



Smithsonian Institution
Scholarly Press

SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 38



Proceedings of the Smithsonian Marine Science Symposium

*Edited by
Michael A. Lang,
Ian G. Macintyre, and Klaus Rützler*

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of “diffusing knowledge” was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: “It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge.” This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Botany
Smithsonian Contributions in History and Technology
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Museum Conservation
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology

In these series, the Institution publishes small papers and full-scale monographs that report on the research and collections of its various museums and bureaus. The Smithsonian Contributions Series are distributed via mailing lists to libraries, universities, and similar institutions throughout the world.

Manuscripts submitted for series publication are received by the Smithsonian Institution Scholarly Press from authors with direct affiliation with the various Smithsonian museums or bureaus and are subject to peer review and review for compliance with manuscript preparation guidelines. General requirements for manuscript preparation are on the inside back cover of printed volumes. For detailed submissions requirements and to review the “Manuscript Preparation and Style Guide for Authors,” visit the Submissions page at www.scholarlypress.si.edu.

Proceedings of the Smithsonian Marine Science Symposium

*Edited by
Michael A. Lang,
Ian G. Macintyre, and Klaus Rützler*



Smithsonian Institution
Scholarly Press
WASHINGTON D.C.
2009

ABSTRACT

Lang, Michael A., Ian G. Macintyre, and Klaus Rützler, editors. Proceedings of the Smithsonian Marine Science Symposium. *Smithsonian Contributions to the Marine Sciences*, number 38, 529 pages, 217 figures, 47 tables, 2009.—The Smithsonian Marine Science Symposium was held on 15–16 November 2007 in Washington, D.C. It represented the first major dissemination of marine research results since the establishment of the Smithsonian Marine Science Network (MSN). The 39 papers in this volume represent a wide range of marine research studies that demonstrate the breadth and diversity of science initiatives supported by the MSN. The first section contains an overview of the MSN along with papers describing the multidisciplinary investigations spanning more than 37 years for the four Smithsonian marine facilities that constitute the Network: the Smithsonian Environmental Research Center at the Chesapeake Bay, Maryland; the National Museum of Natural History's Smithsonian Marine Station at Fort Pierce, Florida; the Caribbean Coral Reef Ecosystems Program, with its Carrie Bow Marine Field Station in Belize; and the Smithsonian Tropical Research Institute in Panama. Subsequent papers represent findings by Smithsonian scholars and their collaborators on overarching topics of marine biodiversity, evolution, and speciation; biogeography, invasive species, and marine conservation; and forces of ecological change in marine systems.

Cover images: (left) *Aurelia aurita* sea jelly with juvenile carangid jacks in its bell, Carrie Bow Cay, Belize; (middle) *Dendronephthya* soft corals and *Anthias* school, The Brothers Islands, Red Sea, Egypt; (right) grey reef shark *Carcharhinus amblyrhynchos*, Kingman Reef, Northern Line Islands (all photos by Michael A. Lang).

Published by Smithsonian Institution Scholarly Press
P.O. Box 37012
MRC 957
Washington, D.C. 20013-7012
www.scholarlypress.si.edu

Library of Congress Cataloging-in-Publication Data

Smithsonian Marine Science Symposium (2007 : Washington D.C.)

Proceedings of the Smithsonian Marine Science Symposium / edited by Michael A. Lang, Ian G. Macintyre, and Klaus Rützler.

p. cm. — (Smithsonian contributions to the marine sciences, ISSN 0196-0768 ; no. 38)

Includes bibliographical references and index.

1. Marine sciences—Congresses. I. Lang, Michael A. II. Macintyre, Ian G. III. Rützler, Klaus.

IV. Title

GC2.S57 2007

578.77—dc22

2009028023

ISSN (print): 0196-0768

ISSN (online): 1943-667X

∞ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48-1992.

Biodiversity and Abundance of Sponges in Caribbean Mangrove: Indicators of Environmental Quality

Maria Cristina Diaz and Klaus Rützler

ABSTRACT. We have long been fascinated by the lush biological diversity seen on subtidal substrates in Caribbean saltwater mangroves. Several groups of plants and sessile invertebrates flourish on the submerged prop roots of red mangrove (*Rhizophora mangle*), competing for space and tolerating a stressful range of ecological variables (temperature, salinity, nutrients, sedimentation) that is quite different from the more stable climate on nearby coral reefs. To test the limits of tolerance, we monitored populations of these organisms, the abundant sponges in particular, at environmentally and geographically dissimilar locations in Panama and Belize. We used relative abundance estimates and frequency counts of major ecologically functional groups and common sponge species to establish baselines, and we repeated our surveys over long time spans (months to years) to find correlations between community and environmental changes. Both study locations demonstrated environmental quality decline during the time of observation, mainly through mangrove clear-cutting, followed by increase of suspended fine sediments from dredging reef sands and filling in intertidal land, and elevation of nutrient levels from terrestrial inputs. Although our methods are still in a stage of refinement, our data are leading the way to responsible monitoring of our most precious coastal resources in the tropics. We find that photosynthetic organisms (cyanobacteria, algae) and filter-feeding invertebrates (sponges, ascidians, bivalves, bryozoans) count among the “canaries in the coal mine” as effective indicators of environmental change.

INTRODUCTION

Red mangrove trees, *Rhizophora mangle*, grow along thousands of kilometers of Caribbean shorelines, protecting them from storm erosion and offering habitat to many organisms (Rützler and Feller, 1988, 1996; de Lacerda et al., 2002). Caribbean mangroves harbor from a handful to more than 100 sponge species at any one particular site (Table 1). Available data indicate that sponges may make up 10% to 70% of epiphytic species diversity on submerged mangrove roots. The best studied mangrove sponge faunas are described from islands off southern Belize, with species richness reported between 50 and 147 species (Rützler et al., 2000; Wulff, 2000; Diaz et al., 2004), followed by faunas from a few islands in the Bocas del Toro Archipelago, Panama, with 65 species (Diaz, 2005), from various mainland and island sites off Venezuela with 62 species (Sutherland, 1980; Diaz et al. 1985; Orihuela et al., 1991; Pauls,

Maria Cristina Diaz, Museo Marino de Margarita, Blvd. El Paseo, Boca del Río, Margarita, Edo. Nueva Esparta, Venezuela. Klaus Ruetzler, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0163, USA. Corresponding author: M. C. Diaz (taxochica@gmail.com). Manuscript received 9 June 2008; accepted 20 April 2009.

TABLE 1. Number of species of Porifera and other epifaunal taxa reported from Caribbean mangroves (n.a. = no data available).

Country	Locality	Porifera	Other taxa	Author
Antilles	Guadalupe, Trinidad, Puerto Rico	4–10	32–70	Toffart (1983)
Bahamas	Bimini	13	n.a.	Rützler (1969)
Belize	Four cays	24	59	Farnsworth and Ellison (1996)
	Twin Cays	54	n.a.	Rützler et al. (2000)
	Pelican Cays	147	217	See Macintyre and Rützler (2000)
Cuba	n.a.	48	n.a.	Alcolado (unpublished data)
Panama	Bocas del Toro	60	n.a.	Diaz (2005)
USA	Indian River, Florida	3	25	Bingham and Young (1995)
Venezuela	Buche Bay	16	32	Sutherland (1980)
	Morrocoy National Park	23	n.a.	Diaz et al. (1985)
	Turiamo Bay	10	n.a.	Pauls (2003)
	Cienaga Bay	26	n.a.	Pauls (1998)
	La Restinga National Park	18	35	Orihuela et al. (1991)
	La Restinga National Park	40	n.a.	Diaz et al. (2003)

1998, 2003; Ramirez, 2002; Diaz et al., 2003; Pérez, 2007), and various mangrove sites in Cuba, with 41 species (Alcolado, unpublished data). Other reports are from Colombia, with 26 species (Zea, 1987; S. Zea, National University of Colombia, personal communication, 2006); Jamaica, with 18 species (Hechtel, 1965; Lehnert and van Soest, 1998); and Trinidad and Guadalupe, with 6 species (Toffart, 1983) (clearly representing only a portion of the mangrove sponge diversity there).

Most of the mangrove systems in the Caribbean remain unexplored, leaving a large void in biodiversity information. Most studies just cited show that the more closely these communities are investigated, the more new species are being discovered. An example is the research by the Caribbean Coral Reef Ecosystems Program in Belize during the past 25 years (Rützler et al., 2000, 2004). In particular, specialists on certain sponge taxa discovered and described numerous species in the families Suberitidae (order Hadromerida) (Rützler and Smith, 1993), Chalinidae (order Haplosclerida) (de Weerd et al., 1991) and Mycalidae (order Poecilosclerida) (Hadju and Rützler, 1998). A recent revision of Caribbean *Lisodendoryx* allowed the reinterpretation of *L. isodyctyalis* (Carter, 1882) and seven other species, four of them new to science (Rützler et al., 2007). Similarly, two unique haplosclerids were found in Belizean and Panamanian mangroves: a thin, erect, and fragile undescribed species of *Haliclona* from Twin Cays, and *Xestospongia bocatorensis*, a thin crust occurring in Bocas del Toro mangroves and reefs. Both are in an endosymbiotic relationship with filamentous Cyanobacteria, a very unusual

occurrence in this order of sponges (Diaz et al., 2007, Thacker et al., 2007).

Besides the importance of sponges species richness, they may be one of the most abundant animal groups in mangrove habitats. In Belize, for instance, on the leeward sides of islands, sponges cover 10% to 50% of the root surfaces, followed in importance by sea anemones, ascidians, and algae (Farnsworth and Ellison, 1996; Diaz et al., 2004). In the Caribbean, epibiont mangrove communities have been interpreted as highly heterogeneous (Rützler, 1969; Sutherland, 1980; Alcolado, 1985; Alvarez, 1989; Calder, 1991a; Bingham, 1992; Diaz et al., 2004) as a result of low recruitment rates (Zea, 1993; Maldonado and Young, 1996), low and fragmented available space (Jackson and Buss, 1975; Sutherland, 1980), and stochastic processes in the long term (Bingham and Young, 1995; Ellison et al., 1996). Abundance and distribution for sponges and algae in these communities have been related to environmental factors, such as light intensity, tides, wave impact, air exposure, and sedimentation (Rützler, 1995), and to biological factors, such as larval supply (Farnsworth and Ellison, 1996), root abundance, competition, and predation (Calder, 1991b; Littler et al., 1985; Taylor et al., 1986; Ellison and Farnsworth, 1992; Rützler, 1995; Rützler et al., 2000; Wulff, 2000). Algae abound on the shallow, well-lit parts of stilt roots, and their abundance and species composition are highly susceptible to the presence of grazers. Sponges are most abundant on the lower subtidal portions of the stilt roots and dominate peat bank walls and undercuts.

The major physical and biological processes are modulated by competitive abilities, such as growth rates and chemical defenses against predation (Wulff, 2000, 2004, 2005; Engel and Pawlik, 2005). Short-term epibiont abundances are likely to be determined by interspecific competitive interactions and predation, while long-term abundances are limited by seasonal environmental changes, such as freshwater inputs during periods of rain, strong tidal currents, waves, and stochastic processes that make these communities unstable (Bingham and Young, 1995; Ellison et al., 1996). Despite important generalizations about mangrove benthos ecology, we lack understanding of the temporal or spatial variation within most epibiont groups and knowledge about species occurrence, abundance, dominance, and interactions. For example, we do not know which species are generally abundant in these communities, how the hierarchy changes with the year's seasons, and if there are predictable succession patterns. Our current lack of knowledge prevents us from discerning between natural variations, for instance, seasonal or yearly dynamics, and artificial disturbances caused by humans.

