

FIGURE 1. Map of research area. The Twin Cays and Pelican Cays ranges are circled.

## MATERIALS AND METHODS

### EXPERIMENTAL DESIGN

Sampling of Pelican Cays and Twin Cays was conducted during May 2008. The sampling design was a split-plot in which the main plot was disturbance type (fixed effect) and the subplot was spatial position relative to the shoreline (fixed effect). Two disturbance levels were designated: undisturbed and disturbed. Undisturbed, reference areas exhibited no visible signs of human activity. Disturbed areas were characterized by removal of mangroves by clear-cutting followed by deposition of dredged marine sediment. Islands with a disturbed area of this type were identified initially by aerial photography. Four islands were selected for soil sampling based on disturbance history and accessibility: one in the Twin Cays range (East Island) and three in the Pelican Cays range (Manatee, Fisherman's, and Ridge Cays). Extent of natural and disturbed areas at each study location was estimated from satellite imagery (Landsat 7, May 2008; <http://landsat.usgs.gov>) and aerial photographs (April 2006, 2007; I. C. Feller, unpublished) and confirmed by ground-truthing (May 2008).

At each island, two transects were established perpendicular to the shoreline and traversing the island to a distance of 100 m inland. One transect was located in the disturbed area and the other in an adjacent undisturbed forest. Fourteen to sixteen sampling stations were preselected along each transect in a stratified-random design; that is, two to four stations occurred within each of five intervals (0–10, 11–30, 31–50, 51–70, and 71–100 m from the shoreline). In the disturbed areas, some portions were not clear cut (but may have been buried by dredged fill) or were clear cut and remained free of dredged fill; these zones were sampled as well. The reference transect originated along the same shoreline and was oriented in the same direction as the disturbed transect, although the length was not always the same (as a consequence of variation in island configuration). Each island was considered to be a replicate block.

At each sampling station, percent cover of herbaceous vegetation and mangrove canopy was estimated visually. The following soil variables were measured: bulk density, texture, shear strength, organic matter content, particle size distribution, and aggregate stability (as described below). A surface core (30 cm depth) was also collected at each disturbed island to determine the thickness of dredged material. Also, deeper cores were collected at one island at Twin Cays (West Island) and one undisturbed island in the Pelican Cays (Cat Cay) to determine the stratigraphy and composition of deposits beneath these islands.

### ANALYSES

#### *Soil Shear Strength*

Soil shear strength was determined with a Torvane device (H-4212 1, Humbolt Manufacturing Company, Durham Geo-Enterprises), which measures the torque required to shear or deform the soil (McGinnis, 1997). Soil strength was measured at the soil surface, and the only selective criterion was flatness, because the Torvane required a flat or nearly flat surface for accurate measurements. Five replicate measurements were made at each sampling station and averaged.

#### *Soil Aggregate Stability*

Duplicate soil cores (2 cm diameter  $\times$  10 cm long) were collected at each station. The cores were carefully extruded onto a board, and the upper 1 cm was severed with a knife, providing a total soil volume of 3.14 cm<sup>3</sup> per sample. One core was used for stability testing and the other was placed into a Ziplock bag for determination of soil bulk density and texture (described below).

Soil aggregate stability was determined based on a modification of standard methods (Angers and Mehuys, 1993; Herrick et al., 2001) to better assess the substrates (peat, marine sediment) and the types of erosive forces (waves, currents) typical of the mangrove habitat. In the field, cores were placed in collection boxes, which protected them from disturbance until processing. Because the soils in this study were naturally moist to saturated, samples were not dried before measurement. Each core was transferred to a sieve (#20 mesh, 850  $\mu$ m) and gently lowered into a container of water, then scored as to initial structural integrity. The core was then gently agitated by repeated dipping (five times) in water and again assessed. Initial stability (based on slaking or disintegration of the core) was scored as 0 (soil too unstable to sample), 1 (50% of structural integrity lost upon immersion or less than 10% of soil remained on sieve after five dips), 2 (10%–25% of soil remained), 3 (25%–75% of soil remained), or 4 (75%–100% of soil remained). After initial assessment, 200 mL water was poured over the sample; the material remaining on the sieve and that washed through the sieve (including the portion from the initial assessment) was transferred to separate bags for drying and weighing. Samples were oven dried at 60°C for 24 h and weighed. The percent by weight of material retained on the sieve was calculated. These two measures were designated as Stability Index 1 and 2, respectively.

### Soil Water Content, Bulk Density, and Texture

At the laboratory, the soil was weighed wet, dried at 60°C to constant mass, and reweighed to determine moisture content (percent water in soil sample). Dry bulk density was calculated by dividing the dry mass by the volume ( $\text{g cm}^{-3}$ ). The dried soil was ashed at 550°C for 6 h to determine mineral mass after organic loss on ignition. Percent organic matter content was calculated as 100 minus the percent ash. Particle size distribution (PSD) was determined (only for mineral sediments) based on a micropipette method (Burt et al., 1993). Subsamples (three or four) collected within each zone along a transect were combined to provide sufficient mass for PSD.

### Peat Coring

Deep cores were collected to the point of refusal with a Russian peat corer, which extracts uncompressed cores in sections 0.5 m long (McKee et al., 2007a). At Twin Cays, seven cores were collected across a transect traversing West Island (west to east) to depths to 10.8 m. At Cat Cay, nine cores were similarly collected, but the maximum depth was 1.5 m because the peat layer was thinner. A deep core was also collected at Manatee Cay (disturbed area). Each core was extracted and transferred to a half-section of polyvinyl chloride (PVC) pipe, wrapped with plastic wrap, and refrigerated until processing. At the field station, each core section was logged, photographed, and thicknesses of major strata measured. Subsamples were taken at intervals of approximately 10 cm and washed

on a 1 mm mesh sieve; plant fragments were identified to species using a key as described previously (McKee and Faulkner, 2000). At all disturbed sites, shallow cores (5 cm diameter  $\times$  30 cm deep) were collected with a piston corer to determine the thickness of the dredged fill.

## RESULTS

### GENERAL OBSERVATIONS

Large areas of Twin Cays, Fisherman's Cay, Manatee Cay, and Ridge Cay were clear cut (Table 1), and marine sediment had been dredged from a nearby reef flat and pumped to the island interior. Scars on the seafloor were visible from the air (Figure 2), showing that large areas (0.6 to 1.0 ha) of reef flat had been disturbed. The mangrove areas disturbed at these four study sites varied from 1.0 to 6.2 ha, accounting for up to 34% of the mangrove area per island (Table 1). In most cases, the woody debris from clear-cutting had been burned and only stumps remained to mark the past presence of mangrove trees. All four disturbed sites had received varying amounts of dredged marine sediment that had created a relatively flat, homogeneous landscape of dry, highly reflective, inorganic substrate (Figure 3). The dredged material varied in depth from 12 to 25 cm and contained coral, shells, and sand that indicated the marine origin of the materials. All the sites examined at the Pelican Cays were filled with material dredged from nearby reef flats, as evidenced by the presence of carbonate sand (*Halimeda* spp.), shells, and coral fragments. At Twin Cays, the dredged fill was composed of

**TABLE 1.** Summary of natural and disturbed mangrove areas at two island ranges: Twin Cays (East and West) and Pelican Cays (Manatee Cay, Fisherman's Cay, and Ridge Cay). A dash (–) indicates data were not obtained.

Measurement	Twin Cays		Pelican Cays		
	East Island	West Island	Manatee Cay	Fisherman's Cay	Ridge Cay
Total island area (ha)	41.4	17.6	12.6	24.3	3.4
Undisturbed area (ha)					
Natural ponds	9.8	2.0	4.3	6.2	0.1
Mangrove	28.7	13.0	6.3	11.9	2.3
Disturbed area (ha)					
Clear-cut only	1.2	1.4	–	–	–
Clear-cut + filled	1.7	1.2	2.0	6.2	1.0
Percent disturbed area					
Island	7%	14%	16%	26%	29%
Mangrove only	9%	17%	24%	34%	30%

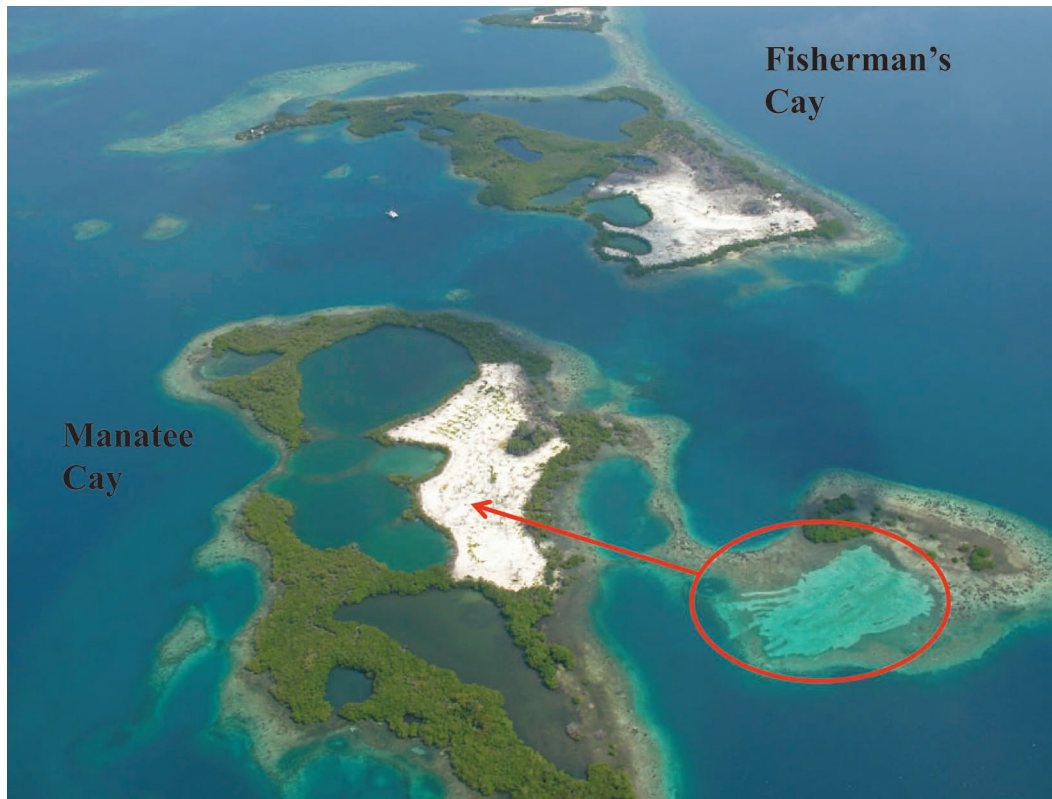


FIGURE 2. Aerial photograph of Fisherman's Cay and Manatee Cay in April 2007 showing mangrove areas that were clear cut and filled with marine sediment dredged from an adjacent reef flat (indicated by red circle and arrow pointing to white filled area on the cay). (Photograph by I. C. Feller.)

quartz sand, indicating a mainland origin. With the exception of a narrow fringe of uncut trees and occasionally a lone tree, no mangrove canopy remained in these disturbed areas. In some cases, dredged material had buried the aerial roots of intact trees along some shorelines, and these trees had subsequently died (Figure 4). At all disturbed sites, mangrove associates (*Conocarpus erectus*) and common coastal beach species were present, but total cover was low (<10%). The most common herbaceous species included *Batis maritima* L., *Sesuvium portulacastrum* (L.) L., *Distichlis spicata* (L.) Greene, *Paspalum distichum* L., *Salicornia virginica* L., *Spartina spartinae* (Trin.) Merr. ex A. S. Hitchc., *Rhabdadenia biflora* (Jacq.) Muell.-Arg., *Cyperus* spp., *Ipomoea pescaprae* ssp. *Brasiliensis* (L.) van Ooststr., *Ageratum littorale* Gray, and *Typha* sp. In unvegetated areas, a biological crust of unidentified composition had sometimes formed a thin surface layer on top of the dredged fill.

In contrast, the reference sites contained intact mangrove canopy (dominant species = *R. mangle* with subdominants = *Avicennia germinans* (L.) L. and *Lagun-*

*cularia racemosa* (L.) Gaertn. f.), low herbaceous cover (<5%; most commonly *B. maritima*), and undisturbed substrate that was dark in color, saturated with water, and composed of live and dead mangrove roots and other organic matter. Abundant aerial roots of intact mangrove vegetation (prop roots and pneumatophores) formed an interlacing network that contributed to the overall structural integrity of the reference areas and also served as substrate for a variety of epiphytes and epibionts. The forest floor was usually covered by algal-microbial mats (Rhodophyta, Chlorophyta, Cyanophycota, Bacillariophyta), typical of mangrove forests in this region (K. L. McKee, unpublished data).

#### SURFACE SOIL CHARACTERISTICS AND EROSION POTENTIAL

Major differences in surface soil characteristics and potential for erosion occurred between reference and disturbed areas (Table 2). The surface soil of reference forests was peat composed of a matrix of live and dead mangrove roots, filamentous algal-microbial mats, and



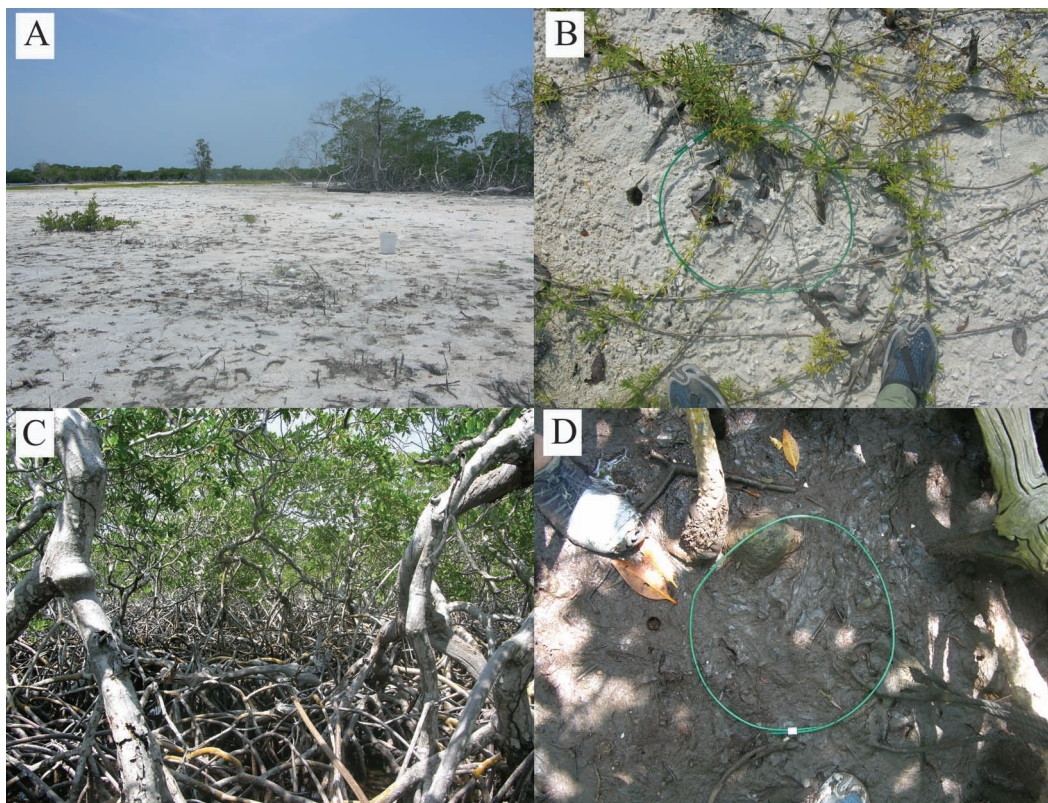


FIGURE 3. Views of disturbed (upper panels, A and B) and reference (lower panels, C and D) areas showing detail of soil surfaces. A circular quadrat in panel D ( $0.1 \text{ m}^2$ ) provides scale.

trapped organic matter that retained its structural integrity even when disturbed by sampling. Bulk density was low ( $0.17 \text{ g cm}^{-3}$ ), and water (68%) and organic contents (60%) were high. Despite its organic nature, the reference soil (peat) had high shear strength (overall mean,  $0.084 \text{ kg cm}^2$ ), which varied little spatially (Figure 5). Core samples retained their shape and showed little or no slaking upon immersion in water (Stability Index 1 = 3.98) and little loss of material upon repeated agitation (Stability Index 2 = 87%). When stability indices were plotted as  $x$ - $y$  coordinates, the reference sites grouped together, indicating little difference among islands (Figure 6).

In contrast, the surface soil in disturbed areas was composed of inorganic carbonate particles derived primarily from calcareous algae (*Halimeda* spp.), coral fragments, and shells (PSD showed that >90% of the mass was sand or larger particles). This material had a high bulk density ( $0.72 \text{ g cm}^{-3}$ ) and low water content (30%) and organic content (9%). Soil shear strength ( $0.044 \text{ kg cm}^2$ ) in disturbed areas was lower overall compared to reference areas and varied spatially (see Figure 5). Aggregate stability was lower overall (Stability Index 1 = 2.14, Sta-

bility Index 2 = 47%), and differed among island locations (see Figure 6). Many cores were friable and readily disintegrated when disturbed mechanically. Where vegetation or biological crusts had developed on the dredged material, the shear strength was higher, but aggregate stability remained low; that is, cores typically did not retain their integrity and exhibited a high degree of slaking in water. The mass retained on the sieve was composed of particles greater than 1 mm in diameter (*Halimeda* chips, coral fragments, shells). Shear strength increased overall with increasing distance along some disturbed transects because of the absence of dredged fill at interior stations where the old peat surface remained exposed (e.g., Twin Cays). In such cases, the exposed peat substrate retained high shear strength and high aggregate stability despite the removal of the mangroves.

#### PEAT STRATIGRAPHY

Mangrove islands in the Twin Cays and Pelican Cays ranges were underlain by deposits of peat, varying in maximum thickness from 1.5 m (Cat Cay and Manatee

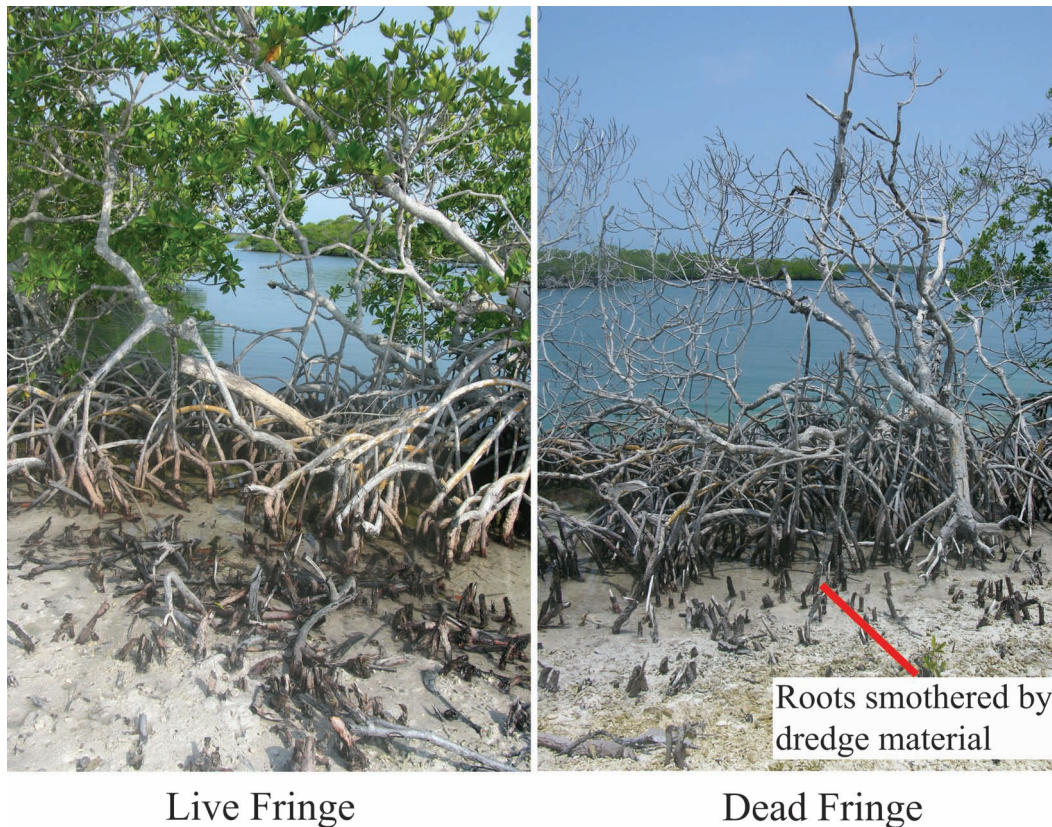


FIGURE 4. Red mangrove trees along the shoreline of disturbed areas: some trees died as a result of burial with dredged fill (right).

Cay) to more than 10 m (Twin Cays) (Figure 7). At Cat Cay, a series of cores traversing the island showed that peat thickness was greatest on the southern, leeward side and decreased toward the northern, windward shore. Botanical matter in the peat consisted predominately of mangrove roots with fragments of leaves and wood. Beneath the peat

layer was sand and/or coral. Deeper peat layers were dominated by *R. mangle*, whereas upper layers (0–50 cm) in the island interior contained remains of *A. germinans*. At Twin Cays, cores across an east–west transect were 7.5 to 10.8 m thick, with two of the cores reaching the limestone platform underlying this range. These cores also consisted

TABLE 2. Summary of analysis of variance (ANOVA) results for soil characteristics. The main plot factor (disturbance) was tested with within-subject error (island); subplot factor (spatial position) and interactions were tested with residual error. Values are the *F* ratio; significance: \**P* = 0.05, \*\**P* = 0.01, \*\*\**P* = 0.001, \*\*\*\**P* = 0.0001, ns = not significant.

Source of error	Shear strength	Aggregate stability		Bulk density	Organic matter	Water content	Vegetative cover	
		Index 1	Index 2				Herbaceous	Mangrove
Disturbance	50.24****	180.0****	86.4****	184.0****	353.2****	350.0****	6.78*	191.3****
Island (block)	6.23**	7.01****	1.93 <sup>ns</sup>	21.2****	5.52**	2.42 <sup>ns</sup>	7.80****	7.95****
Position	1.36 <sup>ns</sup>	4.85**	3.53**	1.23 <sup>ns</sup>	0.68 <sup>ns</sup>	3.02*	1.87 <sup>ns</sup>	1.99 <sup>ns</sup>
Disturbance × position	5.70**	3.95**	1.29 <sup>ns</sup>	6.58****	2.82*	8.67****	1.70 <sup>ns</sup>	1.59 <sup>ns</sup>



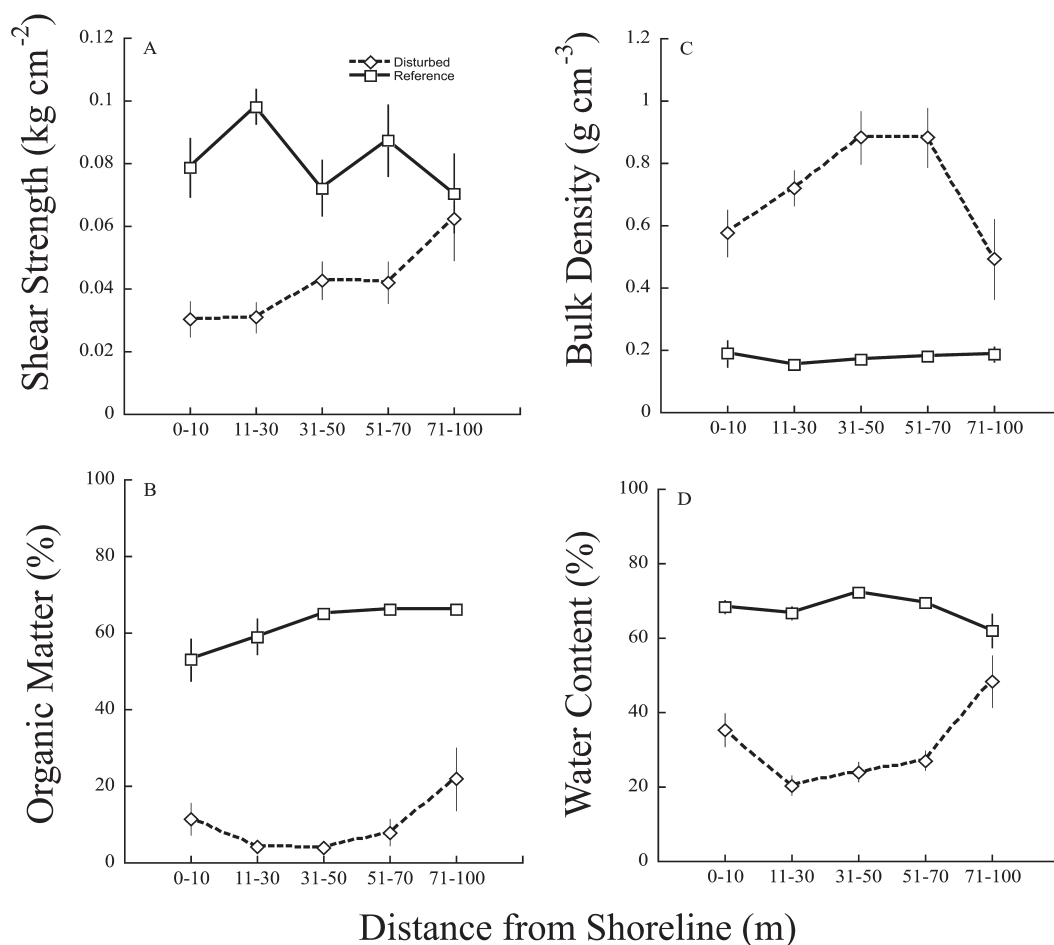


FIGURE 5. Spatial variation in soil shear strength (A), organic matter (B), bulk density (C), and water content (D) in reference (squares) and disturbed (circles) mangrove areas. Values are the mean  $\pm$  SE (note some SE bars are smaller than the symbols).

of mangrove peat, predominately *R. mangle*. In the island interior, surface layers of *A. germinans* peat varied in thickness from 50 to 100 cm, similar to the pattern observed at Cat Cay.

## DISCUSSION

The MBRS is a unique and valuable resource to the Central American countries of Belize, Honduras, and Guatemala ([www.mbrs.org.bz](http://www.mbrs.org.bz); accessed 11 June 2008). Destruction of mangrove islands has rapidly accelerated in this system as a result of attempts to transform these sensitive and fragile habitats into environments more attractive to tourists. Because there are few sand-based islands underlain by shallow limestone platforms and

suitable for development, mangrove-dominated islands have been targeted for conversion. In addition to the two ranges included in this study (Pelican Cays, Twin Cays), other mangrove ranges in the vicinity also have undergone similar mangrove clearing and filling (e.g., Blue Ground Range, Tobacco Range, Coco Plum) (K. L. McKee, personal observation). Survey lines found during this study indicate plans for further development at many of these island ranges.

### EFFECTS OF MANGROVE REMOVAL AND DREDGED FILL ON EROSION

Although the direct and indirect effects of mangrove clear-cutting and marine dredging are many and varied, our study focused on the specific consequences for erosion and

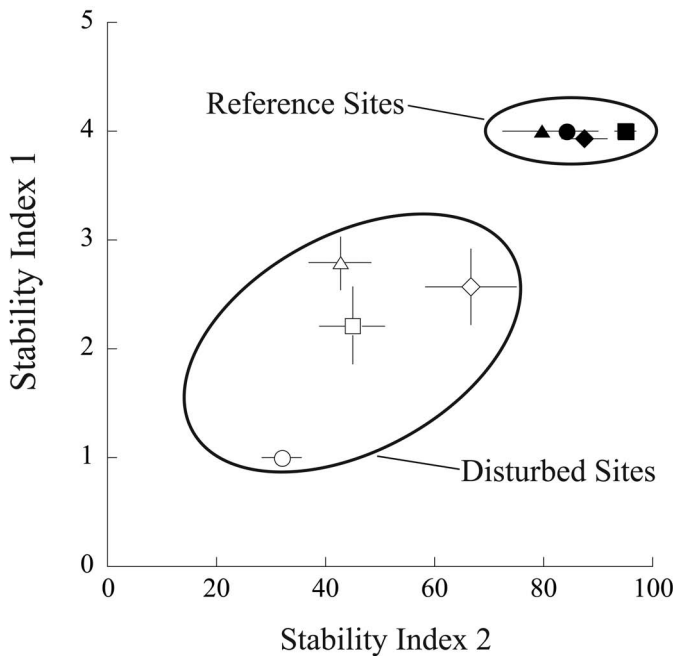


FIGURE 6. Aggregate stability of soils from reference sites (closed symbols) and disturbed mangrove areas (open symbols) at Twin Cays (diamond), Fisherman's Cay (square), Manatee Cay (triangle), and Ridge Cay (circle). Stability indices (mean  $\pm$  SE) are based on maintenance of soil structure upon immersion in water (Index 1) and percent of soil retained on a 850  $\mu$ m sieve (Index 2). Probability ellipses (90% confidence curves) are drawn for each group.

long-term loss of elevation. Removal of mangroves and alteration of the soil surface by dredged fill significantly altered the potential for erosion and substrate stability at Twin Cays and the Pelican Cays. The natural substrate in undisturbed mangroves comprised a strong matrix composed of living and dead fibrous roots as well as filamentous algae, which formed mats on the soil surface. This material was extremely resistant to shearing and retained its integrity even when repeatedly agitated by submersion in water (see Figure 6). Although some interior areas contained natural deposits of flocculent material (e.g., microbial mats) that were soft and friable, they were underlain by solid peat. Work in other locations, such as the Bay Islands of Honduras, found similarly high resistance of mangrove peat soils to shearing (McKee and McGinnis, 2002; Cahoon et al., 2003). These results demonstrate the high resistance to soil erosion afforded by intact mangrove peat.

Removal of mangroves by clear-cutting did not by itself appear to have an immediate effect on soil shear strength or aggregate stability in the areas sampled. In a few cases, clear-cut areas that were not covered by dredged material

were encountered during surveys (e.g., at Twin Cays), and here shear strength was equal to that in reference areas; these were all areas that had been previously occupied by *R. mangle* and had only been altered by removal of trees. Similarly, some mangrove areas in the Bay Islands of Honduras killed by Hurricane Mitch retained shear strength up to two years following mortality because of the strong matrix of *R. mangle* roots forming the peat substrate (Cahoon et al., 2003). However, those areas that had been dominated by *Avicennia germinans* lost soil integrity and collapsed following mortality of the trees. Eventually, however, the lack of live roots and algal mats may lead to loss of shear strength wherever mangroves have been removed.

A review of sediment burial effects on mangroves suggests that some species are more sensitive and may suffer mortality when subjected to excessive rates of sedimentation (Ellison, 1998). We also found that live trees (*R. mangle*) exposed to dredged fill often died—presumably the result of smothering of aerial roots. This outcome was particularly evident where a narrow (<10 m wide) fringe of trees was left intact along the shoreline and the dredged material overflowed into this zone (see Figure 4). In cases where the shoreline tree zone was wider (20–30 m), there was a higher survival. Without a protective mangrove buffer along the shoreline, these islands may rapidly erode. Observations at older sites (Twin Cays) showed rapid shoreline retreat (up to 0.3 m per year) where mangroves had been removed in 1992 (McKee et al., 2007b).

#### LONG-TERM CONSEQUENCES FOR ISLAND STABILITY

Oceanic islands are generally vulnerable to disturbance because of their low-lying position and potential for submergence as well as exposure to tropical storms, hurricanes, and tsunamis that generate strong erosive forces. Mangrove islands in the MBRS have developed and built vertically over thousands of years through deposition of peat derived from mangrove organic matter (McKee and Faulkner, 2000; McKee et al., 2007a). This process occurs in the intertidal zone where abundant mangrove roots are produced and accumulate biomass because of their slow decomposition in the anaerobic environment (Middleton and McKee, 2001). Other biogenic processes include formation of algal and microbial mats on the soil surface (intertidal and subtidal) and carbonate sand formed from calcareous algae (subtidal) in mangrove ecosystems (McKee et al., 2007a; McKee, unpublished data). Growth of mangrove root-algal mats and other biofilms not only contributes to vertical accretion but also stabilizes islands



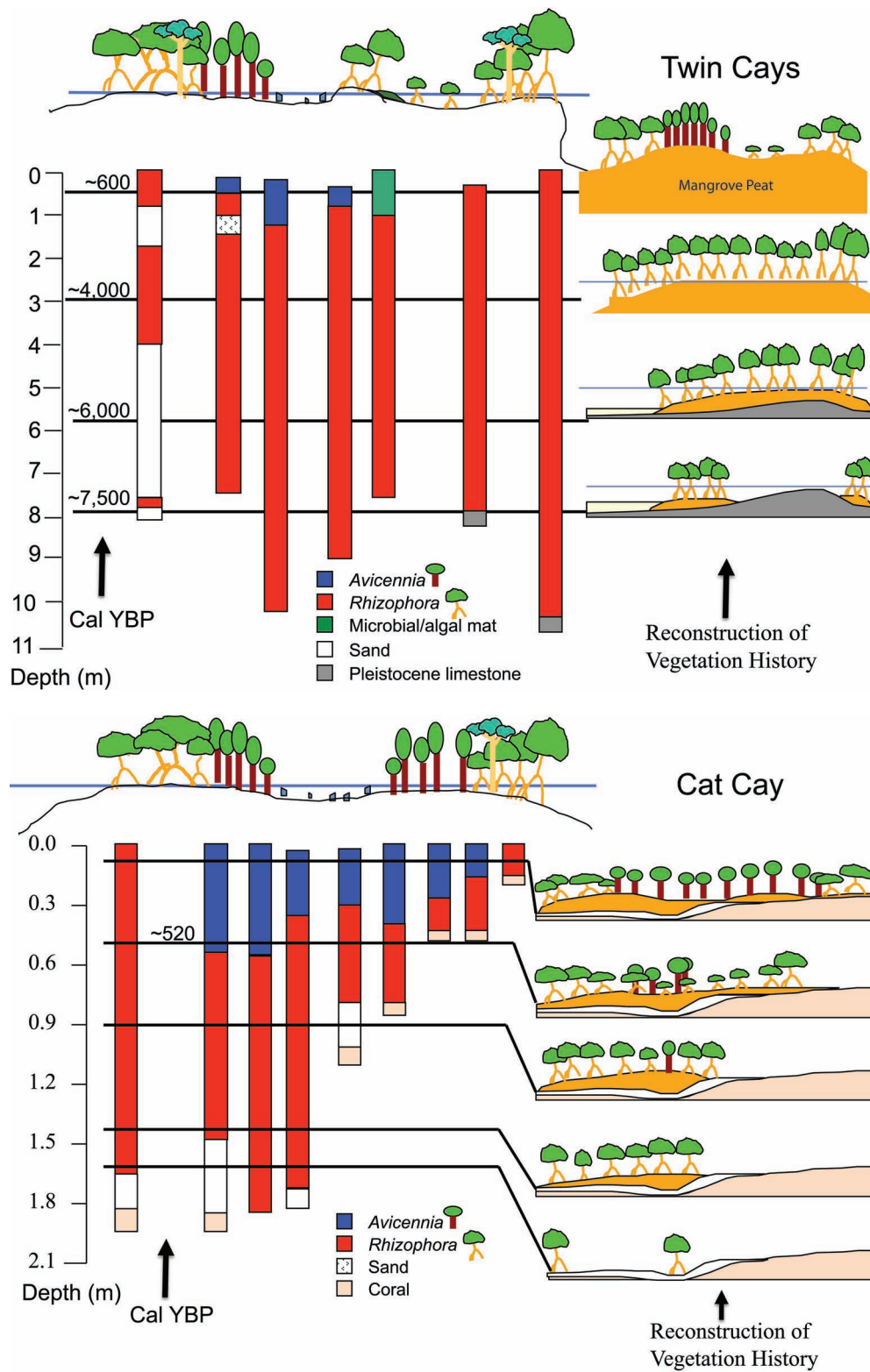


FIGURE 7. Peat stratigraphy across Twin Cays (top) and Cat Cay (Pelican Cays) (bottom) and reconstruction of vegetation history. Radiocarbon dates (calendar years before present [Cal YBP]) are based on previous work (McKee et al., 2007a).

by trapping and consolidating organic and inorganic sediment that is deposited.

To persist, such oceanic islands must accrete vertically to counterbalance both sea-level rise and local rates of subsidence, which vary depending on geomorphology, isostasy, and tectonic movements. Mangrove-dominated islands have the capacity to self-adjust to subsidence and sea-level rise through peat formation. Previous work has shown that mangrove islands in Belize and other Caribbean areas have kept up with changing sea level for thousands of years through the slow accumulation of mangrove roots and other organic material and that vertical building rates are determined by the health and productivity of the mangrove community (McKee and Faulkner, 2000; Middleton and McKee, 2001; McKee et al., 2007a). Peat subsidence rates determined at Twin Cays in vegetated areas averaged  $7 \text{ mm year}^{-1}$  (McKee et al., 2007a). Similar rates of subsidence were found in the Bay Islands, Honduras (Cahoon et al., 2003). Island subsidence combined with eustatic rise in sea level ( $3.5 \text{ mm year}^{-1}$ ; Rahmstorf, 2007) means that the relative rise in sea level in this area is at least  $10.5 \text{ mm year}^{-1}$  (assuming negligible deep subsidence). On undisturbed cays with intact mangroves, vertical building from peat accumulation should maintain surface elevations within the intertidal zone, unless sea-level rise accelerates beyond the capacity of the system to compensate.

Removal of mangroves by clear-cutting eliminates the main mechanism of peat formation and also may alter the environmental conditions necessary for the survival of algal and microbial mats that contribute to sediment trapping and resistance to erosion. Cays disturbed by mangrove clearing and dredged fill deposition will continue to subside, but peat formation will cease. Even if these areas become revegetated with coastal beach vegetation, peat cannot form because of oxidizing conditions (caused by the higher elevations) and lack of the primary peat builder—*R. mangle*. Although disturbed island surfaces have been temporarily raised by dredged fill, the inexorable subsidence of underlying peat and rising seas will lead to submergence. At current rates of peat subsidence and sea-level rise, the elevation gain from dredging will be offset within 20 years.

#### IMPLICATIONS FOR SUSTAINABLE ECOTOURISM

The Caribbean Region, and in particular the MBRS, is a major destination for “eco-tourists,” who are attracted to the tropical climate, clear waters, and abundant marine life (Uyarra et al., 2005; Diedrich, 2007). A prerequisite for sustainable ecotourism is maintenance of a pristine natural environment and protection of all biophysical components necessary for healthy ecosystems and habitat

stability (Casagrandi and Rinaldi, 2002). Unregulated ecotourism enterprises threaten the very features that underpin this industry and, in addition, lead to the degradation of natural resources essential to the livelihood of citizens (e.g., sport and commercial fisheries) (Burger, 2000; Hall, 2001). Although “charismatic” ecosystems such as coral reefs receive much attention by conservationists and tourism regulators (Diedrich, 2007), less emphasis is placed on mangroves. The mangrove destruction occurring in the Belize reef system likely reflects a general misperception that the land beneath mangrove-dominated islands is stable, as well as a failure to recognize mangroves as essential components contributing to habitat stability and marine biodiversity—which is what attracts eco-tourists in the first place (Uyarra et al., 2005).

Our work suggests that the alterations occurring on mangrove islands in the MBRS are inconsistent with sustainable ecotourism. In their natural state, mangroves build a peat substrate that is resistant to erosion and counterbalances subsidence and sea-level rise. In fact, this dynamic peat-building process has allowed mangrove islands such as Twin Cays to persist for the past 8,000 years (Macintyre et al., 2004a, 2004b; McKee et al., 2007a). Attempts to convert mangrove islands to sand islands, with white beaches and coconut palms, will ultimately fail because the underlying peat subsidence and rising seas will eventually prevail. Filling with marine sediment temporarily raises elevations, but without repeated dredging, eventually these cleared areas will become submerged, ultimately reducing the total land area of islands in the MBRS.

Aerial roots of mangroves additionally provide one of the few natural hard substrates for growth of many marine organisms in the MBRS (Ellison et al., 1996; Goodbody, 2000; Macintyre et al., 2000) and also create a permeable barrier that dampens wave energy, decreasing shoreline erosion (Alongi, 2008). Loss of mangrove fringes directly decreases the abundance of marine organisms dependent on mangrove roots for substrate as well as that of reef species dependent on the mangroves as nurseries (Mumby et al., 2004). Although the direct and indirect effects of dredging on reef flats and seagrass beds were not examined in this study, these effects are likely to be substantial, given the sensitivity of such systems to disturbance and sedimentation (Nugues and Roberts, 2003; Erfteimeijer and Lewis, 2006).

Future work should examine the long-term consequences of human activities on the resilience of mangrove islands to global change and the contribution of mangroves to terrestrial and marine biodiversity and fishery productivity. In addition, cost-benefit analyses of man-

grove clearing and dredging and the consequences for sustainable ecotourism should be conducted to provide economic rationales for conservation and management of mangroves and associated habitats.

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#### LITERATURE CITED

- Alongi, D. M. 2008. Mangrove Forests: Resilience, Protection from Tsunamis, and Responses to Global Climate Change. *Estuarine Coastal and Shelf Science*, 76:1–13.
- Angers, D. A., and G. R. Mehuys. 1993. "Aggregate Stability to Water." In *Soil Sampling and Methods of Analysis*, ed. M. R. Carter, pp. 651–657. Boca Raton, Fla.: Lewis Publishers.
- Burger, J. 2000. Landscapes, Tourism, and Conservation. *Science of the Total Environment*, 249:39–49.
- Burt, R., T. G. Reinsch, and W. P. Miller. 1993. A Micro-Pipette Method for Water Dispersible Clay. *Communications in Soil Science and Plant Analysis*, 24:2531–2544.
- Cahoon, D. R., P. Hensel, J. Rybczyk, K. L. McKee, C. E. Proffitt, and B.C. Perez. 2003. Mass Tree Mortality Leads to Mangrove Peat Collapse at Bay Islands, Honduras after Hurricane Mitch. *Journal of Ecology*, 91:1093–1105.
- Cameron, C. C., and C. A. Palmer. 1995. The Mangrove Peat of the Tobacco Range Islands, Belize Barrier Reef, Central America. *Atoll Research Bulletin*, 431:1–32.
- Casagrandi, R., and S. Rinaldi. 2002. A Theoretical Approach to Tourism Sustainability. *Conservation Ecology*, 6:13.
- Diedrich, A. 2007. The Impacts of Tourism on Coral Reef Conservation Awareness and Support in Coastal Communities in Belize. *Coral Reefs*, 26:985–996.
- Ellison, J. C. 1998. Impacts of Sediment Burial on Mangroves. *Marine Pollution Bulletin*, 37:420–426.
- Ellison, A. M., and E. J. Farnsworth. 1992. The Ecology of Belizean Mangrove-Root Fouling Communities: Patterns of Epibiont Distribution and Abundance, and Effects on Root Growth. *Hydrobiologia*, 247:87–98.
- Ellison, A. M., E. J. Farnsworth, and R. R. Twilley. 1996. Facultative Mutualism between Red Mangroves and Root-Fouling Sponges in Belizean Mangal. *Ecology*, 77:2431–2444.
- Erftemeijer, P. L. A., and R. R. Lewis. 2006. Environmental Impacts of Dredging on Seagrasses: A Review. *Marine Pollution Bulletin*, 52:1553–1572.
- Goodbody, I. 2000. Diversity and Distribution of Ascidians (Tunicata) in the Pelican Cays, Belize. *Atoll Research Bulletin*, 480:301–333.
- Hall, C. M. 2001. Trends in Ocean and Coastal Tourism: The End of the Last Frontier? *Ocean and Coastal Management*, 44:601–618.
- Herrick, J. E., W. G. Whitford, A. G. de Soyza, J. W. Van Zee, K. M. Havstad, C. A. Seybold, and M. Walton. 2001. Field Soil Aggregate Stability Kit for Soil Quality and Rangeland Health Evaluations. *Catena*, 44:27–35.
- Macintyre, I. G., I. Goodbody, K. Rützler, D. S. Littler, and M. M. Littler. 2000. A General Biological and Geological Survey of the Rims of Ponds in the Major Islands of the Pelican Cays, Belize. *Atoll Research Bulletin*, 467:13–43.
- Macintyre, I. G., and K. Rützler, eds. 2000. Natural History of the Pelican Cays, Belize. *Atoll Research Bulletin*, 467:466–480.
- Macintyre, I. G., K. Rützler, and I. C. Feller, eds. 2004a. The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change. *Atoll Research Bulletin*, Nos. 509–530.
- Macintyre, I. G., M. A. Toscano, R. G. Lightly, and G. B. Bond. 2004b. Holocene History of the Mangrove Islands of Twin Cays, Belize, Central America. *Atoll Research Bulletin*, 510:1–16.
- McGinnis, T. E. I. 1997. *Shoreline Movement and Soil Strength in a Louisiana Coastal Marsh*. Lafayette, La.: University of Southwestern Louisiana.
- McKee, K. L., D. R. Cahoon, and I. C. Feller. 2007a. Caribbean Mangroves Adjust to Rising Sea Level through Biotic Controls on Change in Soil Elevation. *Global Ecology and Biogeography*, 16:545–556.
- McKee, K. L., and P. L. Faulkner. 2000. Mangrove Peat Analysis and Reconstruction of Vegetation History at the Pelican Cays, Belize. *Atoll Research Bulletin*, 468:46–58.
- McKee, K. L., and T. E. McGinnis. 2002. *Hurricane Mitch: Effects on Mangrove Soil Characteristics and Root Contributions to Soil Stabilization*. USGS Open File Report OFR-02-178. Lafayette, La.: United States Geological Survey National Wetlands Research Center.
- McKee, K. L., J. E. Rooth, and I. C. Feller. 2007b. Mangrove Recruitment after Forest Disturbance is Facilitated by Herbaceous Species in the Caribbean. *Ecological Applications*, 17:1678–1693.
- Middleton, B. A., and K. L. McKee. 2001. Degradation of Mangrove Tissues and Implications for Peat Formation in Belizean Island Forests. *Journal of Ecology*, 89:818–828.
- Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Gorczyńska, A. R. Harborne, C.L. Pescod, H. Renken, C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves Enhance the Biomass of Coral Reef Fish Communities in the Caribbean. *Nature (London)*, 427:533–536.
- Nugues, M. M., and C. M. Roberts. 2003. Coral Mortality and Interaction with Algae in Relation to Sedimentation. *Coral Reefs*, 22:507–516.
- Purdy, E. G., and E. Gischler. 2003. The Belize Margin Revisited: 1. Holocene Marine Facies. *International Journal of Earth Sciences*, 92:532–551.
- Rahmstorf, S. 2007. A Semi-Empirical Approach to Projecting Future Sea-Level Rise. *Science*, 315:368–370.
- Rocha, R. M., S. B. Faria, and T. R. Moreno. 2005. Ascidians from Bocas del Toro, Panama. I. Biodiversity. *Caribbean Journal of Science*, 41:600–612.
- Taylor, D. S. 2000. Biology and Ecology of *Rivulus marmoratus*: New Insights and a Review. *Biological Sciences*, 63:242–255.
- Uyarra, M. C., I. M. Côté, J. A. Gill, R. T. Tinch, D. Viner, and A. R. Watkinson. 2005. Island-Specific Preferences of Tourists for Environmental Features: Implications of Climate Change for Tourism-Dependent States. *Environmental Conservation*, 32:11–19.





# An Overview of Symbiont Bleaching in the Epiphytic Foraminiferan *Sorites dominicensis*

Susan L. Richardson

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**ABSTRACT.** Populations of *Sorites dominicensis*, an epiphytic foraminiferan that possesses dinoflagellate endosymbionts (*Symbiodinium*), were sampled from seagrass meadows located in Florida and Belize and surveyed for evidence of bleaching. Symbiont bleaching was first documented in *S. dominicensis* populations in the Indian River Lagoon, Florida, in August 2003. Subsequent surveys indicated high rates of bleaching in August 2004, followed by a near eradication of the epiphytic foraminiferan population as a result of the 2004–2005 hurricane seasons. Two contrasting sites in Belize, seagrass beds on the reef flat at Carrie Bow Cay and in Boston Bay, Twin Cays, were surveyed in 2005 and 2006. High rates of bleaching characterize the *S. dominicensis* populations living on turtle grass on the reef flat off Carrie Bow Cay, although freshwater runoff from summer storms during the rainy season may trigger localized bleaching events. Moderate rates of bleaching were also observed in *S. dominicensis* populations in Florida Bay in July 2007. Symbiont bleaching in *S. dominicensis* appears to be triggered by multiple environmental factors: increased water temperatures, high levels of irradiance, and influx of freshwater during storm events. Seasonal summer bleaching events may leave already compromised *S. dominicensis* populations vulnerable to periodic disturbance by hurricanes.

