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SCALE-DEPENDENT SPATIAL AND TEMPORAL VARIABILITY IN BIOGEOGRAPHY OF MANGROVE ROOT EPIBIONT COMMUNITIES[1]

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Abstract. Studies across a range of spatial and temporal scales are needed to discern multiple forces structuring communities. Subtidal prop roots of red mangroves host diverse assemblages of sessile marine epibionts that provide a model system for examining community development and maintenance at a variety of discrete spatial scales. During 1991–1992 we twice surveyed 11 sites at four cays in Belize, Central America, to quantify spatial variability and temporal change in distribution and abundance of root-fouling organisms at five sampling scales: (1) fronts and backs of roots (1-cm scale); (2) roots close to and extending away from peat bank (0.5-m scale); (3) along linear transects parallel to shore (1–50 m scale); (4) on leeward and windward shores of cays (0.5-km scale); and (5) among cays (1–10 km scale). Although epibiont community structure differed widely among sites, all cays surveyed had similar seasonal values of water salinity, pH, and temperature. Within cays, windward sites had higher dissolved oxygen levels and water flow rates than leeward sites. At still smaller scales, outer roots and fronts of roots received significantly more light and were subject to higher water flow rates than inner roots and backs of roots. Species richness, diversity, and mosaic diversity patterns indicated that epibiont assemblages were distributed non-randomly in space: leeward sites were more speciose than windward sites, and fronts of roots were more speciose than backs. Jaccard's index of similarity, cluster analysis, and Kendall's coefficient of concordance showed hierarchical patterns of decreasing similarity with increasing sampling distance. Significant spatial autocorrelation among Jaccard values occurred at 2–3 m intervals, possibly reflecting mean larval dispersal distances. Analysis of mosaic diversity among sites indicated the absence of a clear environmental gradient and supported the hypothesis that species distributions may reflect patterns of dispersal from initial source populations. While precise identity of species was unpredictable among roots, species groups based on taxonomy, morphology, and life history showed very consistent distributions among sites that may reflect variability in local root environments: algae were most prevalent in well-lit areas and on windward sites, while sponges and ascidians predominated in leeward areas. Relative importance and dominance of both individual species and species groups changed substantially between 1991 and 1992. Representatives of four species groups were transplanted across three spatial scales to assess whether post-settlement dynamics limit distributions of these taxa. All transplants survived well for the first 6 wk of the experiment. After 6 mo, all transplants exhibited similarly high levels of mortality regardless of treatment. Overall, the results indicate that larval supply may shape epibiont community composition on short time scales and small and very large spatial scales, while variation in physical factors may influence distributions over the long term and at intermediate spatial scales.

Key words: Belize; community structure; epibionts; mangroves; marine invertebrates; mosaic diversity; Rhizophora mangle; *species richness; species diversity.*

INTRODUCTION

Classical approaches to identifying multi-species distribution patterns have focused on the hypothesis that community structure varies across one or more underlying, spatially continuous environmental gradients (reviewed recently by Keddy 1991 and Clarke and Ainsworth 1993). As our means of detecting habitat heterogeneity have improved, we have come to view many ecological systems as complex mosaics of patches (e.g., Paine and Levin 1981, Connell and Keough 1985, Sousa 1985, Forman and Godron 1986, Armstrong 1989, Levin 1992). Recently, it has become apparent that interpretation of community pattern is contingent on the scale at which it is characterized (reviewed in Wiens 1989, Levin 1992). Patches are nested, hierarchical subunits, and abrupt discontinuities in species abundances may reveal breaks in the grain (sensu

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Pielou 1969) of environmental heterogeneity (Allen and Starr 1982, Allen and Wyleto 1983, Kolasa and Strayer 1988, Kolasa 1989). These breaks reflect the fact that different processes controlling community formation and persistence operate at different spatial and temporal scales (Menge and Olson 1990).

Each species in a community responds to spatial and temporal environmental heterogeneity in a unique way, which makes it difficult to explain or predict species distribution patterns. Consequently, many investigations into relationships between community structure and environmental heterogeneity have lumped species into groups defined by anatomy, morphology, and other ecologically meaningful attributes. This simplifying "functional group" approach has proven a useful predictive tool in studies of terrestrial plant communities (e.g., Raunkiaer 1934, Dansereau 1957, Bouchard et al. 1987, Leishman and Westoby 1992, Bycroft et al. 1993, Watkins and Wilson 1994, Wilson and Roxburgh 1994), wetlands (e.g., Boutin and Keddy 1993, Hills et al. 1994, Ellison and Bedford 1995), aquatic animal communities (e.g., Karr et al. 1986, Snoeijs 1989, Poff and Allan 1995), and marine algal and invertebrate assemblages (e.g., Littler and Littler 1980, Padilla 1989, Steneck and Dethier 1994). While community stability rarely is encountered when communities are defined as aggregations of individual species (e.g., Connell and Sousa 1983), many authors have demonstrated stability, persistence, and predictability of communities defined as assemblages of functional groups (reviewed by Steneck and Dethier 1994).

In this paper, we describe scale-dependent patterns of biogeography and diversity of mangrove root epibiont communities in Belize, Central America. These epibiont communities provide a model system for ecological study at several distinct spatial scales ranging from the individual mangrove root, which represents the smallest unit of delineation, to whole mangrove islands, whose geography, age, and physical structure may determine large-scale recruitment and community development patterns. We can apply emerging techniques for spatial and community analysis to these systems (e.g., Sutherland 1980, Bingham 1995), without some of the artefactual problems arising from studies of community dynamics on artificial substrates such as settling plates (reviewed by Warner 1984). Likewise, we can explore the uses of functional groupings in discerning pattern from a complex matrix of coexisting species. We examine scale-dependent patterns in adult epibiont community structure with respect to species and functional groups, and document field experiments designed to identify factors determining observed patterns of epibiont distribution and abundance. In a two-year observational and experimental study at spatial scales ranging from centimetres to kilometres, we have addressed three fundamental questions:

1) Are mangrove epibionts randomly distributed among roots, or are there scale-dependent patterns of variability in epibiont species richness and diversity?

2) Is the species the most appropriate taxonomic unit for detecting these spatio-temporal patterns, or do patterns become clearer when examining higher taxonomic or functional groups?

3) Do factors operate differentially across temporal and spatial scales to influence distribution and abundance of adult epibiont assemblages?

Natural History of the System

Mangroves grow pantropically on protected coasts and host diverse assemblages of marine epibionts: organisms that colonize intertidal and subtidal portions of the trees (e.g., MacNae 1968, Rützler 1969, Bingham 1992, Ellison and Farnsworth 1992). In the Caribbean, red mangroves (*Rhizophora mangle*) produce extensive networks of aerial prop roots >1 cm in diameter that extend below lowest low water (LLW) before reaching and anchoring into peat or silty benthos (Gill and Tomlinson 1977). Subtidal portions of prop roots are fouled by numerous species of invertebrates and algae, many of which are restricted in this otherwise soft-sediment habitat to the hard substrate provided by the roots (e.g., de Weerdt et al. 1991, Goodbody 1993*b*). These epibionts also significantly influence mangrove root growth, and plant and ecosystem productivity (Perry 1988, Rodriguez and Stoner 1990, Steinke and Naidoo 1990, Sheridan 1991, 1992, Ellison and Farnsworth 1992).

Mangrove epibiont communities are common throughout the world, although sessile invertebrate and algal richness are highest (>100 species) in the Caribbean, where erosional cay physiography and small tidal amplitude permit subtidal fouling of roots. Epibiont communities have been described from mangroves in Florida (Mook 1976, Bingham 1992), Puerto Rico (Burkholder and Almodovar 1973, Rodriguez and Stoner 1990), Bermuda (Thomas 1993), the French West Indies (Sheridan 1991, 1992), Belize (Rützler and Feller 1987, Ellison and Farnsworth 1990, 1992, de Weerdt et al. 1991), Costa Rica (Perry 1988), Panama (Jackson et al. 1989, Garrity and Levings 1992), Venezuela (Sutherland 1980, Alvarez I. 1989, Orihuela et al. 1991, Díaz et al. 1992), Brazil (Eston et al. 1991), South Africa (Steinke and Naidoo 1990), and Malaysia (Cheh 1982*a*, *b*). Typical of most speciose assemblages (Preston 1962, Brown 1984), the majority of epibionts in the Caribbean subtidal root communities are "sparse" (sensu Rabinowitz et al. 1986); they occur at many sites, but on few roots and at low percentage cover.

Scale-dependent variation in mangrove epibiont communities has been noted (e.g., Davis 1940, Alvarez I. 1989, Bingham 1992, Ellison and Farnsworth 1992), but not explicitly quantified. In some areas of Belize, >20 epibiont species (drawn from a much larger species pool) may crowd a single, 2-m long root, but pre-

cise species composition varies dramatically from root to root and among mangrove islands, even between islands separated by only hundreds of metres (Ellison and Farnsworth 1992). Because roots are inherently patchy environments for epibiont communities, linear gradients of resources are unlikely to underlie species abundance patterns.

Observed patterns of spatial and temporal variability in mangrove epibiont community structure have been attributed variously to disturbance (Goodbody 1961*a*, *b*, 1993*b*, Sutherland 1980, Alvarez I. 1989, Garrity and Levings 1992); nutrient availability (Goodbody 1984); larval recruitment patterns (Sutherland 1980, Bingham 1992); predation (Perry 1988, Ellison and Farnsworth 1992); competition (Alvarez I. 1989); local flow regimes (Bingham 1992, Ellison and Farnsworth 1992) and frequency of stochastic perturbations (Bingham 1995). However, controlled experiments testing the relative importance of these processes are rare (Sutherland 1980, Perry 1988, Alvarez I. 1989, Bingham 1992, 1995, Ellison and Farnsworth 1992). These studies illustrated that epibiont community composition shows moderate temporal variation (Sutherland 1980), but is not overtly successional (Alvarez I. 1989, Ellison and Farnsworth 1990). Bingham (1992, 1995) showed that larval processes structure epibiont communities at small spatial and temporal scales. He inferred that at larger temporal and spatial scales physical factors (e.g., salinity, flow rates, and exposure) acting on juvenile and adult organisms structure these epibenthic communities. These results parallel conclusions from other marine systems (e.g, Gaines and Roughgarden [1985], Gaines and Bertness [1992]). In general, studies of sessile benthic invertebrate and terrestrial plant communities clearly point out that environmental complexity at many simultaneous spatial scales must be accounted for in explaining pre- and post-recruitment dynamics (e.g., Ardisson and Bourget 1992, Sarnelle et al. 1993, Bourget et al. 1994) and community changes (e.g., Rahel 1990, Thórhallsdóttir 1990).

