

Sponge Community Dynamics on Caribbean Mangrove Roots: Significance of Species Idiosyncrasies

Janie L. Wulff

ABSTRACT. Descriptions of the rich sponge faunas inhabiting mangrove roots at various Caribbean sites are unanimous in pointing out the heterogeneity of species distribution and abundance patterns at all scales, from different portions of a single root to geographic subregions. Abiotic factors have often been implicated by correlation, but ecological interactions, and the life history and morphological characteristics of the sponge species, may also play key roles. Published studies vary widely in methods used, hampering direct comparisons of results, and raising the possibility that conclusions might be influenced by methods. I have been exploring the processes underlying distribution and abundance patterns by applying identical methods to studying community composition and dynamics at two sites in Belize (Twin Cays) and one site in Panama (Bocas del Toro). Established communities on roots have been fully censused, by volume and numbers of individuals, yearly for three years (i.e., four censuses). Community composition, when evaluated in terms of total volume of component species, is very similar at these three sites, although abiotic factors differ and geographic distances between sites range from 330 m to 1,200 km. The nine species found on censused roots at all three sites constituted a total of 89%, 84%, and 73%, respectively, of the total sponge volume at these sites. In general, species exhibited similar patterns of growth, size decrease, and mortality at all sites where they were found, suggesting that these are species-level characteristics. Numbers of individuals and volume provide very different assessments of the relative importance of different species in these communities. Community change over time appeared to be substantial, when measured in terms of shifts in total numbers of individuals or total sponge volume. However, taking into account dynamics of individual species provides a very different view, as most large changes in numbers or volume were not community wide but tended to reflect life history characteristics typical of early successional stage species or idiosyncratic responses of one or a few species to particular environmental circumstances.

INTRODUCTION

Organisms that live in habitats consisting of discrete patches within an uninhabitable matrix have fascinated biologists who are simultaneously attracted to community ecology and to life history evolution. A rich set of conceptual frameworks has developed to explain the dynamics of community assembly and development within each patch in the context of interconnections among patches. Theories of, for example, island biogeography (MacArthur and Wilson, 1967), multiple stable points (Sutherland, 1974), competitive networks (Jackson and

Buss, 1975), the intermediate disturbance hypothesis (e.g., Connell, 1978), and meta-communities (e.g., Mouquet and Loreau, 2002) have helped us understand community dynamics in patchy habitats ranging from oceanic islands and tropical mountaintops to badger mounds, holes in mussel beds, and ponds.

Prop roots of Caribbean red mangrove (*Rhizophora mangle*) trees are easily accessible, experimentally tractable, and extraordinarily colorful examples of inherently patchy communities. The sessile inhabitants that cover the root surfaces colonize in the form of water-borne propagules, and most of them are thereafter confined to the root on which they landed. Although post-recruitment interactions with neighbors and consumers may have relatively deterministic outcomes, a stochastic element, contributed by the uncertainty that any particular species will land on a particular root, is ever present. Throughout the wider Caribbean region sponges are prominent members of the prop root communities, and their abundance and diversity of species, color, and forms have inspired time-series monitoring and experimental manipulations as well as comparative faunal studies (e.g., Sutherland, 1980; Ellison and Farnsworth, 1992; Bingham and Young, 1995; Rützler, 1995; Farnsworth and Ellison, 1996; Rützler and Feller, 1996; Rützler et al., 2000; Diaz et al., 2004; Diaz, 2005; Wulff, 2000, 2004, 2005; Engel and Pawlik, 2005). Specific conclusions relating to how dynamic these sponge communities are, and what processes drive the dynamics and influence distribution and abundance patterns, have differed widely among studies, but a consistent theme is that the resulting distribution and abundance patterns are highly heterogeneous on scales ranging from within individual roots to between geographic subregions.

Sutherland (1980) complemented repeated monitoring of natural communities on prop roots with a study of community development on flat settlement panels suspended among the roots in Venezuela. He concluded that these sponge-dominated communities are relatively stable over time, and that high diversity could be maintained by a trade-off between competitive ability and colonization efficiency, combined with the continued addition of fresh roots that provide refuges for inferior competitors. Farnsworth and Ellison (1996) surveyed prop root communities of mangroves in a variety of abiotic settings in Belize, focusing on spatial scales of distribution patterns. They were able to identify scales of heterogeneity that included backs versus fronts of individual roots, leeward versus windward shores, and coastal versus island mangal. At the 11 sites where they sampled twice, their data corroborated Sutherland's (1980) conclusions that com-

munity change is minimal. Bingham and Young (1995) concluded very differently, from their work in the Florida Keys, that dynamics of sponges on mangrove roots can be extreme, influenced by perturbations from physical disturbance, predators, and asexual recruitment. They attributed differences in community dynamics between sites in the Florida Keys and Venezuela to differences in seasonality (subtropical versus tropical) and abiotic stressors, and suggested that the differences between their study and Sutherland's (1980) study could be explained by equilibrium versus non-equilibrium situations, with the Venezuelan mangrove communities primarily structured by competitive interactions.

Disentangling the effects of biogeography and different suites of abiotic factors by making direct comparisons among studies is hampered by the wide variety of approaches that have been applied. Published studies differ with respect to units of study, time course and frequency of monitoring, and metrics for evaluating abundance. To control for technique, I used identical methods to evaluate sponge community composition and dynamics for three years on mangrove prop roots at three sites in Belize and Panama. Following the fates of individual sponges was a priority, because my chief interest was in how the morphological and life history strategies of the different sponge species constrain or enhance their ability to coexist on the prop roots. Rather than focusing on community-level metrics, such as species diversity or primary space occupancy, I recorded survival and changes in volume of the same individuals over time and attempted to identify the causes of size decrease, fragmentation, or mortality. Two sites near each other in Belize differed in abiotic conditions, and a site in Panama provided a geographic comparison. My goals included (1) assessing the similarity of species composition among sites differing in abiotic factors and geographic distance, (2) comparing community dynamics among sites, with respect to both numbers of individuals and volume, and (3) exploring the possibility that each mangrove sponge species adheres to a characteristic approach for maintaining its representation in this community, regardless of the specific abiotic context and other species present.

METHODS

Three sites characterized by well-developed mangrove prop root epiphytic communities were chosen for yearly censuses. The three sites were chosen primarily because experiments had been established at each several years before, and so regular visits were already required for moni-

toring. Top priorities in initial site choice had been easy access and sufficient sponge individuals for experimental manipulations; species composition was secondary. The two Belize sites, both at Twin Cays, near the Smithsonian Institution's Carrie Bow Cay research station (map and further site descriptions in Rützler et al., 2004; Diaz et al., 2004), allow comparison of a main channel versus a tidal creek near each other (330 m). The Panama site, directly across the channel from the Smithsonian Tropical Research Institute marine laboratory on Isla Colon in Bocas del Toro (map coordinates and description of the overall area are found in Diaz, 2005), adds a geographic comparison (1,200 km distant) between two main channel sites. The submerged portions of the prop roots (i.e., the portion on which sponges could grow) were from 24 to 143 cm long, with the majority between 40 and 80 cm in length.