## INTRODUCTION

*Sorites dominicensis* Ehrenberg, 1839, is one of several living foraminiferan species that are host to algal endosymbionts (Hallock, 1999; Lee et al., 1979). Benthic foraminiferans with algal symbionts occur in several different clades (Soritacea, Alveolinacea, Nummulitacea, Calcarinidae, and Amphisteginidae) and are widely distributed in shallow-water, tropical to subtropical reef-associated marine ecosystems (Langer and Hottinger, 2000). As a group, foraminiferans host a diverse array of endosymbionts, most of which are microbial eukaryotic taxa, including stramenopiles (diatoms and chrysophytes), unicellular rhodophytes, unicellular chlorophytes, and alveolates (dinoflagellates) (Lee, 2006; Hallock, 1999). Cyanobacterial endosymbionts have also been isolated from two different soritid taxa collected from the Red Sea and the Great Barrier Reef (Lee, 2006). Foraminiferans with photosymbionts possess enhanced calcification rates, as well as endogenous sources of nutrition (algal photosynthates) that allow them to allocate more of their energy resources to cell growth and

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maintenance (Lee, 2006; Hallock, 1999; Duguay, 1983; Kremer et al., 1980; Lee and Bock, 1976). The algal endosymbionts presumably benefit from the mutualism as well, gaining access to nutrients that are scarce in oligotrophic environments and to refuge from predation (Lee, 2006; Hallock, 1999).

The mutualistic association of *Sorites* and other taxa in the more inclusive foraminiferal clade Soritida, with dinoflagellate endosymbionts in the *Symbiodinium* clade, is of particular interest to the marine biological community because this clade comprises the zooxanthellae in stony corals, soft corals, gorgonians, anemones, jellyfish, bivalve mollusks, nudibranchs, sponges, and ciliates (Baker, 2003; Douglas, 2003; Glynn, 1996). Originally considered to be a single pandemic species that was symbiotic with a broad range of marine taxa, *Symbiodinium microadriaticum* is now known to be part of a more inclusive and genetically diverse clade composed of eight major subclades, identified by the letters A–H (Pochon and Pawlowski, 2006; Coffroth and Santos, 2005; Baker, 2003; Rowan, 1998; Rowan and Powers, 1991, 1992). *Symbiodinium* symbionts from foraminiferal hosts are found in clades C, D, F, G, and H, with clades F and H being composed almost exclusively of *Symbiodinium* isolated from soritid foraminiferans (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006; Rodriguez-Lanetty, 2003). Although there is relatively high specificity between *Symbiodinium* clades F, G, and H and Foraminifera, there appears to be very little congruence between host and symbiont phylogenies, indicating that coevolution has not taken place, at least not at the taxonomic levels sampled to date (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006). Although DNA sequences have not yet been obtained from the endosymbionts of either the Belizean or Indian River Lagoon populations of *Sorites dominicensis*, *Symbiodinium* sequences from Florida Keys specimens fall within either clade F (subclade F4) or H (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pochon et al., 2006). In all phylogenies published to date, clade H, the dominant phylotype isolated from the Florida Keys, branches as the sister group to clade C, a clade that is widely distributed in the Indo-Pacific, and exhibits more sensitivity to bleaching than the other *Symbiodinium* clades (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006; Rowan, 1998, 2004).

The morphological characteristics of *Symbiodinium* symbionts isolated in culture from specimens of *Sorites dominicensis* collected from the Florida Keys have been

described by Lee et al. (1979, 1997). Symbionts are distributed throughout the foraminiferal cytoplasm, with the highest densities occurring in the intermediate chambers and the lowest densities occurring in the outer chambers where the digestive vacuoles are concentrated (Richardson, 2006; Müller-Merz and Lee, 1976). Similar to other species of foraminiferans, *S. dominicensis* is multinucleate and possesses two different types of nuclei: generative nuclei that participate in reproduction only, and vegetative nuclei that are transcriptionally active and coordinate the day-to-day activities of the cell (Müller-Merz and Lee, 1976). In *S. dominicensis*, the generative nuclei are localized in the central initial chambers of the test (external shell), which are the chambers with the lowest densities of dinoflagellates, whereas the transcriptionally active foraminiferal nuclei are distributed throughout the cytoplasm in regions with the high symbiont densities (Müller-Merz and Lee, 1976).

Estimates of symbiont population size per cell vary depending on the methodology employed (Richardson, 2006; Doyle and Doyle, 1940). Doyle and Doyle (1940) estimated the population of dinoflagellates in a 2-mm sized individual of *S. dominicensis* to be approximately  $1.6 \times 10^4$  using light microscopy. In contrast, confocal microscopy of a 2-mm sized individual of *S. dominicensis* collected from Jupiter Sound yielded an estimated  $4 \times 10^3$  dinoflagellates, equivalent to a density of  $1.27 \times 10^5$  endosymbionts  $\text{cm}^{-2}$  of cytoplasm (Richardson, 2006) (Figure 1). Hemacytometer estimates of endosymbiont densities in live individuals of *S. dominicensis* collected from Jupiter Sound indicate that symbiont densities range from  $6.1 \times 10^2$  to  $4.8 \times 10^5$  dinoflagellates  $\text{cm}^{-2}$ , with an average of  $6.5 \times 10^4$  dinoflagellates  $\text{cm}^{-2}$  ( $n = 85$ ,  $\sigma = 7.9 \times 10^4$ ,  $\sigma^2 = 6.2 \times 10^9$ ) (Ross and Richardson, unpublished data). Endosymbiont populations linearly increase with test size: the average number of symbionts per foraminiferal cell is estimated to be 1,469 ( $n = 85$ ,  $s = 2,919$ ,  $s^2 = 8,523,907$ ) for an individual with a test diameter of 1.42 mm ( $n = 85$ ,  $s = 0.62$ ,  $s^2 = 0.39$ ) (Ross and Richardson, unpublished data).

Live individuals possess a dark yellowish-brown coloration to their cytoplasm as a result of the dense populations of *Symbiodinium* in each cell (Figure 2). In healthy individuals, the coloration is evenly distributed throughout the test, except for the outer chambers, which appear colorless because of the low density or absence of endosymbionts from the zone of cytoplasm where digestion takes place (Figure 2). The distinctive coloration of the foraminiferal cytoplasm makes it easy to recognize bleached or mottled individuals, as described below.

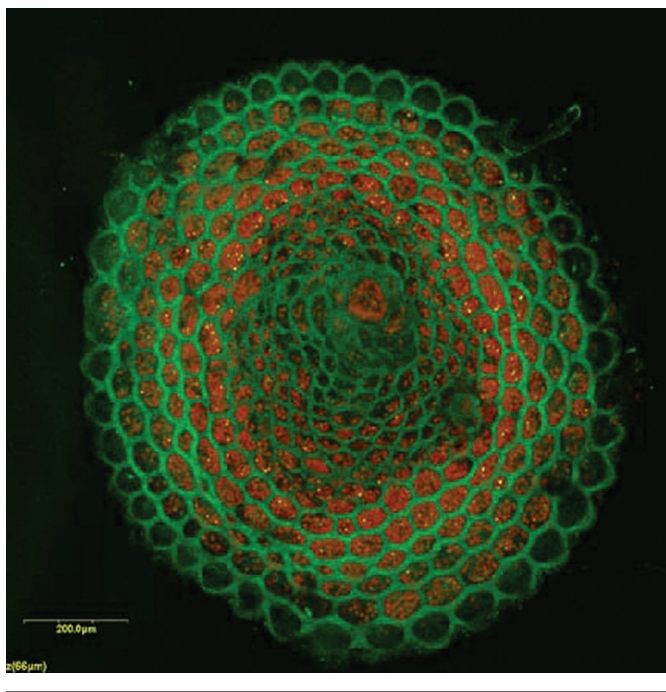


FIGURE 1. Confocal image of live individual of *Sorites dominicensis* from Jupiter Sound, Florida. The foraminiferal test is subdivided into hexagonal chamberlets. The dinoflagellate endosymbionts are most densely packed into the intermediate chambers. Scale bar = 200 μm.

### FIELD OBSERVATIONS OF BLEACHING IN *SORITES DOMINICENSIS*

Symbiont bleaching has been observed in field surveys of epiphytic foraminiferan populations from Florida (Indian River Lagoon and Long Key, Florida Keys) and Belize (Carrie Bow Cay and Twin Cays). Bleaching in *Sorites dominicensis* was first documented in epiphytic populations attached to *Thalassia testudinum* (turtle grass) growing in Jupiter Sound in August 2003 and August 2004, followed by field surveys of populations in Belize in July 2005 and July 2006. Bleaching was also observed in epiphytic populations of *S. dominicensis* surveyed from the Florida Keys in July 2007 (Richardson, unpublished data). Although each of the collecting sites studied hosts seagrass meadows dominated by *T. testudinum*, each locality is subject to different physical factors (salinity, temperature, water clarity, and subaerial exposure), as well as differing levels of anthropogenic impact. Detailed descriptions of the field sites in Florida and Belize are given by Richardson (2006). Although experimental studies of bleaching in *S. dominicensis* have yet to be carried out, field observations

indicate that symbiont bleaching may occur in response to a number of environmental stressors, including increased water temperature, freshwater influx, subaerial exposure during extreme low tides, and periodic disturbance by hurricanes.

### FIELD METHODS

Only epiphytic specimens of the foraminiferan *Sorites dominicensis* that were attached to blades of the seagrass *Thalassia testudinum* were examined in the studies described below. Blades of *T. testudinum* were harvested by wading or snorkeling. Seagrass leaves were removed at the base of the blade, submerged in seawater in a Ziploc bag, and stored in a cooler until return from the field. Both sides of each seagrass blade were examined for the presence of epiphytic foraminiferans using a binocular dissecting microscope (Leica M5). All specimens of the species *S. dominicensis* were removed from the blade using a fine paintbrush or dental pick, measured, and stored on cardboard microslides for additional study and reference material. The cytoplasmic condition (healthy, pale, mottled, totally bleached) and reproductive state (nonreproductive, presence of brood chambers, presence of embryos in brood chambers, or postreproductive)

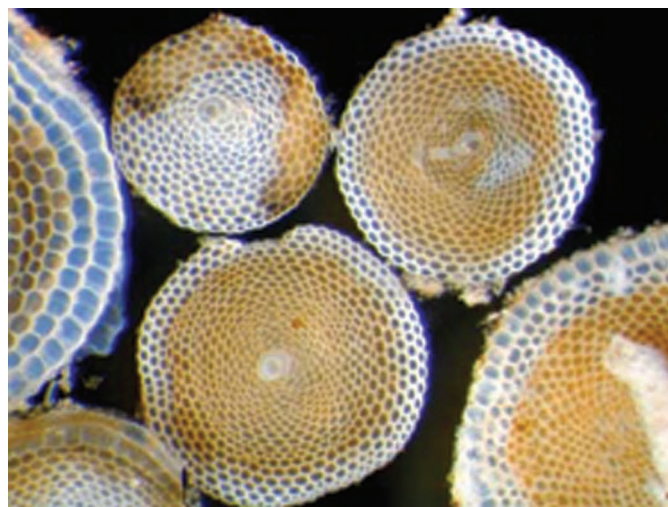


FIGURE 2. Live specimens of *Sorites dominicensis* from Belize, Central America. The two individuals in the upper part of the image show patches of bleached cytoplasm. Note that all specimens, except for the individual in the lower left, possess few, if any, endosymbionts in the outer two or three chambers. The specimen in the lower left is a reproductive individual preparing to undergo multiple fission. The specimen on the upper right is approximately 2 mm in diameter.



of each specimen were noted. Specimens were measured using an optical micrometer calibrated to a stage micrometer. Micrographs of representative individuals (healthy, mottled, and bleached) were taken using a Nikon Coolpix camera with an MCool (Martin Optics) phototube.

Live individuals were recognized by their distinctive cytoplasmic coloration as described below, and/or by the presence of pseudopodial arrays emanating from around the periphery of the protist's test. Bundles of bifurcating pseudopodia in live individuals are usually covered with a light dusting of fine-grained sediment, giving the specimens a star-shaped appearance. Individuals were recorded as having healthy cytoplasm if the cytoplasm possessed an evenly distributed, yellowish-brown coloration (see Figure 2). Individuals were recorded as having a mottled cytoplasm if the cytoplasm contained white-colored patches, interspersed with yellowish-brown sections of cytoplasm (Figure 2). Mottled individuals contained patches of white cytoplasm that were visible on both sides of the disk-shaped test. Specimens were recorded as being totally bleached if the test was completely white. The tests of postreproductive individuals, that is, individuals that had undergone reproduction by multiple fission, were not included in the tallies of bleached specimens. Postreproductive tests are easily distinguished from bleached tests by the presence of fragmented brood chambers, undisseminated embryos, and clusters of dispersed juveniles in close proximity to the parental test. It is assumed that few, if any, of the totally bleached tests had undergone gametogenesis, as microspheric tests (tests formed by syngamy) have never been observed in any of the populations of this species surveyed by the author.

#### WATER TEMPERATURE AND BLEACHING

Studies conducted at both the Jupiter Sound and Belize sites indicate that elevated water temperature, or a combination of elevated water temperature and subaerial exposure, can induce symbiont bleaching in *S. dominicensis*. Bleaching was first observed in the Jupiter Sound populations in 2003 during August (Table 1), when water temperatures are typically at their maximum, often reaching extremes as high as 31°C (RiverKeeper Data, Loxahatchee River District). A relatively low abundance of bleached individuals was recorded in late July 2004; however, a resampling of the site a few weeks later in August indicated that the incidence of bleaching had risen 14 fold (Table 2). In July 2004, water temperatures recorded at the Jupiter Sound site ranged from 30° to 31°C between 1:00 PM and 3:30 PM during an extremely low spring tide that resulted in the subaer-

TABLE 1. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida, during August 2003 ( $n$  = total number of tests examined).

Test condition	Percent of tests	
	2 Aug 2003 ( $n$ = 580)	12 Aug 2003 ( $n$ = 147)
Mottled cytoplasm	1.0%	1.0%
White cytoplasm	15%	12%
Total bleached	16%	13%

ial exposure of major portions of the seagrass bed. No water temperature data are available for Jupiter Sound in August 2004, although the water was uncomfortably hot to the touch at the time of collection (Richardson, unpublished). Bleaching was undetectable in surveys of the *S. dominicensis* populations conducted at other times of the year in both 2003 and 2004 (Richardson, unpublished data).

In Belize, water temperatures were recorded using HOBO Tidbit (Onset) submersible temperature loggers deployed for three days in July 2005. One logger was deployed on the reef flat at Carrie Bow Cay and the other in Boston Bay, Twin Cays. The range of water temperatures recorded for both sites are listed in Table 3 and Figure 3. Although the overall mean temperatures were identical for both sites ( $s = 32^\circ\text{C}$ ), the reef flat off Carrie Bow Cay experienced a wider range of temperatures ( $29^\circ\text{--}40^\circ\text{C}$ ), with higher maximum temperatures recorded during the late afternoon and lower minimum temperatures recorded at night (Figure 3; Table 3). Correspondingly, the rate of bleaching recorded from the reef flat at Carrie Bow Cay was almost five times higher than that observed in Bos-

TABLE 2. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida during July and August 2004 ( $n$  = total number of tests examined).

Test condition	Percent of tests	
	29 Jul 2004 ( $n$ = 446)	19 Aug 2004 ( $n$ = 14)
Mottled cytoplasm	2.0%	29%
White cytoplasm	0%	0%
Total bleached	2.0%	29%



TABLE 3. Characteristics of two collecting sites in Belize.

Characteristic	Carrie Bow Cay	Twin Cays
Water depth	<0.5 m	1.0 m
Exposure	Exposed during low tides	Subtidal
Water clarity	Very clear	High tannins and mangrove detritus
Water movement	Swift current	Sheltered with slower current
Temperature range (1–4 July 2005)	30°–35°C	29°–40°C

ton Bay, Twin Cays (Table 4). Although the water temperatures recorded in Boston Bay, Twin Cays, were not as extreme as those recorded off Carrie Bow Cay, they still were higher than the HotSpot (28.9°C) and bleaching (HotSpot + 1°C) thresholds derived by NOAA/NESDIS for Glovers Reef (Opishinski, 2006). The same sites were resurveyed in July 2006, and the incidence of bleaching on the reef flat at Carrie Bow Cay was observed to be 11 times higher than the incidence of bleaching recorded in Boston Bay, Twin Cays, which exhibited almost negligible levels of bleaching (Table 5).

#### FRESHWATER INFLUX AND BLEACHING

In July and August 2006, continued sampling of the Carrie Bow Cay and Twin Cays field sites in Belize yielded results that indicate that symbiont bleaching in *S. dominicensis* can also be triggered by an influx of freshwater during storm events. In July 2006, field collections were suspended during a three-day period of intense rain then restarted after the storms subsided. After the rainstorms, the incidence of bleaching recorded at both sites rose in all three categories (pale cytoplasm, mottled cytoplasm,

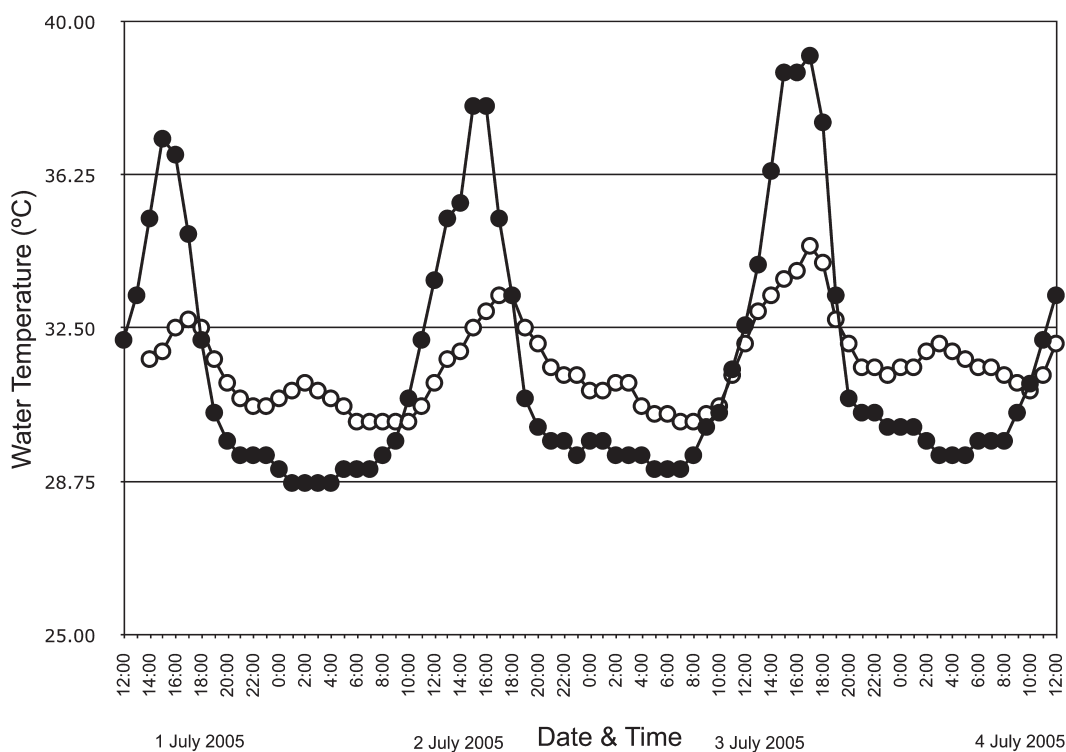


FIGURE 3. Water temperature variations on the reef flat at Carrie Bow Cay and in Boston Bay, Twin Cays, Belize, as measured at noon and every 2.5 hours thereafter during 1–4 July 2005.

TABLE 4. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July 2005 ( $n$  = total number of tests examined).

Test condition	Percent of tests	
	Carrie Bow Cay ( $n$ = 797)	Boston Bay, Twin Cays ( $n$ = 685)
Mottled cytoplasm	4.3%	2.5%
White cytoplasm	14%	1.5%
Total bleached	19%	3.9%

TABLE 5. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July 2006 ( $n$  = total number of tests examined). All specimens were collected before a three-day period of intense rain.

Test condition	Percent of tests	
	Carrie Bow Cay, 21 Jul 2006 ( $n$ = 62)	Boston Bay, Twin Cays, 23 Jul 2006 ( $n$ = 349)
Pale cytoplasm	0%	0%
Mottled cytoplasm	3.2%	0.29%
White cytoplasm	4.8%	0%
Total bleached	8.1%	0.29%

TABLE 6. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July and August 2006 ( $n$  = total number of tests examined). All specimens were collected after a three-day period of intense rain.

Test condition	Percent of tests	
	Carrie Bow Cay, 1 Aug 2006 ( $n$ = 132)	Boston Bay, Twin Cays, 27 Jul 2006 ( $n$ = 369)
Pale cytoplasm	1.5%	0.27%
Mottled cytoplasm	0.76%	2.4%
White cytoplasm	8.3%	16% <sup>a</sup>
Total bleached	11%	19%

<sup>a</sup> Of 60 individuals, 34 were juveniles from the same brood.

and white cytoplasm) (Table 6). Although bleaching on the reef flat at Carrie Bow Cay was slightly higher than the prestorm levels (11% vs. 8.1%), the total poststorm incidence of bleaching in Boston Bay was observed to be more than 65 times higher than that observed just a few days earlier (Table 6). Although the waters in Boston Bay are normally of open ocean marine salinities, during heavy rains and slack tides cold, brackish water drains off Hidden Lake in the Twin Cays and empties into Boston Bay through Hidden Creek (Rützler et al., 2004). Interestingly, juveniles were disproportionately impacted by the bleaching event: 34 of 60 of the tests with white cytoplasm appeared to be individuals from the same brood (Table 6).

## IMPACT OF HURRICANES AND RECOVERY

Seasonal bleaching events cause increased mortality in *S. dominicensis*, resulting in compromised populations that are more sensitive to periodic disturbance by hurricanes. Monthly surveys in 2001, 2003, and 2004 indicate that *S. dominicensis* populations normally plummet in the late summer, stay low throughout the winter, and eventually recover and bloom the following spring in late April and May (Richardson, unpublished data). In September 2004, the Jupiter Sound site was traversed by two hurricanes, Jeanne and Frances (Beven, 2005; Lawrence and Cobb, 2005). The Jupiter site was situated in the south eyewall for both storms, and experienced high winds and storm surges and extensive freshwater inundation. Dark, cloudy, turbid water continued to characterize the site for several months following the hurricanes. Other impacts included loss of shading because of downed trees and overgrowth of the seagrass by cyanobacterial blooms. The entire epiphytic foraminiferal community at the Jupiter Sound site was impacted by the 2004 hurricane season (Richardson, unpublished data). Initially, a dramatic reduction in species diversity and abundance was observed, with two species comprising 92% of the community in April and May 2005. By August 2005 the community had rebounded to 2001 levels of species diversity and density, with the exception of the apparent local eradication of *S. dominicensis* (Richardson, unpublished data). *Sorites dominicensis* is the only species at this site to possess photosynthetic endosymbionts and thus is sensitive to the reduced transmission of light in the water column that resulted from the months of increased turbidity following the 2004 hurricanes.

In October 2005, Jupiter Sound was impacted by Hurricane Wilma (Pasch et al., 2006), although this time the region experienced the high winds of the north eye-

TABLE 7. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida, 4 April 2008, as determined from examination of 446 tests.

Test condition	Percent of tests ( $n = 446$ )
Pale cytoplasm	5.9%
Mottled cytoplasm	7.8%
White cytoplasm	9.8%
Total bleached	24%

wall of the storm. Individuals of *S. dominicensis* were not recovered from the Jupiter Sound site until the summer of 2007 and did not reach their pre-hurricane densities until April 2008 (Richardson, unpublished). A survey of 446 individuals of *S. dominicensis*, collected in April 2008, yielded a high incidence of bleached individuals (24% total), an unusual event for the spring (Table 7). The trigger for this event is unknown; the rainfall during this period was below average as the region was experiencing an extended seasonal drought. It is also not known whether the population recovered through the reproduction of relict populations of *S. dominicensis* that survived the hurricanes of 2004 and 2005 or whether the site was repopulated through immigrants transported by the Gulf Stream from the Florida Keys and/or the Caribbean.

## DISCUSSION

The results from the field studies described above document the occurrence of bleaching in *Sorites dominicensis*, a dinoflagellate-bearing foraminiferan, and delineate some of the environmental stressors that trigger bleaching. As has been observed in corals, bleaching in epiphytic specimens of *S. dominicensis* may be triggered by multiple environmental factors, such as increased irradiance during subaerial exposure at low tide, increased water temperatures, influx of freshwater runoff during storm events, and catastrophic disturbance during hurricanes. The symptoms of bleaching in *S. dominicensis* include decrease in intensity of coloration (pale appearance), the patchy loss of cytoplasmic coloration (mottled appearance), and the total loss of cytoplasmic coloration (white tests). Symbiont bleaching in *S. dominicensis* can be distinguished from the loss of cytoplasmic coloration that occurs during the process of reproduction through multiple fission as the symbiont-rich cytoplasm moves from the central region of the test to the periphery where the brood chambers and

embryos will form. Studies are currently underway to link qualitative observations of bleaching in *S. dominicensis* to quantitative studies of symbiont density in bleached specimens using staining techniques that differentiate necrotic or apoptotic algal cells.

The relatively high water temperatures recorded on the reef flat at Carrie Bow Cay in July 2005 are not unusual for tropical seagrasses, which may experience annual fluctuations in seawater temperatures ranging from 19.8° to 41°C (Campbell et al., 2006). Unusually high water daily temperatures (40°–43°C) have been recorded in seagrass beds growing in shallow water off Papua New Guinea (Fred Short, University of New Hampshire, personal communication, January 2006). In addition to high temperatures, tropical seagrasses growing in shallow-water pools in the intertidal zone are subject to desiccation, extremely high levels of photosynthetically active radiation, and high levels of ultraviolet radiation (Campbell et al., 2006; Durako and Kunzelman, 2002).

Although the underlying mechanisms of bleaching in *S. dominicensis* are unknown, it is hypothesized that several of the proposed mechanisms for bleaching in corals may function in foraminiferans as well, such as reduced efficiency of photosystem II resulting from increased irradiance (Venn et al., 2008; Smith et al., 2005), and the production of damaging reactive oxygen species via several different pathways (Lesser, 2006; Smith et al., 2005).

Soritid foraminiferans have the potential to serve as a model system for bleaching, the need of which was recently emphasized by Weis et al. (2008). Not only do *S. dominicensis* and other soritids possess *Symbiodinium* endosymbionts that are closely related to the zooxanthellae in corals and other metazoans, but the small size of *S. dominicensis* facilitates investigation of symbiont bleaching *in hospite*, using methods such as in situ hybridization, immunofluorescence, and other imaging techniques. Future research will focus on developing culture methods for *S. dominicensis* and on exploring cytological methods that will facilitate the visualization of the cell processes underlying the bleaching response in foraminiferans.

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## LITERATURE CITED

- Baker, A. C. 2003. Flexibility and Specificity in Coral-Algal Symbiosis: Diversity, Ecology, and Biogeography of *Symbiodinium*. *Annual Review of Ecology and Systematics*, 34:661–689.
- Beven, J. L. 2005. Tropical Cyclone Report. Hurricane Frances: 25 August–8 September 2004. NOAA/National Weather Service, National Hurricane Center, Miami, Fla. Available from: <http://www.nhc.noaa.gov/2004/frances.shtml>.
- Campbell, S. J., L. J. McKenzie, and S. P. Kerville. 2006. Photosynthetic Responses of Seven Tropical Seagrasses to Elevated Seawater Temperature. *Journal of Experimental Marine Biology and Ecology*, 330:455–408.
- Coffroth, M. A., and S. R. Santos. 2005. Genetic Diversity of Symbiotic Dinoflagellates in the Genus *Symbiodinium*. *Protist*, 156:19–34.
- Douglas, A. E. 2003. Coral Bleaching—How and Why? *Marine Pollution Bulletin*, 46:385–392.
- Doyle, W. L., and M. M. Doyle. 1940. The Structure of Zooxanthellae. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington*, 32:127–142.
- Duguay, L. E. 1983. Comparative Laboratory and Field Studies on Calcification and Carbon Fixation in Foraminiferal-Algal Associations. *Journal of Foraminiferal Research*, 13:252–261.
- Durako, M. J., and J. I. Kunzelman. 2002. Photosynthetic characteristics of *Thalassia testudinum* measured in situ by pulse-amplitude modulated (PAM) fluorometry: methodological and scale-based considerations. *Aquatic Botany*, 73:173–185.
- Garcia-Cuetos, L., X. Pochon, and J. Pawlowski. 2005. Molecular Evidence for Host-Symbiont Specificity in Soritid Foraminifera. *Protist*, 156:399–412.
- Glynn, P. 1996. Coral Reef Bleaching: Facts, Hypotheses and Implications. *Global Change Biology*, 2:495–509.
- Hallock, P. 1999. “Symbiont-Bearing Foraminifera.” In *Modern Foraminifera*, ed. B. Sen Gupta, pp. 123–139. Dordrecht and Boston, Mass.: Kluwer Academic Publishers.
- Kremer, B. P., R. Schmaljohann, and R. Röttger. 1980. Features and Nutritional Significance of Photosynthates Produced by Unicellular Algae Symbiotic with Larger Foraminifera. *Marine Ecology Progress Series*, 2:225–228.
- Langer, M. R., and L. Hottinger. 2000. Biogeography of Selected “Larger” Foraminifera. *Micropaleontology*, 46 (Suppl. 1):105–106.
- Lawrence, M. B., and H. D. Cobb. 2005. Tropical Cyclone Report. Hurricane Jeanne: 13–28 September 2004. NOAA/National Weather Service, National Hurricane Center, Miami, Fla. Available from: <http://www.nhc.noaa.gov/2004/jeanne.shtml>.
- Lee, J. J. 2006. Algal Symbiosis in Larger Foraminifera. *Symbiosis*, 42:63–75.
- Lee, J. J., and W. Bock. 1976. The Relative Importance of Feeding in Two Species of Soritid Foraminifera with Algal Symbionts. *Bulletin of Marine Science*, 26:530–537.
- Lee, J. J., M. E. McEnery, E. G. Kahn, and F. L. Schuster. 1979. Symbiosis and the Evolution of Larger Foraminifera. *Micropaleontology*, 25:118–140.
- Lee, J. J., J. Morales, S. Bacus, A. Diamont, P. Hallock, J. Pawlowski, and J. Thorpe. 1997. Progress in Characterizing the Endosymbiotic Dinoflagellates of Soritid Foraminifera, and Related Studies on Some Stages in the Life Cycle of *Marginopora vertebralis*. *Journal of Foraminiferal Research*, 27:254–263.
- Lesser, M. 2006. Oxidative Stress in Marine Environments: Biochemistry and Physiological Ecology. *Annual Review of Physiology*, 68:253–278.
- Loxahatchee River District. Research Reports. Available from: <http://www.loxahatcheeriver.org/reports.php> (accessed 5 August 2008).
- Müller-Merz, E., and J. J. Lee. 1976. Symbiosis in the Larger Foraminifera *Sorites marginalis* (with Notes on *Archaias* spp.). *Journal of Protozoology*, 23(3):390–396.
- Opishinski, T. 2006. Carrie Bow Cay Environmental Monitoring System. <http://cbc.riocean.com/cbc2005.htm> (accessed 14 June 2006).
- Pasch, R. J., E. S. Blake, H. D. Cobb, and D. P. Roberts. 2006. Tropical Cyclone Report. Hurricane Wilma: 15–25 October 2005. NOAA/National Weather Service, National Hurricane Center, Miami, Fla. Available from: <http://www.nhc.noaa.gov/HAW2/english/history.shtml#wilma>.
- Pawlowski, J., M. Holzmann, J. F. Fahrni, X. Pochon, and J. J. Lee. 2001. Molecular Identification of Algal Endosymbionts in Large Miliolid Foraminifera: 2. Dinoflagellates. *Journal of Eukaryotic Microbiology*, 48:368–373.
- Pochon, X., T. C. LaJeunesse, and J. Pawlowski. 2004. Biogeographic Partitioning and Host Specialization among Foraminiferal Dinoflagellate Symbionts (*Symbiodinium*; Dinophyta). *Marine Biology*, 146:17–27.
- Pochon, X., J. I. Montoya-Burgos, B. Stadelmann, and J. Pawlowski. 2006. Molecular Phylogeny, Evolutionary Rates, and Divergence Timing of the Symbiotic Dinoflagellate Genus *Symbiodinium*. *Molecular Phylogenetics and Evolution*, 38:20–30.
- Pochon, X., and J. Pawlowski. 2006. Evolution of the Soritids–*Symbiodinium* Symbiosis. *Symbiosis*, 42:77–88.
- Pochon, X., J. Pawlowski, L. Zaninetti, and R. Rowan. 2001. High Genetic Diversity and Relative Specificity among *Symbiodinium*-like Endosymbiotic Dinoflagellates in Soritid Foraminiferans. *Marine Biology*, 139:1069–1078.
- Richardson, S. L. 2006. Endosymbiont-Bleaching in Epiphytic Populations of *Sorites dominicensis*. *Symbiosis*, 42:103–117.
- Rodriguez-Lanetty, M. 2003. Evolving Lineages of *Symbiodinium*-like Dinoflagellates Based on ITS1 rDNA. *Molecular Phylogenetics and Evolution*, 28:152–168.
- Rowan, R. 1998. Diversity and Ecology of Zooxanthellae on Coral Reefs. *Journal of Phycology*, 34:407–417.
- . 2004. Thermal Adaptation in Reef Coral Symbionts. *Nature (London)*, 430:742–743.
- Rowan, R., and D. A. Powers. 1991. A Molecular Genetic Classification of Zooxanthellae and the Evolution of Animal–Algal Symbioses. *Science*, 251:1348–1351.
- . 1992. Ribosomal RNA Sequences and the Diversity of Symbiotic Dinoflagellates (Zooxanthellae). *Proceedings of the National Academy of Sciences of the United States of America*, 89:3639–3643.
- Rützler, K., I. Goodbody, M. C. Diaz, I. C. Feller, and I. G. Macintyre. 2004. The Aquatic Environment of Twin Cays, Belize. *Atoll Research Bulletin*, 512:1–35.
- Smith, D. J., D. J. Suggett, and N. R. Baker. 2005. Is Photoinhibition of Zooxanthellae Photosynthesis the Primary Cause of Thermal Bleaching in Corals? *Global Change Biology*, 11:1–11.
- Venn, A. A., J. E. Loram, and A. E. Douglas. 2008. Photosynthetic Symbioses in Animals. *Journal of Experimental Botany*, 59(5):1069–1080.
- Weis, V. M., S. K. Davy, O. Hoegh-Guldberg, M. Rodriguez-Lanetty, and J. R. Pringle. 2008. Cell Biology in Model Systems as the Key to Understanding Corals. *Trends in Ecology and Evolution*, 23(7):369–376.



# New Perspectives on Ecological Mechanisms Affecting Coral Recruitment on Reefs

*Raphael Ritson-Williams, Suzanne N. Arnold, Nicole D. Fogarty, Robert S. Steneck, Mark J. A. Vermeij, and Valerie J. Paul*

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**ABSTRACT.** Coral mortality has increased in recent decades, making coral recruitment more important than ever in sustaining coral reef ecosystems and contributing to their resilience. This review summarizes existing information on ecological factors affecting scleractinian coral recruitment. Successful recruitment requires the survival of coral offspring through sequential life history stages. Larval availability, successful settlement, and post-settlement survival and growth are all necessary for the addition of new coral individuals to a reef and ultimately maintenance or recovery of coral reef ecosystems. As environmental conditions continue to become more hostile to corals on a global scale, further research on fertilization ecology, connectivity, larval condition, positive and negative cues influencing substrate selection, and post-settlement ecology will be critical to our ability to manage these diverse ecosystems for recovery. A better understanding of the ecological factors influencing coral recruitment is fundamental to coral reef ecology and management.

## INTRODUCTION

Coral reefs are facing unprecedented human impacts and continuing acute and chronic threats that can impact community structure (Nyström et al., 2000). Their ability to resist such changes or to recover from them defines their “resilience” (sensu Holling, 1973). Unfortunately, coral reef ecosystems can be resilient in either the more desirable coral-dominated phase or in the less desirable algal-dominated phase (Hughes et al., 2005). Although we know much about what causes undesirable “phase shifts” (Done, 1992; Hughes, 1994; Pandolfi et al., 2005), we know relatively little about what drives coral community recovery (Connell, 1997).

Scleractinian corals are uniquely important to coral reef ecosystems as ecosystem engineers that structure the habitat (Jones et al., 1994, 1997). The abundance of live coral drives key ecological processes in the wider coral reef community, such as providing recruitment habitat for reef fish, lobsters, and sea urchins (Lee, 2006; Mumby and Steneck, 2008). In the past 30 years, the percent cover of live coral has decreased on a global scale (Gardner et al., 2003; Bruno and Selig, 2007), raising the question: How can we increase the number of corals in these ecosystems for recovery?

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Larval settlement (when they first attach to the benthos) and subsequent survival (recruitment) are processes that can control marine population dynamics (Gaines and Roughgarden, 1985; Doherty and Fowler, 1994; Palma et al., 1999). Although corals can reproduce clonally (Fautin, 2003; Baums et al., 2006), recruitment resulting from sexual reproduction is the primary means of recolonization for most species (Connell et al., 1997) and adds genetic variation to coral populations, which may increase survival of a species. Coral settlement followed by subsequent recruit survival and growth maintains coral populations and is necessary for coral reef recovery. For this cycle to occur on any given reef, larval survival and recruitment are dependent on a sequence of three phases: (1) larval availability, which integrates gamete production, fertilization success, and connectivity; (2) settlement ecology, which relates to larval condition and substrate selection behavior; and (3) post-settlement ecology, including substrate-specific survival and growth (Figure 1).

This review summarizes existing information on ecological factors affecting scleractinian corals during these first three phases of their life, covering the period from

gamete release to juvenile coral colonies (typically described as <40 mm). We discuss factors that are critical for coral recruitment success, and where insufficient data exist, we draw parallels to concepts that have been developed for other marine larvae or adult corals and briefly discuss their relevance for the early life history stages of corals.

## LARVAL AVAILABILITY

Larval supply to a reef depends on sequential processes of gamete production, fertilization success, and larval transport (i.e., larval dispersal and connectivity). Basic life history traits of corals can greatly influence the range of strategies that are used to ensure larval availability. Scleractinians have two main reproductive modes: brooding, where sperm are released into the water column and taken in by conspecifics for internal fertilization, and broadcast spawning, wherein both egg and sperm are released into the environment so that fertilization occurs externally, that is, in the water column (Figure 2; Fadlallah, 1983; Szmant, 1986; Richmond and Hunter, 1990; Richmond, 1997).

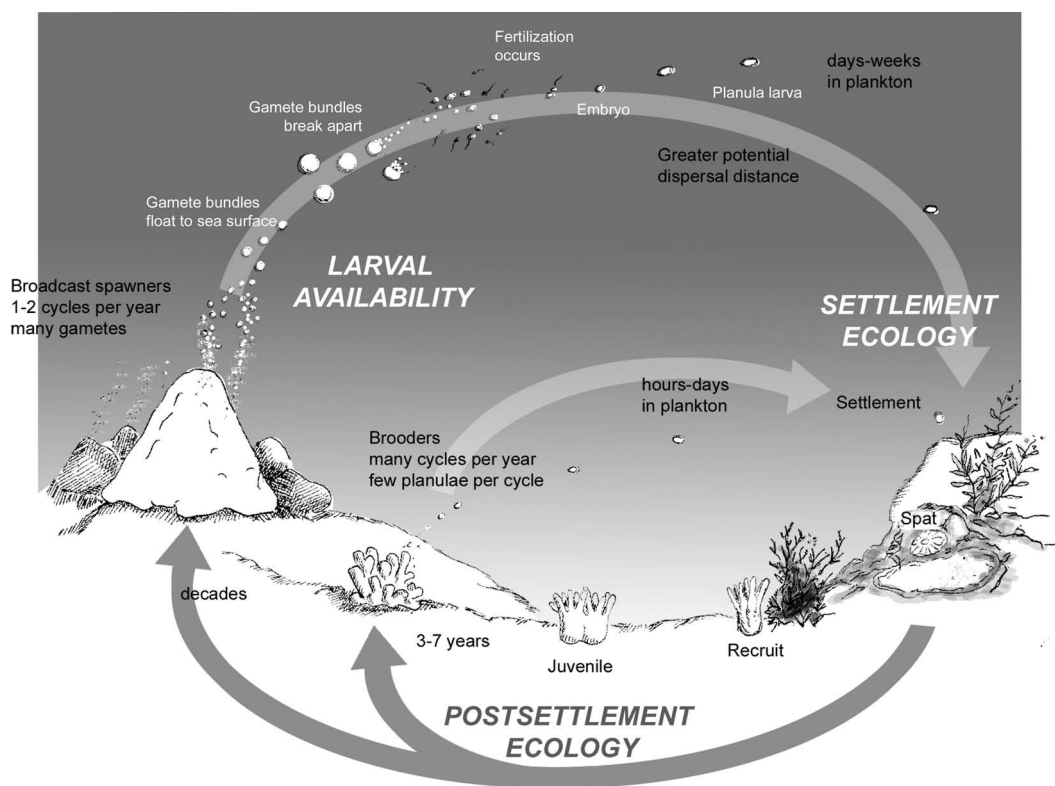
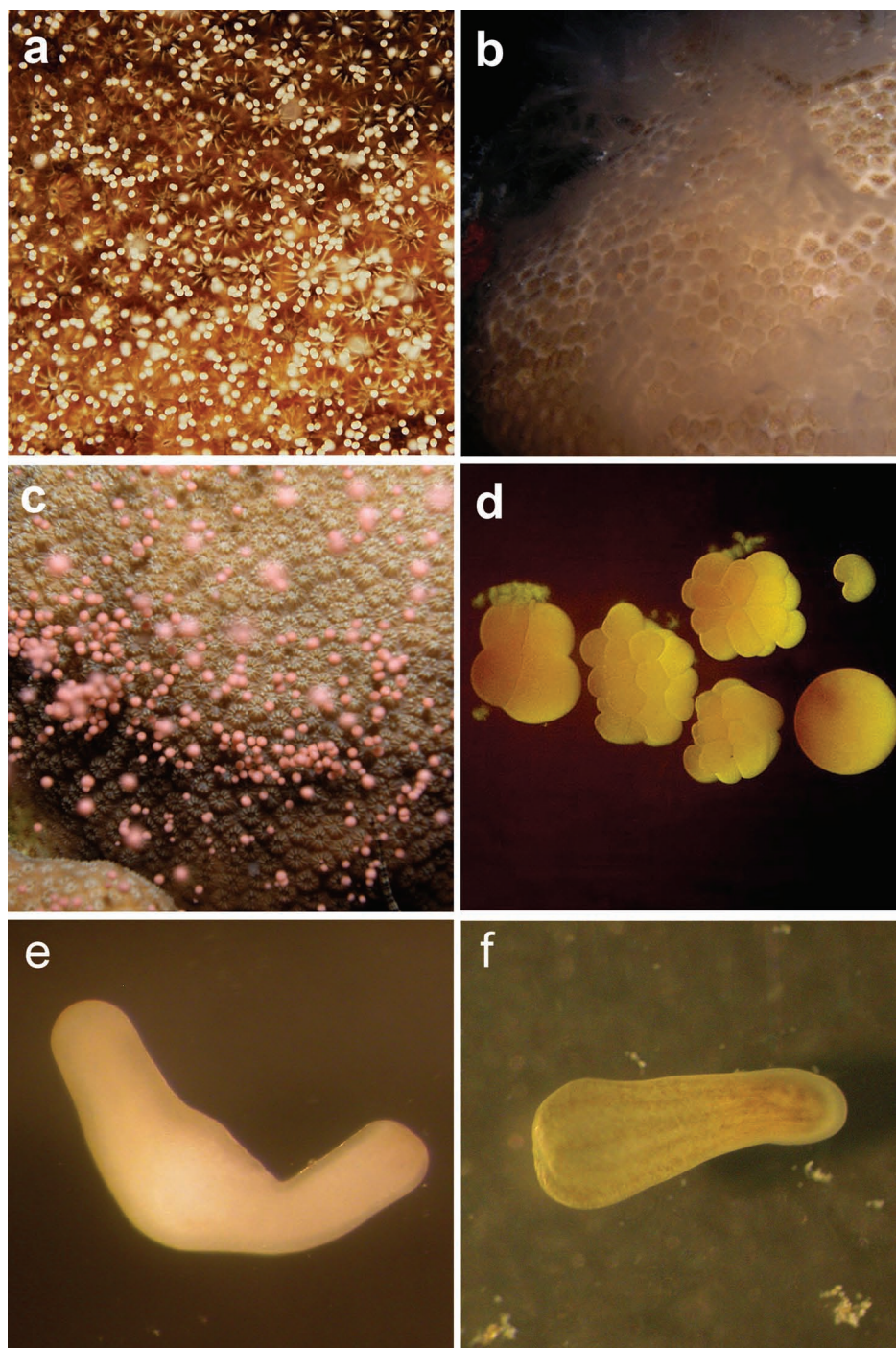


FIGURE 1. Three sequential phases necessary for successful coral recruitment starting with larval availability, progressing to settlement ecology, and ending with post-settlement ecology. (Drawn by Mark Vermeij.)



**FIGURE 2.** Different modes of reproduction influence larval supply in coral species. a, Female *Stephanocoenia intersepta*, a gonochoric spawner, releases eggs. b, A male *S. intersepta* releases sperm. c, The hermaphrodite *Montastraea faveolata* releases eggs and sperm as bundles that float to the surface, where they break apart for fertilization. d, For *Acropora palmata* (and other spawners), fertilization of coral eggs occurs in the water column. e, A larva of *Acropora palmata* completes development in the water column. f, In contrast, a larva of *Porites astreoides* (a brooder) is fully developed when it is released from its parent and contains zooxanthellae. (Photographs a, b, by Mark Vermeij; c, e, f, by Raphael Ritson-Williams; d, by Nicole Fogarty.)



A minority of reef-building coral species worldwide are brooders, but brooding is the dominant reproductive mode found in the Caribbean Sea (Szmant, 1986; Richmond and Hunter, 1990; Smith, 1992). Broadcast spawning is a more common reproductive mode in coral species, and in Australia more than 100 coral species may spawn on a single night (Harrison et al., 1984; Willis et al., 1985; Babcock and Heyward, 1986). Species representing these modes differ in colony size, gametic cycles, larval competency, dispersal distance, and zooxanthellae transmission (Richmond and Hunter, 1990). Brooders are typically smaller than spawning corals and have multiple planulating cycles per year, as opposed to one or two cycles in broadcast spawners (Szmant, 1986).

#### FECUNDITY

Reproductive mode determines the frequency of larval release; however, both abiotic and biotic factors can influence the amount of gametes produced in corals. The production of gametes is only possible when a coral has reached an age, and perhaps more importantly a size, capable of reproduction (Hughes, 1984; Szmant, 1986). It is difficult to measure the impact of stressors on gamete production because it is naturally variable both temporally and between individuals within a species (Chorneskey and Peters, 1987). As coral cover declines in both the Caribbean Sea and the Pacific Ocean (Gardner et al., 2003; Bruno and Selig, 2007) there are fewer and often smaller adult colonies. This change could reduce coral fecundity because small body size reduces gamete production (Szmant, 1986) and low population densities reduce fertilization success (see Fertilization section, below). Even with relatively high adult coral densities the fecundity of individual colonies can be decreased by many stressors before and during gametogenesis.

Coral bleaching has been observed to stop gametogenesis (Szmant and Gassman, 1990), reduce the number of gametes produced (Fine et al., 2001), and decrease fertilization rates in *Acropora* corals (Omori et al., 2001). Nutrients added to the water column decreased the number of successfully developed embryos that were formed in the corals *Acropora longicyathus* and *A. aspera* (Koop et al., 2001). Changes in salinity and sedimentation can also reduce gamete production and fertilization success in corals (Richmond, 1993a, 1993b). Guzman et al. (1994) suggested that the increase in injury levels and slower growth in corals exposed to an oil spill further reduced gamete size, viability, and fecundity. The presence of macroalgae adjacent to coral colonies can decrease fecundity (includ-

ing the number and size of eggs) in the corals *Montastraea annularis* and *Montipora digitata* (Hughes et al., 2007; Foster et al., 2008). Impacts on fecundity are perhaps best summarized by Rinkevich and Loya (1987), who suggested that because reproductive activity involves such high energy expenditure, any stress that diminishes energy reserves will have an effect on adult fecundity.