Study Site

The Caribbean coast of Belize, Central America encompasses the largest continuous barrier reef in the Western Hemisphere, and >100 mangrove cays occur in its lagoon (Stoddart et al. 1982). We selected four cays for biogeographic surveys of epibiont fauna: Peter Douglas Cay (16°43′ N, 88°10′ W), Spruce Cay (16°45′ N, 88°09′ W), Wee Wee Cay (16°46′ N, 88°08′ W), and Twin Cays (16°48′ N, 88°05′ W; referred to as Water Range by Stoddart et al. [1982]). The first three of these are single, isolated cays, while Twin Cays is a 1-km^2 range of four cays bisected by a 30 m wide channel (Fig. 1). All four cays are >5 km from the mainland shore, ≥2 ha in area, and support mature stands of *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa* (taxonomy follows Tomlinson 1986) on thick (>1 m) peat, sand, and muck underlain by coral rubble (Stoddart et al. 1982). Fringing stands (sensu Lugo and Snedaker 1974) of *R. mangle* with subtidal prop roots occur on both windward (northeastern) and leeward (southwestern) shores of these cays. All sites are seawater dominated, with freshwater inputs only from island surface runoff. Tidal amplitude is ≈30 cm throughout the Belizean cays (Kjerfve et al. 1982). The prevailing climate is subtropical–tropical transition (Hartshorn et al. 1984). The rainy season extends from November through February, the dry season extends from March through June, and the hurricane season (generally fair with frequent squalls at sea) extends from June through November. Eastnortheasterly tradewinds prevail, but during winter cold fronts, cool winds blow 27–46 km/h from the northnorthwest (Hartshorn et al. 1984). Despite differences in wind exposure, the barrier reef itself minimizes se-

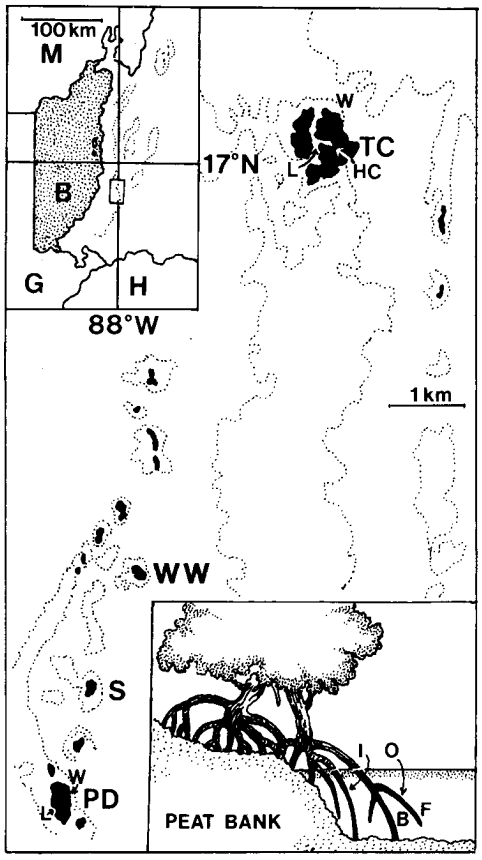

FIG. 1. Map of the study region in Belize, Central America. Insets illustrate study cays; sites where physical factors were measured, transects were conducted, and transplant experiments were performed; and root locations. Key: (Inset map) B, Belize; M, Mexico; G, Guatemala; H, Honduras. (Large map) TC, Twin Cays; WW, Wee Wee Cay; S, Spruce Cay; PD, Peter Douglas Cay; HC, Hidden Creek; W, Windward sites of transplants; L, leeward sites of transplants. Stippling on the two maps indicates coral reef. (Mangrove profile) I, inner roots; O, outer roots; F, fronts of roots; B, backs of roots.

vere wave exposure to the lagoon cays. The study islands receive 1000–1500 mm of rainfall/yr (Hagerman and Smith 1993, A. M. Ellison and E. J. Farnsworth, *unpublished data*).

Within each of the three single cay sites, a windward and a leeward site was selected for investigation (Fig. 1). Two windward and three leeward sites were identified at the Twin Cays complex. Of the Twin leeward set, "Twin West" and "Twin East" referred to the west and east sides of the sheltered main channel bisecting the islands. "Hidden Creek" is a 20 m wide, calm passage enclosed within the east "Twin" island that drains into the main channel. Water depth at the 11 sampling areas ranged from 0.35 to 1.8 m ($\bar{X} \pm 1$ SD; 0.76 ± 0.41 m).

Physical Characteristics of the Sites

Methods

Because abiotic features previously have been posited to influence differences in epibiont community composition, we first characterized local physical parameters at our sampling sites. Both nearshore water temperature and salinity are sensitive to seasonal trends in air temperature and rainfall, as well as local weather events (Ellison and Farnsworth 1992); our sampling regime was designed to detect within- and between-season differences among sites. We measured water salinity and temperature on windward and leeward sides of Peter Douglas, Spruce, and Wee Wee Cays, and at one protected and one exposed site within Twin Cays (Fig. 1). Spruce and Wee Wee samples were taken weekly between 26 December 1991 and 22 January 1992 (encompassing several squalls), whereas samples from Peter Douglas and Twin Cays were taken during summer 1992 (8 June, 18 June, and 22 July). On these dates, we measured salinity (±1 g/L using a hand-held refractometer [Cole-Parmer Model 02940-40, Vernon Hills, Illinois]), pH (Orion 250-A meter with Orion pH electrode, Orion Research, Boston, Massachusetts), and temperature (±0.1°C) of six 50-ml water samples taken at a depth of 0.5 m from each site. Dissolved oxygen (±0.1 mg/L) and pH also were measured at the same depth with a YSI-57 oxygen meter (YSI Incorporated, Yellow Springs, Ohio) on 8 June and 22 July 1992 at 10 stations at Peter Douglas and Twin Cays. Underwater light environments were characterized at Peter Douglas and Twin Cays to assess how incident light intensity varied at different locations within and among roots. "Fronts" of roots were portions facing away from the cay's peat bank; "backs" of roots faced the peat bank (Fig. 1). "Inner" roots occurred ≤30 cm from the peat bank; "outer" roots were those projecting ≈1 m from the peat bank (Fig. 1). On 18 June and 4 July 1992, we measured light availability (in μmoles per square metre per second; LI-COR LI-193SA underwater spherical quantum sensor, averaged over 30 s by a LI-COR LI-1000 data-logger; LI-COR, Incorporated, Lincoln, Nebraska) at the midpoint of backs and fronts of 240 submerged roots (used in the epibiont transplant experiment). Total incident photosynthetically active radiation (PAR) light was measured between 1000 and 1400 at 20 cm below LLW.

We also measured water flow rates at all four cays. Because flow rates within protected channels and on leeward shores were within the range of measurement error of our flow meter, we used clod cards (Doty 1971, Yund et al. 1991, Bingham 1992, Jokiel and Morrissey 1993) to obtain relative, integrated measures of flow over 2–5 d. Pre-weighed 5 cm diameter cylindrical clod cards fashioned of dental plaster (Healthco International, Westboro, Massachusetts) were mounted with silicon onto wire mesh, and then attached with cable ties either to mangrove roots (Twin Cays, Peter Douglas Cay) or to polyvinyl chloride rods inserted among the roots (Wee Wee Cay, Spruce Cay) at a depth of 20 cm. Three clod cards were placed at each windward and leeward location on Wee Wee and Spruce cays in January 1992. On the windward and leeward coasts of Peter Douglas and Twin Cays, six clod cards were placed on inner roots and six were placed on outer roots in July 1992. Clod cards were recovered after 2–5 d, air-dried, and weighed to determine dissolution rates (g/d), which are proportional to water flow velocity (Yund et al. 1991, Jokiel and Morrissey 1993).

Data were analyzed using ANOVA within the MGLH module of SYSTAT version 5.03 (Wilkinson et al. 1992). Cays were considered fixed, while exposure, root position, and root side were considered random effects in the ANOVA, and raw data were transformed when necessary to reduce heteroscedasticity. Homoscedasticity was assessed using normal probability plots. Means ±1 SD (back-transformed) are presented throughout.

Results

Differences in measured environmental parameters generally were small among the sites. No significant differences in water salinity existed among sampling sites (cay × exposure interaction, MS = 2.250, $F_{1,14} = 0.527$, $P = 0.480$) in either summer or winter. Salinity averaged 34.5 g/L (range 32–38 g/L) throughout the year. Water temperature was significantly lower ($P < 0.001$, t test) in winter ($\bar{X} = 25.2$°C, range = 23°–28.8°) than in summer ($\bar{X} = 29.9$°, range = 26.0°–32.0°). There were no significant differences in winter among sampled sites (cay × exposure interaction, MS = 9.901, $F_{1,44} = 0.757$, $P = 0.389$). However, in summer, water was significantly cooler on the windward sides of the cays (these values were: Peter Douglas: windward, 29.7° ± 0.44°; leeward, 30.4° ± 0.40°; Twin Cays: windward, 28.8° ± 0.67°; leeward 30.9° ± 1.18°; cay × exposure interaction, MS = 9.591, $F_{1,76} = 17.542$, $P < 0.001$). Water contained more dissolved oxygen at windward sites in the summer (these values were: Peter Douglas: windward, 9.3 ± 0.71 mg/L; leeward, 6.2 ±

TABLE 1. Clod card dissolution rates, a relative measure of flow rate, at the four cays. Table entries given are $\bar{X}$ percentage change in mass (standard deviation in parentheses). Numbers are back-transformed (ANOVA was done on angular-transformed data), so standard deviations are asymmetrical about the mean. $N = 3$ for Spruce and Wee Wee sites; $N = 6$ for Peter Douglas and Twin sites. Outer roots are > 1 m from the peat bank; inner roots are ≤ 30 cm from the peat bank.‡

Cay†	Leeward exposure*		Windward exposure*	
	Outer roots	Inner roots	Outer roots	Inner roots
Peter Douglas[a]	0.28 (0.206–0.356)	0.28 (0.260–0.308)	0.75 (0.638–0.844)	0.65 (0.550–0.734)
Spruce[b]	0.15 (0.130–0.171)	...	0.47 (0.454–0.494)	...
Wee Wee[b]	0.29 (0.266–0.306)	...	0.47 (0.360–0.574)	...
Twin[a,b]	0.25 (0.208–0.297)	0.22 (0.183–0.266)	0.67 (0.421–0.873)	0.37 (0.279–0.457)

* Windward > leeward; MS = 0.975, $F_{1,52} = 56.920$, $P < 0.001$, ANOVA.

† Cays with different superscripted letters had significantly different overall dissolution rates (cay MS = 0.092, $F_{3,52} = 5.352$, $P = 0.003$, followed by Tukey's HSD test for multiple comparisons among means).

‡ No difference in dissolution rates between inner and outer positions; MS = 0.054, $F_{1,52} = 1.037$, $P = 0.313$.

0.55 mg/L; Twin Cays: windward, 6.9 ± 0.13 mg/L; leeward, 6.8 ± 0.51 mg/L; cay × exposure interaction, MS = 10.680, $F_{1,56} = 38.103$, $P < 0.001$). Water pH was highest at the windward site of Twin Cays (8.3 ± 0.15), but did not differ significantly among the other three sites (Twin Cays: leeward, 8.0 ± 0.04; Peter Douglas: windward, 8.1 ± 0.14; leeward, 8.1 ± 0.11; cay × exposure interaction, MS = 0.371, $F_{1,84} = 27.508$, $P < 0.001$). Clod card dissolution rates, which reflect water flow rates, are affected by temperature, salinity, and pH, and varied in tandem with these latter measurements. Clod cards placed in windward sites dissolved significantly faster than those in leeward sites, indicating higher water flow rates in more exposed areas (Table 1). Clod cards at Spruce and Wee Wee Cays dissolved significantly more slowly than cards at Peter Douglas (Table 1). However, root position relative to the peat bank did not affect dissolution rates (Table 1).

Light reaching root surfaces did not vary with cay (MS = 269 237, $F_{1,480} = 0.252$, $P = 0.252$) or exposure (MS = 204 402, $F_{1,480} = 0.999$, $P = 0.318$), but did vary around each root and with root position (inner vs. outer roots). Fronts of outer roots received significantly more light (433.0 ± 408.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$) than backs of roots (225.9 ± 284.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$; $t_{120} = 4.462$; $P < 0.001$). Because of their proximity to the peat bank, we could not measure light behind inner roots. Considering the fronts of roots only, outer roots received significantly more light (537.6 ± 502.0 $\mu moL \cdot m^{-2} \cdot s^{-1}$) than inner roots (355.4 ± 405.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$; $t_{503} = 4.076$, $P < 0.001$).