At each site, mangrove roots or root clusters were chosen that appeared to be healthy (i.e., no signs of rot or incipient breakage) and on which it was possible to identify and measure all sponges on all sides of each root. Root clusters were added to the initial census at each site until species accumulation curves had leveled off for sponges, and at least 163 sponge individuals (the number of sponges in the first census at the first site) were included: a total of 10 clusters, 1 to 5 roots each (24 roots initially) at Hidden Creek; 13 clusters, 1 to 4 roots each (37 roots initially), at Sponge Haven; and 15 clusters, 1 to 3 roots each (42 roots initially), at the Bocas del Toro site. Roots were labeled with small plastic tags, coded by color and shape, on narrow (1 mm) beaded nylon cable ties. Full censuses were made at approximately 1 year intervals, for a total of 3 years (i.e., four censuses at each site, except for Bocas del Toro, where the 2nd year census was skipped), beginning in March 2004 at both Belize sites and in June 2003 at the Panama site. At each census, every root or root cluster was drawn and root lengths measured. Every sponge was drawn to scale, in place on the root drawings, and sufficient dimensions measured to accurately estimate volume by conglomerations of appropriate geometric solids. In this way, every sponge could be followed for survival, growth, decrease in size, and fragmentation. New recruits were added to the root maps as they were discovered (recruitment data will be reported in a separate publication), and notes were made on interactions between neighboring sponges and other sessile organisms, as well as damage caused by physical disturbance, predation, and disease. Some roots at each site were lost by breakage during the 3 years. To be able to interpret the time-series data clearly, only roots for which at least some portion

persisted throughout the study were included in the time-series data analysis, and the only roots added to the study were those that branched directly off subtidal portions of the originally censused roots.

RESULTS

SPECIES COMPOSITION AND RELATIVE ABUNDANCE, BY VOLUME AND NUMBER OF INDIVIDUALS

A total of 21 sponge species were represented by at least 0.1% of the total sponge volume on censused roots at one or more sites (Table 1). These species represent the demosponge orders Poecilosclerida (8 species), Haplosclerida (6 species), Halichondrida (4 species), and Dictyoceratida (3 species), in a variety of colors, and with growth forms ranging from thinly encrusting to irregularly branching to clusters of volcanoes (Figure 1). Of these most abundant 21 species, 9 were found on censused roots at all three sites, and another 6 were found on censused roots at two of the three sites (Figure 2). Many of the sponge species are relatively rare, and so were present at a site but not on a censused root. Adding three cases in which species were found at a second or third site on roots directly adjacent to at least one censused root increases the number of species shared by all three sites to 10, with an additional 7 species shared by two of the three sites. Geographic distance was not a strong predictor of the percent of species shared. Sponge Haven and Hidden Creek, only 330 m apart, shared 74% (14/19) of their most common species, and Sponge Haven and Bocas del Toro, 1,200 km apart, shared 60% (12/20) of their most common species (comparisons not significantly different by the G test: $0.1 < P < 0.5$). The Hidden Creek and Bocas sites, geographically distant from each other and also differing in abiotic factors, shared 55% (11/20) of their most common species (comparison with the proportion of species shared by Hidden Creek–Sponge Haven by the G test: $0.05 < P < 0.1$).

Census data from all years at each site were added together for an average relative representation of species, with respect to both volume and number of individuals (Figure 3). At all three sites the most abundant species by volume, *Tedania ignis*, accounted for about half (49%–57%) of the total sponge volume. The nine species found on censused roots at all three sites contributed a total of 89%, 84%, and 73% of the total volume at, respectively, Hidden Creek (HC), Sponge Haven (SH), and Bocas del Toro (BT). Similarity of species representation at these sites is also borne out by Morisita's index of community similarity (using volume as abundance measure),

TABLE 1. Sponge species on censused roots at Hidden Creek and Sponge Haven, both at Twin Cays, Belize; and at Isla Colon, Bocas del Toro, Panama. A total of 21 sponge species were represented by at least 0.1% of the total sponge volume on censused roots at one or more sites. Species that rank in the top half of the species on censused roots at a site, with respect to volume, are indicated by “XX”, and those that rank in the bottom half are indicated by “X”. Species that occurred on censused roots at one site but were only seen on a root or roots directly adjacent to at least one censused root at another site are indicated by “x”. A dash (–) indicates species was not found at a site.

Sponge taxon	Location		
	Hidden Creek	Sponge Haven	Bocas del Toro
Order Dictyoceratida			
<i>Dysidea etheria</i> de Laubenfels, 1936	X	x	X
<i>Spongia tubulifera</i> Lamarck, 1814, and <i>S. obscura</i> Hyatt, 1877	XX	XX	XX
Order Halichondrida			
<i>Amorphinopsis</i> sp.	XX	–	–
<i>Halichondria magniconulosa</i> Hechtel, 1965	XX	XX	XX
<i>Halichondria</i> sp.	–	XX	–
<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)	X	x	–
Order Haplosclerida			
<i>Chalinula molitba</i> (de Laubenfels, 1949)	XX	–	X
<i>Haliclona curacaoensis</i> (van Soest, 1980)	X	X	–
<i>Haliclona implexiformis</i> (Hechtel, 1965)	XX	X	X
<i>Haliclona manglaris</i> Alcolado, 1984	X	X	X
<i>Haliclona</i> sp. a	X	x	–
<i>Haliclona</i> sp. b	–	–	XX
Order Poecilosclerida			
<i>Biemna caribea</i> Pulitzer-Finali, 1986	XX	X	X
<i>Clathria campecheae</i> Hooper, 1996	X	X	–
<i>Clathria schoenus</i> (de Laubenfels, 1936)	–	–	XX
<i>Clathria venosa</i> (Alcolado, 1984)	X	X	X
<i>Lissodendoryx isodictyalis</i> (Carter, 1882)	XX	XX	X
<i>Mycale microsigmatosa</i> Arndt, 1927	–	XX	XX
<i>Tedania ignis</i> (Duchassaing and Michelotti, 1864)	XX	XX	XX
<i>Tedania klausii</i> Wulff, 2006	–	XX	XX

with similarities of HC–SH = 0.977, SH–BT = 0.971, and HC–BT = 0.957. These index values are strongly influenced by the similar dominance of *T. ignis* at all three sites, but other species were also consistently either relatively abundant or rare at all sites. When sponge species at each site are divided into those that rank in the top half by volume versus those that rank in the bottom half, pairwise comparisons between sites (see data in Table 1) yield 23 site pairs in which a species was ranked in either the top half or bottom half at both sites and only 7 pairs in which a species was ranked in the top half at one site and in the bottom half at the other site (significantly different from an even distribution by the *G* test at $P < 0.005$).