#### FERTILIZATION ECOLOGY

Because broadcast spawners only have one or two planulating cycles a year, it is imperative that fertilization be successful. In any broadcast species, fertilization success is highly variable and largely depends on the synchronization of gamete release, gamete compatibility (Palumbi, 1994; Levitan et al., 2004), gamete age (Oliver and Babcock, 1992; Levitan et al., 2004), and abundance of spawning adults (Levitan et al., 1992, 2004). However, the health of the spawning colony and environmental conditions during the spawning event also affect fertilization success (Richmond, 1997; Humphrey et al., 2008).

During multispecies spawning events, synchronized gamete release and species-specific gamete recognition are critical for fertilization success and reducing the probability of interspecific fertilization (hybridization), which may result in reduced offspring fitness (Mayr, 1963); however, Willis et al. (2006) suggest a role for hybridization in range expansion and adaptation to a changing environment. Species with overlapping spawning times typically display low interspecific fertilization success in laboratory crosses (Willis et al., 1997; Hatta et al., 1999; Levitan et al., 2004). Interspecific fertilization success is usually higher among morphologically similar species, suggesting they are more closely related or possibly the same species (Willis et al., 1997; Hatta et al., 1999; Wolstenholme, 2004), but interspecific fertilization can also occur between *Acropora* species that have very different branching morphologies (Hatta et al., 1999). Fertilization success during a mass spawning event could be the result of sperm attractant molecules produced by coral eggs (Coll et al., 1994; Babcock, 1995) but could also be regulated by gamete recognition proteins, such as those that ensure species-specific fertilization in spawning sea urchins (Zigler et al., 2005).

If coral colonies spawn asynchronously or encountered gametes are not compatible, eggs may go unfertilized for extended periods of time or sperm may lose its viability. The effect of age on gamete viability and fertilization success differs among coral species; *Platygyra sinensis* showed reduced fertilization after three hours (Oliver and



Babcock, 1992), but in *Acropora* spp. reduced fertilization success occurred after seven to eight hours (Willis et al., 1997; Omori et al., 2001). With increasing gamete age, fertilization success is reduced in conspecific crosses, but aging effects on gamete viability differ between sperm and eggs. *Montastraea* spp. sperm lose viability after two hours but eggs stay viable for more than three hours (Levitan et al., 2004). Another consequence of gamete aging is an increase in the likelihood of interspecific fertilization. Hybridization rates between *Montastraea faveolata* eggs and *M. annularis* and *M. franksi* sperm increased when eggs had aged at least 75 minutes (Levitan et al., 2004). Increased interspecific fertilization may be caused by a breakdown in gamete recognition proteins, but the specific mechanisms remain to be determined.

The density of spawning individuals plays a critical role in fertilization success. If reproductive individual densities are too low, fertilization success will be limited (also referred to as the allee effect) (Levitan and McGovern, 2005). Coma and Lasker (1997) found that fertilization success in gorgonians was influenced by the density of gametes, which was determined by nearest neighbor distances (approximately 10 m), synchronous gamete release, or hydrodynamic processes. These factors probably influence scleractinian fertilization success; however, it is difficult to directly measure species-specific sperm concentrations in situ because a number of coral species spawn synchronously. Field studies examining sperm concentrations have used either of two methods: (1) measuring the percent of fertilized eggs collected at different times and locations on the reef or (2) determining the fertilization potential of collected surface water samples by adding them to unfertilized eggs and recording the proportion of eggs fertilized (Oliver and Babcock, 1992; Levitan et al., 2004). When lower production or dilution resulted in locally lower than normal sperm concentrations, fertilization success was reduced (Oliver and Babcock, 1992; Willis et al., 1997; Omori et al., 2001; Levitan et al., 2004). These studies showed peak fertilization potential during or shortly after coral species spawn (Oliver and Babcock, 1992; Levitan et al., 2004). Hence, synchronized gamete release is a mechanism for the high gamete density needed to ensure fertilization success.

High gamete concentration brings with it a potential risk as well; as sperm densities increase so does the probability of polyspermy, whereby eggs become fertilized by more than one sperm cell, which results in lowered fertilization rates and developmental failure (Styan, 1998; Tomaiuolo et al., 2007). Reduced fertilization success at high sperm concentrations has been described for several coral

species (Oliver and Babcock, 1992; Willis et al., 1997; Levitan et al., 2004), suggesting polyspermic fertilization can occur in scleractinian corals. These findings suggest a trade-off between spawning synchronously (i.e., high gamete density) with other conspecifics to increase fertilization and the potential risk of polyspermy. Polyspermy may therefore act as a negative density-dependent mechanism. Despite the evidence for polyspermy in coral laboratory crosses, field fertilization rates never reached 100% during mass spawning events (97% maximum; Levitan et al., 2004), suggesting that polyspermic conditions are unlikely to occur in nature. In light of recent decreases in adult coral populations, reduced adult density and gamete aging are perhaps the greatest threats to larval production.

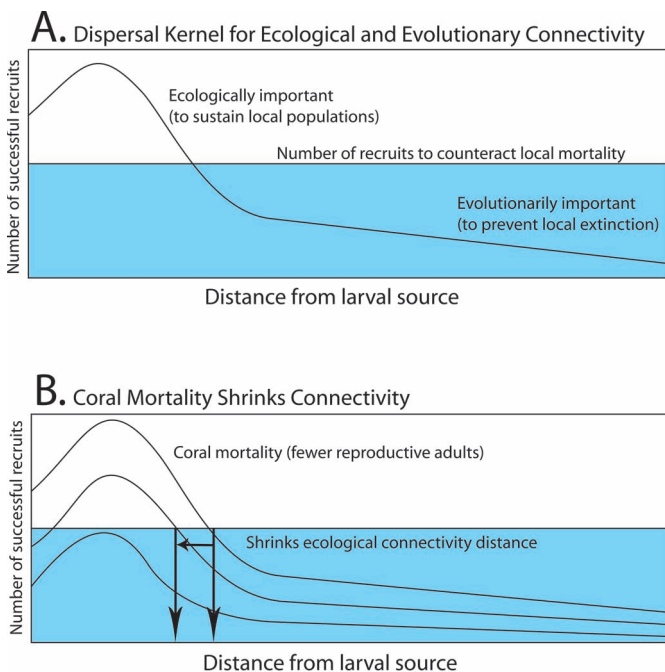
#### LARVAL TRANSPORT: DISPERSAL AND CONNECTIVITY

After gamete fertilization, developing planula larvae transport typically away from reproductive populations (called “dispersal”) and to reefs where they recruit (called “connectivity”) (Levin, 2006). The density of planulae arriving to a reef determines recruitment strength. Larval survival during dispersal varies by means of a combination of hydrodynamic processes, larval energetics, predation pressure (Fabricius and Metzner, 2004), and water quality (Richmond et al., 2007).

Reproductive modes can provide insight into dispersal potential, even though the planktonic duration of coral species can be highly variable and remains undocumented for the majority of scleractinian species. For example, brooders generally settle within hours after release (Carlson and Olson, 1993), whereas broadcast spawners such as *Acropora* spp., *Goniastrea* spp., *Platygyra* spp., and *Montastraea* spp. have planktonic period of 4 to 7 days before they are competent to settle and metamorphose (Babcock and Heyward, 1986; Szmant, 1986). Larvae of the broadcast spawners *Acropora muricata* and *A. valida* settled within 9 to 10 days (Nozawa and Harrison, 2008), but larvae of the spawning corals *Platygyra daedalea* and *Goniastrea favulus* can settle between 2 and 3 days after fertilization, which is sooner than some brooding corals, suggesting that dispersal of these species might be of shorter duration than has been assumed from survival estimates (Miller and Mundy, 2003). In the absence of settlement substrate, a small percentage of *Acropora latistella*, *Favia pallida*, *Pectinia paeonia*, *Goniastrea aspera*, and *Montastraea magnistellata* larvae survived for 195 to 244 days in the water column (Graham et al., 2008). Planulae larvae can probably survive drifting in the plankton for long durations until they encounter suitable settlement substrate;

however, the length of the planktonic period will partially depend on whether the larvae have acquired zooxanthellae, which give them additional energy reserves, from the parent colony (Richmond, 1987).

The frequency of recruitment as a function of distance from a reproductive source population is called a “dispersal kernel” (Steneck, 2006). For most planktonic larvae it was assumed that relatively long larval survival potential in combination with oceanographic transport would generally prevent settlement close to a reproductive source (Cowen et al., 2006). Recent reviews suggest that even though many marine invertebrate larvae have the potential (energy reserves) for long-distance dispersal, they often settle locally because of a combination of oceanographic conditions, larval behavior, and increasing mortality associated with planktonic conditions (Cowen et al., 2000; Strathmann et al., 2002; Levin, 2006). The shape of most dispersal kernels is now thought to be skewed toward the reproductive source, that is, increased rates of local recruitment (Figure 3; Steneck, 2006). Most dispersal and connectivity research to date has focused on fishes;



**FIGURE 3.** Dispersal kernels determine potential connectivity distance between reproductive populations and offspring. A, Distinction between ecologically important recruitment necessary to balance against local mortality and evolutionarily important recruitment to balance against local extinction. B, Shrinking dispersal kernels resulting from adult coral mortality. (After Steneck, 2006.)

however, one study measured ecological connectivity of coral larvae via a field experiment conducted around the isolated Helix Reef in Australia (Sammarco and Andrews, 1988). They reported that 70% of coral recruitment occurred within 300 m of the larval source and that rates of recruitment declined with distance downstream from the reef (Sammarco and Andrews, 1988). Further, as expected, broadcasters dispersed farther than did species of brooding corals, but the estimated ecologically relevant dispersal kernel for both species was remarkably local. A recent review discusses the limited dispersal kernel of coral planulae (Steneck, 2006); however, there is little experimental evidence for the mechanisms that determine coral ecological connectivity.

Recruitment rates must equal or exceed rates of adult mortality to sustain a local population. Most dispersal kernels show high rates of recruitment near the reproductive source, with recruitment decreasing as distance increases (Figure 3). Although that tail is important for gene flow, that low density of settlement is not sufficient to sustain populations. That is, the ecologically relevant portion of a dispersal kernel reflects the sustained rate of recruitment necessary to compensate for rates of mortality. The critical level of settlement to sustain populations (i.e., horizontal line above each shaded half of Figure 3) is not known; however, colonization rates of the introduced orange cup coral *Tubastraea coccinea* can provide some real-world insights into the scale of ecological and evolutionary connectivity. This brooding species was first introduced to the Netherlands Antilles in 1943 and then spread from island to island through the Caribbean, taking 50 years to reach the Bahamas and 60 years to reach Florida (Fenner and Banks, 2004). Once in a region, local populations grew rapidly. This finding is consistent with the concept that the biogeographic spread results from the evolutionarily important “long tail” of the dispersal kernel, whereas the ecologically and demographically significant portion of the dispersal kernel controlling local colonization is much smaller and more local (Figure 3A). Observations of the spread of *T. coccinea* are conservative because some of the spread of this species probably resulted from colonized ships moving among the regions (Fenner and Banks, 2004).

Ecological connectivity necessary to sustain populations against chronic mortality is much more difficult to measure than is evolutionary connectivity. Evolutionary or genetic connectivity can be directly measured using a variety of molecular genetic techniques (reviewed in Hellberg, 2007). In Japan, gene flow between islands 30 to 150 km apart was determined to be consistently higher for the spawner *Acropora tenuis* than for the brooding

species *Stylophora pistillata*, but both coral species had unique genotypes across islands separated by 500 km (Nishikawa et al., 2003). In the Caribbean, a genetic break was detected for *Acropora palmata*, roughly dividing populations from the Greater Antilles and western Caribbean from populations in the Lesser Antilles and the southern and eastern Caribbean (Baums et al., 2005). On the relatively contiguous Great Barrier Reef (GBR), high rates of genetic connectivity were observed for both brooders and spawners. For example, gene flow was detected in all the spawners and three of the five brooders despite being separated by 500 to 1,200 km (Ayre and Hughes, 2000). However, the same species of corals were genetically distinct on Lord Howe Island, which is separated from the GBR by 700 km (Ayre and Hughes, 2004). This observation suggests that coral larvae can use islands within the evolutionarily important tail of the dispersal kernel as “stepping stones” to maintain genetic connectivity between distant reefs separated by long distances (Steneck, 2006).

Although dispersal kernels are useful for visualizing how larval availability declines with distance from a source, their ecological effect can be variable. For example, without changing the shape of the kernel but reducing the number of recruits as a consequence of reduced reproductive output following an adult mortality event (Figure 3B), the range of both the ecological and evolutionary parts of the kernel can shrink. If this happens, connectivity among distant reefs could sever, making recovery following an acute disturbance difficult or impossible.

## SETTLEMENT ECOLOGY

As local and global threats continue to decrease coral cover, it is likely that fewer coral larvae will be supplied to reefs that may or may not have appropriate settlement habitat. For corals, the transitional stage from planktonic planula larvae to sessile benthic juveniles involves a two-step process of settlement and metamorphosis. Settlement is the behavioral response of a larva when it stops dispersal and selects substrate for recruitment. Metamorphosis includes the subsequent morphological and physiological changes that pelagic larvae undergo to become benthic juveniles. Settlement of coral larvae can be influenced by habitat qualities that facilitate or inhibit settlement and metamorphosis of larvae supplied to a reef (Figure 4). Larval settlement behavior can be determined by the conditions the larvae experienced in the plankton or by the presence of positive or negative cues on the benthos or in the water overlying the reef.

## LARVAL CONDITION UPON ARRIVAL

As coral larvae disperse in the plankton they are exposed to water quality conditions that may affect larval health, behavior, survival, and settlement success (Vermeij et al., 2006). Experiences during early life stages (i.e., depleted energy reserves, nutritional stress, environmental stressors, and pollutant exposure) have latent effects on later life stages in numerous marine larvae across different phyla (reviewed in Pechenik, 2006). Even short-term exposure to stressors or a slight delay in metamorphosis can reduce fitness in juveniles and adults (i.e., decrease growth rate, lower competitive ability, reduce survival, and decrease fecundity) (Pechenik, 2006). Although the mechanisms through which latent effects are mediated are not known, it is suspected that transcriptional or translational processes or direct DNA or key enzyme damage are responsible (Pechenik et al., 1998; Heintz et al., 2000; Pechenik, 2006). As very few studies have tested latent effects in coral larvae, we describe some of the patterns found in other marine organisms to highlight how pre-settlement stress might impact post-settlement coral growth and survival.

Marine invertebrate larvae often rely on external cues to trigger metamorphosis. Without these cues, the larval period can be prolonged (reviewed in Pechenik, 1990), and post-settlement fitness may be reduced (Pechenik, 2006). For some invertebrates, including abalones, tunicates, and bryozoans, delayed metamorphosis slowed post-metamorphic development (Wendt, 1998; Roberts and Lapworth, 2001; Marshall et al., 2003). Depleted energy resources during the larval stage may also be an important contributor to post-settlement growth and survival. Bennett and Marshall (2005) found that depleted energy reserves caused by increased activity in larvae of the ascidian *Diplosoma listerianum* were more costly energetically than extending the larval period or completing metamorphosis. Food limitation during the larval period can reduce size, total organic content, energy reserves of metamorphosed animals, juvenile growth rates, and survival (Miller, 1993; Pechenik, 2002; Thiyagarajan et al., 2003; Chiu et al., 2007, 2008).

Water quality conditions can directly reduce coral larval survival and settlement but also may cause latent effects for new recruits. Salinity reductions during pre-settlement periods can reduce post-metamorphic growth rates and survival for various marine invertebrates (Pechenik et al., 2001; Thiyagarajan et al., 2008). Vermeij et al. (2006) tested salinity stress on *Montastraea faveolata* larvae and how that influenced subsequent post-settlement



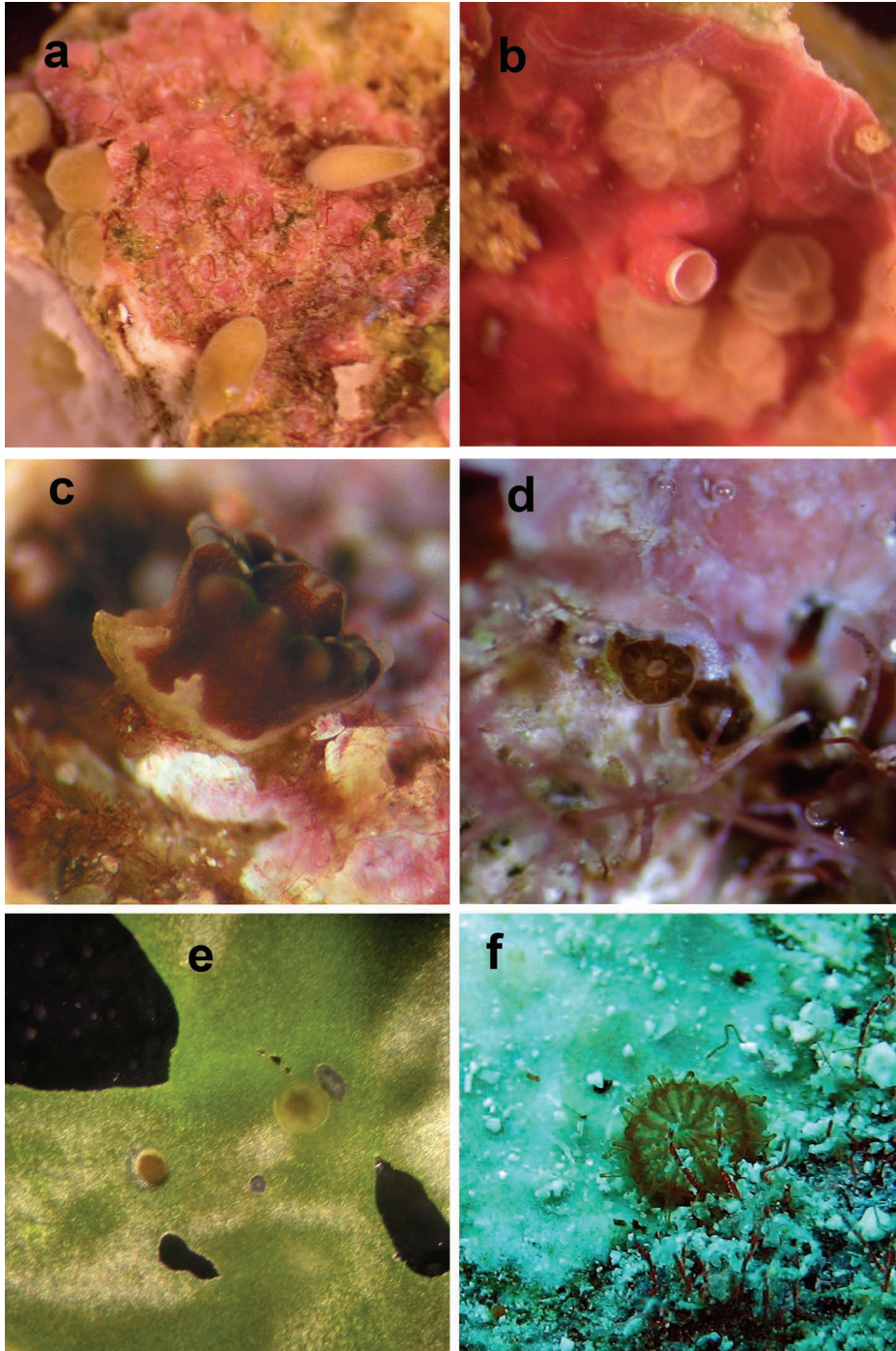


FIGURE 4. Coral larval substrate selection is critical to post-settlement survival. a, *Favia fragum* larvae explore the benthos for a suitable settlement site; some larvae have already attached and are beginning to metamorphose. b, *Acropora cervicornis* settlers are attached to *Titanoderma prototypum* and have metamorphosed. c, A new recruit of *Montastraea faveolata* has settled on coralline algae, which has started to slough its outer layer of tissue, knocking the coral recruit off the substrate. d, *Montastraea faveolata* recruits are being overgrown by a coralline alga. e, *Montipora capitata* larvae have settled on *Ulva* sp., an ephemeral substrate. f, A *Siderastrea radians* recruit has settled in a high-sedimentation environment. (Photographs a, b, by Raphael Ritson-Williams; c, d, by Nicole Fogarty; e, f, by Mark Vermeij.)



performance. Lower than normal seawater salinity caused increased pre- and post-settlement mortality and increased the mobility of coral planulae. It was suggested that the increased activity of the larvae in the lower salinities was an attempt to escape the unfavorable conditions. With increased activity, energy reserves were depleted, which was suggested to be the cause of pre-settlement mortality, smaller post-settlement size, and lower post-settlement survival. Planulae in the lower-salinity treatments settled on a greater range of substrate types. This study emphasized the importance of planktonic conditions on the performance of settling coral larvae, which could then influence post-settlement ecology.

#### LARVAL BEHAVIOR IN OVERLYING WATER

Coral larvae possess a wide array of behaviors that allow them to enhance the likelihood of successful settlement, including, but not limited to, sensitivity to light (Lewis, 1974; Mundy and Babcock, 1998), depth (Carlson, 2001, 2002; Baird et al., 2003; Suzuki et al., 2008), and chemical cues (Morse et al., 1994). One field study showed that multiple behavioral choices determined the larval settlement site of the Caribbean brooder *Agaricia humilis* (Raimondi and Morse, 2000). The larvae swam down when restricted to 3 and 8 m but swam toward the surface when restricted to 25 m. In further field experiments, larvae settled in response to the coralline alga *Hydrolithon boergesenii* but would only settle directly on the coralline alga when it was on the underside of a settlement tile. This study showed that coral larvae are capable of complex behaviors, which are determined to some extent by their ability to detect and discriminate between positive and negative settlement cues in their habitat.

#### POSITIVE SETTLEMENT CUES

Many marine invertebrate larvae use chemical cues to determine the appropriate habitat for settlement (Pawlik, 1992; Hadfield and Paul, 2001). Chemical cues are implicated for both settlement and metamorphosis of corals and may be released by conspecifics and other organisms that indicate appropriate habitat for survival and growth. Research in the Caribbean showed that a membrane-bound carbohydrate complex from the coralline red alga *Hydrolithon boergesenii* induced settlement and metamorphosis in the brooded larvae of *Agaricia humilis* (Morse and Morse, 1991; Morse et al., 1994). It was suggested that many corals require an algal cue for the induction of settlement, indicating a common chemosensory mechanism for settlement and metamorphosis among coral larvae (Morse et al., 1996).

Both the larvae of *Acropora millepora*, a common Indo-Pacific coral species, and coral larvae collected from natural slicks after mass spawning events used coralline algae for settlement and metamorphosis (Heyward and Negri, 1999). Four species of crustose coralline algae, one non-coralline crustose alga, two branching coralline algae, and the skeleton of the massive coral *Goniastrea retiformis* induced metamorphosis. Chemical extracts from both the crustose red alga *Peyssonnelia* sp. and the coral skeleton were highly active, inducing up to 80% larval metamorphosis. Coral larvae can also distinguish among species of coralline algae. The Australian spawning coral *Acropora tenuis* had different rates of settlement in response to different species of coralline algae (Harrington et al., 2004). Settlement choice resulted in higher rates of post-settlement survival on the preferred coralline algae, illustrating the recruitment consequences of larval selectivity. Chemical cues appeared to be involved in this selective behavior, because methanol extracts of the coralline red algae *Titanoderma prototypum* and *Hydrolithon reinboldii* both induced metamorphosis of *A. tenuis*.

Comparative studies have revealed that settlement and metamorphosis in response to crustose coralline algae is not an obligate trait of all coral species. Two brooding Australian corals were compared for their settlement selectivity (Baird and Morse, 2004). *Acropora palifera* larvae only metamorphosed in the presence of coralline red algae, but *Stylophora pistillata* larvae showed some metamorphosis in unfiltered seawater and also metamorphosed onto glass coverslips. A study in Guam found that larvae of the spawning species *Goniastrea retiformis* preferred substrate covered with crustose coralline algae (CCA), but the reef-flat brooding coral *Stylaraea punctata* preferred biofilmed rubble (Golbuu and Richmond, 2007).

Coralline algae have been identified as a positive settlement cue for some corals, but it is unclear if the biofilms present on these algae or the algae themselves are responsible for the observed settlement behavior (Johnson et al., 1991; Webster et al., 2004). Biofilms were isolated from the coralline alga *Hydrolithon onkodes*, and one strain of bacteria alone was enough to induce settlement and metamorphosis of *Acropora millepora* larvae (Negri et al., 2001). When *H. onkodes* was sterilized in an autoclave and treated with antibiotics, it still induced significantly more settlement and metamorphosis than seawater or terracotta tiles. Additionally, coral larvae can distinguish between tiles conditioned at different depths, which could be related to depth-related differences in bacterial community composition of biofilms that formed on tiles (Webster et al., 2004). Whether the coralline algae or its biofilm is producing the inductive compound(s) may depend on the

coral and the coralline algae species tested. The specificity of bacterial communities to different coralline algal species has rarely been investigated (Johnson et al., 1991). With the recent development of more refined genetic techniques it is possible to compare different microbial communities, which might enable the identification of the microbe(s) that can induce coral larval settlement and metamorphosis.

#### NEGATIVE SETTLEMENT CUES

Water quality and substrate conditions impact fertilization rates and also may inhibit some coral larvae from normal settlement and metamorphosis. Low coral recruitment is commonly documented in the field, yet surprisingly few studies have experimentally tested which substrate characteristics might deter coral larval settlement. Coral larval survival and settlement can be reduced by many environmental stresses, such as elevated temperatures (Edmunds et al., 2001), variation in salinity (Vermeij et al., 2006), sedimentation (Hodgson, 1990; Gilmour, 1999), and UVB radiation (Kuffner, 2001; Gleason et al., 2006). Survival and settlement are reasonable ecological metrics for the effects of stress, but an important gap in our knowledge is how sublethal stress influences larval behavior and post-settlement health and success (Downs et al., 2005). New techniques including cellular biomarkers and differential gene expression using microarrays should provide important techniques to measure sublethal stress in coral larvae.

Water quality conditions that are known to impact adult corals also have dramatic effects on larval supply and settlement. Of the physical conditions that negatively influence larval settlement, elevated temperature has received the most attention and has the potential to increase in frequency and duration as ocean temperatures continue to warm. Larvae of the Caribbean brooding coral *Porites astreoides* were killed and had low densities of zooxanthellae when exposed to elevated temperatures for 24 hours (Edmunds et al., 2001, 2005). High temperatures (36°C) killed *Acropora muricata* larvae within 40 hours (Baird et al., 2006), and temperatures of 32°C killed *Diploria strigosa* larvae and reduced their settlement (Bassim and Sammarco, 2003). However, at elevated temperatures (29°C) larvae of *Stylophora pistillata* had the same settlement as at 25°C (Putman et al., 2008), and more larvae settled on the CCA in 25°C than in 23°C. Many of these studies used different experimental conditions, making it difficult to compare the effects of temperature on different species of coral larvae. Temperature is one stress that is relatively well studied, but more research is necessary to understand other physical stressors, such as ocean acidifi-

cation (Albright et al., 2008), that will affect coral larvae in the future.

Larval interactions with the biological inhabitants of reef communities can also reduce larval settlement. Algal turfs, macroalgae, and benthic cyanobacteria can negatively impact the settlement of coral larvae (Kuffner and Paul, 2004; Birrell et al., 2005; Kuffner et al., 2006; Birrell et al., 2008a). In the Florida Keys, two brown algae, *Dictyota pulchella* and *Lobophora variegata*, reduced the total number of *Porites astreoides* settlers (Kuffner et al., 2006). In the Philippines, the algae *Sargassum polycystum* and *Laurencia papillosa* decreased larval settlement of *Pocilloproa damicornis*, but water conditioned with these algae increased settlement over the seawater controls (Maypa and Raymundo, 2004). In Australia, water conditioned with the foliose brown alga *Padina* sp. reduced larval settlement of *Acropora millepora*; however, water conditioned with the brown alga *Lobophora variegata* increased settlement (Birrell et al., 2008a). The cyanobacterium *Lyngbya majuscula* reduced the survivorship of *Acropora surculosa* larvae and settlement and metamorphosis of *Pocillopora damicornis* in studies conducted on Guam (Kuffner and Paul, 2004), and in Florida, the cyanobacterium *Lyngbya polychroa* caused *Porites astreoides* to avoid settling adjacent to it on settlement tiles (Kuffner et al., 2006). Some macroalgae and cyanobacteria can act as settlement inhibitors for coral larvae, but this was not true for all the algae tested. A surprising contrast was observed for *Favia fragum* larvae, which had high rates of settlement and metamorphosis onto live *Halimeda opuntia* when offered with coral rubble (Nugues and Szmant, 2006). Coral larvae of *Montipora capitata* were observed to settle onto *Ulva* sp. (Figure 4e; Vermeij et al., 2009). Why these larvae would settle directly onto blades of algae is unclear as this substrate is ephemeral, thus probably increasing post-settlement mortality. Little research has been done on the mechanisms that algae use to inhibit settlement, but algal qualities such as natural products, shading and abrasion, serving as vectors of bacteria, and releasing dissolved organic matter may contribute to the negative impacts of algae on larval settlement.

Competition from other members of coral reef communities also influences larval behavior. Tissue of the scleractinian coral *Goniopora tenuidens* suspended in seawater inhibited metamorphosis of *Pocillopora damicornis* larvae and reduced the growth of new recruits over seven days (Fearon and Cameron, 1996). The tissue from *Goniopora tenuidens* also caused increased mortality of larvae from *P. damicornis*, *Platygyra daedalea*, *Fungia fungites*, and *Oxyropsis lacera*. Increased research on the types of benthic

organisms and the mechanisms they use for competition with coral larvae is an important area for further study. An integrated approach to larval stress, physiology, and the physical and biological characteristics of settlement substrata will reveal the impact of benthic organisms on coral larval behavior, settlement, and post-settlement survival. Determining what benthic habitat characteristics are necessary for increased settlement will be a critical step for managing reef habitats for increased coral recruitment.

## POST-SETTLEMENT ECOLOGY

Corals, and most benthic marine organisms, suffer high rates of mortality soon after settlement because they are small and vulnerable. Post-settlement processes from the time corals settle (i.e., attach to the benthos) to recruitment (i.e., survive to some later phase) determines much of coral demography (Vermeij and Sandin, 2008). This concept is consistent with the tenet of clonal population biology that states as clonal organisms grow the probability of their death declines but the probability of injury increases (Hughes and Jackson, 1985). Thus, the two rates of early post-settlement mortality and growth can strongly influence the local abundance of corals.

### POST-SETTLEMENT MORTALITY

Coral recruits can die from a myriad of causes including chronic disturbances such as competition and predation and pulse disturbances such as bleaching and disease. However, the chronic disturbances probably drive most post-settlement mortality and thus are serious impediments to reef recovery. Caribbean reefs are a case in point, with incidences of recovery much lower than Indo-Pacific reefs as a result of setbacks from chronic disturbances (Connell et al., 1997).

Algae, encrusting invertebrates, and sediment have all been shown to have deleterious effects on newly settled corals (Figure 5; Rylaarsdam, 1983). Settling corals, with limited stores of energy to invest in competitive interactions, are particularly vulnerable when faced with a well-developed benthic community structure and limited space (Jackson and Buss, 1975; Sebens, 1982; Connell et al., 1997). However, the *mechanisms*, or causes, of reduced growth and mortality of newly settled larvae, recruits, and juveniles have, for the most part, only recently been investigated.

Encrusting invertebrates (particularly sponges) can be especially inhospitable for newly settled corals. In cryptic habitats, newly settled corals are likely to lose out by

overgrowth of fast-growing heterotrophic groups such as sponges, bryozoans, and bivalves (Vermeij, 2005). Aerts and van Soest (1997) determined the impact of sponges on coral survival to be greatly species specific. Physical, chemical, and biological properties of benthic invertebrates may inhibit coral growth and survival. Some studies used chemical extracts of sponges (Sullivan et al., 1983; Pawlik et al., 2007) to show that allelopathy can negatively impact adult corals. Coral recruits are even more susceptible to stress, yet surprisingly few studies have examined secondary metabolites for their impact on the early life history stages of corals. A field study by Maida et al. (1995) suggested that allelopathy reduced recruitment of corals adjacent to the octocorals *Simularia flexibilis* and *Sarcophyton glaucum*, and both the live octocorals and settlement plates with dichloromethane extracts of *S. flexibilis* inhibited coral settlement and survival. More long-term, small spatial scale (millimeters to centimeters) studies are needed to determine the effect of benthic invertebrates on post-settlement survival (Edmunds et al., 2004; Vermeij, 2006).

Areas of high algal biomass are known to be poor nursery habitats for settling corals (Birkeland, 1977; Bak and Engel, 1979; Harriott, 1983; Birrell et al., 2008b; Vermeij and Sandin, 2008; Vermeij et al., 2009). There are several mechanisms by which algae may be deleterious to corals. Algae may interfere with larval settlement by simply preempting available settlement space (Mumby et al., 2006; Box and Mumby, 2007). At least one species of turf algae alone (without sediment) has reduced settlement of corals in laboratory experiments (Birrell et al., 2005). More direct physical interactions including algal shading, abrasion, or basal encroachment can result in reduced coral growth or increased mortality (Lirman, 2001; McCook et al., 2001). Shading by the encrusting brown alga *Lobophora variegata* over six months caused a 50% increase in mortality of juvenile *Agaricia agaricites* (less than 20 mm diameter), and the mere presence of *L. variegata* around the coral reduced colony growth by 60% (Box and Mumby, 2007). However, shading by *Dictyota pulchella* resulted in no direct mortality but caused a 99% decrease in coral growth. Other studies have determined that *Lobophora variegata* (in the absence of grazing) is a superior competitor to Caribbean corals, including *A. agaricites*, *A. lamarcki*, *Meandrina meandrites*, *Mycetophyllia aliciae*, and *Stephanocoenia intersepta*, and to at least one species of Pacific coral, *Porites cylindrica* (De Ruyter van Steveninck et al., 1988; Jompa and McCook, 2003). Thus, it is likely that community phase shifts to high algal biomass decrease recruitment by reducing larval settlement and post-settlement survival (Hughes and Tanner, 2000; Kuffner et al., 2006).



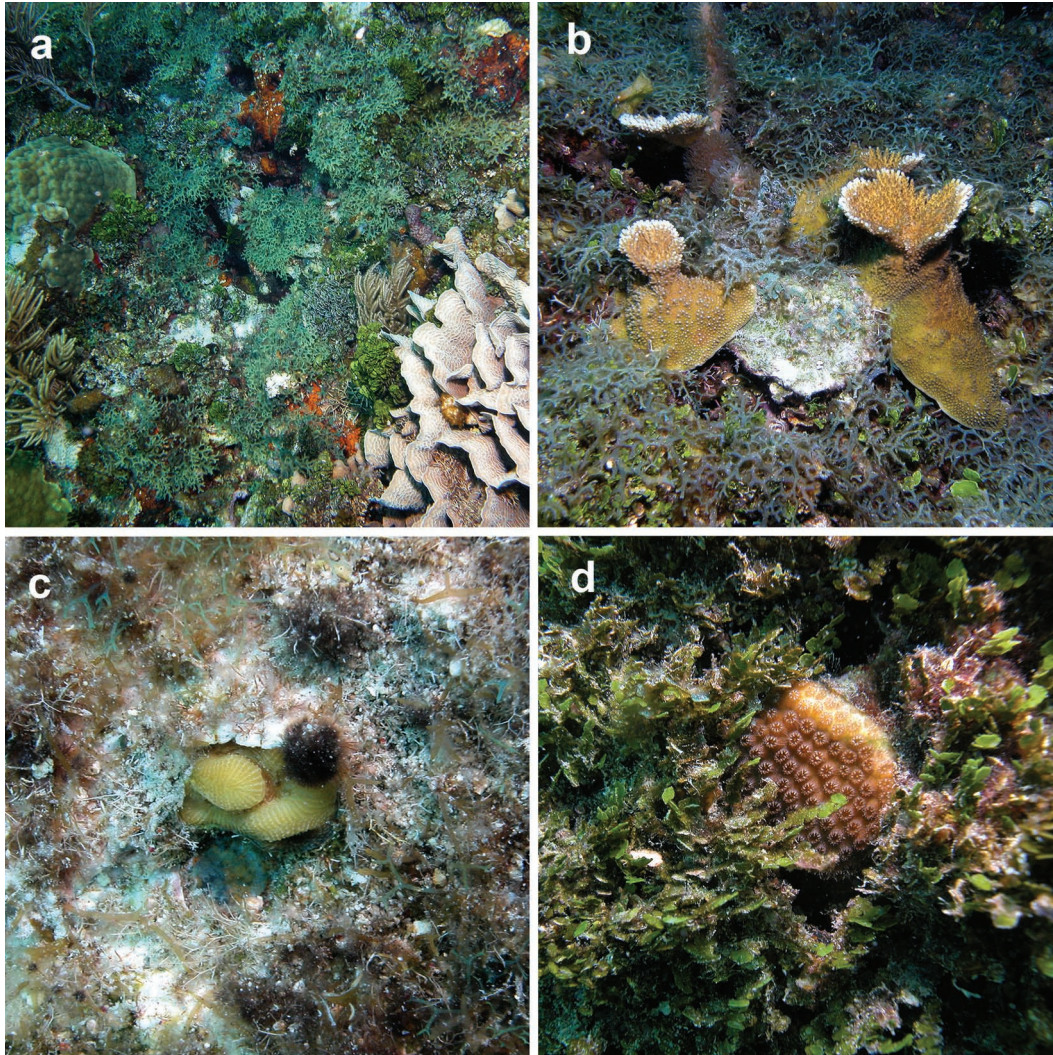


FIGURE 5. Macroalgae can be a dominant space occupier on degraded reefs and can inhibit coral recruitment at multiple life history stages. a, The macroalgae *Dictyota* spp. and *Halimeda opuntia* covered most of the benthos on this Belize reef, potentially inhibiting coral settlement. b, Recruits of *Acropora palmata* surrounded by *Dictyota* sp. c, A new recruit of *Diploria* sp. surrounded by *Gelidiella*, *Jania*, *Dictyota*, and the cyanobacterium *Dichothrix* sp. d, *Montastraea annularis* overgrown by *Halimeda* sp. (All photographs by Raphael Ritson-Williams.)

Reduced coral recruitment in algal-dominated reefs (Edmunds and Carpenter, 2001; Birrell et al., 2005) is thought to be in part the consequence of chemically induced mortality or the increased biomass of fleshy algae actually functioning as a reservoir for coral pathogens (Littler and Littler, 1997; Nugues et al., 2004). Bak and Borsboom (1984) proposed that the reduction in water flow adjacent to macroalgae could cause increased coral mortality through changes in the flow regime and increased allelochemical concentrations. Most recently, enhanced microbial activity caused by algal

exudates has been proposed as a mechanism of competition (Smith et al., 2006; Vermeij et al., 2009). Kline et al. (2006) determined that elevated levels of dissolved organic carbon, which can occur in areas of high algal biomass, increased the growth rate of microbes living in the mucopolysaccharide layer of corals. These studies all suggest that the detrimental effect of algae on corals could be mediated by several properties of macrophytes.

On modern reefs, algal-related post-settlement mortality probably decreases the population density of coral



recruits. Vermeij (2006) compared his recruitment study in Curacao from 1998 to 2004 to that of Van Moorsel (1989) from 1979 to 1981, using the same method in the same location. Recruit densities on the topsides of settlement panels in the more recent study were 5.16 times lower and recruitment on the undersides was 1.14 times lower than the 1979–1981 study. Macroalgae had replaced CCA as the dominant topside space occupier, creating a less-suitable habitat for coral recruitment compared to the crustose algae that had dominated the same site roughly 20 years earlier. In places where *Diadema* urchin recovery and grazing have reduced algal abundance, the population density of juvenile corals has increased (Edmunds and Carpenter, 2001; Aronson et al., 2004; Macintyre et al., 2005).

While herbivory can improve the recruitment potential by keeping reefs relatively free of algae, it can also be a potential cause of mortality for newly settled corals. Grazing rates on exposed outer surfaces of shallow reefs are extremely high, exceeding thousands of bites per square meter per day (Carpenter, 1986; Steneck and Dethier, 1994; Steneck and Lang, 2003). Bites, especially from parrotfish that graze deeply into carbonate substrates, would easily kill a newly settled coral. Few studies have documented recruit mortality resulting from fish grazing (Mumby et al., 2006), although it has been suggested as the cause of the low number of recruits observed on the top surface of settlement plates (Adjeroud et al., 2007). The herbivorous sea urchin *Diadema antillarum* was shown to be a significant agent of mortality for newly settled corals (Sammarco and Carleton, 1981). The highest mortality of newly settled corals is likely to occur on outer exposed surfaces where algal growth rates and herbivore grazing rates are greatest and rates of sedimentation are highest. In shallow reef habitats where algal growth and herbivory rates are greatest, coral recruitment is greater in subcryptic microhabitats (Bak and Engel, 1979). However, which microhabitats increase post-settlement survival has rarely been tested (but see Babcock and Mundy, 1996).

#### POST-SETTLEMENT GROWTH RATES

Given the vulnerability of small size classes, the adaptive advantages of rapid growth rates are obvious. Coral recruit survival is not merely a function of the attributes of the settlement substrate but also of the coral's ability to resist overgrowth by neighboring encrusting invertebrates and algae (Richmond, 1997). As new corals grow, their mortality rates decline (Vermeij and Sandin, 2008), and they are less likely to be overgrown by competitors

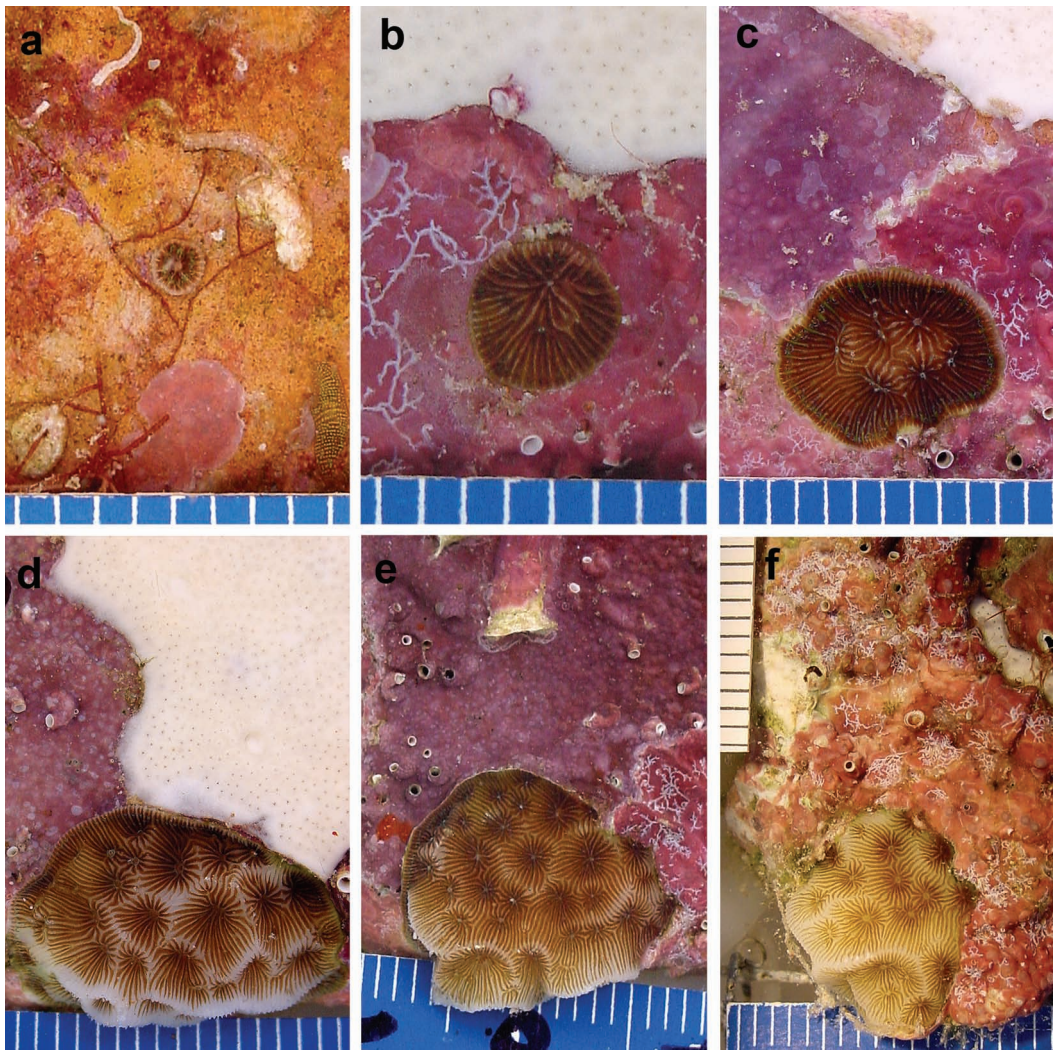
(Hughes and Jackson, 1985). Often, however, the slow growth rates of newly settled corals make this a losing battle, and early post-settlement mortality is generally high (Figure 6; Bak and Engel, 1979; Edmunds, 2000; Vermeij and Sandin, 2008). Even in a controlled environment, laboratory studies showed that a coral that remains less than 3 mm in diameter for two or three months has only a 20% chance of survival (Rylaarsdam, 1983). Field studies report a huge amount of variance in early post-settlement mortality. Babcock (1985) found post-settlement survivorship over the first three to six months ranged from 16% to 71%, whereas more recently Box and Mumby (2007) determined a monthly estimated mortality rate for *Agaricia agaricites* to be 3.5% per month. Annual juvenile coral survivorship estimates range from 0% to 77% (Smith, 1992; Wittenberg and Hunte, 1992; Maida et al., 1994; Smith, 1997; Edmunds, 2000).

Different species of corals have distinctly different rates of growth and ability to recover following a disturbance (Wakeford et al., 2008). Specifically, some of the Indo-Pacific acroporid corals (e.g., *Acropora tenuis*) are extremely “weedy” and are capable of growing nearly 6 cm in 1.5 years (Omori et al., 2008); this translates to an average growth rate of 3.2 mm/month compared to the much slower growth rates reported for *Oxypora* sp. as ranging between 0.2 and 0.5 mm/month (Babcock and Mundy, 1996).

Settlement habitat also influences growth rates of newly settled corals. Subcryptic habitats protect coral recruits from stresses and disturbances common on outer reef surfaces, but they will invariably have lower productivity potential. Diameters of *Platygyra* sp. and *Oxypora* sp. settlers increased one-quarter to one-half as fast in cryptic undersides than they did on upper exposed surfaces for the two species, respectively (Babcock and Mundy, 1996). Importantly, however, new recruits that selected subcryptic microhabitats had higher survivorship despite their slower growth rates (Babcock and Mundy, 1996).

#### VARIABILITY OF POST-SETTLEMENT SURVIVAL AND GROWTH: THE ROLES OF BIODIVERSITY AND LIFE HISTORY STRATEGIES

Before the disease-induced *Acropora* spp. decline in the Caribbean, fundamental differences existed between acroporid-dominated reefs of the Caribbean and Indo-Pacific regions. Caribbean reefs are largely built by two species of *Acropora*. Both species recruit rarely (Rylaarsdam, 1983;



**FIGURE 6.** A time series of the growth of *Agaricia* sp. settled on a terracotta tile in Bonaire over 3.75 years. After March 2007 (e), this recruit is being overgrown by the coralline alga *Titanoderma prototypum*, a known settlement-facilitating species, illustrating just how hazardous the settlement environment can be. a, June 2004, recruit diameter is 1.3 mm; b, March 2005, 3.4 mm; c, July 2005, 8.4 mm; d, June 2006, 15.2 mm; e, March 2007, 16.0 mm; f, March 2008, 12.0 mm. One segment on the scale bar = 1 mm. (All photographs by Suzanne Arnold.)

Sammarco, 1985), but their clonal growth created massive monocultures of rapidly growing reefs capable of keeping up with rising sea level (Adey, 1978). In contrast, there are two orders of magnitude more species of *Acropora* on Indo-Pacific coral reefs, and the population density of their recruits are also orders of magnitude greater on Indo-Pacific reefs than on Caribbean reefs (Hughes et al., 1999).