In summary, with the exception of within-island flow rates and heterogeneity in light availability at the single root scale, measured physical parameters did not differ substantively across spatial scales among sites. Temporal variation in physical parameters followed predictable seasonal patterns. However, we did observe significant differences in both spatial and temporal patterns of distribution and abundance of species at these same scales.

ARE EPIBIONT COMMUNITIES RANDOMLY DISTRIBUTED?

Methods

To characterize species distribution patterns at all 11 sampling sites, we censused epibionts along 50-m line transects laid parallel to shore. Transects contained ≥50 submerged *Rhizophora* prop roots. To explore inter-year variability in species composition, all Twin Cays sites were sampled initially in August 1991 and again in July 1992. To investigate seasonal variability, Peter Douglas, Spruce, and Wee Wee Cays were surveyed first in December 1991, and again in July 1992. The second set of transects at each site began at the same point as the original set, but it is unlikely that we sampled identical roots at each date. Sampling efficiency was assessed with species root curves (analogous to species area curves, where our sampling unit was an individual root) using data from the first set of transects (Fig. 2). We used data from July 1992 transects to illustrate between-site patterns in spatial variation.

At 1-m intervals along each transect, we examined one outer root and one inner root in situ while snorkeling. Not all sample points along each transect hit both outer and inner roots; actual sample sizes for each transect at each site are given in Table 2. Each root was classified as "ground" (rooted in substrate) or "hanging" (tip not in contact with the substrate). All sessile epibionts occurring from the origin to the bottom of each root were noted: separate lists were maintained for root fronts and backs. Epibionts were identified in situ, generally to species, often with the aid of underwater magnification (Underwater Optics, Vancouver, Canada) and macro-photography. Worms were grouped by family, and neither species of crustose coralline red algae nor species of filamentous cyanobacteria were distinguished. On each root, we could identify only the species visible in the outermost, "canopy" layer. Identification of cryptic "understory" species

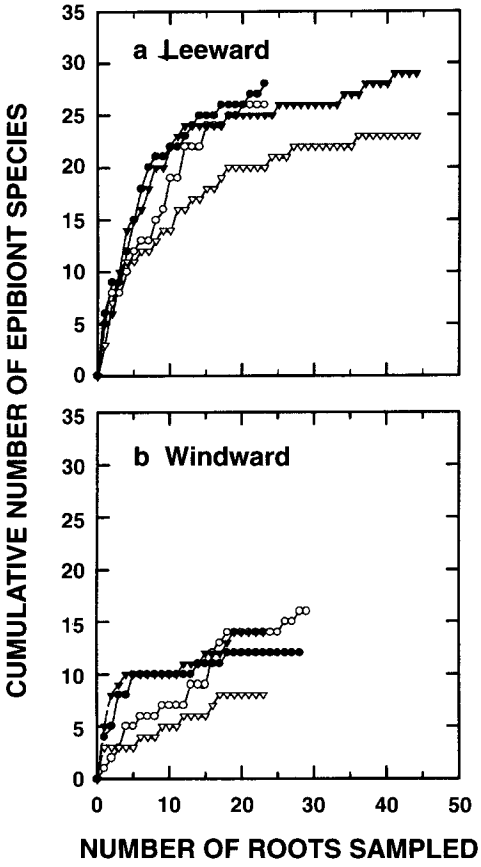

FIG. 2. Representative species root curves for (a) leeward and (b) windward sites at Peter Douglas Cay. Each graph illustrates cumulative number of epibiont species encountered plotted against number of roots sampled. Circles, outer roots; inverted triangles, inner roots; filled symbols, fronts of roots; open symbols, backs of roots.

would have entailed disturbing the communities of interest.

To quantify relative abundance and species diversity patterns of root-fouling communities, we photographed fronts and backs of all available inner and outer roots at 5-m intervals along each line transect. We used a Nikonos V underwater camera with a 28-mm lens and Nikon 1:6 close-up attachment (Nikon Corporation, New York, New York). Each photograph covered a 21-cm section of root. Multiple frames were taken along roots longer than 15 cm to capture the entire root. Slides were scanned with a Cohu video camera (Cohu, Incorporated, San Diego, California), digitized with a PC-VISION+ frame-grabber board (Imaging Technologies, Incorporated, Cambridge, Massachusetts) in a Northgate computer, and analyzed using IMAGE (Rich et al. 1989) to determine projected root surface area (in square centimetres) and the percent of that area occupied by each epibiont.

Hierarchical patterns of similarity among epibiont species assemblages at increasing spatial scales were explored using Jaccard's (1901) index of similarity J, Kendall's coefficient of concordance, W (Daniel 1978), cluster analysis, and affinity analysis (Scheiner 1992). For pairwise comparisons, J was calculated as $c/(a + b + c)$, where c is the number of species in common between two sites, a is the number of species unique to site 1, and b is the number of species unique to site 2. J ranges from 0 to 1, where a value of 0 indicates no species in common between the two sites, and a value of 1 indicates that the two sites are identical. We computed J for: (1) comparisons between fronts and backs of roots within transects (0.01-m scale); (2) all possible between-root comparisons (fronts and backs of roots pooled) within transects and root position (1–50 m scale); (3) comparisons between exposure categories (windward vs. leeward) for each cay, in which we pooled all roots within transects (100–500 m scale); and (4) all possible between-cay comparisons, in which roots were pooled across transects and exposure categories (1–9 km scale).

Kendall's W is a nonparametric measure of agreement among several complete sets of rankings (for example, cays) of a number of objects (here, species). For example, to examine concordance in species abundance patterns among cays, each epibiont species was ranked by the total number of roots occupied by that species. This resulted in a matrix consisting of 4 rows

TABLE 2. Overall epibiont species richness (s) along the sample transects at the four cays. Number of roots of each type sampled is given in parentheses.

		Root type								
Cay	Location	All	Outer	Inner	Ground	Hanging	Outer ground	Outer hanging	Inner ground	Inner hanging
Peter Douglas	Leeward	48	38	43	37	43	···	38 (17)	37 (23)	38 (28)
	Windward	28	25	19	17	25	11 (4)	25 (46)	15 (6)	13 (7)
Spruce	Leeward	46	31	40	41	33	14 (4)	27 (16)	39 (42)	17 (7)
	Windward	45	33	35	38	32	14 (5)	29 (24)	34 (17)	24 (19)
Wee Wee	Leeward	42	33	37	38	32	21 (11)	31 (15)	36 (40)	19 (7)
	Windward	27	24	20	25	18	21 (23)	18 (15)	20 (19)	9 (5)
Twin	Western main channel (leeward)	52	47	40	17	51	···	47 (38)	17 (9)	37 (24)
	Eastern main channel (leeward)	53	37	47	46	45	···	37 (13)	46 (32)	31 (14)
	Hidden Creek (leeward)	49	37	29	25	45	···	37 (23)	25 (19)	35 (25)
	Eastern outer coast (windward)	32	15	28	27	24	6 (1)	19 (21)	26 (32)	18 (15)
	Western outer coast (windward)	24	24	12	21	21	21 (24)	21 (22)	11 (4)	4 (1)

(cays) × 96 columns (taxa). We tested the null hypothesis that the ranked species abundance patterns were independent of cays by computing:

$$W = \frac{12 \cdot \Sigma R_j^2 - 3m^2n(n+1)^2}{m^2n(n^2-1)},$$

where m is the number of sets of rankings (four cays), n is the number of ranked objects (96 species), and R_j is the sum of the ranks assigned to the jth object (Daniel 1978). Kendall's W ranges from 0 (no association) to 1 (perfect association). The test statistic:

$$\chi^2 = m(n-1)W$$

is distributed as a chi-square with $(n-1)$ degrees of freedom. Kendall's W was computed using Friedman's test within the NPAR routine of SYSTAT version 5.03 (Wilkinson et al. 1992).

Cluster analysis (within SYSTAT) and affinity analysis (version 4.3, Scheiner 1992) were used to provide additional information about relative similarities and differences among the 11 sites, and to infer mechanisms that may control overall pattern diversity among the four cays. Affinity analysis measures compositional pattern diversity as the relationship between variation in species richness among communities and variation in species evenness across communities. The metric, mosaic diversity (m), is the slope of the line regressing average site affinity (the average relative "distance" in hyperdimensional space between one site and all other sites) on average site similarity (the average similarity [Jaccard] between each site and all other sites). The standard error of m was computed using a jackknifing procedure, and comparisons between observed patterns of mosaic diversity and expected patterns from several null distributions were computed using 100 bootstrapped replicates (Scheiner 1992). Details of the null distributions are given in *Results*.

Results

Spatial variation in distribution and abundance of epibionts.—We identified 96 taxa on mangrove roots during the two years of sampling (Appendix). Dominant taxa in terms of frequency and cover on roots included algae (*Bryopsis pennata, Enteromorpha flexuosa,* and *Halimeda opuntia*), sponges (*Haliclona implexiformis* and *Tedania ignis*), ascidians (*Distaplia corolla, Perophora bermudensis,* and *Diplosoma glandulosa*), and cnidarians (*Aiptasia pallida* and *Dynamena crisioides*). Visual inspection of species root curves in 1991 illustrated that ≈90% of the species within a transect normally were encountered within the first 10–15 m of the transect (Fig. 2). This figure illustrates representative data only from Peter Douglas Cay; the other sites showed similar asymptotic behavior in species encounters. The magnitude of this asymptote, which reflects total species richness (S) for the community, varied by aspect (front vs. back) and position of root (inner vs. outer) among roots within

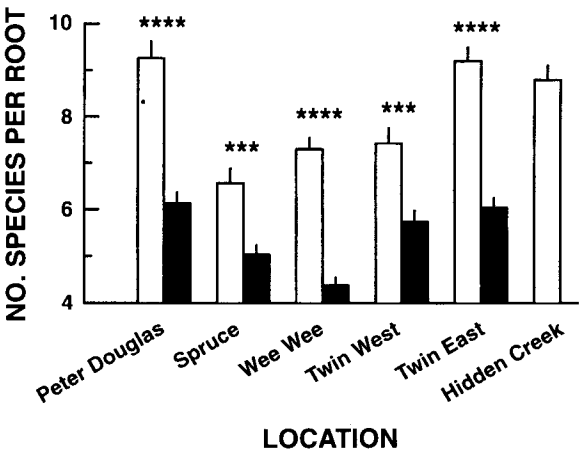

FIG. 3. Mean number of species per root (1992 data) at the four cays. Open bars, leeward sites; filled bars, windward sites. Hidden Creek is a protected channel within the Twin Cays complex (see Fig. 1). Error bars represent 1 SD. ***$P < 0.005$, ****$P < 0.001$; t tests.

sites, and among cays (Table 2). We found 79 taxa at Twin Cays, the largest site sampled, 62 taxa at Peter Douglas, 60 taxa at Spruce, and 49 taxa at Wee Wee Cay. The relationship between $\log_{10}$(cay perimeter), one measure of the "area" available for space occupiable by epibionts, and $\log_{10}$(number of species) was linear ($\beta = 0.23$, $r^2 = 0.96$).

