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THE AQUATIC ENVIRONMENT OF TWIN CAYS, BELIZE

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Red mangrove *(Rhizophora mangle)* hanging roots are the primary solid substrata along mangrove channels at Twin Cays and their vertical orientation assures optimal protection from silting. Sponges and ascidians make up most of the biomass of epibionts. Sponges shown include *Lissodendoryx* cf. *isodictyalis* (bluish gray), *Tedania ignis* (orange massive), *Scopalina ruetzleri* (orange encrusting), and *Haliclona manglaris* (turquoise); the ascidians are *Distaplia corolla* (deep orange knobby structures), which also overgrow sponges. (Photo, L. M-Penland).

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KLAUS RÜTZLER[1], IVAN GOODBODY[2], M. CRISTINA DIAZ[3], ILKA C. FELLER[4], AND IAN G. MACINTYRE[5]

ABSTRACT

The rich fauna and flora of Twin Cays off southern Belize were explored and compared with coral and turtle-grass habitats of the surrounding Belize lagoon and the nearby barrier reef. Among the many subtidal habitats found in these cays, some 20 stations were routinely sampled to study the composition of plankton and benthos, sediment and peat bottoms, and to investigate the parameters that determine distribution. The work also focused on distribution patterns, animal behavior, and community development over geological time scales. Each station is examined for its particular properties, including topography, substratum types, environmental parameters, and predominant organisms and communities, particularly the sessile benthos.

INTRODUCTION

Twin Cays off the southern coast of Belize are so named because a wide tidal channel splits the roughly oval mangrove island into two unequal parts. These islands are the closest mangrove development to Carrie Bow Cay and the Smithsonian's Carrie Bow Marine Field Station, less than 4 km to the northwest. They are among hundreds of mangrove cays perched on the leeward top of the Belize barrier reef platform (Plate 1a). We call this type of tidal forest "island mangrove," to distinguish it from "mainland mangroves," which fringe the continental shores, including the tidal mouths of freshwater rivers and creeks (Rützler and Feller, 1996) and are awash by full-oceanic-salinity seawater. By contrast, mainland mangroves are subjected to a salinity gradient ranging from freshwater to fully oceanic, caused by coastal runoff. The absence of freshwater at Twin Cays' marine environment (except during periods of heavy rains), combined with

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the area's small tidal range accounts for the extensive and diverse development of marine habitats in these islands.

Twin Cays (16° 49' 48" N, 88° 06' 11" W; at their center) are part of the Stann Creek District and are situated 15.5 km due 81° (ENE) of Sittee Point, the nearest mainland, and 20 km due 142° (SE) from Dangriga, the nearest town. The islands crown the N-S directed barrier-reef carbonate platform which at that location is 8 km wide and 0-7 m (average 2.5 m) deep. To the west of Twin Cays, the platform extends for about 5 km where its depth drops rapidly to about 20 m, the average for the trough-like main lagoon, including the Inner Channel that is a protected shipping lane for large vessels. The lagoon has a sediment bottom covered mainly by seagrass, *Thalassia testudinum.* About 2 km to the east of Twin Cays, the reef platform is delineated by the intertidal barrier-reef-crest. From there, the reef slopes rapidly, within a distance of 400 m, toward the continental dropoff (Rützler and Macintyre, 1982).

Barring unusual currents and storms, the lagoon water west of Twin Cays is influenced by mainland runoffs; the water east of the islands has open-ocean bluewater characteristics that are enhanced by a series of three 600 to 800 m wide and 5 to 8 m deep breaks through the barrier reef, South Water, Carrie Bow, and Curlew cuts. Within the perimeter of the cays, topography, water depth, extent and kind of vegetation, and seasonal and meteorological events determine habitat- and water quality parameters, including substratum composition and inclination, suspended and settled sediments, water level and flow velocity, temperature, salinity, turbidity, dissolved substances, and nutrients.

In the following sections we summarize and illustrate the habitat characteristics of a number of tidal and subtidal locations throughout Twin Cays that served as sites for collecting, observation, illustration, and experimentation of sessile organisms for many researchers over the years since 1984 (see also, Calder, 1991a, b; Diaz et al., 2004; Goodbody, 2004a; Littler and Littler, 2000; Littler et al., 2004; Ott and Bright, 2004; Parrish and Ryan, 2004; Richardson, 2004; Winston, 2004; Wulff, 2004).

STUDY AREA AND METHODS

Twin Cays actually consist of four fully established mangrove islands. To identify the various topographic features, they were labeled by newly invented place names (no traditional local designations existed) suggested by participants of the Smithsonian Caribbean Coral Reef Ecosystems (CCRE) program (Fig. 1). The largest cay is East Island; it measures 52.1 ha in area, is 1400 m in maximum length, and 674 m at its widest point, just south of its center. East Island is nearly cut in half by the west-east oriented, 16 to 58 m wide Lair Channel, separating a northern and southern portion. Both include in-shore ponds, lakes, and tidal mudflats. The northern section contains Candy's, East, and Hummingbird ponds and Aanderaa Flats; the southern part is distinguished by Hidden Lake and Boa Flats. West Island, the second largest cay and nearly a smaller mirror image of the former, extends over 21.5 ha and measures 895 x 377 m. It is separated from East Island by the s-shaped Main Channel which tapers from 136 m width at the south entrance into Twin Cays to 8 m at the northern exit. West Island includes the tidal West

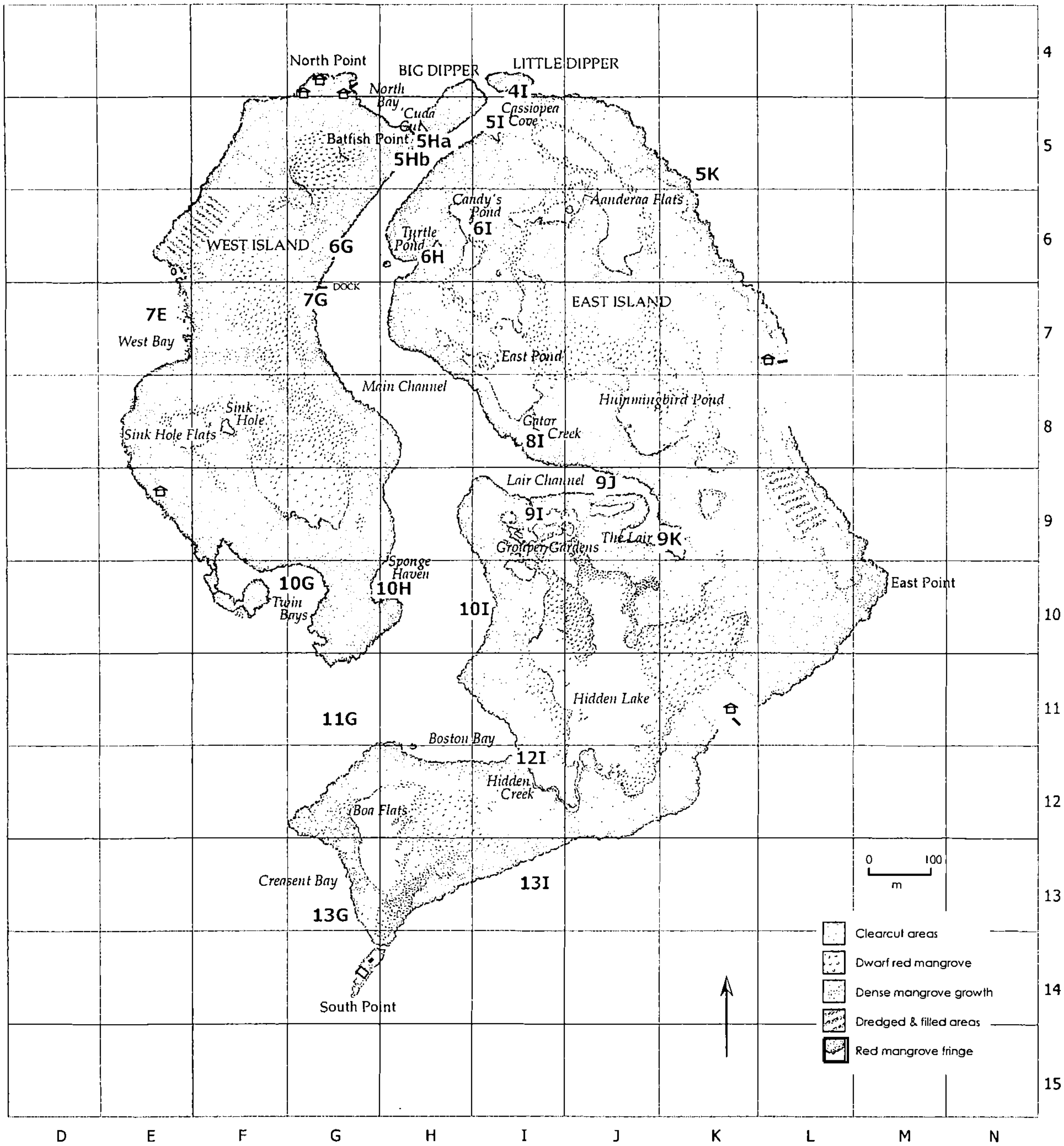

Figure 1. Map of Twin Cays based on aerial photographs taken in 2002, with station numbers (grid coordinates used in this survey (map, M. K. Ryan).

Pond and Sinkhole Flats; its northward extension is formed by two islets, Big Dipper (0.5 ha, 132 x 64 m) and Little Dipper (0.2 ha, 65 x 39 m). Several smaller islets, or, rather, isolated stands of mangrove trees, developed and vanished in different places over the past 20 years of our study, for instance, the one just outside Turtle Cove (Figs. 1, 7).

The total shoreline of Twin Cays (excluding interior ponds, lakes, and mudflats) is 8.1 km long, more than half of that made up by the inshore mangrove fringe, the rest directly exposed to the open Belize lagoon. The tide is micro-tidal and of mixed semidiurnal type, with a mean range of 15 cm (Kjerve et al., 1982); maximum fluctuations have a range of 40 cm. Water surface temperature (lagoon at Carrie Bow Cay) averages 25° C in February, 30° C in August, with recorded extremes of 23.5°–31.5°; air temperature minima and maxima differ only slightly, 22.5°–34.5° C (Koltes et al. 1998). Predominant wind direction during October through February is from the northwest, the rest of the year it is northeast to east. Monthly preciptation is lowest between March and May (0–25 mm), highest between June and November (100–480 mm) (Rützler and Ferraris, 1982; Koltes et al., 1998). Salinity in the open lagoon is fully oceanic, 35–36‰. Reactive silica content of interstitial water from sediments collected off Twin Cays (South Point) reaches 1.2–1.5 mg SiO_2/l (as compared with 0.3–0.4 mg around Carrie Bow Cay), with terrigenous particulate silica (87–92%) dominating the sediment fine fraction, ≤0.25 mm (0% at Carrie Bow) (Rützler & Macintyre, 1978).

Station numbers were assigned from an arbitrary grid (mesh-size ca. 135 m) superimposed on a 1985 version of a Twin Cays map (Fig. 1). Large-scale measurements and water-depth values outside Twin Cays were taken from nautical chart 28167 (U. S. Defense Mapping Agency, Hydrographic/Topographic Center, Washington, DC; 1984 edition). Topographic measurements at Twin Cays were based on a map from aerial and satellites images (Rodriguez and Feller, 2004).

DESCRIPTION OF STATIONS

These descriptions are presented in sequence from north to south and west to east. Station numbers are based on number-letter combinations from the aforementioned grid (Twin Cay locations are covered by the ranges 4–14 and E–M). Estimates of prevailing environmental conditions are expressed as follows: L=light exposure; C=current flow (+ is strong, ± moderate, – low); T=temperature and S=salinity. These latter parameters are not mentioned if they are normal (close to open-lagoon water conditions) but are listed as "stressful range" (with measured range values where available) if they vary beyond the fluctuations of the open lagoon.

Sta. 4 I, Little Dipper (Figs. 1, 2; Plate 1b)

Location and Topography. South shore of the islet, facing Main Channel.

Habitats. Mixture of free hanging roots and roots embedded in substratum. Sandy bottom with turtle grass *(Thalassia testudinum)*.

Depth. 1.5 m.

Environmental Conditions. L: +; C: +.

Sediment. Fine-grained sand.

Communities. Algae *(Caulerpa, Halimeda, Dictyota)* and a modest number of sponges on roots *(Lissodendorys* cf. *isodictyalis, Tedania ignis)* and peat bank *(Haliclona mucofibrosa)*.

Figure 2. Aerial view of Twin Cays looking southeast. Little Dipper (sta. 4I), Big Dipper, and 'Cuda Cut (5Ha) (left to right) are in the foreground, Cassiopea Cove (5I) is seen directly behind Big Dipper; Batfish Point South (5Hb) is in the Main Channel, turning right after passing 'Cuda Cut (photo, D. Littler).

Figure 3. Low-altitude aerial view of 'Cuda Cut and Batfish Point (background) (sta. 5Ha; photo, D. Littler).