At each site species were present on censused roots that were represented by volumes of less than 0.1% of the total. Among these species were *Scopalina ruetzleri* (Wiedenmayer, 1977) at Hidden Creek, *Clathrina coriacea*

(Montagu, 1818) at Hidden Creek and Sponge Haven, and *Mycale magnirhaphidifera* (van Soest, 1984) at Sponge Haven; and *Hyrtilios violaceus* (Duchassaing and Michelotti, 1864), *Haliclona vansoesti* (de Weerd, de Kluijver, and Gomez, 1999), *Haliclona caerulea* (Hechtel, 1965), and *Tethya actinia* (de Laubenfels, 1950), all at Bocas del Toro, as well as several as yet unidentified species.

In general, number of individuals and total volume provide very different views of the relative importance of the species in these communities (see Figure 3). This discrepancy is strikingly illustrated by the high representation by numbers of individuals of *Haliclona manglaris* (15.2%, 27.9%, and 50.1% at HC, SH, and BT, respectively), which also consistently contributed minimal volume (0.06%, 0.08%, and 0.37%). By contrast, *Tedania ignis*, which contributed half the volume at each site, contributed only 8.4% to 20.4% of the individuals.



FIGURE 1. Photographs of some of the most common sponge species inhabiting mangrove prop roots at Hidden Creek and Sponge Haven, Twin Cays, Belize, and across the channel from the STRI Bocas del Toro Marine Station, Isla Colon, Panama. Top row, from left to right: *Clathria venosa*, *Haliclona curacaoensis*, *Haliclona manglaris* (turquoise) and *Haliclona* sp. b (purple), *Dysidea etheria* (ethereal blue). Second row: *Chalinula molitba*, *Mycale microsigmatosa*, *Biemna caribea*, *Tedania ignis* (three individuals). Third row: *Lissodendoryx isodictyalis*, *Tedania klausii*, *Haliclona* sp. a. Bottom row, from left: *Halichondria magniconulosa*, *Haliclona implexiformis* (purple). Authors of species are given in Table 1.

Sponge species on mangrove prop roots

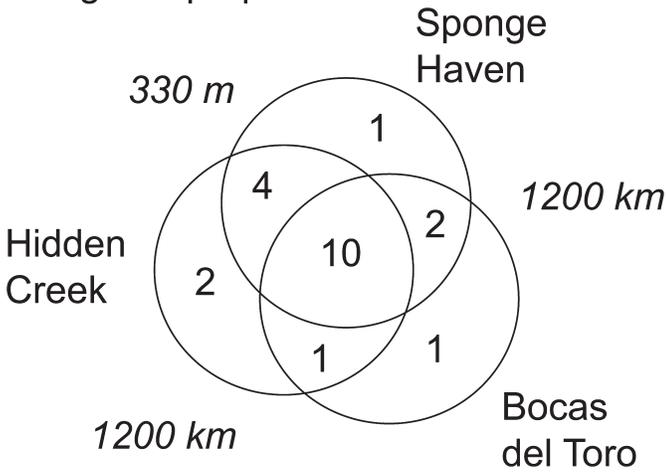


FIGURE 2. Diagram showing sponge species shared among two sites in Belize (Hidden Creek and Sponge Haven) and one site in Panama (Bocas del Toro). Only the 21 species that each constituted at least 0.1% of the total sponge volume on censused roots at a minimum of one of the three sites are included.

Mean density of numbers of sponge individuals per unit length of subtidal prop root was similar for all three sites (15, 11, and 15 individuals per meter length of root for Hidden Creek, Sponge Haven, and Bocas del Toro, respectively). Reflecting a relative preponderance of small individuals at the Bocas del Toro site, sponge density measured as volume per unit length of subtidal prop root was only 5.7 cm³/cm at Bocas, compared with 20.8 cm³/cm at Hidden Creek and 15.7 cm³/cm at Sponge Haven. Although variation in root diameter renders root length imprecise as a measure of substratum area monitored, length was deemed a better measure than number of roots because of the sixfold variation in root lengths (i.e., from 24 to 143 cm).

SPONGE COMMUNITY DYNAMICS COMPARED WITHIN AND BETWEEN SITES, BY VOLUME AND NUMBER OF INDIVIDUALS

During the three years of monitoring, the largest difference between the highest and lowest total sponge volume was 12%, 35%, and 27% at, respectively, Hidden Creek, Sponge Haven, and Bocas del Toro; and the largest difference between the highest and lowest number of sponge individuals was 50%, 34%, and 39%, respectively (Figure 4). Based on these total abundance values, com-

munity-wide change appears to be substantial. However, comparison over time of abundance of individual species, with respect to both volume and numbers of sponge individuals, sheds light on the components of change and provides a very different picture. In many cases, large overall changes in total volume or numbers in the course of a particular year reflect changes in just one or a few species. For example, the drop in total sponge volume between 2005 and 2006 at Sponge Haven (see Figure 4) was mostly caused by losses from *Halichondria* sp., *Halichondria magniconulosa* (almost to the point of elimination),

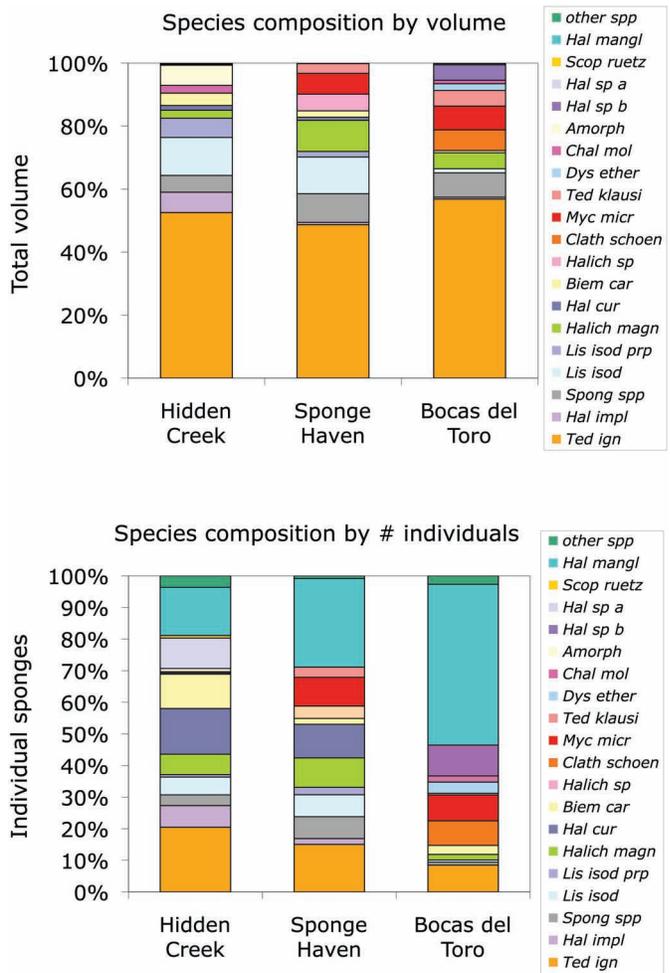


FIGURE 3. Sponge species assemblage composition, with respect to total volume contributed by each species, and with respect to the total number of individuals of each species, on mangrove prop roots at three Caribbean sites. These average relative abundances were calculated by adding together the volume or numbers of individuals for all four yearly census dates (three dates in the case of Bocas del Toro). See Table 1 for complete spelling of species names.