At the smallest sampling scale, the single root, within-root S ranged from 1 to 17 species ($\bar{X} = 6.9 \pm 2.71$). Fronts of roots had more species ($S = 5.6 \pm 2.29$) than backs of roots ($S = 4.7 \pm 2.18$; $t = 7.205$, $P < 0.001$, $N = 743$ roots pooled over root position, wind exposure, and cay). We found identical patterns within cays, within types of roots (hanging vs. ground), and within root locations (inner vs. outer): S of fronts of roots was always $\geq S$ on the backs of roots. Despite the high correlation of island area with species richness, no such tight relationships occurred among root species richness and individual root surface area. Only loose linear correlations existed between $\log_{10}$(number of species per root) and $\log_{10}$(surface area of root) ($\beta = 0.14$, $r^2 = 0.109$, $N = 1221$ for all roots pooled).

To compare S among roots of different types at the different sites (each cay × location combination of Table 2), fronts and backs of roots were combined to give total within-root S values. Total species richness of ground roots and hanging roots did not differ within or between root positions (inner or outer) within 10 of the 11 sites ($P > 0.1$, t tests on all cases, subject to table-wide Bonferroni correction). Only at Hidden Creek, S of hanging roots (9.6 ± 2.79) was greater than S of ground roots (6.9 ± 2.0; $t_{42} = 3.55$, $P = 0.01$). Within each cay, roots on leeward sites were more speciose than roots on windward sites (Fig. 3). Leeward sites overall were more speciose (42–53 species) than windward sites (27–45 species; Table 2).

Species diversity (H') was consistently low within

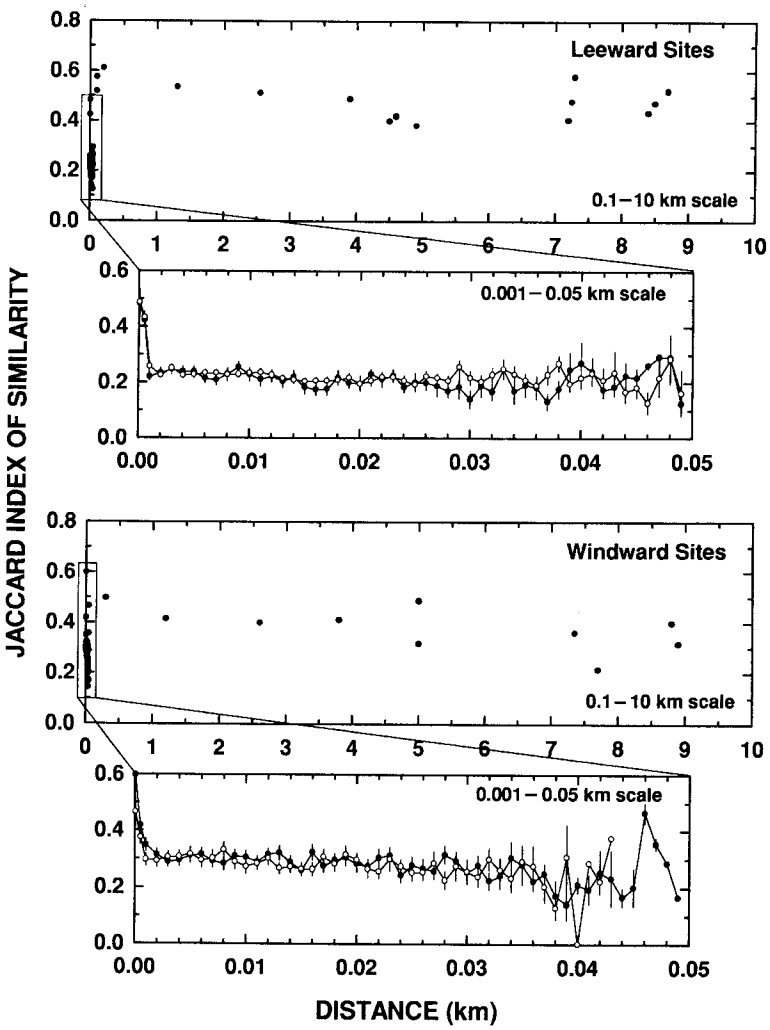

FIG. 4. Pair-wise similarities between epibiont communities at leeward and windward sites (1992 data). Small-scale graphs (0.1–10 km) illustrate all pair-wise comparisons among (upper graph) the six leeward sites or (lower graph) five windward sites. Large-scale insets (0.001–0.05 km) illustrate pair-wise comparisons between roots within transects on leeward or windward sites: solid symbols, outer roots; open symbols, inner roots. Within the insets, each point shown is the mean pair-wise similarity of all roots separated by a given distance. Error bars represent ± 1 SD.

roots at all spatial scales (range = 0.80–1.68), reflecting the fact that on the majority of roots, one or two species dominated each assemblage. There was little bare space (percentage of total root area) available for recruitment or expansion on any roots. Leeward roots had significantly less bare space than windward roots ($\bar{X}$ = 5.2 ± 6.1%, range = 0–23% at leeward sites; $\bar{X}$ = 9.5 ± 7.9%, range = 2–26% at windward sites; P = 0.003, t test).

Fig. 4 shows the relationship between Jaccard's index of similarity J and distance between each paired comparison at windward and leeward sites. The largest values of J were found at the smallest spatial scale, when we compared between fronts and backs of roots (leeward roots: J = 0.48; windward roots: J = 0.60). Within transects (1–50 m scale), J appeared to oscillate regularly among both inner and outer roots (Fig. 4). Spectral analysis using fast Fourier transforms (within the SERIES module of SYSTAT version 5.03) revealed significant spatial autocorrelation among Jaccard indices at 3 m for leeward roots and 2 m for windward roots. Oscillations became irregular above 36 m, which we interpret as an artefact of declining sample sizes for comparisons between roots as the distance between them increased. Within cays, similarity values among leeward sites ranged from 0.4 to 0.6, and from 0.2 to 0.6 for windward sites. J declined slightly, but not significantly, with distance between cays. The slope of the decline was slightly more negative for windward sites (β_1 = −0.017), indicating slightly less similarity of these sites over long distances than for leeward sites (β_1 = −0.010).

We tested for concordance among root epibiont assemblages at three scales: between root positions (inner

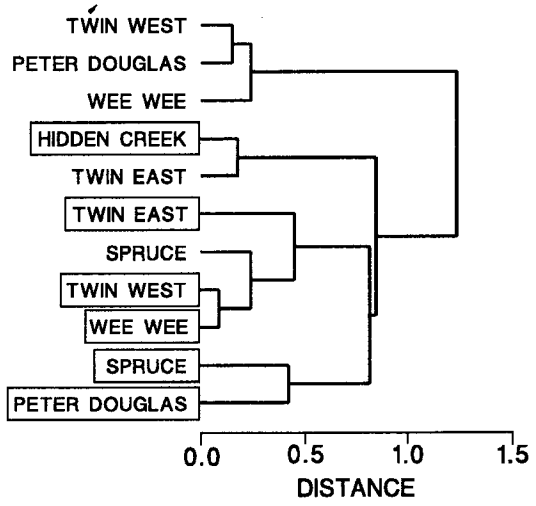

FIG. 5. Cluster analysis of windward and leeward sites, based on presence/absence data of all species (1992 data). Cluster distances based on $1 - g_{ij}$, where g_{ij} is the Goodman-Kruskal gamma correlation coefficient (Goodman and Kruskal 1954, Wilkinson et al. 1992) between pairs of sites. Leeward sites indicated by boxes.

vs. outer roots, pooling among cays and exposure); between the two exposure types (windward vs. leeward, pooling among cays and position with respect to shore); and among the four cays (pooling all roots within a cay, regardless of exposure and position with respect to shore). Inner and outer roots had the highest concordance ($W = 0.922$, $P < 0.001$), exposure type showed intermediate concordance ($W = 0.742$, $P = 0.003$), and among-cay comparisons were less similar ($W = 0.624$, $P < 0.001$). In other words, at spatial scales on the order of metres, epibiont assemblages were similarly structured with respect to species rank abundance, but this similarity declined with distance between roots (tens to hundreds of metres that separate the windward from leeward sides of cays, and kilometres between cays).

Cluster analysis was used to clarify relationships between the 11 sites sampled during 1992 (Fig. 5). One windward and five leeward sites clustered together (both sides of Spruce Cay, together with the leeward sides of Peter Douglas and Wee Wee, and the protected sites of Twin East and West Main Channel; Fig. 5). Three windward sites formed another cluster (Twin West Outer Coast, and the northeastern sides of Peter Douglas and Wee Wee; Fig. 5). Hidden Creek clustered together with the windward side of that island, and this smaller cluster was clustered with the "leeward" cluster described (Fig. 5). The first pairing of each cluster also reflect distances between islands (Fig. 1), with the exception of the Twin West Outer Coast–Peter Douglas windward cluster.

This pattern was amplified by affinity analysis (Fig. 6). The modal site (highest average similarity relative to all other sites) was Hidden Creek ($J = 0.45 \pm 0.15$), which shared on average more species (27.5) with other sites. The windward sites at Peter Douglas and Twin West Outer Coast were both "outliers": sites with little in common with the others because of their low species richness. Note that these two sites also grouped together in the cluster analysis (Fig. 5). As with the cluster analysis, the five other leeward sites and the exposed coast of Spruce Cay had relatively high similarities and had higher affinities with each other than did the other windward sites. Mosaic diversity (m), the slope of the line in Fig. 6, was a relatively high 3.6 ± 0.44, indicating a "complex landscape with either many ecological gradients or no particularly strong gradient" (Scheiner 1992: page 1865) determining species composition.

We compared the overall mean similarity and mosaic diversity with three null distributions generated by bootstrapping the 11 site × 96 species data matrix. The first null distribution was generated by randomly assigning species to sites, the only constraint being that the overall total number of species in the matrix was identical to the original. The second null distribution constrained the number of species within each site to be the same as was actually observed in 1992, while the third null distribution constrained the number of sites at which any species occurred to be the same as the observed. Scheiner (1992), like Simberloff and Connor (1981) and Diamond and Gilpin (1982), points out that if the observed data match the first null model, species distributions were likely determined by chance historical pattern; if the second, that species number is limited by some upper bound (carrying capacity of the

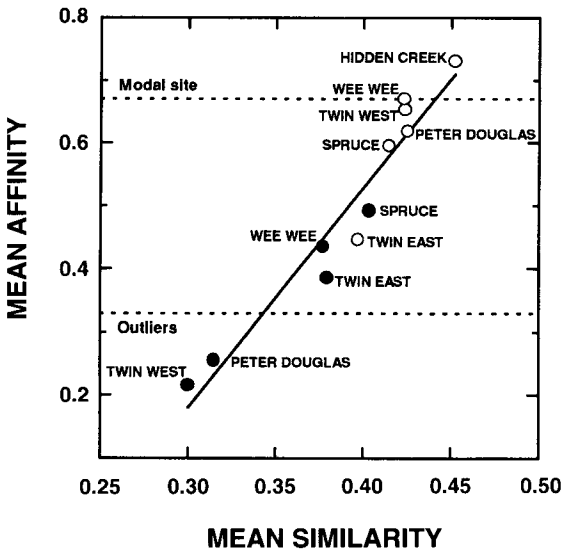

FIG. 6. Relationship between overall mean similarity (mean pairwise Jaccard similarity between each site and all other sites) and mean affinity (average relative distance in hyperdimensional space between one site and all other sites; Scheiner 1992) for the leeward (open symbols) and windward (solid symbols) sites. The slope of the regression line between these two variables (=3.6) is the mosaic diversity of this landscape.

TABLE 3. Mean similarity and mosaic diversity measured for the 11 sites given in Table 1, and comparisons with three null models generated using a bootstrap by constraining species frequencies across sites, total frequencies within sites, and matrix total frequencies. Values ($\bar{X} \pm$ SE) that are significantly different ($P < 0.001$) from each other (based on a Z statistic; α-level reduced to account for 12 pairwise comparisons) are indicated by different superscripted letters.

