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Proceedings of the Smithsonian Marine Science Symposium

*Edited by
Michael A. Lang,
Ian G. Macintyre, and Klaus Rützler*

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ABSTRACT

Lang, Michael A., Ian G. Macintyre, and Klaus Rützler, editors. Proceedings of the Smithsonian Marine Science Symposium. *Smithsonian Contributions to the Marine Sciences*, number 38, 529 pages, 217 figures, 47 tables, 2009.—The Smithsonian Marine Science Symposium was held on 15–16 November 2007 in Washington, D.C. It represented the first major dissemination of marine research results since the establishment of the Smithsonian Marine Science Network (MSN). The 39 papers in this volume represent a wide range of marine research studies that demonstrate the breadth and diversity of science initiatives supported by the MSN. The first section contains an overview of the MSN along with papers describing the multidisciplinary investigations spanning more than 37 years for the four Smithsonian marine facilities that constitute the Network: the Smithsonian Environmental Research Center at the Chesapeake Bay, Maryland; the National Museum of Natural History's Smithsonian Marine Station at Fort Pierce, Florida; the Caribbean Coral Reef Ecosystems Program, with its Carrie Bow Marine Field Station in Belize; and the Smithsonian Tropical Research Institute in Panama. Subsequent papers represent findings by Smithsonian scholars and their collaborators on overarching topics of marine biodiversity, evolution, and speciation; biogeography, invasive species, and marine conservation; and forces of ecological change in marine systems.

Cover images: (left) *Aurelia aurita* sea jelly with juvenile carangid jacks in its bell, Carrie Bow Cay, Belize; (middle) *Dendronephthya* soft corals and *Anthias* school, The Brothers Islands, Red Sea, Egypt; (right) grey reef shark *Carcharhinus amblyrhynchos*, Kingman Reef, Northern Line Islands (all photos by Michael A. Lang).

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Caribbean Coral Reef Ecosystems: Thirty-Five Years of Smithsonian Marine Science in Belize

Klaus Rützler

ABSTRACT. With foresight and tenacity, Smithsonian Institution marine scientists have devoted more than three decades to understanding and preserving one of the planet's vital natural resources: the coral-reef ecosystem. In the late 1960s marine scientists from the Smithsonian National Museum of Natural History, Washington, founded a long-term Caribbean coral-reef field program, now known as Caribbean Coral Reef Ecosystems (CCRE), to investigate the biodiversity, community structure and dynamics, and environmental processes that control this ecosystem. Its core group of botanists, zoologists, paleobiologists, and geologists found an ideal study site—with high biological diversity, significant geological features, and minimal anthropogenic disturbance—on the barrier reef off Southern Belize, and in 1972 established a field station on one of its tiny islands, Carrie Bow Cay. Within a radius of less than 2 km lie a great variety of richly populated habitats, from mangrove to fore-reef. The Belize mainland and three offshore atolls are within easy reach by small boat. Each year, up to 120 Smithsonian staff and associated scientists, with assisting students and technicians, study the area's reefs, nearby mangroves, and seagrass meadows. Their “whole-organism” expertise encompasses many fields of biology—systematics, evolution, paleobiology, ecology, and ecophysiology—supported by molecular techniques to expand upon traditional morphological taxonomic analyses. An oceanographic-meteorological monitoring station on Carrie Bow Cay records environmental data, now available on the World Wide Web, and monitors the productivity of selected reef, mangrove, and seagrass communities. Field research is complemented by the large resources of the Smithsonian home base. Today, the CCRE program is a member of the Smithsonian's Marine Science Network, which includes coastal laboratories in Panama, Florida, and Maryland. In these and other respects—CCRE now has more than 800 papers in print—the program's accomplishments are indeed impressive.

INTRODUCTION

How does one summarize in a few pages 35 years of research on a complex ecosystem by more than 200 investigators? Clearly, it cannot be done in a complete fashion. With apologies for any omissions, I present this review as a tribute to every single participant in the Caribbean Coral Reef Ecosystems program (CCRE) dating back to the late 1960s, when it was titled Investigations of Marine Shallow-Water Ecosystems (IMSWE). The founders' unifying objective was to apply a multidisciplinary, long-term team approach to studies of marine shallow-water animals and plants, and to examine their interactions in

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their environment—today as well as in the past—for information on the determinants of community structure and evolutionary change. A coral-reef ecosystem, we agreed, is the most extensive and biologically productive shallow-water community on Earth and thus would fully meet our purposes. After conducting literature reviews and several joint surveys throughout the Caribbean, we chose Belize (then British Honduras) as the program's locale because of its pristine environment and high diversity of organisms and reef types.

