ignis*, *Hyrtios proteus*, *Spongia tubulifera*, and *Clathrina* aff. *coriacea*. Comparing with the 1997 survey we find that *T. ignis*, *H. proteus* and *S. tubulifera* maintained their wide distribution, but *Haliclona manglaris*, *Clathria venosa*, and *Scopalina ruetzleri* were found at only four sites. *C. nucula* seemed to have disappeared from the Twin Cays sites whereas in 1997 it was found to be either common (Sponge Haven South) or rare (Hidden Creek). *M. magniraphidifera* and *Clathria microchelus* which were, respectively, rare or absent in 1997, are found at all sites in the present survey. We should also note the absence of four typical mangrove species of *Haliclona*, that is, *H. curacaoensis*, *H. implexiformis*, *H. manglaris*, and *H. tubulifera* from the recently surveyed area at Manatee Cay Lagoon C.

Sponge Species Relative Abundance

The most abundant species at the Twin Cays sites are: *Haliclona manglaris* (9-47%), *H. curacaoensis* (11-44%), *H. implexiformis* (2-36%), *Biemna caribaea* (2-34%), *Tedania ignis* (11-34%), *Lissodendoryx* aff. *issodyctialis* (10-24%), *H. magniconulosa* (17-25%), *Hyrtios proteus* (6-20%), and *Clathrina* aff. *coriacea* (1-16%). Comparing these results with the 1997 survey, we find that *M. magniraphidifera* changed its

abundance from rare to common, and that *G. papyracea* decreased its high abundance (in Hidden Creek, and Sponge Haven South) to an apparent absence. In Manatee Cay we found that the most abundant species were *T. ignis* (26%), *Halichondria magniconulosa* (21%), *C. nucula* (19%), *C. aff. coriacea* (16%), *A. erina* (9%), *Hyrtios proteus* (6%), and *S. tubulifera* (6%). *H. magniconulosa* was absent in Manatee Cay during the 1997 survey but became an abundant species in 2003.

Grouped Taxa Relative Abundance

In the present work, the frequency of occurrence of grouped taxa is used as an indicator of their abundance (Table 6). Sponges were the most common root colonizer (67-88%) at all Twin Cays sites, ascidians were second (27-47%). At Manatee Cay,

Table 6. Frequency (%) of occurrence of the 10 most common epibiont taxa on mangrove aerial roots at five sites on the southern barrier reef of Belize during a survey in August 2003.

Root numbers and taxa	The Lair	Sponge Haven South	Sponge Haven North	Hidden Creek	Manatee Lagoon
No. of roots surveyed	105	99	121	59	89
Cyanophytes (filamentous)	31	36	37	12	16
Chlorophytes (fleshy)	23	8	17	15	25
Chlorophytes (calcareous)	1	5	1	2	0
Rhodophytes (fleshy)	18	9	16	25	20
Rhodophytes (calcareous)	0	15	5	0	2
Macroalgae turf	8	10	0	14	0
Sponges	67	79	88	75	87
Cnidarians (<i>Aiptasia</i> sp.)	10	20	24	8	0
Bivalves (mangrove oyster)	12	7	5	5	3.4
Ascidians	34	47	27	41	90

sponges were second (occupying 87% of roots) after ascidians (90%). At Twin Cays sites, ascidians were followed by filamentous cyanobacteria (12-36%), fleshy chlorophytes (8-25%), and the anthozoan *Aiptasia* sp. (8-24%).

DISCUSSION

Sponge Diversity

Data presented here and elsewhere show that sponges constitute one of the most diverse single groups of animals among the epibiont community of mangrove aerial roots. Species richness data from different Caribbean localities reveal sponge diversities from a few up to 147 species (Table 4), depending apparently on a combination of physical parameters, such as water turbidity, salinity, wave exposure, root density, and tidal ranges, and biological factors, such as competition, larval supply, and predation (Calder, 1991; Littler et al., 1985; Taylor et al., 1986; Ellison and Farnsworth, 1992; Rützler, 1995; Rützler et al. 2000; Wulff, 2000). Calm, clear, open-ocean-influenced deeper lagoons or channels seem to favor sponge colonization and growth.

The variability of species richness reported from Caribbean sites may be the result of different sampling methods. For example, in the current study we recorded 28 sponge species when surveying a 30 m transect along the fringe at Manatee lagoon. Previously, in 1997, seven sponge experts collected 95 species while swimming along the entire 638 m perimeter of the same lagoon (Rützler et al., 2000). A similar example is a study of red mangrove root epifauna at La Restinga National Park (Venezuela) where Orihuela et al. (1988) reported 18 species at five study sites. Subsequently, one of us involving 12 students found 33 species, including two new records for Venezuela, while swimming along the fringe for one hour at each of three sites (Diaz et al., 2003). This discrepancy in results is mostly due to the patchiness of species distribution and to the fact that 60% of the species are rare, that is, they are found only once or twice in a survey. It is therefore necessary to determine optimal transect length and numbers to determine an accurate measure of species richness.