		Bootstrapped data sets		
	Original data	Constrain matrix total (Model 1)	Constrain species frequencies within sites (Model 2)	Constrain species frequencies across sites (Model 3)
Mean similarity	0.39 ± 0.010^a	0.27 ± 0.006^a	0.26 ± 0.006^b	0.39 ± 0.001^b
Mosaic diversity	3.61 ± 0.449^a	8.63 ± 0.945^c	5.92 ± 0.474^b	8.61 ± 1.071^c

community); and if the data match the third null model, that species distributions reflect patterns of dispersal from initial source populations. Results of this bootstrap analysis are given in Table 3. Observed mean similarity did not differ from that of the null model that constrained frequencies of species across sites (null model 3), indicating that dispersal may play a key role. Observed mosaic diversity was significantly different from that of all three of the bootstrapped datasets, because by increasing variation among sites or species, the constraints increase variation among species and sites, and hence increase m substantially (Scheiner 1992).

Temporal variation in distribution and abundance of epibionts.—At all 11 sites, species distribution among roots was similar in the 1991 and 1992 transects. We first compared frequency of occurrence of each species along transects. Each species was assigned a rank based on the number of roots on which it occurred, and statistics comparing between years were done on these ranks. As with between-year comparisons of frequency-of-occurrence, we compared temporal changes in percentage cover by assigning each species a rank based on its average percentage cover on each root at a given site (the five most abundant species in each year are superscripted in the Appendix). The number of roots occupied (ranked) by a given species in 1991 was significantly correlated with the number of roots occupied by the same species in 1992 at all sites (Table 4). However, within-root percentage cover of epibiont species in 1991 was not correlated with percentage cover of the same species in 1992 (Table 4). In 1991, number of roots occupied by each species (ranked) was significantly correlated ($P < 0.008$ following Bonferroni table-wide correction) with its percentage cover (ranked) at all but three sites (the eastern leeward site and Hidden Creek at Twin Cays, and the windward coast of Spruce Cay). However, the frequency of roots occupied and percentage cover were not correlated at any site in 1992 ($P > 0.111$ all cases).

In addition, few across-site patterns emerged when we examined which species occurred on many roots along transects, or which showed high mean percentage cover on individual roots. With the exception of three species of algae (*Enteromorpha flexuosa, Ceramium nitens,* and *Wrangelia argus*), one hydroid (*Dynamena crisioides*), and three sponges (*Haliclona curacaoensis, Spirastrella* sp., and *Tedania ignis*), species that were either frequent or dominant at a given site were not necessarily so at other sites. Even for these species, high frequency of occurrence among roots or abundance within roots was not consistent between years. Most of these epibionts occurred sparsely on few roots per site at low percentage cover, yet were found at a broad range of sites. Pooled over all sites in 1992, mean rank frequency of occurrence (in terms of percentage

TABLE 4. Relationship between frequency of roots occupied by species in 1991 and 1992 transects, and mean percentage cover of each species in 1991 and 1992 photographs along the transects. Each species was ranked based on the number of roots on which it was found in the 1991 and 1992 transect for number of root comparisons, and ranked based on its average percentage cover in 1991 and 1992 for percentage cover comparisons. Values shown are correlations (Pearson's r) between 1991 rank and 1992 rank for each site. No photographs were taken on the east windward site at Twin Cays in 1991.

Cay	Location	r (no. roots)	r (% cover)
Peter Douglas	Leeward	0.687****	−0.042
	Windward	0.548****	0.291*
Spruce	Leeward	0.369***	−0.192
	Windward	0.238*	−0.133
Wee Wee	Leeward	0.510****	0.595****
	Windward	0.447****	0.006
Twin	Western main channel (leeward)	0.568****	0.219
	Eastern main channel (leeward)	0.662****	0.087
	Hidden Creek (leeward)	0.600****	0.113
	Western outer coast (windward)	0.502****	0.223
	Eastern outer coast (windward)	0.522****	...

* $P < 0.05$; *** $P < 0.005$; **** $P < 0.001$.

of roots on which a given species occurred) and mean rank percentage cover within a root were not correlated (Spearman's rank correlation $r_s = 0.117$, $P = 0.313$), indicating species that were common were not necessarily widespread. We therefore grouped species into higher taxonomic categories and/or functional groups to examine more qualitatively across-site similarities and differences in epibiont community structure.

Distribution and Abundance of Epibiont Taxon Groups

Methods

We assigned each epibiont taxon to 1 of 10 categories based on taxonomic affiliation, adult morphology, and life history: filamentous algae, fleshy algae, corallines (coralline algae, encrusting corals, *Millepora,* and bryozoa), soft-bodied cnidaria (small hydroids and larger anemones), massive sponges, encrusting sponges, ascidians, barnacles, bivalves, and worms. Spatio-temporal variation in number of species within higher taxonomic groups was explored initially for three groups: fleshy algae, massive sponges, and ascidians.

The almost complete absence of sponges and ascidians from windward sites (Appendix) implied the existence of systematic differences in relative importance and abundance of various taxa across sites. From presence/absence data on individual taxa, we derived relative importance (RI) values for all 10 of the species groups. We define RI as the fraction of roots occupied by any member of the group at each site (percentage of total roots sampled). While species richness varied significantly between the fronts and backs of roots, RI of taxa did not ($P \geq 0.123$ for all comparisons by ANOVA on angular-transformed data), so data were pooled within roots to obtain means for comparisons between roots at different positions within sites, and between exposure types among cays. Spatio-temporal patterns in species group abundances (percentage covers) were calculated from photographs digitized as described.

Results

Spatial variation in distribution and abundance of epibiont taxon groups.—Fig. 7 illustrates representative patterns of species richness (1991 data) of algae, sponges, and ascidians at leeward and windward sites of Peter Douglas and western leeward and windward sites of Twin Cays (similar patterns were found for Spruce, Wee Wee, and the east island of Twin Cays). These cays showed similar profiles of species richness within groups. Algae were more speciose, and sponges and ascidians were virtually absent, on windward roots. On leeward roots, algae, sponges, and ascidians were similarly speciose. Outer roots (which are predominantly hanging; Table 2) supported more speciose assemblages of algae at both leeward and windward sites, and ascidians at leeward sites. Inner roots (which are more evenly divided between hanging and ground

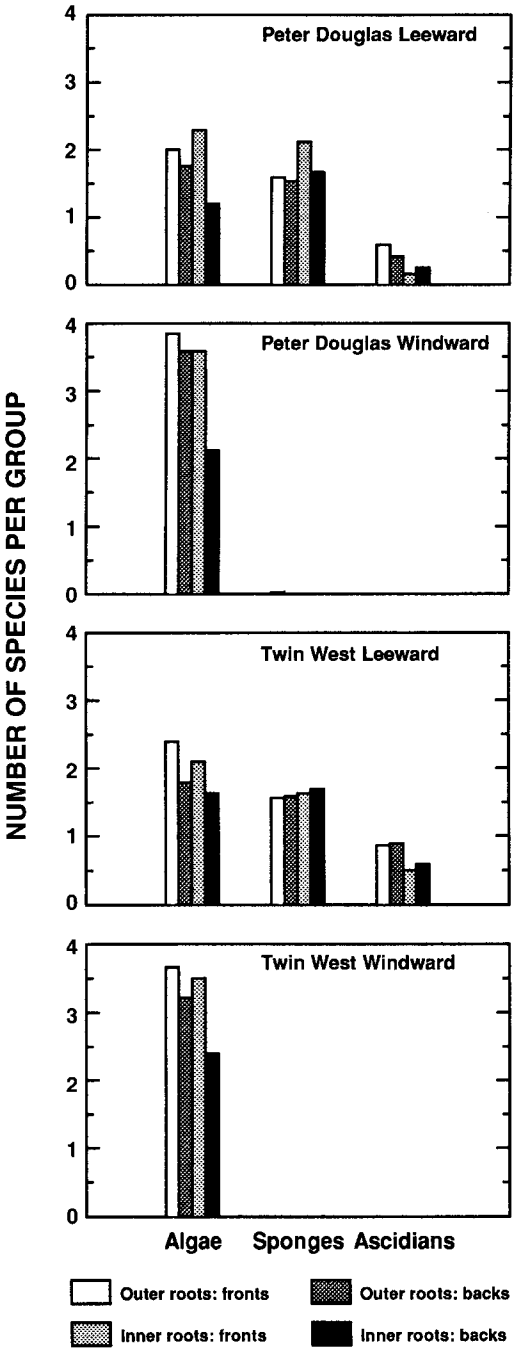

FIG. 7. Mean number of species per species group at two representative cays (1991 data).

roots; Table 2) had slightly more species of sponges than did outer roots. Fronts of roots typically supported more species of algae than did backs of roots, but ascidian and sponge species richness did not vary between fronts and backs of single roots.

Relative importance of the 10 groups showed considerable variation with both root position and exposure (Fig. 8). Encrusting sponges, barnacles, bivalves, and

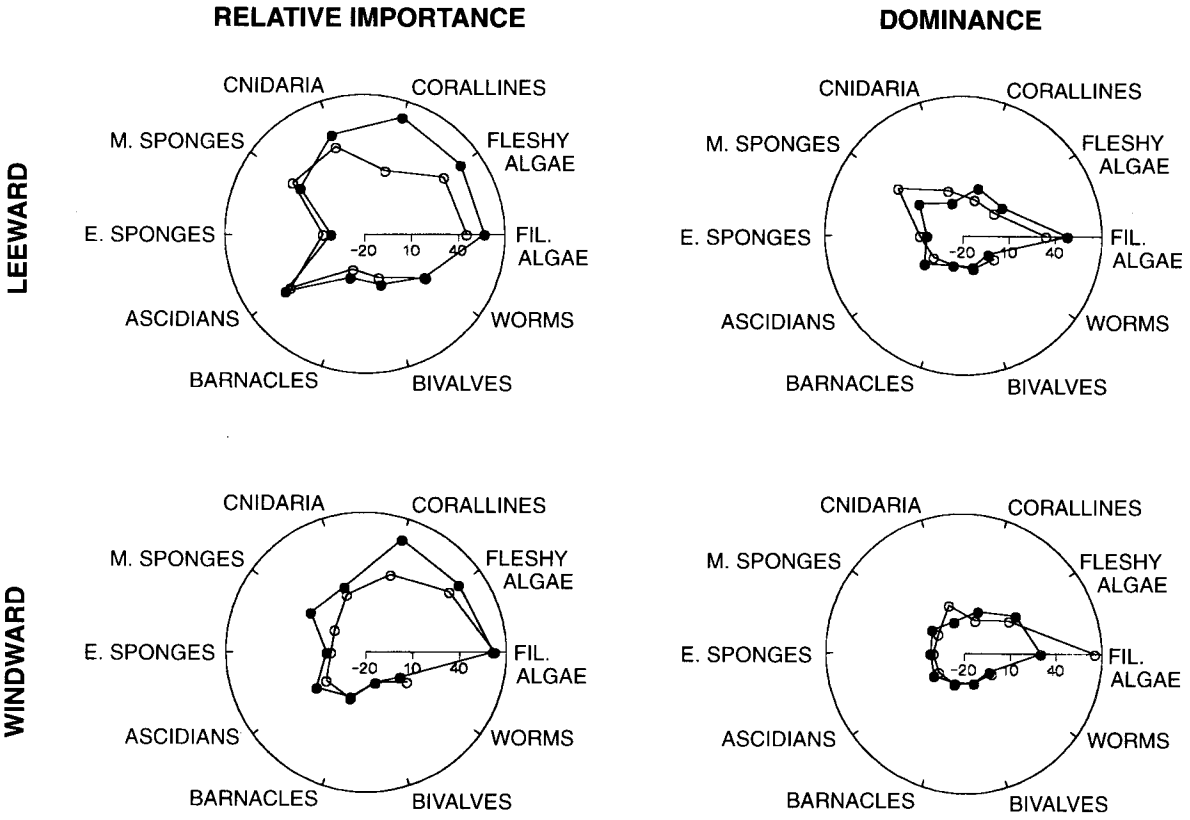

FIG. 8. Polar plots illustrating changes in (left panels) relative importance and (right panels) dominance (percentage cover) of species groups on (top panels) leeward and (bottom panels) windward sites in (open symbols) 1991 and (solid symbols) 1992. Each point illustrates, as distance along the radius, average relative importance (RI) or percentage cover of each species group. For clarity, 0% cover is a small distance from the center of the plot.

worms were uncommon at all sites, and were found most commonly on leeward inner roots. Soft-bodied cnidaria were similarly uncommon, occurring on 2–14% of roots surveyed; this group occurred mostly on windward outer roots. Massive sponges and ascidians were moderately common, and occurred most frequently on leeward roots. Filamentous and fleshy algae were observed on 10–54% of roots, and were the dominant epibionts on windward roots; certain fleshy algae (primarily *Caulerpa* spp.) completely covered leeward roots on which they occurred.