Sta. 5 Ha, Batfish Point—'Cuda Cut (Figs. 1, 3, 4; Plates 1, 2a)

Location and Topography. The north coast of West Island, from its northeast corner (Batfish Point) to North Bay, opposite Big Dipper (the passage between the two

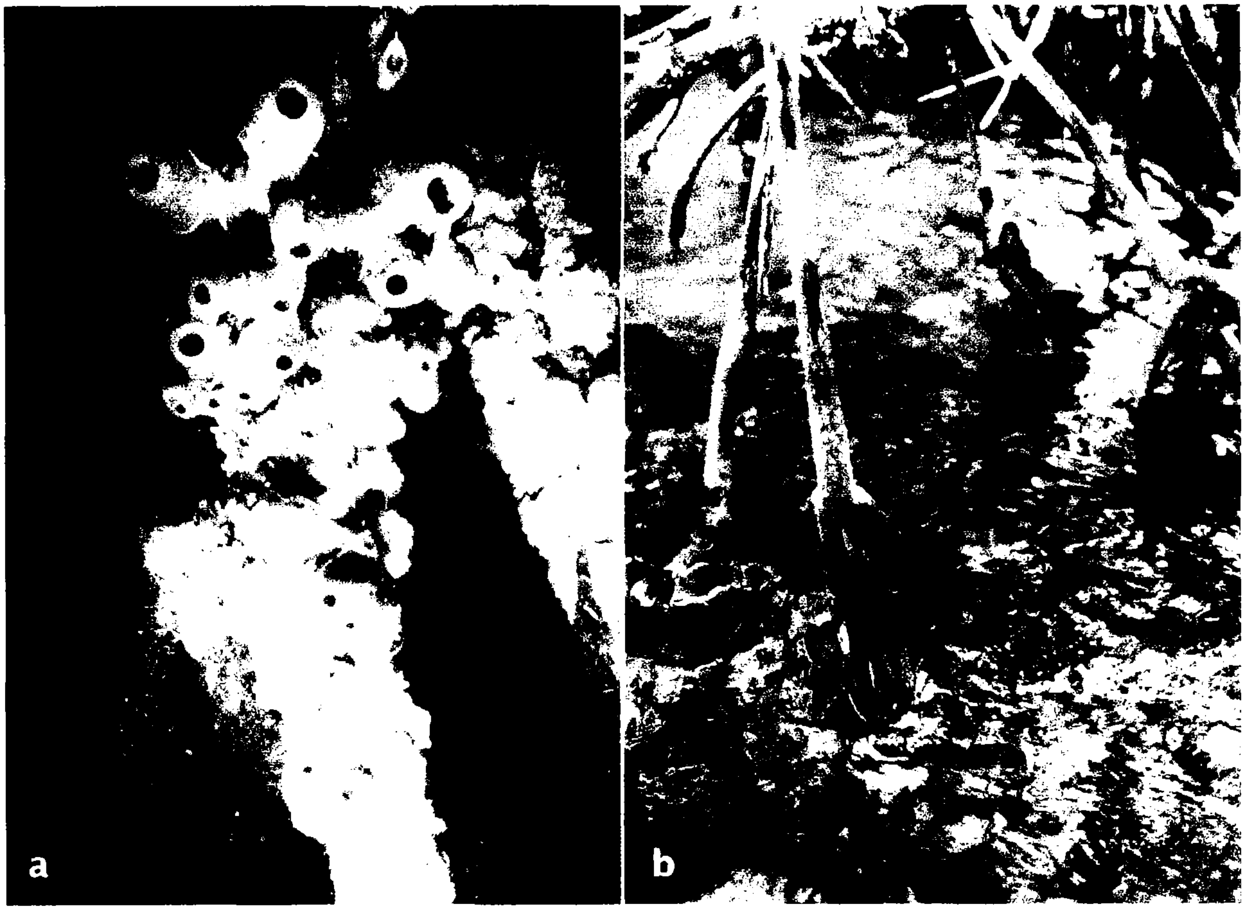

Figure 6. Mangrove roots at Main Channel Northwest: *a,* root covered by sponges, purple *Haliclona implexiformis* (tubes) and orange *Scopalina ruetzler* (encrusting); *b,* mangrove oysters, *Isognomon alatus.*

Tedania, and *Hyrtios;* they alternate with clusters of mangrove oysters *(Isognomon alatus)* and alga-like fuzz of the bryozoan *Zoobotryon verticillatum* (Winston, 2004). Because a counter-current creates pockets of calm water, there are accumulations of light-green floats of cyanobacterial mats composed mainly of filamentous *Lyngbya* sp.

Sta. 6 H, Turtle Cove and Turtle Pond (Figs. 1, 7; Plate 2e)

Location and Topography. A deeply cut bay 30 m wide and 45 m long in the northwest shoreline of East Island. Its entrance from the Main Channel is partly blocked by a small mangrove patch that developed on a sandbank during the past 15 years (25 m diameter in 2003). About 100 m south of the entrance, sand deposits account for a very shallow shoreline covered by seagrass and lined by long hanging roots. The cove extends toward the northeast through a narrow, shallow channel (2–3 m wide, 31 m long), which ends in a deeper (2 m) pond, 16 x 12 m in diameters. Garbage dumping in Turtle Pond has interrupted research at this location for several years.

Figure 5. Low-altitude aerial photograph of Northeast coast looking northwest (photo D. Littler).

Sta. 6 G, Main Channel Northwest (Figs. 1, 6, 7)

Location and Topography. Western shore of the Main Channel, along the coast of West Island between the Dock and Batfish Point.

Habitats. Steep and strongly eroded peat bank (1.5 m tall), with overhanging red-mangrove roots of low density protruding in 2–3 m distance from the bank. *Thalassia* seagrass sparsely covering the bottom of the channel which at this location is 55 m wide, 1.5–2 m deep.

Depth. 2–3 m.

Environmental Conditions. L: +; C: + (wind-generated waterflow through the cuts to the open lagoon).

Sediment. Abundance of fine sediments that tend to be resuspended by heavy boat traffic through the channel; it covers most substrata and ebibionts.

Communities. Algal fuzz composed of calcareous red algae *(Jania* cf. *adhaerens)* and cyanobacteria *(Lyngbya, Schizothrix* spp.), fleshy green algae *(Caulerpa verticillata)* and red algae *(Acanthophora spicifera),* sponges *(Lissodendoryx, Tedania, Scopalina ruetzleri, Haliclona implexiformis, H. manglaris, Spongia tubifera),* and a few ascidians *(Didemnum* spp.) on the roots. Sponges are partly covered by rusty red cyanobacteria (*Schizothrix* spp.) and leafy greens (cf. *Anodyomene).* On the peat bank, one finds among other sponges the encrusting *Clathria venosa;* the sea urchin *Lytechinus variegatus* is abundant. Near the Dock there is an abundance of solitary ascidians *(Phallusia nigra, Microcosmus exasperatus),* which are rare elsewhere at Twin Cays.

Swimming across the channel one encounters large mounds caused by burrowing crustaceans, and *Cassiopea* jellyfish among the turtlegrass. The opposite bank looks very much like its western counterpart but the roots are closer to shore, algae are more common than sponges, and there is more deposited fine sediment. Algae include cyanobacterial mats, *Caulerpa,* and *Halimeda.* Most sponges belong to *Lissodendoryx,* Islands; 'Cuda Cut, was named for its abundance of schooling barracudas). Outward (north) of North Bay, the water is very shallow (<0.5 m) because of sand deposits covered by turtle grass.

Habitats. The southern shore of the passage has an intertidal peat bank protruding over a curved or nearly vertical peat wall, 3 m tall. The wall is recessed 1–3 m from the distal edge of the bank, thus creating an extensive cave habitat. Red mangrove is anchored on top of the bank, its roots protruding here and there from the otherwise smooth or somewhat pitted, compact peat; stilt roots hanging over edge of the bank.

Depth. 3–4 m.

Environmental Conditions. L: + to –; C: +.

Sediment. Sand with mollusk fragments; very fine sand and soft, carbonate mud toward the center of the channels, extensively worked by crustacean burrowers.

Communities. Peat banks are covered by tufts of algae and hydroids, coralline algae, calcified green alga *(Halimeda),* and a number of encrusting or cushion-shaped sponges *(Scopalina ruetzleri, Spongia tubulosa)* and ascidians *(Diplosoma* sp.) and populated by seaurchins *(Lytechinus variegatus).* Sea anemones *(Condylactis gigantea, Bartholomea annulata)* and sabellid polychaetes are anchored in fissures and depressions of the peat wall. The most common encrusting sponges on the dark cave wall and ceiling peat substrata are the orange *Scopalina ruetzleri* and the yellow *Amorphinopsis* sp. and *Clathrina* cf. *coriacea.* Other abundant species in this habitat are *Chondrilla nucula, Clathria venosa, Mycale citrina, M. microsigmatosa,* and *Haliclona mucofibrosa,* and sheet-like forms of ascidians, including *Diplosoma listerianum, D. glandulosum, Lissoclinum abdominale* and *Didemnum conchyliatum.* Crisp white patches of sulfur-fixing bacteria *(Beggiatoa)* are conspicuous on the peat wall near the muddy bottom. Ascidians with a higher profile tend to be confined to hanging roots, as are fleshy macro-algae, and massive sponges such as *Lissodendoryx* cf. *isodictyalis, Mycale laxissima* (also large-growing and common on fully light-exposed peat walls), and *Tedania.* Many of the light-exposed sponges are covered (as observed in August 2004) by rusty-red veils of cyanobacteria *(Schizotrix* spp.). The sediment bottom near the banks is barren except for sporadic algae and seagrass but the Main Channel floor off Batfish Point is covered by stands of *Thalassia* seagrass, and *Halimeda* and *Caulerpa* algae interspersed with characteristic mounds and holes indicating the presence of burrowing decapods *(Glypturus, Alpheus).* Numerous specimens of the benthic jellyfish *(Cassiopea xamancha)* and of the starfish *Oreaster reticulatus* are also regularly encountered. Exiting north into and beyond North Bay one commonly encounters an encrusting black sponge *(Artemisina melana)* covering coral rubble and dead gorgonians.

Sta. 5 Hb Batfish Point South (Figs. 1, 2; Plate 2b,c)

Location and Topography. Main Channel west, northeast shore of West Island just south of Batfish Point.

Habitats. Intertidal, root-consolidated peat-bank with long adventitious red-mangrove roots covered mainly by sponges hanging in front of the bank. About 20 m toward the south, the peat bank decreases in height to about 0.5 m.

Depth. 1–3.5 m.

Environmental Conditions. L: + to –; C: + (wind-generated water flow through the cuts to the open lagoon).

Sediment. Sand with mollusk fragments and *Halimeda* chips.

Communities. Encrusting or low-growing algae, sponges, and ascidians on the bank, like at 'Cuda Cut (Sta. H 5A); ascidian numbers decrease with diminishing waterflow toward the south. Seagrass *(Thalassia)* appears where the current through the cuts slows and sediment accumulates on the bottom. Opposite across the channel (East Island), cool water entering through 'Cuda Cut stimulates a rich community of algae, sponges *(Mycale microsigmatosa, Lissodendoryx, Tedania),* and colonial ascidians *(Didemnum* spp., *Botrylloides nigrum).*

Sta. 5 I, Cassiopea Cove (Figs. 1, 2; Plate 2d)

Location and Topography. North end of Main Channel, a small bay on East Cay, opposite Big Dipper islet.

Habitats. Soft sedimentary bottom with *Thalassia* seagrass. Mangrove stilt-roots along the shore.

Depth. 0.5–2 m.

Environmental Conditions. L: +; C: +.

Sediment. Fine-grained sand and carbonate mud. Median grain diameter of the sand fraction has a range of 94–268 μm, the mud fraction (<63 μm) is 17–33% and the organic content 5.4–9.7% (Dworschak and Ott, 1993). The mud fraction tends to become resuspended during high winds, causing high turbidity.

Communities. Large population of the benthic upside-down jellyfish *Cassiopea xamancha.* Sediment mounds and funnel-shaped holes among stands of algae *(Penicillus, Halimeda)* indicate the presence of burrowing decapods *(Alpheus* spp., *Glypturus acanthochirus).* Stilt or hanging prop roots are covered by algae and a few ascidians *(Perophora)* but much of the epifauna tends to become smothered by whitish flock from resuspended and resettling fine sediment.

Sta. 5 K, East Island, Northeast Coast (Figs. 1, 5)

Location and Topography. Northernmost part of the highly exposed outer shoreline that faces northeast.

Habitats. Mangrove fringe with *Rhizophora* stilt roots hanging freely, or (further to the southeast) firmly embedded in sandy substratum. About 30-40 m offshore, a shallow sandbank covered by turtle grass *(Thalassia)* parallels the coast and separates it from the extended turtle grass meadows of the lagoon.

Depth. 0.5-1 m

Environmental Conditions. L: +; C: +.

Sediment. Medium to coarse sand with ample *Halimeda* chips.

Communities. Algal turf (bostrychietum) and a few ascidians *(Didemnum)* on roots; *Halimeda* algae and *Thalassia* seagrass covering the bottom.

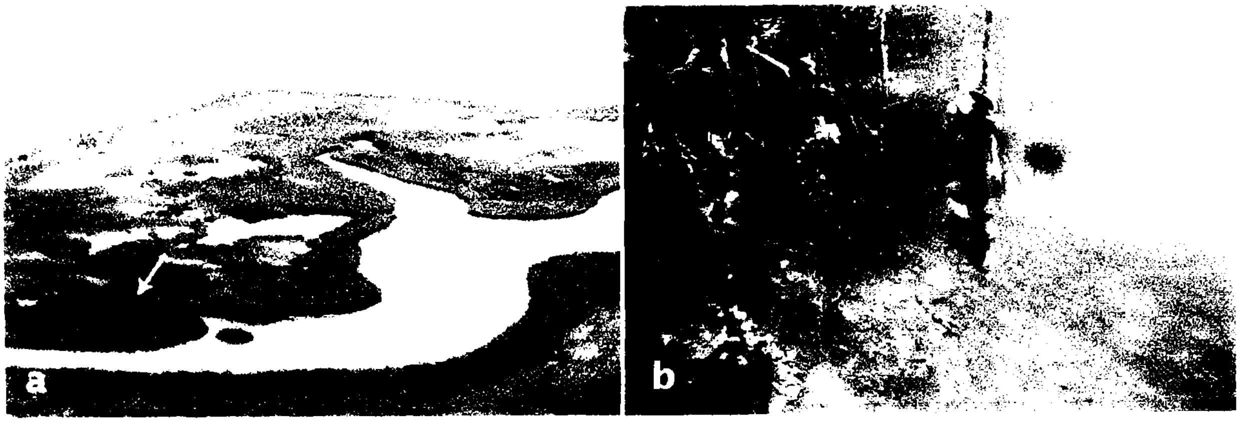

Figure 7. Habitats near the northern Main Channel: a, aerial photograph looking southeast (across Main Channel Northwest, 6G), onto Turtle Cove and Turtle Pond (6H, arrow), which are connected by Turtle Creek; Candy's Pond (6I) is to the far left; b, underwater view of Turtle Creek (photo, M. Carpenter).