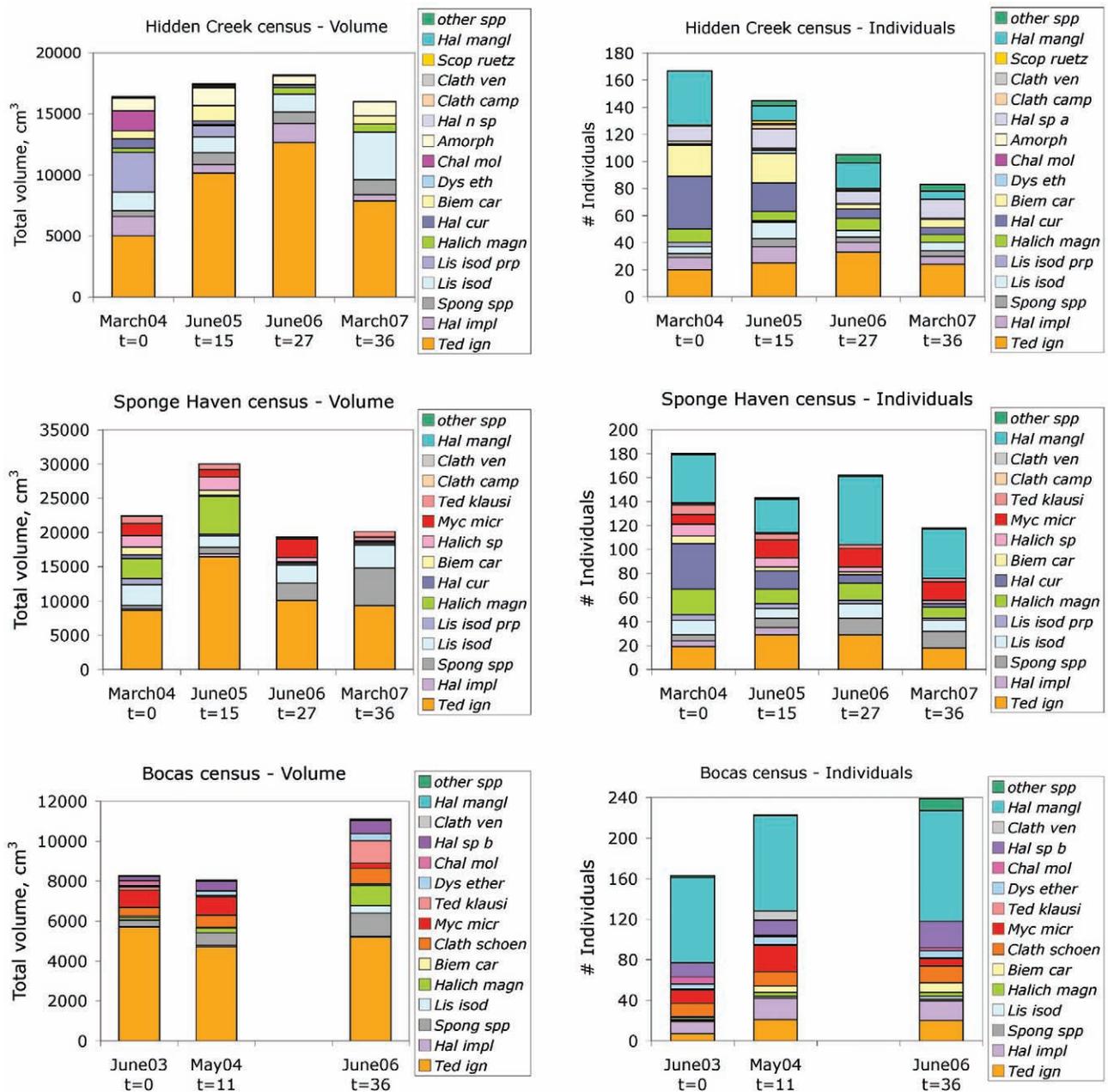


FIGURE 4. Community dynamics for sponges on mangrove prop roots at three Caribbean sites. Relative abundance of the species is represented by both total volume and total numbers of individuals. See Table 1 for complete spelling of species names.

and *T. ignis*. For the second and third species these losses primarily consisted of size decreases and fragmentations of sponges that were subsequently able to regenerate; and thus for both of these species, abrupt and dramatic changes in volume between the second and third censuses are not reflected in tandem changes in numbers of individuals (e.g., *H. magniconulosa* was represented by 12 individuals of total volume 5,518 cm³ in 2005, 14 individuals of total volume 187 cm³ in 2006, and 9 individuals of total volume 225 cm³ in 2007). Large differences in maximum size achieved by sponges of different species further promote asynchronous changes in overall volume and numbers of individuals. For example, during this same year in which total sponge volume at Sponge Haven decreased by 35%, the number of individual sponges there increased by 13%, largely the result of a doubling of the number of *Haliclona manglaris* individuals. Yet each *H. manglaris* individual is so small that, even in the aggregate, they scarcely register in the overall volume tally (0.2% for the June 2006 census; see Figure 4).

Similarly, progressive loss of individuals of *Biemna caribea* and *Haliclona curacaoensis* at Hidden Creek resulted in decreases in total numbers of individuals by more than half in the course of three years (Figure 5). If these species are removed from the “Hidden Creek census – Individuals” graph in Figure 4 (along with the very small bodied *H. manglaris*), the community can be seen to otherwise remain very similar throughout the three years with respect to relative representation of the component species by numbers of individuals. During this same time period, the total volume of all sponges at this site remained very similar, although there were large volume changes for individual species (see Figure 4). The Sponge Haven data show the same pattern of progressive loss of *H. curacaoensis* (see Figure 5) and also *B. caribea*, although the latter species was not as abundant to begin with at this site.

Not all changes in abundance of particular species were abrupt or negative. Volume of *Spongia* spp. steadily increased at all sites (see Figure 5), with little increase in numbers, reflecting high survival of the individuals that were present at the first census. Illustrating a third pattern of dynamics, the volume of *T. ignis* fluctuated at all three sites, but at the end of the three years the total volume of this species at each site was similar to what it was at the start of the study (Figure 5).