The present work pursues the overall goal of a better understanding of diversity, biogeography, and ecological dynamics and their causes among the sponges in Caribbean mangroves. It encompasses two major aspects: evaluation of our current knowledge of epiphytic sponge taxa and the contribution of new data on causes for species richness, distribution, abundance, and dynamics, particularly from the examples of mangrove in Panama and Belize. The survey carried out in Bocas del Toro (Panama) intends to follow short-term changes (over one year) in the epiphytic fauna of mangrove roots, whereas the study in Belize will clarify shifts in distribution of taxa over a longer period (four years).

METHODS

SPONGE SPECIES DISTRIBUTION IN CARIBBEAN MANGROVES

The distribution of species in Caribbean mangroves was determined from currently published data or unpublished data provided to the authors. Faunas from different regions were compared by using a cluster analysis with the Bray-Curtis dissimilarity coefficient, which is part of the Multivariate Statistical Package (MVSP 3.1) (van Soest, 1993).

SPONGE IDENTIFICATION

Specimens were identified *in situ* or, when necessary, briefly characterized and photographed, with a sample

preserved in ethanol. In the laboratory, routine microscope preparations were made by cleaning spicules in household bleach and hand-cutting perpendicular and tangential sections, which were dehydrated and mounted in Permount and examined under the light microscope.

PHYSICOCHEMICAL VARIABLES

Temperature and salinity were measured at 0 and 50 cm depth at the Belize sites (January and August 2004), and in Bocas del Toro (February, June, and September 2004). Sedimentation rates were estimated from accumulations in buried sediment traps (plastic pipes, 10 cm diameter, 50 cm length) left in place for 210 days in Belize and 150 days in Panama. The trapped sediment was oven-dried (50°C), and its composition was determined as percentage of mud (including the very fine clay fraction) (<0.002–0.05 mm) and sand (0.05–2 mm). Approximate values of calcium carbonate content were determined from weight loss after exposure to changes of dilute hydrochloric acid, and sediment deposition rates were calculated (g/m²/day). Seawater samples (500 mL each) were taken in Belize (September 2003) and at Bocas del Toro (September 2004) at low and high tide, filtered (0.2 µm, GF/F filter) and frozen for nutrient analysis (Astor, 1996). Nutrient values were determined by spectrophotometric technique using the procedure described earlier (Diaz and Ward, 1997). Qualitative observations about habitat types surrounding the mangrove fringe were recorded, as well as an estimate of the level of human disturbance.

SURVEY SITES, BOCAS DEL TORO, PANAMA

Four sites within a perimeter of 10 km were selected and surveyed during 2004 (Figures 1, 2): (1) STRI Point: location of the Smithsonian Tropical Research Institute's laboratory, several mangrove stands close to reef patches in the southwest of Colon Island, and near a well-developed area with a housing complex that is part of the station; (2) Solarte In: a protected lagoon in the east of Solarte Island, site of a modest housing development; (3) Solarte Out: a pristine mangrove island close to reef patches to the west side of Solarte Island; and (4) Big Bight: a pristine, mangrove-lined lagoon surrounded by a well-developed terrestrial forest on Colon Island, less than 5 km northwest of STRI Point. General physicochemical characterization and geographic location of the sites are presented in Table 2 and the nutrient regime in Table 3.

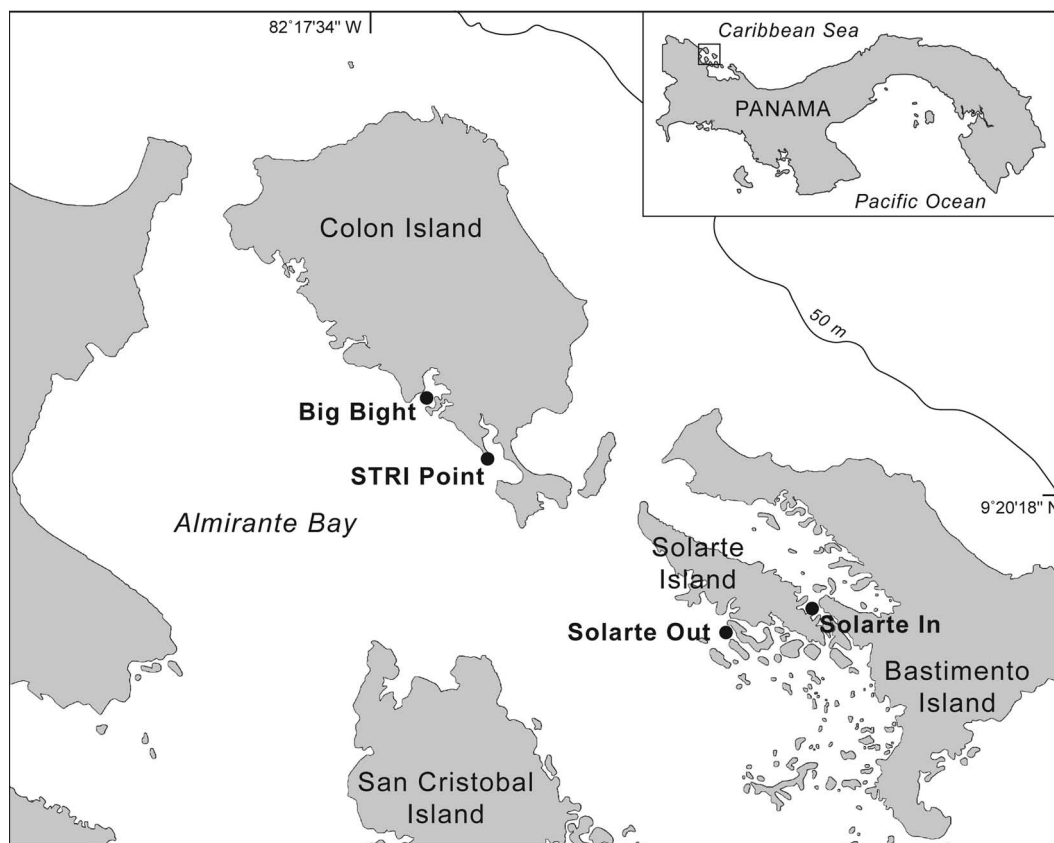


FIGURE 1. Map of research area at Bocas del Toro, Panama (STRI = Smithsonian Tropical Research Institute).

Mangrove prop roots (25 per site) were haphazardly selected within a 30 m length of the mangrove fringe. The front side (facing the channel) of each selected root was photographed along its entire length and set to scale by tying a transparent measuring tape to the high-tide water mark. The tape was prevented from floating by attaching a metal weight to its lower end. Three to seven photographs were taken, depending on the root length. Roots were rephotographed four times during the year (February 2004, June 2004, September 2004, and February 2005). From these images, abundance values of epifauna were estimated by measuring the projected area of each species using the CPCe program. The area (cm^2) covered by each taxon was divided by the root length (m), so that the relative abundance values are related to a measure of available substrate. Cover of each taxon is reported as the sum of its abundances (cm^2/m root) on all roots at a particular site. Eight categories of epiphytes were distinguished: cyanobacterial mats (monospecific stands

of cyanobacteria), green algae, red algae (including both crustose calcareous and fleshy species), turf (mixture of densely packed red, green, and cyanobacterial filaments), sponges, hydroids, bivalves, and ascidians; the ninth category was “empty” (spaces not occupied by macrofauna or macroalgae). When small organisms were found overgrowing a large one (such as *Spongia tubulifera*, *Hyrtios proteus*) the projected area of both species was included. The number of roots finally analyzed per studied site was reduced to 14–22 because there was some accidental loss of photographic data.

SURVEY SITES, TWIN CAYS AND PELICAN CAYS, BELIZE

Three sites at Twin Cays and one in the Pelican Cays were surveyed in August 2003 and four years later in August 2007 (Figures 3, 4; see Tables 2, 3). Two of the Twin Cays sites, the Lair Channel and Hidden Creek, are deep creeks that branch off the Main Channel; Sponge Haven



FIGURE 2. Views of research locations at Bocas del Toro, Panama. Top row from left: STRI Point looking south, where the transect was located in the right foreground; Solarte Island, with transect location Solarte In near the center. Bottom row from left: mangrove fringe at Solarte In; underwater view of mangrove prop roots showing a specimen of sponge, *Chalinula molitba*; mangrove roots covered by the encrusting sponge *Halisarca* sp. (undescribed; note scale in centimeters [cm] to the left), along with bivalves, algae, bryozoans, ascidians, and other fouling invertebrates.

is a bay in the southwest of the Main Channel. The Pelican Cays site was in the northern part of the lagoon of Manatee Cay. Transects (30 m long) were placed along the red mangrove fringe at each site, with number of roots ranging between 52 and 143. In all, the presence of the six most conspicuous epiphyte categories was recorded on each root within each transect: cyanobacterial mats, macroalgae, sponges, sea anemones (*Aiptasia pallida*), bivalves, and ascidians.

RESULTS

CARIBBEAN MANGROVE SPONGE SPECIES RICHNESS AND DISTRIBUTION

The distribution of 177 sponge species currently reported from Caribbean mangroves is presented in Table 4. A cluster analysis (Figure 5) of the best studied sites (Belize, Cuba, Panama, Venezuela) shows the highest similarity between Venezuela (62 species) and Panama (65 species).

TABLE 2. Characterization of study sites in Panama and Belize.

Country and locality	Habitat ^a (depth, m)	Human impact ^b	Temperature range (°C)	Salinity range (ppm)	Sedimentation			Coordinates	
					Type	CaCO ₃ (% dry wt)	Rate (g/m ² /day)		Turbidity ^b
Panama									
STRI Point	PR (1.5–2)	+	26–29	29–34	Mud	14–23	34–41	±/+	09°21'29.1"N, 82°16'28.9"W
Solarte In	SG (2–2.5)	-/+	26–29	27–32	Sand	4–24	28–58	–	09°17'05.0"N, 82°10'03.3"W
Solarte Out	PR (1)	–	27–29	29–33	Sand	80–98	88–248	–	09°17'35.6"N, 82°12'08.3"W
Big Bight	SG (1.5–2)	-/+	27–29	27–34	Mud/ sand	25	40	-/+	09°22'31.1"N, 82°17'38.3"W
Belize									
Sponge Haven	SG (1–1.8)	±	26–32	33–35	Mud	48.75	25	±	16°49'40.5"N, 88°06'16.5"W
Hidden Creek	TC (2–2.5)	±/+	25.5–33	32–36	n.a.	n.a.	n.a.	±	16°49'40.5"N, 88°06'16.5"W
Lair Channel	TC (1.5–1.8)	–	25.3–33	32–36	Mud	25.9	44	–	16°49'33.7"N, 88°06'11.6"W
Manatee Lagoon	PR/SG (1–2)	-c/+ ^d	25.5–32	35–36	Mud	38.9	45	–	16°40'03.3"N, 88°11'32.4"W

^a Habitat abbreviations: PR = mangrove prop roots; SG = seagrass (*Thalassia*); TC = tidal creek with peat walls and undercuts.

^b Human impact and turbidity designations: +, high; ±, medium; –, low.

^c Survey of 2003.

^d Survey of 2007.

TABLE 3. Ranges of nutrient concentrations (low tide to high tide) at the study sites: Panama samples taken in September 2004 and Belize samples taken in September 2003.

Country and locality	Phosphate (μmol/L)	Ammonium (μmol/L)	Nitrate (μmol/L)
Panama			
STRI Point	0–0.048	1.32–0.988	0.26–0.253
Solarte In	0.02–0.85	0.845–0.88	0.264–0.23
Solarte Out	0.024–0.048	0.096–0.071	0.345–0.276
Big Bight	0.048–0.048	1.55–1.100	0.345–0.230
Belize			
Sponge Heaven	0.528–0.624	4.79–1.88	0.5–0.41
Hidden Creek	0.336–0.786	3.19–2.35	1.1–0.39
Lair Channel	0.384–0.672	2.72–1.59	1.06–1.24
Manatee Lagoon ^a	0.576	1.41	0.32

^a Only one sample taken, at intermediate tide.