Habitats. Dense bed of seagrass *(Thalassia)* at the entrance to the cove; otherwise muddy bottom. Ample free-hanging *Rhizophora* roots from overhanging trees that line cove, channel, and pond. (Roots at this location were measured to grow 0.2–0.4 mm per day.)

Depth. 1–2 m.

Environmental Conditions. L: –; C: –; T, S: stressful range (connection with nearby inshore Candy's Pond).

Sediment. Fine, organics-rich mud.

Communities. Intertidal parts of the roots are covered by algal fuzz and clusters of mangrove oysters *(Isognomon alatus).* Subtidal zones support brown cyanobacteria, algae *(Ulva* sp., *Caulerpa racemosa),* small sponges *(Haliclona implexiformis, Biemna* sp.) and, toward the tips of roots, an abundance of ascidians *(Perophora regina, Didemnum conchyliatum, Eudistoma olivaceum)* competing with serpulid worms and a few sponges *(Haliclona curacaoensis).* Owing to current patterns and the deposit of suspended sediments and other matter (such as loose seagrass leaves left from manatee feeding), roots on the south flank of the cove are less densely colonized by epibionts than the north side. Long-bladed *Thalassia* seagrass predominates the shallow bank just south of Turtle Pond where hanging mangrove roots have a poorly developed epibiont community with a few sponges and anemones. Patches of lower intertidal peat banks are covered by *Halimeda* algae.

Sta. 6 I, Candy's Pond (Figs. 1, 7; Plate 2f)

Location and Topography. An inshore pond on East Island, 65 m from the Main Channel, accessible from Turtle Pond through a narrow, mangrove-overgrown canal, 1.5 m wide, 0.5 m deep, and 45 m long. This is actually a double pond, two equal-sized lagoons of about 200 m^2 area joined by a narrow neck of water. Only the northern pond is being considered here, which is elongate, 50 m long, and 8–30 m wide.

Habitats. Rhizophora roots. Muddy bottom of decaying plant materials.

Depth. 1–1.5 m.

Environmental Conditions. L: +; C: –. T, S: stressful range; 34°, 37‰ (highest values recorded, May, 1985). Strongly impacted by heavy rains and periods of evaporation over the surrounding swamp.

Sediment. Very loose organic flock, up to 1 m deep.

Communities. Abundance of ascidian *Eudistoma olivaceum,* known for its high stress tolerance, and *Didemnum.* Sponges are rare (mainly *Haliclona implexiformis).* Small sabellid polychaetes *(Bispira melanostigma),* hydroids (cf. *Myrionema),* and a bryozoan *(Bowerbankia,* which always seems to grow near the water surface) are fairly common. The only fishes observed were mangrove snapper and small barracuda. Bacterial mats cover areas of the muddy bottom.

Sta. 7 E, West Bay (Figs. 1, 2, 8; Plate 3c)

Location and Topography. A recess of the outer (western, lagoon-ward) shoreline of West Island. The bay measures about 175 by 45 m, with a ragged shoreline.

Habitats. Rhizophora mangrove lines the fringe, with stout roots firmly anchored in coarse sand along the shallow (0.5 m) coastal zone of West Island. The bay bottom is made up by a variety of coral rock rock, shell (bivalve, conch shells), and sand covered by calcareous and fleshy algae and patches of turtle grass. A barren sandy apron extends from close to shore several hundred meters outward into the lagoon at the southern part of the bay.

Depth. 0.2–3.5 m.

Environmental Conditions. L: +; C: +.

Sediment. Poorly sorted but mainly coarse sand and gravel, patches of medium fine sand.

Communities. The fauna and flora of West Bay are rich, possibly benefiting from nutrient input from the adjacent mangrove, lack of very fine sediments, and a moderate temperature-salinity regime. Mangrove roots support crustose coralline and *Halimeda* algae, algal turfs, and a reef-like fauna of a few sponges *(Clathria venosa, Mycale laevis, Niphates* sp.), coral *(Porites porites and P. atroides, Millepora complanata),* and serpulid worms. The bay floor is covered by a variety of algae *(Halimeda, Penicillus, Rhipocephalus, Caulerpa), Thalassia* and *Halodule* seagrass, clusters of bivalves and coral *(Manicina areolata)* with stands of octocoral, and numerous sea urchins *(Lytechinus variegatus, Clypeaster rosaceus),* and the occasional batfish *(Ogcoephalus).* Cushion-shaped and branching sponges occur on rock (e.g., *Amphimedon viridis, A. compressa, Niphates erecta),* ascidians are rather rare except for a few small patches on seagrass blades (didemnids, *Ecteinascidia minuta)* and a small burrowing form buried around *Thalassia* roots *(Pyura munita).*

Sta. 7 G, Main Channel West, the Dock (Figs. 1, 9)

Location and Topography. West coast of Main Channel (central eastern shore of West Island). The Dock itself, a wooden structure, was built by CCRE Program participants to facilitate access to the swamps of West Island; its submerged pilings are fouled mainly by algae and sponges and are used as support for various experimental setups (settling frames, tide and temperature probes).

Figure 8. Habitats at West Bay: *a*, sieving sand samples in front of the mangrove fringe bordering the bay; *b*, Turtle grass surrounding sand patches with unattached solitary coral, *Manicina;* b, coral *(Porites)* and hydrocoral *(Millepora)* growing on *Rhizophora* stilt roots that are firmly embedded in sand.

Habitats. Dense seagrass, *Thalassia,* comes up to the fringe where there is a low peat bank and roots are covered by sponges. Fallen trees and driftwood are stranded in places and entangled among the prop roots.

Depth. 0.5–1 m.

Environmental Conditions. L: ±; C: ±.

Sediment. Carbonate mud with patches of *Halimeda* chips.

Communities. Fleshy and calcareous algae *(Caulerpa, Halimeda, Jania),* sponges *(Lissodendoryx* cf. *isodictyalis, Chondrilla nucula, Clathria venosa, Tedania ignis, Clathrina* cf. *coriacea),* and mangrove oysters *(Isognomon)* cover the roots. Juvenile fishes are common in protected areas where floating *Sargassum* seaweed is often trapped, particularly in spring. *Thalassia* seagrass covers the bottom.

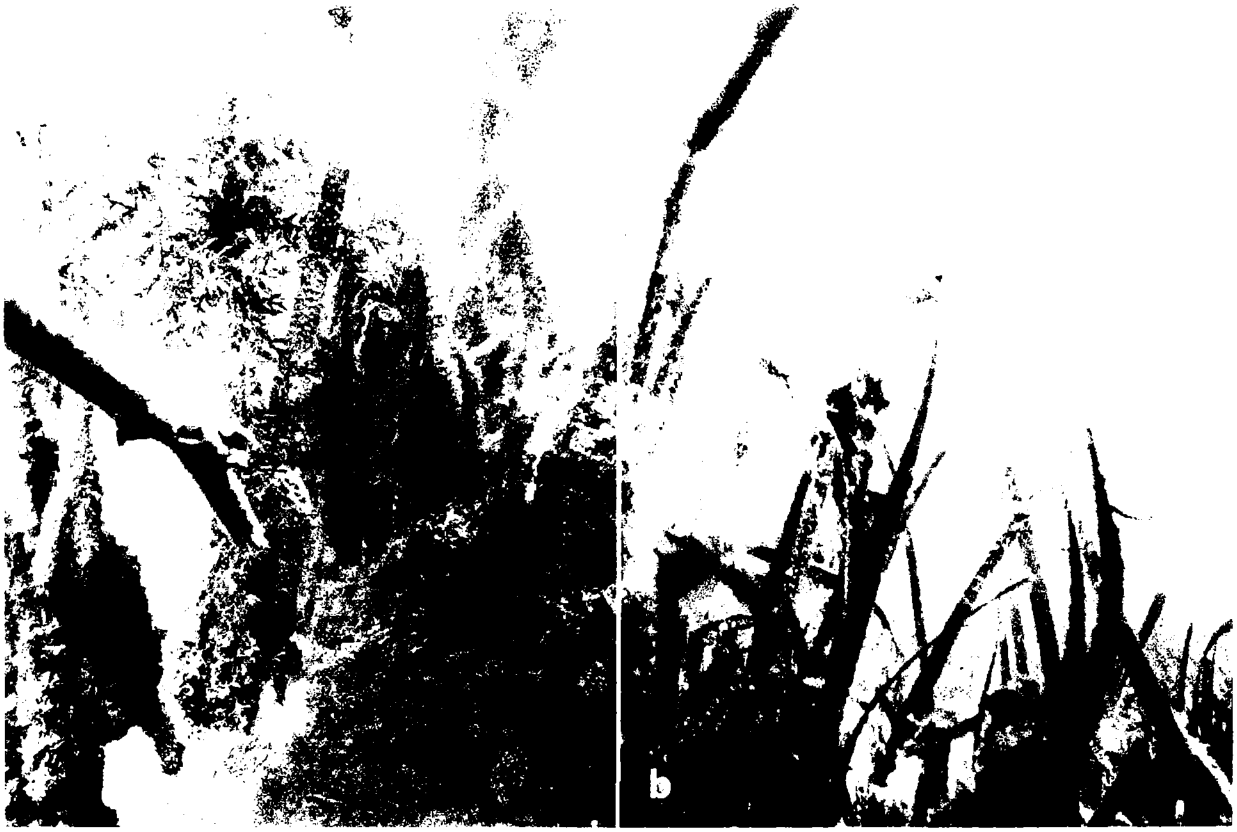

Figure 9. Main Channel West, the Dock: *a,* floating *Sargassum* seaweed entangled among *Rhizophora* roots (photo, M. Carpenter); *b,* tall *Thalassia* seagrass populated by epibionts (photo, L. M-Penland).

Figure 10. View over 'Gator Creek near its entrance into East Pond.

Sta. 8 I, 'Gator Creek (Figs. 1, 10; Plates 3d–f, 4a)

Location and Topography. East Island, starting at the northern flank of the entrance to Lair Channel, and meandering north to East Pond.

Habitats. Rhizophora mangrove roots, peat bank, mud bottom covered by decaying mangrove litter.

Depth. 0.5 m (entrance) 1.5 –3 m.

Environmental Conditions. L: –; C: +. T, S: stressful range, due to tidal drainage of water (heated-hypersaline, or cooled-brackish, depending on the weather) derived from the large, shallow East Pond.

Sediment. Organic mud; patches of *Halimeda* chips.

Communities. The Lair channel bottom slopes up to the creek's entrance where *Thallassia* seagrass becomes dense in 0.5 m depth and interspersed with some algae, mainly *Caulerpa racemosa*. Mollusk and polychaete egg cases crowd the muddy areas. Near the mouth of the creek along the north-shore of Lair Channel, there are clusters of mangrove oyster *(Isognomon)* on the roots, as well as ascidians *Eudistoma olivaceum* and *Didemnum conchyliatum,* the latter a hardy species tolerant of a wide range of environmental extreme (see Goodbody, 2004a) and often found on root tips and at the leaf bases of *Thalassia* seagrass. Algae *(Caulèrpa)* and big sponges grow on the mangrove roots flanking the entrance *(Tedania, Lissodendoryx).*

The channel is rich in cyanobacterial mats and tufts, algae *(Halimeda, Caulerpa),* sponges, hydroids, anemones *(Aiptasia tagetes, Condylactis gigantea),* and juvenile fishes hiding among the epibionts. Common sponges on mangrove roots and peat bank include *Lissodendoryx, Biemna, Tedania, Tethya* cf. *actinia, Cinachyrella apion* (mainly on peat walls), *Dysidea etheria, Dysidea* sp. (a large, undescribed bluish gray form also found in Hidden Creek), *Haliclona implexiformis, H. curacaoensis, H. manglaris, H. twincayensis, H. tubifera, H. magnifica* (on peat walls), and *Chalinula molitba.* Sponges are also found loose among the mangrove litter of the channel floor *(Lissodendoryx, Biemna),* together with low-growing algae *(Avrainvillea),* or buried in organic sediment flock (*H. magnifica).* Bryozoans *(Zoobotryon verticillatum, Amathia vidovici)* and small colonies of ascidians *(Eudistoma olivaceum)* are co-occurring with sponges on roots and along the peat wall lining the creek. A conspicuous population of a telestinid gorgonian with brilliant white polyps *(Carijoa riisei),* and two color morphs of *Tedanis ignis* (red-orange and orange-red) with opposite color-morph *Parazoanthus swiftii* (orange-red and red orange) covering their surfaces were observed near the outer one-third distance into the creek in 1984. Four years later (1988), these organisms had disappeared, except for a few small colonies of the telestid, which reappeared in larger numbers by 1992 but were not noted during a survey in 2004. The *Tedania-Parazoanthus* population was never seen again since the original observation.