Portions of many roots were lost during the three years of the study, but new roots sprouting from subtidal portions of censused roots nearly balanced the losses during some time periods. Thus the total length of prop roots

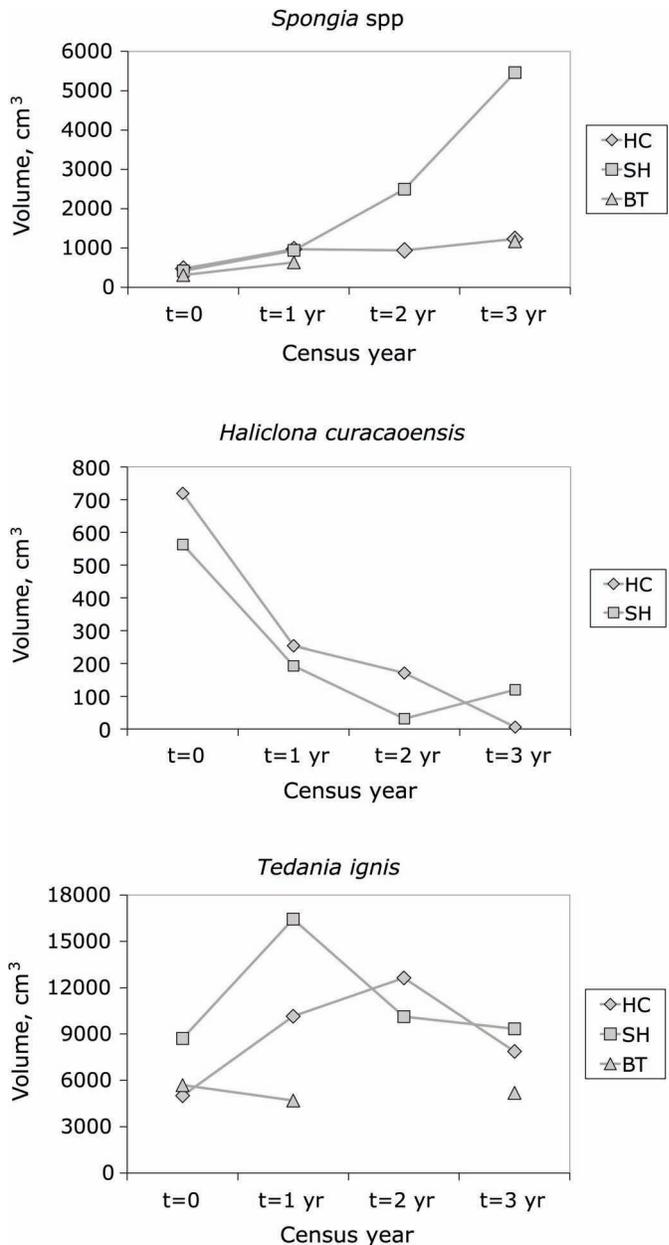


FIGURE 5. Representative population dynamics graphs for three sponge species inhabiting mangrove prop roots at sites where yearly censuses were made (HC = Hidden Creek; SH = Sponge Haven; BC = Bocas del Toro). Total volume of *Spongia* spp. consistently increased between monitoring periods at all three sites; volume of *Haliclona curacaoensis* decreased between monitoring periods at both sites in which it was found; *Tedania ignis* total volume fluctuated over time but ended up very similar to what it had been at all three sites at the start of the study three years earlier.

included in the census was very similar for the first three censuses at Hidden Creek, and for the first two censuses at Bocas del Toro and Sponge Haven, and then, after a decrease, also for the final two censuses at Sponge Haven. Total length (in cm) for the four censuses at Hidden Creek was 968, 896, 995, and 562; for Sponge Haven, 1,847, 1,787, 1,162, and 1,179; and for Bocas del Toro, 1,483, 1,583, and (after two years) 1,203. Substratum available was not necessarily related to sponge abundance with respect to either numbers of individuals or total volume (compare abundance measures reported in Figure 4 with total root lengths censused); for example, sponge volume and total root length were inversely associated over the three years at the Bocas del Toro site.

VARIATION AMONG SPONGE SPECIES
IN INDIVIDUAL PERSISTENCE

Because individual sponges were mapped and measured, their fates from one census to the next could be recorded as (a) increased in size, (b) fragmented, (c) decreased in size, or (d) disappeared. To characterize each species at each site independently of environmental circumstances during a particular time interval, data from all 1 year intervals between censuses (and one 2 year interval in the case of the Bocas del Toro site) were added together in Figure 6. Three patterns emerge from these graphs. First, fragmentation and size decrease are important aspects of persistence for many of these species. The only species represented entirely by individuals that increased in size or vanished (i.e., none decreased in size or fragmented) between censuses were *Spongia* spp. and *Amorphinopsis* sp. Second, at each site variation among species in the degree to which individuals persisted was clear. Yearly rates of loss ranged from 0% (e.g., *Spongia* spp.) to 100% (e.g., *Chalinula molitba*). Third, many species exhibited the same characteristics at each site where they occurred. For example, a set of species characterized by at least 40% of the individuals increasing in size from one yearly census to the next were evident at each site: *Tedania ignis*, *Haliclona implexiformis*, *Spongia* spp., *Lissodendoryx isodictyalis*, and *Halichondria magniconulosa*. The only exceptions were *Haliclona implexiformis* in Bocas del Toro and *Halichondria magniconulosa* at Sponge Haven. The reason for the *H. implexiformis* difference at the Bocas site was not obvious, but individuals of this species were always very small there. At Sponge Haven, both *H. magniconulosa* and *T. ignis* suffered high rates of size decrease and fragmentation between the second and third censuses. These

