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SPONGES ON MANGROVE ROOTS, TWIN CAYS, BELIZE: EARLY STAGES OF COMMUNITY ASSEMBLY

BY

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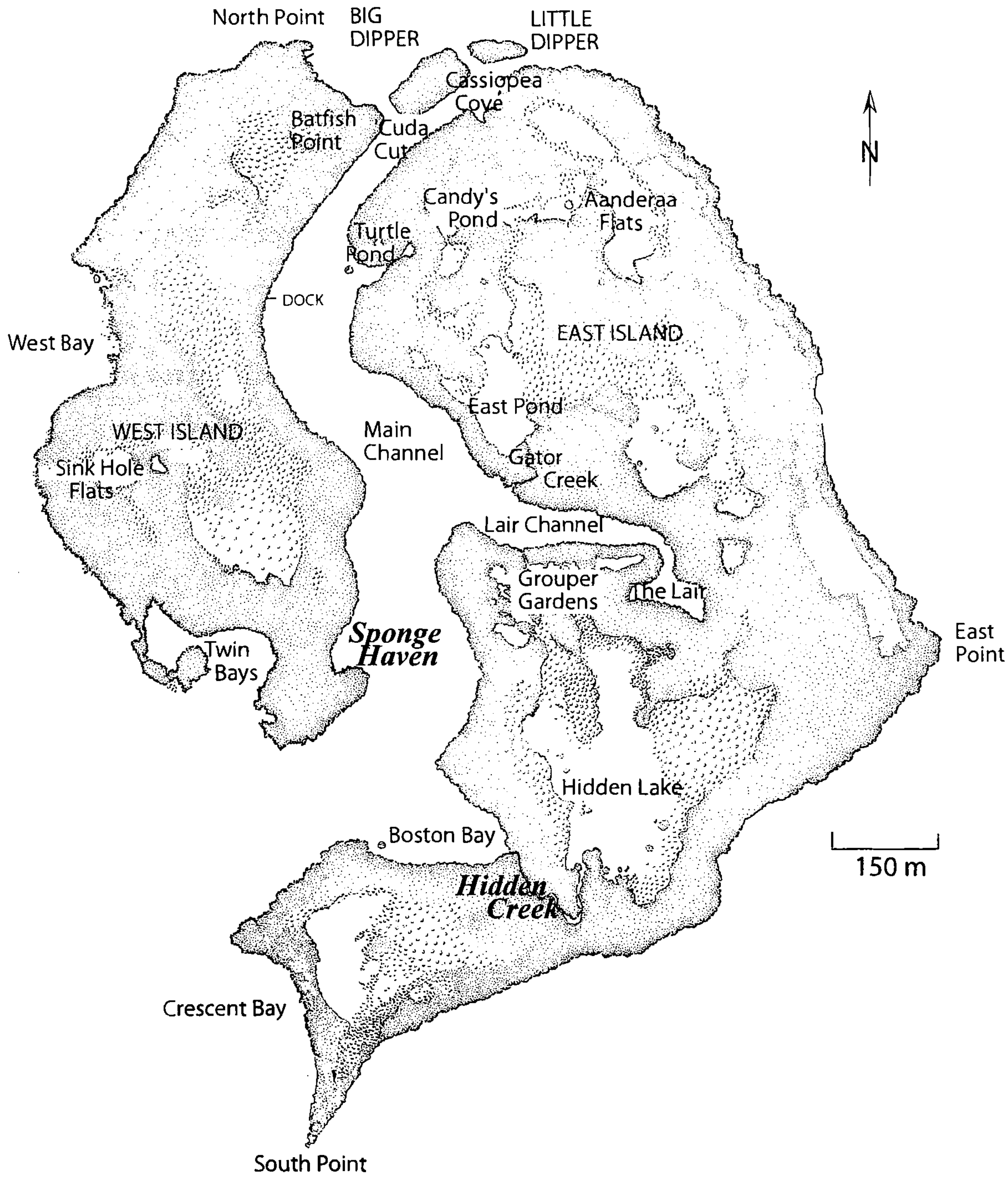

Figure 1. Index map of Twin Cays showing Sponge Haven and Hidden Creek study sites.