PROGRAM FOUNDERS AND OBJECTIVES

Coral reefs are among the true wonders of the world: they cover 190 million km² of the world's ocean floors, are tremendously productive, protect tropical continental coasts and islands from the eroding forces of the oceans, supply humans with large quantities of high-quality protein, and are a unique recreational resource. For all their aesthetic and economic value, coral reefs remain invisible to most people unless they live close to tropical coasts or engage in skin or scuba diving. Without such contact, many are insensitive to the catastrophic effects of pollution and uncontrolled land development, which can rapidly decimate entire communities and thus their benefits, or are unaware of the effects of natural phenomena such as global warming and acid rain.

Fortunately, the unique composition of the Smithsonian Institution, with specialists in many disciplines of the life and earth sciences, provided a substantial number of researchers interested in reefs and willing to team up for the common good of an integrated study. Some experts from other institutions were expected to join for specific tasks. Our original team, all staff of the Natural Museum of Natural History (NMNH), consisted of Walter H. Adey, Department of Paleobiology, a specialist in fossil and modern coralline algae; Ian G. Macintyre, Paleobiology, a carbonate sedimentologist studying calcification, reef-building organisms, and reef evolution; Arthur L. Dahl, Botany, an algal ecologist; Mary E. Rice, Invertebrate Zoology, an expert in sipunculan worm systematics and developmental biology; Tom Waller, Paleobiology, a malacologist focusing on the systematics and distribution of scallops in time and space; Arnfried Antonius, a postdoctoral fellow in Invertebrate Zoology working on stony corals; and myself, Invertebrate Zoology, a sponge biologist with an interest in reef ecology and bioerosion. We were joined in our early search for the optimal research site by David R. Stoddart, a geographer at the University of Cambridge, England; Porter M. Kier, an actinopaleontologist (later a director of

the Natural History Museum) looking for modern clues to interpreting fossil echinoderm assemblages; Richard S. (Father Joe) Houbrick, a former priest turned malacologist and working at the Smithsonian Marine Sorting Center; Ernst Kirsteuer, an invertebrate zoologist specializing in nemertine worms at the American Museum of Natural History, New York; and Fred Hotchkiss, a postdoctoral fellow in Invertebrate Zoology specializing in ophiuroid echinoderms. David Stoddart was a particular asset because he had a wealth of research experience with the distribution, geomorphology, terrestrial botany, and dynamics of Belizean islands (cays), having been a member of the 1959 Cambridge Expedition to British Honduras (Carr and Thorpe, 1961) and participant in numerous post-Hurricane Hattie (1961) surveys (Stoddart et al., 1982).

Our main objective was to study the historical and present conditions in a well-developed coral reef far removed from the stressful impacts of an industrial society with a view to compiling baseline data on how an established reef community adjusts to natural environmental parameters. These data would include information on diagenetic alteration of the reef structure, as revealed in drill cores. With the resulting information, we hoped to develop a predictive model of the impact of anthropogenic stress. As we quickly discovered, most previous reef studies consisted of short-term surveys during large-scale expeditions, with superficial sampling during a single season; moreover, many of the reports on reef fauna and flora had been prepared by specialists who had never observed the organisms and processes in the field. A complex ecosystem such as a coral reef obviously required a more rigorous, long-term, and multidisciplinary approach if we had any hope of determining the relative importance of diversity, biomass, energy flow, and environment to community function.

CARRIE BOW CAY, BASE OF A NEW MARINE FIELD STATION

The team chose a Caribbean reef site for several reasons: most of us had already worked in that area, and it would be "close to home," would permit comparison with the already-stressed reefs of Florida, and would minimize travel time and cost. Equally important, to be sure, was the fact that all the characteristic reef types and zones were within workable distance, reef growth was vigorous with a good geological record of past development, and the locale was remote from terrestrial and human influences.

Moving ahead with small grant awards from Smithsonian Institution endowments, we purchased an inflatable boat with an outboard motor, dive tanks, a small compressor, and tents for reconnaissance trips across the Carib-

bean. In another step forward, the U.S. National Science Foundation provided support for a planning meeting on Glovers Reef atoll, Belize, attended by representatives of some 40 academic institutions. We envisioned starting up the program there and eventually conducting comparative studies on an Indo-Pacific atoll. As fate would have it, the proposal emanating from this meeting was not funded.