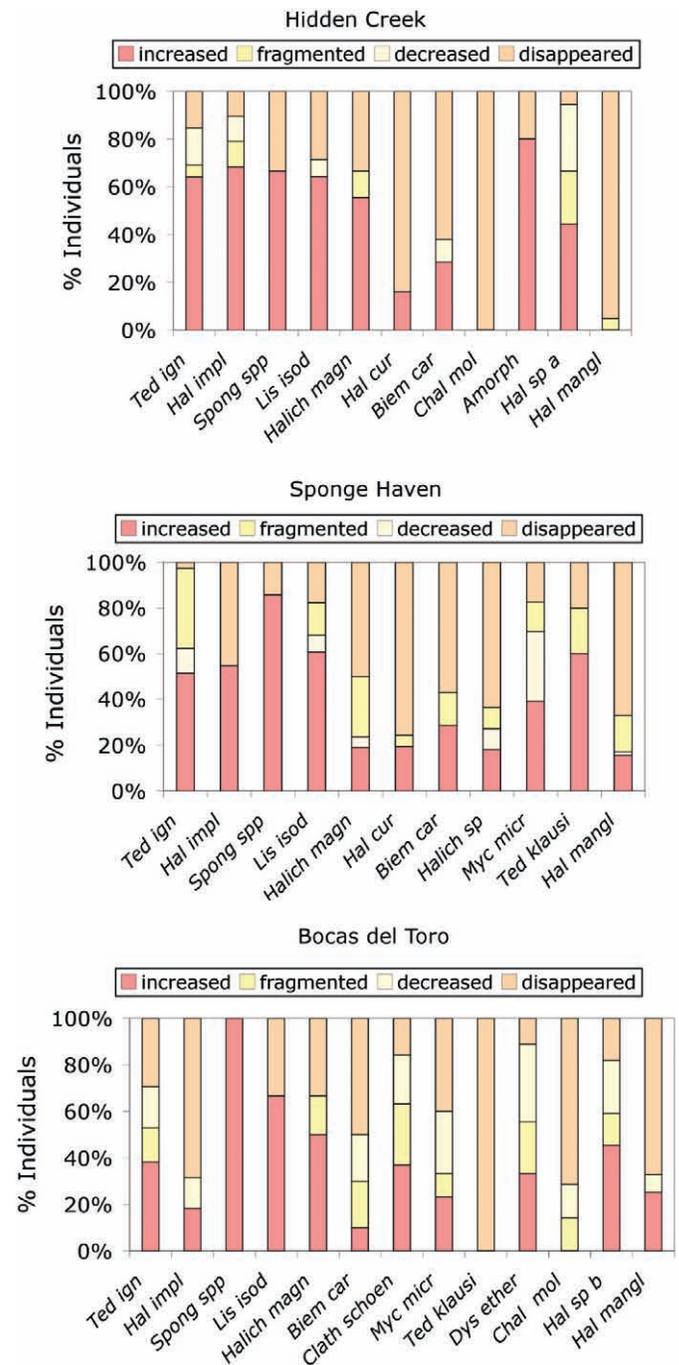


FIGURE 6. Proportions of sponge individuals of each species that increased in volume, fragmented, decreased in volume, or disappeared entirely between yearly census dates at three Caribbean mangrove sites. Although the fate of each individual was recorded in a single category at the time of observation, the distinction between “fragmented” and “decreased” can be fuzzy, as it depends on whether or not fragments generated survive until the time of observation. See Table 1 for complete spelling of species names.

departures from their usual pattern (i.e., most individuals increasing in size during a year) coincided with the unusual and fleeting presence of a couple of French angelfish just before the third census. French angelfish have been demonstrated to readily consume these two species (Wulff, 2005) and *Halichondria* sp. (in preparation), which also decreased in volume during the same time interval. Species that only occurred at two sites also exhibited similar characteristics with respect to persistence at both sites. For example, no *Chalinula molitba* individuals increased in size from year to year at either Hidden Creek or Bocas del Toro, and *Haliclona curacaoensis*, *H. manglaris*, and *Biemna caribea* had consistently low survival at each site. In contrast, *Tedania klausii* survived well at Sponge Haven, but suffered an extreme decline on censused roots at the Bocas del Toro site, coinciding with observed high losses of only this species throughout the site to disease (Wulff, 2006).

DISCUSSION

COMMUNITY COMPOSITION

These three sites that differ in abiotic factors and in geographic distance from each other have very similar species compositions, not only with respect to species present but also with respect to their relative abundance. The 9 species that are shared by all three sites constituted 89%, 84%, and 73% of the total sponge volume at, respectively, Hidden Creek, Sponge Haven, and Bocas del Toro. The ubiquity and consistent local dominance of the fire sponge *Tedania ignis* contributes heavily to similarity among these sites. Previous studies also concur that *T. ignis* is a signature species for this ecosystem throughout the wider Caribbean region, and it was the sole species, of 23, that was recorded in all eight prop root faunal surveys compiled by Wulff (2000) and in four of five of the studies compared by Diaz et al. (2004). Not only does it occur at most sites, it tends to be among the most abundant species by any metric. At five sites in Belize (including Hidden Creek and Sponge Haven), Diaz et al. (2004) recorded *T. ignis* as present on 11% to 34% of the roots, in the top 3 species ranked by frequency of occurrence. By measuring area covered from photographs, Bingham and Young (1995) estimated that 16.7% of the root area at their Florida Keys site was covered by *T. ignis*. Using line transects, along which the length of root covered by each sponge was measured, Sutherland (1980) estimated 5%–12% coverage by *T. ignis* in Bahía de Buche, Venezuela. Evaluating abundance by volume boosts the proportional representation of this species because of its massive

growth form, and thus in this study *T. ignis* constituted from 49% to 57% of the total sponge volume on censused roots. This species not only holds a large proportion of the primary substratum space, but it also participates in a mutualism with the mangroves, enhancing the persistence and health of the entire ecosystem by protecting the roots from attacks by boring isopods (Ellison and Farnsworth, 1990; Ellison et al., 1996).

Tedania ignis is not the only species that is both nearly ubiquitous and locally abundant, although it stands out as the most extreme. Consistently *Lissodendoryx isodictyalis*, *Halichondria magniconulosa*, *Spongia* spp., *Haliclona implexiformis*, *Haliclona manglaris*, and *Dysidea etheria* appear on faunal lists and, where authors indicate relative abundance, by whatever metric, they rank highly (Wulff, 2000; Diaz et al., 2004).

Although the three sites in this study are similar with respect to these widespread typical mangrove root sponge species, there are two types of differences among the sites: (1) a few species that are abundant at one site but do not occur elsewhere (e.g., *Amorphinopsis* sp. at Hidden Creek), and (2) many rare species that appear to differ among sites. The virtual lack of overlap of these rarer species on species lists from different sites does not necessarily indicate constrained distribution but may simply reflect their rareness. Diaz et al. (2004) discuss this sampling issue with the highly diverse Caribbean mangrove root sponge fauna and illustrate it well with their data. Diaz et al. (2004) also point out the great degree to which community composition can vary along a particular mangrove fringe. The three sites in the present study are known to share additional sponge species if entire contiguous stretches of mangrove are included (Rützler et al., 2000). For example, at Sponge Haven, *Clathria schoenus* is not found near the censused roots but appears on roots at this site that are further toward the mouth of the main channel.

Sponge species composition differences among sites characterized by very different abiotic circumstances have been well documented, and some sites are sufficiently extreme in abiotic factors that sponges are scarcely present (Farnsworth and Ellison, 1996) or succumbed to unfavorable conditions while being studied (Pawlik et al., 2007). At least some of the differences in species composition between Hidden Creek and Sponge Haven, only 330 m apart, have already been ascribed to less hospitable abiotic factors in the narrow, tidal Hidden Creek. Transplants of 5 species that are conspicuous at Sponge Haven thrived initially in Hidden Creek, but nearly all (61/63) died over the course of one year (Wulff, 2004), possibly implicating episodically wide fluctuations in temperature and salinity.

The similarity between the three sites in this study is especially interesting, considering that they were chosen for accessibility and overall sponge abundance, rather than for species composition, and that they have demonstrated differences in abiotic factors and span a geographic distance of 1,200 km.

METHODS FOR STUDYING SPONGES ON MANGROVE
PROP ROOTS CAN INFLUENCE EVALUATIONS
OF COMMUNITY SIMILARITY BETWEEN SITES
AND COMMUNITY STABILITY OVER TIME

Methods of studying composition and dynamics of sponge communities on mangrove roots have varied with respect to metrics for evaluating abundance, sampling unit, choice of which units to sample, time interval of sampling, and materials, size, and shape of recruitment surfaces. This variety reflects the many different questions posed by researchers, and the difficulty of quantifying sponges; but methods may also influence conclusions.