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ABSTRACT

A combination of transplant experiments and provision of recruitment surfaces has been initiated to determine the degree to which differences in sponge diversity and species composition at two Twin Cays sites, Hidden Creek and Sponge Haven, reflect differences in abiotic factors, ecological interactions, and recruitment history. This report contains the first stages of this project. The Hidden Creek sponge fauna differs from the Sponge Haven fauna largely by deletions. To determine if the cause might be stressful abiotic factors in Hidden Creek, five sponge species common at Sponge Haven, but absent from Hidden Creek, were transplanted to Hidden Creek. After 12 months, all but two transplanted individuals had died (97% mortality), suggesting distribution constraint by episodically unfavorable abiotic factors. To follow recruitment and community development from a start on bare substrata, pipes of pvc, each 25 cm long and 2.2 cm outside diameter, were suspended among prop roots in Hidden Creek. After 20 months, 69 sponge individuals representing 11 species were living on eight pipes. Differences in species composition and relative abundance between pipes and roots underscore the importance of postrecruitment processes in community development.

INTRODUCTION

Effects of abiotic environmental factors, interactions with other organisms, and historical events combine to determine the assortment of species that co-occur at a site. Lurking within this simple and obvious statement are the complexities of actually learning the relative importance of these factors in a particular system. Consistent correlations of environmental factors with distribution patterns can provide hints about physical and chemical requirements of species, but manipulative experiments and long-term studies often provide surprisingly additional insights and are required for understanding dynamics.

Sponges are one of the dominant groups inhabiting submerged portions of prop roots of Caribbean mangroves with respect to numbers of species, numbers of individuals, and total biomass (e.g. Rützler and Feller, 1996). Some species are found on mangrove roots and not in other habitats with sufficient predictabililty that they can be referred to as "typical mangrove sponge species" (e.g., summary of other faunal studies in Wulff, 2000), but variations on this typical fauna have been documented. A particularly striking variation is found in the Pelican Cays where sponge species typically found on

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shallow coral reefs inhabit prop-roots (Rützler et al., 2000). Overlap in species composition between the Pelican Cays prop-root sponge fauna and the more typical assortment at Twin Cays, 18 km distant, is only 22% of a total of 166 species and forms (Fig. 2a). Species inhabiting both sets of cays tend to be rare in one or the other set, e.g., only three species were designated with the highest abundance rank of "3" (on a 1-2-3 scale; Rützler, et al., 2000) at sites in both sets of cays. The large differences in species composition and diversity (Rützler et al., 2000) between the Pelican Cays (146 species) and the more typical mangrove-root sponge fauna at Twin Cays (56 species) may reflect differences in processes influencing community composition (Wulff, in press). Faster-growing typical mangrove sponge species can prevent typical reef species from inhabiting Twin Cays mangrove roots by outcompeting them. Diversity is relatively low as expected in a system in which competitive dominants eliminate some species. By contrast, spongivorous fishes can prevent some typical mangrove species from inhabiting Pelican Cays mangrove roots by consuming them. This may prevent competitive exclusion, allowing an especially high diversity of typical reef species to coexist on the roots.

Comparisons among sites within Twin Cays reveal species composition and diversity differences as well. This study reports on the first stages of an investigation into differences between Hidden Creek and Sponge Haven, which are only separated by 330 m across a shallow bay and the channel between the cays (map on page facing title page). While differences in species composition between the Pelican Cays and Twin Cays reflect the low number of shared species, the Hidden Creek sponge fauna differs from those in Sponge Haven primarily by deletions (Fig. 2b). Species shared by these two sites constitute 39% of the combined species and those shared species are 73% of the Hidden Creek sponge fauna suggesting that periodically stressful abiotic conditions in the tidally influenced creek (Rützler, 1995) might inhibit some typical mangrove species from living there.

A combination of transplant experiments and provision of recruitment surfaces have been initiated to determine the degree to which differences in diversity and composition of these two Twin Cays sites reflect chance historical differences that are maintained by limited larval dispersal, ecological interactions that differ between sites and abiotic factor differences that favor some species over others. In a more general context, these data address the influence of trade-offs among growth, recruitment, predator defenses, and ability to cope with environmental stresses on community development in systems characterized by discrete substrata.