Sta. 9 I Grouper Gardens (Figs. 1, 11; Plate 4)

Location and Topography. A cluster of at least six interconnected ponds just south of the Lair Channel, which can be entered through a north-south-directed creek located 100 m to the east of the Main Channel. The Lair channel bottom outside Grouper Gardens is 2 m deep and sparsely covered by turtle grass. It slopes up to 0.5 m toward the

Figure 11. Grouper Gardens, underwater view along a connecting channel between two ponds, with free-hanging, heavily colonized mangrove roots.

creek where *Thalassia* becomes tall and dense. There are patches of *Halimeda* sand and healthy populations of this alga crowd the nearby *Rhizophora* roots. The creek at its entrance is relatively deep (3 m), but quickly shallows where it connects to the first pond (0.5 m). Most ponds and passages between them are 0.3 m or less deep and difficult to explore by swimming.

Habitats. Vertical peat walls and overreaching hanging stilt roots, soft muddy bottom with seagrass and, particularly in the remote ponds, thick stands of seaweed *(Avrainvillea).*

Depth. 0.1–3 m.

Environmental Conditions. L: +; C: ±.

Sediment. Fine sand with *Halimeda* chips; peat and detritic mud cover the bottoms of ponds and connecting canals.

Communities. The mangrove roots outside the entrance to Grouper Gardens are covered mainly by *Halimeda opuntia triloba.* Just inside, the roots and peat walls are overgrown by sponges *(Tedania, Lissodendoryx, Haliclona implexiformis, H. tubifera, Spongia tubulifera, Calyx podatypa, Geodia papyracea),* more *Halimeda* algae, algal turfs (including intertidal bostrychietum), hydroids, anemones *(Bartholomea annulata, Condylactis gigantea, Aiptasia tagetes),* and a few colonies of the ascidian *Eudistoma olivaceum.* Extensive reddish veils covering epibions and streamer-like strands (up to 2 m long) formed by cyanobacteria *(Lyngbya* spp.) were noted during the month of August (2004).The astrophorid sponge *Geodia papyracea* there has periodically been overcome by stress-related disease involving its own cyanobacterial symbionts (Rützler, 1988). The bottom is covered by stands of turtle grass, *Thalassia,* and patches of *Halimeda* and other algae. The encrusting orange ascidian *Didemnum conchyliatum* is common and often attached to seagrass blades. Short, 1 m deep tidal channels connect the ponds, which average 0.5 m in depth. Mangrove roots in the current flow here support clusters of mangrove oysters *(Isognomon),* a diverse population of sponges *(Spongia tubulifera,* *Haliclona curacaoensis, H. manglaris, Biemna caribaea, Dysidea etheria, Clathrina* cf. *coriacea),* hydroids, and algae *(Caulerpa verticillata).* The bottom of the shallow ponds consists mostly by stands of tall green algae *(Avrainvillea longicaulis* f. *laxa)* and supports populations of *Cassiopea* jellyfish and *Tridachia* nudibranchs. Some sponges *(Haliclona spp., Lissodendoryx)* that for some reason had lost their solid root substrate are surviving despite being buried in deep detritus.

Sta. 9 J, Lair Channel (Figs. 1, 12; Plates 4a, 5a–c)

Location and Topography. Second-largest channel (after the Main Channel, from where it originates) cutting west–east into East Island and blind-ending in a pond, known as The Lair. The channel is about 260 m long, widest at its mouth (56 m), and gradually narrows to 14 m (neck of the Lair channel), where it makes a sharp turn to the south and, after 40 m more, opens into a terminal pond, The Lair. Along the flanks of the Lair's neck are extensive peat-bank undercuts, dark cave-like features suggesting that the Lair was once connected to the open lagoon and that water run more briskly through the channel than now, eroding its banks. The undercuts occur along both the west and east banks of the Lair Channel neck, undercutting the root-peat bank horizontally to 0.5–3. Along the western shore the caves are deepest where the Lair neck first turns south, at the east bank they are best developed near the entrance point into The Lair proper, further supporting the idea that they were washed out by current rather than other mechanisms of erosion. Cave ceiling clearance at the entrance of undercuts is 0.4–1.4 m, tapering to 0.3–0.8 m near the rear peat wall.

Habitats. Fringe of hanging *Rhizophora* roots, particularly along the south (west) shore, muddy bottom with sparse seagrass and macrophytes restricted to shallow (<1m) areas and patches of coarse *Halimeda*-chip sand. *Rhizophora*-root reinforced peat undercuts and caves with sediment-free walls and ceiling and detritus-rich, pudding-like mud bottom. The center channel bottom is bare mud with *Cassiopaea* jellyfish, no seagrass.

Depth. 0.8–1.9 m (fringe); to 2–3 m (channel bottom).

Environmental Conditions. L: + to –; C: ± to –. T, S: stressful range, due to tidal drainage of water from surrounding shallow ponds and flats. Particularly affected are sessile communities (algae, sponges, ascidians) on shallow, bank-side roots because water flowing from the flats may differ by several degrees temperature and per-mille salinity from the channel ambient conditions (total range measured, 27°–36° C and 30–34‰ , in May 1985, February and April 1990, and April 1991).

Sediment. Calcareous and detrital mud stabilized by mucuous components; patches of fine sand and *Halimeda* chips. Suspended fine sediments, mainly detritus, were observed to flow out of the creek at ebb tide (February, 1988).

Communities. Thick sponge clusters on roots at both sides of the channel *(Lissodendoryx, Tedania, Spongia tubulifera, Hyrtios proteus, Amorphinopsis* sp., *Biemna caribea, Haliclona curacaoensis, H. manglaris, H. implexiformis, Mycale* spp.). Also, bunches of green algae *(Halimeda, Caulerpa)* and alga-like soft bryozoans *(Zoobotryon),* and ascidians *(Perophora bermudensis)* grow hanging into the water flow.

The light-exposed peat banks are covered by algae *(Halimeda, Caulerpa, Anodyamene),* sponges *(Lissodendoryx, Amorphinopsis, Biemna, Spongia obtusa),* cyanobacterial webs *(Lyngbya),* and anemones *(Aiptasia, Bartholomea).* Colorful small to medium-large sponge crusts or cushions populate the dark cave- or overhang-ceilings of the Lair Channel neck where there is no competition from algae (yolk yellow *Biemna* and *Amorphinopsis*, red *Tedania,* greenish *Haliclona manglaris,* pink *H. implexiformis,* sulfur-yellow *Clathrina),* along with the white calcareous tubes of serpulid polychaetes, patches of the soft filmy cream-colored ascidian *Diplosoma,* and bright-white accumulations of bacteria, *Beggiatoa.*

Here and there, the mud bottom is covered by cyanobacterial mats (see Joye & Lee, 2004) but otherwise is bare except for jellyfish *(Cassiopea),* mollusk egg cases, and a few protruding sponge fistules (for instance *Lissodendoryx);* these sponges seem to have fallen off stilt roots that decayed after death of the tree or from borer's action (Kohlmeyer et al., 1995) and survive on and in the mud substratum. Turtle grass occurs only in small patches the shallow fringe areas and is often populated by anemones *(Aiptasia).*

Near drainage points of interior swamp water into the Lair Channel, large clusters of mangrove oyster, *Isognomon*, appear as well as dense populations of the ascidians *Perophora* spp., suggesting that nutrient-rich water and particulate matter become available; swarms of the mysid *Mysidium columbiae* are also seen concentrated near these drainage locations. Another ascidian common in this community is *Distaplia corolla,* which settles preferentially on the shaded side of free-hanging roots but was all but eliminated (at least to a depth of 0.3 m below low-tide level) during a massive mortality event in early 1986, possibly by unusually warm, hyposaline water draining off the swamp, or by exposure at a very low tide.

Extensive microbial mats harboring a rich community of dinoflagellates, protozoans, and small invertebrates develop in protected (calm-water) locations and may become dislodged by the buoyancy of photosynthetic oxygen bubbles and float to the surface ("floating muck") until oxygen is consumed or dissipated and causes the mat to sink back to the bottom (Faust and Gulledge, 1996). Dense growth of *Thalassia* seagrass covers the light exposed parts of the channel bottom west of the Lair neck. The turtle grass blades are extensively colonized by different color morphs of the ascidian *Diplosoma glandulosum.*

Sta. 9 K, The Lair (Figs. 1, 13; Plate 4a)

Location and Topography. This terminal pond of Lair Channel is elongate and oriented parallel to the channel, but perpendicular to the orientation of the neck that make a sharp bend to the south before entering. It is 100 m long, 12 m wide at its west end, 45 m at its east end.

Habitats. Rhizophora mangrove roots along the margins. Soft, flocculent detritus bottom.

Figure 12 (opposite). Lair Channel: *a,* view along the channel from one of its taller surrounding trees; *b,* cave-like peat undercut at the western flank of the channel's neck; *c,* seagrass along the shallow fringe populated by sea anemones *(Aiptasia); d,* algae-like bryozoans *(Zoobotryon)* on roots; *e,* detached sponges *(Lissodendoryx)* surviving partially buried in the detrital bottom of decomposed mangrove litter; a sediment-covered spherical sponge *(Cinachyrella)* is attached to the peat bank to the right.

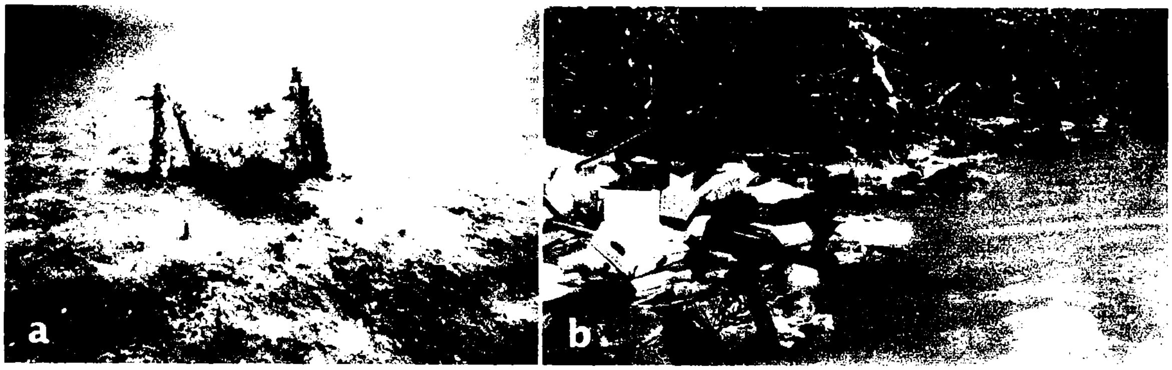

Figure 13. The Lair: *a,* detritus bottom in 2 m depth; the structure in the center is a square experimental frame with settlement plates that became partly buried after one year of exposure; *b,* garbage dumped in May 1990 (photo, M. Carpenter).

Depth. 2 m, at center.

Environmental Conditions. L: + to ±; C: –. T, S: stressful range (see Lair Channel, above). A series of measurements during high and low tide (September 2003) were in the range of 30.5°–33° C temperature and 35.7–36.7‰. Nutrient levels measured in subtidal sites (0.5 m) are highest in the Lair, lowest in the Main Channel stations and locations in direct water exchange with the channel (Sponge Haven North, Sponge Haven South, Hidden Creek entrance). Comparative values (high: low, in January 2003, were: 1.2: 0.2 μMol/l phosphate; 5.5: 1.4 μMol/l ammonium; 0.4: 0.1 μMol/l nitrite, and 1.3: 0.4 μMol/l nitrate. Garbage dumping prevented research for a number of years but was recently discontinued.

Sediment: fine detritus, mainly from decomposed plant material.

Communities. Not as rich as root communities observed elsewhere. Mangrove oysters (*Isognomon)* are common, as well as members of the ascidian family Perophoridae (see Goodbody, 2004a). A few sponges *(Mycale microsigmatosa, Haliclona tubifera)* and anemones (*Aiptasia)*. Algae *(Halimeda, Caulerpa)* and 5 to 8 cm mucuous balls (polychae egg cases) populate the bottom. Cyanobacterial mats are abundant (see 9 J above).

Sta. 10 G, Twin Bays (Figs. 1, 14; Plate 5d)

Location and Topography. A shallow double bay just west of the southern tip of West Island. The outer bay (80 m long x 90 m wide) has a 60 m wide mouth that opens toward the southwest into the main lagoon, to the left (north of the Main Channel entrance. The triangular inner bay (60 x 20 m) is connected by a 10 m wide passage. Regrettably, by 1989 garbage dumping had made Twin Bays unsuitable for research and was excluded as a research site pending future developments.

Habitats. A low (0.5 m) peat bank along the inner margin of the bays with overhanging red-mangrove roots that do not quite touch the bottom. Sandy bottom covered with sparse *Thalassia* seagrass, denser seagrass at the entrance.

Depth. 0.2–1 m.

Environmental Conditions. L: +; C: ± (protected form prevailing north-east winds).

Figure 14. Twin Bays are the first to the left (west) off the Main Channel entrance, viewed from the south (photo, M. Carpenter).

Sediment. Fine calcareous sand and mud.

Communities. Few sponges on the roots, some overgrown by a large population of an ascidian with two color morphs, *Distaplia corolla* (see Goodbody, 2004a). This species was (in 1984) particularly abundant at the western margin of the bank, close to the entrance to the inner bay. Other ascidians are the orange encrusting *Didemnum conchyliatum,* which is widespread and highly tolerant to environmental stress and often overgrows the root tips of mangrove, and the solitary *Phallusia nigra* and *Microcosmus exasperatus,* both characteristic of mildly eutrophic conditions (Goodbody, 2004b). On the bottom of the inner bay margin, specimens of the scyphozoan jellyfish *Cassiopea frondosa* and coral *Manicina areolata* were common.