These faunas were paired with Twin Cays (54 species) and Cuba (48 species). The most dissimilar fauna in the analyses resulted from comparison with the Pelican Cays mangroves (147 species).

MANGROVE SURVEYS AT BOCAS DEL TORO, PANAMA

Changes in Abundance of Major Epifaunal Taxa

The relative abundance of major taxa at each of the four localities studied between February 2004 and February 2005 is shown in Figure 6. In terms of the hierarchy of major taxa, sponges were first or second in abundance on mangrove roots at all sites, followed by algal turfs. An exception to this pattern was found in Solarte In (see Figure 1), where large mats of green algae, mostly *Caulerpa verticillata* and *Halimeda* spp., dominated over the sponges in February 2004 and 2005. Bivalves were the third most abundant group, followed closely by unoccupied (empty) spaces.

The abundance of the two most dominant groups, sponges and algae/cyanobacteria, showed a considerable decrease at STRI Point and Solarte In by the end of the



FIGURE 3. Map of research areas at Twin Cays and Pelican Cays, Belize.

study (February 2005), whereas abundance of both groups increased or stayed at similar levels at the other two sites.

Sponge Species Abundances per Site

Because of the high level of heterogeneity in sponge composition and dominance among sites, the relative abundance of the most conspicuous epiphytic sponge species is presented separately, by sites.

STRI Point

Sixteen of a total of 23 species found at this site comprise 99% of total sponge abundance. Most of them (13 species) belong to the order Haplosclerida, specifically the family Chalinidae, and to the order Poecilosclerida. *Tedania*

ignis was the most abundant, followed by *Clathria schoenus*, *Spongia tubulifera*, *Mycale microsigmatosa*, *Chalinula molitba*, *Haliclona manglaris*, and *H. tubifera*. Figure 7a shows the relative abundance of the six most common species at this site, which added up to 87% of the total sponge abundance. It is interesting to note that the presence of both *T. ignis* and *Clathria schoenus* had decreased considerably by February 2005, whereas *S. tubulifera* remained with similar abundance throughout the year. *Chalinula molitba* shows a considerable increase (>200%) for June 2004 and a decrease to its initial values by February 2005.

Solarte In

Eight of 14 species found at this site constituted 99% of the total sponge abundance. Figure 7b demonstrates



FIGURE 4. (facing page) Views of research locations at Twin Cays and Pelican Cays, Belize. Top left, aerial view of Twin Cays looking south, where transect locations were in the Lair channel (branching from the Main Channel center toward the left), in Sponge Haven (the small bay at the top right), and Hidden Creek (a narrow, deep tidal channel hidden by mangrove canopy, connecting the Main Channel in the far right background with Hidden Lake in the center background); top right, aerial view of Manatee Cay where a transect was placed in the large lagoon to the left (Cat Cay is in the background); middle left, mangrove fringe at Sponge Haven; middle right, red mangrove prop roots hanging free near the Pelican Cays site and covered mainly by the ropy sponge *Iotrochota birotulata*; bottom left, close-up of *Tedania ignis* and *Tedania* sp. (probably *T. klausii* Wulff, a species described after this survey was made), both red, attached to exposed roots in the main channel of Twin Cays; bottom right, close-up of purple ascidian (*Clavelina puertosecensis*) with sponges (turquoise *Haliclona curacaoensis*, primarily) on root at Manatee Cay lagoon.

TABLE 4. Distribution of sponge species reported from Caribbean mangrove localities by various researchers (X = presence). Localities are abbreviated as follows: BEL, Belize; TC, Twin Cays; PC, Pelican Cays; PAN, Panama; COL, Colombia; VEN, Venezuela; TRI, Trinidad; GUA, Guadalupe; JAM, Jamaica; and CUB, Cuba. Data sources are given in table footnotes.

Species ^a	BEL ^b		PAN ^c	COL ^d	VEN ^e	TRI ^f	GUA ^f	JAM ^g	CUB ^h
	TC	PC							
<i>Plakina jamaicensis</i>	—	X	—	—	—	—	—	—	—
<i>Plakinastrella onkodes</i>	—	X	—	—	—	—	—	—	—
<i>Plakortis halichondriodes</i>	X	X	—	—	—	—	—	—	—
<i>Plakortis angulospiculatus</i>	—	—	X	—	—	—	—	—	X
<i>Oscarella</i> sp. 1 (purple)	X	X	X	—	—	—	—	—	—
<i>Oscarella</i> sp. 2 (drab)	—	X	X	—	—	—	—	—	—
<i>Cinachyrella apion</i>	X	X	X	—	X	—	—	—	—
<i>Ecionemia dominicana</i>	—	X	—	—	—	—	—	—	—
<i>Myriastrra kallitetilla</i>	X	—	—	—	—	—	—	X	X
<i>Erylus formosus</i>	—	X	—	—	—	—	—	—	—
<i>Geodia gibberosa</i>	—	X	—	—	X	—	X	X	X
<i>Geodia papyracea</i>	X	X	X	—	X	—	—	X	—
<i>Dercitus</i> sp.	—	X	—	—	—	—	—	—	—
<i>Chondrilla caribensis</i>	X	X	X	—	X	—	—	—	X
<i>Chondrosia collectrix</i>	—	X	X	—	—	—	—	—	X
<i>Cervicornia cuspidifera</i>	—	X	—	—	—	—	—	—	—
<i>Cliona caribbaea</i>	—	X	—	—	—	—	—	—	—
<i>Cliona raphida</i>	—	—	—	—	X	—	—	—	—
<i>Cliona varians</i>	X	X	—	—	—	—	—	—	X
<i>Cliona</i> sp.	—	X	—	—	—	—	—	—	—
<i>Placospongia intermedia</i>	—	X	X	—	X	—	—	—	—
<i>Diplastrella megastellata</i>	—	X	—	—	—	—	—	—	—
<i>Spirastrella coccinea</i>	—	X	—	—	—	—	—	—	—
<i>Spirastrella bartmani</i>	—	X	—	—	—	—	—	—	—
<i>Spirastrella mollis</i>	X	X	X	—	—	—	—	—	—
<i>Aaptos duchassaingii</i>	—	X	—	—	—	—	—	—	—
<i>Aaptos lithophaga</i>	—	—	—	—	—	—	—	—	X
<i>Terpios fugax</i>	—	X	—	—	—	—	—	—	X
<i>Terpios manglaris</i>	X	X	X	—	X	—	—	—	—
<i>Prosuberites laughlini</i>	—	—	X	—	X	—	—	X	—
<i>Suberites aurantiaca</i>	—	X	—	—	X	—	—	X	—
<i>Tethya actinia</i>	X	X	X	—	X	—	—	—	X
<i>Tethya</i> aff. <i>seychellensis</i>	—	—	X	—	X	—	—	X	—
<i>Discodermia dissoluta</i>	—	—	X	—	—	—	—	—	—
<i>Paratimea</i> ? sp.	X	—	—	—	—	—	—	—	—
<i>Timea unistellata</i>	—	X	—	—	—	—	—	—	—
<i>Agela conifera</i>	—	X	—	—	—	—	—	—	—

continued

TABLE 4. *continued*

Species ^a	BEL ^b		PAN ^c	COL ^d	VEN ^e	TRI ^f	GUA ^f	JAM ^g	CUB ^h
	TC	PC							
<i>Phorbas amaranthus</i>	—	X	—	—	—	—	—	—	—
<i>Coelosphaera raphidifera</i>	—	X	—	—	—	—	—	—	—
<i>Lissodendoryx colombiensis</i>	—	X	X	—	—	—	—	—	—
<i>Lissodendoryx isodictyalis</i>	X	X	X	—	X	—	X	—	X
<i>Lissodendoryx sigmata</i>	X	—	—	—	—	—	—	—	—
<i>Monanchora arbuscula</i>	—	X	—	—	X	—	—	—	—
<i>Desmapsamma anchorata</i>	—	X	X	—	X	—	—	—	—
<i>Biemna caribea</i>	X	—	X	—	X	—	—	—	X
<i>Desmacella janiae</i>	—	X	—	—	—	—	—	—	—
<i>Desmacella meliorata</i>	—	X	—	—	X	—	—	—	—
<i>Neofibularia nolitangere</i>	—	X	—	—	—	—	—	—	—
<i>Hymedesmia</i> sp.	—	X	—	—	—	—	—	—	—
<i>Acarus</i> sp.	—	X	—	—	—	—	—	—	—
<i>Artemisina melana</i>	—	X	X	—	X	—	—	—	—
<i>Clathria affinis</i>	—	X	—	—	—	—	—	—	—
<i>Clathria</i> cf. <i>ferrea</i>	—	—	X	—	X	—	—	—	—
<i>Clathria microchela</i>	—	X	—	—	X	—	—	—	—
<i>Clathria schoenus</i>	X	—	X	—	X	—	—	—	X
<i>Clathria</i> aff. <i>schoenus</i>	X	—	—	—	—	—	—	—	—
<i>Clathria spinosa</i>	—	X	—	—	—	—	—	—	—
<i>Clathria venosa</i>	X	X	X	—	X	—	—	—	—
<i>Clathria virgultosa</i>	X	—	—	—	—	—	—	—	—
<i>Mycale</i> cf. <i>americana</i>	—	—	—	—	X	—	—	—	—
<i>Mycale angulosa</i>	—	—	—	—	X	—	—	—	—
<i>Mycale arenaria</i>	—	—	—	—	—	—	—	—	—
<i>Mycale arndti</i>	—	X	—	—	—	—	—	—	—
<i>Mycale carmigropila</i>	X	X	X	—	X	—	—	—	—
<i>Mycale citrina</i>	X	—	—	—	X	—	—	—	—
<i>Mycale escarlatei</i>	—	—	—	—	—	—	—	—	—
<i>Mycale laevis</i>	X	—	—	—	—	—	—	X	—
<i>Mycale laxissima</i>	X	X	—	X	X	—	—	—	—
<i>Mycale magniraphidifera</i>	X	X	X	—	X	—	—	—	X
<i>Mycale</i> aff. <i>magniraphidifera</i>	X	X	X	—	—	—	—	—	—
<i>Mycale microsigmatosa</i>	X	X	X	X	X	X	—	X	X
<i>Mycale</i> aff. <i>microsigmatosa</i>	—	X	—	—	—	—	—	—	—
<i>Mycale paresperella</i>	—	X	X	—	—	—	—	—	—
<i>Iotrochota birotulata</i>	—	X	X	—	X	—	—	—	—
<i>Strongylacidon</i> sp.	—	X	—	—	—	—	—	—	—
<i>Ectyoplasia ferox</i>	—	X	—	—	X	—	—	—	—
<i>Eurypon laughlini</i>	—	X	X	—	X	—	—	—	—
<i>Tedania ignis</i>	X	X	X	—	X	—	—	X	X
<i>Tedania</i> aff. <i>ignis</i>	—	X	—	—	—	—	—	—	—
<i>Dragmacidon reticulata</i>	—	X	—	—	—	—	—	—	—
<i>Pseudaxinella</i> ? sp.	—	X	—	—	—	—	—	—	—
<i>Ptilocaulis walpersi</i>	—	X	—	—	—	—	—	—	—
<i>Dictyonella</i> sp.	X	X	—	—	—	—	—	—	—
<i>Scopalina hispidata</i>	—	X	—	—	X	—	—	X	X
<i>Scopalina ruetzleri</i>	X	X	X	X	X	—	—	—	X
<i>Scopalina</i> ? sp.	—	X	—	—	—	—	—	—	—
<i>Ulosa funicularis</i>	—	X	—	—	—	—	—	—	—
<i>Amorphinopsis</i> sp. 1	—	X	—	—	X	—	—	—	—
<i>Amorphinopsis</i> sp. 2	—	X	—	—	—	—	—	—	—
<i>Ciocalyptra</i> ? sp.	—	X	—	—	—	—	—	—	—
<i>Halichondria corrugata</i>	—	—	—	—	—	—	—	—	X
<i>Halichondria magniconulosa</i> ?	X	X	X	—	X	X	X	—	X
<i>Halichondria melanadocia</i>	X	X	X	X	X	—	—	X	X
<i>Halichondria poa</i> ?	X	X	—	—	—	—	—	—	—