Average percentage cover (dominance) of each group was also predicted most reliably by exposure (Wilks' $\lambda = 0.724$, $F_{10,425} = 16.216$, $P < 0.001$, MANOVA on 1991 data; Fig. 8). In general, leeward roots supported a higher percentage of both massive and encrusting sponges (10–50% cover), larger anemones (5–15% cover), and ascidians (5–10% cover) than windward roots. In contrast, windward roots were dominated by filamentous algae (60–75% cover), fleshy algae (5–35% cover), and small hydroids (40% cover). Corallines, bivalves, and barnacles occupied consistently low proportions of root space across all communities. Root position affected only fleshy algae and worms, both of which were more abundant on outer roots (fleshy algae: MS = 0.130, $F_{1,434} = 4.402$, $P = 0.036$, univariate F test on the effect of root position on percentage cover of fleshy algae; worms: MS = 0.077, $F_{1,434} = 7.370$, $P = 0.007$; Wilks' $\lambda = 0.958$, $F_{10,425} = 0.051$, $P = 0.043$ overall MANOVA for the effect of root position on all species groups). However, there was no exposure × root position interaction (Wilks' $\lambda = 0.982$, $F_{10,425} = 0.776$, $P = 0.652$). Within roots, filamentous algae were more abundant on backs of roots than on fronts of roots (MS = 0.389, $F_{1,434} = 4.119$, $P = 0.043$, univariate F test on the effect of root side on percentage cover of filamentous algae; Wilks' $\lambda = 0.954$, $F_{10,425} = 1.948$, $P = 0.026$ overall MANOVA for the effect of root position on all species groups), but no other species group had different patterns of percent cover on fronts vs. backs of roots ($P > 0.1$, all other univariate F tests).

Temporal variation in distribution and abundance of epibiont species groups.—We observed substantial changes in RI of species groups from 1991 to 1992 (Fig. 8). Because transects at Twin Cays were surveyed in the summer of each year, while transects at the other islands were surveyed in December 1991 and summer of 1992, we could contrast between-season (within-year) changes in group frequencies with between-year

(within-season) changes in group frequencies. We compared relative changes in RI ($\Delta RI = [RI_{time1} - RI_{time2}]/RI_{time1}$) of each group at Twin Cays (sampled in August 1991 and July 1992) to ΔRI of each group at Spruce, Wee Wee, and Peter Douglas Cays (sampled in December 1991 and July 1992). All groups showed positive ΔRI from January 1992 to July 1992 (a seasonal shift), whereas ΔRI of worms, sponges, and bivalves was negative across years. When windward and leeward sites were considered separately, the highest overall ΔRI was observed between seasons at windward sites. In contrast, the largest between-year ΔRI occurred among groups in the leeward regions (except for sponges and fleshy algae). Analysis of variance indicated no significant among-site differences in seasonal vs. annual ΔRI, as variance was very high. Thus, we present data from the 1991 summer and winter censuses together as "1991" data, and contrast these pooled data with the summer 1992 data to illustrate 1991 to 1992 ΔRI (Fig. 8). The largest changes in relative importance from "1991" to 1992 occurred among fleshy algae, corallines, and ascidians: all increased in RI in all root classes (Fig. 8). In contrast, percentage of roots occupied by filamentous algae decreased slightly in all areas. Encrusting sponges and massive sponges declined in frequency at leeward sites, but increased at windward sites (Fig. 8). All other groups had similar RI during the 1991 and 1992 samples.

Changes in percentage cover of species groups were assessed through analysis of digitized photographs, and are illustrated in Fig. 8. Echoing their decreases in RI between years, massive sponges on leeward roots uniformly declined from 1991 to 1992 by 5–30% across all root types. This decline in sponge cover occurred in all leeward areas checked during summer 1992, and does not appear to be an artefact of seasonal vs. yearly sampling regimes. Encrusting sponges also showed slightly reduced percentage cover among leeward roots. As with their ΔRI, filamentous algae, fleshy algae, corallines, and ascidians all exhibited slight (1–10%) increases in percentage cover on leeward roots over the same period. On windward roots, percent cover of filamentous algae declined 10–40% and percentage cover of soft-bodied cnidaria declined 15–25%. The other species groups remained comparatively stable.

Do Post-Settlement Factors Determine Mangrove Epibiont Community Structure?

Methods

While exact species composition of mangrove root epibiont communities could not be predicted accurately at a given site, patterns were clarified by grouping species into higher taxonomic groups. We then designed transplant experiments to test the null hypothesis suggested by this observation: that all groups can survive and grow equally well on both protected and exposed coasts. Acceptance of this null hypothesis would indicate that environmental differences between sites do not account for differences in local species composition of the adults we identified on roots. The affinity analysis results (Table 4, Fig. 6) indicated that dispersal of spores and larvae may limit distribution and abundance of epibionts locally.

To determine if planktonic larval abundance correlated with apparent species distribution patterns of epibionts, we conducted plankton tows using a 63-μm mesh plankton net dragged for 50 m parallel to shore, on leeward and windward coasts of Wee Wee Cay on seven dates in 1992 corresponding to new and full moons (4 January, 20 January, 19 March, 31 May, 16 June, 30 June, and 15 July). However, no larvae of sessile epibiont species were captured, so we were unable to measure directly temporal patterns in larval release and dispersal. Together with our inability to monitor continuously larval release, the virtual absence of information on timing of reproduction and larval/spore biology of most mangrove root epibionts in Belize (but see Goodbody 1988, 1993*a*, Havenhand 1993, Rützler 1993) precluded us from directly testing the hypothesis that larval supply limits distribution and abundance patterns of epibionts. However, monitoring the performance of adult transplants eliminates environmental forces on adults as a factor, and allows us to infer whether a combination of larval supply and early post-settlement survivorship and growth are selective filters in community formation and persistence. Post-hoc analysis of performance of transplants of different sizes provides a starting point for distinguishing between the effects of larval supply and early post-settlement processes in structuring these epibiont communities.

We transplanted sections of hanging mangrove roots at four different spatial scales relative to the original location of the root, to assess whether adults of epibiont species characteristic of certain mangrove sites were able to survive at other locations. Species groups were the focus of the transplant experiments because the majority of individual epibiont species were rare, and we sought to minimize overall root damage resulting from adequate replication in this experiment. At each of four sites (windward and leeward sides of Peter Douglas Cay and the east island of Twin Cays; Fig. 1), six root sections per taxon group were transplanted as follows (four treatments): fronts of roots to backs of roots; outer roots to inner roots; leeward (windward) roots to windward (leeward) locations; and transplant controls. Each transplanted section of root was covered predominantly (>50%) by one of the four most common species groups: massive sponges, ascidians, algae, and soft-bodied cnidaria. Each section hosted one or two epibiont species of the relevant species group. The most common (>10% of sections) massive sponge species used in this experiment were *Ulosa ruetzleri* (33% of the transplants), *Tedania ignis* (28%), and *Haliclona implexiformis* (12%). The most common ascidians were

Didemnum conchyliatum (31%), *Distaplia corolla* (29%), and *Botrylloides nigrum* (17%). Algae were represented most commonly by *Acanthophora spicifera* (22%), *Caulerpa racemosa* (17%), and *Ceramium nitens* (13%). Only the predominant species of anemone, *Aiptasia pallida,* was used for the cnidarian transplants.

Each root section transplant was labelled with a plastic numbered band and trimmed to 10 cm long, so that one taxonomic grouping covered the majority of each section. Front-to-back transplant sections were removed from the main root cable, rotated 180° to face the peat bank, and attached to the remaining section of root with two plastic cable ties. Outer-to-inner root transplant root sections were cut from the parent tree and attached to roots directly landward (≤1 m) of the donor root. Leeward-to-windward and windward-to-leeward transplants were cut and transferred immediately from one side of each island to the other, keeping them constantly submerged in a well-oxygenated bucket of sea water. Transplant controls were severed from the main root cable and re-attached in place with no change in orientation. Massive sponges, ascidians, algae, and large anemones were all common on leeward sides of these two cays, and so all four taxon groups were used for within-leeward (outer-to-inner and front-to-back) and leeward-to-windward transplant treatments. Because only algae predominated in windward locales, they were the only group used for within-windward and windward-to-leeward transplants.

We photographed each transplant immediately after the experiment was set up (18 June 1992), 16 d later (4 July), and once again on 27 December 1992. We examined the transplants for survivorship (but did not photograph them) 34 d later, on 22 July 1992. Photographs were digitized to quantify survivorship and change in percentage cover of each transplanted species. We recorded percentage cover of the two most common species within the transplanted species group, which together normally accounted for >75% cover on the section. We also recorded the incidence and amount of overgrowth of the transplants by other epibionts. We terminated the experiment in late December 1992, when root sections were beginning to disintegrate.

Results

At the beginning of the experiment, the single dominant species on each root accounted for 58 ± 23% of the epibiont cover on each section (all roots pooled). However, there were significant differences among species groups (sponges = algae > anemones > ascidians) in degree of dominance by the most abundant species on the root section (MS = 30 830, $F_{3,212} = 8.746$, $P < 0.001$, ANOVA). Dominant species on sponge roots and algae roots accounted for 65 ± 21% and 63 ± 21%, respectively. *Aiptasia* covered 53 ± 25% of their root transplants. Dominant ascidians covered 48 ± 21% in that group of transplants. The second most abundant species (algae, sponge, and ascidian roots only) covered 19 ± 13% of each root section, and there were no differences among species groups in the abundance of these subordinate taxa (MS = 847, $F_{2,88} = 1.220$, $P = 0.300$, ANOVA).