Sta. 10 H, Sponge Haven (Figs. 1, 15; Plate 5e)

Location and Topography. Shallow, open bay near the southeast tip of West Island, facing the Main Channel. The opening is 65 m, directed eastward, recess is 25 m from the West Island shoreline, at that location. The shoreline is made up of a low (0.2–0.5 m) peat bank with numerous free-hanging and anchored roots in front; this feature extends around the point south of the bay, where the peat bank is even more eroded and recessed and roots hang free and clear of sediments. In the back of the bay there are accumulations of fine-sediment close in and under the roots; along the entrance

Figure 15. Sponge Haven South, fringe seen from the Main Channel looking south toward the channel entrance.

there is a shallow longitudinal bank supporting tall seagrass. The northern flank of Sponge Haven ("Sponge Haven North," see Diaz et al., 2004) is also exposed to fine sediment and to accumulations of detached seagrass leaves, floating cyanobacterial mats, and other debris. The coastline of the southern point ("Sponge Haven South," facing the Main Channel Entrance) has clean lagoon water prevailing along the fringe.

Habitats. Hanging and anchored *Rhizophora* roots, peat bank with some undercuts; sandy and seagrass-covered bottom.

Depth. 0.5–1 m.

Environmental Conditions. L: + to ±; C: + (clockwise water circulation, counter the predominant north-south flow in the Main Channel). Measurements taken during high and low tide (September 2003) ranged from 30.4° to 32.1° C in temperature and 35.2 to 35.6‰ salinity.

Sediment. Fine calcareous sand and mud.

Communities. Highly diverse sponge fauna on roots, particularly along Sponge Haven South, including the very common *Geodia papyracea, Clathria venosa, Tedania ignis, Halichondria magniconulosa, H. manglaris, H. mucifibrosa, Calyx podatypa, Hyrtios proteus, Spongia tubifera,* and a few specimens of large *Ircinia strobilina.* Specimens of the sea urchin *Echinometra lucunter* abound along the bank. Many roots are covered by anemones *(Aiptasia)* and mangrove oysters *(Isognomon)* and, in clear water without much sediment loading, by *Halimeda* sp. Algae, the coral *Porites,* sabellid worms, and the ascidians *Diplosoma listerianum* and *Distaplia corolla.* The orange *Scopalina ruetzleri* encrusts large areas of the peat bank and undercuts. Red and green fleshy algae are common on hanging roots along with clumps of cyanobacteria *(Lyngbya* spp.). Extended patches of long-leaved *Thalassia* seagrass with a rich epifauna (hydroids, didemnids, stinging anemone *Bunodeopsis antillensis)* border the fringe and extend into the Main Channel; burrowing alpheid crustaceans abound in sand.

Sta. 10 I, Main Channel Southeast (Figs. 1, 16)

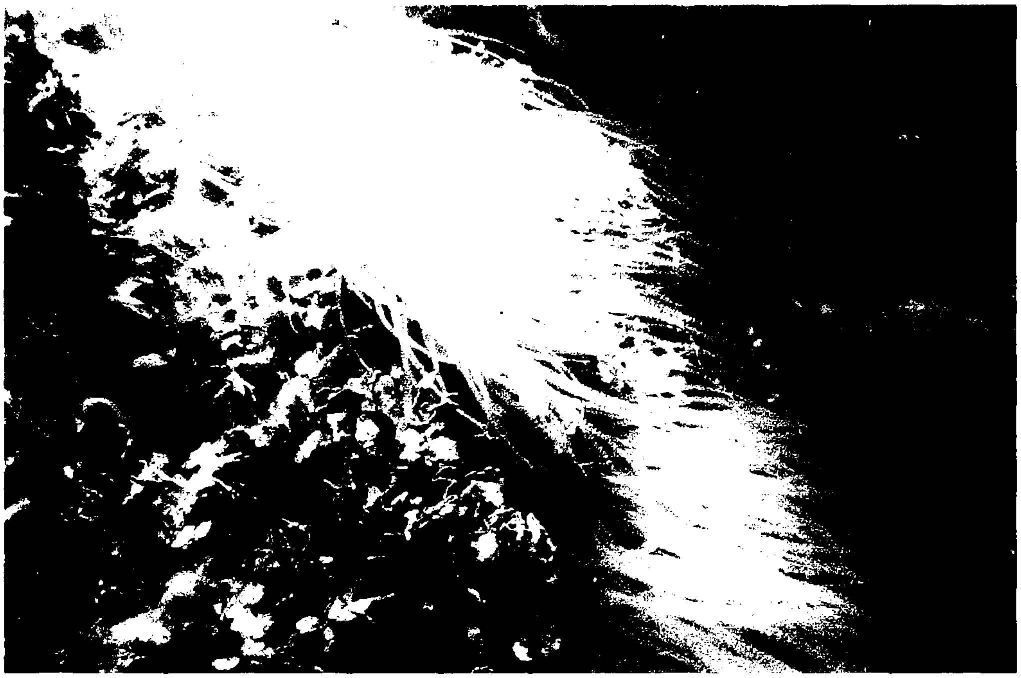

Figure 16. Main Channel Southeast, characteristic community of *Halimeda* algae with sea anemone *Batholomea.*

Location and Topography. West coast of East Island, facing the Main Channel, across from Sponge Haven. It is a gently curved, shallow fringe with low but steep and eroded peat bank that is pitted and exposes old *Rhizophora* roots.

Habitats. Peat bank, some mangrove stilt roots in shallow water, sand banks with *Thalassia* seagrass.

Depth. 0.2–0.5 m.

Environmental Conditions. L: +; C: +. A surface layer of brown swamp-water runoff was noted in places.

Sediment. Fine calcareous sand.

Communities. Halimeda occurs in dense patches on the peat, along with a few sponges *(Mycale microsigmatosa, Haliclona tubifera)* and sea urchins *(Diadema antillarum).* Shallow *Rhizophora* roots are covered by the bostrychietum algal community and other algae, anemones *(Condylactis, Bartholomea),* coral *(Diploria strigosa),* and sporadic ascidians *(Microcosmus exasperatus).* Extended beds of *Thalassia* with long and dense grass blades are populated by juvenile fishes and in places disturbed, indicating that manatees had grazed there.

Sta. 11 G, Main Channel Entrance (Figs. 1, 14, 17; Plate 5f)

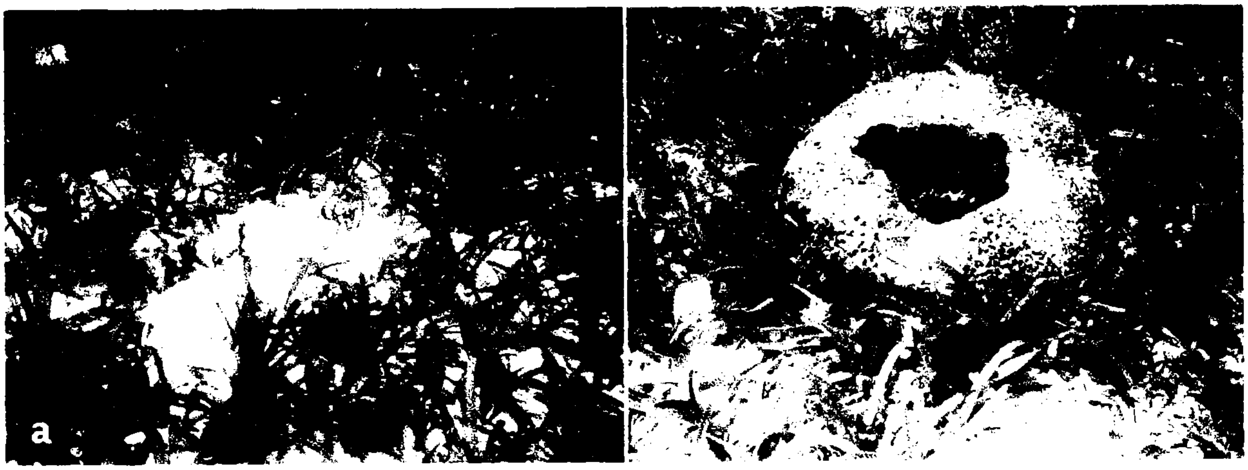

Figure 17. Underwater images of habitats at Main Channel entrance: *a,* turtle grass alternating with sand mounds produced by the burrowing of shrimp *Glypturus; b,* large sponge (60 cm across) among turtle grass, *Spheciospongia,* is the reef-like center of a community of endobiotic invertebrates.

Location and Topography. The funnel-shaped mouth of Main Channel that separates West and East islands and faces west, and some open-lagoon bottom just in front (west) of it. Width of the Channel mouth is about 110 m.

Habitats. Mini-reefs composed of clusters of coral, sponge, algae, and octocoral and large loggerhead sponges *(Spheciospongia vesparium)* with associated epi- and endofauna. Firm sandy bottom with dense stands of *Thalassia* seagrass to the north (West Island), a bare sand apron along the southern shore (East Island).

Depth. 0.5–3 m.

Environmental Conditions. L: +; C: + (open lagoon conditions, but exposure modest because of orientation away from the predominant northeast winds).

Sediment. Medium-grained sand-size fraction (267–426 μm median diameters), with mud-size (<63 μm) fraction 9–21%, organic content 3.9–4.6% (Dworschak and Ott, 1993).

Communities. The mini-patch reefs are formed by coral, *Porites porites* and *P. astreoides* (the latter often adorned by the colorful crowns of sessile polychaetes, *Spirobranchus),* and by sponges *(Spheciospongia vesparium, Tectitethya crypta),* bound together by algae, sponges *(Lissodendoryx colombiensis, Clathria schoenus, A. erina, Hyrtios proteus, Aplysina fulva),* and gorgonians. Associated with these reefs are seagrass *(Thalassia, Halodule),* several algae *(Caulerpa, Halimeda, Rhipocephalus, Udotea),* and anemones *(Condylactis).* Seagrass *(Thalassia, Syringodium)* growing between rubble and conch hides a number of sponges *(Tedania ignis, Amphimedon compressa, Ircinia felix),* sea urchins *(Lytechinus),* and, here and there, specimens of the bivalve *Pinna carnea* and large, erect leathery tubes occupied by the polychaete *Eunice aphroditois.* In sandy areas, small (<10 cm) mounds decorated with pieces of shell indicate the presence of a burrowing shrimp *(Glypturus acanthochirus).* Divers or swimmers in this area are regularly attacked by biting but otherwise harmless isopods, *Rocinela signata.* Along the east bank of the Entrance are shallow, anchored *Rhizophora* roots with *Halimeda* algae.

Sta. 12 I, Hidden Creek (Figs. 1, 18; Plate 6)

Location and Topography. The creek originates from deeply cut but shallow Boston Bay at the southern end of East Island. The mouth of the bay opens into the Main Channel. Hidden Creek starts at the opposite end and meanders first east, then south, and finally turning and running north, enters the large and shallow Hidden Lake. The creek is

Figure 18. Hidden Creek and Lake: *a,* low-altitude aerial view of Hidden Creek looking west; Hidden Lake is to the right, Boston Bay to the back; in the background one can see the Main Channel with Twin Bays (left) and Sponge Haven (right); *b,* detail of the creek; *c,* entrance into the lake.

a constant 3–4 m wide and 2–3 m deep (shallower toward its end), and about 20 m long. Hidden Lake covers an area of over 3 ha and is on average less than 0.5 deep (depth depending on tide).

Habitats. Peat banks and undercuts, hanging *Rhizophora* roots, soft sandy bottom rich in detritus and covered by varying density of seagrass. The bottom of Boston Bay near the Creek's entrance is covered by turtle grass; the seafloor of Hidden Lake consists of soft detritus deposited on firm peat floor.

Depth. 0.5–3 m.

Environmental Conditions. L: + to –; C: + (with each tidal change). T, S: stressful range, due to tidal drainage of water from Hidden Lake that may be hot and hypersaline after a period of exposure to full sun, or cold and brackish after heavy rains. Water drains from nearby Boa Flats (in the south) into Boston Bay and Hidden Creek as well. During the cold season (January, February), the lake can approach the air temperature of a cold night, whereas the deeper lagoon acts as a buffer. Measurements by thermistor recorder just inside the Hidden Creek entrance show a combined maximum temperature range of 18.5°–30° C (January 1990, February 1998) and 28°–37° C (August 1989, 1999). Salinity range at the same location measured by refractometer (April 1993, February 1998, August 1999) ranged from 22 to 38‰ (subsurface), depending on rainfall and direction and timing of tidal current flow.

There were several observations of strong exposure to suspended sediments that may enter through tidal flow from either Hidden Lake or Boston Bay; some of these events may have been caused by boat traffic, a rare but not unusual occurrence.

Sediment. Bottom samples taken at the entrance in 1.3 m depth, and 10 m into the creek (1.9 m) consisted of fine sand (70% less than 2 mm diameter), with larger *Halimeda* chips and shell fragments and a substantial amount (17% dry weight) of detritus (plant material). A similar sample taken near the mangrove fringe in Boston Bay, just outside the creek entrance, revealed mostly decaying plants (detritus) with a small amount (11%) of carbonate chips and shell. Samples included just trace amounts of broken sponge spicules despite the close proximity of large sponge populations.