Species ^a	BEL ^b		PAN ^c	COL ^d	VEN ^e	TRI ^f	GUA ^f	JAM ^g	CUB ^h
	TC	PC							
<i>Hymeniacion caerulea</i>	—	X	—	—	—	—	—	—	—
<i>Myrmekioderma rea</i>	—	X	—	—	—	—	—	—	—
<i>Topsentia ophiraphidites</i>	—	X	—	—	—	—	—	—	—
<i>Callyspongia arcesiosa</i>	—	—	—	—	X	—	—	—	—
<i>Callyspongia fallax</i>	—	X	X	—	—	—	—	—	X
<i>Callyspongia pallida</i>	—	X	X	—	—	—	—	—	—
<i>Callyspongia vaginalis</i>	—	X	—	—	—	—	—	—	—
<i>Haliclona caerulea</i>	—	X	X	—	X	—	X	X	—
<i>Haliclona curacaoensis</i>	X	X	X	—	X	—	—	—	X
<i>Haliclona aff. curacaoensis</i>	—	X	—	—	—	—	—	—	—
<i>Haliclona implexiformis</i>	X	X	X	X	X	—	—	—	X
<i>Haliclona aff. implexiformis</i>	—	X	—	—	—	—	—	—	X
<i>Haliclona magnifica</i>	X	X	X	—	X	—	—	—	—
<i>Haliclona manglaris</i>	X	X	X	—	X	—	—	—	X
<i>Haliclona mucifibrosa</i>	X	X	X	—	—	—	—	—	—
<i>Haliclona picadaerensis</i>	X	X	X	—	X	—	—	—	—
<i>Haliclona tubifera</i>	X	X	X	X	X	—	—	—	X
<i>Haliclona aff. tubifera</i>	—	X	—	—	—	—	—	—	—
<i>Haliclona twincayensis</i>	X	X	X	—	X	—	—	—	—
<i>Haliclona vermeuleni</i>	X	X	X	—	—	—	—	—	—
<i>Chalimula molitba</i>	X	X	X	—	X	—	—	X	X
<i>Chalimula zeae</i>	—	—	X	—	—	—	—	—	—
<i>Amphimedon compressa</i>	—	X	—	—	X	—	—	X	—
<i>Amphimedon erina</i>	X	X	—	X	X	—	—	—	—
<i>Amphimedon aff. erina</i>	—	X	—	—	—	—	—	—	—
<i>Amphimedon viridis</i>	—	—	—	—	—	—	—	—	X
<i>Niphates caicedoi</i>	—	X	X	—	—	—	—	—	—
<i>Niphates digitalis</i>	—	X	—	—	—	—	—	—	—
<i>Niphates erecta</i>	—	X	X	—	X	—	—	—	—
<i>Niphates sp.</i>	—	X	—	—	—	—	—	—	—
<i>Petrosia pellarca</i>	—	X	—	—	—	—	—	—	—
<i>Petrosia weimbergi</i>	—	X	—	—	—	—	—	—	—
<i>Strongylophora davilai</i>	—	X	—	—	—	—	—	—	—
<i>Xestospongia carbonaria</i>	—	X	—	—	—	—	—	—	—
<i>Xestospongia muta</i>	—	X	—	—	—	—	—	—	—
<i>Xestospongia proxima</i>	—	X	—	—	—	—	—	—	—
<i>Xestospongia subtriangularis</i>	—	X	—	—	X	—	—	—	—
<i>Aka coralliphaga</i>	—	X	—	—	—	—	—	—	—
<i>Aka siphona</i>	—	X	—	—	—	—	—	—	—
<i>Aka sp.</i>	—	X	—	—	—	—	—	—	—
<i>Calyx podatypa</i>	X	X	X	—	—	—	—	—	—
<i>Oceanapia nodosa</i>	—	—	X	—	X	—	—	—	—
<i>Oceanapia oleracea</i>	—	—	X	—	—	—	—	—	—
<i>Cacospongia sp.</i>	—	X	—	—	—	—	—	—	X
<i>Fasciospongia? sp.</i>	—	X	—	—	—	—	—	—	—
<i>Hyrtios proteus</i>	X	X	X	—	X	—	—	—	X
<i>Hyrtios sp.</i>	X	X	—	—	—	—	—	—	—
<i>Smenospongia aurea</i>	—	X	—	—	—	—	—	—	—
<i>Ircimia campana</i>	—	X	X	—	—	—	—	—	—
<i>Ircimia felix</i>	X	X	X	X	X	—	—	X	X
<i>Ircimia strobilina</i>	X	X	—	—	X	—	—	—	X
<i>Spongia pertusa</i>	X	X	X	—	X	—	X	—	X
<i>Spongia tubulifera</i>	X	X	X	X	X	—	—	—	X
<i>Dysidea etheria</i>	X	X	X	X	X	—	X	—	X
<i>Dysidea fragilis</i>	—	—	—	—	—	—	—	X	—
<i>Dysidea janiae</i>	—	X	—	—	—	—	—	—	X
<i>Aplysilla glacialis</i>	X	X	X	—	X	—	—	—	—
<i>Chelonaplysilla aff. erecta</i>	—	X	X	X	X	—	—	—	X
<i>Darwinella rosacea</i>	—	X	—	—	X	—	—	X	X

continued

TABLE 4. *continued*

Species ^a	BEL ^b		PAN ^c	COL ^d	VEN ^e	TRI ^f	GUA ^f	JAM ^g	CUB ^h
	TC	PC							
<i>Halisarca caerulea</i>	—	X	—	—	—	—	—	—	—
<i>Halisarca</i> sp. (white)	X	X	X	—	X	—	—	—	—
<i>Aiolochoxia crassa</i>	—	X	—	—	—	—	—	—	—
<i>Aplysina archeri</i>	—	X	—	—	—	—	—	—	—
<i>Aplysina fistularis</i>	—	X	—	—	X	—	—	—	X
<i>Aplysina insularis</i>	—	X	—	—	—	—	—	—	—
<i>Aplysina fulva</i>	—	X	—	—	—	—	—	—	X
<i>Aplysina lacunosa</i>	—	X	—	—	—	—	—	—	—
<i>Verongula rigida</i>	—	X	—	—	—	—	—	—	—
<i>Clathrina primordialis</i>	X	X	—	—	—	—	—	—	X
<i>Sycon</i> sp.	X	—	X	—	X	—	—	—	—
<i>Leucandra aspera</i>	—	—	X	—	X	—	—	—	—

^a Species are listed in taxonomic order according to class, order, and family.

^b Rützler et al., 2000.

^c Diaz, 2005; Lehnert and van Soest, 1998.

^d Zea, 1987; unpublished data.

^e Sutherland, 1980; Diaz et al., 1985; Orihuela et al., 1991; Pauls, 1998, 2003; Ramirez, 2002; Diaz et al., 2003; Perez, 2007.

^f Toffart, 1983.

^g Hechtel, 1965.

^h Alcolado, unpublished data.

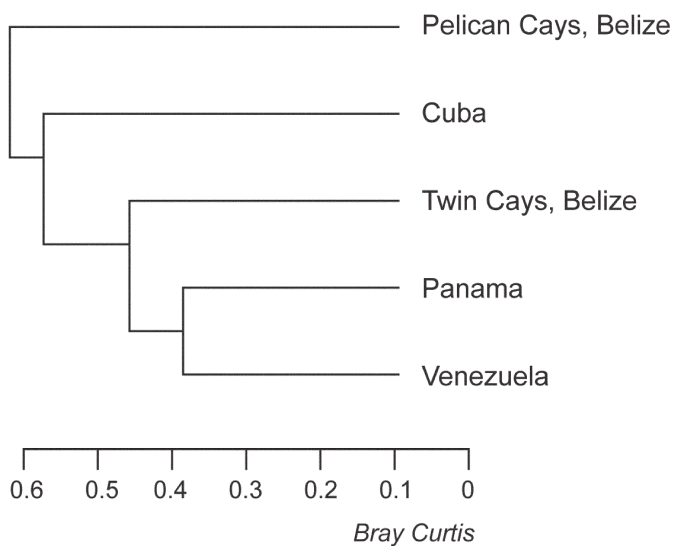


FIGURE 5. Similarities of mangrove sponge faunas from Belize, Panama, Venezuela, and Cuba. The dendrogram is built from a binary matrix (presence or absence) of species distribution using an unweighted pair-group method with arithmetic mean (UPGMA) clustal analysis program, with the Bray-Curtis distance index.

the relative abundance of the six most common species, which comprised 96% of all sponges. *Tedania ignis* and *Mycale microsigmatosa* were among the top species; *Halisarca* sp. (a species so far undescribed) and *Mycale carmigropila* appeared to be among the major components. Similar to STRI Point, most of the dominant species decreased in abundance or disappeared by the end of the study, while *Halisarca* remained steady in abundance throughout the study period. Three of the common species at this site (*Dysidea etheria*, *Haliclona curacaoensis*, and *Mycale carmigropila*) show an increase of sponge growth in the warmer periods (either June or September 2004), followed by a decrease in size during cooler periods (February 2005).

Solarte Out

Six of nine species found at this site made up 99% of total sponge abundance (Figure 7c). *Tedania ignis* continues to dominate, followed by three species not seen in the previously discussed sites: *Spirastrella mollis*, *Haliclona vermeuleni*, and *H. caerulea*. It is notable that the (projected) area coverage of the dominant species is much lower here than that at the other sites (most values are less than 500 cm²/m).