METHODS

Recruitment and Community Development

Lengths of pvc pipe, 2.2 cm outside diameter and 25 cm long, were suspended among the mangrove roots in Hidden Creek in June, 2001. By March, 2003 (i.e., 20 months after deployment) the pipes were covered by a variety of sessile organisms, chiefly sponges. All dimensions of every individual on each of the eight pipes were measured for nondestructive determinations of volume. The pipes were left undisturbed

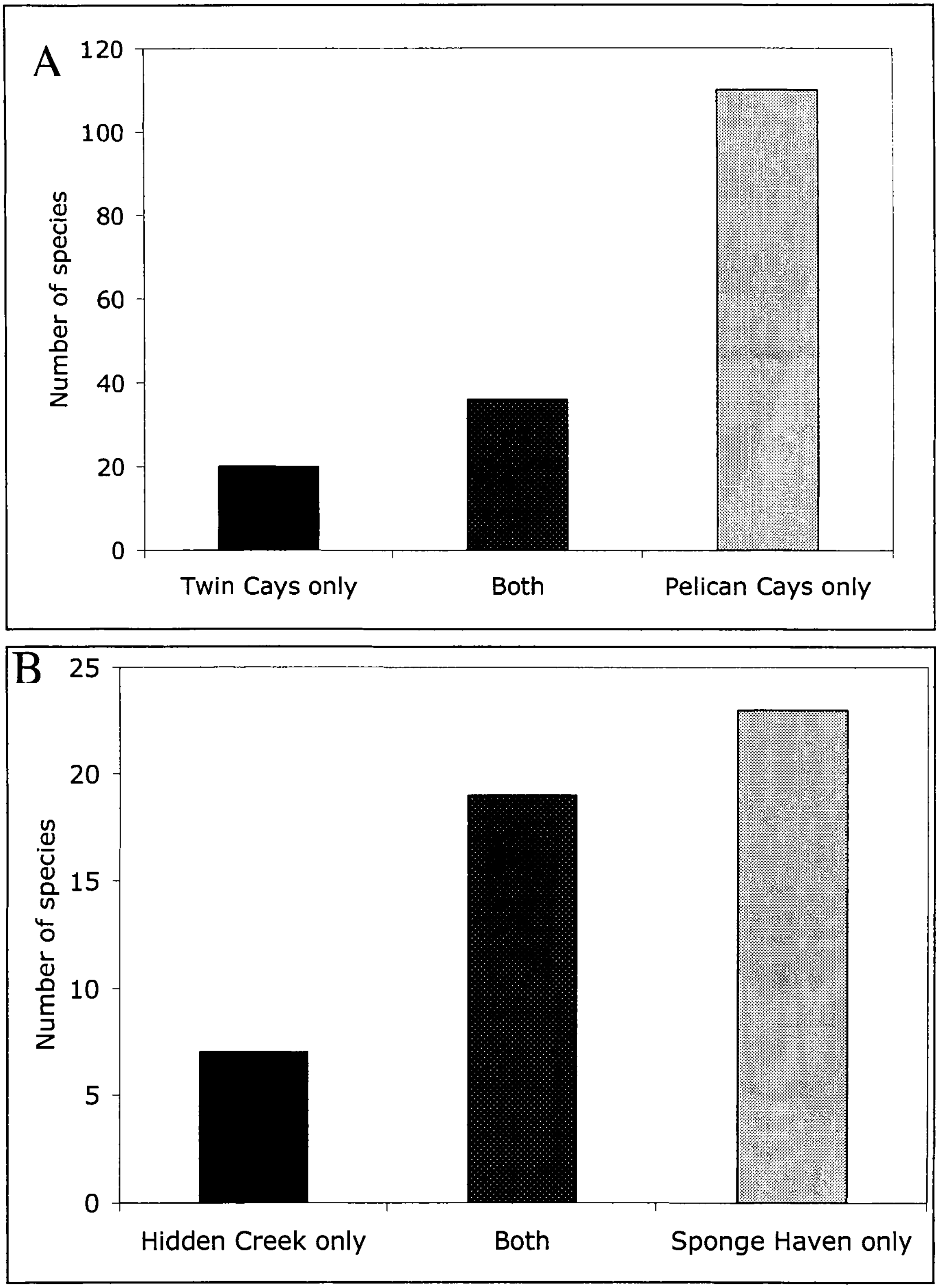


Figure 2 A, B. Comparison of the patterns of shared and not-shared species at: A) two sets of mangrove cays, Pelican Cays and Twin Cays; and B) two sites within Twin Cays, Sponge Haven and Hidden Creek.

so community development could be followed but tiny pieces of individuals to which names could not be applied confidently in the field were collected for identification in the lab.