Communities. Thalassia at the Boston Bay entrance is heavily overgrown by filamentous cyanobacteria *(Lyngbya)*, anemones *(Bunodeopsis)*, bryozoans *(Zoobotryon)*, and ascidians *(Didemnum)*. Algae, a great variety of sponges, sabellid polychaetes, and ophiuroids on the peat banks. Roots dominated by sponges and anemones *(Aiptasia, Bartholomea, Condylactis)*, also *Halimeda* and *Caulerpa* algae, hydroids, ascidians, and clusters of mangrove oyster *(Isognomon)* in the intertidal. Common sponge species on the peat bank are *Cinachyrella apion, Biemna caribea, Scopalina ruetzleri, Hyrtios proteus,* and *Clathrina.* On the roots we find *Spongia tubulosa. S. pertusa, Geodia papyracea,* very large specimens of *Lissodendoryx, Scopalina, Biemna caribea, Mycale magniraphidifera, Tedania, Amorphinopsis* sp., *Halichondria* cf. *magniconulosa, Haliclona implexiformis, H curacaoensis,* and *Dysidea* sp. Clusters of bivalve *(Isognomon)* shells in the lower intertidal zone offer additional substratum to small and encrusting sponges (e.g., *Halisarca*, *Clathrina, Sycon)*, hydroids, and ascidians *(Ecteinascidia minuta, Styela canopus)*. During the early 1980s, the green alga *Halimeda* was nearly as prominent as sponges but the population has since diminished. Some algae *(Udotea, Halimeda, Caulerpa)* are scattered over the bottom and sponges *(Haliclona magnifica)* and sabellid polychaetes are embedded in the soft sediment and attached to the bases of algae in protected side branches and near the entrance into Hidden Lake. Sponges that have fallen from broken or decayed mangrove roots are surviving partially buried in the muddy bottom (for instance, *Lissodendoryx, Haliclona permollis)* and *Udotea* algae were observed supporting small invertebrate settlers (e.g., the ascidian *Botryllus tuberatus).* Polychaete and mollusk egg cases are commonly encountered on the muddy bottom among decayed mangrove litter.

Sta. 13 G, Crescent Bay (Figs. 1, 19)

Figure 19. Aerial photograph of south Twin Cays looking toward the northwest; Crescent Bay (sta. 13G) is behind South Point (occupied by a ranger station of the South Water Cay Marine Reserve); in the center foreground is Southeast Coast (13I).

Location and Topography. A wide (>200 m), gently curved bay located at the southwest end of East Island, just south of the entrance to Main Channel and open toward the west; its southern limit is South Point.

Habitats. Short *Rhizophora* roots along the margin with bostrychietum fuzz but no large invertebrates, anchored in sand. Sandy bottom with seagrass; a large, bare, near-shore sandy patch to the north.

Depth. 0.2–2 m.

Environmental Conditions. L: +; C: + (fully exposed to west and southwest winds); water flow at ebb-tide from the adjacent Boa Flats may affect the organisms living close to the mangrove margin).

Sediment. Fine to medium-grained calcareous sand, rich in *Halimeda* chips.

Communities. Seagrass *Thalassia* and *Halimeda* algae, with solitary coral *(Manicina areolata)* and bivalves (*Pinna carnea, Atrina* sp.). Sandy bottom with traces (mounds) of burrowing shrimps.

Sta. 13 I, East Island, Southeast Coast (Fig. 1, 19)

Location and Topography. South exposed shore (open lagoon)extending east from South Point.

Habitats. Short, stout *Rhizophora* roots anchored in sand along the fringe. Sandy bottom with dense *Thallassia* seagrass and algae *(Halimeda, Penicillus, Rhipocephalus),* very similar to other peripheral sites such as 5 K, 13 G, but not as diverse as the more protected West Bay (7 E).

Depth. 0.2–1.5 m.

Environmental Conditions. L: +; C: + (fully exposed to southerly and south-easterly winds).

Sediment. Fine to medium-sized calcareous sand; coarser *Halimeda* chips.

Communities. Mangrove roots are populated mainly by bostrychietum and some encrusting hydrocoral *(Millepora)* but no large invertebrates. Turtlegrass and *Halimeda* algae, sponge clusters attached to dead shell, particularly *Hyrtios proteus* and *Amphimedon erina*. The only location in the Carrie Bow area where the symbiotic sponge (with filamentous cyanobacteria) *Hyrtios violacea* is common (Rützler, 1990).

DISCUSSION

This account of subtidal localities in the Twin Cays mangrove concentrates on sessile fauna (sponges and ascidians, in particular) because these organisms are excellent indicators of long-term environmental conditions and community health. Algae too are highly diverse in mangroves (Norris & Bucher, 1982; Littler and Littler, 1997; Littler et al., 2004) but occur in different ecological niches and are more tolerant of environmental changes. Algae in fact are powerful competitors for the limited supply of substratum space and seem to flourish during the warmer summer months, overgrowing epifauna on stilt roots.The habitats described represent diverse topographic features that are unique to mangrove islands and are influenced by a wide range of environmental parameters, from near-oceanic quality of outer coasts to the life-restricting conditions of inshore ponds.

Mangroves are forests composed of a diverse collection of salt-tolerant plants, but in the subtidal realm only one species has direct impact on the marine community: the red mangrove *(Rhizophora mangle).* Growth of these trees over thousands of years resulted in an accumulation of peat that is consolidated, eroded, and shaped by various physical and biological processes (Macintyre et al. 1995; McKee and Faulkner, 2000; Macintyre et al., 2004).

Primary Substrata

Availability of solid surfaces distant from sediment bottoms is the key to the existence of most sessile shallow-water invertebrates. In the mangrove, hard substrata are provided mainly by the stilt roots of *Rhizophopra,* many of which hang freely into the water if they are young and where the bottom is too deep to reach, for instance along deep-cut tidal creeks. Second in importance are the vertical surfaces of eroded peat banks lining canals and ranging from 0.2 m to nearly 3 m in height. Peat banks are eroded by past or present water currents that have also created deep undercuts and caves where they were forced to bend. Most of the Main Channel's west coast is lined by peat banks where the water flows fastest. High walls are found along 'Gator Creek (station 8I), Grouper Gardens channel (9I), and Hidden Creek (12I). Cave-like undercuts occur at Batfish Point (5Ha) where currents from the open lagoon are the strongest. Undercut caves also occur at the neck of Lair Channel (9J), where water is quite stagnant but flow conditions may have been different in the past when there was a connection to the open lagoon.

Under good conditions, mangrove adventitious roots grow several centimeters per year and therefore constantly provide new substrata for settlement. On the other hand, roots or entire trees may die, causing substrata to rot and leaving the entire epibiont community to sink into the muddy bottom. Most sessile invertebrates become smothered, but a few sponges (notably species of *Haliclona, Lissodendoryx,* and *Ircinia)* were observed buried in detritus and healthy for at least three years. Some developed fistulose structures, presumably for the increase of surface area to compensate for the restricted water and nutrient flow into the incurrent canal system of the sponge.

Secondary Substrata

Although *Rhizophora* roots and peat are the primary substrata for sessile mangrove organisms, secondary space becomes available as the community develops. One of the organism that provide new substrata are the bivalve *Isognomon alatus,* the mangrove oyster, a species that develops clusters of individuals, often near the water surface at the top of a hanging root. Although adjacent shells may be in close juxtaposition, two species of ascidians regularly make use of the shells as a settlement surface. These are the colony-forming *Ecteinascidia minuta* and the solitary species *Styela canopus* (Goodbody, 2004a). Other colonial ascidians, such as *Diplosoma listerianum* and *Didemnum conchyliatum,* and sponges (for instance, *Biemna caribaea, Haliclona curacaoensis, H. manglaris, H. tubulifera,* and *Clathrina* cf. *coriacea),* are more common on the outside of a bivalve cluster but still penetrate the intershell space. Sponges too provide biological surfaces for secondary settlement space, particularly *Spongia tubulifera,* which is always overgrown by other sponges and by algae, ascidians, hydroids and serpulid polychaetes. Other important members of the benthic community such as turtlegrass *(Thalassia)* and calcareous green algae *(Halimeda)* regularly provide secondary space, particularly for hydroids, *Didemnum,* anemones, such as the small but strongly stinging *Bunodeopsis antilliensis, Aiptasia tagetes,* and foraminiferans (Richardson, 2004).

Tides

One condition that determines the existence and structure of subtidal mangrove epifauna is tidal range. Twin Cays, like most parts of the Caribbean, has a small range (mean 20 cm), thus keeping habitats permanently submerged except for an upper, near-surface transition zone to the intertidal populated by species with some resistance to short-term exposure to dessication (Rützler, 1995). In two recorded El Niño years, tides of 30 cm below mean low during noon hours caused mass mortalities of all organisms in the uppermost subtital zone.

Light

Most organisms in this shallow-water ecosystem are adapted to strong illumination, but in some locations light, or the lack of it, determines the community structure. Photosynthetically active radiation determines most notably the distribution and density of seagrass, *Thalassia,* which is not found on deep channel bottoms with turbid water (for instance, part of Lair Channel, 9J; Lair, 9K). It is also sparse or missing in narrow creeks shaded by overhanging trees and flooded by (brown-colored) water high in tannin content as it returns from the swamp (Gator Creek, 8I; Hidden Creek, 12I) (Calem and Pierce, 1993). Algae and cyanobacteria are more tolerant and successfully compete with sessile animals for free space. Exceptions are peat overhangs and caves, and some recessed peat banks under a dense canopy, where light levels are very low. Sponges flourish under these conditions, without competing algae and (on cave ceilings) free of sediment. Although no unique cryptic species were found, the sponge diversity per area is highest in caves. One cream-colored ascidia *(Diplosoma)* was also found to be a common member of the cave community.

Temperature

Because much of the water in the mangrove occurs in shallow lakes and ponds, it is directly subjected to heating and cooling of the atmosphere. Tidal signature and timing strongly influences the temperature regime. Since the ponds are too shallow and muddy to support large populations of sessile animals, the effect of temperature change is mainly noticeable in the channels where water moves with each tidal cycle and is very hot when the ponds empty after noon hours of full sunshine in summer, very cold following a chilly night in winter. Swamp water also drains sideways into the channels, flowing across the peat banks and noticeable because of its tannin-brown color. The presence of large populations of filter feeders such as sponges and ascidians near the outflow of swamp water indicates high contents in nutrients (dissolved and particulate, mainly as bacterioplankton) overriding the limiting effects of temperature fluctuations. Measurements were taken on numerous occasions but unfortunately, long-term in situ recordings of temperature together with correlated parameters (tide, salinity, rainfall, dissolved organics) are still missing.

Temperature changes in one tidal cycle during winter (January–March) can vary from 18° to 32° C (ocean mean temperature, 26° C); during summer (July–September), they fluctuate from 28° to 41° C (ocean mean, 29° C).

Salinity

Normal seawater in the area has a salinity of 35–36‰. At Twin Cays, the range was measured after heavy overnight rains when ebb tide drained the swamp in the early morning. Samples along the main channel had lower salinity of 21‰ at the surface, 23‰ at 50 cm depth. The same phenomenon has been recorded from the Port Royal, Jamaica, mangroves where it was demonstrated that if the low salinity water goes too deep it causes heavy mortality among sessile communities in which most organisms lack mechanisms for osmotic control (Goodbody 1961).

During some tidal exchanges after heavy rains, freshwater tends to form the top layer although it is colder by several degrees than the denser but warmer seawater. Intertidal and upper subtidal communities are strongly affected by this phenomenon, as reflected by extensive mortality after such conditions occurred repeatedly.

Sediments

Fine calcareous sand and mud, that is, rich in organics, make up the bottom of the Main and Lair channels and support stands of seagrass *(Thalassia, Halodule)* and algae *(Halimeda, Penicillus, Avrainvillea)*, large populations of upside-down jellyfish *(Cassiopea),* and an ubiquitous burrowing crustacean endofauna that forms characteristic mounds, deposits from its tunneling activity (Dworschak and Ott, 1993). Despite the plant cover and consolidation by mucuous substances derived from bacteria, cyanobacterial mats, fecal pellets, and other sources, the sediment is easily disturbed and resuspended by storms, manatee feeding, and boat traffic. The wake of passing boats may also indirectly cause resuspension of sediments by moving thickly populated free-hanging roots with growth tips close to the bottom. Because most mangrove epibionts are filter-feeders with limited capability to clear themselves from sediment cover, these disturbances may result in burial and smothering. Sponges and ascidians are only successful in these mangroves because many of the hard substrata (mangrove roots, peat banks) have vertical orientation, keeping siltation to a minimum. Nevertheless, increased boat traffic through the channels in recent years may have contributed to a decline in populations, particularly of the rich sponge fauna in Sponge Haven (10H; Diaz et al., 2004). Habitats with anchored roots and strong currents are mostly found along the perimeter of Twin Cays (stations 5 K, 7 E, 11 G, 13 G, 13 I).

The bottoms of inshore ponds and creeks are equally soft but primarily made up by flock of fibrous, broken-down plant materials. As already mentioned above, some sponges are able to flourish being buried in this substratum.

Water Flow

Storms resuspend fine sediments but tidal and wind-generated currents help clear exposed substrata and bring nutrient- and bacteria-rich water from the interior of the swamp to the sessile benthos that is either filter or particle feeding. Water flow is most constant in the main channel because prevailing winds push water either from north or south and create conditions close to those of nearby coral reefs. Some narrow and long creeks connecting the outer lagoons to interior ponds ('Gator Creek 8 I; Hidden Creek, 12 I) display the strongest currents within the system (20 cm/sec were measured) but depend on tidal signature and often combine the beneficial factor of strong flow, washing silt away from settlers, with less desirable poor (hot, cold, high or low salinity, tannin-rich) water quality. The wake of passing boats my indirectly cause resuspension of fine sand and mud by moving heavily populated free-hanging roots with growth tips near the bottom, thus affecting the epibionts both by wave action and by sedimentation.

Biotic Factors

Diversity and species composition are influenced not only by abiotic factors but also by differences in ecological interactions and recruitment history. Transplant experiments and new artificial substrata make it possible to highlight these parameters for sponge communities (Wulff, 2004; Ruetzler, in preparation).