Although the high diversity of acroporid corals in the Pacific spans the spectrum of life history characteristics from weeds (i.e., high reproductive output and rapid

growth rate; Omori et al., 2008) to trees (i.e., competitively dominant, large colonies; Baird and Hughes, 2000), the two acroporid species comprising Caribbean reefs require long adult lives and considerable clonal propagation. However, since the acroporid die-off in the early 1980s, Caribbean reefs have fundamentally changed. Because of the resultant algal phase shift (Hughes, 1994), acroporid reefs have become hostile to the rare acroporid recruits, and they have lost their receptivity for reattachment of encrusting fragments (Williams et al., 2008). These changes on many

Caribbean reefs may be the primary reason why they appear less capable of recovering from widespread disturbances such as coral disease and bleaching.

The massive, slow-growing coral *Montastraea annularis* is also a broadcast spawner and framework builder in the Caribbean. It also has very low rates of recruitment (Hughes and Tanner, 2000) and thus requires long adult life to establish its dominance. Although it dominates Caribbean reefs today (Kramer, 2003) and is relatively hardy, it too has shown elevated levels of disease in recent years (Pantos et al., 2003) and has increased susceptibility to disease after bleaching (Miller et al., 2006). Again, the long-term prognosis for this Caribbean reef builder is poor.

Weedy, brooding species such as *Agaricia* spp. and *Porites* spp. are the thrust behind the current rates of coral recruitment in the Caribbean. The Caribbean brooder *Agaricia agaricites* is often the most abundant recruit on Caribbean reefs in recent times (Bak and Engel, 1979). This species has well-documented high rates of recruitment and adequate sediment-rejection capabilities yet regenerates poorly from lesions and is often outcompeted by other corals (Bak and Engel, 1979). In the past 30 years *Agaricia tenuifolia* has replaced other corals to dominate the community on two reefs that had historically different community compositions (Aronson et al., 2004). The increasing community dominance observed for *Porites astreoides* at six sites in the Caribbean is being driven by a constant recruitment rate coinciding with reduced percent cover of other coral species (Green et al., 2008).

It is possible that these life history-related differences are fundamentally changing Caribbean reefs. Are Caribbean reefs today following the paths of forests and other marine ecosystems in their shift to weedy, stress-tolerant species? (see Knowlton, 2001). A recovery such as seen in Palau following the 1998 bleaching event, where sexual recruitment and remnant regrowth were equal contributors (Golbuu et al., 2007), has yet to be recorded in the Caribbean. Success stories of Caribbean recoveries led by broadcast spawning species are scarce (but see Idjadi et al., 2006). Thus, the relative importance of sexual versus asexual reproduction to recovery in the Caribbean needs to be addressed by long-term observations with particular focus on recovery following large-scale disturbances such as major storms and bleaching events.

Thus, it seems that Caribbean reefs were built by corals that have been successful since the Pleistocene (Pandolfi and Jackson, 2006) with a strategy of low recruitment, considerable clonal growth, and low post-settlement mortality. However, that strategy may not be broadly viable today, given the global climate trajectory

(Hoegh-Guldberg et al., 2007) and patterns of human activities. While Indo-Pacific reefs are not immune to declines in rates of coral recruitment in recent years (Wakeford et al., 2008), the higher biodiversity and range of recruitment and post-recruitment strategies (e.g., high rates of growth) allow reefs there to be more resilient.

## CONCLUSIONS

Coral mortality has increased in recent decades, making coral recruitment more important than ever before in sustaining coral reef ecosystems and contributing to their resilience. We identified three critical sequential phases to the recruitment process of corals: larval availability, larval settlement, and post-settlement ecology. All three factors are necessary for coral recruitment and, ultimately, for maintenance or recovery of coral reef ecosystems.

Most coral planulae available for recruitment are probably from relatively local reproduction and relatively short-distance connectivity. As adult coral abundance declines, both fertilization success and the effective dispersal distance of corals (see Figure 3B) will likely decline as well. Physiological stress on reproducing corals might also result in fewer and possibly weaker coral larvae arriving, thereby reducing the per capita rate of settlement success.

Once in the vicinity of a coral reef, settling corals respond to a hierarchy of environmental cues both in the water and from the reef. Several studies have identified organisms that facilitate or inhibit the settlement and metamorphosis of corals. Crustose coralline algae can facilitate coral settlement but, disturbingly, this group of algae is becoming rarer on coral reefs as macroalgae become increasingly dominant. Macroalgae are known inhibitors of settlement, which may result from their ability to rapidly occupy settlement habitat, their suite of secondary metabolites, their microbial communities, or a combination of some or all of these mechanisms.

Stressors that impact multiple life history stages of corals have the most potential to greatly reduce coral recruitment. Poor water quality (such as sedimentation and increased temperatures) and the increased abundance of macroalgae are known to decrease coral recruitment and negatively impact corals at many different life history stages. Human impacts on the water quality of marine systems continue to grow, and few locations remain untouched (Halpern et al., 2008). These and other stressors may decrease the reproductive output of corals, physiologically stress the larvae, block subcryptic nursery habitats, create negative settlement cues, and result in increased post-settlement mortality.



Globally, many Indo-Pacific reefs have higher rates of settlement, recruitment, and recovery from disturbances, which could be the result of higher biodiversity in the region. In contrast, Caribbean reefs may have evolved a strategy of low recruitment and considerable clonal growth, with low post-settlement mortality for its few reef-building acroporid corals. Unfortunately, that strategy may be ineffective in the future given the global climate trajectory of higher ocean temperatures, acidification, and greater disturbance from tropical storms, which will continue to physiologically stress corals. Because Indo-Pacific reefs have two orders of magnitude more acroporid species, weedy and potentially resilient strategies could succeed. If current trends continue on modern reefs, it is possible that reefs in the future will differ from those of the recent past.

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#### LITERATURE CITED

- Adey, W. 1978. Coral Reef Morphogenesis: A Multidimensional Model. *Science*, 202:831–837.
- Adjeroud, M., L. Penin, and A. Carroll. 2007. Spatio-temporal Heterogeneity in Coral Recruitment around Moorea, French Polynesia: Implications for Population Maintenance. *Journal of Experimental Marine Biology and Ecology*, 341:204–218.
- Aerts, L.A.M., and R. W. M. van Soest. 1997. Quantification of Sponge/Coral Interactions in a Physically Stressed Reef Community, NE Colombia. *Marine Ecology Progress Series*, 148:125–134.
- Albright, R., B. Mason, and C. Langdon. 2008. Effect of Aragonite Saturation State on Settlement and Post-settlement Growth of *Porites astreoides* Larvae. *Coral Reefs*, 27:485–490.
- Aronson, R.B., I. G. Macintyre, C. M. Wapnick, and W. O. O'Neill. 2004. Phase Shifts, Alternative States, and the Unprecedented Convergence of Two Reef Systems. *Ecology*, 85:1876–1891.
- Ayre, D. J., and T. P. Hughes. 2000. Genotypic Diversity and Gene Flow in Brooding and Spawning Corals along the Great Barrier Reef, Australia. *Evolution*, 54:1590–1605.
- . 2004. Climate Change, Genotypic Diversity and Gene Flow in Reef-Building Corals. *Ecology Letters*, 7:273–278.
- Babcock, R. 1985. Growth and Mortality in Juvenile Corals: The First Year. *Proceedings of the 8th International Coral Reef Symposium*, 2:1197–1202.
- . 1995. Synchronous Multispecific Spawning on Coral Reefs: Potential for Hybridization and Roles of Gamete Recognition. *Reproduction, Fertility and Development*, 7:943–950.
- Babcock, R., and C. Mundy. 1996. Coral Recruitment: Consequences of Settlement Choice for Early Growth and Survivorship in Two Scleractinians. *Journal of Experimental Marine Biology and Ecology*, 206:179–201.
- Babcock, R. C. and A. J. Heyward. 1986. Larval Development of Certain Gamete-Spawning Scleractinian Corals. *Coral Reefs*, 5:111–116.
- Baird, A. H., R.C. Babcock, and C. P. Mundy. 2003. Habitat Selection by Larvae Influences the Depth Distribution of Six Common Coral Species. *Marine Ecology Progress Series*, 252:289–293.
- Baird, A. H., J. Gilmour, T. M. Kamiki, M. Nonada, M. S. Pratchett, H. H. Yamamoto, and H. Yamasaki. 2006. Temperature Tolerance of Symbiotic and Non-symbiotic Coral Larvae. *Proceedings of the 10th International Coral Reef Symposium*, 1:351–358.
- Baird, A. H., and T. P. Hughes. 2000. Competitive Dominance by Tabular Corals: An Experimental Analysis of Recruitment and Survival of Understory Assemblages. *Journal of Experimental Marine Biology and Ecology*, 251:117–132.
- Baird, A. H., and A. N. C. Morse. 2004. Induction of Metamorphosis in Larvae of the Brooding Corals *Acropora palifera* and *Stylophora pistillata*. *Marine and Freshwater Research*, 55:469–472.
- Bak, R. P. M., and J. L. A. Borsboom. 1984. Allelopathic Interaction between a Reef Coelenterate and Benthic Algae. *Oecologia (Berlin)*, 63:194–198.
- Bak, R. P. M., and M. S. Engel. 1979. Distribution, Abundance and Survival of Juvenile Hermatypic Corals (Scleractinia) and the Importance of Life History Strategies in the Parent Coral Community. *Marine Biology*, 54:341–352.
- Bassim, K. M., and P. W. Sammarco. 2003. Effects of Temperature and Ammonium on Larval Development and Survivorship in a Scleractinian Coral (*Diploria strigosa*). *Marine Biology*, 142:241–252.
- Baums, I. B., M. W. Miller, and M. E. Hellberg. 2005. Regionally Isolated Populations of an Imperiled Caribbean Coral, *Acropora palmata*. *Molecular Ecology*, 14:1377–1390.
- . 2006. Geographic Variation in Clonal Structure in a Reef-Building Caribbean Coral, *Acropora palmata*. *Ecological Monographs*, 76:503–519.
- Bennett, C. E., and D. J. Marshall. 2005. The Relative Energetic Costs of the Larval Period, Larval Swimming and Metamorphosis for the Ascidian *Diplosoma listerianum*. *Marine and Freshwater Behaviour and Physiology*, 38:21–29.
- Birkeland, C. 1977. The Importance of Rate of Biomass Accumulation in Early Successional Stages of Benthic Communities to the Survival of Coral Recruits. In *Proceedings of the 3rd International Coral Reef Symposium, Miami*, 1:15–21.
- Birrell, C. L., L. J. McCook, and B. L. Willis. 2005. Effects of Algal Turfs and Sediment on Coral Settlement. *Marine Pollution Bulletin*, 51:408–414.
- Birrell, C. L., L. J. McCook, B. L. Willis, and L. Harrington. 2008a. Chemical Effects of Macroalgae on Larval Settlement of the Broadcast Spawning Coral *Acropora millepora*. *Marine Ecology Progress Series*, 362:129–137.



- Birrell, C. L., L. J. McCook, B. L. Willis, and G. A. Diaz-Pulido. 2008b. Effects of Benthic Algae on the Replenishment of Corals and the Implications for the Resilience of Coral Reefs. *Oceanography and Marine Biology: An Annual Review*, 46:25–63.
- Box, S. J., and P. J. Mumby. 2007. Effect of Macroalgal Competition on Growth and Survival of Juvenile Caribbean corals. *Marine Ecology Progress Series*, 342:139–149.
- Bruno, J. F., and E. R. Selig. 2007. Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLOS One*, 8:1–8.
- Carlson, D. B. 2001. Depth-Related Patterns of Coral Recruitment and Cryptic Suspension-Feeding Invertebrates on Guana Island, British Virgin Islands. *Bulletin of Marine Science*, 68:525–541.
- . 2002. Production and Supply of Larvae as Determinants of Zonation in a Brooding Tropical Coral. *Journal of Experimental Marine Biology and Ecology*, 268:33–46.
- Carlson, D. B., and R. R. Olson. 1993. Larval Dispersal Distance as an Explanation for Adult Spatial Pattern in Two Caribbean Reef Corals. *Journal of Experimental Marine Biology and Ecology*, 173:247–263.
- Carpenter, R. C. 1986. Partitioning Herbivory and Its Effects on Coral Reef Algal Communities. *Ecological Monographs*, 56:343–363.
- Chiu, J. M. Y., T. Y. T. Ng, W. X. Wang, V. Thiyagarajan, and P. Y. Qian. 2007. Latent Effects of Larval Food Limitation on Filtration Rate, Carbon Assimilation and Growth in Juvenile Gastropod *Crepidula onyx*. *Marine Ecology Progress Series*, 343:173–182.
- Chiu, J. M. Y., H. Wang, V. Thiyagarajan, and P. Y. Qian. 2008. Differential Timing of Larval Starvation Effects on Filtration Rate and Growth in Juvenile *Crepidula onyx*. *Marine Biology*, 154:91–98.
- Chornesky, E. A., and E. C. Peters. 1987. Sexual Reproduction and Colony Growth in the Scleractinian Coral *Porites astreoides*. *Biological Bulletin*, 172:161–177.
- Coll, J. C., B. F. Bowden, G. V. Meehan, G. M. Konig, A. R. Carroll, D. M. Tapiolas, P. M. Aliño, A. Heaton, R. De Nys, P. A. Leone, M. Maida, T. L. Aceret, R. H. Willis, R. C. Babcock, B. L. Willis, Z. Florian, M. N. Clayton, and R. L. Miller. 1994. Chemical Aspects of Mass Spawning in Corals. I. Sperm-Attractant Molecules in the Eggs of the Scleractinian Coral *Montipora digitata*. *Marine Biology*, 118:117–182.
- Coma, R., and H. R. Lasker. 1997. Effects of Spatial Distribution and Reproductive Biology on *In Situ* Fertilization Rates of a Broadcast-Spawning Invertebrate. *Biological Bulletin*, 193:20–29.
- Connell, J. H. 1997. Disturbance and Recovery of Coral Assemblages. *Coral Reefs*, 16:S101–S113.
- Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-Year Study of Coral Abundance, Recruitment, and Disturbance at Several Scales in Space and Time. *Ecological Monographs*, 67:461–488.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of Marine Populations: Open or Closed? *Science*, 287:857–859.
- Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of Connectivity in Marine Populations. *Science*, 311:522–527.
- de Ruyter van Steveninck, E. D., L. L. Van Mulekom, and A. M. Bree-man. 1988. Growth Inhibition of *Lobophora variegata* (Lamouroux) Womersley by Scleractinian Corals. *Journal of Experimental Marine Biology and Ecology*, 115:169–178.
- Doherty, P., and T. Fowler. 1994. An Empirical Test of Recruitment Limitation in a Coral Reef Fish. *Science*, 263:935–939.
- Done, T. 1992. Phase Shifts in Coral Reef Communities and Their Ecological Significance. *Hydrobiologia*, 247:121–132.
- Downs, C. A., C. M. Woodley, R. H. Richmond, L. L. Lanning, and R. Owen. 2005. Shifting the Paradigm of Coral-Reef ‘Health’ Assessment. *Marine Pollution Bulletin*, 51:486–494.
- Edmunds, P. J. 2000. Patterns in the Distribution of Juvenile Corals and Coral Reef Community Structure in St. John, US Virgin Islands. *Marine Ecology Progress Series*, 202:113–124.
- Edmunds, P. J., J. F. Bruno, and D. B. Carlson. 2004. Effects of Depth and Microhabitat on Growth and Survivorship of Juvenile Corals in the Florida Keys. *Marine Ecology Progress Series*, 278:115–124.
- Edmunds, P. J., and R. C. Carpenter. 2001. Recovery of *Diadema antillarum* Reduces Macroalgal Cover and Increases Abundance of Juvenile Corals on a Caribbean Reef. *Proceedings of the National Academy of Sciences of the United States of America*, 98:5067–5071.
- Edmunds, P. J., R. D. Gates, and D. F. Gleason. 2001. The Biology of Larvae from the Reef Coral *Porites astreoides*, and Their Response to Temperature Disturbances. *Marine Biology*, 139:981–989.
- Edmunds, P. J., R. D. Gates, W. Leggat, O. Hoegh-Guldberg, and L. Allen-Requa. 2005. The Effect of Temperature on the Size and Population Density of Dinoflagellates in Larvae of the Reef Coral *Porites astreoides*. *Invertebrate Biology*, 124:185–193.
- Fabricius, K. E., and J. Metzner. 2004. Scleractinian Walls of Mouths: Predation on Coral Larvae by Corals. *Coral Reefs*, 23:245–248.
- Fadlallah, Y. H. 1983. Sexual Reproduction, Development and Larval Biology in Scleractinian Corals. *Coral Reefs*, 2:129–150.
- Fautin, D. G. 2003. Reproduction of Cnidaria. *Canadian Journal of Zoology*, 80:1735–1754.
- Fearon, R. J., and A. M. Cameron. 1996. Larvotoxic Extracts of the Hard Coral *Goniopora tenuidens*: Allelochemicals That Limit Settlement of Potential Competitors? *Toxicon*, 34:361–367.
- Fenner, D., and K. Banks. 2004. Orange Cup Coral *Tubastraea coccinea* Invades Florida and the Flower Garden Banks, Northwestern Gulf of Mexico. *Coral Reefs*, 23:505–507.
- Fine, M., H. Zibrowius, and Y. Loya. 2001. *Oculina patagonica*: A Non-Lessepsian Scleractinian Coral Invading the Mediterranean Sea. *Marine Biology*, 138:1195–1203.
- Foster, N. L., S. J. Box, and P. J. Mumby. 2008. Competitive Effects of Macroalgae on the Fecundity of the Reef-Building Coral *Montastraea annularis*. *Marine Ecology Progress Series*, 367:143–152.
- Gaines, S., and J. Roughgarden. 1985. Larval Settlement Rate: A Leading Determinant of Structure in an Ecological Community of the Marine Intertidal Zone. *Proceedings of the National Academy of Sciences of the United States of America*, 82:3707–3711.
- Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term Region-wide Declines in Caribbean Corals. *Science*, 301:958–960.
- Gilmour, J. 1999. Experimental Investigation into the Effects of Suspended Sediment on Fertilization, Larval Survival and Settlement in a Scleractinian Coral. *Marine Biology*, 135:451–462.
- Gleason, D. F., P. J. Edmunds, and R. D. Gates. 2006. Ultraviolet Radiation Effects on the Behavior and Recruitment of Larvae from the Reef Coral *Porites astreoides*. *Marine Biology*, 148:503–512.
- Golbuu, Y., and R. H. Richmond. 2007. Substratum Preferences in Planula Larvae of Two Species of Scleractinian Corals, *Goniastrea retiformis* and *Stylaraea punctata*. *Marine Biology*, 152:639–644.
- Golbuu, Y., S. Victor, L. Penland, D. Idip, C. Emaurois, K. Okaji, H. Yukihiro, A. Iwase, and R. van Woesik. 2007. Palau’s Coral Reefs Show Differential Habitat Recovery Following the 1998 Bleaching Event. *Coral Reefs*, 26:319–332.
- Graham, E. M., A. H. Baird, and S. R. Connolly. 2008. Survival Dynamics of Scleractinian Coral Larvae and Implications for Dispersal. *Coral Reefs*, 27:529–539.
- Green, D. H., P. J. Edmunds, and R. C. Carpenter. 2008. Increasing Relative Abundance of *Porites astreoides* on Caribbean Reefs Mediated by an Overall Decline in Coral Cover. *Marine Ecology Progress Series*, 359:1–10.

- Guzman, H. M., K. A. Burns, and J. B. C. Jackson. 1994. Injury, Regeneration and Growth of Caribbean Reef Corals after a Major Oil Spill in Panama. *Marine Ecology Progress Series*, 105:231–241.
- Hadfield, M. G., and V. J. Paul. 2001. Natural Chemical Cues for Settlement and Metamorphosis of Marine Invertebrate Larvae. In *Marine Chemical Ecology*, ed. J. McClintock and B. Baker, pp. 431–462. Boca Raton: CRC Press.
- Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A Global Map of Human Impact on Marine Ecosystems. *Science*, 319:948–952.
- Harrington, L., K. Fabricius, G. De'ath, and A. Negri. 2004. Recognition and Selection of Settlement Substrata Determine Post-settlement Survival in Corals. *Ecology*, 85:3428–3437.
- Harriott, V. J. 1983. Reproductive Seasonality, Settlement, and Post-settlement Mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. *Coral Reefs*, 2:151–157.
- Harrison, P. L., R. C. Babcock, G. D. Bull, J. K. Oliver, C. C. Wallace, and B. L. Willis. 1984. Mass Spawning in Tropical Reef Corals. *Science*, 223:1186–1189.
- Hatta, M., H. Fukami, W. Q. Wang, M. Omori, K. Shimoike, T. Hayashibara, Y. Ina, and T. Sugiyama. 1999. Reproductive and Genetic Evidence for a Reticulate Evolutionary History of Mass-Spawning Corals. *Molecular Biology and Evolution*, 16:1607–1613.
- Heintz, R. A., S. D. Rice, A. C. Wertheimer, R. F. Bradshaw, F. P. Thrower, J. E. Joyce, and J. W. Short. 2000. Delayed Effects on Growth and Marine Survival of Pink Salmon *Oncorhynchus gorbuscha* after Exposure to Crude Oil During Embryonic Development. *Marine Ecology Progress Series*, 208:205–216.
- Hellberg, M. E. 2007. Footprints on Water: The Genetic Wake of Dispersal among Reefs. *Coral Reefs*, 26:463–473.
- Heyward, A. J., and A. P. Negri. 1999. Natural Inducers for Coral Larval Metamorphosis. *Coral Reefs*, 18:273–279.
- Hodgson, G. 1990. Sediment and the Settlement of Larvae of the Reef Coral *Pocillopora damicornis*. *Coral Reefs*, 9:41–43.
- Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Calderira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatzioles. 2007. Coral Reefs under Rapid Climate Change and Ocean Acidification. *Science*, 318:1737–1742.
- Holling, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4:1–23.
- Hughes, T. 1984. Population Dynamics Based on Individual Size Rather Than Age: A General Model with a Reef Coral Example. *American Naturalist*, 123:778–795.
- Hughes, T., and J. B. C. Jackson. 1985. Population Dynamics and Life Histories of Foliose Corals. *Ecological Monographs*, 55:141–166.
- Hughes, T. P. 1994. Catastrophes, Phase-Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, 265:1547–1551.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschanivskij, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 1999. Patterns of Recruitment and Abundance of Corals along the Great Barrier Reef. *Nature (London)*, 397:59–63.
- Hughes, T. P., D. R. Bellwood, C. Folke, R. Steneck, and J. Wilson. 2005. New Paradigms for Supporting the Resilience of Marine Ecosystems. *Trends in Ecology and Evolution*, 20:380–386.
- Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanivskij, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology*, 17:360–365.
- Hughes, T. P., and J. E. Tanner. 2000. Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals. *Ecology*, 81:2250–2263.
- Humphrey, C., M. Weber, C. Lott, T. Cooper, and K. Fabricius. 2008. Effects of Suspended Sediments, Dissolved Inorganic Nutrients and Salinity on Fertilisation and Embryo Development in the Coral *Acropora millepora* (Ehrenberg, 1834). *Coral Reefs*, 27:837–850.
- Idjadi, J. A., S. C. Lee, J. F. Bruno, W. F. Precht, L. Allen-Requa, and P. J. Edmunds. 2006. Rapid Phase-Shift Reversal on a Jamaican Coral Reef. *Coral Reefs*, 25:209–211.
- Jackson, J. B. C., and L. Buss. 1975. Allelopathy and Spatial Competition among Coral Reef Invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 72:5160–5163.
- Johnson, C. R., C. D. Muir, and A.-L. Reysenback. 1991. Characteristic Bacteria Associated with the Surfaces of Coralline Algae: A Hypothesis for Bacterial Induction of Marine Invertebrate Larvae. *Marine Ecology Progress Series*, 74:281–294.
- Jompa, J., and L. J. McCook. 2003. Contrasting Effects of Turf Algae on Corals: Massive *Porites* spp. Are Unaffected by Mixed-Species Turfs, But Killed by the Red Alga *Anotrichium tenue*. *Marine Ecology Progress Series*, 258:79–86.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. *Oikos*, 69:373–386.
- . 1997. Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, 78:1946–1957.
- Kline, D. I., N. M. Kuntz, M. Breitbart, N. Knowlton, and F. Rohwer. 2006. Role of Elevated Organic Carbon Levels and Microbial Activity in Coral Mortality. *Marine Ecology Progress Series*, 314:119–125.
- Knowlton, N. 2001. The Future of Coral Reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 98:5419–5425.
- Koop, K., D. Booth, A. Broadbent, J. Brodie, D. Bucher, D. Capone, J. Coll, W. Dennison, M. Erdmann, P. Harrison, O. Hoegh-Guldberg, P. Hutchings, G. B. Jones, A. W. D. Larkum, J. O'Neil, A. Steven, E. Tentori, S. Ward, J. Williamson, and D. Yellowlees. 2001. ENCORE: The Effect of Nutrient Enrichment on Coral Reefs. SYNTHESIS OF RESULTS AND CONCLUSIONS. *Marine Pollution Bulletin*, 42:91–120.
- Kramer, P. A. 2003. Synthesis of Coral Reef Health Indicators for the Western Atlantic: Results of the AGRRA Program (1997–2000). *Atoll Research Bulletin*, 496:1–58.
- Kuffner, I. B. 2001. Effects of Ultraviolet Radiation on Larval Recruitment of the Reef Coral, *Pocillopora damicornis*. *Marine Ecology Progress Series*, 217:251–261.
- Kuffner, I. B., and V. J. Paul. 2004. Effects of the Benthic Cyanobacterium *Lyngbya majuscula* on the Larval Settlement of the Reef Corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs*, 23:455–458.
- Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. Beach. 2006. Inhibition of Coral Recruitment by Macroalgae and Cyanobacteria. *Marine Ecology Progress Series*, 323:107–117.
- Lee, S. C. 2006. Habitat Complexity and Consumer-Mediated Positive Feedbacks on a Caribbean Coral Reef. *Oikos*, 112:442–447.
- Levin, L. A. 2006. Recent Progress in Understanding Larval Dispersal: New Directions and Digressions. *Integrative and Comparative Biology*, 46:282–297.
- Levitan, D. R., H. Fukami, J. Jara, D. Kline, T. M. McGovern, K. E. McGhee, C. A. Swanson, and N. Knowlton. 2004. Mechanisms of Reproductive Isolation among Sympatric Broadcast-Spawning Corals of the *Montastraea annularis* Species Complex. *Evolution*, 58:308–323.
- Levitan, D. R., and T. M. McGovern. 2005. *The Allee Effect in the Sea*. Washington, D.C.: Island Press.

- Levitán, D. R., M. A. Sewell, and F. S. Chia. 1992. How Distribution and Abundance Influence Fertilization Success in the Sea Urchin *Strongylocentrotus franciscanus*. *Ecology*, 73:248–254.
- Lewis, J. B. 1974. The Settlement Behavior of Planulae Larvae of the Hermatypic Coral *Favia fragum* (Esper). *Journal of Experimental Marine Biology and Ecology*, 15:165–172.
- Lirman, D. 2001. Competition Between Macroalgae and Corals: Effects of Herbivore Exclusion and Increased Algal Biomass on Coral Survivorship and Growth. *Coral Reefs*, 19:392–399.
- Littler, M. M., and D. S. Littler. 1997. Disease-Induced Mass Mortality of Crustose Algae on Coral Reefs Provides Rationale for the Conservation of Herbivorous Fish Stocks. *Proceedings of the 8th International Coral Reef Symposium*, 1:719–724.
- Macintyre, I. G., P. W. Glynn, and F. Hinds. 2005. Evidence of the Role of *Diadema antillarum* in the Promotion of Coral Settlement and Survivorship. *Coral Reefs*, 24:273.
- Maida, M., J. C. Coll, and P. W. Sammarco. 1994. Shedding New Light on Scleractinian Coral Recruitment. *Journal of Experimental Marine Biology and Ecology*, 180:189–202.
- Maida, M., P. W. Sammarco, and J. C. Coll. 1995. Effects of Soft Corals on Scleractinian Coral Recruitment. I: Directional Allelopathy and Inhibition of Settlement. *Marine Ecology Progress Series*, 121:191–202.
- Marshall, D. J., J. A. Pechenik, and M. J. Keough. 2003. Larval Activity Levels and Delayed Metamorphosis Affect Post-larval Performance in the Colonial Ascidian *Diplosoma listerianum*. *Marine Ecology Progress Series*, 246:153–162.
- Maypa, A. P., and L. J. Raymundo. 2004. Algae-Coral Interactions. Mediation of Coral Settlement, Early Survival, and Growth by Macroalgae. *Silliman Journal*, 45:76–95.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, Maine: Belknap Press.
- McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition Between Corals and Algae on Coral Reefs: A Review of Evidence and Mechanisms. *Coral Reefs*, 19:400–417.
- Miller, J., R. Waara, E. Muller, and C. Rogers. 2006. Coral Bleaching and Disease Combine to Cause Extensive Mortality on Reefs in the US Virgin Islands. *Coral Reefs*, 25:418.
- Miller, K., and C. Mundy. 2003. Rapid Settlement in Broadcast Spawning Corals: Implications for Larval Dispersal. *Coral Reefs*, 22:99–106.
- Miller, S. E. 1993. Larval Period and Its Influence on Postlarval Life History: Comparison of Lecithotrophy and Facultative Planktotrophy in the Aeolid Nudibranch *Phestilla sibogae*. *Marine Biology*, 117:635–645.
- Morse, A. N. C., K. Iwao, M. Baba, K. Shimoike, T. Hayashibara, and M. Omori. 1996. An Ancient Chemosensory Mechanism Brings New Life to Coral Reefs. *Biological Bulletin*, 191:149–154.
- Morse, D. E., and A. N. C. Morse. 1991. Enzymatic Characterization of the Morphogen Recognized by *Agaricia humilis* (Scleractinian Coral) Larvae. *Biological Bulletin*, 181:104–122.
- Morse, D. E., A. N. C. Morse, P. T. Raimondi, and N. Hooker. 1994. Morphogen-Based Chemical Flypaper for *Agaricia humilis* Coral Larvae. *Biological Bulletin*, 186:172–181.
- Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. *Science*, 311:98–101.
- Mumby, P. J., and R. Steneck. 2008. Coral Reef Management and Conservation in the Light of Rapidly Evolving Ecological Paradigms. *Trends in Ecology and Evolution*, 23:555–563.
- Mundy, C. N., and R. C. Babcock. 1998. Role of Light Intensity and Spectral Quality in Coral Settlement: Implications for Depth-Dependent Settlement? *Journal of Experimental Marine Biology and Ecology*, 223:235–255.
- Negri, A. P., N. S. Webster, R. T. Hill, and A. J. Heyward. 2001. Metamorphosis of Broadcast Spawning Corals in Response to Bacteria Isolated from Crustose Algae. *Marine Ecology Progress Series*, 223:121–131.
- Nishikawa, A., M. Katoh, and K. Sakai. 2003. Larval Settlement Rates and Gene Flow of Broadcast-Spawning (*Acropora tenuis*) and Planula-Brooding (*Stylophora pistillata*) Corals. *Marine Ecology Progress Series*, 256:87–97.
- Nozawa, Y., and P. L. Harrison. 2008. Temporal Patterns of Larval Settlement and Survivorship of Two Broadcast-Spawning Acroporid Corals. *Marine Biology* 155:347–351.
- Nugues, M. M., G. W. Smith, R. J. Van Hooindonk, M. I. Seabra, and R. P. M. Bak. 2004. Algal Contact as a Trigger for Coral Disease. *Ecology Letters*, 7:919–923.
- Nugues, M. M., and A. M. Szmant. 2006. Coral Settlement onto *Halimeda opuntia*: A Fatal Attraction to an Ephemeral Substrate? *Coral Reefs*, 25:585–591.
- Nyström, M., C. Folke, and F. Moberg. 2000. Coral Reef Disturbance and Resilience in a Human-Dominated Environment. *Trends in Ecology and Evolution*, 15:413–417.
- Oliver, J., and R. Babcock. 1992. Aspects of the Fertilization Ecology of Broadcast Spawning Corals: Sperm Dilution Effects and *In Situ* Measurements of Fertilization. *Biological Bulletin*, 183:409–417.
- Omori, M., H. Fukami, H. Kobinata, and M. Hatta. 2001. Significant Drop of Fertilization of *Acropora* Corals in 1999. An After Effect of Heavy Coral Bleaching? *Limnology and Oceanography*, 46:704–706.
- Omori, M., K. Iwao, and M. Tamura. 2008. Growth of Transplanted *Acropora tenuis* 2 Years after Egg Culture. *Coral Reefs*, 27:165.
- Palma, A. T., R. S. Steneck, and C. J. Wilson. 1999. Settlement-Driven, Multiscale Demographic Patterns of Large Benthic Decapods in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, 241:107–136.
- Palumbi, S. R. 1994. Genetic Divergence, Reproductive Isolation, and Marine Speciation. *Annual Review of Ecology and Systematics*, 25:547–572.
- Pandolfi, J. M., and J. B. C. Jackson. 2006. Ecological Persistence Interrupted in Caribbean Coral Reefs. *Ecology Letters*, 9:818–826.
- Pandolfi, J. M., J. B. C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Ogden, H. P. Possingham, and E. Sala. 2005. Are U.S. Coral Reefs on the Slippery Slope to Slime? *Science*, 307:1725–1726.
- Pantos, O., R. P. Cooney, M. D. A. Le Tissier, M. R. Barer, A. G. O'Donnell, and J. C. Bythell. 2003. The Bacterial Ecology of a Plague-like Disease Affecting the Caribbean Coral *Montastraea annularis*. *Environmental Microbiology*, 5:370–382.
- Pawlik, J. R. 1992. Chemical Ecology of the Settlement of Benthic Marine Invertebrates. *Oceanography and Marine Biology: An Annual Review*, 30:273–335.
- Pawlik, J. R., L. Steindler, T. P. Henkel, S. Beer, and M. Ilan. 2007. Chemical Warfare on Coral Reefs: Sponge Metabolites Differentially Affect Coral Symbiosis *In Situ*. *Limnology and Oceanography*, 52:907–911.
- Pechenik, J. A. 1990. Delayed Metamorphosis by Larvae of Benthic Marine Invertebrates. Does It Occur? Is There a Price to Pay? *Ophelia*, 32:63–94.
- . 2002. Relationships Between Larval Nutritional Experience, Larval Growth Rates, Juvenile Growth Rates, and Juvenile Feeding Rates in the Prosobranch Gastropod *Crepidula fornicata*. *Journal of Experimental Marine Biology and Ecology*, 280:63–78.
- . 2006. Larval Experience and Latent Effects: Metamorphosis Is Not a New Beginning. *Integrative and Comparative Biology*, 46:323–333.



- Pechenik, J. A., R. Berard, D. D. Gleason, T. R. Gleason, and D. Champlin. 2001. Influence of Lowered Salinity and Elevated Cadmium on the Survival and Metamorphosis of Trochophores in *Capitella* sp. *Invertebrate Biology*, 120:142–148.
- Pechenik, J. A., D. E. Wendt, and J. N. Jarrett. 1998. Metamorphosis Is Not a New Beginning. *Bioscience*, 48:901–910.
- Putnam, H. M., P. J. Edmunds, and T.-Y. Fan. 2008. Effect of Temperature on the Settlement Choice and Photophysiology of Larvae from the Reef Coral *Stylophora pistillata*. *Biological Bulletin*, 215:135–142.
- Raimondi, P. T., and A. N. C. Morse. 2000. The Consequences of Complex Larval Behavior in a Coral. *Ecology*, 81:3193–3211.
- Richmond, R. H. 1987. Energetics, Competency, and Long-Distance Dispersal of Planula Larvae of the Coral *Pocillopora damicornis*. *Marine Biology*, 93:527–533.
- . 1993a. Coral Reefs: Present Problems and Future Concerns Resulting from Anthropogenic Disturbance. *American Zoologist*, 33:524–536.
- . 1993b. Effects of Coastal Runoff on Coral Reproduction. In *Proceedings of the Colloquium and Forum on Global Aspects of Coral Reefs: Health, Hazard, and History*, ed. R. N. Ginsburg, pp. 360–364. University of Miami, Miami, Fla.
- . 1997. Reproduction and Recruitment in Corals: Critical Links in the Persistence of Reefs. In *Life and Death of Coral Reefs*, ed. C. E. Birkeland, pp. 175–198. New York: Chapman & Hall.
- Richmond, R. H., and C. L. Hunter. 1990. Reproduction and Recruitment of Corals: Comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series*, 60:185–203.
- Richmond, R. H., T. Rongo, Y. Golbuu, S. Victor, N. Idechong, G. Davis, W. Kostka, L. Neth, M. Hamnett, and E. Wolanski. 2007. Watersheds and Coral Reefs: Conservation Science, Policy, and Implementation. *Bioscience*, 57:598–607.
- Rinkevich, B., and Y. Loya. 1987. Variability in the Pattern of Sexual Reproduction of the Coral *Stylophora pistillata* at Eilat, Red-Sea: A Long-Term Study. *Biological Bulletin*, 173:335–344.
- Roberts, R. D., and C. Lapworth. 2001. Effect of Delayed Metamorphosis on Larval Competence, and Post-Larval Survival and Growth, in the Abalone *Haliotis iris* Gmelin. *Journal of Experimental Marine Biology and Ecology*, 258:1–13.
- Rylaarsdam, K.W. 1983. Life Histories and Abundance Patterns of Colonial Corals on Jamaican Reefs. *Marine Ecology Progress Series*, 13:249–260.
- Sammarco, P. W. 1985. The Great Barrier Reef Versus the Caribbean: Comparisons of Grazers, Coral Recruitment Patterns and Reef Recovery. In *Proceedings of the 5th International Coral Reef Symposium*, 4:391–398.
- Sammarco, P. W., and J. C. Andrews. 1988. Localized Dispersal and Recruitment in Great Barrier Reef Corals: The Helix Experiment. *Science*, 239:1422–1424.
- Sammarco, P. W., and J. H. Carleton. 1981. Damselfish Territoriality and Coral Community Structure: Reduced Grazing, Coral Recruitment, and Effects on Coral Spat. In *Proceedings of the 4th International Coral Reef Symposium*, 2:525–535.
- Sebens, K. P. 1982. Competition for Space: Growth Rate, Reproductive Output, and Escape in Size. *American Naturalist*, 120:189–197.
- Smith, J. E., M. Shaw, R. A. Edwards, D. Obura, O. Pantos, E. Sala, S. A. Sandin, S. Smriga, M. Hatay, and F. L. Rohwer. 2006. Indirect Effects of Algae on Coral: Algae-Mediated, Microbe-Induced Coral Mortality. *Ecology Letters*, 9:835–845.
- Smith, S. R. 1992. Patterns of Coral Recruitment and Post-settlement Mortality on Bermuda's Reefs: Comparisons to Caribbean and Pacific Reefs. *American Zoologist*, 32:663–673.
- . 1997. Patterns of Coral Settlement, Recruitment and Juvenile Mortality with Depth at Conch Reef, Florida. *Proceedings of the 8th International Coral Reef Symposium*, 2:1197–1202.
- Steneck, R. S. 2006. Staying Connected in a Turbulent World. *Science*, 311:480–481.
- Steneck, R. S., and J. C. Lang. 2003. Rapid Assessment of Mexico's Yucatan Reef in 1997 and 1999: Pre- and Post-Mass Bleaching and Hurricane Mitch (Stony Corals, Algae and Fish). *Atoll Research Bulletin*, 496:294–317.
- Steneck, R. S., and M. N. Dethier. 1994. A Functional Group Approach to the Structure of Algal-Dominated Communities. *Oikos*, 69:476–498.
- Strathmann, R. R., T. R. Hughes, A. M. Kuris, K. C. Lindeman, S. G. Morgan, J. M. Pandolfi, and R. R. Warner. 2002. Evolution of Local Recruitment and Its Consequences for Marine Populations. *Bulletin of Marine Science*, 70:377–396.
- Styan, C. A. 1998. Polyspermy, Egg Size, and the Fertilization Kinetics of Free-Spawning Marine Invertebrates. *American Naturalist*, 152:290–297.
- Sullivan, B., D. J. Faulkner, and L. Webb. 1983. Siphonodictidine, a Metabolite of the Burrowing Sponge *Siphonodictyon* sp. That Inhibits Coral Growth. *Science*, 221:1175–1176.
- Suzuki, G., T. Hayashibara, Y. Shirayama, and H. Fukami. 2008. Evidence of Species-Specific Habitat Selectivity of *Acropora* Corals Based on Identification of New Recruits by Two Molecular Markers. *Marine Ecology Progress Series*, 355:149–159.
- Szmant, A. M. 1986. Reproductive Ecology of Caribbean Reef Corals. *Coral Reefs*, 5:43–53.
- Szmant, A. M., and N. J. Gassman. 1990. The Effects of Prolonged Bleaching on the Tissue Biomass and Reproduction of the Reef Coral *Montastraea annularis*. *Coral Reefs*, 8:217–224.
- Thiyagarajan, V., L. A. Gosselin, and P. Y. Qian. 2008. Juvenile Growth in Barnacles: Combined Effect of Delayed Metamorphosis and Sublethal Exposure of Cyprids to Low-Salinity Stress. *Marine Ecology Progress Series*, 344:173–184.
- Thiyagarajan, V., T. Harder, J. W. Qiu, and P. Y. Qian. 2003. Energy Content at Metamorphosis and Growth Rate of the Early Juvenile Barnacle *Balanus amphitrite*. *Marine Biology*, 143:543–554.
- Tomaiuolo, M., T. F. Hansen, and D. R. Levitan. 2007. A Theoretical Investigation of Sympatric Evolution of Temporal Reproductive Isolation as Illustrated by Marine Broadcast Spawners. *Evolution*, 61:2584–2595.
- Van Moorsel, G. W. N. M. 1989. Juvenile Ecology and Reproductive Strategies of Reef Corals. Leiden: Backhuys Publishers.
- Vermeij, M. J. A. 2005. Substrate Composition and Adult Distribution Determine Recruitment Patterns in a Caribbean Brooding Coral. *Marine Ecology Progress Series*, 295:123–133.
- . 2006. Early Life-History Dynamics of Caribbean Coral Species on Artificial Substratum: The Importance of Competition, Growth and Variation in Life-History Strategy. *Coral Reefs*, 25:59–71.
- Vermeij, M. J. A., N. D. Fogarty, and M. W. Miller. 2006. Pelagic Conditions Affect Larval Behavior, Survival, and Settlement Patterns in the Caribbean Coral *Montastraea faveolata*. *Marine Ecology Progress Series*, 310:119–128.
- Vermeij, M. J. A., and S. A. Sandin. 2008. Density-Dependent Settlement and Mortality Structure: The Earliest Life Phases of a Coral Population. *Ecology*, 89:1994–2004.
- Vermeij, M. J. A., J. E. Smith, C. M. Smith, R. V. Thurber, and S. A. Sandin. 2009. Survival and Settlement Success of Coral Planulae: Independent and Synergistic Effects of Macroalgae and Microbes. *Oecologia*, 159:325–336.
- Wakeford, M., T. J. Done, and C. R. Johnson. 2008. Decadal Trends in a Coral Community and Evidence of Changed Disturbance Regime. *Coral Reefs*, 27:1–16.
- Webster, N. S., L. D. Smith, A. J. Heyward, J. E. M. Watts, R. I. Webb, L. L. Blackall, and A. P. Negri. 2004. Metamorphosis of a Scleractinian Coral in Response to Microbial Biofilms. *Applied and Environmental Microbiology*, 70:1213–1221.



- Wendt, D. E. 1998. Effect of Larval Swimming Duration on Growth and Reproduction of *Bugula neritina* (Bryozoa) under Field Conditions. *Biological Bulletin*, 195:126–135.
- Williams, D. E., M. W. Miller, and K. L. Kramer. 2008. Recruitment Failure in Florida Keys *Acropora palmata*, a Threatened Caribbean Coral. *Coral Reefs*, 27:697–705.
- Willis, B. L., R. Babcock, P. L. Harrison, and T. K. Oliver. 1985. Patterns in Mass Spawning of Corals on the Great Barrier Reef from 1981 to 1984. In *Proceedings of the 5th International Coral Reef Symposium*, 4:343–348.
- Willis, B. L., R. C. Babcock, P. L. Harrison, and C. C. Wallace. 1997. Experimental Hybridization and Breeding Incompatibilities within the Mating Systems of Mass Spawning Reef Corals. *Coral Reefs*, 16:S53–S65.
- Willis, B. L., M. van Oppen, D. J. Miller, S. V. Vollmer, and D. J. Ayre. 2006. The Role of Hybridization in the Evolution of Reef Corals. *Annual Review of Ecology, Evolution, and Systematics*, 37:489–517.
- Wittenberg, M., and W. Hunte. 1992. Effects of Eutrophication and Sedimentation on Juvenile Corals I. Abundance, Mortality and Community Structure. *Marine Biology*, 112:131–138.
- Wolstenholme, J. K. 2004. Temporal Reproductive Isolation and Gametic Compatibility Are Evolutionary Mechanisms in the *Acropora humilis* Species Group (Cnidaria; Scleractinia). *Marine Biology*, 144:567–582.
- Zigler, K. S., M. A. McCartney, D. R. Levitan, and H. A. Lessios. 2005. Sea Urchin Bindin Divergence Predicts Gamete Compatibility. *Evolution*, 59:2399–2404.



# Do Indian River Lagoon Wetland Impoundments (Eastern Florida) Negatively Impact Fiddler Crab (Genus *Uca*) Populations?

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**ABSTRACT.** Quantitative sampling of fiddler crabs was performed in June–July between 1992 and 1994 along transects at three St. Lucie County mosquito impoundments, Florida, running from the Indian River Lagoon (IRL) shore and across the impoundment perimeter dikes, and in one impoundment across the perimeter ditch. A total of 929 specimens representing four species were found: *Uca pugilator*, *Uca rapax*, *Uca speciosa*, and *Uca thayeri*. The quantitative sampling showed that there was no correlation between the number of *Uca* burrow openings on the sediment surface and the actual number of crabs in the sediment. Differences were recorded in abundance and distributional patterns between impoundments, but no correlation was recorded between substrate organic content and species distributional patterns. The male/female ratio was close to 1 for all species, except for *U. thayeri*; the males dominated for this species (ratio, 1.8:1). High water temperatures potentially lethal to fiddler crabs occurred in the impounded marsh in the summer. *U. pugilator* and *U. rapax* were unlikely to be impacted by the impoundment flooding as they are highly motile and not very site specific. *U. speciosa* and *U. thayeri* were more restricted to the very soft, dark, and wet substrate along perimeter ditch banks and may therefore be impacted during periods of flooding because they are dependent on nonflooded areas for feeding and reproduction.

## INTRODUCTION

Burrowing crustaceans, such as fiddler crabs, impact the ecology of associated infaunal communities and, consequently, the ecosystem as a whole (Crane, 1975; Montague, 1982; Dittman, 1996). According to Montague (1980), fiddler crabs are the most abundant macrobenthic crustacean inhabitants of North American estuaries. Their impacts on bioturbation activity and oxygenation of the substrate are considerable (Bertness, 1985). Fiddler crabs may also play an important role in recycling nutrients (Macintosh, 1982; Bertness, 1985). They feed by scraping up and ingesting surface sediment (Crane, 1975; Kraeuter, 1976; Heard, 1982; Macintosh, 1982; Weis and Weis, 2004) and are in that respect very important in overturn of substrates. Fiddler crabs are also an important food source for birds, fish, and mammals (Peterson and Peterson, 1979; Montague, 1980; Grimes et al., 1989; Gilmore et al., 1990). There is a relatively diverse *Uca* species assemblage within the Indian River Lagoon (IRL) region, with seven species reported in the IRL (Salmon, 1967; Kerr, 1976; M. Salmon, Florida

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Atlantic University, personal communication, 1992), four tropical species, *Uca rapax* (Smith), *Uca thayeri* Rathbun, *Uca speciosa* (Ives), and *Uca mordax* (Smith), and three temperate species, *Uca pugnax* (Smith), *Uca pugilator* (Bosc), and *Uca minax* (Le Conte). Only four species were found during these studies: *Uca pugilator*, *U. rapax*, *U. speciosa*, and *U. thayeri*.