Transplanted Sponges

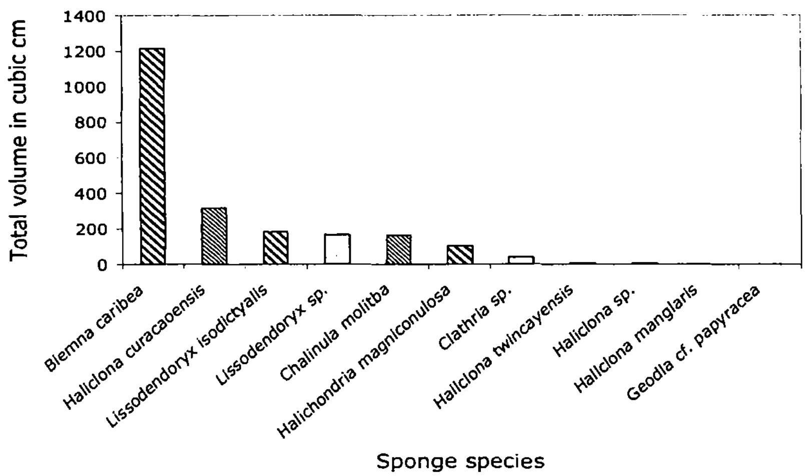
In March 2003, 12-13 individuals of each of five sponge species commonly inhabiting prop-roots, and sometimes the peat, at Sponge Haven, *Mycale microsigmatosa*, *Calyx podatypa*, *Spirastrella mollis*, *Halichondria* cf. *poa*, and aff. *Tedania ignis* (noticeably different in overall morphology and color from *Tedania ignis* and treated consistently differently by predators but with the same spicule complement), across the Twin Cays channel from Hidden Creek were transplanted to roots in Hidden Creek where they had not been found. Immediately after the sponges were collected at Sponge Haven they were transported in a bucket of seawater (transferred into and out of the bucket underwater) to Hidden Creek. Volume, initially 2-8 cm^3, was determined for each individual by immersion in a graduated cylinder and the measured sponges were then attached to bare spots on the roots with small (1 mm in diameter) labeled cable ties. Transplants were checked daily for 10 days and again after one year.

RESULTS

Recruitment and Community Development

After 20 months, all eight pipes were nearly completely covered with sessile organisms with bare space ranging from 0 to 21.2 cm^2 out of a total surface area of 175 cm^2 for an individual pipe (i.e., <12.1% bare space on any particular pipe and only 4.3% of the total). In addition to sponges, macroscopic colonists included colonial ascidians, algae, polychaete worms, a few anemones and one spiny oyster. Sponges were by far the most abundant with respect to both surface area covered and total volume of live tissue.

Eleven sponge species were identified on the pipes (Figure 2 a,b,c). Abundance on the pipes (with respect to number of individuals or total volume), or even presence or absence, was not consistently related to abundance on the roots, either negatively or positively (Figure 3a,b,c). Four of the 11 species were among those designated as "abundant" (i.e., 3 on a scale of 1-2-3) by a team of Caribbean sponge experts (Rützler et al., 2000), three species had been given an abundance rank of 2, and two species a rank of 1. The other three species inhabiting the pipes could not be assigned confidentally to described species but are in genera found in Hidden Creek (*Clathria, Lissodendoryx,* and *Haliclona*). Conversely, three of the seven species that were given the high abundance rank of 3 on the Hidden Creek roots were not found on the pipes at all (*Tedania ignis*, *Haliclona implexiformis*, and *Amorphinopsis* sp.). It is very possible that additional species were represented on the pipes as individuals that were too small to be seen in the field. Because the time course of community development was an important focus for this study, leaving the pipes relatively undisturbed in the field was deemed more important than risking losses by bringing them to the lab for microscopic evaluation.