Algae and cyanobacteria affect invertebrate epibionts through space competition at settlement as well as in later stages of community development. During the winter months, large quantities of floating *Sargassum* seaweed enter the Main Channel from the north and prevailing winds push them against the western shore of the channel. Wave or boat wash causes the weed to move up and down along the roots in such a manner as to have an abrasive action damaging or destroying elements of the epibiont community, as was demonstrated by newly marked colonies of the ascidian *Diplosoma glandulosum* (July 1984), many of which were lost or damaged by the following February.

A more serious threat to many epibionts, particularly filter-feeding sponges and ascidians, is the seemingly increasing presence of filamentous cyanobacteria, which tend to overgrow roots and everything settling on them. One common kind develops thick, hair-like filaments of tan, brown, to red color and covers substrata as entangled tufts or clumps, or forms strands that hang into the current like streamers, up to 15 cm wide and 2 m long (for instance, in Grouper Gardens, 9I; August 2004). The main species incorporated in these clusters are *Lyngbya polychroa* and *Lyngbya* sp. Dislodged strands may accumulate as thick masses forming bright green floats (bleached from full exposure to sun light) after they drifted into calm-water bays, such as the cove outside Turtle Pond. Another kind is commonly found as rust-red heavy drapes coating roots, sponges and other surfaces on mangrove roots and is composed mainly of *Schizothrix tenerrima* and *Schizothrix* sp. Their filaments are shorter and more fragile than *Lyngbya* and flake off and disperse easily. This phenomenon was already recorded in 1986 (May) when growths of this organism took over the lowest part of roots that were otherwise occupied by the ascidian *Eudistoma olivaceum.* Today, cyanobacterial accumulations seem ubiquitous throughout Twin Cays, at least during the summer months (July–September), and it remains to be investigated whether it is related to the increase of dissolved organic substances in the lagoon water. An ongoing project attempts to determine what environmental parameters (in particular, nutrient levels, temperature, current flow) stimulate growth of cyanobacteria and to what degree sponge and other sessile invertebrates are affected by microbial competitors and pathogens (Diaz et al., 2004). Shifts in community composition of physiologically sensitive epibionts such as sponges may be useful indicators of long-term environmental health.

Pollution caused by human activities and rapidly increasing with economic development has particularly severe consequences in mangroves because as a tidal community they are affected by both terrestrial and aquatic stresses. Live trees make up the framework and principal components of the community and if lost they cannot be replaced in our life time, maybe never once the substratum buildup is washed away. Effects of clear-cutting are discussed in another contribution (Rodriguez and Feller, 2004). Peat and hanging and anchored roots are the principal solid substratum for sessile organisms and hence the pillars of the rest of the marine community, as we have demonstrated after examining the effects of an oil spill in another Caribbean mangrove (Rützler and Sterrer, 1970).

Unfortunately, many people still believe that mangroves are areas of decay and therefore suitable dumping grounds for garbage. This notion has caused severe damage to the Twin Cays mangrove community, not to mention setbacks in ongoing research in places such as Turtle Pond (6H), The Lair (9K), and Twin Cays (10K). Repeatedly over the years, these secluded locations were apparently considered good hiding places and, unlike the more spectacular nearby coral reefs not affected by unsightly appearance, were subjected to excessive release of nutrients from kitchen waste and heavy metals from batteries, or the smothering action of large plastic bags.

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PLATES

Plate 1

Plate 1. Aerial views and habitats of northern Twin Cays: *a,* The archipelago looking southeast toward the barrier reef and some of its cays (left to right, South Water Cay, Carrie Bow Cay, and Curlew Bank; *b,* northern shore and channels; *c,* peat undercut and hanging roots at Batfish Point; *d,* peat wall with sponge; *e,* hanging root covered by fire sponge *(Tedania ignis); f,* gray ascidian, *Diplosoma glandulosum; g,* orange sponge *(Scopalina ruetzleri)* on root.

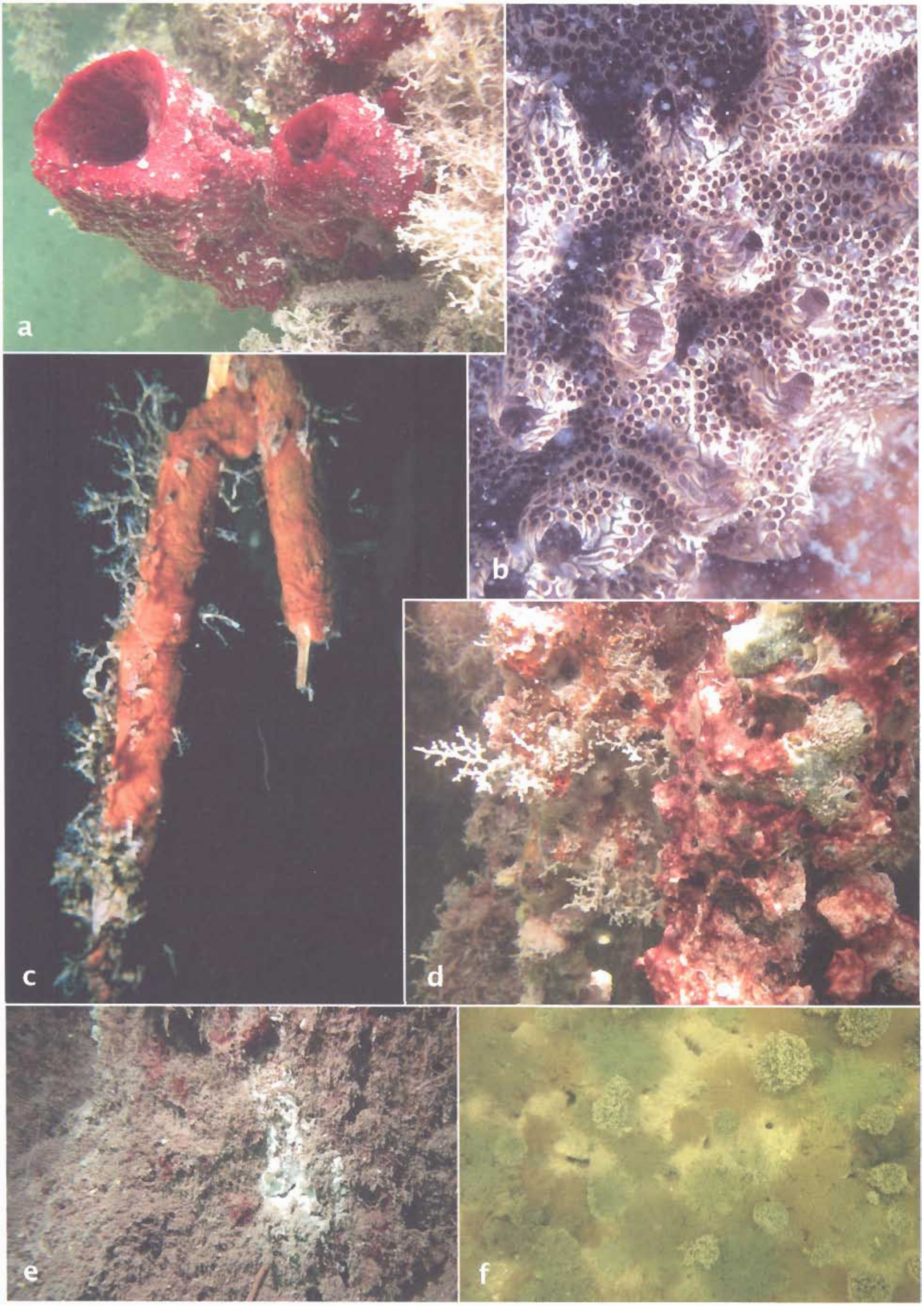

Plate 2

Plate 2. Sessile organisms and habitats of northern Twin Cays: *a, Mycale laxissima,* a sponge typical for the banks of 'Cuda Cut; *b, Botrylloides nigrum,* a common ascidian at Batfish Point; *c,* common encrusting sponge, *Mycale microsigmatosa*; *d,* filamentous cyanobacteria, *Schizothrix* spp., coating many sponges, such as *Lissodendoryx; e,* peat wall in the rear of an undercut showing patch of sulfur-fixing bacteria, *Beggiatoa; f,* vertical view of mud bottom at Cassiopea Cove showing the upside-down jellyfish that gave the cove its name (yellowish-green disks), algae (fluffy green balls), *Penicillus,* and fine sand with openings of tunnels made by burrowing shrimps *(Glypturus, Alpheus).*

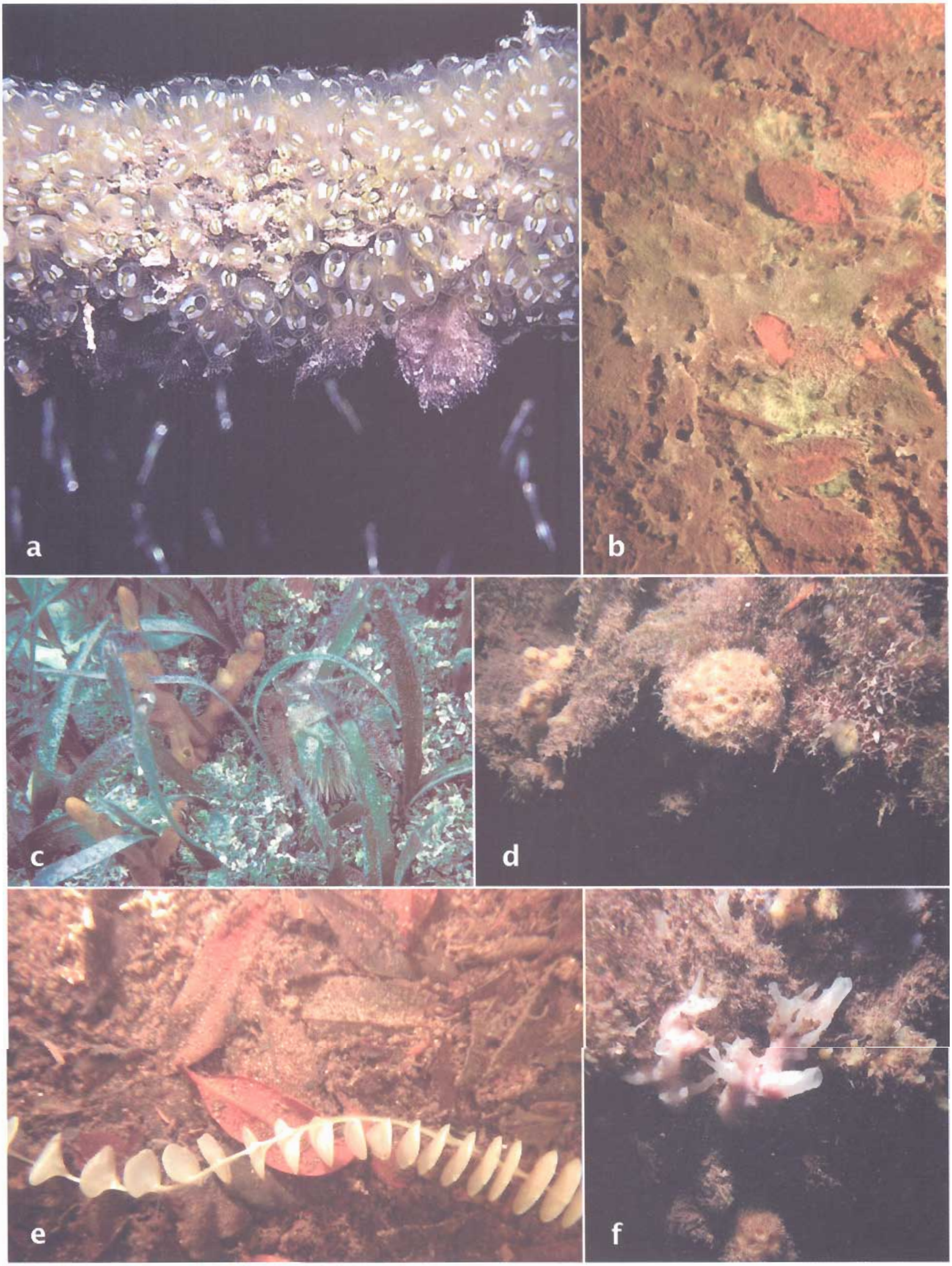

Plate 3

Plate 3. Sessile invertebrates and views of habitats in ponds and bays of northern Twin Cays: *a,* ascidians, *Perophora regina* on a mangrove root at the type locality, Turtle Pond; *b,* typical loose organic-flock bottom in Turtle Pond, with decaying mangrove leaves and covered by a bacterial matt; *c,* West Bay, mini-reef cluster among turtlegrass consisting of green calcareous *Halimeda* algae and sponge *(Clathria schoenus),* visited by a sea urchin *(Lytechinus); d,* 'Gator Creek, the yellow sponge *Cinachyrella apion,* ornamented by porocalices (cups containing pores and oscula) and tiny buds, is typical for the peat wall lining the deep channel; *e,* mollusk egg case on the channel's soft bottom of mangrove litter; *f, Haliclona magnifica,* a sponge with long oscular tubes is common on the peat bank and buried in detritus bottom of 'Gator Creek, its type locality.