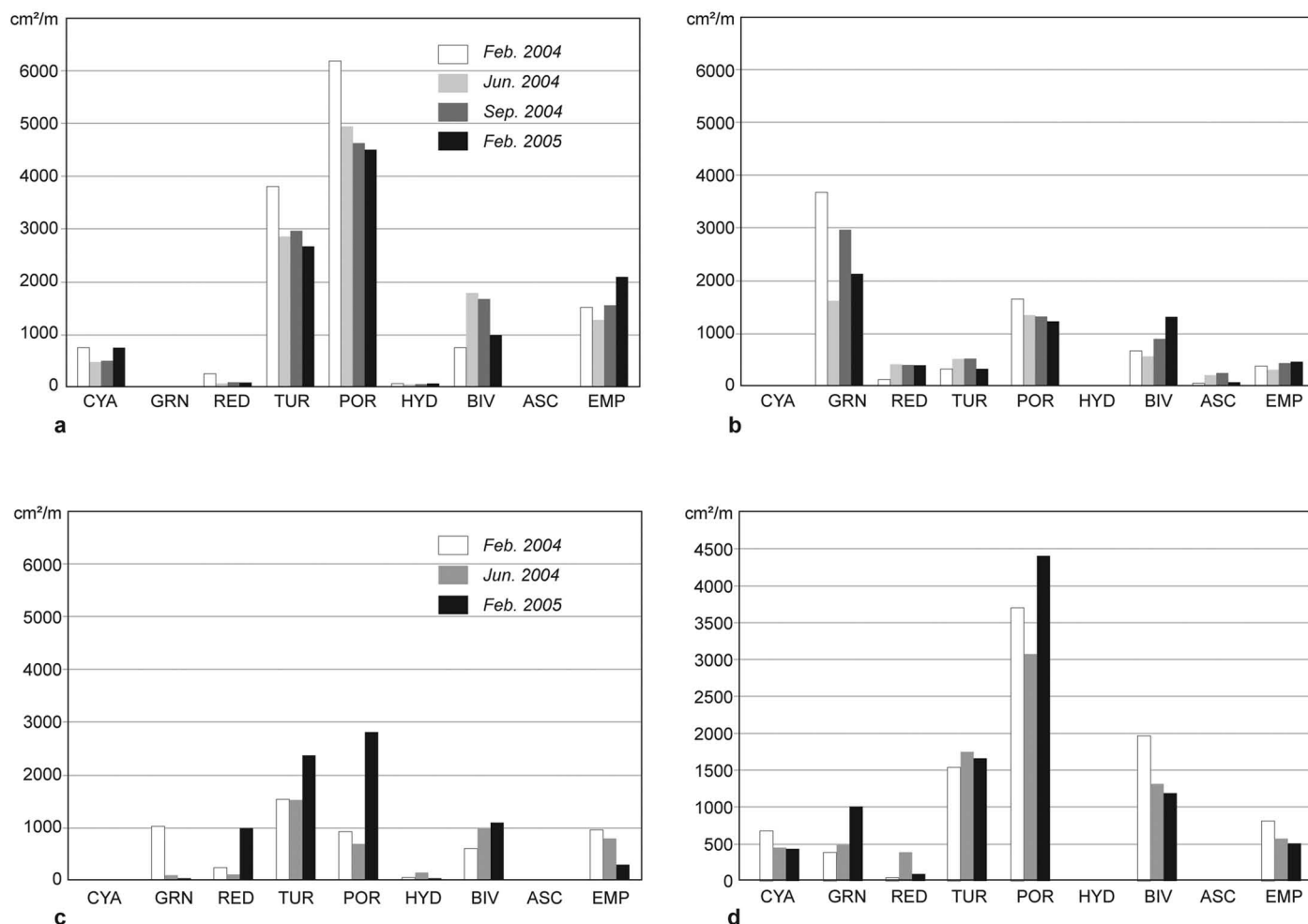


FIGURE 6. Relative abundance of major functional groups growing on mangrove roots (expressed as projected area [cm^2] per length [m] of root) at four Bocas del Toro sites, between February 2004 and 2005: a, STRI Point; b, Solarte In; c, Solarte Out; d, Big Bight. (ASC = ascidians; BIV = bivalves; CYA = Cyanobacteria; EMP = empty space; GRN = green algae; HYD = hydroids; POR = sponges [Porifera]; RED = red algae; TUR = algal–cyanobacterial turf.)

Big Bight

Twelve of 17 species found at Big Bight comprised 99% of the total sponge abundance; 6 of these amounted to 90% (Figure 7d). The most abundant species—*Tedania ignis*, *Mycale microsigmatosa*, and *Haliclona manglaris*—increased in size throughout the year, whereas *Lissodendoryx colombiensis* and *Dysidea etheria* gained in size up to September 2004 but disappeared altogether in February 2005. It is worth pointing out the large values for area coverage, as compared to the other locations. The September 2004 data from this site were accidentally lost.

Sponge Species Ranks

The most common sponges at each site amount to 21 species, from a total of 40 distinguished in the studied areas. Abundance ranks from each site are listed in Table 5. Only one species, *Tedania ignis*, maintained the same rank at all sites, as the most abundant species. The second and third most abundant species were *Clathria schoenus* and *Spongia tubulifera* at STRI Point, *Mycale microsigmatosa* and *Halisarca* sp. at Solarte In, *Spirastrella mollis* and *Haliclona manglaris* at Solarte Out, and *M. microsigmatosa* and *H. manglaris* in Big Bight. Seven of these 21 common sponges were only found at one site.

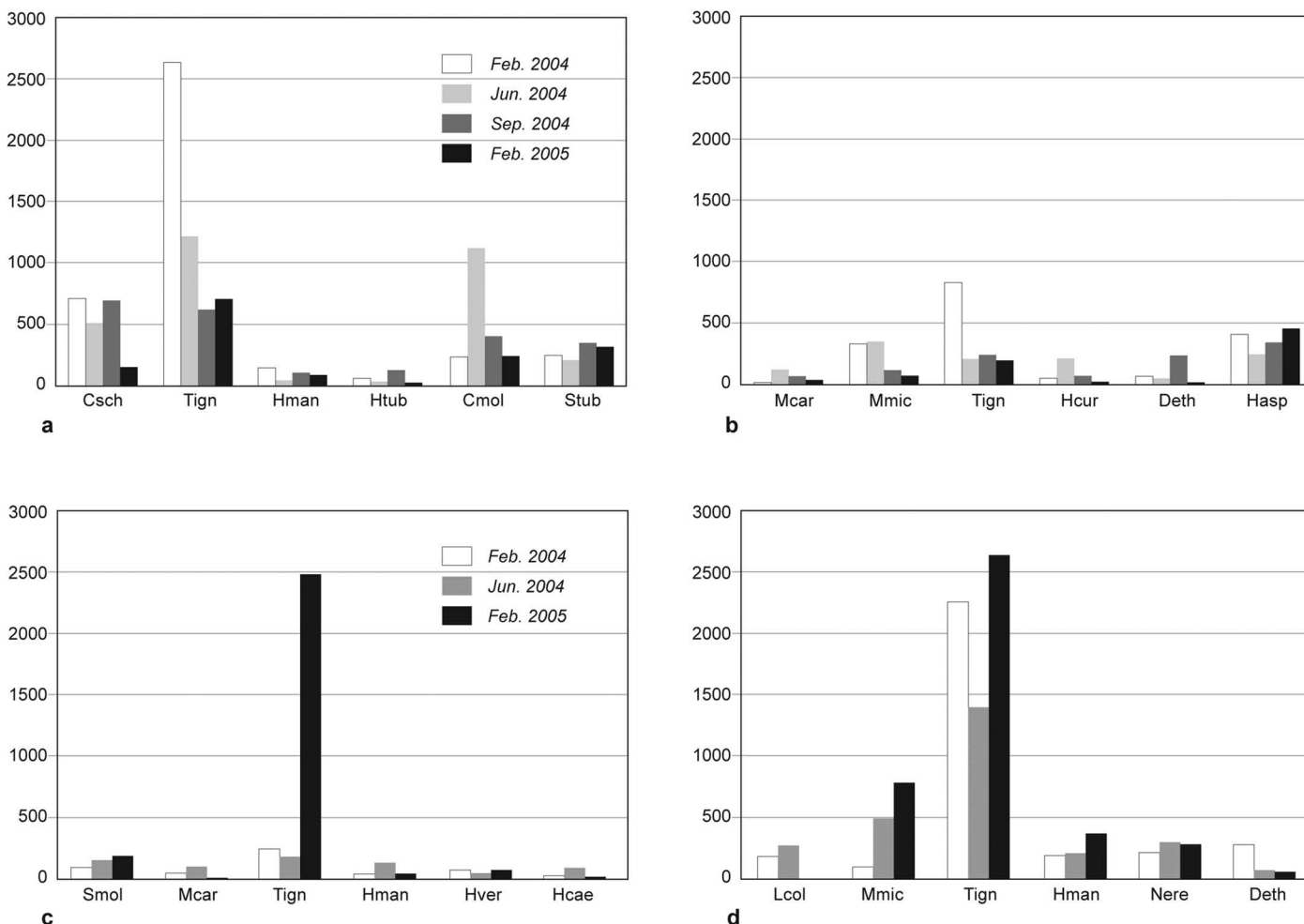


FIGURE 7. Relative abundance of most common sponge species growing on mangrove roots (expressed as projected area [cm²] per length [m] of root) at four Bocas del Toro sites between February 2004 and 2005: a, STRI Point; b, Solarte In; c, Solarte Out; d, Big Bight. (Cmol = *Chalinula molitba*; Csch = *Clathria schoenus*; Deth = *Dysidea etheria*; Hasp = *Halicarca* sp.; Hcae = *Haliclona caerulea*; Hcur = *H. curacaoensis*; Hman = *H. manglaris*; Hpro = *Hyrtios proteus*; Htub = *Haliclona tubifera*; Hver = *H. vermeulei*; Lcol = *Lissodendoryx colombiensis*; Mcar = *Mycale carmigropila*; Mmic = *M. microsigmatosa*; Nere = *Niphates erecta*; Smol = *Spirastrella mollis*; Stub = *Spongia tubulifera*; Tign = *Tedania ignis*).

MANGROVE SURVEYS IN BELIZE

Changes in Frequency of Occurrence of Major Functional Groups

We determined the frequency of occurrence of important functional groups growing on mangrove roots to be able to assess changes over time (Figure 8). The six compound groups recorded in our surveys were cyanobacteria, algae, sponges, sea anemones, bivalves, and ascidians. In terms of the hierarchy, sponges were first or second at all

sites, followed by colonial ascidians, macroalgae, and cyanobacteria. Only at Manatee Cay had sponge occurrence on roots decreased since 2003, whereas at the other three sites it either increased or stayed nearly the same. Ascidian occurrence decreased considerably (10%–26%) at all sites between 2003 and 2007. These changes in sponge and ascidian populations were accompanied by cyanobacterial blooms at three sites (Lair Channel, Hidden Creek, and Manatee Cay), where increases of 10% to 57% of these organisms were recorded. One of the less abundant

TABLE 5. Ranking of the most common sponge species according to their abundance at each studied site in the Bocas del Toro region, 2004–2005.

Species	Rank in abundance			
	STRI Point	Solarte In	Solarte Out	Big Bight
<i>Spirastrella mollis</i>	0	0	2	0
<i>Lissodendoryx colombiensis</i>	0	0	0	5
<i>Lissodendoryx isodicyialis</i>	11	0	0	11
<i>Clathria schoenus</i>	2	0	0	12
<i>Mycale carmigrphila</i>	16	4	6	16
<i>Mycale microsigmatosa</i>	5	2	0	2
<i>Iotrochota birotulata</i>	7	0	0	0
<i>Tedania ignis</i>	1	1	1	1
<i>Haliclona caerulea</i>	0	0	5	0
<i>Haliclona curacaoensis</i>	13	5	0	0
<i>Haliclona implexiformis</i>	10	0	0	0
<i>Haliclona manglaris</i>	6	7	3	3
<i>Haliclona tubifera</i>	8	0	0	0
<i>Haliclona vermeuleni</i>	0	0	4	0
<i>Chalimula molitba</i>	4	0	0	10
<i>Amphimedon</i> sp.	0	0	0	8
<i>Niphates erecta</i>	0	0	0	4
<i>Hyrtios proteus</i>	15	0	0	6
<i>Spongia tubulifera</i>	3	8	0	13
<i>Dysidea etheria</i>	0	6	0	7
<i>Halisarca</i> sp.	0	3	0	18

groups, the sea anemone *Aiptasia pallida* (Cnidaria), is worth mentioning for its striking change in occurrence at the Twin Cays sites. Although the population remained steady at Hidden Creek (8%), it doubled in Lair Channel (10%–24% of roots occupied), but it apparently disappeared from Sponge Haven where it had been present on 20% of the roots in 2003. The number of roots available for settlement per site increased considerably at Sponge Haven and Manatee Cay lagoon, although it decreased in Hidden Creek and Lair Channel.

Sponge Species Frequencies per Site

The distinctive species composition and richness at each site warrant separate presentations.

Sponge Haven

Most mangrove-specific species, such as *Halichondria magniconulosa*, *Haliclona curacaoensis*, *H. manglaris*, *H. implexiformis*, *Hyrtios proteus*, *Lissodendoryx isodictia-*

lis, and *Spongia tubulifera*, remained the most common among sponges, and some even increased in frequency between 2003 and 2007 (Figure 9a).