That the impoundment of 90% of the marginal wetlands (primarily for mosquito control) of the IRL has a potential negative impact on regional *Uca* populations has been a controversial issue for many years. Each impoundment and the management procedures are described in detail in Rey and Kain (1991). Preliminary studies by Gilmore et al. (1991) revealed that no *Uca* spp. were observed from marsh-mangrove habitats in flooded (short-term and long-term) impoundments, while they were present in large numbers at unimpounded sites adjacent to impoundments. This difference could be associated with a number of factors, because many aspects of the reproduction of *Uca* (including courtship, female receptivity, egg maturation, and hatching) are closely synchronized with the semidiurnal and semilunar tidal cycles (Fingerman, 1957; Barnwell, 1968; Wheeler, 1978; Zucker, 1978; Montague, 1980; DeCorsey, 1983; Salmon et al., 1986). However, according to Fingerman (1957), the tidal rhythm differs between species (*U. pugilator* and *U. speciosa*). The exclusion of natural tidal cycles within several impoundments may therefore have serious impacts on populations of *Uca* spp. In addition, prolonged periods of inundation that usually occur from May to September (management for mosquito control) may displace *Uca* spp., which need periods of exposure of the burrow entrances for survival. Periods of heavy precipitation, mainly during the summer, may also drastically reduce the salinity within these impoundments.

The main objectives of this study were (a) to evaluate survival and adaptation of *Uca* populations to manipulated ecological conditions along the impoundment perimeter ditches (compared with the natural IRL conditions), (b) to determine if these potential adaptations differed among species, and (c) to elucidate zonation patterns of each species (from the IRL shore, across the dike road, down to the impoundment ditch).

## METHODS

Figure 1 shows the location of the three studied impoundments, which are described in detail in Rey and Kain (1991). Blue Hole Point (impoundment [Imp.] #23)

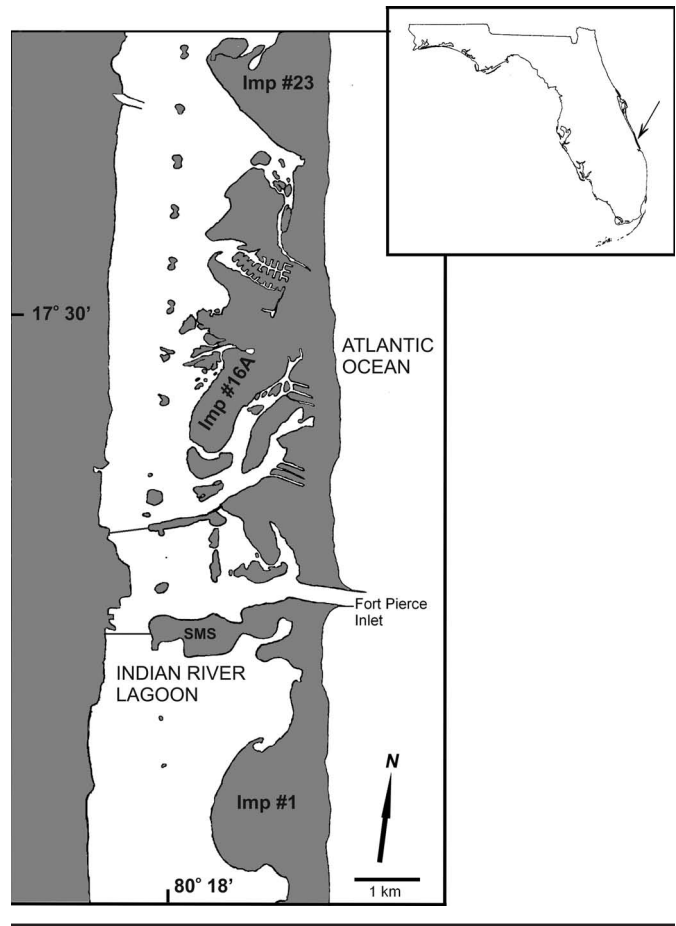
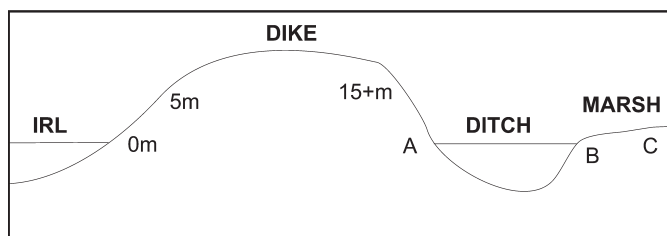


FIGURE 1. The three sampling impoundments (Imp) within St. Lucie County, Florida; SMS = Smithsonian Marine Station.

is a 122 ha breached impoundment. The 20 m breach in the western dike allowed natural tidal access between the impoundment and the IRL. This breach was a result of a severe 1981 winter storm and was left open to the natural tidal cycles of the IRL. The main reason for not repairing the breach was that this impoundment could be used as a reference/control site for numerous impoundment studies (James R. David, St. Lucie County Mosquito Control District, personal communication, 1992). Jack Island State Preserve (Imp. #16A) is a 161 ha impoundment divided into four cells. This impoundment was open via culverts to the IRL during the winter months but was artificially flooded during the summer months (early May through August). Bear Point (Imp. #1) is a 255 ha impoundment. Since August 1993, the culverts here were left open to tidal exchange.

Quantitative sampling was performed in these impoundments, Imp. #23 and Imp. #16A in June-July 1992,

1993, and 1994 and Imp. #1 in July 1994 along a portion of transect lines previously established for burrow counts (Gilmore et al., 1991). One transect line had been established in each impoundment. These transects ranged from the edge of the IRL (0 m), continued across the artificial dike, and ended at the impoundment perimeter ditch (Figure 2). Four permanent metal stakes indicated the sampling sites (see below). Because of the very hard substrate on top of the actual dike (the road), it was impossible to sample these sites (10 m and 15 m) quantitatively (see below). The 0 m stake was placed at the waterline (low tide) on the IRL side, and the other three stakes (markers) were placed at 5 m intervals across the dike, with the 0 m stake as the starting point. The 15+ m site was between the 15 m stake and the upper bank of the perimeter ditch (Gilmore et al., 1991; see Figure 2). Additional sites were also established for the studies: site A was at the edge of the water (low tide) on the dike side of the perimeter ditch and site B in the corresponding area of the impoundment marsh side of the ditch (Figure 2). It was not possible to establish a site B in Imp. #16A, because of the summer artificial flooding, or in Imp. #1, because it was flooded naturally. The width of the perimeter ditches was about 5 to 6 m. The ditch shores in all impoundments had a very dense (but only about 1.5 to 2 m wide) mangrove vegetation (primarily *Rhizophora mangle*). Two additional sites were established in Imp. #23: site C, about 2 m into the impoundment marsh from site B, immediately behind the dense mangrove vegetation along the ditch shore (see Figure 2), and site D on the sand flat within the marsh (25 m from the ditch). The distance from site 0 m to site C was about 25 m and to site D about 47 m. The sampling sites were 2 × 2 m permanent squares situated at each marker (sites 0 m, 15+ m, C, and D), within which four replicate samples were randomly collected on each sampling



**FIGURE 2.** Cross section of a typical mosquito impoundment in the Indian River Lagoon (IRL), showing locations of the fiddler crab sampling sites. The dike road was approximately 1.5 m above low tide level in the IRL at three investigated sites (site D is not shown).

date. Sites A and B were sampled the same way (on the exposed substrate at low tide) close to the dense mangrove vegetation at each side of the perimeter ditch. The Imp. #23 impoundment marsh was never flooded during my studies. The random sampling was performed by means of a stainless steel cylinder (0.1 m<sup>2</sup>, 40 cm high) with a sharpened bottom edge. Sampling was always performed at low tide and when no, or very few, specimens were observed on the sediment surface. Sampling was never performed when many crabs were observed out of their burrows. Sampling at such times would have resulted in erroneous quantitative results because *Uca* spp., when disturbed on the sediment surface, seek shelter in the closest burrow or even migrate out into the water. The cylinder was forced down to a sediment depth of at least 25 cm. The number of *Uca* burrows within the cylinder area was recorded, and then the sediment was removed with a shovel (with a straight edge). The uppermost fraction (0–10 cm) was sieved (in the field) in seawater through a 2 mm stainless steel mesh sieve. In the remaining fraction (10–25 cm) the crabs were removed by hand in the field. This procedure was deemed acceptable as small crabs only occurred in the uppermost layer of the sediment. The specimens were transferred to plastic bags and kept in a cooler in the field. In the laboratory, the samples were either processed immediately or stored in a freezer for later processing. The crabs were sorted by hand in a tray filled with seawater. They were then placed in labeled glass jars in a solution of 5% borax-neutralized formalin, diluted in seawater. After 4 to 5 days the formalin was replaced with 70% ethanol. All specimens larger than 5 mm carapace width (CW) were later identified and weighed (wet weight) and have been archived for possible future studies. All individuals smaller than 5 mm were regarded as “juveniles.” It was not possible to identify these to species level with certainty. The literature sources used for species determination were Tashian and Vernberg (1958), Salmon (1967), and Crane (1975). A total of 140 quantitative samples were collected during the entire study period: 84 in Imp. #23, 40 in Imp. #16A, and 16 in Imp. #1.

Water temperature was measured midafternoon on 26 July 1993 and 1 August 1994 within the marsh of Imp. #16A (which was artificially flooded), in the middle of the adjacent perimeter ditch, and in the IRL (about 5 m from the shore). The measurements were taken at 5 cm water depth.

Because many impoundments are closed for natural tidal exchange to the estuarine waters of the IRL during the artificial flooding periods (impoundment pumps), salinity may drop rapidly during periods of heavy rainfall.

An experiment was therefore performed to investigate tolerance to rapid salinity changes among the four *Uca* species. The laboratory setup consisted of twenty 2 L round plastic containers equipped with a lid. A separate air supply was provided to each container. Four treatments and one control (four replicates per treatment) were established: 100%, 75%, 50%, 25%, and 0% seawater. Laboratory-supplied seawater was diluted with distilled water. The salinities of the different treatments were 100% = 36–37 ppt (parts per thousand), 75% = 27–29 ppt, 50% = 19 ppt, 25% = 9–10 ppt, and 0% = 0 ppt, measured with an ocular refractometer. The water temperature was very stable during the experimental period, 24.0°–26.0°C. Each experiment lasted for seven days. The crabs were collected 48 hours before each experiment and acclimated in 100% aerated seawater during this period. Seven randomly selected female crabs of each species were placed in each experimental container. It was not possible to find enough specimens of *U. thayeri* during the period for these studies. Therefore only 25% and 0% seawater were used as treatments, and each replicate contained five crabs. The experiments were monitored twice a day, and any dead crabs were removed. Water was changed only in the containers where dead crabs were found. These experiments were performed between 4 July and 27 July 1994.

Sediment samples for analysis of organic content (loss on ignition) were collected in 1994 along the three transects. Three sediment cores (inner diameter, 30 mm) were collected to a depth of 5 cm at randomly chosen points at each site. As stated above it was not possible to establish a site B in Imp. #16A or in Imp. #1. The sediment was treated in the laboratory according to the procedures described in Holme and McIntyre (1971).

A one-way analysis of variance (ANOVA) (Holm–Sidak method) was performed to compare the respective monitored sites in the three impoundments regarding organic content (LOI) in the sediment (Table 1).

## RESULTS

### ABUNDANCE

Abundance data from the three transects sampled in 1992, 1993, and 1994 at Imp. #23 and Imp. #16A are presented in Figures 3 and 4, and the one transect sampled in 1994 at Imp. #1 in Figure 5. High water levels prevented sampling 0 m (IRL) at Imp. #16A in 1992 and site A (ditch shore) in 1994.

The results from Imp. #23 were similar the three sampling years (Figure 3). *U. pugilator* and *U. rapax* were relatively evenly distributed across the transect, and a few specimens of *U. rapax* were sometimes observed on the dike road (DIKE; see Figure 2). *U. speciosa*, the dominant species, was found only at site 0 m, and in very high densities in the wet, soft, and dark mud on both sides of the perimeter ditch (sites A and B). *U. thayeri* was also found on both sides of the perimeter ditch (sites A and B), in addition to a few specimens at site 0 m in 1992.

In contrast, at Imp. #16A (Figure 4), *U. pugilator* dominated in abundance at site 5 m whereas *U. rapax* was most abundant at site A (perimeter ditch shore). *U. speciosa* was almost exclusively found at site A and *U. thayeri* at site 0 m.

At Imp. #1 the distributional patterns were similar to the other impoundments. However, *U. pugilator* was found in comparatively low densities, whereas *U. rapax* was abundant at both sites 0 m and 5 m. *U. speciosa* was found in high densities in the wet muddy areas at site 0 m and at site A. *U. thayeri* was found at the 0 m site and to even a greater extent at site A (dike side of the ditch).

No statistical tests were performed to elucidate any potential difference between years at each site, but it was of higher interest to statistically compare abundance patterns between impoundments. Therefore, correlation analyses (Pearson product moment correlation) were performed on the mean abundance data (1992, 1993, 1994) for sites 0 m

TABLE 1. One-way analyses of variance (Holm–Sidak method) concerning differences in organic content (LOI) between the different impoundment and sampling sites. Significant differences (*P* values) are in **bold italic**.

Impoundment no.	Site					
	0 m	5 m	15+	A	C	D
23 vs. 16A	<b>0.025</b>	0.068	0.158	<b>0.0002</b>	<b>0.0001</b>	<b>0.001</b>
23 vs. 1	0.148	<b>0.044</b>	0.123	0.124		
16A vs. 1	<b>0.004</b>	<b>0.003</b>	<b>0.014</b>	<b>0.00006</b>		



### IMPOUNDMENT #23

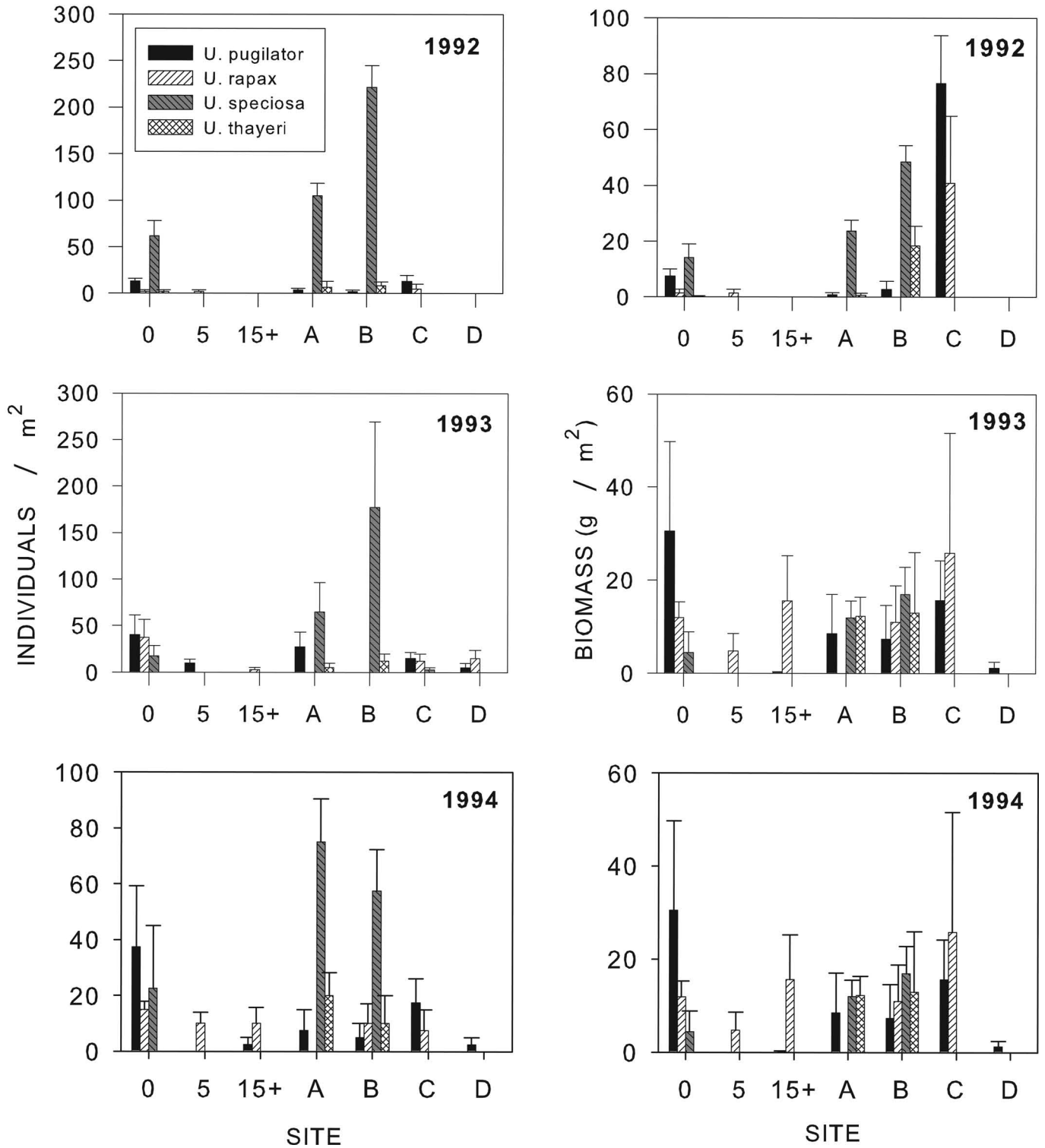


FIGURE 3. Abundance and biomass (wet weight) between 1992 and 1994 of the four fiddler crab species along the impoundment #23 transect. Error bars represent + standard error values ( $N = 4$ ). Note the different scaling on the y-axes.

### IMPOUNDMENT #16A

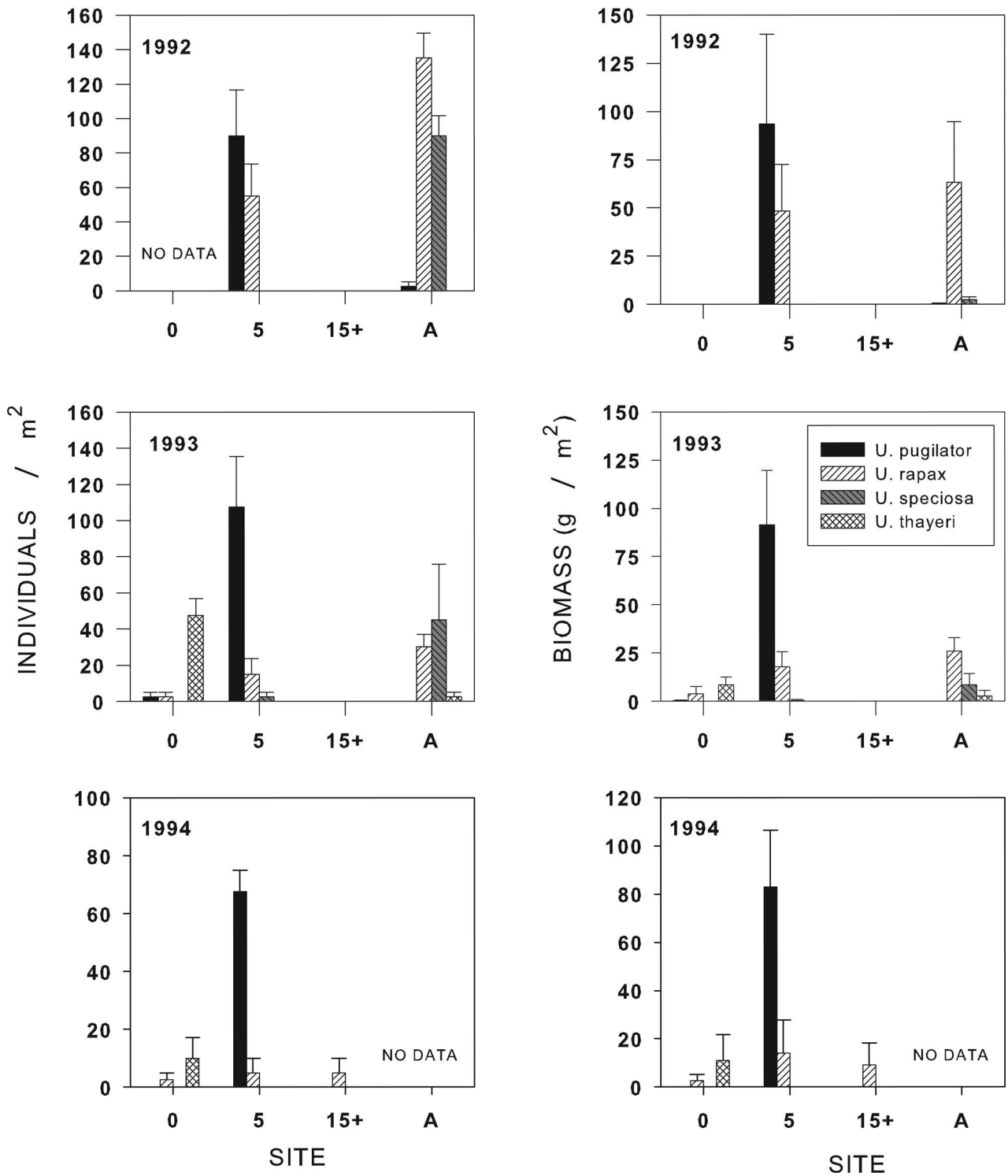


FIGURE 4. Abundance and biomass (wet weight) between 1992 and 1994 of the four fiddler crab species along the transect within impoundment #16A. Error bars represent + standard error values (N = 4). Note different scaling on y-axes.

## IMPOUNDMENT #1 (1994)

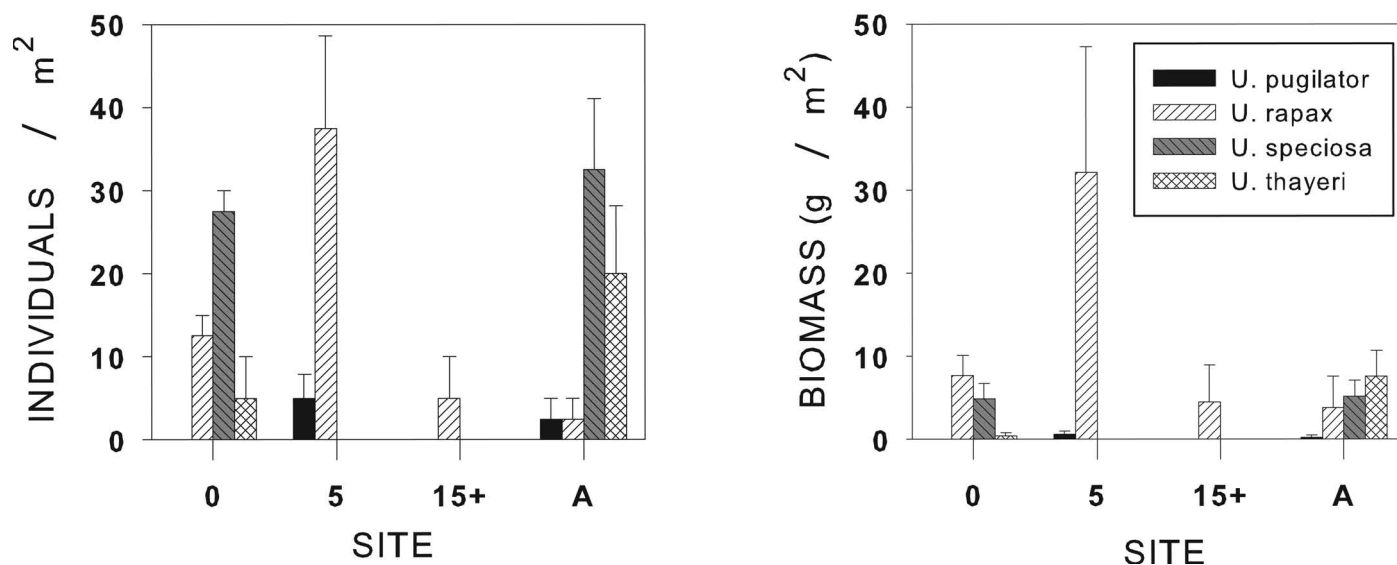


FIGURE 5. Abundance and biomass in 1994 of the four fiddler crab species along the transect within impoundment #1. Error bars represent + standard error values ( $N = 4$ ).

to A for each of the four species separately between Imp. #23 and Imp. #16A. However, no correlation ( $P > 0.05$ ) could be found for any of the species. The same analyses were performed for the 1994 data from Imp. #23, Imp. #16A, and Imp. #1. The only correlation (positive) found was for *U. thayeri* between Imp. #23 and Imp. #1 (correlation coefficient, 0.968;  $P$  value, 0.031).

### BIOMASS

The biomass (g wet weight) measurements are presented in Figures 3–5. No significance tests were performed concerning the biomass difference among the three years for each species.

However, the biomass calculations for the three years in Imp. #23 (Figure 3) indicate that changes took place, but these changes are based on subjective observations. High biomass values were recorded for *U. pugilator* in 1992 at site C and in 1993 and 1994 at site 0 m. High values were recorded for *U. rapax* throughout the entire transect, especially in 1993 and 1994, except at site D. The highest biomass values for *U. speciosa* were recorded on both sides of the perimeter ditch (sites A and B), especially on the marsh side of the ditch (site B). High *U. thayeri* biomass values were recorded along the perimeter ditch (sites A and B).

At Imp. #16A the biomass values for *U. pugilator* were high at site 5 m all three years (see Figure 4). Relatively high biomass values were recorded for *U. rapax* at sites 5 m and A in 1992. However, data for site A in 1994 are not available. Low biomass values were recorded for *U. speciosa* at site A in 1992 and 1993. *U. thayeri* was only recorded at low biomass values at site 0 m in 1993 and 1994 and at site A in 1993 and at site 0 m in 1994.

At Imp. #1 low values were observed for *U. pugilator* throughout the transect (see Figure 5), but *U. rapax* was, by far, the most dominant (biomass) species across the entire transect. The only exception was site A, where the values for *U. speciosa* and *U. thayeri* were somewhat higher.

### REPRODUCTION AND SEX DISTRIBUTION

The percentage of “juveniles” found in 1993 and 1994 at the different sites within Imp. #23 and Imp. #16A is presented in Figure 6. More juveniles were found at site 0 m at Imp. #16A compared with Imp. #23. Many juveniles were also recorded along these impoundment ditch shores (sites A and B in Imp. #23 and site A in Imp. #16A). The sex distribution among adults of the four species from the 1992, 1993, and 1994 (combined) collections (June–July) is presented in Figure 7 with the number



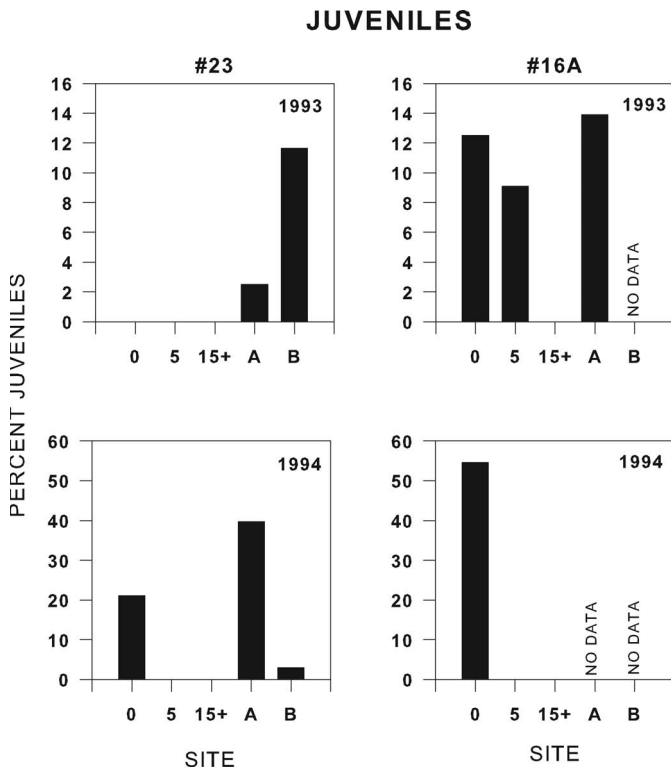


FIGURE 6. Percentage specimens having a carapace width (CW) less than 5 mm (juveniles) of all collected individuals of *Uca* spp. from each site in 1993 and 1994. Note different scaling on y-axes.

of ovigerous females. As shown, the sex ratio was near to 1.0 among all four species except for *U. thayeri* where the male/female ratio was approximately 1.8:1. The highest ovigerous rate was found among *U. pugilator* (22.0%) and the lowest among *U. rapax* (3.4%). The corresponding figures for *U. speciosa* and *U. thayeri* were 6.9% and 10.0%, respectively.

### BURROWS

The correlation between the number of burrows and the actual number of crabs found within each sample in 1992 and 1993 is presented in Figure 8. A Wilcoxon signed-rank test showed that there was no correlation between these two parameters:  $P = 0.097$  (linear regression:  $R^2 = 0.02$ ,  $P$  [analysis of variance] = 0.23). This finding has also been reported by Colby and Fonseca (1984). The same lack of correlation was also found by the author in a larger and more detailed multiyear study at Merritt Island impoundments (close to Cape Canaveral, eastern Florida.).

### TEMPERATURE AND SALINITY TOLERANCE

The summer water temperatures within Imp. #16A, the perimeter ditch, and in the IRL is presented in Table 2. The water temperature was higher within the impoundment marsh than in the perimeter ditch and in the IRL.

The laboratory experiment showed that no species showed any disturbance or mortality in 100%–25% seawater. However, the reaction toward 0% seawater was severe (Figure 9). *U. speciosa* and *U. thayeri* showed very low tolerance toward 0% seawater while *U. pugilator* showed the highest tolerance. The reaction from *U. rapax* was intermediate.

### SEDIMENT

The results of the sediment analyses are presented in Figure 10. The loss on ignition (organic content) was higher in Imp. #16A than in Imp. #23 and Imp. #1 (see

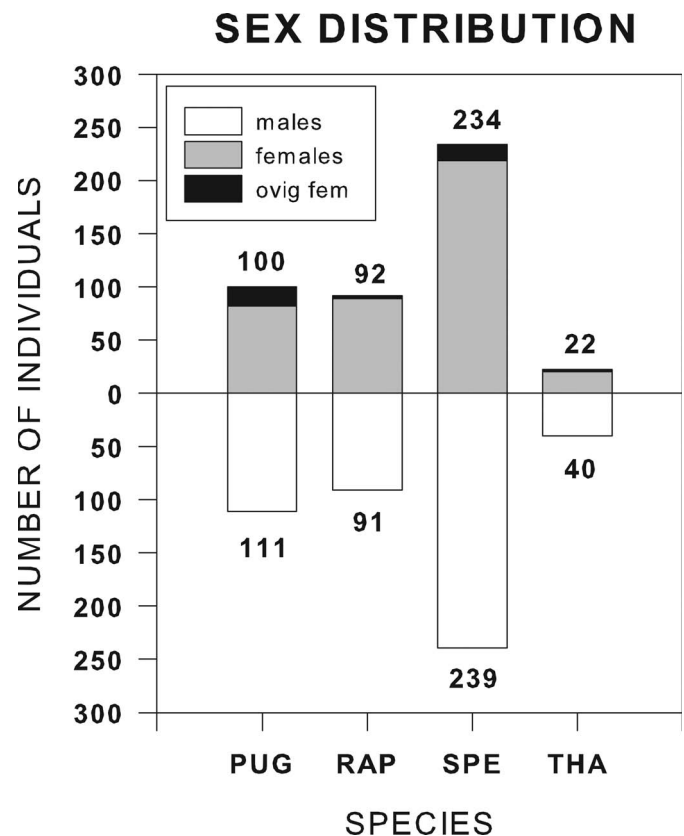


FIGURE 7. Sex distribution of all fiddler crab individuals larger than 5 mm collected during 1992–1994 combined within impoundments #23, #16A, and #1. The bars show sex distribution for each species found throughout the study period; PUG = *Uca pugilator*; RAP = *U. rapax*; SPE = *U. speciosa*; THA = *U. thayeri*.

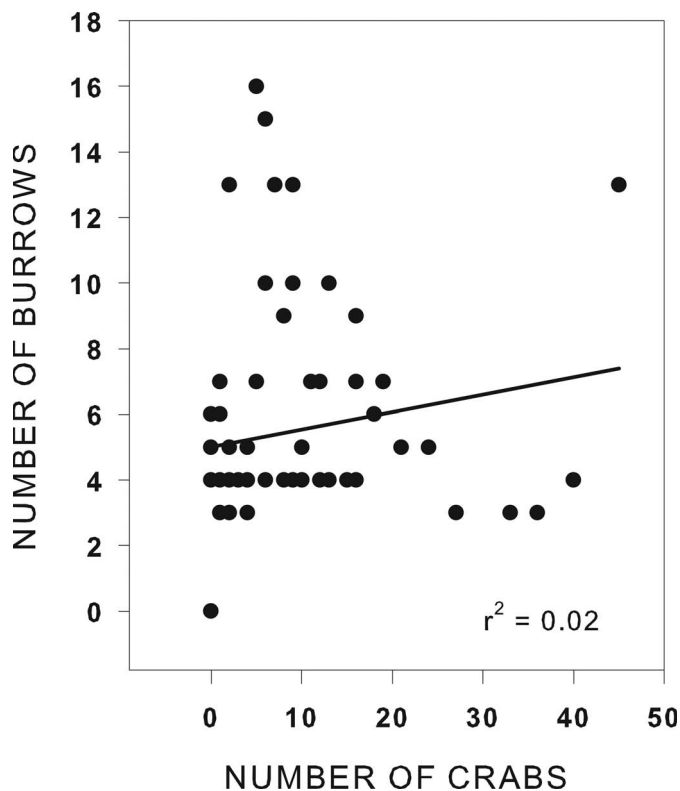


FIGURE 8. Relationship between number of burrows and number of fiddler crabs found in each quantitative sample.

Table 1). The lowest values on the IRL side (site 0 m) were recorded from Imp. #1 and the highest from Imp. #16A. At the ditch (site A) the highest organic value was recorded at Imp. #16A and the lowest at Imp. #1. Within the marsh (site C) (Imp. #23 and Imp. #16A only), the loss on ignition was very high within Imp. #16A and very low within Imp. #23. As indicated in Table 1, Imp. #16A deviated significantly the most from the other two impoundments, with generally the highest organic content (LOI).

TABLE 2. Water temperatures (°C, 5 cm water depth) at impoundment site #16A, measured in midafternoon during July 1993 and July 1994.

Location <sup>a</sup>	1993	1994	Mean
Marsh	44.3	42.4	43.4
Ditch	37.1	36.1	36.6
IRL	37.5	35.2	36.4

<sup>a</sup> Marsh = impoundment marsh; ditch = impoundment perimeter ditch; IRL = Indian River Lagoon.

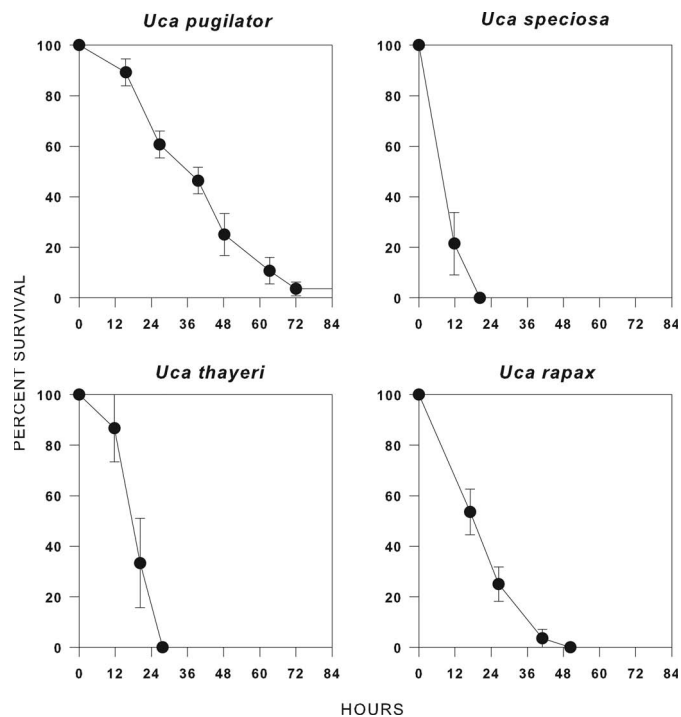


FIGURE 9. Percent survival in fresh (distilled) water of the four fiddler crab species. Error bars represent standard error values (N = 4).

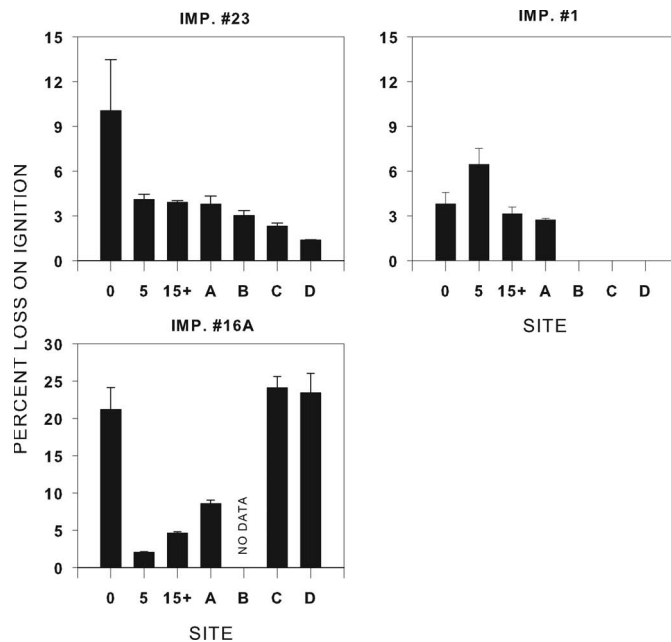


FIGURE 10. Sediment organic content (percent weight loss on ignition) at the sampling sites within the three impoundments in 1994. The error bars represent standard error values (N = 3). Note different scaling on y-axes.

Pearson product moment correlation tests were used to elucidate any potential correlation between the organic content of the sediment (LOI) and the distributional pattern (along the transects) of the four different species. All tests were performed on the mean values of each parameter. Only transects where a significant amount of information was available were used for these tests: Imp. #23 in 1993 and 1994, and Imp. #16A in 1994 (see explanation above). No significant correlation ( $P > 0.05$ ) was recorded for any species between abundance and organic content, except for *U. pugilator* at Imp. #23 in 1994, with a correlation coefficient of 0.797 and a  $P$  value of 0.032.

## DISCUSSION

Different species of fiddler crabs prefer different substrates and salinities for reasons of their specific physiological tolerances and environmental preferences (Teal, 1958; Vernberg et al., 1973). However, the artificial environment of the impoundments in the IRL, with the perimeter ditch and dike, poses a completely new, different type of environment for the *Uca* populations. The occurrence and distributional patterns of the different species of fiddler crabs in these impoundment dikes and perimeter ditches have not been investigated earlier, so this is a first basic study on these populations. The results from this study indicate that more detailed studies are needed in the future in these very extensive artificial environments in the IRL.

*Uca speciosa* and *U. thayeri* were the most "site- and substrate-specific" species within these environments, whereas *U. pugilator*, and in some cases also *U. rapax*, were more "generalists." *Uca speciosa* and *U. thayeri* were almost exclusively found in the very soft, black, and wet substrate close to the water (primarily sites A and B), which is clearly demonstrated by the data presented from Imp. #23. The highest abundances of *U. speciosa* were here recorded on the perimeter ditch "shores" (sites A and B). Given the rich mangrove vegetation, it was expected that the very fine, wet, and muddy sediment on the ditch perimeter shores (sites A and B) would have a comparatively high organic content, but this was not the case (see Figure 10). Because no correlation between the organic content of the substrate and the abundance pattern of the different species were found, the grain-size distribution, water content, the chemical content of the sediment, root mat density, physiological tolerances, and interspecific interactions may be more important factors in fiddler crab distributional patterns (Teal, 1958; Ringold, 1979; Bertness and Miller, 1984). No root mat areas were investigated in this

study. The large differences in substrate organic content (LOI) between Imp. #23 and Imp. #16A are noteworthy (see Table 1).

Large numbers of *U. rapax* (and to some extent also *U. pugilator*) were quite often observed on the dike roads, but *U. speciosa* and *U. thayeri* were never seen there. Thompson et al. (1989) have also demonstrated that some species of desiccated fiddler crabs, among these *U. pugilator*, can rehydrate on damp sand.

When the impoundments are being flooded, it appears that *U. rapax*, and most likely also *U. pugilator*, are able to migrate under water, across the perimeter ditch (often anoxic and with  $H_2S$  in the sediment), to more suitable areas. It is, however, important to note that this has so far been confirmed only for *U. rapax*. Therefore, the ability to relocate to more suitable habitat may be the decisive factor in survivorship among *Uca* species. The banks of the perimeter dike (immediately above site A) may therefore act as a temporary "refuge" for some species during periods of impoundment flooding. It is also possible that further migration takes place toward the IRL shores (*U. rapax*, *U. pugilator*). However, this question does not apply to the rim and road of the dike because of the unsuitable substrate. Furthermore, the distance to the water table is also too great (at least 1 m).

The two species *U. rapax* and *U. pugilator* are probably not adversely affected by impoundment management. Visual observations, and also in situ experiments, have revealed that these species are highly motile within the impoundment areas. According to Thurman (2003) *U. rapax* is typically collected in brackish water. Yoder et al. (2005) have also found that the "herding behavior" in *U. pugilator* is a water-conserving group effect, and this behavior makes them less vulnerable to desiccation. Many specimens of *U. pugilator* and *U. rapax* have been observed (by the author) to migrate over long distances within and outside the impoundments (marked individuals, not reported here). However, further studies need to be performed to clarify these patterns.

Although *U. pugilator* and *U. rapax* thrive in these areas, the fate of the other two species is more uncertain. According to the quantitative sampling results and intensive visual in situ studies, *U. speciosa* and *U. thayeri* are confined to substrate-specific areas of the impoundments, and this may have a negative effect on the populations of these species when the impoundments are being managed (flooded). However, the results from Imp. #16A, which was flooded frequently for mosquito control, seem to contradict this assumption. In spite of this management, a rich community of *U. speciosa* was recorded on the ditch shore (site A), but with low densities of *U. thayeri*.

Even though the data on the occurrence of juveniles are limited, they indicate that fiddler crab reproduction (species unknown) occurs also in the impoundment perimeter ditch (site A and B). As shown in Figure 6, juveniles were, as expected, mainly found close to the water (sites 0 m, A, and B).

The dilution experiments indicate that none of the four species is sensitive to low salinities, a situation that rarely occurs within the impoundments. During this experiment *U. pugilator* was the most tolerant species. Thurman, (2003) investigated the osmoregulation of eight *Uca* species and found that *U. speciosa* and especially *U. pugilator* are able to withstand high “osmotic challenge.” Additionally, Thurman (2005) reported that *U. rapax* is best equipped for living in brackish habitats and that *U. thayeri* and *U. speciosa* are best suited physiologically to inhabit low and moderately saline habitats. This observation may explain why the latter two species are able to successfully inhabit the impoundment ditch “shores” (sites A and B). *U. rapax*, and most likely also *U. pugilator* are, as discussed earlier, able to migrate over long distances, for example, across the perimeter ditches (when the impoundments are being flooded) and dikes (studies by the author on ~1,200 of marked *U. rapax* individuals). However, this is most likely not the case with *U. speciosa* and *U. thayeri*. As *U. speciosa* is a comparatively small species, it may therefore be more vulnerable to desiccation than the other three species (Pellegrino, 1984).

High summer temperatures in the shallow impoundment water (see Table 2) pose a threat to the fiddler crab populations. Even though the temperature measurements only were performed twice within Imp. #16A (Table 2), they show that the temperature in the shallow (flooded) areas in the impoundment marsh may reach at least 44°C, which is significantly higher than in the nearby IRL. Large numbers of dead individuals were observed in very shallow water during these high temperature periods (within the marsh of Imp. #16A), but never at lower temperatures, and it was assumed that death was the result of short-term hyperthermia. Replicated laboratory experiments on *U. pugilator* and *U. rapax* collected inside Imp. #23 showed that lethal water temperatures (LD<sub>50</sub>) on individuals from this area are 41°–42°C. Teal (1958) reported a lethal temperature (LD<sub>50</sub>) between 39.5° and 40.0°C for *U. pugilator*, *U. minax*, and *U. pugnax*, and Vernberg and Tashian (1959) found that *U. rapax* was more resistant to temperatures of 42°–44°C than was *U. pugnax*. Wilkens and Fingerman (1965) performed a thorough study on lethal temperatures for *U. pugilator* in both saturated and dry air. LD<sub>50</sub> in saturated air was reached at 40.7°C, which

corresponds well to the results from my observations. Powers and Cole (1976) have also demonstrated that burrow temperature decreased rapidly with depth, proving the major heat refuge for *U. panacea* on open sand flats during a study on Mustang Island, Texas. Edney (1961), in a study on a number of fiddler crabs at Inhaca Island, Mozambique, found that the temperature within the burrows during the warmer months was considerably cooler than the sand on the surface. Preliminary results within this study (not presented) also indicate that the temperature drops significantly with sediment depth in the mosquito impoundments.

Genoni (1985), on a study on *U. rapax* in Florida, reported that there were more burrows than fiddler crabs in the sediment. Even if there was no correlation between fiddler crabs (all species) and burrows in the present study, the results were often the opposite from the results by Genoni (1985). Mouton and Felder (1996) investigated the quantitative distribution of *U. spinocarpa* and *U. longisinalis* by quantitatively counting the number of *Uca* burrows along transects in a Gulf of Mexico salt marsh. However, no studies were performed regarding the number of individuals (and species) living in these burrows. Excavating the substrate is a very labor-intensive procedure but obviously necessary to be able to evaluate the actual fiddler crab species distribution and abundance within specific areas (see Methods, above). The studies performed by the author in the three St. Lucie County impoundments and at Merritt Island (Cape Canaveral) impoundments (not reported here) did not produce any correlation between burrows and number of *Uca* specimens. Actually, in several cases when no burrows at all were found on the sediment surface within the 0.1 m<sup>2</sup> sampling area, large amounts of fiddler crabs were found in deeper areas when excavating the substrate within the sampling area according to the description above. Therefore, only counting *Uca* burrows does not seem to give correct data regarding *Uca* population abundance and species distributional pattern. Further detailed studies are therefore needed to elucidate this relationship.

In conclusion, these studies in the St. Lucie impoundments do not indicate that the construction and management of IRL mosquito impoundments pose a serious threat to fiddler crab populations. However, the impoundments may change the distributional patterns of the different species. It is important to note that new, highly suitable habitats were created when the impoundments were constructed, such as the perimeter ditch margins (sites A and B), especially preferred by *U. speciosa* and *U. thayeri* in impoundments with tidal access to the IRL. However, the



fate of these two species at the marsh side of the perimeter ditch (site B) during the prolonged artificial summer flooding is still unknown.