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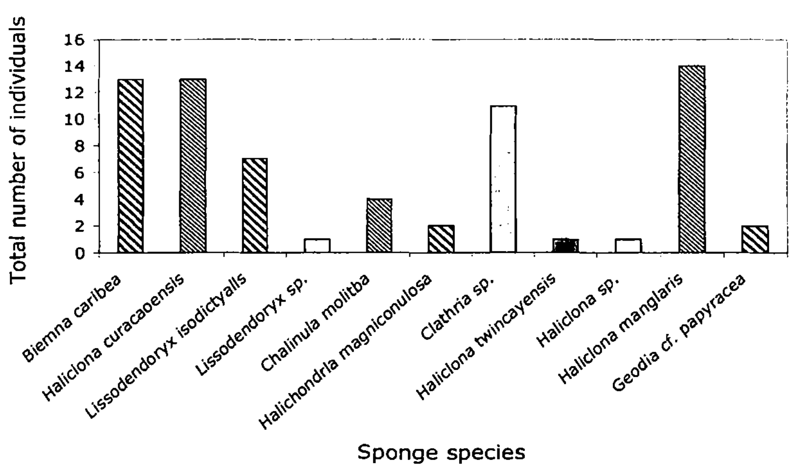

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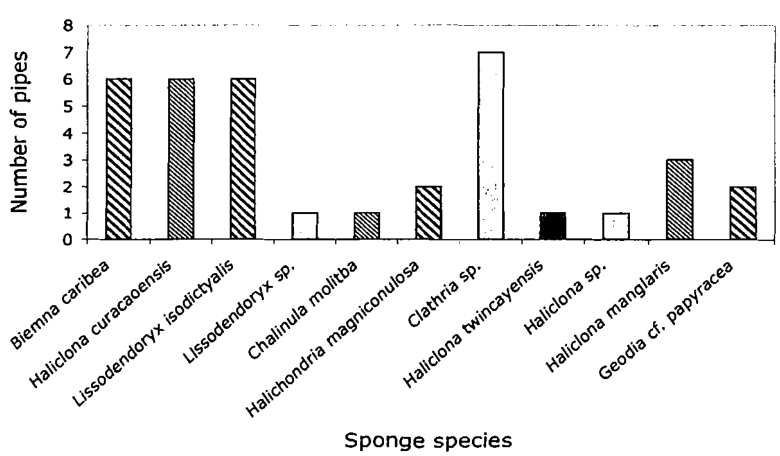

C

Figure 3 A,B,C. Sponges inhabiting eight pvc pipes suspended among mangrove prop roots at Hidden Creek, Twin Cays, for 20 months from June 2001 to March 2003. Relative abundance of these species on unmanipulated mangrove roots as designated by a team of Caribbean sponge experts (Rützler, et al., 2000) is indicated as follows: "abundant" = course diagonals; "common" = fine diagonals; "rare" = dark grey; "not present" = light grey.

Four orders of Demospongiae were represented on the pipes: five species in Haplosclerida (all in the genus *Haliclona*), four in Poecilosclerida (two in the genus *Lissodendoryx*); one in Astrophorida; and one in Halichondrida. Abundance on the pipes was not correlated with taxon on the order or genus level. For example, the five *Haliclona* species had abundance ranks (with respect to total volume) among the 11 species of 2, 5, 8, 9, 10 (Fig. 3a).

Growth-form variation of the sponges inhabiting the pipes was limited, relative to the full range of possibilities among demonsponges, but still varied from encrusting (*Clathria* sp.) to broad-based massive-fistulose (*Lissodendoryx isodictyalis*, *Lissodendoryx* sp., *Halichondria magniconulosa*, and *Geodia* cf. *papyracea*), to clusters of fistulose branches that are relatively loosely substratum-bound (*Biemna caribea*, *Chalinula molitba*), to clusters of low mounds (*Haliclona curaçaoensis*), encrusting cushions, sometimes with thin stolons (*H. manglaris*) and very thin branches (*H. twincayensis*). No patterns in abundance on the pipes were related to growth form with the exception that the species that was represented by the most individuals and on the most pipes (*Clathria* sp.) was an encrusting species, a growth form rarely seen on the roots.

Growth rate did not appear to be related to abundance on pipes. Growth rates had been measured over seven months for six of the most common species in Hidden Creek (Wulff in review). One of the species that increased in volume most rapidly (*Biemna caribea*) was also the species that was most abundant by volume on the pipes and among the most abundant with respect to numbers of individuals and numbers of pipes colonized. But another species that grew rapidly (*Tedania ignis*) did not appear on the pipes at all and the third rapid grower (*Halichondria magniconulosa*) was represented at intermediate levels by all three abundance measures (Fig. 3 a,b,c).