Three surveys carried out at Twin Cays over the past 10 years resulted in three different estimates of sponge species richness: 20 species from three sites (Farnsworth and Ellison, 1996), 54 species from four sites (Rützler et al., 2000), and 35 species from four sites (this study). Two major factors might have contributed to these differences. First, the area covered by the surveys, which for Rützler et al. (2000) included the entire fringe, for Farnsworth and Ellison (1996) and our own study was restricted to discontinuous 50 m and 30 m transects, respectively. Farnsworth and Ellison (1996) surveyed 50 roots within each transect whereas we examined 59–121 roots per site, thus registering a larger species number despite the shorter transects. Another possible factor contributing to these differences is the level of sponge expertise of the surveyor. It is probable that more species can be differentiated by a person who is familiar with the morphological variations in this group. Considering the different methods, efforts, and skill levels employed in the various studies of sponge diversity, we believe that the richness of sponge species in Caribbean mangroves is far underestimated. We conclude that an accurate estimate of sponge biodiversity in mangroves, as in other habitats, requires large survey areas or long transects (for instance, along the fringe of the forest) and inclusion of several topographically representative sites at each island or location, rather than short random transects.

The most diversified sponge taxa recorded in our study belong to the family Chalinidae (6 *Haliclona* spp., 2 *Chalinula* spp.) and the Mycalidae (4 *Mycale* spp.). Three to 21 percent of the roots supported 2–3 chalinid species (Sponge Haven South 3%, The

Lair 17%, Hidden creek 11 %, Sponge Haven North 21 %). In contrast, although only second in importance, rarely is more than one mycalid species found on one root.

Sponge Distribution and Abundance

About half of the sponges from mangrove roots in Twin Cays are rare or low in abundance, that is, occurring only at one or two of the various study sites (20 of 40 spp. in 2003). The comparison between the two surveys carried out in southern Belize (Rützler et al.; 2000; and present study) allows to conclude that the majority of the species that are widely distributed across the region (*Clathria venosa*, *Scopalina ruetzleri*, *Tedania ignis*, *Haliclona manglaris*, *Hyrtios proteus*, *Spongia tubifera*) maintained a wide geographic distribution during this six year period. Few species increased their geographic distribution, such as *Biemna caribaea*, *Clathria microchelus*, *Mycale magnirhaphidiphera*, *Halichondria magniconulosa*, and *Clathrina* aff. *coriacea*, and others, such as *Geodia papyracea* and *Chondrilla* aff. *nucula*, decreased it. Farnsworth and Ellison (1996) found that the rank a major species had in frequency of occurrence (number of roots occupied by a species) was maintained during their two year study. However, the relative importance and dominance (% area coverage) of individual species and species groups varied substantially between two years of sampling. In general, it seems that widely distributed species tend to be frequent colonizers, and this status tends to be maintained through time. On the other hand, there are other less common species that might be restricted to one island or locality but occur there in very high abundance. This is the case for *Mycale microsigmatosa* and *Clathria schoenus* (20% each at Sponge Haven North) and *Dysidea etheria* (15% at The Lair). Table 7 lists the species that have been reported in various studies as the most frequent or abundant mangrove root colonizers. As can be seen, *Haliclona* spp, *T. ignis*, *Lissodendoryx issodyctialis*, *S. ruetzleri*, *Dysidea janiae*, and *H. magniconulosa* represented the most conspicuous species on the mangroves in at least two Caribbean localities. Among these species, some are mangrove specialist species (*L. issodyctialis*, *H. magniconulosa*, and *Haliclona* spp.), whereas others are generalists found also in seagrass beds and on some coral reefs (*T. ignis*, *S. ruetzleri*).

Sponges as Biological Indicators of Mangrove Health

Owing to the high natural variability of sponge diversity among mangrove islands, we do not recommend the use of species numbers as indicators of the health status of a particular mangrove system without a baseline study that allows interpretation of changes over time. On the other hand, certain sponge species could serve as biological indicators of mangrove health. Sponges have been recognized as good indicators of organic and oil pollution in subtidal reef habitats (Alcolado and Herrera, 1987; Muricy et al., 1989). Some of the requisites are that selected species are normally abundant in the study area, easy to sample in quantity, and show clear responses to the stress factors affecting the community (Linton and Warber, 2003). The first two requirements are easily satisfied by several species inhabiting Belizean mangroves. However, among these common species, one must distinguish two groups: Generalists with wide habitat preference that inhabit mangrove roots and peat walls, seagrass, and coral reefs, and mangrove specialists that inhabit predominantly mangrove roots. In Belizean mangrove

Table 7. Sponge species recognized as the most frequent or abundant in Caribbean mangrove systems. (MS= mangrove specialist; G= generalist found in mangroves, seagrass beds, and coral reefs; U= preference not known.)