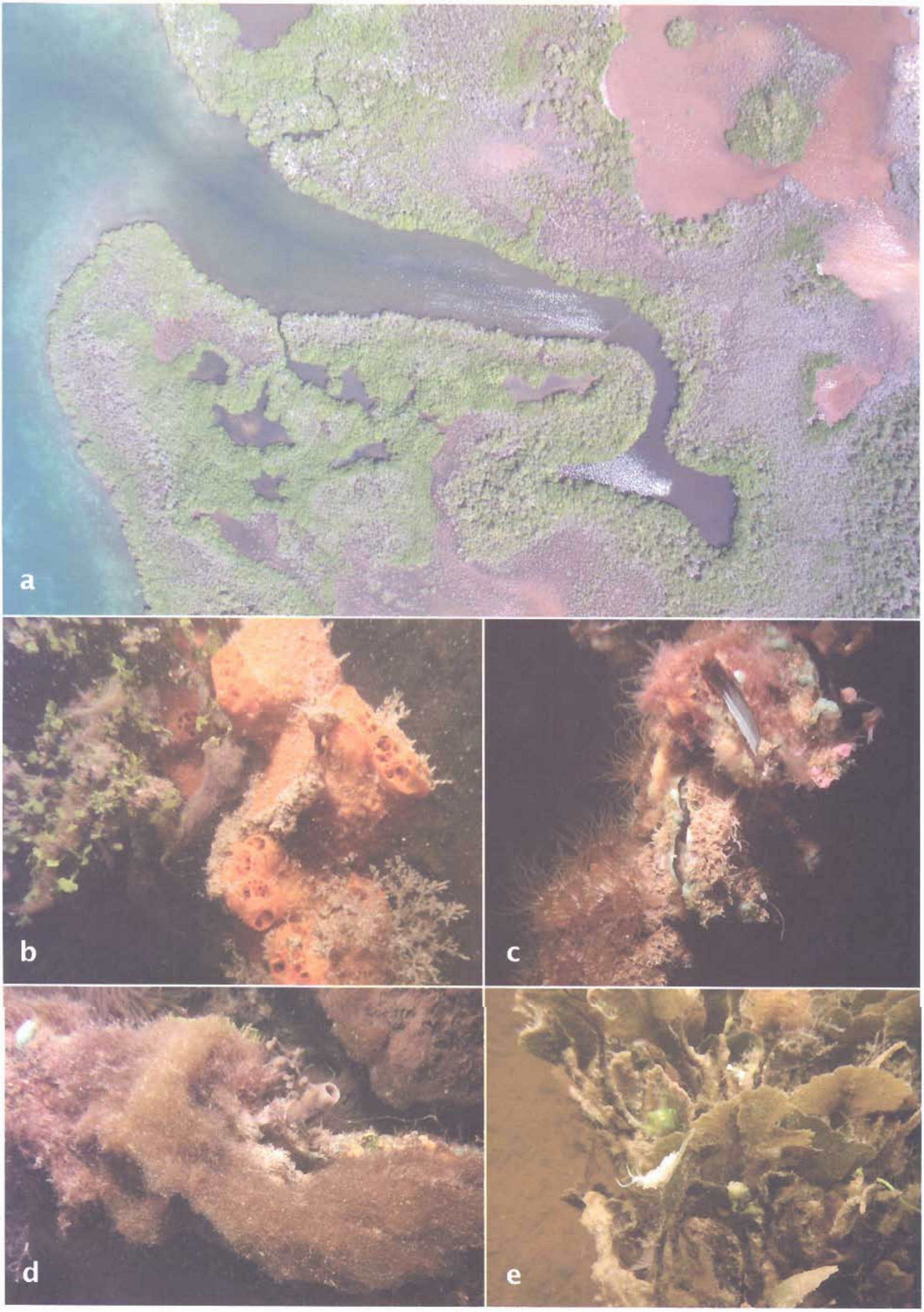

Plate 4

Plate 4. Lair Channel and associated biotopes: *a,* bird's eye view of Lair Channel, leading from the Main Channel eastward (right) through the channel's neck into The Lair; 'Gator Creek branches off at the channel's mouth, toward the north (top left); Grouper Gardens, a cluster of small ponds, is entered through a narrow passage cutting into the opposite (south) bank; *b,* calcified algae, *Halimeda,* and fire sponge, *Tedania* line the entrance to Grouper Gardens; *c,* bunches of mangrove oysters *(Isognomon)* grow on many roots along the canals connecting ponds and serve as a secondary substratum for small sponges, sea anemones, serpulid worms, and ascidians; *d,* in the back of Grouper Gardens entrance sponges, such as this *Calyx podatypa,* may be threatened by thick layers of filamentous cyanobacteria *(Lyngbya),* which develop in masses during the summer months (July to September); *e,* the bottom of Grouper Gardens ponds is overgrown by tall *Avrainvillea* algae which provide shelter for invertebrates, such as this opisthobranch, *Tridachia.*

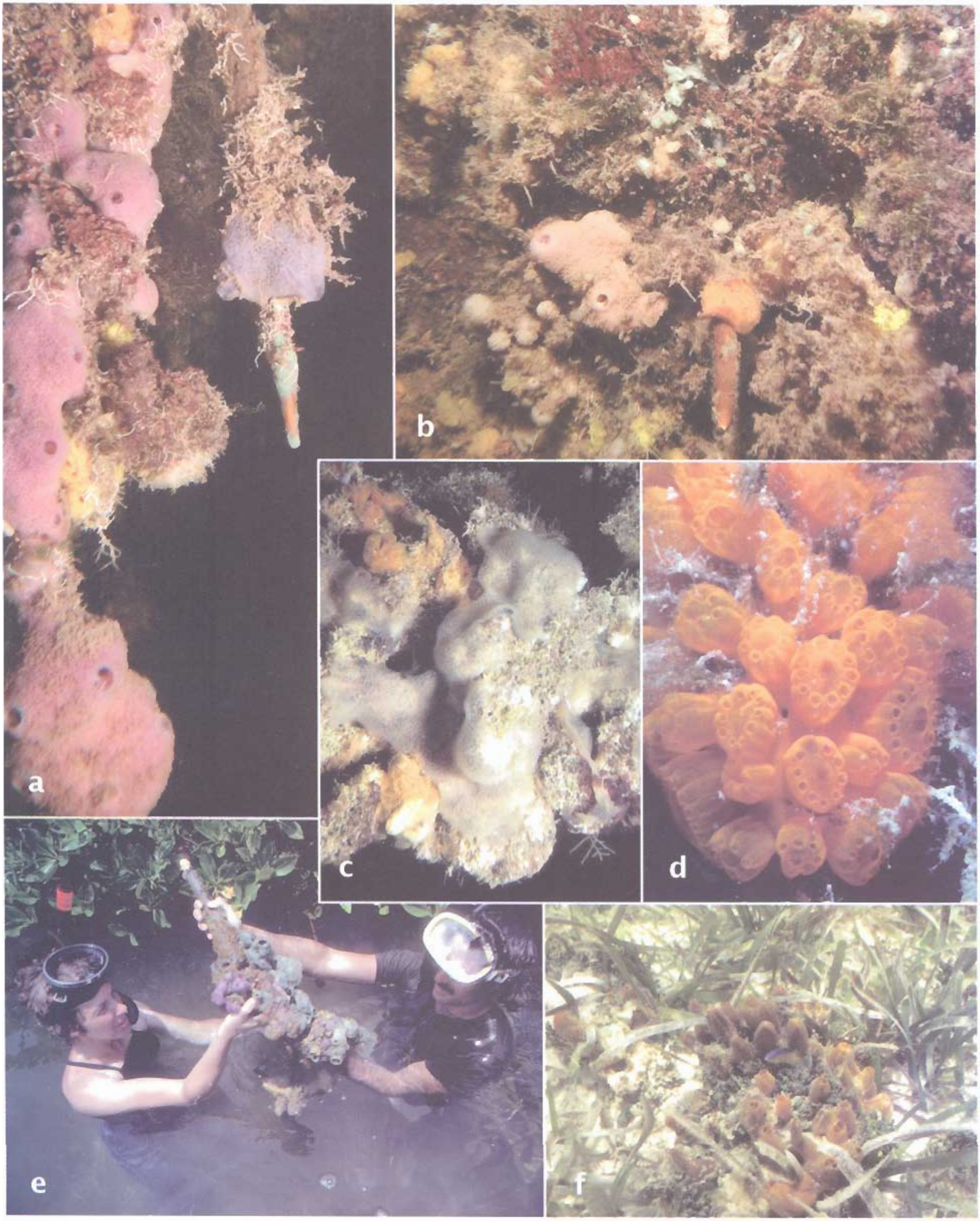

Plate 5

Plate 5. Habitats of south Twin Cays locations: *a,* mangrove root at Lair Channel neck; the older root (right) is covered by the sponges *Haliclona implexiformis* (violet) and *Biemna caribea* (yellow); the sprout is overgrown by *Clathria venosa* (gray) and, on the new tip, turquoise *H. manglaris; b,* dark ceiling of peat cave covered by sponges, with mangrove root sprouting from above; sponges include *H. implexiformis* (pinkish violet), *H. curacaoensis* (light gray), *H. manglaris* (turquoise), *Clathrina* cf. *coriacea* (yellow); c, same habitat as *b* above, soft, cream colored ascidian crust, *Diplosoma* sp.; *d,* ascidian *Distaplia corolla,* a prominent colonizer of mangrove substrata at Twin Bays (sta. 10G); *e,* Sponge Haven fringe (sta. 10H) with researchers displaying a mangrove root heavily populated by sponges; *f,* Main Channel entrance, mini-reef among *Thalassia* seagrass composed of fire sponge *(Tedania ignis)* agglutinating calcified algal *(Halimeda)* thalli.

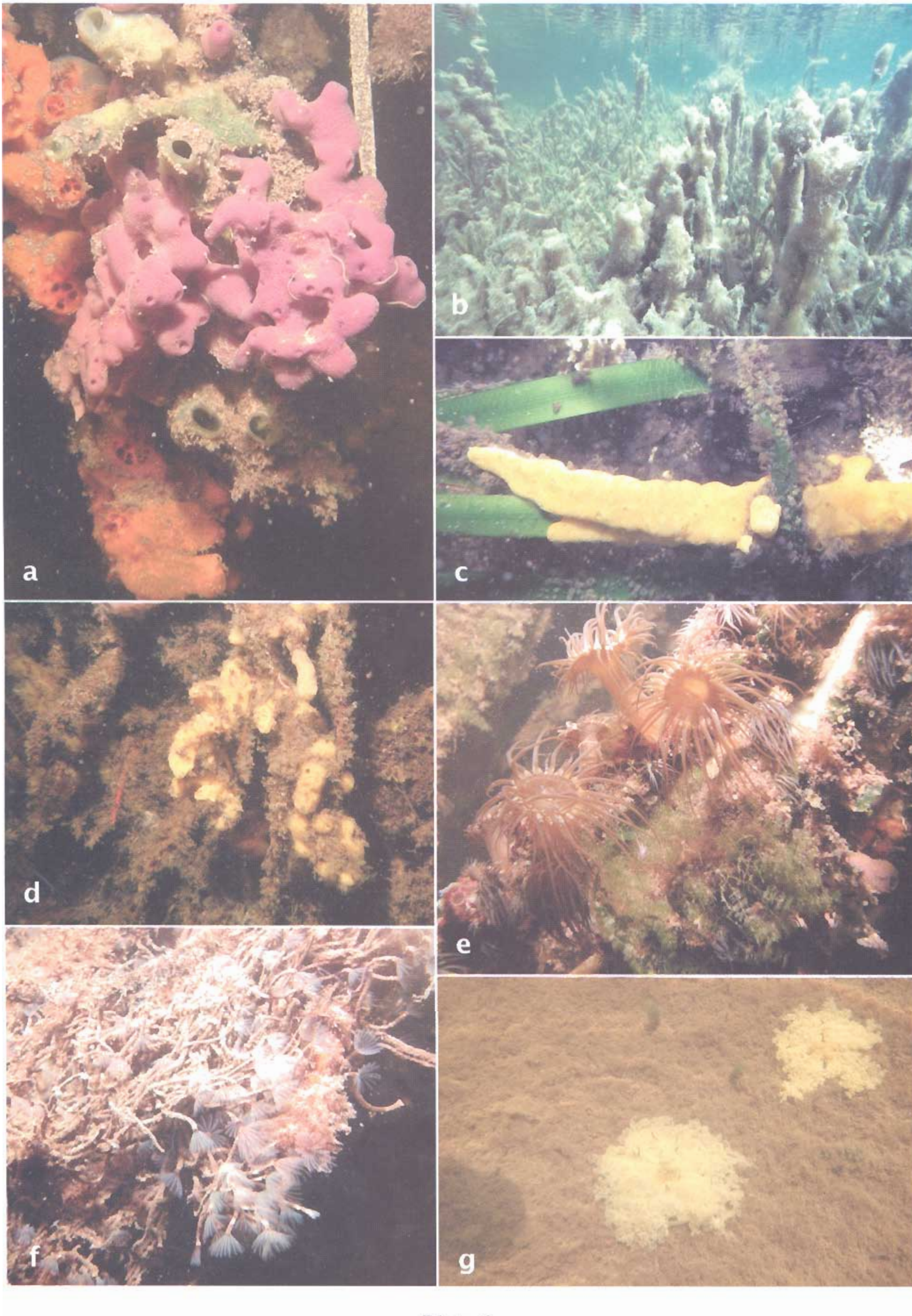

Plate 6

Plate 6. Hidden Creek habitats and common organisms: *a,* mangrove root hanging over peat-bank undercut overgrown by sponges, *Chalinula molitba* (purple), *Lissodendoryx* (greenish gray), and *Tedania* (orange red); *b,* seagrass *Thalassia* at Boston Bay entrance heavily overgrown by filamentous cyanobacteria, *Lyngbya; c,* turtlegrass blades covered by ascidian, *Didemnum conchyliatum; d,* corroded peat bank with partially exposed mangrove roots covered by sponge, *Biemna caribea; e,* anemones, *Aiptasia tagetes* on roots; *f,* unidentified sabellid worms; *g,* Hidden Lake bottom with upside-down jellyfish, *Cassiopea.*