Lair Channel

In this mangrove channel most species remained in place between survey periods; some increased in root occurrence (*Tedania ignis*, *Haliclona manglaris*, *H. tubifera*, *Dysidea etheria*) and a few decreased (*Haliclona curacaoensis*, *H. implexiformis*, *Hyrtios proteus*) (Figure 9b). Overall, this change was accompanied by a slight decrease in root numbers (from 105 to 91) and an increase in all non-sponge groups except ascidians.

Hidden Creek

This tidal channel site is opposed to Sponge Haven in its changes between 2003 and 2007 (Figure 9c). Ten of the 12 sponge species found on the transect decreased considerably in occurrence on roots; only the opportunistic

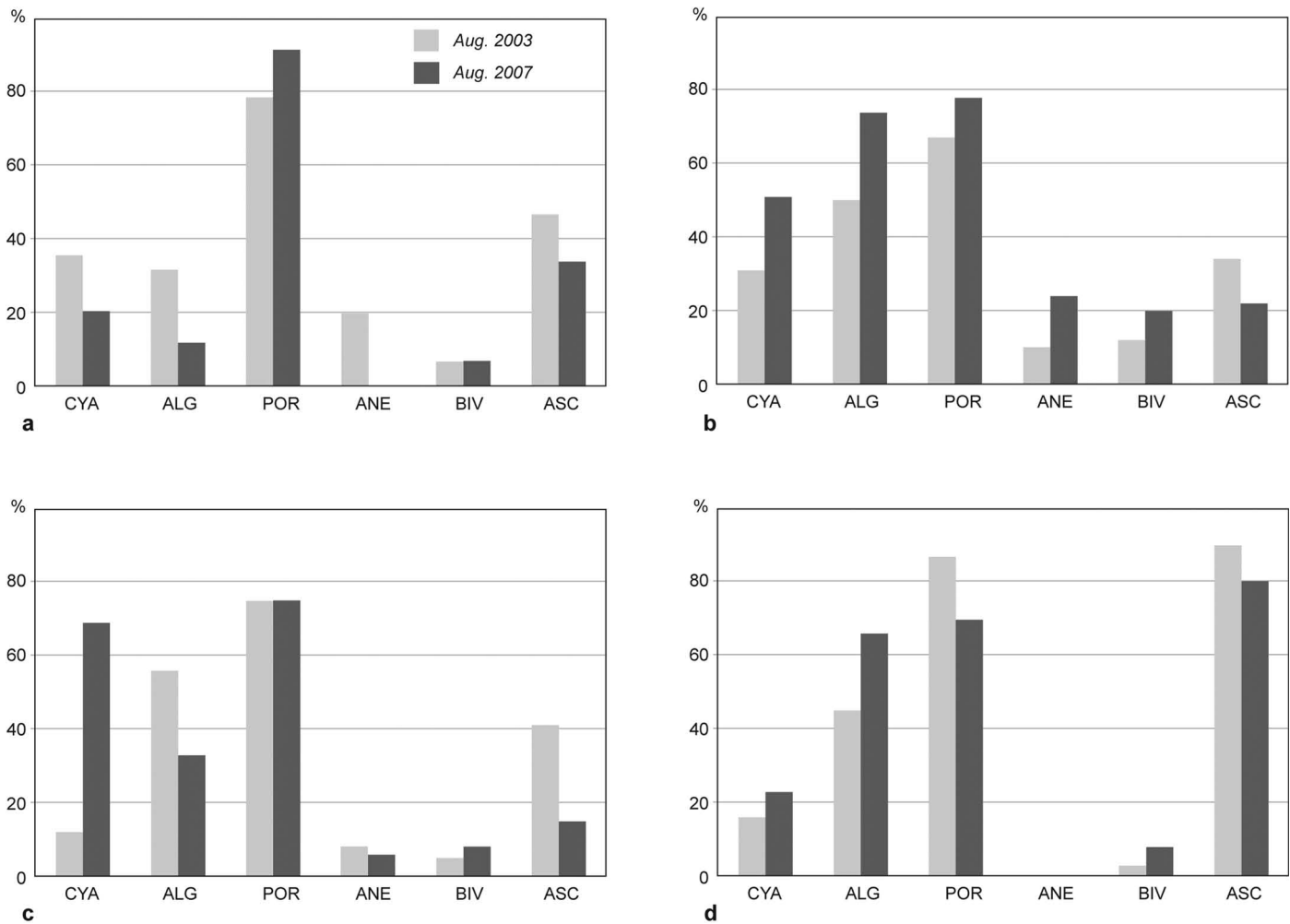


FIGURE 8. Frequency of occurrence (% of roots occupied) of major functional groups growing on mangrove roots at four sites in Belize: a, Sponge Heaven, Twin Cays; b, Lair Channel, Twin Cays; c, Hidden Creek, Twin Cays; d, Manatee Lagoon, Pelican Cays. (ALG = algae; ANE = sea anemones [*Aiptasia pallida*]; ASC = ascidians; BIV = bivalves; CYA = cyanobacteria; POR = sponges [Porifera]).

generalist *Tedania ignis* and *Lissodendoryx isodictyalis* increased slightly.

Manatee Cay

At this lagoon site, abundance of most typical mangrove sponge species decreased considerably during the survey period while two common opportunistic species (*Tedania ignis*, *Clathria schoenus*) experienced a considerable boost in their populations (Figure 9d). This trend coincided with a major increase in root numbers (from 89 to 123), similar to that which took place at Sponge Haven during the same time span.

DISCUSSION

BIOGEOGRAPHY OF CARIBBEAN MANGROVE SPONGES

Available reports describing sponge species distribution in Caribbean mangroves suggest the importance of geographic vicinity, with high similarities between the faunas of Panama and Venezuela. On the other hand, this geographic concept is upset by the incongruence of faunas encountered at two nearby sites in Belize (Twin Cays and the Pelican Cays). This dissimilarity is caused mostly by the presence of several unique or usually coral reef-associated species in the mangroves of Manatee Lagoon, an environment of particular geomorphological structure and prevailing ecologi-

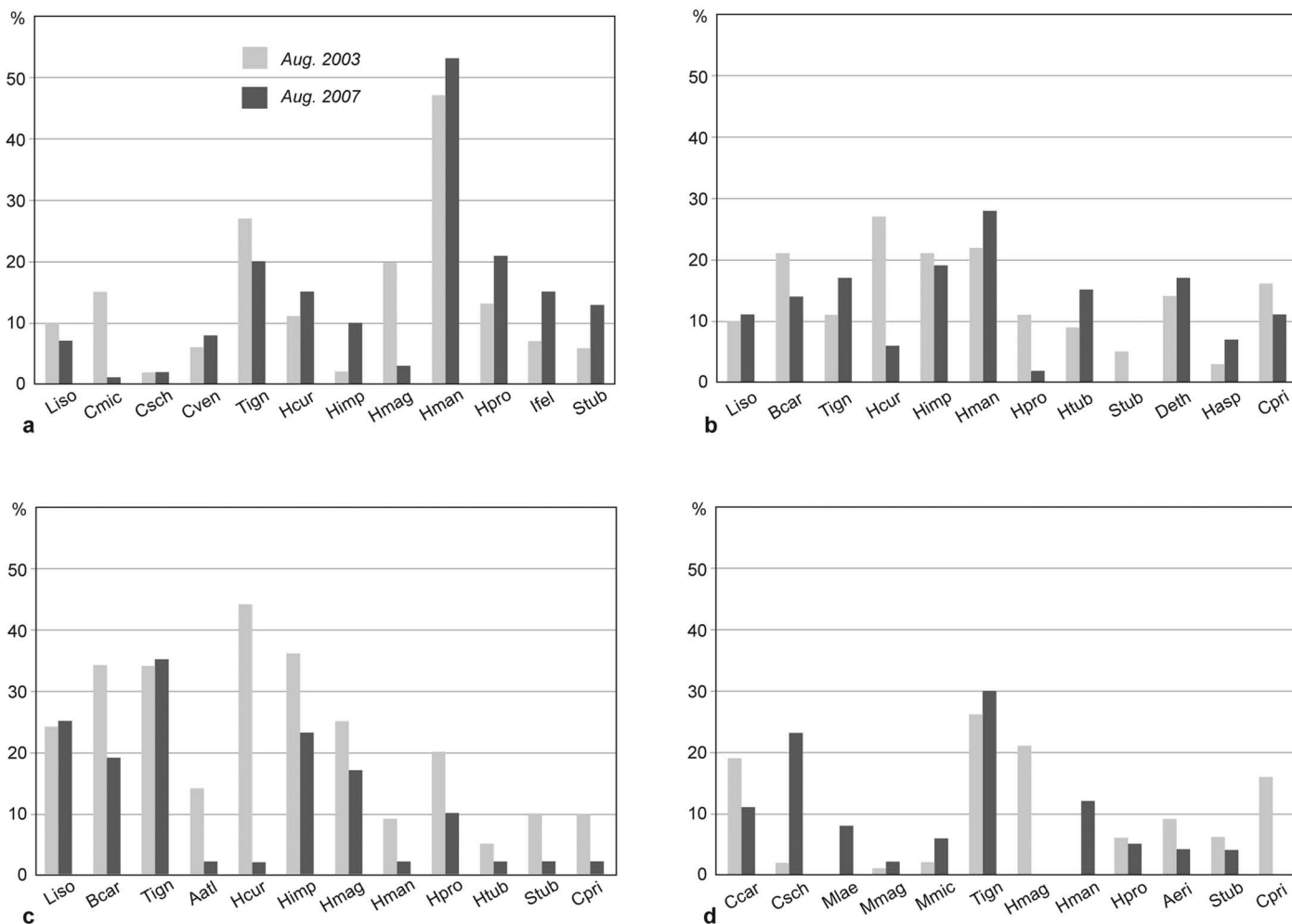


FIGURE 9. Frequency of occurrence (% of roots occupied) of sponge species growing on mangrove roots at four sites in Belize: a, Sponge Heaven, Twin Cays; b, Lair Channel, Twin Cays; c, Hidden Creek, Twin Cays; d, Manatee Lagoon, Pelican Cays. (Aatl = *Amorphinopsis atlantica*; Aeri = *Amphimedon erina*; Bcar = *Biemna caribbea*; Ccar = *Chondrilla caribensis*; Cmic = *Clathria microchela*; Cpri = *Clathrina primigenia*; Csch = *Clathria schoenus*; Cven = *Clathria venosa*; Deth = *Dysidea etheria*; Hasp = *Halisarca* sp.; Hcur = *Haliclona curacaoensis*; Himp = *H. implexiformis*; Hmag = *Halichondria magniconulosa*; Hman = *Haliclona manglaris*; Hpro = *Hyrtios proteus*; Htub = *Haliclona tubifera*; Ifel = *Ircinia felix*; Liso = *Lissodendoryx isodictyalis*; Mlae = *Mycale laevis*; Mmag = *M. magniraphidifera*; Mmic = *M. microsigmata*; Stub = *Spongia tubulifera*; Tign = *Tedania ignis*.)

cal conditions in the Pelican Archipelago (Macintyre and Rützler, 2000; Rützler et al., 2000; Wulff, 2000).

SHORT-TERM DYNAMICS OF MANGROVE
EPIFAUNA IN PANAMA

Major Functional Groups

As previously reported, mangrove-root epiphytic communities in Bocas del Toro are dominated either by

sponges or by algae/cyanobacteria (Farnsworth and Ellison, 1996; Diaz et al., 2004; Pérez, 2007). Elsewhere in the Caribbean, other groups, such as bivalves, anemones, or ascidians, may rival these taxa in abundance (Sutherland, 1980; Toffart, 1983; Bingham, 1992). The dominance of macroalgae at the protected lagoon of “Solarte In” might be a consequence of the eastward orientation of this site (as opposed to the westward orientation of the other three sites), which would expose the mangrove fringe to sunlight

for longer periods, thus promoting the growth of typical shallow-water algal species. However, further studies are required to sustain this hypothesis. There were no observations of seasonal changes in the composition of epiphytic taxa from one sampling period to the other at any site. The decrease in abundance (20%–35%) found for the most dominant groups at two sites (STRI Point and Solarte In) coincides with housing developments that occurred since the study started in 2004. Increases in suspended sediments and incidences of sponges covered by silt, which were observed at STRI Point during September and February 2005, may have impacted the community. In contrast, at the more pristine sites (Solarte Out and Big Bight), these same organisms demonstrated considerable quantitative increases.