Species on the pipes fell into two categories with respect to how evenly they were represented among the pipes. *Clathria* sp., *Biemna caribea*, *Haliclona curaçaoensis*, and *Lissodendoryx isodictyalis* were each found on six-to-seven of the eight pipes; but the other species were each on three or fewer pipes and four of them were on only one pipe (Fig. 3c).

Transplanted Sponges

Most individuals of *Calyx podatypa*, *Spirastrella mollis*, *Halichondria* cf. *poa*, and aff. *Tedania ignis* that were transplanted from Sponge Haven to Hidden Creek appeared to be reattached and healthy by the end of 10 days. Several individuals of one species, *Mycale microsigmatosa*, developed necrotic patches where the cable ties held them onto the mangrove roots but the undamaged portions attached within a day and began to grow so quickly that encrusting portions extended as far as 1.5 cm from the transplant by 10 days.

After one year, however, only two of the 63 transplanted individuals survived. Specific growth rates of these two individuals, both of which were *Calyx podatypa*, were high (6.8 and 15 in a year; starting sizes were 3.5 and 6 cm^3, and ending sizes were 27.3 and 96.1 cm^3). A few transplants and their labels were missing because entire roots had been lost, especially near the mouth of Hidden Creek, but most of the labeled cable ties were found indicating the clear demise of the transplants.

DISCUSSION

Distribution Constraints by Abiotic Factors

Intolerable abiotic factors are often accepted as explanations of constraints on distributions of species because of consistent correlations of distribution patterns with particular abiotic factors. Sometimes transplant experiments give surprising results, demonstrating that the actual constraints are interactions with other organisms or recruitment patterns (e.g., Wulff, in press). In this study, however, the hypothesis that some common Sponge Haven species are inhibited from living in Hidden Creek because of unfavorable abiotic factors is not rejected by the data. Transplants reattached and grew for at least the first 10 days suggesting that conditions sufficiently unfavorable to kill the Sponge Haven species are episodic. The other possibility that was not tested is that a smooth pufferfish, *Testudineus sphoeroides*, which is common in Hidden Creek but which I have never observed at Sponge Haven, may have consumed the transplanted species. The two *C. podatypa* individuals that were thriving had both become partially covered by dense mats of *Halimeda* suspended from roots, possibly protecting them from predators.

If more transplants had survived, the possibility would have to be considered that these species are missing from the Hidden Creek fauna due to lack of larval dispersal into Hidden Creek. But the mortality of 97% of the transplants suggests that conditions would not be reliably favorable in Hidden Creek for at least some of the species that are common at nearby Sponge Haven even if their larvae were able to travel over to Hidden Creek.

Intermediate Stages of Sponge Species Assembly on Twin Cays Prop-Roots

Although most bare space on the pipes was filled by sessile organisms at 20 months, this time period appears to have been insufficient for development of the usual prop-root community for Hidden Creek. On the other hand, the crowded conditions on the pipes made it clear that 20 months is long enough that much post-recruitment sorting may have already occurred.

Results from the few studies that have focussed specifically on recruitment of Caribbean sponges provide insights that may aid interpretation. In Zea's (1993) study of sponge recruitment on acrylic plates in six reef and rocky-shore sites in the Colombian Caribbean, recruitment was on the whole low and highly variable among plates. Zea concluded that proximity to abundant adult sponges was the best predictor of abundance of recent recruits although recently settled sponges were not identified by species. Zea's point that even his bimonthly sampling scheme allowed some invisible recruitment, i.e., sponges which both settled and died between sampling periods, cautions against interpreting the assortment of species on pipes after 20 months in this study as a full record of recruitment.

Two of the most common Hidden Creek species, *Tedania ignis* and *Halichondria magniconulosa*, were included in a study of recruitment of four species on shallow (< 2m) boulders and cobbles in the Indian River Lagoon, FL by Maldonado and Young (1996). They distinguished four microhabitats by light and current flow conditions and determined that adult abundance of each of the four species was associated with a different set of water flow and light conditions. However, in all four microhabitats *T. ignis* was by far the most abundant recruit after 35 days although it dropped in abundance by 96 days. For three of the four species, adult abundance had no statistical association with larval recruitment.