Methods for evaluating abundance have included analysis of photographs for percent cover, line transects down roots with distance covered by each species recorded, point counts through acetate sheets, and presence/absence on each root, as well as the total numbers of individuals and volume of each individual. The advantages and disadvantages of evaluating sponge abundance with respect to volume, area covered, or numbers of individuals have been previously compared in the context of coral reefs (Rützler, 1978; Wulff, 2000, 2001). Choice of metric is influenced by expediency in the field, and also by whether functional roles, life histories, species diversity, or some other aspect of these communities is the central focus of a study. One advantage to measuring sponge abundance by volume is that growth rates can then be calculated if the same sponge individuals are followed over time. As well, functional roles related to trophic interactions, such as filtering food particles from the water column and provision of food to spongivores, probably scale with volume. Unfortunately, sponge volume is time consuming to measure nondestructively in the field, decreasing the number of individuals that can be monitored.

Area can be a problematic measure of sponge abundance, as the amount of sponge tissue under a particular point can range over orders of magnitude. At these three sites, for example, sponges on prop roots varied in thickness 150 fold, from 0.1 to 15 cm. Evaluating mangrove sponge abundance in terms of area is further complicated by the prevalence of epizooism, which results in points falling simultaneously over more than one sponge species.

At least one functional role of sponges in mangroves may be related to substratum area covered: protection of mangrove roots from boring isopods (Ellison and Farnsworth, 1990, 1992).

Numbers of individuals are difficult to interpret in the contexts of sponge population dynamics and functional roles, as numbers can increase either by recruitment or fragmentation, and individual size can vary over many orders of magnitude. The lack of concordance between population dynamics of individual species measured in terms of numbers of sponges versus total volume on the same roots (see Figure 4) underscores how divergent conclusions can be when different metrics are chosen for evaluating sponge abundance. Evaluating abundance using two or more metrics at the same site can strengthen understanding of processes underlying the dynamics. For example, data indicating a small increase in numbers of individuals of *Halichondria magniconulosa* at Sponge Haven allowed the coincident large decrease in volume to be interpreted as extensive partial mortality and some fragmentation, rather than heavy losses of individuals.

An abundance measure that lends itself well to biodiversity surveys in this inherently fragmented habitat is presence/absence of a species on each root. Diaz et al. (2004) evaluated relative abundance of sponge species at Hidden Creek and Sponge Haven by prevalence on roots. Specific ranks of the species by prevalence were different from ranks assigned by volume in this study, but the match between the 10 most abundant species with respect to percent of prop roots inhabited (Diaz et al. 2004) and the 10 most abundant species with respect to volume (this study) is 80% at Hidden Creek and 60% at Sponge Haven. Resolution of systematic challenges may increase the match; for example, a second species of *Tedania* was only formally identified (Wulff, 2006) at Sponge Haven after the study by Diaz et al. (2004) was published.

Evaluating abundance by presence/absence can also address an important community assembly issue: the probability that the community on a root will include a particular species. Sutherland (1980) pointed out the great importance of habitat division into small discrete patches by explicitly comparing the course of community development on prop roots versus on the 20 × 122 cm asbestos panels he deployed for evaluating recruitment. The larger area of the panels increased the probability that the competitively dominant, but inefficiently recruiting, *Tedania ignis* recruited onto every physically separated substratum patch. Once settled on a panel, this species was able to continue its growth in every direction, and each panel became quickly dominated by it. Each root had much less

surface area, providing a smaller target for settling larvae of competitively dominant species. As predicted, if the roots are therefore more reliable refuges for competitively inferior species, the species composition on the roots was far more heterogeneous (Sutherland, 1980).

For ranking species by relative abundance, the greatest discrepancies between abundance measures (i.e., volume, area, number of individuals, and percent of roots) emerge when applied to thinly encrusting species, as their volume can be trivial even when they cover large areas (e.g., see Wulff, 2001, for an explicit comparison in a coral reef sponge community). The possibility that encrusting species may be relatively ephemeral because they are easily overgrown is supported by a comparison between the pattern of recruitment of the thinly encrusting species *Clathria campecheae* onto initially bare polyvinyl chloride (PVC) pipes at Hidden Creek (Wulff, 2004) and its abundance in the established community on prop roots. This species was described from coral reefs and had not been reported from mangroves, and yet it distinguished itself by occurring on more pipes (7/8) than any other species at 20 months after they were suspended among the mangrove roots. Once the possibility of its occurrence on mangrove roots was raised, it was discovered at a very low level on prop roots at Hidden Creek and Sponge Haven.

This finding raises the question of how the successional stage of communities on censused roots might influence the evaluation of similarity of assemblages between sites and over time. Sutherland (1980) labeled 116 roots that had not yet entered the water, in addition to 260 roots that had already been colonized below the water surface. Sponge species that specialize on colonizing fresh roots would have therefore been included in his assessment of the total fauna. Because I followed roots with already established sponge faunas, and only added new roots that sprouted from subtidal portions of previously included roots (i.e., new roots that could be colonized by sponge growth from already censused portions), the earliest successional stages were not included in my assessment of community dynamics. *Clathria campecheae*, mentioned above, was not the only species that was disproportionately well represented on PVC pipes deployed for recruitment at Hidden Creek 20 months earlier. *Haliclona curacaoensis*, *Biemna caribea*, and *Haliclona manglaris* were also conspicuous with respect to numbers of individuals, percent of pipes colonized, and (for *H. curacaoensis* and *B. caribea*) volume, in this relatively early stage of community development on initially bare pipes (Wulff, 2004: fig. 3). The pattern of loss of these species from one census

to the next (see Figures 4–6) is consistent with the possibility that these are early succession species that are progressively lost from roots as sponge species that are superior competitors accumulate over time. These data support Sutherland's (1980) suggestion that the mangrove root inhabitants illustrate a trade-off between colonization rate and ability to persist in the community, and raise the possibility that stability of these communities, if measured as change over time, will depend on the successional stage on the monitored roots. The earlier in succession the assemblage on a root is, the more likely that subsequent censuses will reveal changes in species composition. Apparent instability will be further magnified if percent cover is the metric chosen for abundance, as thinly encrusting species that are efficient recruiters, but may be eliminated as superior competitors recruit, will initially have very high abundances with respect to area covered.

Observational units in previous studies have ranged from camera framer-length segments of roots to root clusters. Bingham and Young (1995) monitored 21 cm long root segments at 1 and 2 month intervals. Their analysis revealed how changes in abundance appear at different monitoring intervals, providing insight into the complex and rapidly changing dynamics of these communities at particular locations on roots. Their spatial position-focused analysis is complementary to the individual organism-focused analysis in the present study. Because the position of sponge individuals can shift along the prop roots as they increase and decrease in size, it is possible for them to move into a particular root segment without a recruitment event and to move out of a root segment while still persisting on the root. Thus a sponge assemblage within a root segment may appear less stable than the assemblage on that entire root. Differences in conclusions of Sutherland and Bingham and Young were attributed by the latter authors to greater influence of physical disturbance and seasonality on a subtropical site (Florida Keys) relative to a tropical site (Venezuela), but it is possible that difference in choice of observational unit might have also influenced evaluations of stability.