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#### LITERATURE CITED

- Barnwell, F. H. 1968. The Role of Rhythmic Systems in the Adaptation of Fiddler Crabs to the Intertidal Zone. *American Zoologist*, 8:569–583.
- Bertness, M. D. 1985. Fiddler Crab Regulation of *Spartina alterniflora* Production on a New England Salt Marsh. *Ecology*, 66:1042–1055.
- Bertness, M. D., and T. Miller. 1984. The Distribution and Dynamics of *Uca pugnax* (Smith) Burrows in a New England Salt Marsh. *Journal of Experimental Marine Biology and Ecology*, 83:211–237.
- Colby, D. R., and M. S. Fonseca. 1984. Population Dynamics, Spatial Distribution and Somatic Growth of the Sand Fiddler Crab *Uca pugilator*. *Marine Ecology Progress Series*, 16:269–279.
- Crane, J. 1975. *Fiddler Crabs of the World (Ocypodidae)*. Princeton, N.J.: Princeton University Press.
- DeCorsey, P. J. 1983. "Biological Timing." In *The Biology of Crustacea*, ed. D. E. Bliss, pp. 107–162. New York: Academic Press.
- Dittman, S. 1996. Effects of Macrobenthic Burrows on Infaunal Communities in Tropical Tidal Flats. *Marine Ecology Progress Series*, 134:119–130.
- Edney, E. B. 1961. The Water and Heat Relationships of Fiddler Crabs (*Uca* spp.). *Transactions of the Royal Society of South Africa*, 36:71–91.
- Fingerman, M. 1957. Relation Between Position of Burrows and Tidal Rhythm of *Uca*. *Biological Bulletin*, 112:7–20.
- Genoni, G. P. 1985. Increased Burrowing by Fiddler Crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae) in Response to Low Food Supply. *Journal of Experimental Marine Biology and Ecology*, 87:97–110.
- Gilmore, R. G., R. E. Brockmeyer Jr., and D. M. Scheidt. 1991. A Preliminary Report: Spatial and Temporal Dynamics of *Uca* Populations in High Marsh Habitats Vegetated with Algae, Herbaceous and Woody Flora under Managed Hydrological Cycles. Ft. Pierce, Fla.: Harbor Branch Oceanographic Institute.
- Gilmore, R. G., D. M. Scheidt, R. E. Brockmeyer Jr., and S. Vader Kooy. 1990. Spatial and Temporal Dynamics of Secondary Productivity in High Marsh Habitats Vegetated with Algae, Herbaceous and Woody Flora under Managed Hydrological Cycles. *Final Report, Coastal Zone Management 258*. Tallahassee, Fla.: Florida Department of Environmental Regulation.
- Grimes, B. H., F. T. Huish, J. H. Kerby, and D. Xoran. 1989. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)-Atlantic Marsh Fiddler. *U.S. Fish and Wildlife Service Biology Report 82*. Vicksburg, Miss.: U.S. Army Corps of Engineers Coastal Ecology Group.
- Heard, R. W. 1982. *Guide to the Common Tidal Marsh Invertebrates of the Northeastern Gulf of Mexico*. Ocean Springs, Miss.: Mississippi-Alabama Sea Grant Consortium.
- Holme, N. A., and A. D. McIntyre, eds. 1971. *Methods for the Study of Marine Benthos*. Oxford and Edinburgh: Blackwell Scientific Publications.
- Kerr, G. A. 1976. Indian River Coastal Zone Study, Inventory 1975. *Annual Report, Volume II*. Fort Pierce, Fla.: Harbor Branch Consortium.
- Kraeuter, J. N. 1976. Biodeposition by Salt-Marsh Invertebrates. *Marine Biology*, 35:215–223.
- Macintosh, D. J. 1982. "Ecological Comparison of Mangrove Swamp and Salt Marsh Fiddler Crabs." In *Wetlands Ecology and Management. Proceedings of the First International Wetlands Conference (New Delhi, India, 10–17 September 1980)*, ed. B. Gobal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, pp.243–257. Jaipur, India: National Institute of Ecology & International Scientific Publications.
- Montague, C. L. 1980. A Natural History of Temperate Western Atlantic Fiddler Crabs (Genus *Uca*) with Reference to Their Impact on the Salt Marsh. *Contributions in Marine Science*, 23:25–55.
- . 1982. "The Influence of Fiddler Crab Burrows on Metabolic Processes in Salt Marsh Sediments." In *Estuarine Comparisons*, ed. V. S. Kennedy, pp. 283–301. New York: Academic Press.
- Mouton, E. C., and D. L. Felder. 1996. Burrow Distribution and Population Estimates for the Fiddler Crabs *Uca spinacrapa* and *Uca longisignalis* in a Gulf of Mexico Salt Marsh. *Estuaries*, 19:51–61.
- Peterson, C. H., and N. M. Peterson. 1979. The Ecology of Intertidal Flats of North Carolina: A Community Profile. *Biological Services Program Report FWS/OBS-79/39*. Sidell, La.: U.S. Fish and Wildlife Service.
- Pellegrino, C. R. 1984. The Role of Desiccation Pressure and Surface Area/Volume Relationships on Seasonal Zonation and Size Distribution of Four Intertidal Decapod Crustacea from New Zealand: Implications for Adaptation to Land. *Crustaceana*, 47(3):251–268.
- Powers, L. W., and J. F. Cole. 1976. Temperature Variation in Fiddler Crab Microhabitats. *Journal of Experimental Marine Biology and Ecology*, 21:141–157.
- Rey, J. R., and T. Kain. 1991. *A Guide to the Salt Marsh Impoundments of Florida*. Vero Beach, Fla.: The Florida Entomology Laboratory.
- Ringold, P. 1979. Burrowing, Root Mat Density, and the Distribution of Fiddler Crabs in the Eastern United States. *Journal of Experimental Marine Biology and Ecology*, 21:141–157.
- Salmon, M. 1967. Coastal Distribution, Display and Sound Production by Florida Fiddler Crabs (Genus *Uca*). *Animal Behaviour*, 15:449–459.

- Salmon, M., W. H. Seiple, and S. G. Morgan. 1986. Hatching Rhythms of Fiddler Crabs and Associated Species at Beaufort, North Carolina. *Journal of Crustacean Biology*, 6:24–36.
- Tashian, R. E., and F. J. Vernberg. 1958. The Specific Distinctness of the Fiddler Crabs *Uca pugnax* (Smith) and *Uca rapax* (Smith) at their Zones of Overlap in Northeastern Florida. *Zoologica*, 43:89–92.
- Teal, J. M. 1958. Distribution of Fiddler Crabs in Georgia Salt Marshes. *Ecology*, 39:185–193.
- Thompson, W. E., P. J. Molinaro, T. M. Greco, J. B. Tedeschi, and C. W. Holliday. 1989. Regulation of Hemolymph Volume by Uptake of Sand Capillary Water in Desiccated Fiddler Crabs *Uca pugilator* and *Uca pugnax*. *Comparative Biochemistry and Physiology*, 94A:531–538.
- Thurman, C. L. 2003. Osmoregulation in Fiddler Crabs (*Uca*) from Temperate Atlantic and Gulf of Mexico Coasts of North America. *Marine Biology*, 142:77–92.
- . 2005. Comparison of Osmoregulation among Subtropical Fiddler Crabs (*Uca*) from Southern Florida and California. *Bulletin of Marine Science*, 77:83–100.
- Vernberg, F. J., and R. E. Tashian. 1959. Studies on the Physiological Variation between Tropical and Temperate Zone Fiddler Crabs of the Genus *Uca*. I. Thermal Death Limits. *Ecology*, 40:589–593.
- Vernberg, W. B., P. J. DeCoursey, and W. J. Padgett. 1973. Synergistic Effects of Environmental Variables on Larvae of *Uca pugilator*. *Marine Biology*, 22:307–312.
- Weis, J. S., and P. Weis. 2004. Behavior of Four Fiddler Crabs, Genus *Uca*, in Southern Sulawesi, Indonesia. *Hydrobiologica*, 523:47–58.
- Wheeler, D. E. 1978. Semilunar Hatching Periodicity in the Mud Fiddler Crab *Uca pugnax* (Smith). *Estuaries*, 1:268–269.
- Wilkins, J. L., and M. Fingerman. 1965. Heat Tolerance and Temperature Relationships of the Fiddler Crab, *Uca pugilator*, with Reference to Body Coloration. *Biological Bulletin*, 128:133–141.
- Yoder, J.A., K. A. Reinsel, J. M. Welch, D. M. Clifford, and E. J. Rellingner. 2005. Herding Limits Water Loss in the Sand Fiddler Crab, *Uca pugilator*. *Journal of Crustacean Biology*, 25:141–145.
- Zucker, N. 1978. Monthly Reproductive Cycles in Three Sympatric Hood-Building Tropical Fiddler Crabs (Genus *Uca*). *Biological Bulletin*, 155:410–424.



# Dynamic Hydrology of a Mangrove Island: Twin Cays, Belize

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**ABSTRACT.** The hydrology of an overwashed mangrove island is shown to be both complex and dynamic, with a strong interaction between tide-induced flow and the resident red mangrove (*Rhizophora mangle* L.) root system. A topographic map of the tidally flooded area of the island was made and related to the tide-induced water levels. The flooded area approximately doubled during the usual tidal event. The bottom topography is highly irregular with a maximum channel water depth of about 1.5 m, but much of the flooded area experiences a water depth of less than 0.5 m. Water elevations were recorded by automatic water level loggers for periods of time up to 9 months. The usual symmetrical parabolic tide signal was transformed into a highly asymmetrical form as it moved landward through the tangled root system of the red mangrove forest. A normal tide range of 13 cm at the island margin attenuated to 3 cm at a distance of 200 m landward, with a lag time of 2 h for highs and 6 h for lows. Maximum flow velocities of 5 cm/s were measured in the main channels with marked reduction in regions of dense mangrove root and shallow water depth. The combined frictional resistance of the bottom and associated mangrove roots is characterized by a Manning's roughness coefficient,  $n$ , that ranged from 0.084 to 0.445. The changing flow pattern within the flooded mangrove swamp was mapped during a 7 h high-to-low tide period using aerial photography to track the movement of slugs of visible dye placed at three locations. Analysis of the sequential time-related photos showed limited lateral dispersion in the tortuous main channel but strong tidally controlled flow direction changes and dispersion along the channel axis. A strong circulatory pattern is observed in a shallow pond at the south central terminus of the tidally affected flow system. This large shallow pond is sparsely populated by dwarf red mangrove and is some 350 m from a primary connection with the surrounding lagoon. Poor flushing of the pond creates water temperatures ranging from 25°C in the winter to 40°C in the summer. High surface water evaporation creates a hypersaline condition of 45 ppt salinity in summer. In winter, with the infusion of fresh rainwater, salinity of surface water in the pond can be less than 5 ppt. Because of its role in the transport of nutrients and detritus, and its flushing action, the dynamic hydrological system of the mangrove island is a highly important ecological feature of the overwashed mangrove island.

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## INTRODUCTION

Mangrove forests are tropical wetlands with a specialized vegetation adapted to waterlogged and saline conditions (Lugo and Snedaker, 1974; Hutchings and Saenger, 1987; Ball, 1988). These forests provide energy-absorbing buffers from



hurricane-driven seas, prevent coastal erosion, provide a protective habitat for many fish juveniles, and are a nutrient source for the surrounding waters (Odum and Heald, 1972, 1975; Twilley, 1988; Danielson et al., 2005; Barbier, 2006, Constanza et al., 2008), as well as a filtering mechanism for sediments and pollution (Alongi and McKinnon, 2005). Under natural conditions mangroves live in a highly dynamic environment and in synergistic balance with their natural neighbors. Mangroves have evolved features that enable them to cope with an ever-changing regime of tidal water ranges, variable salinity and temperature, and anoxic soil conditions, but within limits (Tomlinson, 1986). The biggest enemy appears to be man, who can directly or indirectly destroy, in days, whole mangrove communities that have taken thousands of years to develop (Alongi, 2002; Macintyre et al., 2004; Rodriguez and Feller, 2004; Taylor et al. 2007; Duke et al., 2007).

It is widely recognized that hydrological patterns determine mangrove structure and function at the ecosystem scale (Lugo and Snedaker, 1974; Forman and Godron, 1986; Twilley, 1995), and general models of mangrove hydrodynamics have been developed (Wolanski et al., 1992). In these coastal wetlands, tidal flooding and surface drainage influence many ecological processes, including habitat quality, water movement, filtration, and nutrient cycling (Forman and Gordon, 1986). Water flow also influences the dispersal and establishment of mangrove propagules (Mazda et al., 1999).

The significant role of vegetation and the effect of intertidal root density on tidal movement in mangrove channels has been described by Wolanski et al. (1980) and over the broader mangrove swamp environment by Wolanski et al. (1992), Furukawa and Wolanski (1996), Mazda et al. (1997), and Mazda et al. (2005). Thus, there is a synergistic relationship for the development and growth of a mangrove forest that depends on the dynamics and magnitude of tidal inundation into the swamp. Concurrently, the frictional resistance of the mangrove roots controls the degree of tidal inundation and patterns of movement in the mangrove swamp (Wright et al., 1991).

Based on long-term experiments on offshore mangrove islands in Belize, hydrodynamics have been linked to distinct patterns of nitrogen (N) and phosphorus (P) limitation across the intertidal flow system (Feller et al., 2003). Lovelock (2008) suggested that differences in tidal inundation also influence soil respiration and below-ground carbon sequestration via root production, which is the source of the deep peat deposits underlying these islands. McKee et al. (2007) predicted that the ability of islands such as Twin Cays to keep pace with rising sea

levels is dependent on the tight coupling between peat formation and hydrology.

Although these and other studies based at Twin Cays have identified tidal flooding as an important drive of ecological processes, there is limited knowledge on the specific pattern of water movement across these islands. Thus the objective of this research was to conduct a detailed analysis of tidal characteristics and flushing patterns of West Island, the smaller of the two main islands in the Twin Cays Archipelago.

## LOCATION

The Twin Cays Archipelago lies some 22 km off the coast of Belize (Figure 1) on the edge of the Belizean Barrier Reef (16°50'N, 88°06'W). Islands of the Barrier Reef and its surrounding waters have been the locations for scientific ecosystem studies by the Smithsonian Institution since 1972 (Rützler and Macintyre, 1982). Because of their pristine condition and relative isolation from anthropogenic effects, the islands and contiguous waters of Twin Cays were selected for detailed scientific research of oceanic mangroves and associated marine ecosystems (Rützler and Feller, 1996). Field studies of the dynamic hydrology of the Twin Cays mangrove ecosystems were begun in 1986 and have continued since that time. This particular study focuses on the surface hydrology of West Island of Twin Cays (Figure 1), a 21.5 ha kidney-shaped landmass approximately 900 m long and 400 m wide. According to the classification of Lugo and Snedaker (1974), the island is an "overwashed mangrove island," one frequently overwashed by tides and with high organic export.

## ISLAND CHARACTERISTICS

The land cover on West Island and effect of man are shown in Figure 2, which depicts the natural mangrove growth and the man-made clear-cut and dredge-fill as mapped by I. C. Feller of the Smithsonian Institution in 2002. Since then even more mangrove destruction has occurred on the east side of the island. The island is dominated by the red mangrove, *Rhizophora mangle* L., with black mangrove (*Avecennia germinans* L.) on somewhat higher topography in the intertidal zone and white mangrove (*Laguncularia racemosa* L.) above the intertidal zone (Rützler and Feller, 1988; Rodriguez and Feller, 2004). It is to be noted that the density of the mangrove is far from uniform, with sparse dwarf red mangrove dominating the interior, and much more vigorous red mangrove growth on the island perimeter

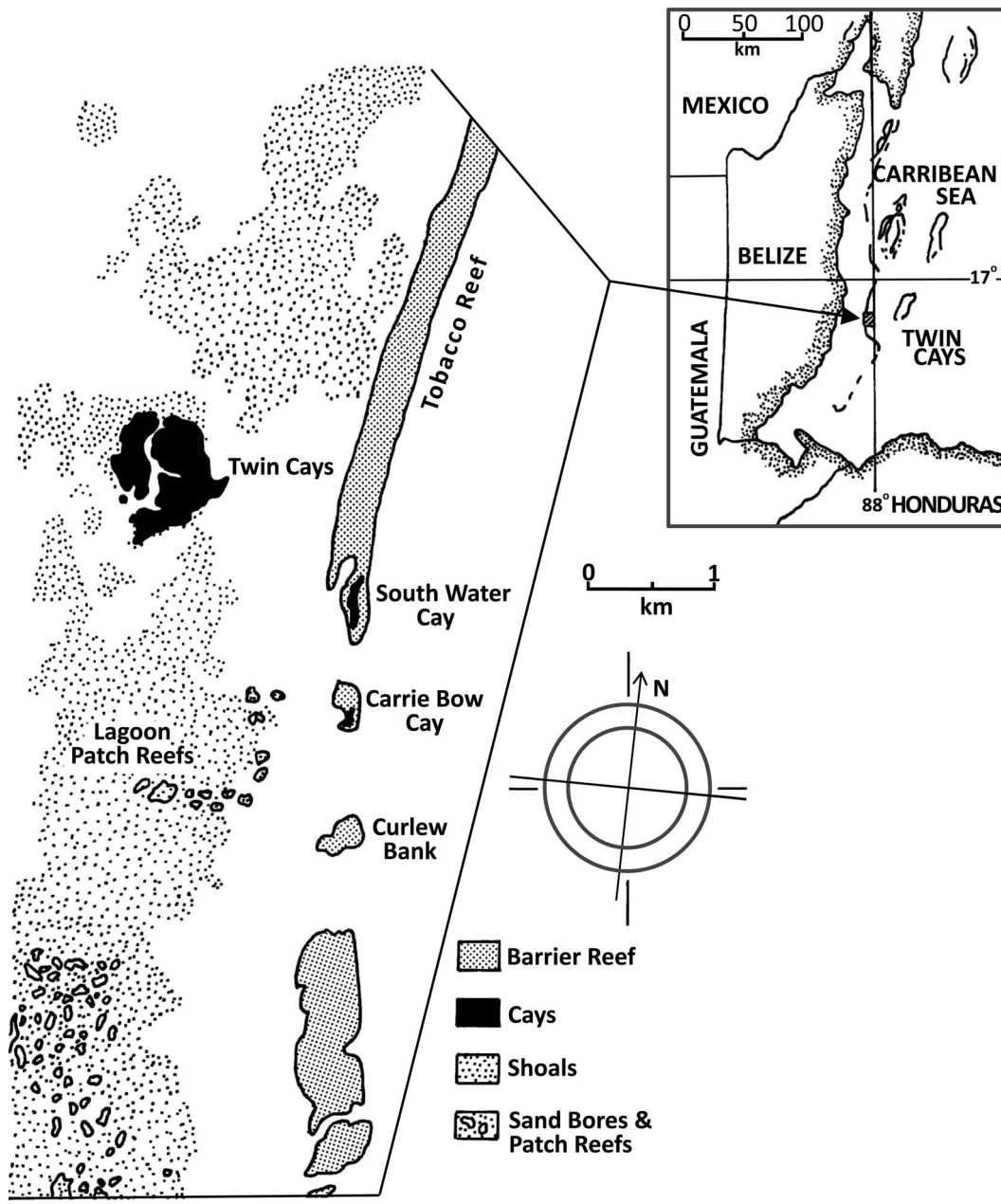


FIGURE 1. Location map of Twin Cays, Belize, Central America. (Adapted from Rützler and Macintyre, 1982.)

and in areas of greater tidal movement. Figure 3 is a photograph taken from the island interior showing the dwarf red mangrove in the foreground and the distant background of taller dense red mangrove growth that characterizes the island perimeter. Figure 4 provides a botanical rendering of the cross section of the scrub red mangrove, showing the relationship between mangrove foliage, stem and root structure, average tidal range, and

hydrogeologic strata. It is to be noted that the typical low tide level is near the top of the organic ooze.

The mangroves of Twin Cays have developed on an ancient limestone plateau over the past 8,000 years (Macintyre et al., 2004). During this time 9–12 m of Holocene mangrove deposits have accumulated on the underlying limestone substrate and kept pace with rising sea level (Toscano and Macintyre, 2003; Macintyre

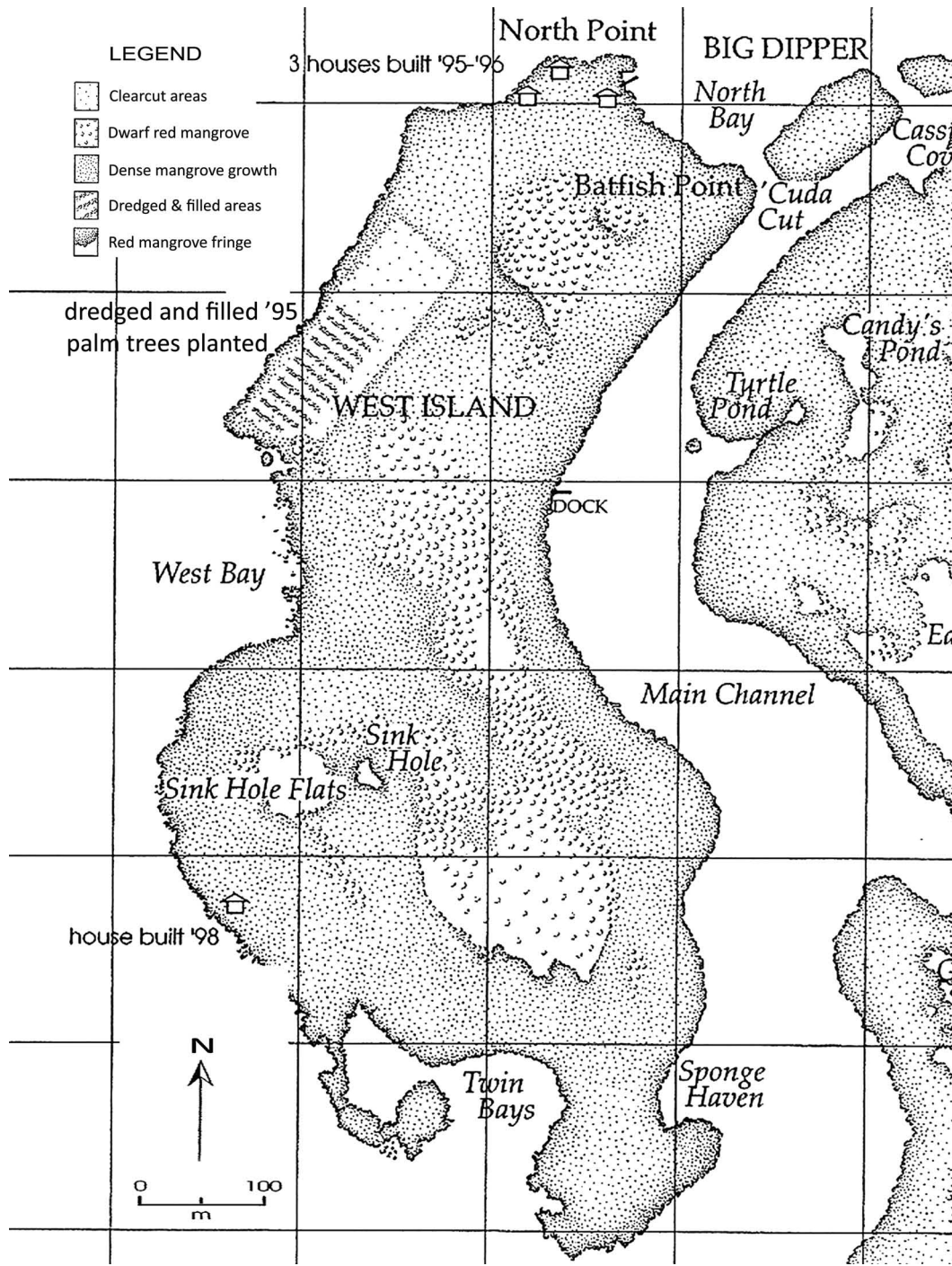


FIGURE 2. Land cover characteristics of West Island, Twin Cays, Belize, based on aerial photographs taken in 2002 that show mangrove density and clear-cut areas. (Drawn by Molly K. Ryan of the Smithsonian Institution in 2002.)





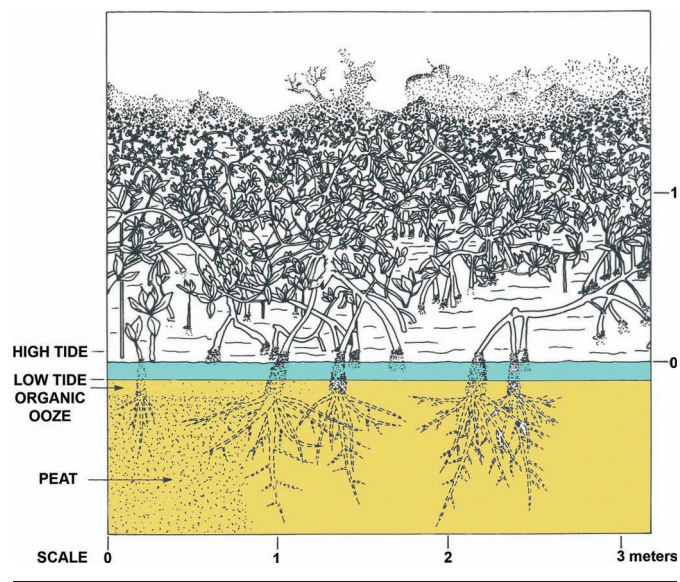
**FIGURE 3.** Photograph of West Island, Twin Cays, showing dwarf red mangrove of island interior with much more vigorous fringe red mangrove growth in distance along periphery of the island.

et al., 2004; McKee et al., 2007). Macintyre and Toscano (2004) found Pleistocene limestone at depths of 8.3 to 10.8 m below mean sea level in cores at West Island. As sea level rose to cover a subaerially eroded limestone plateau fringing the coastline, mangrove peat appears in the stratigraphic record. The highest topography of the island is on the seaward side where deposited sand is no more than 1 m above mean sea level. The limestone is now found at depths of 9 to 10 m below present sea level (Macintyre et al., 2004). The swamp bottom is composed largely of soft silty organic detritus. Exceptions of harder bottoms are found in the nearshore swamp channels where stronger tide-induced velocities have scoured the channel bottoms.

The climate of Twin Cays is marine tropical with air temperatures ranging during the year from 24°C in January to 29°C in June; humidity averages about 78% (Rützler and Ferraris, 1982). Lagoon water temperatures range from 23°C in the winter to 31°C in the summer. The microclimate of West Island, particularly that of the interior water, has a much greater range. The estimated annual precipitation at Twin Cays is about 1,885 mm, based on 4 years of complete records at the climatological station on Carrie Bow Cay, 4 km away. This precipitation is about 80% of the annual precipitation of the nearest mainland climatological station, the Melinda Forest Station, 30 km to the northwest. The monthly pattern is much the same for both stations. Hurricanes cause seawater to completely

overwash the low-lying island. However, the natural mangrove ecosystem seems resilient and well suited to survival from natural events, viz. hurricanes. No significant adverse effects have been observed on Twin Cays; the same cannot be said for the response to man-made features, where mangrove clearing results in severe coastal erosion.

Tides in the lagoon area surrounding the island are microtidal with an average range of about 15 cm and are of the mixed semidiurnal type (Kjerfve et al., 1982). The tides exhibit semidiurnal high and lows with a tidal cycle periodicity of approximately 12 h and 25 min, but display a marked asymmetry with a large tide range following a smaller one. In some cases the larger range is as much as 40 cm, followed by a range of only 10 cm. At times the smaller range is so small as to appear nonexistent. In other cases certain components of the tide occur simultaneously and create a range as great as 50 cm. Once the tidal signal enters the tangled root system of the mangrove, the signal changes from a form that is approximately parabolic to a highly asymmetrical pattern, in which the rising limb of the flood tide is much steeper than the falling limb. Concurrently the amplitude is attenuated, and the highs and lows of the tidal signal lag the open lagoon tide. The spring–neap tidal cycle is about 29.5 days and can cause monthly tidal ranges that completely “dry up” the interior of the island.



**FIGURE 4.** Botanical rendering of cross section of dwarf red mangrove showing relationship between mangrove foliage, stem and root structure, average tide range, and hydrogeologic strata. (Drawn by Molly K. Ryan of the Smithsonian Institution in 1989.)



## METHODOLOGY

The information required for a study of the dynamic hydrology of West Cay encompassed both spatial and temporal data and a wide variety of methods. These methods included field surveying techniques for obtaining the island topography and bathymetry, automated water level recorders for water levels, automated temperature loggers, electromagnetic water current meters, conductivity meters for determination of water salinity, and aircraft for photographic recording of dye flows, among a host of lesser equipment and measuring devices that were employed over the study period of 18 years (1988–2006).

### TOPOGRAPHY

Topography was determined for the tidal flood region extending from open lagoon water at the west side of the island along the 350 m long channel and the southern interior pond (Urish et al., 2003; Wright et al., 1991). Some 36 semipermanent monitor locations were established in 1988 in the intertidal swamp to obtain water level and water quality measurements. The locations were marked with 2 cm diameter polyvinyl chloride (PVC) pipes driven into the ground in a grid pattern. Horizontal control was established by field measurement with a 35 m long tape and conventional level and transit surveying techniques (Wolf and Ghilani, 2006), later located with Global Positioning System (GPS) technology using a Garmin GPS 76. These data were later used for georeferencing of all island features (Rodriguez and Feller, 2004). Vertical control for land and water measurements was determined from a primary datum reference point on the east side of the island to which an arbitrary datum was assigned. The initial elevation assigned to this reference point was 3.05 m with all readings later adjusted to an approximate mean lower low water (MLLW) after several years of time segments of about 2 weeks; one long record of 9 months of tidal data was obtained. A datum lower than the typical terrestrial datum of “mean sea level” was used to maintain both topography and water level values positive to the extent possible.

Two principal surveying transects across the island were established: (1) from the lagoon to the bend in the channel along an east-to-west run including 6 points (F1 to A1) and (2) from the bend in the channel to the south pond along a north-to-south run of 12 more points (A1 to A12). In addition, 3 to 5 points were determined perpendicular to each transect point. These secondary points were spaced approximately 15 m apart. These established

points, as located on Figure 5, were the primary location references for all subsequent data collection.

Automated pressure transducer water level loggers (In-Situ Environmental Data Logger Model SE 1000c with pressure transducer probes) were employed at five locations for short-term (1–2 weeks) measurements. These units were vented to automatically compensate for ambient atmospheric pressure. Later in the study period 12 of these locations became long-term monitoring stations with automated self-contained water level loggers (Remote Data Systems, Navassa, N. C.) that remained in place for as long as 12 months to record data at 30 min intervals with an accuracy of about 3 mm. Self-contained automated temperature loggers (Optic Stowaway by Onset Computer Corporation) were also deployed to record temperatures at 30 min intervals for as long as 9 months. In addition to the monitor locations, stilling wells consisting of slotted 15 cm diameter PVC pipe for both manual and instrumented tide measurements were established at both shorelines of the island, and later in the study these were correlated with a primary oceanographic/climatological data collection station established at the Smithsonian Research Station on Carrie Bow Cay, 4 km southeast. The tops of the stilling wells were initially assigned an elevation based on the same arbitrary datum as used at the key datum reference points. Elevations were established on the tops of all reference station pipes using survey leveling techniques with a Topcon Automatic Level (model ATF-1A). The coordination of tides at West Island and Carrie Bow Cay was accomplished by comparison of a series of six separate short-term tidal cycle measurements taken concurrently at both stations.

### HYDROLOGY

Water flow direction and velocities during various positions of the tide cycle were determined using conventional stream gauging techniques along channel cross-sections, or “reaches:” section A–A’ was defined between survey points A1 and D1 and reach B between survey points D1 and E1. The measurements were taken at various times during the tidal cycle using a Marsh-McBirney electromagnetic current velocity meter and standard stream channel cross-sectioning methods (Watson and Burnett, 1995). Velocities and water depths were measured at 0.6- to 1.5 m intervals perpendicular to the flow to provide 25 to 50 individual measurements at each cross section. These measurements were then plotted to determine flow volumes and flow friction factors and to examine trends.

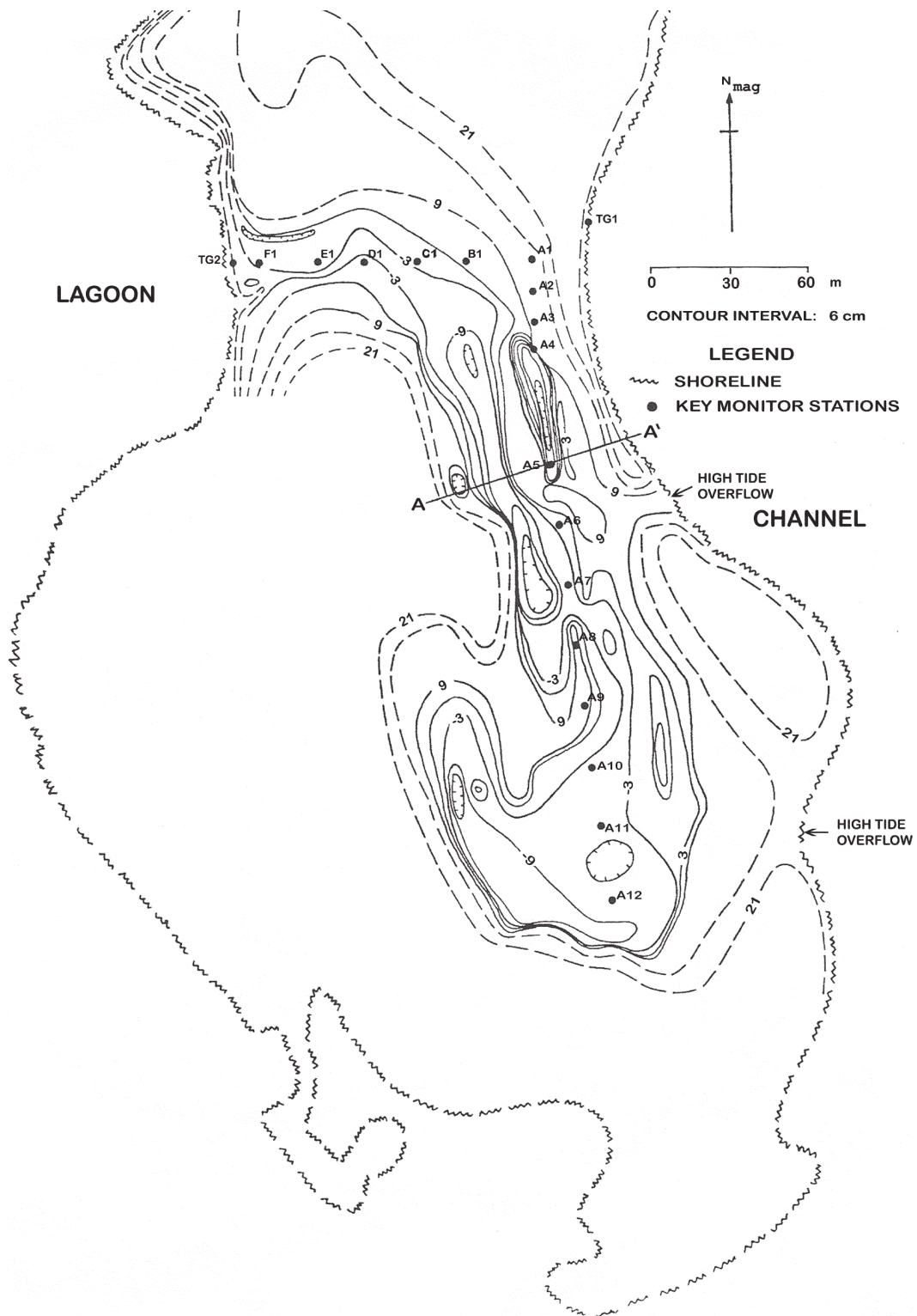


FIGURE 5. Topographic contour map of interior of West Island showing locations of key monitoring stations and representative channel cross section A-A'. Elevation datum = mean lower low water (MLLW). Contour interval = 6 cm.

Water salinity ( $\pm 0.1$  ppt), conductivity ( $\pm 0.1$   $\mu$ S), and temperature ( $\pm 0.1^\circ\text{C}$ ) were measured with a YSI 30 S-C-T (Yellow Springs, OH) in the field and in the laboratory. Salinity measurements were also made in the field using a refractometer (model 366ATC; Vista) with an accuracy of  $\pm 1$  ppt.

Flow patterns were also observed and evaluated by use of dye studies, both at the surface water level and by helium balloon low-level photography in 1990 and 1991, and later by high-level aircraft photography during a tidal cycle in 1993. Although the balloon photography was only of limited value because upper air wind currents caused the balloon to drift off the island, aircraft photography was highly successful. Large targets, approximately  $1 \times 2$  m in size, were marked and placed at each station for dye movement referencing. Continuing runs at 0.5 h intervals were made across the island on the same flight path at an altitude of 150 m. Photographs were taken during each run with a SLR camera with AF Zoom 35-70 mm lens (Minolta 5000 MAXXUM), thus enabling both the flow directions and dispersion within the mangrove system to be observed. Slugs of Rhodamine fluorescent dye, a highly visible but nontoxic dye, were placed at three stations at the start of the observation period. The dye remained highly visible during one tidal cycle. Continuing, but diminishing, levels of the fluorescence were measured in the laboratory on water samples taken during three subsequent tidal cycles. The series of photographs taken from the aircraft runs were reduced to a time sequence of plots and then used by George L. Venable of the Smithsonian Institution to produce an animated video of the dye movement for further study.

## RESULTS

### TOPOGRAPHY

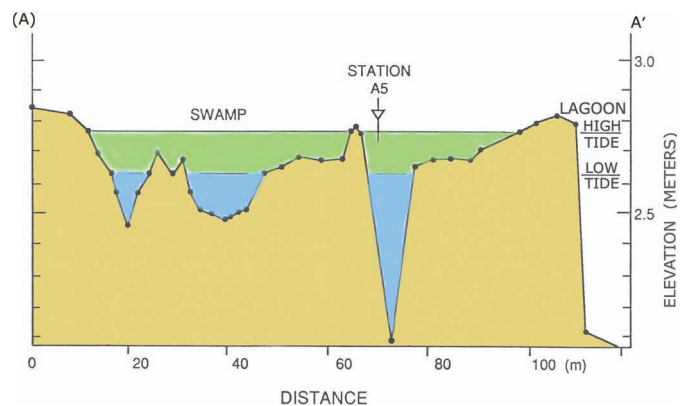
A topographic map of the intertidal flood zone region of West Island is shown as Figure 5. The highly irregular nature of the bottom is evident by inspection of the contour pattern. The region of tidal flow and flooded area is characterized by relatively flat areas with water depths frequently only about 25 cm over much of the flow system, but highlighted by sections more than 1 m in depth, such as occur between stations A4 and A5. Such deep holes are not necessarily coherent with the main flow channel. A cross-section (A–A') plot (Figure 6) at station A5 depicts the extreme changes in channel bottom that exist at this location. In contrast, the other significant feature of the system is a very large shallow pond of about 2.2 ha at sta-

tions A10 to A12 at the south central part of the island. This region contains only sparse dwarf red mangrove with a flooded depth of about 0.25 m. Additionally, examination of the topographic map shows ground level at the east shoreline of this pond is about 6 cm lower than the rest of the island periphery. At high tides these limited lower topographic zones allow lagoon water from outside to enter the internal swamp flow system. In particular, high tide waters overtop the island perimeter at two other locations on the east side into the central region, causing short-term hydrological anomalies of temperature and salinity, as well as a somewhat irregular tidal signal, in the system.

### HYDROLOGY

Figure 7 is a five-day plot showing the typical tidal signal as it enters the swamp system at TG2. As the signal enters the mangrove system, the frictional resistance of the roots cause attenuation in tide amplitude as well as a time lag in the highs and lows.

The unique hydrological nature of the flow in the mangrove ecosystem is characterized by a very shallow water depth that averages only about 0.5 m at low tide to 0.67 m at high tide, although great variations exist. However, because of the very flat topography, even this low tidal fluctuation causes an extensive and significant hydroperiod of wetting and drying with important implications to the mangrove ecosystem. As depicted on Figure 8, the area typically covered by water during high tide is about double that covered by water during low tide. Doyle (2003) states that his controlled field experiments



**FIGURE 6.** West Island cross section A–A' at station A5 showing relative relationship of high and low tides to bottom contours. Green = range of flooding from the tide; blue = low tide flow. Elevation datum is arbitrary.

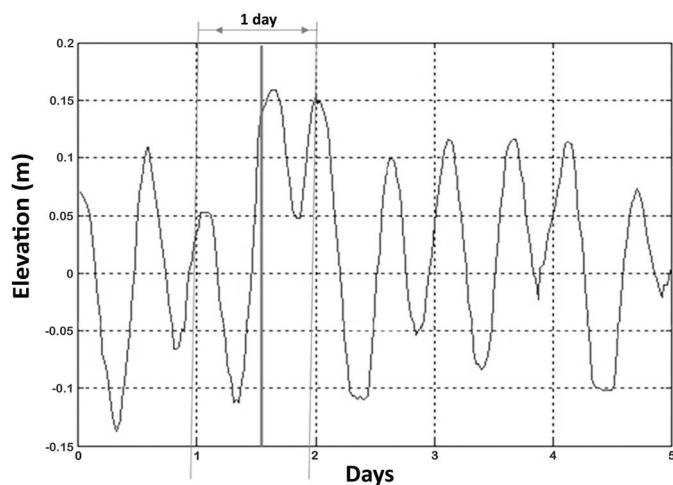


FIGURE 7. Plot of five-day tide sequence showing relative ranges and asymmetry of the tide at West Island. Elevation datum = approximate mean sea level.

“suggest that the hydroperiod—the rate and level of tidal exchange—plays a much more important role in determining mangrove growth and success than previously documented.” Figure 9 presents a conceptual plot showing the wetting–drying cycle during the sequential phases of the tide. Perhaps even more important, the tide range is sufficient to cause reversal of flow direction and velocity throughout the system during each cycle.

Figure 10 shows the changing characteristics of the tidal signal at three stations as it moves inland in a tortuous path through the mangrove ecosystem. A tide range of 13 cm at the island margin is attenuated to 8 cm at a location 50 m landward and to 3 cm at a location 200 m landward in the main flow channel. Concurrently, there is a lag time of 1 h for high tide and 2 h for low tide at 50 m landward, and of 2 h for high tide and 6 h for low tide at 200 m landward. The great difference in lag time between highs and lows is caused by the much greater influence of root density during a receding tide; this is also illustrated by the asymmetrical characteristic of the tidal signal as it transposes landward.

The seasonal climatic variations had a profound effect on the monthly hydrological budget, especially when the high evapotranspiration was considered. Figure 11 shows the approximate seasonal relationships of precipitation, surface water evaporation, and vegetation transpiration (evapotranspiration), assuming a total annual rainfall of 1,885 mm. This value and the estimated monthly values are based on limited (about 5 years) available data that

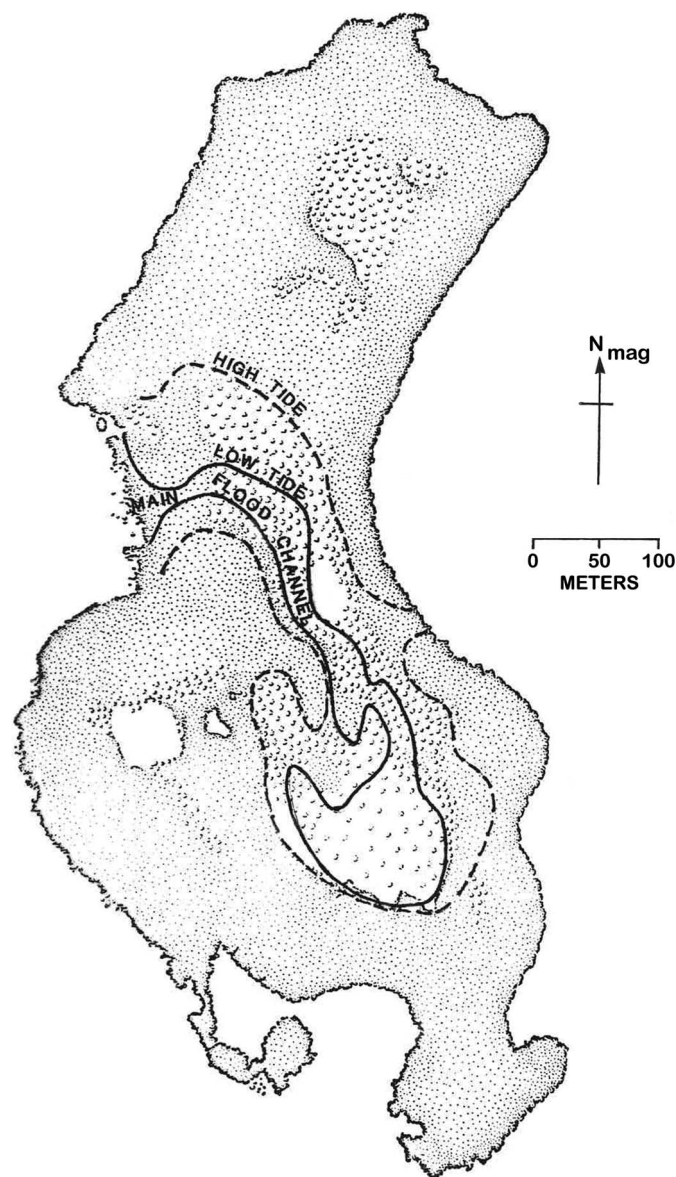


FIGURE 8. Plan of West Island showing aerial extent of tidal flooding between average daily low and high tides. Stippling on map shows relative density of vegetation. (Adapted from drawing by Molly K. Ryan of the Smithsonian Institution in 2002.)

have been collected at Carrie Bow Cay and correlated with the longer-term record at the mainland Melinda Forest Station. The potential evapotranspiration values for each month were calculated from the Thornthwaite equation (Dunne and Leopold, 1978; Thornthwaite and Mather, 1987) using a partial record of temperature and solar radiation available for Carrie Bow Cay. Examination of the water budget shows a deficit of precipitation as



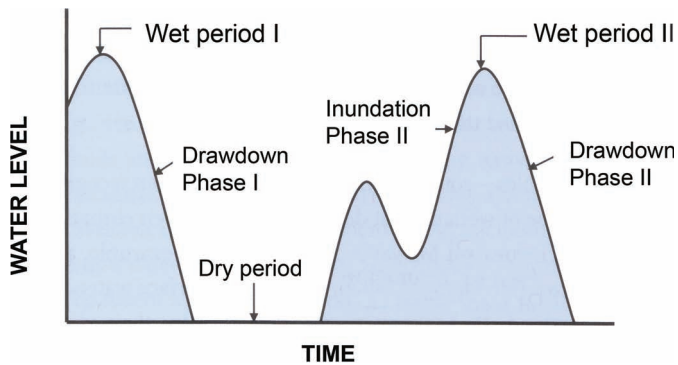


FIGURE 9. Conceptual plot of tidal phases during mixed semidiurnal hydroperiod event. (Adapted from Boulton and Brock, 1999.)

compared with evapotranspiration February through June during the “dry” season and a surplus during the “wet” season months from July through January. This “dry” season water deficit has an extreme effect on the surface water in the semienclosed interior swamp system, especially in the poorly flushed shallow pond at the south end of the island. Figure 12 is a composite plot of water temperature and salinity measured along the main flood channel over several years during the “dry” and “wet” seasons. Near the inflowing/outflowing location at station F1 the values approach those of lagoon water at the periphery of the

island, but in the shallow pond the value ranges are much more extreme, with salinity ranging from 5 to 45 ppt and temperatures ranging from 25°C to 40°C. Some temperature and salinities even exceed these values in particularly isolated locations.

The elevations of the water surfaces and velocities at three stations within the first 150 m inland from the shore, as compared with the primary tide signal at shore station TG2, are shown in Figure 13. It is to be noted that at all stations the maximum velocities occur during the middle of the falling tide, with the highest velocities found nearest shore. This pattern is comparable with the tidal asymmetry and velocity patterns found by Bryce et al. (2003) in mangrove creek systems in Australia. The distribution of flow and variations of velocity for a typical channel section are illustrated in Figure 14 for a cross section at station A4. The data were acquired during a mid-tide flood tide at a time of maximum velocity. The upper part of Figure 14 shows depths of water across the section at the specific time of the velocity measurements shown in the lower part. The velocities shown are an average determined from a series of velocities measured at a series of depths over the shortest time period possible. As indicated the velocity changes dramatically, from 2.0 to 0 cm/s, across the section, although there is a general pattern of greater velocity at the deeper parts. However, this is contradictory to the observation that the deeper part on the right side does not

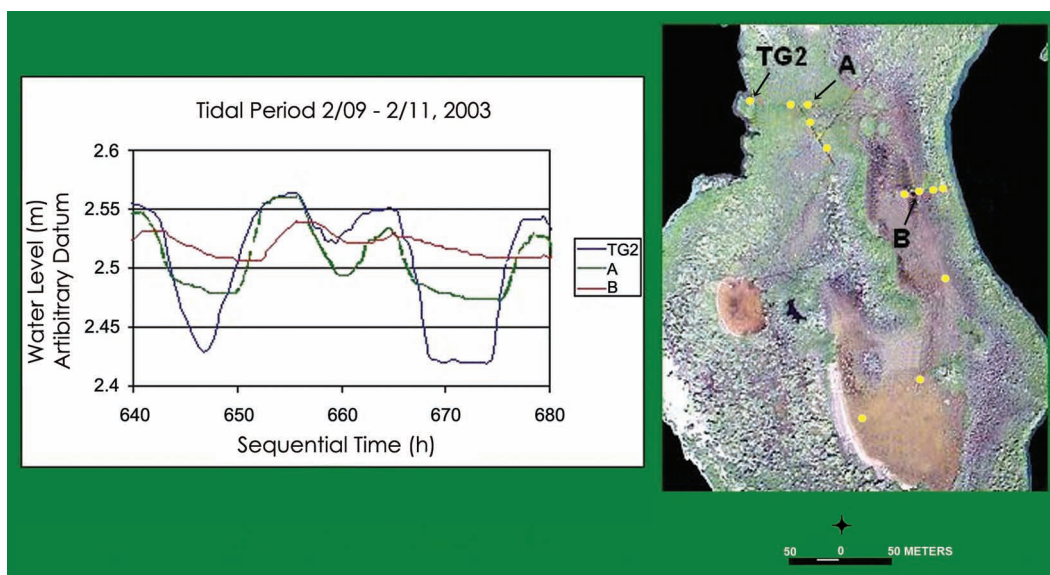


FIGURE 10. Tidal fluctuation plots at three interior monitoring stations—TG2, A, and B, as shown on photograph at right—during maximum velocity of flood tide on 27 May 1988. Yellow dots on the photograph are locations of monitor stations. Elevation datum is arbitrary.