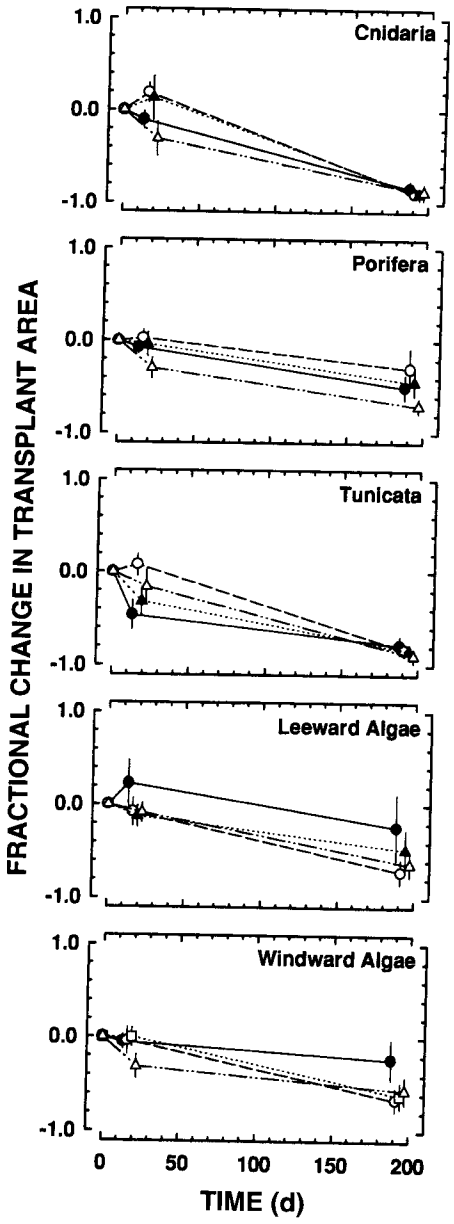

FIG. 9. Performance of epibiont transplants over 6 mo. A value of 0 indicates no change in area of root occupied; a value of −1 indicates that the colony disappeared completely. Values shown are means ±1 SE; $N = 12$ per point. Solid circles, controls; open circles, front-to-back; open triangles, outer-to-inner; solid triangles, leeward-to-windward; open squares, windward-to-leeward (bottom panel only).

Within the first 16 d of the experiment, many transplanted epibionts grew (Fig. 9), indicating little transplant shock. However, there were no significant differences in 16-d percentage cover changes (angular-transformed data) among species groups (MS = 0.600,

$F_{3, 287} = 1.194$, $P = 0.312$), treatments (MS = 1.297, $F_{3, 287} = 2.579$, $P = 0.06$), or group × treatment interaction (MS = 0.169, $F_{9, 287} = 0.336$, $P = 0.962$). Likewise, there was no apparent site effect on relative change (pooled over species groups and treatment) in transplant percentage cover (cay × exposure interaction, MS = 0.284, $F_{2, 300} = 0.563$, $P = 0.640$). Few transplanted epibionts died between the establishment of the experiment in mid-June and late July. On 22 July, 90% of the anemone and sponge transplants, 88% of the algal transplants, and 81% of the ascidian transplants still had the original dominant taxon on the root sections (no difference among species groups: $\chi^2 = 2.764$, df = 3, $P = 0.429$, G test).

Between July and December, all dominant species in all treatment classes declined in percentage cover. This decline (relative to initial percentage cover) was not affected significantly by site of transplant (Peter Douglas or Twin Cays), original exposure of transplant (windward or leeward), type of transplant (front-to-back, outer-to-inner, leeward-to-windward, or windward-to-leeward), or any interaction between these factors ($P > 0.2$, all manipulated sources of variation, parametric ANOVA on rank-transformed data [Seaman et al. 1994]). However, the magnitude of this decline did vary significantly among species groups (Fig. 9). Of their original percentage cover, dominant sponges lost 50 ± 27%, dominant algae lost 58 ± 62%, dominant ascidians lost 84 ± 26%, and *Aiptasia* lost 88 ± 22% (MS = 24 205.4, $F_{3, 140} = 8.427$, $P < 0.001$, parametric ANOVA on rank-transformed data, followed by Tukey's HSD post-hoc test for multiple comparisons among means).

The second most abundant species on each root at the start of the experiment also declined in area between July and December (17 ± 187% loss in area), but there was no relationship between the decline of the subordinate species and any of the treatment variables ($P > 0.4$, all manipulated sources of variation, ANOVA on rank-transformed data). To distinguish whether small, sub-dominant (possibly younger) colonies and large, dominant (possibly older) colonies responded differently to the treatments, initial colony size (percentage cover) was used as a covariate in an ANCOVA assessing relative change in percentage cover June 1991–December 1991 as a function of transplant treatment. Initial colony size was not a significant predictor of final relative change for either dominant taxa (MS = 8109, $F_{1, 211} = 2.658$, $P = 0.105$) or secondary taxa (MS = 1105, $F_{1,82} = 2.239$, $P = 0.138$).

As transplanted taxa declined in abundance, other taxa colonized many (69%) root sections. Average growth of invading taxa (52 ± 27%) was not affected significantly by cay, exposure, or transplanted species group ($P > 0.11$, parametric ANOVA on rank-transformed data). There was a tendency for transplants of one species group to be colonized by other species within the same species group ($\chi^2 = 14.62$, df = 9, $P = 0.102$, G test). The most frequent algal colonists were *Enteromorpha flexuosa, Caulerpa racemosa,* and *Halimeda incrassata*; sponge colonists were *Tedania ignis, Ulosa ruetzleri, Haliclona implexiformis,* and *Haliclona curacaoensis*; cnidaria colonists were *Halecium nanum* and *Myrionema amboinense*; and ascidian colonists were *Eudistoma olivaceum* and *Didemnum conchyliatum.* Algal and cnidarian colonists grew significantly faster (MS = 23 314, $F_{3, 146} = 16.130$, $P < 0.001$, ANOVA) than sponge or ascidian colonists. By December 1992, colonizing algae and hydroids had reached 61 and 62% mean cover on transplanted roots, respectively, whereas sponge colonists attained 36% mean cover and ascidian colonists only 28%.

Discussion

The majority of studies of distribution and abundance of benthic species assemblages have focused on relationships between apparent environmental gradients and observed spatio-temporal variation in these communities (reviewed by Field et al. 1982, Clarke and Ainsworth 1993, Warwick and Clarke 1993). Alternatively, spatial or temporal variation in community structure can result from discrete patterning of the landscape (or seascape) resulting in a complex mosaic of species or habitat patches (e.g., Paine and Levin 1981, Connell and Keough 1985, Sousa 1985). The size and complexity of patch geometry can significantly influence larval settlement (Butman 1987, Carleton and Sammarco 1987, Chabot and Bourget 1988, Le Tourneux and Bourget 1988, Bourget et al. 1994) and adult persistence (Menge and Olson 1990). The importance of identifying relevant scales at which community structuring factors operate is similarly clear in terrestrial plant and animal communities (e.g., Allen and Starr 1982, Allen and Wyleto 1983, Kolasa and Strayer 1988, Kolasa 1989, Pickett et al. 1989, Levin 1992).

Mangrove root fouling assemblages on Belizean cays can be considered "patchy" communities that are readily identifiable and manipulable at a number of scales. Mangrove cays within the lagoon complex, separated by one to several kilometres, are trivially recognizable as unique islands, yet nonetheless share a suite of characteristics. Different parts of each cay are exposed to predictable variation in flow, wave action, water depth, and insolation (Table 1). Within each island sector, the thicket of mangrove roots is resolved into concentric bands of roots far from shore and appressed into the peat bank. Each root itself is a patch of hard substrate in an otherwise soft-sediment community. At a still finer scale, ambient conditions (especially water flow and insolation) differ predictably as one moves around the root (Table 1). Our identification of distinct mangrove root fouling communities at each of these scales points to scale-dependent mechanisms structuring them. Given the superficial complexity of these species-rich communities at root and

island scales, individual species and taxon groupings both revealed pattern in assemblage structure.

Although we sampled epibionts at only four cays, we found a clear linear relationship between area available for epibiont colonization (island perimeter) and number of different species encountered along our transects. The slope of the log-log plot (0.23) is, given the sample size, remarkably close to the general area richness relationship found for many island communities (MacArthur and Wilson 1967). However, it is not clear what the "source" assemblage is for these communities. Some species may recruit from nearby coral reef complexes and adjacent seagrass beds, some are ubiquitous constituents of shallow-water fouling assemblages, whereas others are known presently only from mangrove habitats (e.g., Goodbody and Cole 1987, Calder 1991, de Weerdt et al. 1991). Adjacent cays clustered together in terms of species composition (Figs. 5 and 6), indicating that species-sharing via larval transport must occur over relatively short distances.

Most epibiont species encountered were "sparse" (sensu Rabinowitz et al. 1986), with broad ranges but low relative abundances within sites. Early studies into the persistence of chronically sparse plant species in North American prairies indicated that low reproductive output, limited dispersal, and poor germination were not significant factors in either patterns of distribution and abundance or their persistence (Rabinowitz and Rapp 1980, 1981). Rabinowitz et al. (1989) suggested that sparse plant species may persist by maintaining consistently high reproductive output and dispersal in the face of high levels of spatial and temporal environmental heterogeneity. However, environmental heterogeneity is less obvious in the near-shore marine environment than it is in the prairie, and reproductive buffering may be less important in determining marine species distribution and abundance patterns. The importance of dispersal and recruitment in maintaining populations of sparse species has not been studied in physically more homogeneous environments. Our data suggest that larval dynamics—supply and dispersal—may figure prominently in determining epibiont distributions in mangrove systems.

The majority of invertebrate species listed in the Appendix have lecithotrophic larvae that remain in the water column for a very short time (e.g., ascidians, sessile polychaetes, and bryozoa), or sexually reproduce only rarely (sponges: Rützler 1993). These species were sparser than algae, which produce resistant, long-lived spores and are ubiquitous on leeward and windward coasts (Table 2, Fig. 8). Bingham (1992, 1995) found that Florida mangrove root communities similarly are dominated by species with short-lived larvae. There, larval recruitment to and community development on bare mangrove roots are very slow and highly patchy.

Within cays, leeward coasts and individual roots were much more species-rich than windward coasts (Table 2) and roots (Figs. 2 and 3). Precise species composition varied dramatically in space and time at both of these scales (Table 4, Appendix), but exposure was the key variable linking communities (Figs. 5 and 6). Exposure also was the most reliable predictor of percentage cover of all taxon groupings. Roots on protected, leeward coasts were dominated by massive sponges, ascidians, large anemones, and occasionally fleshy algae, whereas roots on high-energy windward coasts were dominated by small hydroids and filamentous and fleshy algae (Figs. 7 and 8). Despite changes in the relative abundances of individual species between sampling dates, these large-scale dominance patterns remained consistent throughout 1991–1992. Our transplant experiments showed that over short time scales (<6 mo), adult epibionts could survive in habitats where they were not otherwise encountered (Fig. 9). With the exception of water flow rates and summer temperatures, few environmental factors differed significantly among leeward or windward sites or cays. This evidence implies that environmental differences alone cannot adequately explain patterns of adult distribution. Such patterns could result from flow-dependent failure of algal spores and invertebrate larvae to arrive at sites where adults were not normally found, or from failure of arriving spores and larvae to successfully settle and grow on existing mangrove roots. Analysis of size-specific performance of transplanted adults indicated no size-dependent responses to treatments. This result suggests that early post-settlement events are less important than recruitment in determining patterns of epibiont distribution. Finally, rapid turnover of short-lived adults could result in patchy distribution patterns, but other studies have shown that most mangrove root epibionts are relatively long-lived (Sutherland 1980, Bingham 1995).