Sponge Species

The six most common species at each site constitute from 87% to 99% of the total root area covered by sponges. These dominant species differed between sites, bringing the number of the most abundant sponges to 21, of a total diversity of 40 species. Only *Tedania ignis* was the most common species at all sites. At Solarte In the second most common species was a thin crust of the genus *Halisarca*, whereas at STRI Point it was *Clathria schoenus*, a species with a highly variable growth form (thick crusts to branching), supporting the common observation that mangrove fauna can be highly heterogeneous within one biogeographic region. It is interesting to note that 5 species that ranked near the top at the four sites were encrusting sponges (*Mycale microsigmatosa*, *Dysidea etheria*, *Haliclona manglaris*, *Halisarca* sp., *Clathria schoenus*, and *Spirastrella mollis*). This result suggests that, at least in Bocas del Toro, encrusting species are highly successful competitors. The dominance of *Tedania ignis* was also reported from other Caribbean locations (Toffart, 1983; Sutherland, 1980; Wulff, 2004; Diaz et al., 2004) and is probably related to its high and nearly year-around production of larvae (Ruetzler, unpublished data) and rapid growth rate (Wulff, 2005).

Dominant species were not always consistent in abundance at all sites. For example, during the observation time *Tedania ignis* decreased considerably at STRI Point and Solarte In but increased at Solarte Out and Big Bight. Furthermore, increase or decrease in abundance was not necessarily restricted to certain species or localities. Certain locality trends, however, were observed. At STRI Point, where *T. ignis* and *Clathria schoenus* decreased or disappeared entirely from the roots, the few large specimens of *Spongia tubulifera* remained with

only slight size changes throughout the year. At least at one location, Solarte In, deterioration of sponges appeared to be coinciding with the aforementioned housing development, which caused an increase in suspended and deposited sediment.

An interesting trend is the predominance of large sponges at Big Bight versus the much smaller sizes at Solarte Out. Solarte Out is a shallow habitat in an exposed position and subjected to strong wave action and scouring by predominantly sandy sediments (see Table 2). These parameters must impede the growth of large individuals, with the result that small and better adapted forms, such as *Haliclona vermeuleni*, *H. caerulea*, and *Spirastrella mollis*, become very abundant. Even an opportunistic species such as *Tedania ignis*, common and large-growing elsewhere, tends to be considerably restricted in size there. On the other hand, Big Bight sponges were found to have rapid growth rates that can be attributed to high nutrient concentrations measured at this site, possibly related to runoff from the dense forest that surrounds this lagoon (see Table 3). The high variability of sponge species composition between contiguous sites corroborates previous reports that the mangrove sponge fauna is rather heterogeneous in species distribution and dominance within relatively small geographic areas (Farnsworth and Ellison, 1996; Ruetzler et al., 2000; Diaz et al., 2004). This characteristic is probably the result of low recruitment rate in most species studied and, in some cases, selective physicochemical variables, such as those described for Solarte Out. A third aspect that became evident in this study is the intrinsic growth dynamics of species over time, high in species such as *Tedania ignis* and *Chalinula molitba*, and low or barely noticeable in *Hyrtios proteus* and *Spongia* spp. It must be recognized that species have different lifespans, growth rates, growth periods, and frequency of reproduction. Understanding these processes is essential to the interpretation of community dynamics.

LONG-TERM DYNAMICS OF MANGROVE EPIFAUNA IN BELIZE

Major Functional Groups

The distribution of the four primary components of mangrove-root epiphytic communities in Belize—cyanobacteria, macroalgae, sponges, and ascidians—varied differently at each of the four studied sites between August 2003 and 2007. Sponges were the most frequent occupants at all four locations in 2003; by 2007, the population had either increased (Sponge Heaven, The Lair), decreased (Manatee Lagoon), or remained steady. The decrease at Manatee Cay seemed to be related to macroalgal blooms

that coincided with the recent clear-cutting of the mangrove adjacent to this lagoon and to dredging for land-fill that released large quantities of fine sediments. Ascidian occurrence followed a similar pattern, indicating that all filter feeders are impacted by environmental events such as increase of sedimentation and blockage of vents by cyanobacterial blooms. The effect of changing root numbers seems to be obscured by the environmental factors, because there was no obvious relationship between changes in root number and frequency of any of the major taxa in the community.

Sponge Species

Comparing species composition and frequency at the four study sites in Belize, we found that they varied considerably during the four years between observation periods. The most obvious parameters affecting sponge populations were space competitors (cyanobacteria, macroalgae), number of roots available for settlement, and anthropogenic destructive events. The considerable decrease in cyanobacteria and macroalgae and increase in root numbers (from 99 to 143) in Sponge Haven may be related to the strong increase of mangrove-specific sponges because important competitors were no longer present and new substrata became available. In contrast, at Hidden Creek, the increase of filamentous cyanobacteria (to 57% of substrate area) and decrease in root numbers (from 59 to 52) must have caused the dramatic reduction of most mangrove-specific sponge species. In Manatee Cay Lagoon, mangrove-specific species lost in frequency while opportunistic species (*Tedania ignis*, *Clathria schoenus*) gained. Overall, however, there was a reduction of sponge populations despite an addition in root numbers. This trend can be explained by increased algal competition and an artificial incursion, the clear-cutting of mangrove trees and dredging of fill material for a housing development sometime before the 2007 survey. The dredge operation in particular can be blamed in the short term as it causes suspension of fine sediment, affecting the delicate filtration system of the sponges. A shift of species toward more robust opportunists rather than typical mangrove forms is therefore not surprising.

COMMENTS ON METHODS FOR EVALUATING MANGROVE PROP-ROOT COMMUNITIES

Two criteria were used in the present study to evaluate epiphytic communities on mangrove roots. To determine short-term dynamics (within one year; Bocas del Toro),

it was expected that specimen size rather than numbers would change. Therefore, a photographic record was made of a specific number of roots (25) along their entire lengths (the side facing the open water), and planimetry was used to measure projected area cover of the fouling organisms. From these values and the record of root length, an index of species abundance could be calculated. Area cover has been extensively used to compare the abundances of plant and sessile animal communities, and it has been proven a most practical and reliable method for reef surveys (Weinberg, 1981). Considering that in mangroves substrate availability is quite low, measuring area cover gives a good indication of how important an organism is in this community. The limitation of this method applies mostly to stoloniferous organisms for which cover may underestimate their importance. The photo-transect method proved to be most useful in areas where visibility was very good, but it was problematic in locations with high freshwater or sediment input. Such conditions caused whole sets of photographs to be impossible to interpret. This method is also time consuming, both the work underwater and that during photo analysis in the lab. For this reason there was a limit to the root numbers that could be included in each survey. Usually, to complete a survey of 25 roots in one site it was necessary to visit twice, and evaluation of all (3–8) photos for one root took from 30 to 60 min. In the end, after excluding useless images, the data set was reduced to only 14 to 22 recorded roots, depending on the site.

Alternatively, in Belize we used data on the presence or absence of taxa on each root and thus were able to survey a much larger number of roots (50–150), from which we determined the frequency of occurrence of major taxonomic groups and species of sponges. These data allowed monitoring the presence of each group or species and change in distributions over time. This type of survey follows the fate of the community rather than fluctuations in biomass. The method also aids detection of a species or community reaction to particular environmental disturbances. In terms of time investment, it takes only 2 to 5 h to obtain frequency data from a 30 m transect along the mangrove fringe. The data were in hard copy once the fieldwork was completed and were independent of visibility conditions and other variables that may ruin photographic data.

CONCLUSIONS

Many more Caribbean mangroves must be studied before we can expect a full understanding of the biodiversity and the biogeographic relationships of their unique and

fascinating prop-root fouling communities, particularly the sponges. The rather disjunct pattern of sponge species distribution found in the Panama and Belize study sites suggests that biodiversity is better evaluated by surveying extended stretches of mangrove fringe at numerous sites in any region rather than short lengths of transects. Interpretation of species composition and interactions can be based on smaller-scale levels of inquiry. The most abundant organisms in the studied sites were sponges, macroalgae, cyanobacteria, ascidians, and bivalves. The hierarchical ranking of these groups showed great variability on spatial and temporal scales, making generalization and prediction of structure and dynamics of communities very difficult.

The one-year study of four sites in the Bocas del Toro region, Panama, showed various important aspects of abundance changes in these fouling communities. First, a few sponge species contribute most of the abundance; second, the identity of major community components varies within a small geographic scale; third, species have adopted distinct life strategies (in growth potential, recruitment rates, and asexual reproduction capabilities) that allow for adaptations to resist stressful environmental variables; and fourth, the combination of the factors of large sediment grain size and energy from wave or current action limits species habitat access, survival, and growth, as demonstrated by the increase in turbidity from land-filling and development in some areas.

The four-year observations in Belize made it evident that the frequency of occurrence of sponge species and other taxa, such as cyanobacterial and macroalgal blooms, is a relatively simple and fast measure to detect major environmental changes. Even if sponge frequency on the roots is not much affected by algal blooms, the presence of mangrove-specific species certainly shows a decline; only a couple of generalist species seem to profit from such stressful events. The degree of disappearance of ascidians at all four sites in Belize suggests that these organisms may be even more sensitive to algal and cyanobacterial competition, as well as suspended fine sediments, than sponges. We find, both in Belize and in Panama, that two sponge growth forms are highly successful among sponge root occupiers: encrusting and irregularly massive. This observation is in contrast to open reef environments where tubular and ramose forms predominate.

Close monitoring of the abundance and frequencies of key mangrove benthos at specific sites and their correlation with short-term or long-lasting environmental impacts and stress will be a useful tool for assessing mangrove health throughout the Caribbean region in the future.

ACKNOWLEDGMENTS

We thank Mike Carpenter, Kathleen Smith, Estrella Villamizar, and Martha Nicholas for support of fieldwork based at Carrie Bow Cay, Belize; likewise, we thank Gabriel Jacome and Plinio Gondola for assistance with logistics at the Smithsonian Bocas del Toro field station, Panama. Molly Kelly Ryan designed the maps and rendered the graphs in final form; Carla Piantoni prepared the color figures and helped with editorial tasks. We acknowledge the National Coral Reef Institute for lending us the CPCe (Coral Point Count with Excel extensions) program for area calculations. Photographs for this paper were taken by the following Smithsonian staff or associates: Cristina Diaz, Ilka Feller, Diane Littler, Elisabeth McLean, Tony Rath, and Klaus Ruetzler. This is contribution number 855 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund.