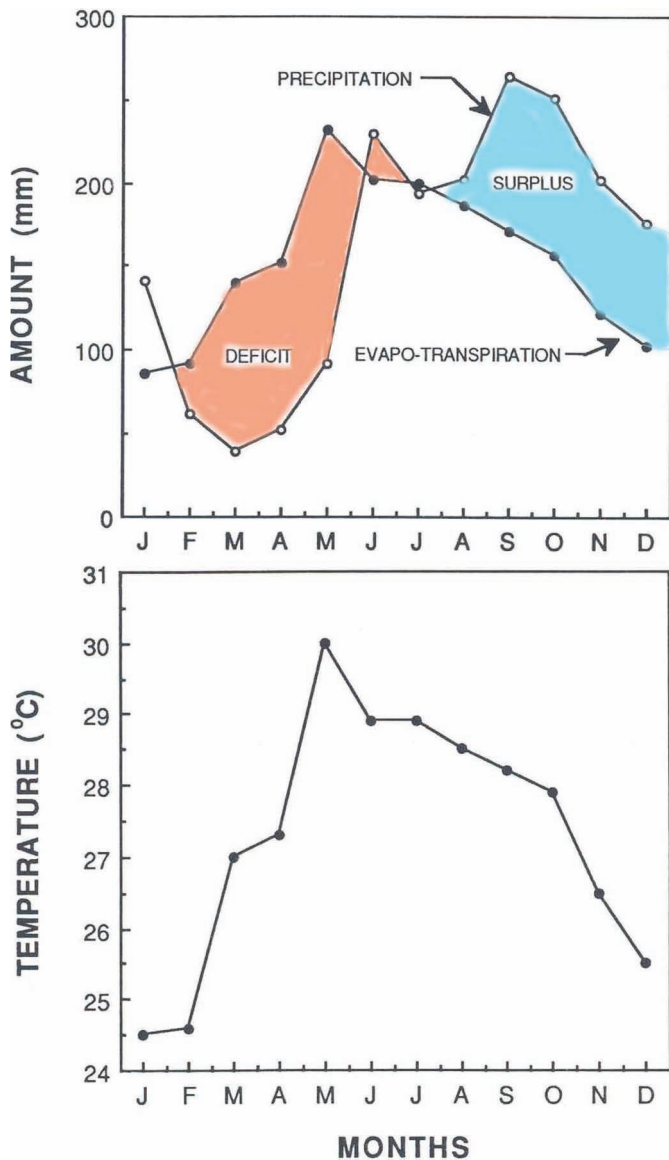


FIGURE 11. Hydrological budget for West Island showing annual pattern of precipitation, evapotranspiration, and temperature. Shaded orange area = the “dry season” with net deficit of water from evapotranspiration; blue shaded area = the “wet season” with a surplus of precipitation.

have a high velocity. Inspection of the topographic plan (see Figure 5) provides the explanation: The deeper right-hand feature is a part of a closed depression, whereas the deeper part on the left is continuous with the main channel flow.

The average flow velocity between points in the swamp is reflective of both the tortuous path of flow through the mangroves and the frictional resistance of the mangrove root system and the channel bottom. This resistance can

be quantified by inverse calculation of the Manning equation for stream flow (Watson and Burnett, 1995). Although the Manning equation was originally developed for stream flow, it has a logical deterministic relationship that has been used successfully by other researchers for mangrove flow characterization and modeling (Wolanski et al., 1980). The Manning equation in MKS unit format (Lindsley and Franzini, 1979) is

$$V = 1/n R^{2/3} S^{1/2},$$

where  $V$  is the average velocity,  $n$  is the Manning roughness coefficient,  $R$  is the hydraulic radius (cross-section area divided by wetted perimeter), and  $S$  is the slope, or hydraulic gradient, of the water surface.

Manning’s roughness coefficient,  $n$ , was determined at various locations in the flow system and at various times in highly fluctuating stream depth and current direction. The determined values of  $n$  for these measurements ranged

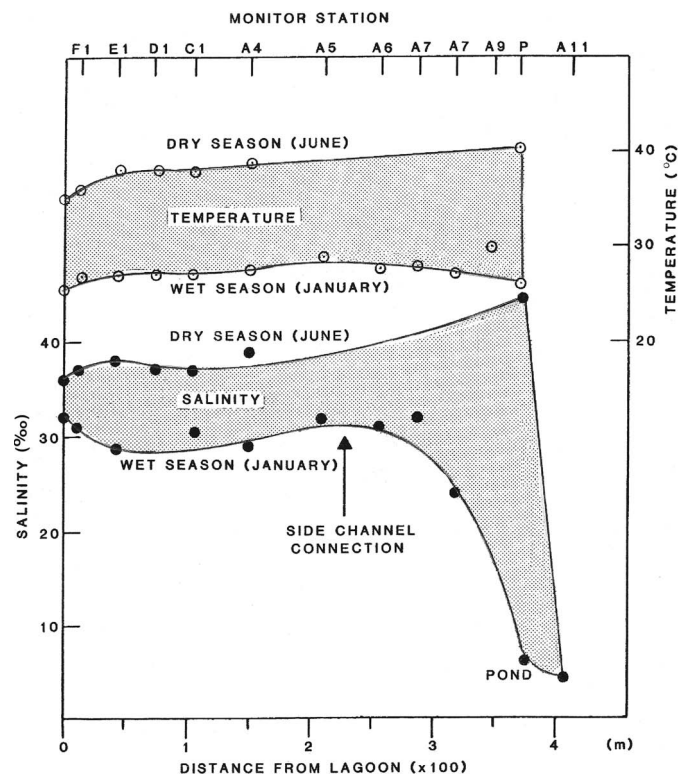


FIGURE 12. Plot showing ranges of salinity (black dots) and temperature (circles) during “dry” and “wet” season conditions at the southern shallow pond on West Island. Monitoring stations (see Figure 5) with distances from the open water lagoon at the west periphery of the island are indicated.

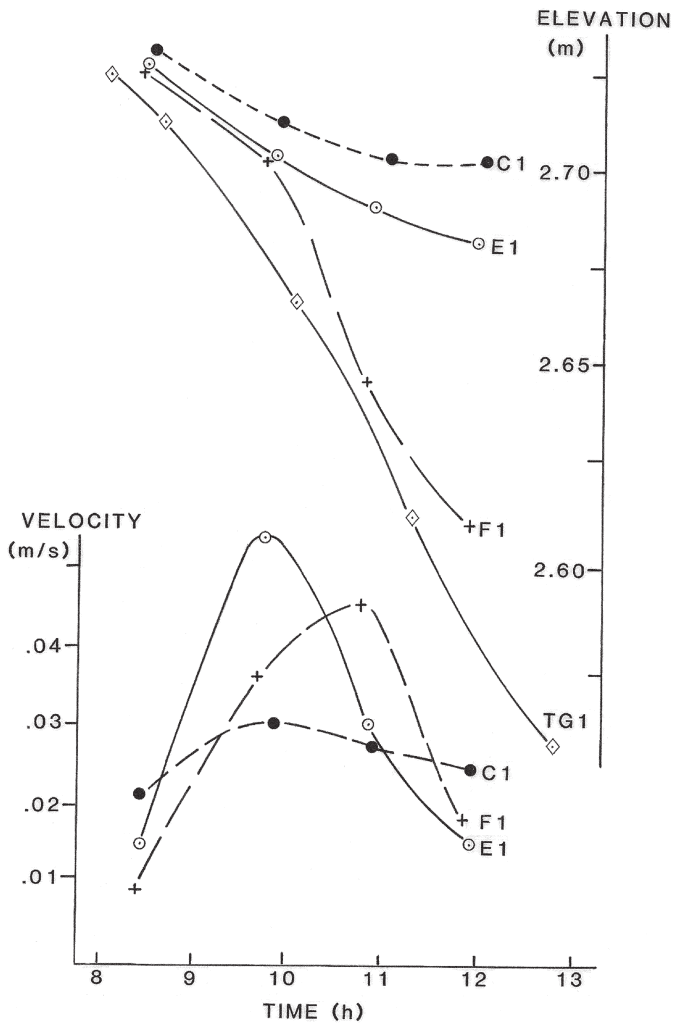


FIGURE 13. Plot of relative elevations (arbitrary datum) and velocities during falling limb of tide at monitor stations C1, E1, and F1 (see Figure 5).

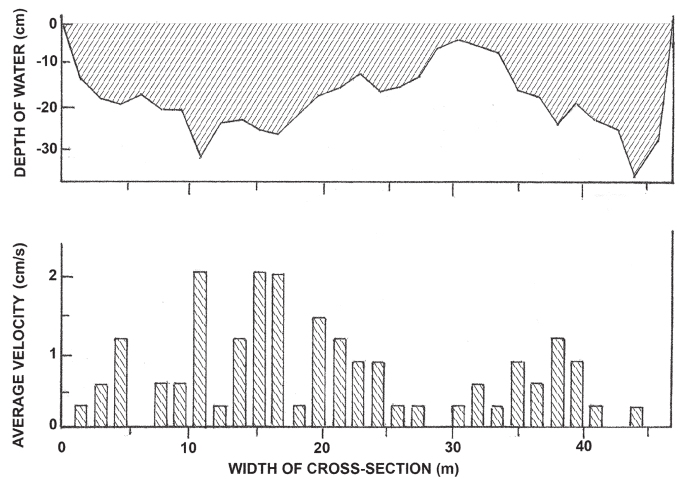


FIGURE 14. Water depths and velocities at cross-section A-A', at monitoring station A4 (see Figure 5) during a flood tide with maximum velocities, on 27 May 1988.

from 0.084 to 0.445, far higher than the typical 0.035 found even for natural channels with stones and weeds. These values however are comparable to those ranges of 0.2 to 0.7 determined by Wolanski et al. (1992) for flow in southern Japan mangrove systems. Based on earlier studies, Wolanski et al. (1980) had earlier suggested that  $n$  is of the order of 0.2–0.4 in mangrove swamps. Table 1 shows the parameters and results for calculation of the Manning coefficient for section A-A', with depth and velocity characteristics as depicted in Figure 14. It is to be noted in Table 1 that the value of  $n$  is greatest at shallow water depth and lower velocities. Again, this is comparable to the findings of Wolanski et al. (1992).

TABLE 1. Summary of hydraulic parameters for cross-section A-A' at Station A4 (see Figure 5).

Observation <sup>a</sup>	Average water depth (cm)	Hydraulic slope, S (m/m)	Average velocity (cm/s)	Flow (m <sup>3</sup> /s)	Manning's coefficient, n
1	11.9	0.000117	0.6	0.034	0.415
2	13.4	0.000110	0.6	0.037	0.445
3	14.3	0.000102	1.3	0.085	0.206
4	14.6	0.000098	1.1	0.069	0.261
5	16.4	0.000086	1.3	0.097	0.210
6	20.3	0.000055	1.6	0.145	0.159

<sup>a</sup> Each observation with the associated calculations is based on 30 measurements across cross-section A-A' as detailed in Figure 14.



A dye flow study was accomplished during a high tide period on 5 June 1993. Single slugs of Rhodamine fluorescent dye, which produced a distinctive red color, were placed at three locations (monitor stations D1, A6, and A10; see Figure 5) along the main channel early in the morning. Large visual targets were placed at the monitor stations in the mangrove swamp to enable referencing the dye positions during movement.

The movement of dye was documented by aerial photography from an aircraft flown in a fixed flight pattern, and at a fixed altitude of 150 m (500 ft.), Runs were made at 0.5 h intervals. Figure 15 is a series of drawings made from 11 of these runs, depicting the leading edge of the dye with time. The 7 h period of measurement relative to the position of the tide at the exterior lagoon is depicted on the inset tide plot of Figure 15. Figure 16 is a high oblique photograph of West Island taken from an altitude of about 600 m (2,000 feet) showing the position of the dye at 9:10 AM, shortly after high tide. The aircraft run pattern starts over monitor station TG 2 and progresses east, turning

south to proceed over the large pond at the south end of the island. The series of photographs have been converted to an animated visual program by George L. Venable of the Smithsonian Institution (URL <http://www.uri.edu/cve/dye.mov>) that clearly shows the oscillation of the water of the mangrove swamp water as the dye at station D1, some 70 m from the lagoon, first went to the east, then reversed to finally discharge into the lagoon. The dye flow at station A6 also oscillated, then merged with the outgoing dye from station A10 approximately 120 m south of A6, toward the pond. Interestingly, the dye placed at A10, at the north margin of the pond, also moved into the pond and then flowed in a circulatory pattern. This pattern may be caused by new lagoon water overflowing the rim of the pond to the east because the tide during the period of observation was a relatively high spring tide. Finally the dye from D1 discharges into the lagoon, and the merged A6/A10 dye moves north. Previous water level studies with measured levels of fluorescent dye indicated that this dye persists at continuing reduced levels in the central locations

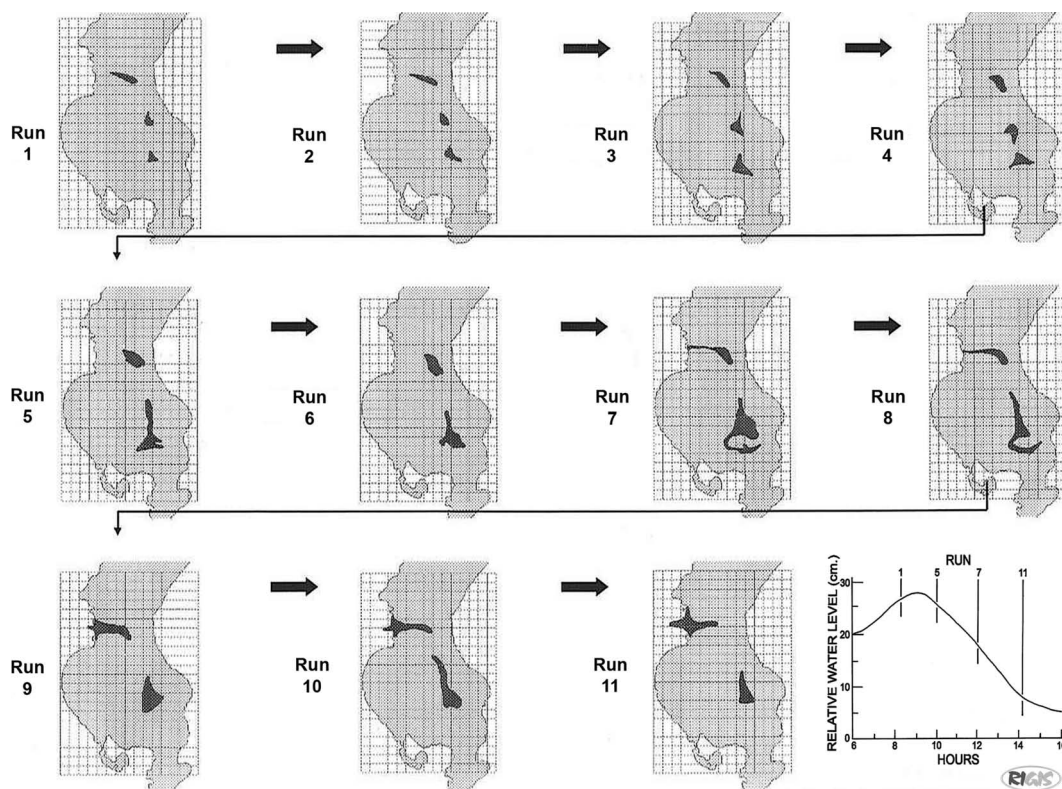


FIGURE 15. Sequential plots of dye flow patterns over a 7 h period from high tide through low tide, during dye flow test on 5 June 1993. The plot in the lower right-hand corner shows the relative time position of runs with tide levels at station TG2.





**FIGURE 16.** Aerial photograph of West Island looking to the northwest from an altitude of 600 m during the 5 June 1993 dye flow test, corresponding approximately to the time of run 4 of Figure 15. The dye is evident as the red configuration in the south pond.

for several tidal cycles before finally being flushed and dissipated into the lagoon.

## DISCUSSION

An intimate knowledge of the topography of the flow and flood area is essential to an understanding of the ecosystem of a semiclosed mangrove hydrosystem such as West Island. The interior water system of West Island is primarily tide-induced flow, with modifications caused by precipitation and seasonal climatic change. Hence, it is also very important that the climatic factors be considered in conjunction with the hydrographic characteristics.

The tidally induced hydrodynamics of the water flow in tidal channels and ponds of an overwashed mangrove island, in conjunction with the topography, greatly affect the ecosystem and vitality of the resident mangrove systems. Analysis of the temporal and spatial characteristics

of a 21.5 ha island hydrological flow system shows that where flooding and current flow becomes more vigorous, the growth of the red mangrove is enhanced. It was found, during the 18-year period of this study, that hydrological changes such as increased tidal flow, from anthropogenic as well as natural causes, enhanced the growth of the red mangrove. On the other hand, observations of relict tree remains indicate that historically the interior of the island experienced a transition in mangrove species from black mangrove to dwarf red mangrove, possibly because of higher water levels and with poor flushing in the island interior. This concept is in concurrence with findings of Knight et al. (2008) in studies of patterns of tidal flooding within a mangrove forest in Southeast Queensland, Australia, that “mangrove basin types represent a succession in mangrove forest development that corresponds with increasing water depth and tree maturation over time.”

Detailed mapping of the topography of the intertidal interior region of the island reveals poorly defined flow

channels that vary greatly in depth and width. Within this system anomalous deep sections exist, further contributing to the complexity of flow. The root structure of the mangroves and the irregular bottom result in a frictional resistance to the flow, quantified by Manning's  $n$  as being as much as 10 times greater than that of conventional terrestrial stream channels. In studies in mangrove swamps on Iriomote Island, Japan, Kobashi and Mazda (2005) stress the importance of the hydraulic resistance of mangrove vegetation in determining the flow patterns, especially in reducing the velocity component perpendicular to the main channel. Accordingly, the interaction of the mangrove itself is a determinate factor in stream flow and the resulting flushing action, important to the vitality of the mangrove. It appears to be particularly relevant to the transport of nutrients and other physicochemical conditions important to the growth of the mangrove. The driving force for the flow within the mangrove hydrosystem is the ever-changing hydraulic gradient induced by the tide. Accordingly, the flow moves, at varying velocities, in and out of the interior mangrove swamp with the tide. As a result the seawater entering the mangroves not only follows a constantly changing path, but is regularly reversed in direction, and consequently it takes at least several tidal cycles for flushing of the island interior. There are indications that the central part of West Island is flooding more over a span of years, causing commensurate changes in the mangrove types capable of surviving in the changed regime, a process described by Knight et al. (2008). In other areas the geomorphology of the land is changing consequent to sediment transport, detritus deposition, and subsidence from peat compaction. In this regard Bryce et al. (2003), in studies of a small mangrove creek system near Townsville, Australia, evaluated the role of hydrodynamics in the sediment transport process. Importantly they observed that sediment transport appears to be a seasonal phenomenon, with net flux going either landward or seaward, but they conclude that the net sediment transport for the overall system may be close to long-term equilibrium. They do state that mangrove swamp areas (in the tidal overflow regions) are most likely to be places of sediment accumulation; if so, the more shallow areas of West Island, when flooded at high tide, may experience accumulation from redistribution of sediment within the system as well as from direct leaf drop and in situ detritus accumulation.

The data showed that the annual pattern of precipitation and temperature greatly affects temperature and salinity in the poorly flushed interior pond. On an annual basis there was a net discharge of water from island to the

exterior lagoon because of precipitation. However, when the monthly climatic factors are considered it is apparent that during the "dry period" of February to May there is a net loss of freshwater in the island water budget, with high evaporation creating high-temperature hypersaline water in the interior. When the island is in the rainy season, July through December, the reverse is true, with the interior water becoming cooler and fresher from the rains (see Figure 12). In the extreme case, as described by Wolanski et al. (1992) for tropical mangrove systems on the coast of northern Australia, "The balance between rainfall and evaporation, in conjunction with tidal variations, is the key factor in determining if the upper levels of the swamp are (tidally flushed) swamp or (hypersaline) tidal flat." A further important implication for the shallow pond in the south part of West Island is, as stated by Wolanski et al. (1992), "rainfall significantly affects porewater salinity and it is likely that it also affects nutrient levels within the swamp substrate, particularly in areas where regular flooding by the tides does not occur." On West Island, during the "dry period" of February through May, evapotranspiration is approximately three times that of precipitation. However, during the "wet period" of June through December, conditions are reversed with evapotranspiration being approximately one-half that of precipitation (see Figure 11). Thus, the net effect on the poorly flushed interior areas of the West Island mangrove system is that of greatly increased salinity during the "dry season" and short periods of nearly fresh water from rain storms in the wet season (see Figure 12).

The effects of human intrusion into the natural ecosystem are illustrated by Figure 17, an aerial photograph showing the survey lines newly cut in 1993. At that time the strongest flow from the coastal seawater was some 25 m south of the west-east running survey cut, as identified by the darker, more vigorous vegetation. By 2003 the main flow had moved north to the survey cut itself as the cutting as well as foot traffic in the cut had deepened that area. During the course of the investigations, it was observed that the previous dwarf red mangrove trees alongside these survey lines initiated signs of vigorous growth as a result of the increased flushing, as illustrated by the photograph in Figure 18.

Although previous studies have shown that for the past 8,000 years the mangrove growth has managed to keep up with rising sea level because of peat accretion, the future may be in doubt because of anticipated greatly increasing sea-level rise rates (Mckee et al., 2007). The ability of the island to adjust to rising sea level has important implications for a future that will include sea levels rising





**FIGURE 17.** Aerial photograph taken in 1993 (looking south) showing survey lines that were newly cut in 1993. The original principal tidal flow path is evident as the darker green vegetation approximately 30 m south of the 1993 east–west survey line.

at a rate much greater than that experienced over the past 8,000 years when mangroves first appeared and flourished on Twin Cays. As McKee et al. (2007) have stated, “Rates of subsurface plus subsurface (root) accretion in fringe, transition and interior zones at Twin Cay were 10.4, 6.3, and 2.0 mm/year. Fringe mangroves have kept up and could accommodate eustatic sea level rise of 4 mm/year if current rates of accretion were maintained. If eustatic rates exceed 5 mm/year then these mangrove islands would not be likely to persist, assuming all other conditions remain unchanged.”

The islands of Twin Cays, with a history of comprehensive ecological research, remain an important location for measuring and evaluating changes in the mangrove and associated ecosystems because they occur in a world of dramatic coastal change. Much analytical work remains to link the dynamic hydrology of the mangrove island to the physiological parameters essential to mangrove growth. The research site of Twin Cays, with three decades of baseline data and research, is a very important asset for better understanding the ecosystem of the mangrove. It is very important that this work continue and build on the substantial foundation of information that now exists.

## CONCLUSIONS

Overwashed mangrove islands are extremely complex ecosystems. They are essentially self-dependent, and the vitality of the resident mangrove species is primarily a result of the tide that produces the essential hydrological functions of flushing and nutrient transport. The topography, the geomorphology, and even the existence of a mangrove island are products of the island vegetation itself. This interaction affecting the island configuration is constantly changing as the mangrove forest with its multiple species adjusts to higher sea levels and the resultant changes in hydrological flow and flooding parameters.

The interior of the island is subject to extremes of temperature (20°–40°C) and salinity (5–45 ppt) with limited flushing that may adversely affect the vitality and existence of the mangrove, as well as the natural selection of mangrove species. A comparison of the hydrological parameters and flow regimes in the regions of vigorously growing red mangrove with that of dwarf red mangrove strongly suggests that enhanced communication with external lagoon water is best for the vitality of the red mangrove on Twin Cays.

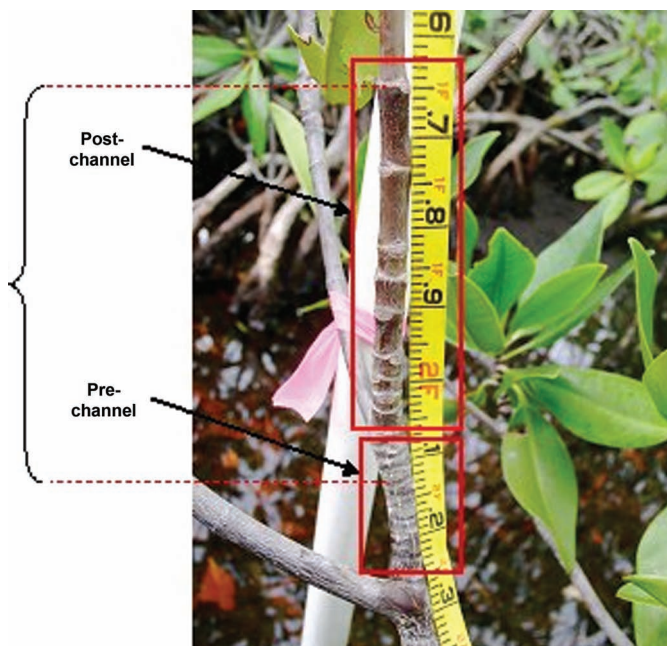


FIGURE 18. Photograph of red mangrove branch taken in 2003 near monitoring station D1 (see Figure 5) showing progressive increase of growth between sequential growth rings after survey lines were cut approximately 10 years previously. Note that the tape is marked decimally in feet.

The flow within the island is strongly influenced by the substantial frictional resistance of the mangrove root system. This dense root system serves to greatly attenuate the tidal amplitude as it progresses into the island, creating a reduced hydraulic gradient for water movement. The resultant reduced flow creates a poorly flushed island interior with poor mangrove growth.

Extensive land clearing, especially along the coastal margins, has long-term continuing effects of mangrove loss from which the island may never recover (Macintyre et al., 2009). In contrast, limited incursions such as the observed survey line cutting may shift, but enhance, channel flow, promoting more vigorous red mangrove growth. In extensive field research (Feller et al., 2003), it was found that the patterns of nutrient availability within and among mangrove ecosystems are complex. Feller et al. (1999) showed the dramatic effects of nutrient enrichment on mangrove growth as well the changes in nutrient limitations that can take place within relatively short distances in swamp ecosystems. At least in the case of the nutrient-poor (P-limitation) condition of the sparse red mangrove in the interior of the island, the cause of nutrient limitation seems to be poor flushing, which limits the refreshing of

the system with phosphorus-rich lagoon water from tidal flooding.

A further concern is that of the effect of rising sea level on the ability of the mangrove to survive. The hydrodynamics of the mangrove system greatly influences the mangrove ecosystem both by transport of nutrients and sediment and by the direct ability of the geomorphology of the island to develop to keep pace with rising sea level as it has in the past (McKee et al., 2007). At the least it appears that differential growth of mangroves will occur as flooding occurs and the hydrodynamics of the system changes.

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#### LITERATURE CITED

- Alongi, D. M. 2002. Present State and Future of the World's Mangrove Forests. *Environmental Conservation*, 24:331–349.
- Alongi, D. M., and A. D. McKinnon. 2005. The Cycling and Fate of Terrestrially-Derived Sediments and Nutrients in the Coastal Zone of the Great Barrier Reef Shelf. *Marine Pollution Bulletin*, 51:239–252.
- Ball, M. C. 1988. Salinity Tolerance in the Mangroves *Aegiceras corniculatum* and *Avicennia maria*. I. Water Use in Relation to Growth, Carbon Partitioning, and Salt Balance. *Australian Journal of Plant Physiology*, 15:447–464.
- Barbier, E. B. 2006. Natural Barriers to Natural Disasters: Replanting Mangroves After the Tsunami. *Frontiers in Ecology and the Environment*, 4(3):124–131.



- Boulton, A. J., and M. A. Brock. 1999. *Australian Freshwater Ecology: Processes and Management*. Adelaide, Australia: Gleneagles Publishing.
- Bryce, S., P. Larcombe, and P. V. Ridd. 2003. Hydrodynamics and Geomorphological Controls on Suspended Sediment Transport in Mangrove Creek Systems, a Case Study: Cocoa Creek, Townsville, Australia. *Estuarine, Coastal and Shelf Science*, 56:415–431.
- Costanza, R., O. Perez-Maquico, M. L. Martinez, P. Sutton, S. L. Anderson, and K. Mulder. 2008. The Value of Coastal Wetlands for Hurricane Protection. *Royal Swedish Academy of Sciences*, 37(4):241–248.
- Danielson, F., M. K. Sørensen, M. F. Olwig, V. Selvam, F. Parish, N. D. Burgess, T. Hiraishi, V. M. Karunagaran, M. S. Rasmussen, L. B. Hansen, A. Quarto, and N. Suryadiputra. 2005. The Asian Tsunami: A Protective Role for Coastal Vegetation. *Science*, 310:643.
- Doyle, T. W. 2003. Effects of Hydrology on Red Mangrove Recruits. U. S. Geological Survey Report USGS 023-03. Lafayette, La.: National Wetlands Research Center.
- Duke, N. C., J. O. Meynecke, S. Dittman, A. M. Ellison, K. Anger, U. Berger, C. Cannicci, K. Diele, K. C. Ewell, C. D. Field, N. Koedam, S. Y. Lee, C. Marchand, I. Nordhaus, and F. Dahdouh-Guebés. 2007. A World Without Mangroves? *Science*, 317:41–42.
- Dunne, T., and L. B. Leopold. 1978. *Water in Environmental Planning*, pp. 135–138. San Francisco: W. H. Freeman and Company.
- Feller, I. C., K. McKee, D. F. Whigham, and J. P. O'Neill. 2003. Nitrogen vs. Phosphorous Limitation across an Ecotonal Gradient in Mangrove Forest. *Biogeochemistry*, 62:145–175.
- Feller, I. C., D. F. Whigham, J. P. O'Neill, and K. M. McKee. 1999. Effect of Nutrient Enrichment Within-Stand Nutrient Cycling in Mangrove Ecosystems in Belize. *Ecology*, 80:2193–2205.
- Forman, R. T. T., and M. Godron. 1986. *Landscape Ecology*. New York: John Wiley and Sons.
- Furukawa, K., and E. Wolanski. 1996. Sedimentation in Mangrove Forests. *Mangroves and Salt Marshes*, 1:3–10.
- Hutchings, P. A., and P. Saenger. 1987. *Ecology of Mangroves*. St. Lucia: University of Queensland Press.
- Kjerfve, B., K. Rützler, and G. H. Kierspe. 1982. "Tides at Carrie Bow Cay, Belize." In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*, ed. K. Rützler and I. G. Macintyre. *Smithsonian Contributions to the Marine Sciences*, 12:47–51.
- Knight, J. M., P. E. R. Dale, R. J. K. Dunn, G. J. Broadbent, and C. J. Lemckert. 2008. Patterns of Tidal Flooding within a Mangrove Forest: Coombabah, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, 76:580–593.
- Kobashi, D., and Y. Mazda. 2005. Tidal Flow in Riverine-type Mangroves. *Wetlands Ecology and Management*, 13:315–619.
- Lindsley, R. K., and J. B. Franzini. 1979. *Water Resources Engineering (Open Channel)*. New York: McGraw Hill, pp. 251–256.
- Lovelock, C. E. 2008. Soil Respiration and Belowground Carbon Allocation in Mangrove Forests. *Ecosystems*, 11:342–354.
- Lugo, A. E., and S. C. Snedaker. 1974. The Ecology of Mangroves. *Annual Review of Ecology and Systematics*, 5:39–64.
- Macintyre, I. G., and M. A. Toscano. 2004. The Pleistocene Limestone Foundation below Twin Cays, Belize, Central America. *Atoll Research Bulletin*, 511:1–16.
- Macintyre, I. G., M. A. Toscano, I. C. Feller, and M. Faust. 2009. Decimating Mangrove Forests for Commercial Development in the Pelican Cays, Belize: Long-Term Ecological Loss for Short-Term Gain? *Smithsonian Contributions to the Marine Sciences*, No. 38:281–289.
- Macintyre, I. G., M. A. Toscano, R. G. Lightly, and G. B. Bond. 2004. Holocene History of the Mangrove Islands of Twin Cays, Belize, Central America. *Atoll Research Bulletin*, 510:1–16.
- Mazda, Y., N. Knazawa, and T. Kurokawa. 1999. Dependence of Dispersion on Vegetation Density in a Tidal Creek-Mangrove Swamp System. *Mangrove and Salt Marshes*, 3(1):59–66.
- Mazda, Y., D. Kobashi, and S. Okada. 2005. Tidal Scale Hydrodynamics Within Mangrove Swamps. *Wetlands Ecology and Management*, 13:647–655.
- Mazda, Y., E. Wolanski, B. King, A. Sase, O. Otsuka, and M. Magi. 1997. Drag Forces due to Vegetation in Mangrove Swamps. *Mangroves and Salt Marshes*, 1:193–199.
- McKee, K. L., D. Cahoon, and I. C. Feller. 2007. Caribbean Mangroves Adjust to Rising Sea Level Through Biotic Controls on Soil Elevation Change. *Global Ecology and Biogeography*, 16:546–556.
- Odum, W. E., and E. J. Heald. 1972. Trophic Analyses of an Estuarine Mangrove Community. *Bulletin of Marine Science*, 22:671–738.
- . 1975. "The Detritus-Based Food Web of an Estuarine Mangrove Community." In *Estuarine Research*, ed. L. E. Cronin, pp. 265–286. New York: Academic Press.
- Rodriguez, W., and I. C. Feller. 2004. Mangrove Landscape Characterization and Change in Twin Cays, Belize Using Aerial Photography and IKONOS Satellite Data. *Atoll Research Bulletin*, 513:1–22.
- Rützler, K., and I. C. Feller. 1988. Mangrove Swamp Communities. *Oceanus*, 30(4):16–24.
- . 1996. Caribbean Mangrove Swamps. *Scientific American*, 274(3):94–99.
- Rützler, K., and J. D. Ferrais. 1982. "Terrestrial Environment and Climate, Carrie Bow Cay, Belize." In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*, ed. K. Rützler and I. G. Macintyre. *Smithsonian Contributions to the Marine Sciences*, 12:77–91.
- Rützler, K., and I. G. Macintyre. 1982. "Introduction." In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*, ed. K. Rützler and I. G. Macintyre. *Smithsonian Contributions to the Marine Sciences*, 12:1–7.
- Taylor, D. S., E. A. Reyier, W. P. Davis, and C. C. McIvor. 2007. Mangrove Removal in the Belize Cays: Effects on Mangrove-Associated Fish Assemblages in the Intertidal and Subtidal. *Bulletin of Marine Science*, 80(3):879–890.
- Thornwaite, C. W., and J. R. Mather. 1987. *Instructions and Tables for Computing Potential Evapo-transpiration and the Water Balance*, pp. 185–311. Centerton, N.J.: Laboratory of Climatology.
- Tomlinson, P. B. 1986. *The Botany of Mangroves*. London: Cambridge University Press.
- Toscano, M. A., and I. G. Macintyre. 2003. Corrected Western Atlantic Sea-Level Curve for the Last 11,000 Years Based on Calibrated <sup>14</sup>C Dates from *Acropora palmate* Framework and Intertidal Mangrove Peat. *Coral Reefs*, 22:257–270.
- Twilley, R. R. 1988. "Coupling of Mangroves to the Productivity of Estuarine and Coastal Waters." In *Coastal Offshore Biosystem Interactions*, ed. B. O. Jansson, pp. 155–180. Berlin: Springer-Verlag.
- . 1995. "Properties of Mangrove Ecosystems in Relation to the Energy Signature of Coastal Environments." In *Maximum Power*, ed. G. A. S. Hall, pp. 43–62. Boulder: University Press of Colorado.
- Urish, D. W., R. M. Wright, and O. Viator. 2003. *Topographic and Hydrographic Study in the Overwash Mangrove Islands of Twin Cays, Belize*. CCRE Report for 2002–2003. Washington, D.C.: Smithsonian Institution, National Museum of Natural History.
- Watson, I., and A. D. Burnett. 1995. *Hydrology: An Environmental Approach*, pp. 460–465. Boca Raton, Fla.: CRC Press.
- Wolanski, E., M. Jones, and J. S. Bunt. 1980. Hydrodynamics of a Tidal Creek-Mangrove Swamp System. *Australian Journal of Marine and Freshwater Research*, 31:431–450.
- Wolanski, E., Y. Mazda, and P. Ridd. 1992. Mangrove Hydrodynamics. *Coastal and Estuarine Studies (Tropical Mangrove Ecosystems)*, 41:43–62.
- Wolf, P. R., and C. D. Ghilani. 2006. *Elementary Surveying: An Introduction to Geomatics*, pp. 72–144. Upper Saddle River, N. J.: Pearson Prentice and Hall.
- Wright, R. W., D. W. Urish and I. Runge. 1991. The Hydrology of a Caribbean Mangrove Island. In *Coastlines of the Caribbean, Coastal Zone '91 Conference-ASCE, Long Beach, CA July 1991*, ed. G. Cambers, pp. 171–184. New York: American Society of Civil Engineers.

# Ecological Characteristics of *Batis maritima* in Florida and Belize

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**ABSTRACT.** *Batis maritima*, a low-growing perennial species with woody stems and succulent leaves, occurs in mangroves and, to a lesser degree, in salt marshes in the Neotropics. It spreads by clonal growth, occurs in a wide range of habitats, and at times forms monotypic stands. Sites that are permanently flooded or are flooded regularly by tides and salt pans are the only mangrove habitats in which *B. maritima* does not occur or occurs as a few scattered plants. On mangrove-dominated islands in Belize, the coverage and height of *B. maritima* were highest in open habitats, including sites disturbed by human activities. In a mangrove-dominated mosquito impoundment in Florida, *B. maritima* occurred in all habitats sampled and, similar to observations in Belize, coverage and height were greatest in the most open habitats. The abundance and, at times, dominance of *B. maritima* suggests that it may play an important role in the dynamics of mangrove ecosystems, especially in the recruitment and establishment of mangrove seedlings. Mangrove seedlings and saplings were present in most of the plots that were sampled in Belize and Florida, but there was no relationship between the percent cover of *B. maritima* and the density of seedlings and saplings.

## INTRODUCTION

*Batis*, the only genus in the family Bataceae, has two species. *Batis maritima* L. occurs in the Neotropics in coastal salt marshes and mangroves from Georgia and Brazil on the Atlantic coast and California to Peru on the Pacific Coast of North and South America. The species is widely distributed in the Caribbean basin. The second species, *Batis agrillicola* P. Royan, is endemic to coastal areas of northern Australia.

*Batis maritima*, a low-growing C<sub>3</sub> perennial species with woody stems and succulent leaves, is associated with saline soils and has been described as a species that responds to disturbance in mangroves and salt marshes (Rey et al., 1990; Pennings and Richards, 1998; Pennings and Callaway, 2000). An important ecophysiological characteristic of *B. maritima* is the ability to adjust photosynthetic rates to increasing soil salinity by making adjustments to leaf sap osmolalities (Lüttge et al., 1989). The ability to propagate clonally (Pennings and Callaway, 2000) is another characteristic that enables it to respond rapidly to altered environmental conditions.

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Despite its widespread distribution, there have been relatively few ecological studies of *B. maritima*. In Georgia salt marshes, Pennings and Richards (1998) found a positive relationship between the presence of wrack (accumulated litter) and the abundance of *B. maritima*. Pennings and Callaway (2000) found that clonal integration was an important factor in the ability of the species to colonize bare salt pans. The responses of *B. maritima* to altered hydrological conditions appear to vary with differing environmental settings. In hypersaline coastal wetlands in Texas, *B. maritima* cover expanded following inundation with freshwater (Alexander and Dunton, 2002). Conversely, the opposite occurred in Baja California (México) where its cover increased following the construction of a dike that eliminated tidal flooding and increased soil salinity (Ibarra-Obando and Poumian-Tapia, 1991). *Batis maritima* cover was also dynamic in mangroves in Florida that were impounded for mosquito control. The cover of all herbaceous halophytic species, including *B. maritima*, decreased following the construction of dikes and the subsequent impoundment and flooding of mangroves in the Indian River (Rey et al., 1990). Several years later, when tidal exchange between the impoundment and estuary was restored, *B. maritima* recolonized areas that were no longer flooded continuously. Another important ecological feature of *B. maritima* is its inability to tolerate prolonged periods of shade in mangrove-dominated wetlands (López-Portillo and Ezcurra, 1989). Along Florida's Gulf Coast, Milbrandt and Tinsley (2006) observed a greater number of black mangrove (*Avicennia germinans* (L.) Stearn) seedlings in existing *B. maritima* patches compared to surrounding mudflats. They hypothesized that this improved seedling success was the result of a slight increase in elevation provided by the *B. maritima* root system. In contrast, McKee et al. (2007) found that on offshore islands in Belize *B. maritima* did not appear to have an effect on recruitment of red mangrove (*Rhizophora mangle* L.) seedlings.

Other than the experimental research on coastal salt marshes (Pennings and Richards, 1998; Pennings and Callaway, 2000), little is known about the ecological role of *B. maritima* in coastal wetlands, especially in mangroves where it most frequently occurs. Is it a fugitive species that only persists because it is capable of responding to changing environmental conditions? Alternatively, is it an important species in mangroves because of its impact on patterns of nutrient cycling or its ability to influence the establishment of mangrove trees (i.e., *R. mangle*, *A. germinans*, *Laguncularia racemosa* (L.) Gaertn. f. [white mangrove], *Conocarpus erectus* L. [buttonwood])? Although

*B. maritima* is a common component of mangrove forests throughout the Neotropics, there is limited knowledge on distribution patterns within the intertidal landscape or on the ecological roles of this species across a range of mangrove habitats.

Our objective was to describe the distribution of *B. maritima* in Florida and Belize as part of our overall goal to determine its ecological role in mangrove ecosystems. Here we describe our initial efforts to characterize the ecology of *B. maritima* at two of the Smithsonian's long-term research sites (Figure 1) that also represent the range of conditions (subtropical and tropical) where this species associates with mangroves. For Florida (subtropical), we focus on *B. maritima* in four habitats in a mangrove-dominated impoundment along the Indian River Lagoon (IRL) that has a history of intervention for purposes of mosquito control (Rey et al., 1990). For Belize (tropical), we focus on *B. maritima* in disturbed and undisturbed sites on offshore mangrove islands. For both sites, we also present data on the relationships between percent cover of *B. maritima* and the density of mangrove seedlings.

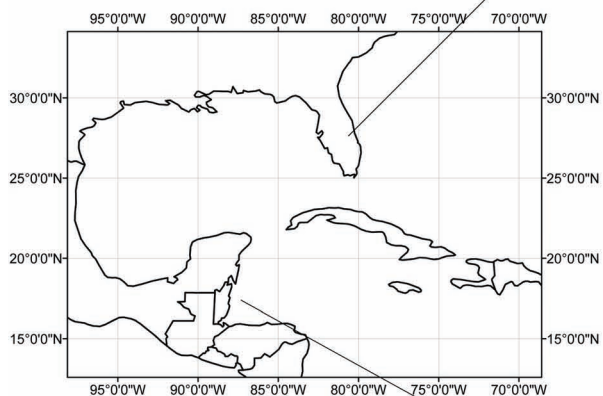
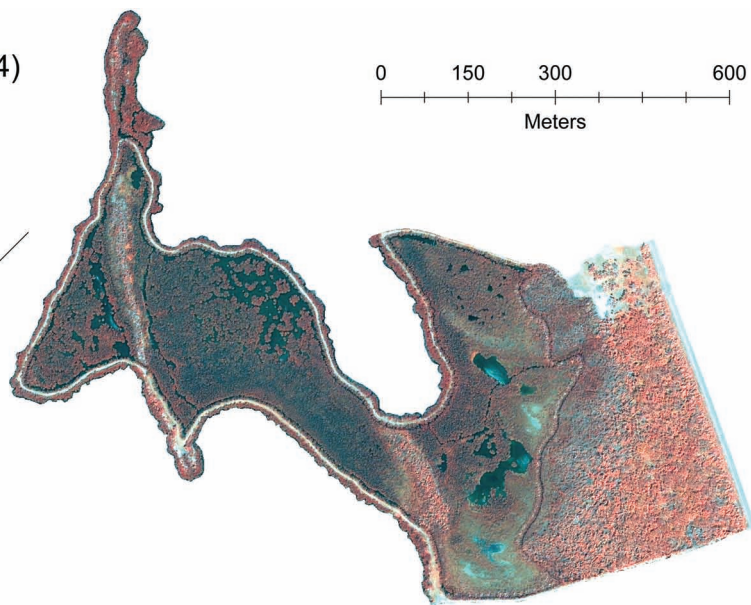
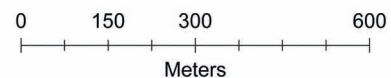
## STUDY SITES

### BELIZE

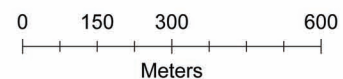
Twin Cays is the focus of our *B. maritima* studies in Belize. Twin Cays (91.5 ha) is an archipelago of peat-based mangrove islands (Figure 1) located near the crest of the barrier reef of central Belize. These islands are located approximately 17 km east of the mainland, and the only source of freshwater is precipitation. Vegetation on Twin Cays is dominated by the mangroves *R. mangle*, *A. germinans*, and *L. racemosa*. The forest structure is heterogeneous and characterized by gradients in hydrology and tree height that include a seaward fringe of *R. mangle* around the periphery of the islands, along tidal creeks, and in perennially flooded ponds (Feller et al., 1999). *Avicennia germinans* and *L. racemosa* primarily occur in habitats that are not water covered at low tide. Vegetation patterns on Twin Cays are complex, and the dynamics have been the focus of many studies (Feller, 1995; Feller and McKee, 1999; Rodriguez and Feller, 2004; Lovelock et al., 2006a). However, none of the previous research has focused on the distribution or ecology of *B. maritima* even though it occurs in almost all habitats except those that do not experience prolonged flooding (D. Whigham, personal observation). Human activities have altered parts of Twin Cays (Rodriguez and Feller, 2004; McKee et al., 2007), and the primary anthropogenic activity has been the clearing



Mangrove-dominated wetland (SLC 24)  
 Indian River Lagoon, Florida  
 IKONOS 2005 (UTM Zone 17N)



Twin Cays Archipelago  
 Belize, Central America  
 IKONOS 2003 (UTM Zone 16N)



**FIGURE 1.** Approximate locations of SLC24 and Twin Cays (inset map) and IKONOS images of the two study sites. For SLC 24, the white line that is seen around the impoundment is a dike. Dark areas within the impoundment are dredged from adjacent subtidal habitats. Darker areas on the two large islands are internal tidally influenced ponds that are most often shallowly water covered.



of mangroves with or without the addition of sediments dredged from nearby subtidal habitats. In this study, we compared the distribution of *B. maritima* in disturbed and undisturbed mangrove habitats at Twin Cays (described in further detail below).

#### FLORIDA

An impounded, mangrove-dominated wetland (SLC 24) in St. Lucie County in the IRL is the focus of the Florida studies (see Figure 1). SLC 24 has been managed in a variety of ways since it was diked in 1970. Rey et al. (1990) describe management activities and patterns of vegetation change in SLC 24 between 1970 and 1987. SLC 24 was hydrologically isolated from the IRL by a dike (Figure 1) until 1985 when a culvert was installed to remove excess water deposited during two tropical storms. Once water levels were lowered, the culvert was sealed, and the impoundment remained isolated until 1987 when the culvert was reopened and other culverts were installed. The cover of all vegetation decreased from 75% to near 30% following construction of the diked impoundment in 1970. Over subsequent years, the cover of herbaceous halophytes, including *B. maritima*, changed in response to variations in the timing and duration of flooding and the establishment and growth of mangroves. Rey et al. (1990) concluded that a steady decline in the cover of herbaceous halophytes after 1984 was primarily caused by shading as the canopies of mangroves developed. Vegetation patterns are also complex in the numerous impoundments that have been established in the IRL, and they have been the focus of several studies focused primarily on nutrient limitation within mangroves (Feller et al., 2003; Lovelock and Feller, 2003; Lovelock et al., 2006b). We sampled *B. maritima* in three mangrove-dominated habitats and areas associated with salt pans where dwarf *A. germinans* (sensu Feller et al., 2003) occurs as scattered individuals or in patches with almost continuous cover. Details of sampling locations and methods are given below.