Species	Rützler (1969)	Diaz et al. (1985)	Alcolado (unpublished data)	Farnsworth & Ellison, 1996	Present study	Habitat preference
<i>Myriastra kalitetilla</i>	X					MS
<i>Chondrilla nucula</i>	X					G
<i>Lissodendoryx isodictyalis</i>		X	X		X	MS
<i>Biemna caribaea</i>					X	MS
<i>Liosina monticulosa</i>			X			U
<i>Desmacella janiae</i>		X	X			U
<i>Clathria</i> (as <i>Raphidophlus</i>) <i>schoenus</i>		X				G
<i>Mycale microsigmatosa</i> ¹			X			G
<i>Tedania ignis</i>	X		X	X	X	G
<i>Scopalina ruetzleri</i>			X		X	G
<i>Halichondria magniconulosa</i>		X	X		X	MS
<i>Haliclona implexiformis</i>				X	X	MS
<i>H. curacaoensis</i>				X	X	MS
<i>H. manglaris</i>					X	MS
<i>Haliclona</i> sp.	X					G
<i>Amphimedon viridis</i>		X				G
<i>Hyrtios proteus</i>					X	G
<i>Ircinia felix</i>	X		X			G
<i>Spongia</i> spp.		X			X	G
<i>Dysidea etheria</i>			X			G
<i>Clathrina</i> aff. <i>coriacea</i>					X	G

¹This species has been found by one of us (CMD) growing profusely on pilings and other artificial substrates near Bocas del Toro, Panamá.

islands, the first group includes, in order of importance, *Tedania ignis*, *Hyrtios proteus*, *Spongia tubulifera*, *Chondrilla nucula*, and *Scopalina ruetzleri*. The second group is made up primarily by *Haliclona manglaris*, *H. curacaoensis*, *H. implexiformis*, *Mycale magniraphidiphera*, *M. microsigmatosa*, *Clathria venosa*, and *Geodia papyracea*. Knowing the life histories of these species in terms of growth and recruitment rates, longevity, microhabitat preference, competitive abilities, and chemical toxicity allows us to interpret responses to possible stressors, such as changes in distribution and abundance. Muricy et al., (1989) demonstrated this concept among common inhabitants of rocky subtidal habitats in Brazil that have been subjected to organic and oil pollution,

that is, *T. ignis*, *C. nucula*, *S. ruetzleri* and *M. microsigmatosa*. An increase of generalist species (such as, *T. ignis*) on the mangrove roots at the expense of the disappearance of a mangrove specialist could be a sign of alarm that physical or biological conditions are dropping to levels that only ecologically resilient species might be able to confront and survive. Among the specialist species encountered in our study, members of the families Chalinidae and Mycalidae have great potential owing to their high diversification and abundance in mangrove ecosystems. In Belizean mangroves, the best candidates to serve as biological indicators of mangrove health are *H. manglaris*, *H. curacaoensis*, *H. implexiformis*, *M. magniraphidiphera*, and *M. microsigmatosa*; they have widespread distribution and high colonization frequency on mangrove roots.

Relative Abundance of Functional Groups

Our data on the abundance of major functional groups on roots along the fringe of Twin Cays channels reflect Farnsworth and Ellison's (1996) descriptions of leeward sites of islands where sponges and ascidians are the most frequent colonizers whereas algae and hydroids dominate windward locations. Toffart (1983) examining mangrove sites in Guadalupe found two major communities: one in the tidal canals where roots are covered mainly by annelid tube worms and amphipod crustaceans, the other along the lagoonal shoreline characterized by ascidians and sponges. Alcolado (personal comm.) reports that sponge populations are absent in areas close to river inputs and in very shallow water with high suspended-sediment content, but abound in locations that are influenced by the sea, with dense foliage shading the habitats, and depths exceeding 1 m. Similar epibiont community structure on mangrove roots has also been noted elsewhere in the Caribbean (Rützler, 1969; Sutherland, 1980; Toffart, 1983; Alvarez, 1989; Bingham, 1992). Roots on the wind-ward side of islands, in shallow water (<1 m), or touching the ground tend to have the lowest species numbers. Toffart (1983) differentiated three types of roots in the mangrove fringe according to the abundance of sponges and tunicates: the outermost roots (type I) where sponges and tunicates covered >30% of the root surface, the middle roots (type II) where sponges and tunicates cover < 30% of the root surface, and the inner root (type III) where sponges and tunicates are absent. We conclude that the relative abundance of functional groups is a good biological parameter to monitor because each group responds differently to physico-chemical parameters (temperature, salinity, sedimentation, light, nutrients). For instance, we noted an increase of filamentous-cyanobacterial coatings and mats at some sites at Twin Cays that may be worth monitoring because this group is always present but not known for having large abundances in healthy Caribbean mangroves.

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