LITERATURE CITED

- Alcolado, P. M. 1985. Distribución de la abundancia y composición de las comunidades de esponjas en la macrolaguna del Golfo de Batabanó. [Distribution and Abundance of Sponge Communities in the Macrolagoon of the Gulf of Batabanó.] In *Proceedings of the Symposium on Marine Sciences and 7th Scientific Meeting of the Institute of Oceanography (20th Anniversary)*, pp. 5–10. Havana: Academy of Sciences of Cuba.
- Alvarez, A. I. 1989. Establecimiento, desarrollo y mantenimiento de una comunidad epibentónica tropical. [Settlement, Development and Maintenance of a Tropical Epibenthic Community.] Licenciature Thesis, Universidad Central de Venezuela, Caracas, Venezuela.
- Astor, Y. 1996. "Manual de análisis de aguas para la acuicultura y las ciencias del mar." ["Manual for Water Analysis in Aquaculture and Ocean Studies."] In Fundación La Salle de Ciencias Naturales Contribución Número 192. *Colección Cuadernos FLASA. Serie Ciencia y Tecnología*, 8:1–89.
- Bingham, B. L. 1992. Life Histories in an Epifaunal Community: Coupling of Adult and Larval Processes. *Ecology*, 73:2244–2259
- Bingham, B. L., and C. M. Young. 1995. Stochastic Events and Dynamics of Mangrove Root Epifaunal Community. *Marine Ecology*, 16:145–163.
- Calder, D. R. 1991a. Abundance and Distribution of Hydroids in a Mangrove Ecosystem at Twin Cays, Belize, Central America. *Hydrobiology*, 216/217:221–228.
- . 1991b. Associations Between Hydroid Species Assemblages and Substrates Types in the Mangal Twin Cays, Belize. *Canadian Journal of Zoology*, 69:2067–2074.
- de Lacerda, L. D., J. E. Conde, B. Kjerfve, R. Alvarez-León, C. Alarcón, and J. Polanía. 2002. "American Mangroves." In *Mangrove Ecosystems: Function and Management*, ed. L. D. de Lacerda, pp. 1–62. Berlin: Springer-Verlag.
- de Weerd, W. H., K. Ruetzler, and K. Smith. 1991. The Chalinidae (Porifera) of Twin Cays, Belize, and Adjacent Waters. *Proceedings of the Biological Society of Washington*, 104:189–205.

- Diaz, H., M. Bevilaqua, and D. Bone. 1985. *Esponjas en Manglares del Parque Nacional Morrocoy*. [Mangrove Sponges of Morrocoy National Park.] Caracas: Fondo Editorial Acta Científica Venezolana.
- Diaz, M. C. 2005. Common Sponges from Shallow Marine Habitats from Bocas del Toro Region, Panama. *Caribbean Journal of Science*, 41(3):466–475.
- Diaz, M. C., S. Pauls, E. Villamizar, A. Alvizu, M. E. Amaro, M. Cellamare, S. Grune, I. Hernandez, S. Narciso, A. Perez, J. Perez, I. Ramirez, R. Ramos, M. P. Romero, and P. Young. 2003. *Porifera Biodiversity in Nueva Esparta, Venezuela: Common Species from La Restinga and Cabugua Island*. Abstract. The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change. Report from a Workshop, Smithsonian Marine Station, Fort Pierce, Florida, December 2003. Washington, D.C.: Smithsonian Institution.
- Diaz, M. C., K. A. Smith, and K. Rützler. 2004. Sponge Species Richness and Abundance as Indicators of Mangrove Epibenthic Community Health. *Atoll Research Bulletin*, 518:1–17.
- Diaz, M. C., R. W. Thacker, K. Rützler, and C. Piantoni. 2007. “Two New Haplosclerid Sponges from Caribbean Panama with Symbiotic Filamentous Cyanobacteria, and an Overview of Sponge–Cyanobacteria Associations.” In *Proceedings of the 7th International Sponge Symposium: Porifera Research: Biodiversity, Innovation and Sustainability*, pp. 31–39. Rio de Janeiro, Brazil: Museu Nacional.
- Diaz, M. C., and B. B. Ward. 1997. Sponge-mediated Nitrification in Tropical Benthic Communities. *Marine Ecology Progress Series*, 156:97–107.
- Ellison, A. M., and E. J. Farnsworth. 1992. The Ecology of Belizean Mangrove-Root Fouling Communities: Patterns of Epibiont Distribution and Abundance, and Effects on Root Growth. *Hydrobiologia*, 247:87–98.
- Ellison, A. M., E. J. Farnsworth, and R. R. Twilley. 1996. Facultative Mutualism Between Red Mangroves and Root-Fouling Sponges in Belizean Mangal. *Ecology*, 77(8):2431–2444.
- Engel, S., and J. R. Pawlik. 2005. Interactions among Florida Sponges. II. Mangrove Sponges. *Marine Ecology Progress Series*, 303: 145–152.
- Farnsworth, E. J., and A. M. Ellison. 1996. Scale Dependent Spatial and Temporal Variability in Biogeography of Mangrove-Root Epibiont Communities. *Ecological Monographs*, 66:45–66.
- Hadju, E., and K. Rützler. 1998. Sponges, Genus *Mycale* (Poecilosclerida: Demospongiae: Porifera), from a Caribbean Mangrove and Comments on Subgeneric Classification. *Proceedings of the Biological Society of Washington*, 11(4):737–773.
- Hechtel, G. J. 1965. A Systematic Study of the Demospongiae of Port Royal, Jamaica. *Bulletin of the Peabody Museum of Natural History*, 20:1–103.
- Jackson, J. B. C., and L. Buss. 1975. Allelopathy and Spatial Competition Among Coral Reef Invertebrates (Species Interactions/Community Structure). *Proceedings of the National Academy of Sciences*, 72(12):5160–5163.
- Lehnert, H., and R. W. M. van Soest. 1998. Shallow Water Sponges of Jamaica. *Beaufortia*, 48(5):71–103.
- Littler, M. M., P. R. Taylor, D. S. Littler, R. H. Sims, and J. N. Norris. 1985. The Distribution, Abundance, and Primary Productivity of Submerged Macrophytes in a Belize Barrier-Reef Mangroves System. *Atoll Research Bulletin*, 289:1–20.
- Macintyre, I. G., and K. Rützler, eds. 2000. Natural History of the Pelican Cays, Belize. *Atoll Research Bulletin*, 466–480:1–333.
- Maldonado, M., and C. M. Young. 1996. Bathymetric Patterns of Sponge Distribution on the Bahamian Slope. *Deep-Sea Research I*, 43(6):897915.
- Orihuela, B., H. Diaz, and J. E. Conde. 1991. Mass Mortality in a Mangrove Roots Fouling Community in a Hypersaline Tropical Lagoon. *Biotropica*, 23:592–601.
- Pauls, S. 1998. *Estudio Sistemático y Biodiversidad de Porifera y Cnidaria en la Bahía de la P. N. Henri Pittier*. [Systematic and Diversity Study of Porifera and Cnidaria of the Ciénaga de Ocumare de la Costa Bay, Henri Pittier National Park.] Caracas: Escuela de Biología, Universidad Central de Venezuela.
- . 2003. “Esponjas.” In *Biodiversidad en Venezuela*. [“Sponges.” In *Biodiversity of Venezuela*.], ed. M. Aguilera, A. Azocar, and E. Gonzales, pp. 210–219. Caracas, Venezuela: Polar Foundation and Ministry of Science and Technology.
- Pérez, A. 2007. Biodiversidad y Estructura Comunitaria de Poríferos Asociados a Raíces del Manglar, *Rhizophora mangle*, en el P. N. Laguna de La Restinga, Nueva Esparta, Venezuela. [Biodiversity and Community Structure of Poríferos Associated to Mangrove Roots, *Rizophora mangle*, in Laguna de La Restinga National Park, Nueva Esparta, Venezuela.] Licenciante’s Thesis, Universidad Central de Venezuela, Caracas, Venezuela.
- Ramirez, I. 2002. Taxonomía de Esponjas (Porifera: Demospongiae) de la Laguna de Bocaripo, Estado Sucre, e Islote Caribe, Dependencia Federal, Venezuela. [Taxonomy of the Sponges (Porifera: Demospongiae) of Bocaripo Lagoon, Estado Sucre, and Caribe Island, Dependencia Federal, Venezuela.] Licenciante’s Thesis, Universidad de Oriente, Cumaná.
- Rützler, K., 1969. “The Mangrove Community: Aspects of Its Structure, Faunistics, and Ecology.” In *Memorias, Simposio Internacional Lagunas Costeras, 1967*, pp. 515–536. Mexico City: Universidad Nacional Autónoma de México.
- . 1995. Low-Tide Exposure of Sponges in a Caribbean Mangrove Community. *P.S.Z.N. I: Marine Ecology*, 16:165–179.
- Rützler, K., M. C. Diaz, R. W. M. van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. Wulff. 2000. Diversity of Sponge Fauna in Mangroves Ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, 477:231–248.
- Rützler, K., and I. C. Feller. 1988. Mangrove Swamp Communities. *Oceanus*, 30(4):16–24.
- . 1996. Caribbean Mangrove Swamps. *Scientific American*, 274(3):94–99.
- Rützler, K., I. Goodbody, M. C. Diaz, I. C. Feller, and I. G. Macintyre. 2004. The Aquatic Environment of Twin Cays, Belize. *Atoll Research Bulletin*, 512:1–49.
- Rützler, K., C. Piantoni, and M. C. Diaz. 2007. *Lissodendoryx*: Rediscovered Type and New Tropical Western Atlantic Species (Porifera: Demospongiae: Poecilosclerida: Coelospharidae). *Journal of the Marine Biological Association of the United Kingdom*, 87:1491–1510.
- Rützler, K., and K. P. Smith. 1993. The Genus *Terpios* (Suberitidae) and New Species in the “*Lobiceps*” Complex. *Scientia Marina*, 57(4):381–393.
- Sutherland, J. P. 1980. Dynamics of the Epibenthic Community on Roots of the Mangrove *Rhizophora mangle*, at Bahía de Buche, Venezuela. *Marine Biology*, 58:75–84.
- Taylor, P. R., M. M. Littler, and D. S. Littler. 1986. Escapes from Herbivory in Relation to the Structure of Mangrove Island Macroalgal Communities. *Oecologia (Berlin)*, 69:481–490.
- Thacker, R. W., M. C. Diaz, K. Rützler, P. M. Erwin, S. J. A. Kimble, M. J. Pierce, and S. L. Dillard. 2007. Phylogenetic Relationships Among the Filamentous Cyanobacterial Symbionts of Caribbean Sponges and a Comparison of Photosynthetic Production Between Sponges Hosting Filamentous and Unicellular Cyanobacteria. *Proceedings of the 7th International Sponge Symposium: Porifera Research: Biodiversity, Innovation and Sustainability*, pp. 621–626. Rio de Janeiro, Brazil: Museu Nacional.

- Toffart, J. L. 1983. Les Peuplements des racines de palétuviers en Guadeloupe (Antilles Françaises). I. Analyse floristique et faunistique; méthodologie et premier résultats. [Populations of Mangrove Roots in Guadeloupe (French Antilles). I. Floristic and Faunistic Analysis; Methodology and First Results.] *Bulletin d'Ecologie*, 14(4):227–239.
- Van Soest, R.W. M. 1993. Affinities of the Marine Demosponge Fauna of the Cape Verde Islands and Tropical West Africa. *Courier, Forschungsinstitut Senckenberg*, 159:205–219.
- Weinberg, S. 1981. A Comparison of Reef Survey Methods. *Bijdragen tot de Dierkunde*, 5:199–218.
- Wulff, J. L. 2000. Sponge Predators May Determine Differences in Sponge Fauna Between Two Sets of Mangrove Cays, Belize Barrier Reef. *Atoll Research Bulletin*, 477:250–263.
- . 2004. Sponges on Mangrove Roots, Twin Cays, Belize: Early Stages of Mangrove Community Assembly. *Atoll Research Bulletin*, 519:1–10.
- . 2005. Trade-Offs in Resistance to Competitors and Predators, and Their Effects on the Diversity of Tropical Marine Sponges. *Journal of Animal Ecology*, 74:313–321.
- Zea, S. 1987. *Esponjas del Caribe Colombiano*. [*Sponges of the Colombian Caribbean*.] Bogota, Columbia: Instituto de Investigaciones Marinas y Costeras “José Benito Vives de Andrés.”
- . 1993. Recruitment of Demosponges (Porifera, Demospongiae) in Rocky and Coral Reef Habitats of Santa Marta, Colombian Caribbean. *Marine Ecology*, 14:1–21.