### METHODS

#### BELIZE

We sampled *B. maritima* in two disturbed sites and six undisturbed sites on Twin Cays. One disturbed site is a 2 ha area on West Island that was cleared of mangroves and burned in 1991 and covered with material dredged from the adjacent subtidal area in 1995 (Rodriguez and Feller, 2004; McKee et al., 2007). The other disturbed site was clear cut in 2004, but no dredged material was added. In

both disturbed sites, we sampled *B. maritima* in 10 randomly located plots (each 1 × 1 m) in which we made visual estimates of its cover, measured its height at five randomly chosen locations in each plot, and identified and counted all mangrove seedlings and saplings. Seedlings of *A. germinans* and *L. racemosa* had cotyledons present. Seedlings of *R. mangle* were individual, with no more than one pair of true leaves. Saplings were defined as individuals less than 50 cm in height with no cotyledons present, or with more than one pair of true leaves in the case of *R. mangle*.

For our undisturbed sites at Twin Cays, we sampled *B. maritima* in three forested habitat types (Fringe, Transition, Interior), which were located at different distances from the ecotone between the mangrove forest and open water. Fringe habitats, which were dominated by trees 4 to 5 m tall, were at the outer boundary between mangroves and open water, either along ponds located in the interior of Twin Cays or along the ocean. *Avicennia germinans* was the dominant tree in the three Fringe habitats adjacent to interior ponds. *Rhizophora mangle* was the dominant tree in the three Fringe habitats adjacent to the ocean. Transition and Interior habitats were all dominated by *A. germinans*. Transition habitats were located approximately 15 m further into the mangrove forest from the Fringe habitats, and Interior habitats were located approximately an additional 15 m beyond the Transition habitats. We sampled 5 randomly located plots (same procedures as described above) in each of the 90 plots (5 plots × 3 habitat types × 6 sites) in undisturbed mangrove.

#### FLORIDA

We sampled *B. maritima* in SLC 24 in four habitat types (Fringe = *R. mangle*, Dense = *A. germinans*, Sparse = *A. germinans*, Dwarf = *A. germinans*). The Fringe habitats, dominated by *R. mangle* 4 to 6 m tall with scattered *A. germinans*, were located at the boundary between mangroves and open water. The two habitats dominated by taller (3–6 m) *A. germinans* (Dense, Sparse) differed in the size and spatial configuration of the dominant trees. The Dense *A. germinans* habitat had trees that were mostly 4 to 6 m tall and formed a continuous canopy dominated by *A. germinans*. The Sparse *A. germinans* habitat was also dominated by *A. germinans* but the trees were usually shorter (3–5 m) and were more widely spaced, resulting in a more open canopy. The Dwarf *A. germinans* habitat was always adjacent to salt pans that were mostly unvegetated or only had a few scattered dwarf trees (usually less than 1 m tall). We sampled *B. maritima* in one randomly located plot in each of the replicate sites for each habitat

type. In each  $1 \times 1$  m plot, we made the same set of measurements as described above for Belize.

## DATA ANALYSIS

Because of the different sampling regimes, we made separate statistical comparisons for the Belize and Florida data sets. Based on initial screening of the data (Proc Univariate; SAS Institute, 1990), we determined that none of the data were normally distributed either in their original form or any of the possible transformations. We used the nonparametric PROC NPAR1WAY (SAS Institute, 1990) to make comparisons of *B. maritima* data (percent cover, height) and the number of mangrove seedlings + saplings for the different habitat types at both locations.

## RESULTS

### BELIZE

Percent cover of *B. maritima* differed (Figure 2a) significantly ( $df = 4$ , chi-square for Kruskal–Wallis test = 27.9272,  $P < 0.0001$ ) among the sites on Twin Cays. Mean percent cover ranged from 50% to 53% for the two disturbed sites and the undisturbed Fringe habitat. Percent cover decreased from the Fringe to the Transition ([mean  $\pm 1$  SE] =  $35.5\% \pm 4.7\%$ ) and Interior ( $16.9\% \pm 2.9\%$ ) undisturbed sites. The average height of *B. maritima* also differed significantly between sites (Figure 2b;  $df = 4$ , chi-square for Kruskal–Wallis test = 29.0273,  $P < 0.0001$ ). Heights were similar at the two disturbed sites ( $24.4 \pm 2.3$  cm = clear-cut + fill;  $26.4 \pm 1.0$  cm = clear-cut). At the undisturbed sites, height was greatest at the Fringe habitat ( $61.7 \pm 18.5$  cm) and decreased toward the interior of the mangrove forest ( $40.4 \pm 2.2$  = Transition;  $34.7 \pm 2.0$  = Interior).

The number of mangrove saplings + seedlings also differed across sites (Figure 2c), and there were significant differences for all three species and for the total of all species ( $df = 4$ , chi-square for Kruskal–Wallis test = 38.9958,  $P < 0.0001$ ; 12.5551,  $P > 0.0137$ ; 11.3187,  $P < 0.0232$ ; 15.5953,  $P < 0.0036$  for *R. mangle*, *A. germinans*, *L. racemosa*, and total mangroves, respectively).

The total number of mangrove saplings + seedlings was higher at the clear-cut and filled site ( $24.6 \pm 13.8$  m<sup>-2</sup>) compared to the clear-cut site ( $2.5 \pm 0.8$  m<sup>-2</sup>) and undisturbed mangrove habitats (mean for all three undisturbed sites was  $7.3 \pm 1.2$  m<sup>-2</sup>). *Avicennia germinans* saplings + seedlings at the clear-cut and filled site were less than 1 m<sup>-2</sup> (Figure 2c). *Rhizophora mangle* was the most abundant species at the Fringe habitat, whereas *A. germinans* was

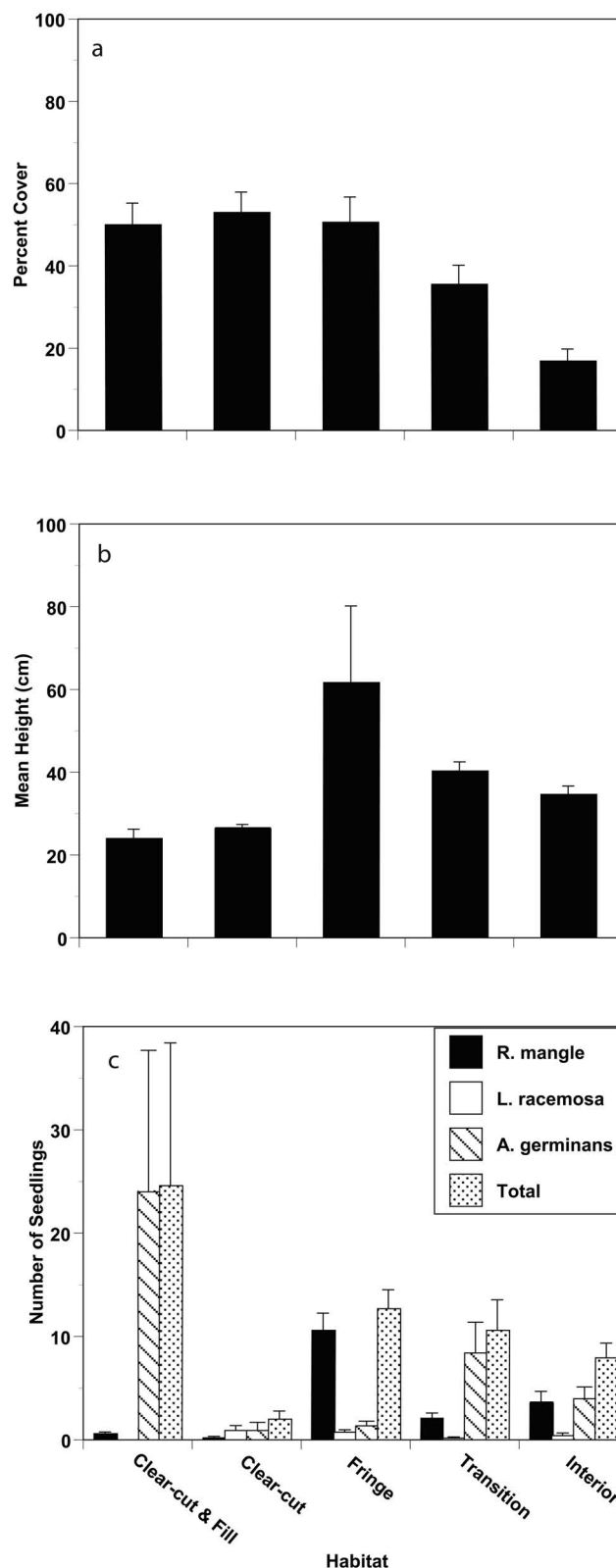


FIGURE 2. Cover (a), height (b), and sapling + seedling (c) data for two disturbed and three undisturbed habitats on Twin Cays (Belize). Values are means  $\pm 1$  SE.

the most abundant species at the Transition and Interior habitats.

#### FLORIDA

Percent cover ( $df = 3$ , chi-square for Kruskal–Wallis test = 38.9252,  $P < 0.0001$ ) and height ( $df = 3$ , chi-square for Kruskal–Wallis test = 33.0923,  $P < 0.0001$ ) of *B. maritima* differed between the four habitat types in SLC 24 (Figure 3a). There was no *B. maritima* in the plots that were sampled in the Fringe *R. mangle* habitat, and the cover ( $2.8\% \pm 1.2\%$ ) was very low in the Dense *A. germinans* habitat. Percent cover was  $42.9 \pm 8.1$  and  $27.8 \pm 4.6$  in the Sparse and Dwarf *A. germinans* habitats, respectively. Height differences (Figure 3b) among the four habitats had the same pattern with the tallest plants occurring in the Sparse *A. germinans* habitat ( $48.9 \pm 4.5$ ) and shortest in the Dense *A. germinans* habitat ( $13.1 \pm 5.4$ ). The total number of saplings + seedlings and the means for each mangrove species also differed significantly (Figure 3c) among the four habitat types ( $df = 3$ , chi-square for Kruskal–Wallis test = 11.5483,  $P < 0.0091$ ; 12.7678,  $P < 0.0052$ ; 16.4377,  $P < 0.0009$ ; 13.4660,  $P < 0.0037$  for *R. mangle*, *A. germinans*, *L. racemosa*, and total mangroves, respectively).

### DISCUSSION

The objective of this initial investigation of *Batis maritima* was to quantify aspects of its distribution in a variety of habitats in mangroves at long-term Smithsonian study sites in Belize and Florida. The impetus for the research was the observation that *B. maritima* is widespread in mangroves and, in some habitats, its high abundance and cover suggest that it potentially plays an important role in these systems. There have, however, been few studies that shed light on its possible ecological importance in mangroves. Studies in salt marshes near its northern limit found that it was not a dominant species and did not compete well with other marsh plants (Zedler, 1977). There is some suggestion that *B. maritima* may be a fugitive species because it is common in disturbed sites (Milbrandt and Tinsley, 2006). Pennings and Richards (1998), for example, found that stands of *B. maritima* were associated with areas that were disturbed by wracks of litter in a Georgia salt marsh.

*Batis maritima* has been described as a species that does not do well in shaded conditions or under conditions of continuous flooding (Rey et al., 1990; Alexander and Dunton, 2002). However, Keer and Zedler (2002) found

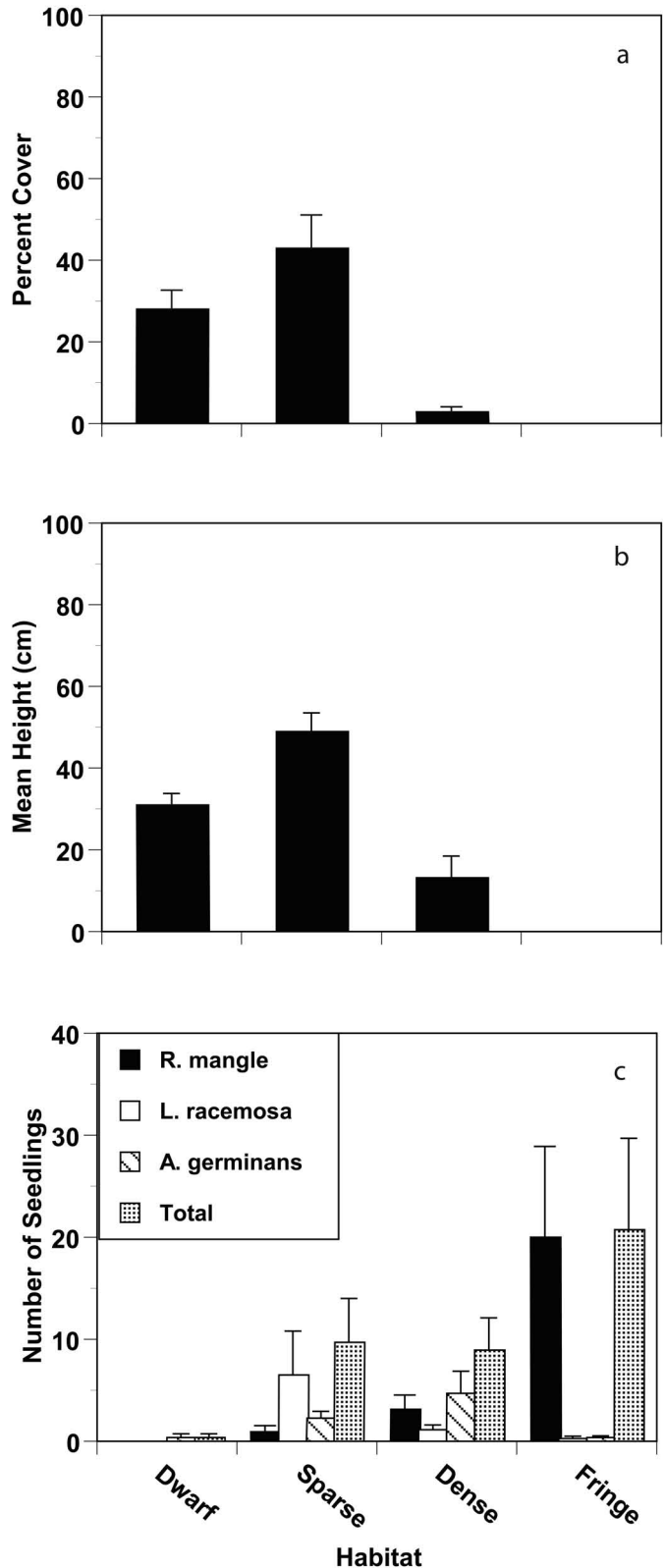


FIGURE 3. Cover (a), height (b), and sapling + seedling (c) data for four habitats in mosquito impoundment SCL 24 in the Indian River Lagoon, Florida. Values are means  $\pm$  1 SE.

that it can tolerate prolonged flooding, and it does well in waterlogged conditions when light is not limiting (Zedler, 1980). It also responds positively to increasing salinity (Ibarra-Obando and Poumian-Tapia, 1991) but is eliminated under hypersaline conditions (Zedler et al., 1986; Dunton et al., 2001).

The only long-term study of *B. maritima* in changing environmental conditions occurred in one of our study sites, SCL 24 in Florida. Rey et al. (1990) examined a sequence of aerial photographs taken over a period of time when hydrological conditions varied from years when there was continuously flooding, to years when the impoundment was drained, and to years when there was partial tidal exchange with the IRL. Vegetation almost completely disappeared when the impoundment was continuously flooded. Once the impoundment was opened to limited tidal exchange, herbaceous halophytes increased in abundance and cover and *B. maritima* eventually became the dominant species. Over time, mangroves recruited and eventually dominated the vegetation in most parts of the impoundment. As the abundance and size of mangroves increased, *B. maritima* declined along with other herbaceous halophytes in response to increased shading by mangroves (Rey et al., 1990).

Results of our surveys support several of the earlier studies and suggest that light levels, regular tidal flooding, and soil salinity are three important factors that determine where *B. maritima* occurs and how abundant it is. There have been at least two studies (Pennings and Richards, 1998; Milbrandt and Tinsley, 2006) suggesting that *B. maritima* is a fugitive species that colonizes high-light disturbed sites. In Belize, the highest percent cover was at the two disturbed sites and the Fringe habitat in the undisturbed mangroves (see Figure 2a). Even though the mean cover of *B. maritima* in the undisturbed sites on Twin Cays was lower ( $34.3\% \pm 3.1.9\%$ ) than the disturbed sites, the highest *B. maritima* cover ( $80.3\% \pm 2.6\%$ ) of any of the habitats sampled was in the three Fringe habitats that were associated with interior ponds. Edge habitats associated with interior ponds are mostly in full sun and are exposed to tidal flooding, but the flooding is rarely more than a few centimeters deep (D. Whigham, personal observations). The substrates are almost always waterlogged, and the sediments are soft, mostly composed of floc that accumulates on the downwind side of the interior ponds. The highest *B. maritima* cover in SCL 24 in Florida also occurred at sites that had no overhead mangrove canopy or only a discontinuous canopy.

The mean cover of *B. maritima* was least in the shaded habitats in Florida and Belize, supporting the suggestions of López-Portillo and Ezcurra (1989) that low light levels

can limit its abundance and distribution. The absence of *B. maritima* in the sample plots at the Fringe habitat associated with SCL 24 and the lower cover in the Fringe habitats closest to the ocean on Twin Cays ( $20.9\% \pm 2.9\%$ ) also support the suggestions that regular inundation by tidal flooding has a negative effect on the species (Alexander and Dunton, 2002).

The mean height of the *B. maritima* canopy also varied among habitats, and the patterns are most likely the result of variations in light and salinity (Zedler et al., 1986; Dunton et al., 2001). In SCL 24, mean height decreased from the more open Dwarf and Sparse *A. germinans* habitats to the shadier Dense *A. germinans* habitat (Figure 3b). At the undisturbed sites in Belize, mean height decreased from the Fringe to the Interior, most likely in response to decreasing light. The height of the plants was greatest in the Fringe habitat associated with the Edge sites that were closest to the Interior ponds. Mean height at the Fringe habitats associated with the ponds was  $85.4 \pm 27.1$  cm compared to  $40.4 \pm 2.2$  at the more shaded Fringe habitats closest to the ocean. Taller average height associated with the Edge habitats may be the result of higher phosphorus concentrations in the sediments. In a separate fertilization experiment, we found that *B. maritima* responded significantly to the addition of phosphorus at all the undisturbed sites on Twin Cays, but the smallest response was at the Edge habitat associated with interior ponds, suggesting that phosphorus was more available in those sediments (D. Whigham, unpublished data). Compared to the Fringe habitats on Twin Cays and the Sparse *A. germinans* habitat in the SCL 24, mean height decreased toward the sites with no mangrove canopy (Dwarf *A. germinans* habitat in SCL 24 and the two disturbed sites at Twin Cays). Lower mean height at the open sites is likely the result of increased salinity as the Dwarf *A. germinans* site in SCL 24 is hypersaline (i.e., soil salinity as high as 100‰; D. Whigham unpublished data). In addition, soil salinity at the clear-cut and filled site on Twin Cays, while variable during an annual cycle, can be more than 60‰ (McKee et al., 2007).

Mangrove seedlings are widely dispersed, and their occurrence varies spatially in response to light levels and their ability to withstand flooding, salinity, and attacks from herbivores (Ellison and Farnsworth, 1993; Olusegun and Creese, 1997). If *B. maritima* facilitates the establishment of mangrove seedlings, we would expect a positive relationship between percent cover and the number of seedlings + saplings for one or more of the mangrove species. Milbrandt and Tinsley (2006) found that the presence of *B. maritima* had a positive effect on the survival of *A. germinans* seedlings. McKee et al. (2007), however, found that *B. maritima* had no effect on the recruitment and survival



of mangrove seedlings, even though mangrove seedlings benefited by the presence of other herbaceous species (i.e., *Distichlis spicata*, *Sesuvium portulacastrum*) at clear-cut and filled sites sampled in this study. Although there were habitat differences in the number of seedlings + saplings, the presence of seedlings + saplings in 88% of the plots sampled in Belize and 55% of the plots in Florida indicated that mangrove establishment may have been facilitated by *B. maritima*. We found no relationship, however, between the amount of *B. maritima* cover and the density of seedlings + saplings for any of the mangrove species (Figure 4). The potential for *B. maritima* to influence the distribution and growth of mangroves trees and other mangrove plants and animals remains unknown. But, given the abundance of the species across a range of habi-

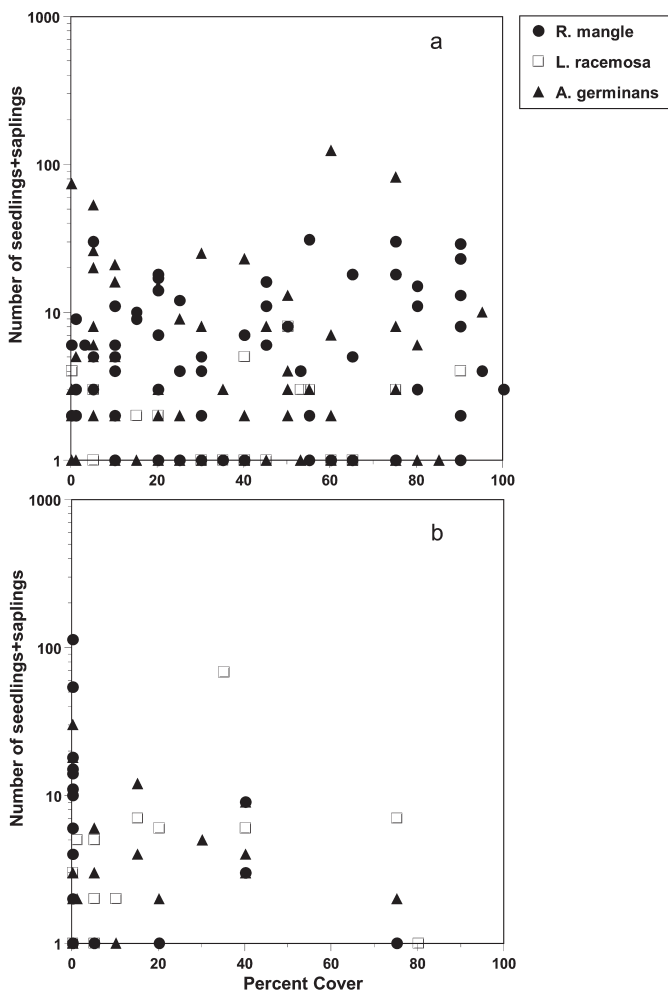


FIGURE 4. Number of mangrove saplings + seedlings ( $\# \text{m}^{-2}$ ) plotted against percent cover of *Batis maritima* for  $1 \times 1$  m plots sampled in Belize (a) and Florida (b) study sites.

tats, the potential seems high, especially in areas where it is the dominant species.

In summary, *B. maritima* was widespread in most mangrove habitats at both our study locations, and there were significant interhabitat differences in all the variables measured. Mangrove seedlings and saplings were common in areas occupied by *B. maritima*, but we found no evidence that the establishment of mangroves benefited by increasing cover of this common halophytic species. The ubiquitous distribution of *B. maritima* at all the sites sampled, however, indicates that its role in mangrove ecosystems deserves further consideration.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- Alexander, H. D., and K. H. Dunton. 2002. Freshwater Inundation Effects on Emergent Vegetation of a Hypersaline Salt Marsh. *Estuaries*, 25:142–1435.
- Dunton, K. H., B. Hardegee, and T. E. Whitledge. 2001. Response of Estuarine Marsh Vegetation to Interannual Variations in Precipitation. *Estuaries*, 24:851–861.
- Ellison, A. M., and E. J. Farnsworth. 1993. Seedling Establishment, Growth, and Response to Disturbance in Belizean Mangal. *American Journal of Botany*, 80:1137–1145.
- Feller, I. C. 1995. Effects of Nutrient Enrichment on Growth and Herbivory in Dwarf Red Mangrove (*Rhizophora mangle*). *Ecological Monographs*, 65:477–505.
- Feller, I. C., and K. L. McKee. 1999. Light-Gap Creation in a Belizean Red-Mangrove Forest by a Wood-Boring Insect. *Biotropica*, 31:607–617.
- Feller, I. C., D. F. Whigham, K. L. McKee, and C. E. Lovelock. 2003. Nitrogen Limitation of Growth and Nutrient Dynamics in a Disturbed Mangrove Forest, Indian River Lagoon, Florida. *Oecologia (Berlin)*, 134:405–414.
- Feller, I. C., D. F. Whigham, J. P. O'Neill, and K. M. McKee. 1999. Effects of Nutrient Enrichment on Within-stand Nutrient Cycling in Mangrove Ecosystems in Belize. *Ecology*, 80: 2193–2205.
- Ibarra-Obando, S. E., and M. Poumian-Tapia. 1991. The Effect of Tidal Exclusion on Salt Marsh Vegetation in Baja California, México. *Wetlands Ecology and Management*, 1:131–148.
- Keer, G. H., and J. B. Zedler. 2002. Salt Marsh Canopy Architecture Differs with the Number and Composition of Species. *Ecological Applications*, 12:456–473.

- López-Portillo, J., and E. Ezcurra. 1989. Zonation in Mangrove and Salt Marsh Vegetation at Laguna de Mecoacán, México. *Biotropica*, 21:107–114.
- Lovelock, C. E., and I. C. Feller. 2003. Photosynthetic Performance and Resource Utilization of Two Mangrove Species Coexisting in Hypersaline Scrub Forest. *Oecologia (Berlin)*, 134:455–462.
- Lovelock, C. E., M. C. Ball, B. Choat, B. M. J. Engelbrecht, N. M. Holbrook, and I. C. Feller. 2006a. Linking Physiological Processes with Mangrove Forest Structure: Phosphorus Deficiency Limits Canopy Development, Hydraulic Conductivity and Photosynthetic Carbon Gain in Dwarf *Rhizophora mangle*. *Plant, Cell and Environment*, 29:793–802.
- Lovelock, C. E., I. C. Feller, M. C. Ball, B. M. J. Engelbrecht, and M. L. Ewe. 2006b. Differences in Plant Function in Phosphorus and Nitrogen Limited Mangrove Ecosystems. *New Phytologist*, 172:514–522.
- Lüttge, U., M. Popp, E. Medina, W. J. Cram, M. Diaz, H. Griffiths, H. S. J. Lee, C. Schäfer, J. A. C. Smith, and K. H. Stimmel. 1989. Ecophysiology of Xerophytic and Halophytic Vegetation of a Coastal Alluvial Plain in Northern Venezuela. *New Phytologist*, 111:283–291.
- McKee, K. L., J. E. Rooth, and I. C. Feller. 2007. Mangrove Recruitment After Forest Disturbance is Facilitated by Herbaceous Species in the Caribbean. *Ecological Applications*, 17:1678–1693.
- Milbrandt, E. C., and M. N. Tinsley. 2006. The role of *Batis maritima* in regeneration of degraded mangrove forests. *Hydrobiologia*, 568:369–377.
- Olusegun, O. O., and R. G. Creese. 1997. Population Structure, Spatial Pattern and Seedlings Establishment of the Grey Mangrove, *Avicennia marina* var. *australasica*, in New Zealand. *Australian Journal of Botany*, 45:707–725.
- Pennings, S. C., and R. M. Callaway. 2000. The Advantage of Clonal Integration under Different Ecological Conditions: A Community-Wide Test. *Ecology*, 81:709–716.
- Penning, S. C., and C. L. Richards. 1998. Effects of Wrack Burial in Salt-Stressed Habitats: *Batis maritima* in a Southwest Atlantic Salt Marsh. *Ecography*, 21:630–638.
- Rey, J. R., R. A. Crossman, and T. R. Kain. 1990. Vegetation Dynamics in Impounded Marshes along the Indian River Lagoon, Florida, USA. *Environmental Management*, 14:397–409.
- Rodriguez, W., and I. C. Feller. 2004. Mangrove Landscape Characterization and Change in Twin Cays, Belize Using Aerial Photography and IKONOS Satellite Data. *Atoll Research Bulletin*, 513:1–22.
- SAS Institute. 1990. SAS Language: Reference. Version 6. First Edition. Cary, N. C.: SAS Institute, Inc.
- Zedler, J. B. 1977. Salt Marsh Community Structure in the Tijuana Estuary California USA. *Estuarine and Coastal Marine Sciences*, 5:39–53.
- . 1980. Algal Mat Productivity: Comparisons in a Salt Marsh. *Estuaries*, 3:122–131.
- Zedler, J. B., J. Covin, C. Nordby, P. Williams, and J. Boland. 1986. Catastrophic Events Reveal the Dynamic Nature of Salt Marsh Vegetation in Southern California. *Estuaries*, 9:75–80.



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

*Janie L. Wulff*

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

## INTRODUCTION

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

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

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

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

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

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

## METHODS

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

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

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

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

## RESULTS

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

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

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

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

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

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

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

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

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





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



Sponge species on mangrove prop roots

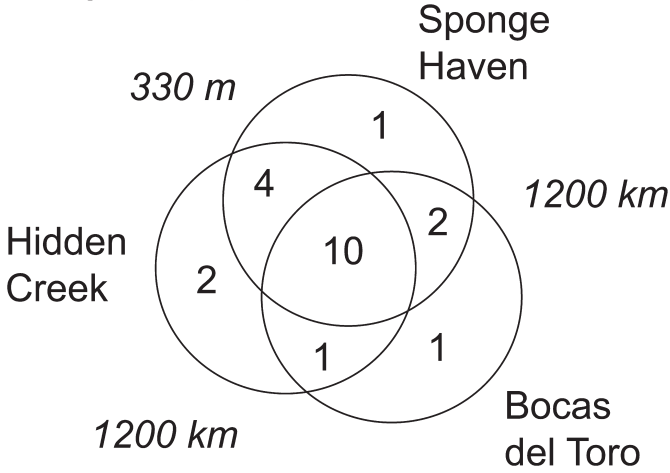


FIGURE 2. Diagram showing sponge species shared among two sites in Belize (Hidden Creek and Sponge Haven) and one site in Panama (Bocas del Toro). Only the 21 species that each constituted at least 0.1% of the total sponge volume on censused roots at a minimum of one of the three sites are included.

Mean density of numbers of sponge individuals per unit length of subtidal prop root was similar for all three sites (15, 11, and 15 individuals per meter length of root for Hidden Creek, Sponge Haven, and Bocas del Toro, respectively). Reflecting a relative preponderance of small individuals at the Bocas del Toro site, sponge density measured as volume per unit length of subtidal prop root was only 5.7 cm<sup>3</sup>/cm at Bocas, compared with 20.8 cm<sup>3</sup>/cm at Hidden Creek and 15.7 cm<sup>3</sup>/cm at Sponge Haven. Although variation in root diameter renders root length imprecise as a measure of substratum area monitored, length was deemed a better measure than number of roots because of the sixfold variation in root lengths (i.e., from 24 to 143 cm).

Sponge Community Dynamics Compared Within and Between Sites, by Volume and Number of Individuals

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

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

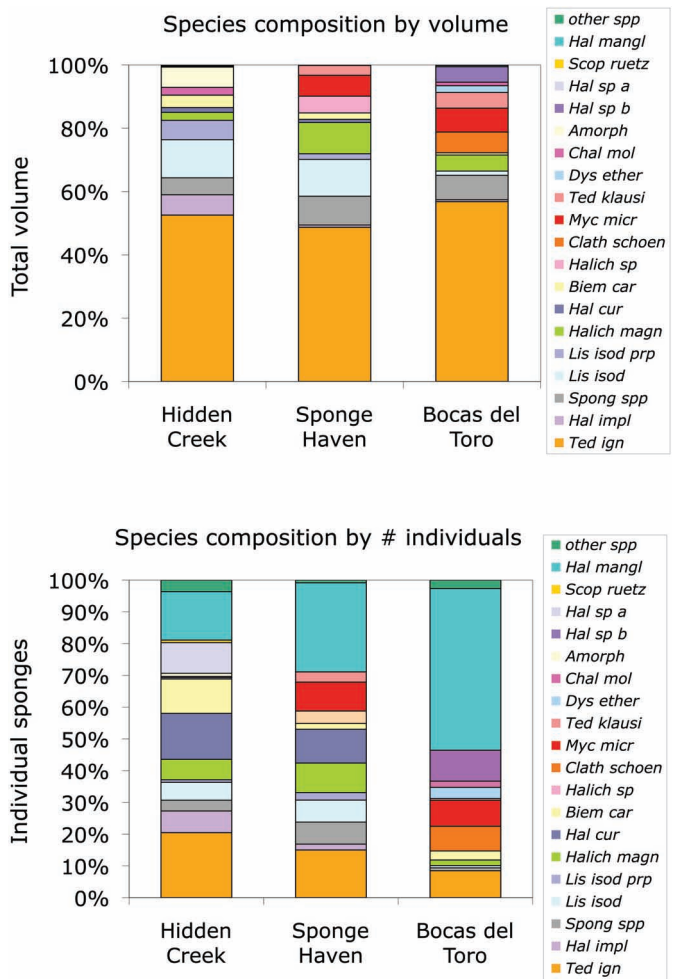


FIGURE 3. Sponge species assemblage composition, with respect to total volume contributed by each species, and with respect to the total number of individuals of each species, on mangrove prop roots at three Caribbean sites. These average relative abundances were calculated by adding together the volume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

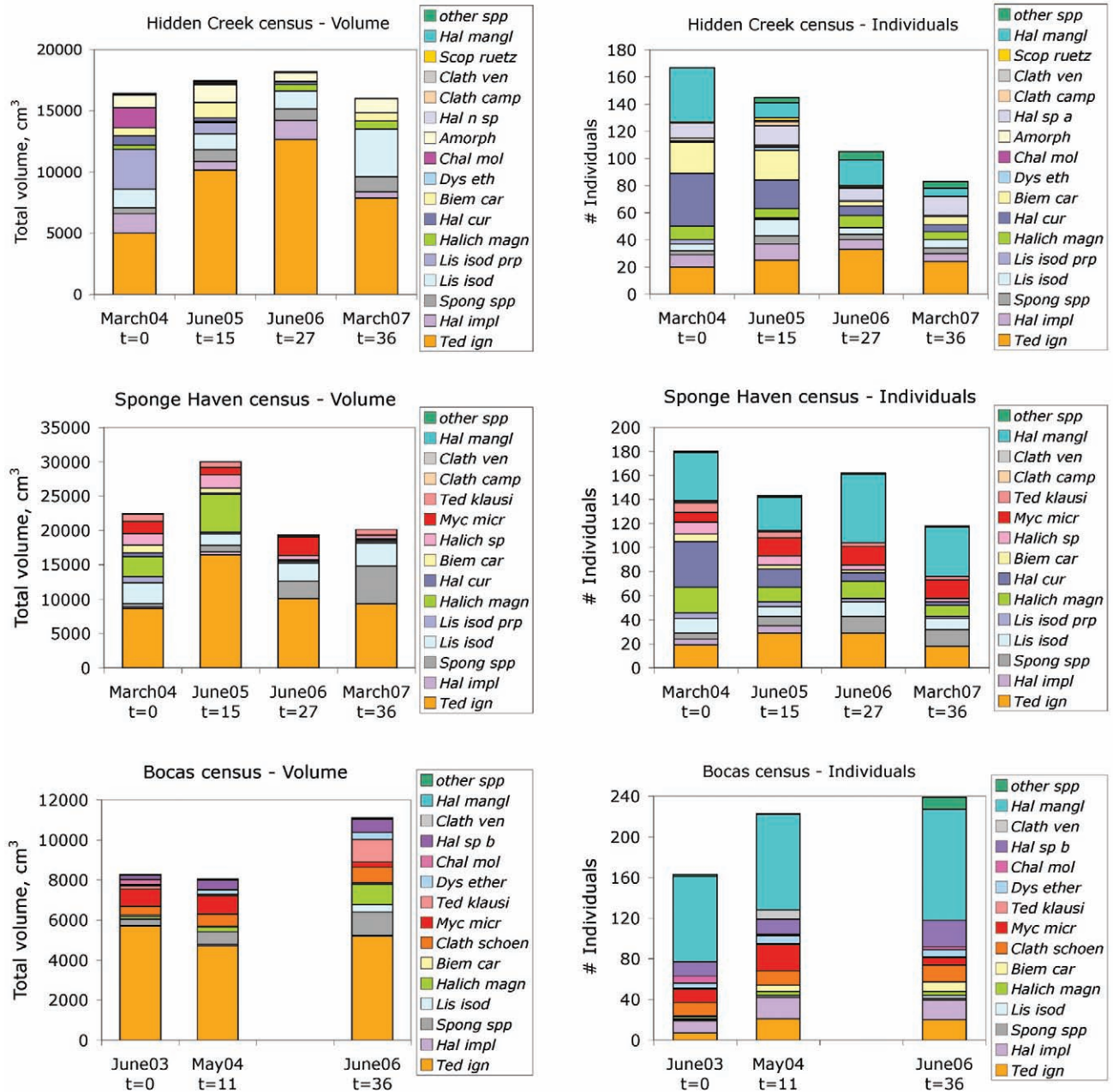


FIGURE 4. Community dynamics for sponges on mangrove prop roots at three Caribbean sites. Relative abundance of the species is represented by both total volume and total numbers of individuals. See Table 1 for complete spelling of species names.

and *T. ignis*. For the second and third species these losses primarily consisted of size decreases and fragmentations of sponges that were subsequently able to regenerate; and thus for both of these species, abrupt and dramatic changes in volume between the second and third censuses are not reflected in tandem changes in numbers of individuals (e.g., *H. magniconulosa* was represented by 12 individuals of total volume 5,518 cm<sup>3</sup> in 2005, 14 individuals of total volume 187 cm<sup>3</sup> in 2006, and 9 individuals of total volume 225 cm<sup>3</sup> in 2007). Large differences in maximum size achieved by sponges of different species further promote asynchronous changes in overall volume and numbers of individuals. For example, during this same year in which total sponge volume at Sponge Haven decreased by 35%, the number of individual sponges there increased by 13%, largely the result of a doubling of the number of *Haliclona manglaris* individuals. Yet each *H. manglaris* individual is so small that, even in the aggregate, they scarcely register in the overall volume tally (0.2% for the June 2006 census; see Figure 4).

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

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

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

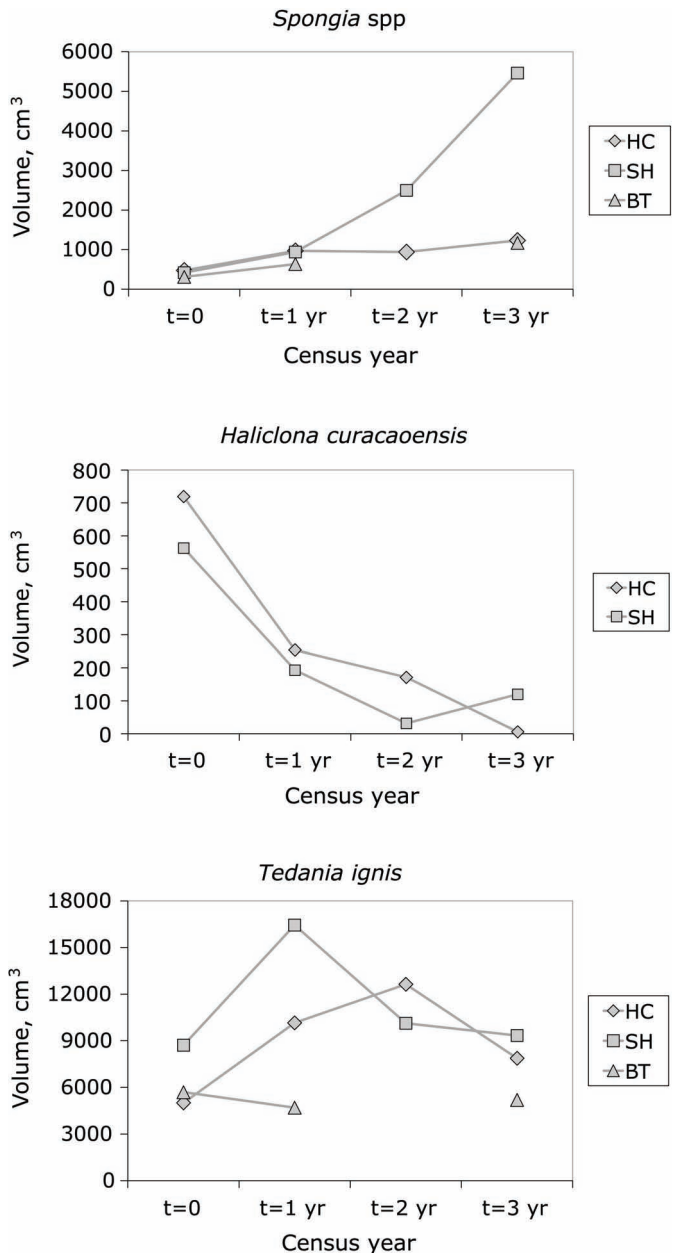


FIGURE 5. Representative population dynamics graphs for three sponge species inhabiting mangrove prop roots at sites where yearly censuses were made (HC = Hidden Creek; SH = Sponge Haven; BC = Bocas del Toro). Total volume of *Spongia* spp. consistently increased between monitoring periods at all three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



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

VARIATION AMONG SPONGE SPECIES  
IN INDIVIDUAL PERSISTENCE

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

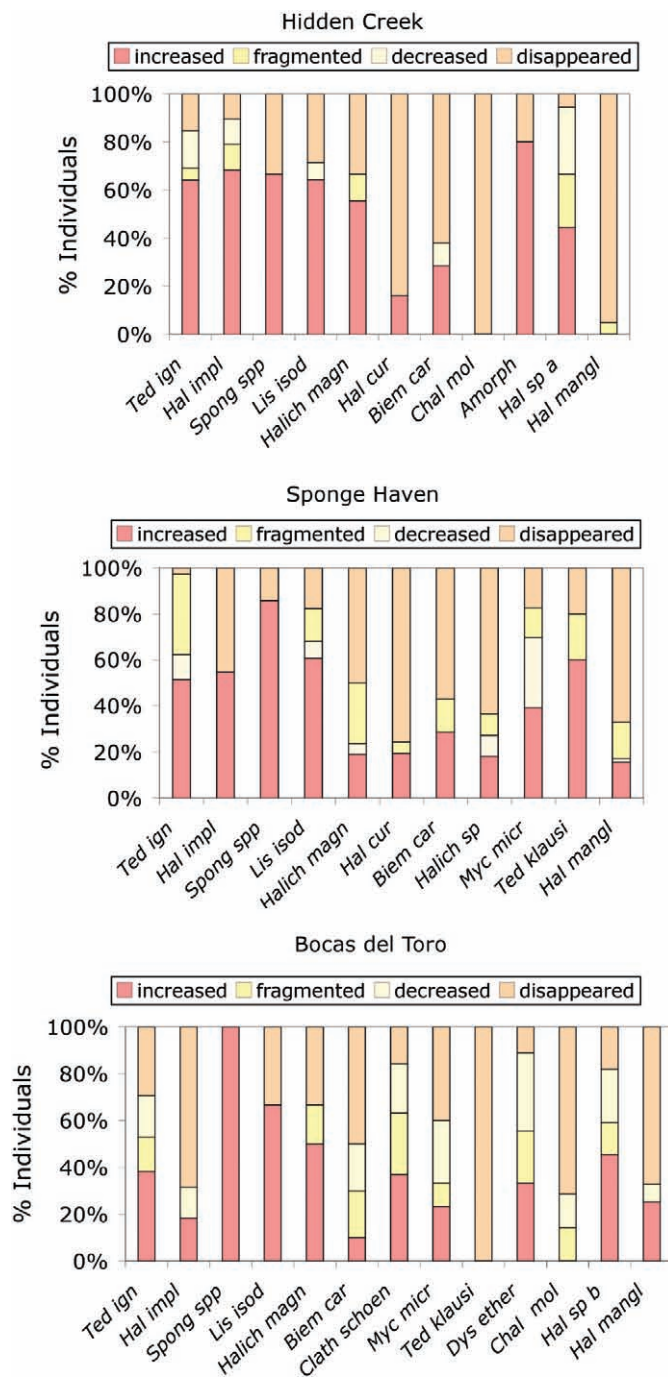


FIGURE 6. Proportions of sponge individuals of each species that increased in volume, fragmented, decreased in volume, or disappeared entirely between yearly census dates at three Caribbean mangrove sites. Although the fate of each individual was recorded in a single category at the time of observation,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



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

## DISCUSSION

### COMMUNITY COMPOSITION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

#### SIGNIFICANCE OF ECOLOGICAL CHARACTERISTICS OF SPONGE SPECIES

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

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

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

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## LITERATURE CITED

- Bingham, B. L., and C. M. Young. 1995. Stochastic Events and Dynamics of a Mangrove Root Epifaunal Community. *P.S.Z.N.I.: Marine Ecology*, 16:145–163.
- Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science*, 199:1302–1310.
- Diaz, M. C. 2005. Common Sponges from Shallow Marine Habitats from Bocas del Toro Region, Panama. *Caribbean Journal of Science*, 41:465–475.
- Diaz, M. C., K. P. Smith, and K. Rützler. 2004. Sponge Species Richness and Abundance as Indicators of Mangrove Epibenthic Community Health. *Atoll Research Bulletin*, 518:1–11.
- Ellison, A. M., and E. J. Farnsworth. 1990. The Ecology of Belizean Mangrove-Root Fouling Communities. I. Epibenthic Fauna Are Barriers to Isopod Attack of Red-Mangroves. *Journal of Experimental Marine Biology and Ecology*, 142:91–104.
- . 1992. The Ecology of Belizean Mangrove-Root Fouling Communities: Patterns of Epibiont Distribution and Abundance, and Effects on Root Growth. *Hydrobiologia*, 247:87–98.
- Ellison, A. M., E. J. Farnsworth, and R. R. Twilley. 1996. Facultative Mutualism Between Red Mangroves and Root-Fouling Sponges in Belizean Mangal. *Ecology*, 77:2431–2444.
- Engel, S., and J. R. Pawlik. 2005. Interactions among Florida Sponges. II. Mangrove Habitats. *Marine Ecology Progress Series*, 303:145–152.
- Farnsworth, E. J., and A. M. Ellison. 1996. Scale-Dependent Spatial and Temporal Variability in Biogeography of Mangrove Root Epibiont Communities. *Ecological Monographs*, 66:45–66.
- Jackson, J. B. C., and L. W. Buss. 1975. Allelopathy and Spatial Competition among Coral Reef Invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 72:5160–5163.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, N. J.: Princeton University Press.
- Mouquet, M., and N. Loreau. 2002. Coexistence in Metacommunities: The Regional Similarity Hypothesis. *American Naturalist*, 159:420–426.
- Pawlik, J. R., S. E. McMurray, and T. P. Henkel. 2007. Abiotic Factors Control Sponge Ecology in Florida Mangroves. *Marine Ecology Progress Series*, 339:93–98.
- Rützler, K. 1978. "Sponges in Coral Reefs." In *Coral Reefs: Research Methods. Monographs on Oceanographic Methodology*, Volume 5, ed. D. R. Stoddart and R. E. Johannes, pp. 299–313. UNESCO: Paris.
- . 1995. Low-Tide Exposure of Sponges in a Caribbean Mangrove Community. *P.S.Z.N.I.: Marine Ecology*, 16:165–179.
- Rützler, K., M. C. Diaz, R. W. M. van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. Wulff. 2000. Diversity of Sponge Fauna in Mangrove Ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, 476:230–248.
- Rützler, K., and I. C. Feller. 1996. Caribbean Mangrove Swamps. *Scientific American*, 274(3):94–99.
- Rützler, K., I. Goodbody, M. C. Diaz, I. C. Feller, and I. G. Macintyre. 2004. The Aquatic Environment of Twin Cays, Belize. *Atoll Research Bulletin*, 512:1–49.
- Sutherland, J. P. 1974. Multiple Stable Points in Natural Communities. *American Naturalist*, 108:859–873.
- . 1980. Dynamics of the Epibenthic Community on Roots of the Mangrove *Rhizophora mangle*, at Bahia de Buche, Venezuela. *Marine Biology*, 58:75–84.
- Wulff, J. L. 2000. Sponge Predators May Determine Differences in Sponge Fauna Between Two Sets of Mangrove Cays, Belize Barrier Reef. *Atoll Research Bulletin*, 477:250–263.
- . 2001. Assessing and Monitoring Coral Reef Sponges: Why and How? *Bulletin of Marine Science*, 69:831–846.
- . 2004. Sponges on Mangrove Roots, Twin Cays, Belize: Early Stages of Community Assembly. *Atoll Research Bulletin*, 519:1–10.
- . 2005. Trade-Offs in Resistance to Competitors and Predators, and Their Effects on the Diversity of Tropical Marine Sponges. *Journal of Animal Ecology*, 74:313–321.
- . 2006. Sponge Systematics by Starfish: Predators Distinguish Cryptic Sympatric Species of Caribbean Fire Sponges, *Tedania ignis* and *Tedania klausi* n. sp. (Demospongiae, Poecilosclerida). *Biological Bulletin*, 211:83–94.

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