Sutherland (1980) also noted the lack of relationship between adult abundance and larval recruitment for sponge species inhabiting mangrove roots in Venezuela. He evaluated recruitment of mangrove sponges by suspending asbestos panels, 20 cm by 122 cm, among the prop roots for 18 months and comparing communities that developed on the panels with those on the roots. None of the five most abundant (by % cover) species on the roots were among the top five species in recruitment. The discrepancy between abundance on roots and panels was so extreme in some cases that the ranks for recruitment rates of the three most abundant sponge species (*Tedania ignis*, *Mycale microsigmatosa*, and *Sigmadocia* cf. *caerulea*) were 24, 7, and 10 (out of a total of 25). These results led Sutherland to conclude that accumulation of species in this community reflects results of competition with neighbors after settlement.

The importance of the size and shape of substrata provided for settlement was stressed by Sutherland (1980). Communities on his panels were more similar to each other than those on roots reflecting two differences between panels and roots: 1) each of the much larger panels was more likely to sample all possible larvae available for settlement; and 2) the continuity of the panel substrata allowed superior competitors to continue growing over large areas instead of having to recruit onto each small patch. Thus dissimilarity in species composition among roots results from the low rate of recruitment and the discontinuity of the substrata. Sutherland pointed out how this combination increases species diversity by slowing the elimination of inferior competitors from the system, a point that had also been made by Jackson and Buss (1975) based on their studies of communities on undersurfaces of foliaceous corals.

Seasonality of recruitment was not observed by Sutherland (1980) in Venezuela, but Zea (1993) found recruitment to be influenced strongly by seasonal temperature changes associated with upwelling at Santa Marta, Colombia. In Rützler's (1987) study of settlement on acrylic plates among mangrove roots at Twin Cays, recruitment onto the plates occurred throughout the year but with variations among species depending on the season and prior recruits. This result raises the interesting possibility that differences among sponge species in timing of larval release could increase diversity of mangrove root inhabitants by allowing different species to be the initial colonists of roots entering the water at different times of the year.

The importance of acceptable microhabitats for recruitment is demonstrated by consistent reports of higher rates of settlement by sponge larvae in darker microhabitats (e.g., Zea, 1993; Maldonado and Young, 1996) for Caribbean species. Although materials used for experimentally provided settlement surfaces appear to have minimal impact (Zea, 1993; Reiswig, 1973; Rützler, this volume), the lack of microtopographic features and dark areas that might inspire increased recruitment may have decreased recruitment on smooth pvc pipes. However, the pipes do mimic the prop roots well as the roots are also cylindrical and smooth when they first enter the water. Depth may be an important aspect of microhabitat. Rützler's (1995) study of influence of tidal fluctuations in water level on mangrove sponges demonstrated differences in the depths at which some common Hidden Creek species live on the roots. The pipes in the present study were suspended so that the tops were always at least 20 cm below the lowest tide marks, possibly decreasing representation on them of species such as *Haliclona implexiformis* and *Lissodendoryx isodictyalis* that can tolerate emersion better than other species (Rützler, 1995) although these species also grow on deeper portions of roots.

At Hidden Creek, differences in species composition and relative abundance between the pipes and roots that are still clear and consistent after 20 months indicate that development of the communities on roots is a longer-term process involving sorting of the species that recruit initially. Positive correlation between specific growth rate and survival of six of the most abundant species in Hidden Creek (Wulff, in press) suggest that competition, mediated by growth rate, influences species composition. There are too few published studies to be confident of the pattern yet, but it is intriguing that Zea's (1993) study of sponge recruitment on coral reefs demonstrated a positive relationship between adult abundance and recruitment, whereas studies on habitats with discrete substrata, mangrove roots and cobbles, showed no relationship (Maldonado and Young, 1996; Sutherland, 1980; this study). Interplay between competition and recruitment success is of especially great importance in systems characterized by discrete substrata. In this system, provision of new substrata as roots grow and enter the water for the first time ensures that there are chances for inferior competitors to inhabit roots that are not colonized by superior competitors if they can balance their lack of competitive ability with recruitment success.

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