The balance between numbers of individuals monitored, frequency of monitoring, and method of evaluating abundance must be struck with the ultimate aim in mind. Following individual sponges over time and evaluating their size with respect to volume were essential to the aims of this study, which were to understand the life history and morphological strategies employed by each species. Inevitably the number of individuals and roots that could be followed in such detail suffered, as did the frequency of

monitoring. Some compensation for these failings is made by the detail of the time-series drawings of entire roots. Detailed maps of the location of each sponge and comments about its shape and size at each census allowed fragmentation, size decrease, and addition of new recruits to be unambiguously distinguished, even when the causes of size change were not obvious. It is likely that new sponges recruited and vanished, and resident sponges changed in size in multiple ways, during the year-long intervals between censuses, and so my data only indicate the net result of months of unmonitored dynamics.

SIGNIFICANCE OF ECOLOGICAL CHARACTERISTICS OF SPONGE SPECIES

Proportions of sponges that increased, decreased, fragmented, or disappeared were similar for given species among sites, suggesting that these may be species-level characteristics. With a few exceptions, the set of species that reliably exhibited 40% to 100% of individuals increased between censuses were the same at all three sites (*Tedania ignis*, *Haliclona implexiformis*, *Lissodendoryx isodictyalis*, *Spongia* spp., *Halichondria magniconulosa*), and constituted large proportions of the total sponge volume (85%, 82%, and 72% at HC, SH, and BT, respectively) at each site. Numbers of individuals of these species found on eight initially bare PVC pipes 20 months after they were suspended among prop roots at Hidden Creek, ranged from 0 (*T. ignis*, *H. implexiformis*, and *Spongia* spp.) to 7 (*L. isodictyalis*) (Wulff, 2004). By contrast, the set of species for which only 0% to 30% of the individuals increased in size between censuses (i.e., *B. caribea*, *H. curacaoensis*, *H. manglaris*, *Clathria campecheae*) were each represented on the recruitment pipes by 11 to 14 individuals (Wulff, 2006). These patterns hint at the possibility of integrated sets of ecological characteristics that help to maintain all these species in the mangrove prop root system. Population dynamics of at least some of the typical mangrove root sponge species may be tied to their each being most suited to a particular time period in community development.

Overall community change, measured by total biomass, species diversity, numbers of individuals, and space occupied, can be functionally of great importance on an ecosystem level. However, an exclusive focus on these community-level metrics can obscure the components of community change—that is, changes in the component species—and therefore hamper our understanding of underlying processes. Consideration of the characteristics of individual

species, such as their probability of persisting from year to year; their efficiency at recruiting; susceptibility to particular biotic mortality sources such as predators, competitors, or pathogens; and the frequency with which they fragment or suffer partial mortality, may explain much of the community dynamics. Combining these new data on persistence with previously reported recruitment data (Wulff, 2004) indicates that some of the heterogeneity in space and time among mangrove prop root communities may be the result of the community on each root progressing independently through a successional sequence that is mediated, at least in part, by an inverse relationship between ability to hold space on mangrove roots and recruitment into the community that was first suggested by Sutherland (1980). Adding to these life cycle-mediated patterns the observed idiosyncratic responses of particular species at a particular site, such as *Tedania klausii* succumbing to disease at the Bocas del Toro site or *Halichondria magniconulosa* targeted for consumption by a pair of French angelfish at Sponge Haven, allows community dynamics to be understood as the result of a complex set of interactions among individual sponges representing species that are characterized by specific physiological tolerances and morphological and life history traits.

ACKNOWLEDGMENTS

I am grateful to the Caribbean Coral Reef Ecosystems Program (CCRE), of the National Museum of Natural History (NMNH), Smithsonian Institution, for the privilege of being able to do fieldwork at the Carrie Bow Cay field station in Belize; and to Mike Carpenter, Klaus Ruetzler, and the volunteer station managers who make the Carrie Bow station an unparalleled resource, supporting comprehensive research on tropical marine ecosystems. I also thank Gabriel Jacome for always facilitating my fieldwork at the Bocas del Toro station of the Smithsonian Tropical Research Institute. I thank two reviewers for helpful comments, and Carla Piantoni (CCRE) and Molly K. Ryan (Department of Invertebrate Zoology, NMNH) for help with the figures. My field research was supported by the National Science Foundation under Grant No. 0550599, and by the Marine Science Network of the Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Endowment. This is contribution number 854 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund.

LITERATURE CITED

- Bingham, B. L., and C. M. Young. 1995. Stochastic Events and Dynamics of a Mangrove Root Epifaunal Community. *P.S.Z.N.I.: Marine Ecology*, 16:145–163.
- Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science*, 199:1302–1310.
- Diaz, M. C. 2005. Common Sponges from Shallow Marine Habitats from Bocas del Toro Region, Panama. *Caribbean Journal of Science*, 41:465–475.
- Diaz, M. C., K. P. Smith, and K. Rützler. 2004. Sponge Species Richness and Abundance as Indicators of Mangrove Epibenthic Community Health. *Atoll Research Bulletin*, 518:1–11.
- Ellison, A. M., and E. J. Farnsworth. 1990. The Ecology of Belizean Mangrove-Root Fouling Communities. I. Epibenthic Fauna Are Barriers to Isopod Attack of Red-Mangroves. *Journal of Experimental Marine Biology and Ecology*, 142:91–104.
- . 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*, 77:2431–2444.
- Engel, S., and J. R. Pawlik. 2005. Interactions among Florida Sponges. II. Mangrove Habitats. *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.
- Jackson, J. B. C., and L. W. Buss. 1975. Allelopathy and Spatial Competition among Coral Reef Invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 72:5160–5163.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, N. J.: Princeton University Press.
- Mouquet, M., and N. Loreau. 2002. Coexistence in Metacommunities: The Regional Similarity Hypothesis. *American Naturalist*, 159:420–426.
- Pawlik, J. R., S. E. McMurray, and T. P. Henkel. 2007. Abiotic Factors Control Sponge Ecology in Florida Mangroves. *Marine Ecology Progress Series*, 339:93–98.
- Rützler, K. 1978. “Sponges in Coral Reefs.” In *Coral Reefs: Research Methods. Monographs on Oceanographic Methodology*, Volume 5, ed. D. R. Stoddart and R. E. Johannes, pp. 299–313. UNESCO: Paris.
- . 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 Mangrove Ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, 476:230–248.
- Rützler, K., and I. C. Feller. 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.
- Sutherland, J. P. 1974. Multiple Stable Points in Natural Communities. *American Naturalist*, 108:859–873.
- . 1980. Dynamics of the Epibenthic Community on Roots of the Mangrove *Rhizophora mangle*, at Bahia de Buche, Venezuela. *Marine Biology*, 58:75–84.
- 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.
- . 2001. Assessing and Monitoring Coral Reef Sponges: Why and How? *Bulletin of Marine Science*, 69:831–846.
- . 2004. Sponges on Mangrove Roots, Twin Cays, Belize: Early Stages of 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.
- . 2006. Sponge Systematics by Starfish: Predators Distinguish Cryptic Sympatric Species of Caribbean Fire Sponges, *Tedania ignis* and *Tedania klausii* n. sp. (Demospongiae, Poecilosclerida). *Biological Bulletin*, 211:83–94.