At longer time scales, seasonal climatic changes, accompanied by increased rainfall, sedimentation, and reduced water temperature affect local epibiont abundances. Goodbody (1961*b*) reported mass mortality of Jamaican ascidians and sponges following heavy rains. Rützler (1987) observed seasonal degeneration of didemnid ascidians on settling plates at Twin Cays, while sponges persisted for two years. Bingham (1995) found similar seasonal dynamism in Florida. At Lark Cay, further south in the Belize lagoon complex, we observed severe mortality of root-fouling ascidians, sponges, and fleshy algae, and concomitant rapid growth of filamentous and coralline algae in the winters of 1989 and 1990, coincident with the onset of winter rains (A. M. Ellison and E. J. Farnsworth, *unpublished manuscript*). Although it is problematic to infer trends from the two-date sampling regime in this study, our inter-season surveys, as well as the overall decline on our transplanted root sections in species percentage cover between June and December paralleled our observations at Lark Cay. Despite fluctuations in individual species abundance, dominance relationships be-

tween taxon groups remained consistent from year to year between windward and leeward sites. Likewise, most species colonizing marked roots at Lark Cay during the spring recoveries had previously occupied the site: new species rarely recruited from outside Lark Cay (A. M. Ellison and E. J. Farnsworth, *unpublished manuscript*). Many subtidal root epibionts are sensitive to sudden changes in water conditions (Ellison and Farnsworth 1992), although some *Haliclona* spp. and *Perophora* spp. at Twin Cays can tolerate modest oscillations in salinity and temperature (de Weerdt et al. 1991, Goodbody 1994). Thus, the relationship between larval processes and differential adult tolerances of changing physical conditions in controlling within-cay root epibiont community structure will likely depend in part on the timing of sexual reproduction in these species relative to seasonal changes in climate.

Considering still smaller spatial scales, hanging and ground roots, as well as inner and outer roots, had similar numbers of species (Table 2, Fig. 7). However, similarity in epibiont species composition between roots within transects ranged from 12 to 25% (Fig. 4), and showed 2–3 m oscillations. The relatively low similarity between roots separated by only 1 m implies that species composition on any given root may represent the outcome of a lottery-type model of colonization and coexistence (sensu Sale 1977, Chesson and Warner 1981), while the 2–3 m periodicity of peaks in similarity may reflect average larval transport distances.

Within transects, additional patterns were apparent when we considered species groups. Roots further from shore received twice as much sunlight as roots close to the peat bank, and fronts of roots were brighter than backs of roots; both algal species richness and percentage cover consequently were higher on outer roots and fronts of roots (Table 2, Fig. 8). Presence of other species groups made up of sessile suspension- or filter-feeders did not correlate with light availability. Algal species richness was also higher on hanging roots (Fig. 7). Taylor et al. (1986) demonstrated experimentally that herbivorous urchins cannot climb onto hanging roots, which thus provide refuges from predation for fleshy algae. The general importance of herbivory and predation in determining epibiont species distribution and abundance remains to be investigated.

Conclusions

This study demonstrates that species composition of an individual mangrove root is the product of processes occurring at a number of scales. Larval behavior and longevity may limit the identity of species that can recruit to certain locales. Frequent sampling of invertebrate larvae at a variety of scales and very long-term monitoring of marked natural roots as an alternative to artificial settling plates are required to elucidate species-specific trajectories and spatio-temporal changes in community structure (Bingham 1995). With sporadic colonization and disturbance events, the species composition of an island may change over several years, yet assembly rules governing which species groups predominate appear to be stable. Seasonal or periodic disturbance can remove certain members of species assemblages, as we witnessed with the decline in massive sponge abundance between 1991 and 1992. In turn, these perturbations create space for new colonists, which come largely from local sources. Within an island, epibionts may spread from root to root, increasing in local commonness, as larvae are released and resettle over a distance of a few metres. Within the root, coexistence may be promoted by microclimate variability, preferential herbivory, or be discouraged by competition and overgrowth. Determinants of community structure are challenging to identify in complex, species-rich assemblages like the ones studied here. An analytical perspective encompassing a range of spatial and temporal scales is recommended.

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APPENDIX

Species found (checks indicate species present) on mangrove roots along 50-m transects at the four cays during the summer of 1992. Roman numeral subscripts (I–V) indicate the five most common species (in terms of number of roots occupied) during 1991 (I is most common); Arabic numeral subscripts (1–5) indicate the five most common species during 1992 transects (Crustose coralline algae, *Bostrychia* spp., and Cyanobacteria, each of which occurs on virtually every root, are excluded from this tally). Roman numeral superscripts (I–V) indicate the five most abundant species (in terms of average percentage cover) during 1991 (I is most common; no data for the east windward site at Twin Cays for 1991); Arabic numeral superscripts (1–5) indicate the five most abundant species during 1992 transects. The designation spp. indicates more than one species in a genus occurred at all checked sites; see footnotes for the list of those species. Nomenclature for algae follows Littler et al. (1989), sponges follow Wiedenmayer (1977), de Weerdt et al. (1991), and Rützler and Smith (1992); hydroids follow Calder (1988, 1990, 1991); isopods follow Kensley and Schotte (1989); bivalves follow McLean (1951); all others follow Sterrer (1986).

	Twin Cays					Spruce Cay		Wee Wee Cay		Peter Douglas Cay	
Taxa	West lee-ward	East lee-ward	Hidden Creek	West wind-ward	East wind-ward	Lee-ward	Wind-ward	Lee-ward	Wind-ward	Lee-ward	Wind-ward
Cyanobacteria											
Scytonema polycystum	√	√	√	√	√	√	√	√	√	√	√
Chlorophyta											
Acetabularia crenulata	√	√									√
Bryopsis pennata var.	√	√	3√		√	√	4√	√	II,5√IV	√	III,√V
Caulerpa mexicana	√	√	√		√		√			√	
Caulerpa paspalloides						√				√5	
Caulerpa racemosa	√	√	√	√1	√		√IV	√		√	√1
Caulerpa sertularioides		√									
Caulerpa taxifolia		√					√	√			√
Caulerpa verticillata	√			√							
Codium spp.*						√	√	√	√3		√
Dasycladus vermicularis		√		√			√				
Dictyosphaeria spp.†		√		√			√		√		
Enteromorpha flexuosa	√	I,5√	√	III,2√	5√	3√	II,2√V	√	3√	III,2√	I,1√II
Halimeda incrassata	√	√	√		√	√		√V	√		
Halimeda tuna		√									
Halimeda opuntia	√		√3		√		√III				
Neomeris annulata	√			4√					√		√
Ulva fasciata		√	√	√		√	√	√	√		√
Valonia macrophysa	√2	√2		√		√5		√3			√
Ventricaria ventricosa				√		√	√	√			√
Udotea sp.		√5				√2	√3				
Phaeophyta											
Dictyota cervicornis		√	√1	√2	√3		√1	√	√		
Dictyota divaricata	√1	√3		V√		√1		√1	√	√1	√III,2I
Lobophora variegata			√	II√II	√						√
Padina sanctae-crucis		√		√			√5	√	√V		√
Rhodophyta											
Acanthophora spicifera	√	√	√	√V	√	√	√	√	√2	√	V,4√IV
Asparagopsis taxiformis		√	√		√						
Bostrychia spp.‡	√	√	√	√	√	√	√	√	√	√	√
Ceramium nitens	√	II√	5√4	I,5√III	√4	2√	√		III,4√III	√	√
Coelothrix irregularis								√			√
Crustose coralline algae	√	√	√5	√	√	√	√	√	√5	√4	√
Galaxaura oblongata				√		√					2√
Jania adherens	√	IV,1√II		√			√	√5			
Laurencia intricata	√			IV,3√			√		√		5√
Spyridia hypnoides							√				
Wrangelia spp.§	√	III,2√I	II,2√IV	1√IV	II,1√1	IV,4√IV	1√1	5√2	I,1√I,1	3√IV	IV,3√
Porifera											
Adocia amphioxa			√		√	√			√		
Amphimedon compressa	√		√		√	√	√	√	√	√	
Amphimedon viridis		√	√		√			III√	√	√	
Biemna microstyla	√		√		√	√	√				
Biemna tubulata			√			√	√	√		√	
Cinachyrella apion										√	
Clathrina coriacea	√		√		√	√	√	√	√	√	
Dysidea etheria						√					
Geodia papyracea				√3		√	√	√		√V	
Haliclona curacaoensis	II,3√III	√	V√		V√	III√	√	I,3√II		√	
Haliclona implexiformis	√	√	I,√V			√III		√	√	√	
Haliclona magnifica	√		√								
Haliclona manglaris	√										

APPENDIX. Continued.

Taxa	Twin Cays					Spruce Cay		Wee Wee Cay		Peter Douglas Cay	
	West lee-ward	East lee-ward	Hidden Creek	West wind-ward	East wind-ward	Lee-ward	Wind-ward	Lee-ward	Wind-ward	Lee-ward	Wind-ward
Haliclona mucifibrosa			√								
Haliclona pseudomolitiba	√		√								
Haliclona tubifera			√								
Ircinia felix	√	√	√			√		√		√	
Leucetta microraphis		√									
Lissodendoryx sp.	V√	√	III√			II√	√			√	
Mycale microsigmatosa										√	
Niphates erecta		√	√		√	√	√			√	
Spirastella sp.	5√	V√IV	√		III√	√	√	V,2√IV	√	V√	
Tedania ignis	√IV	√III	√III		√	5√II		√		√	
Ulosa ruetzleri	√V	3√	√1							IV,5√	
Cnidaria (Hydrozoa)											
Dynamena crisioides	√	√V	1√	√I	IV,2√	I,1√II	II,3√II	IV,1√I	IV,2√II,4	√III	√I
Halecium nanum							√	√		√	
Millepora alcicornis								√			
Myrionema amboinense						√3	IV√				√4
Tridentata turbinata							√				√
Cnidaria (Anthozoa)											
Aiptasia pallida	IV,2√I	√	√II			√	√	√		II,4√3	
Bartholomea annulata		√		√4							
Bunodeopsis antillensis						√					
Diplora strigosa					√						
Palythoa caribaea						√		√III			
Porites astreoides				√5	√5	√					
Annelida											
Spirorbis formosus	√					√	√	√		√	√
Sabellidae	√	√	√			√			√	√	
Serpulidae		√	√		√			√	V√	√	
Crustacea (Cirripedia)											
Balanus eberneus	√					√4	√	√		√	
Chthamalus angustitergum	√		√	√	√	√	√	√	√	√	II√
Crustacea (Isopoda)											
Phycolimnoria clarkae	√	√	√	√	√	√	√	√	√	√	√
Mollusca (Bivalvia)											
Crassostrea rhizophorae	√	√	√		√	√	√4	√		I,1√	√
Chama macerophylla						√		√		√	
Isognomon alatus		√1	√				√			√	
Teredinidae (shipworms)	I,1√II	√	IV√			√V		√		√	
Bryozoa	√	√				√	√	√		√	
Chordata (Tunicata)											
Ascidia nigra	√	√								√	
Botrylloides nigrum	√3	√	√		√2	√		√4		√2	√5
Botrylloides sp.	√										
Didemnum conchyliatum	4√	4√	√			√	V√	II√		√	
Didemnum psammathodes	√										
Diplosoma glandulosum	√	√4	√2			√	√	4√		√	
Diplosoma listerianum							√			√	
Distaplia corolla	III√4	√	√		4√		√2			√	
Ecteinascidia spp.‖	√5		√			V√	√				
Eudistoma olivaceum		√	√			√	5√		√	√	
Microcosmus exasparatus	√									√	
Perophora bermudensis	√	√	4√		I,5√						√3
Perophora viridis	√	√	√		√					√	
Tridemnum savignyi		√					√			√	

* Includes *Codium intertextum* and *C. repens.*
† Includes *Dictyosphaeria cavernosa* and *D. ocellata.*
‡ Includes *Bostrychia montagnei* and *B. tenella.*
§ Includes *Wrangelia argus* and *W. penicillata.*
‖ Includes *Ecteinascidia turbinata* and *E. minuta.*