Returning to Glovers Reef in February 1972 to retrieve our IMSWE equipment from storage, Arnfried Antonius and I discovered a small unoccupied islet with three shuttered buildings on the southern Belize barrier reef. Its name, we learned, was Carrie Bow Cay ($16^{\circ}48'N$, $88^{\circ}05'W$; originally spelled Caye), and it was owned by the family operating the Pelican Beach Motel in Dangriga (Stann Creek District), a small town on the mainland (Figures 1, 2). To our happy surprise, this reef tract met all our scientific requirements, studies there would garner generous cooperation from Belize's Fisheries Department, and excellent local logistical support would be available. The motel, now called Pelican Beach Resort, was owned and operated by Henry Bowman, Jr., and his wife Alice. After negotiating storage for our equipment, we initiated a contract to lease part of Carrie Bow Cay, including the two smaller cottages, for a three-month research period that spring and summer.

Carrie Bow Cay was owned by Henry Junior's father, Henry T. A. Bowman, a third-generation descendant of Scottish settlers. The enterprising Henry senior was a citrus grower, businessman, and one-time legislator who had bought the island from his father as a vacation retreat, changed its name (from Ellen or Bird Caye) to Carrie for his wife, and put up an old farmhouse that he had bought on the mainland and carried out to the cay in sections. With his love of fishing, "Sir Henry" (as I referred to him when we became friends) and some of his relatives (daughter Norma and daughter-in-law Alice, in particular) developed a keen interest in the sea and the reef's myriad animals and plants. This interest persuaded him to allow us unrestricted access to most of his island and provided many opportunities to share our observations over drinks during the sunset hour.

A great concern for both of us then, and for all of CCRE today, was the rate of coastal erosion, mainly the consequence of frequent hurricanes, which had reduced the size of the island from 2 acres (0.8 ha) in the 1940s to a little more than half that in the 1970s. In his delightful autobiography (Bowman, 1979), Henry took the blame himself, admitting that he had carelessly removed mangrove trees "that build and bind these cayes." At the same time, he did make a significant contribution to the island's mor-

phology: in 1942 he built a 27 m long concrete boat dock on the leeward (lagoon) side. It has remained unchanged to this day and has served as a reference in our mapping of the geomorphology and communities nearby.

Since then, both Henrys have passed away, but their naturalist spirit lives on. Therese Rath, who is Junior and Alice's daughter (Sir Henry's granddaughter), runs Pelican Beach with her mother and continues to offer us logistical support on Carrie Bow. Therese's husband, Tony Rath—one of our early volunteer station managers who moved to Dangriga from Minnesota two decades ago—is a successful nature photographer and runs the premier web design business in Belize; he still helps us out as a naturalist adviser and provides documentary photography.

FACILITIES AT START-UP

Between 1972 and 1975, our team operated on a shoestring. The relatively small grants available to us (the Smithsonian has no direct access to National Science Foundation funding) kept the field station open for no more than four months a year and supported up to 25 scientists and assistants per season. Our facilities consisted of a small three-room building with a tin roof to the south of the main house (it contained our lab, living quarters for two, and a kitchen); a 4 m² shed that could house two; and a tent, when needed, that could accommodate up to six. The dive compressor and a small generator were installed in improvised shelters.

Our shower consisted of a spray-head on a pipe screwed into the bottom of a huge wooden vat that collected rainwater running off the roof of the main building. To preserve decency, there was an enclosure (its sign read: "Save Water, Shower with a Friend"). The toilets for all island occupants were two outhouses accessed from a wooden pier extending over the reef flat to the island's east. The cabin's seats were rough-cut planks with holes. However, its window opening allowed a spectacular view of the reef flat, barrier reef, and unobstructed horizon, with pelicans and 1 m long parrotfish jumping and feeding in the foreground.

After getting used to us, Sir Henry turned his children's "museum" in the main house into a station manager's quarters by adding some wood siding for walls and a door. It was a roofed-over corner of the house's wide, upper-level porch, where Norma and Alice had kept and displayed an assortment of shells, corals, quirky driftwood, and stranded and mummified algae, invertebrates, and fishes. Working for a museum ourselves, we found that a quaint step forward.

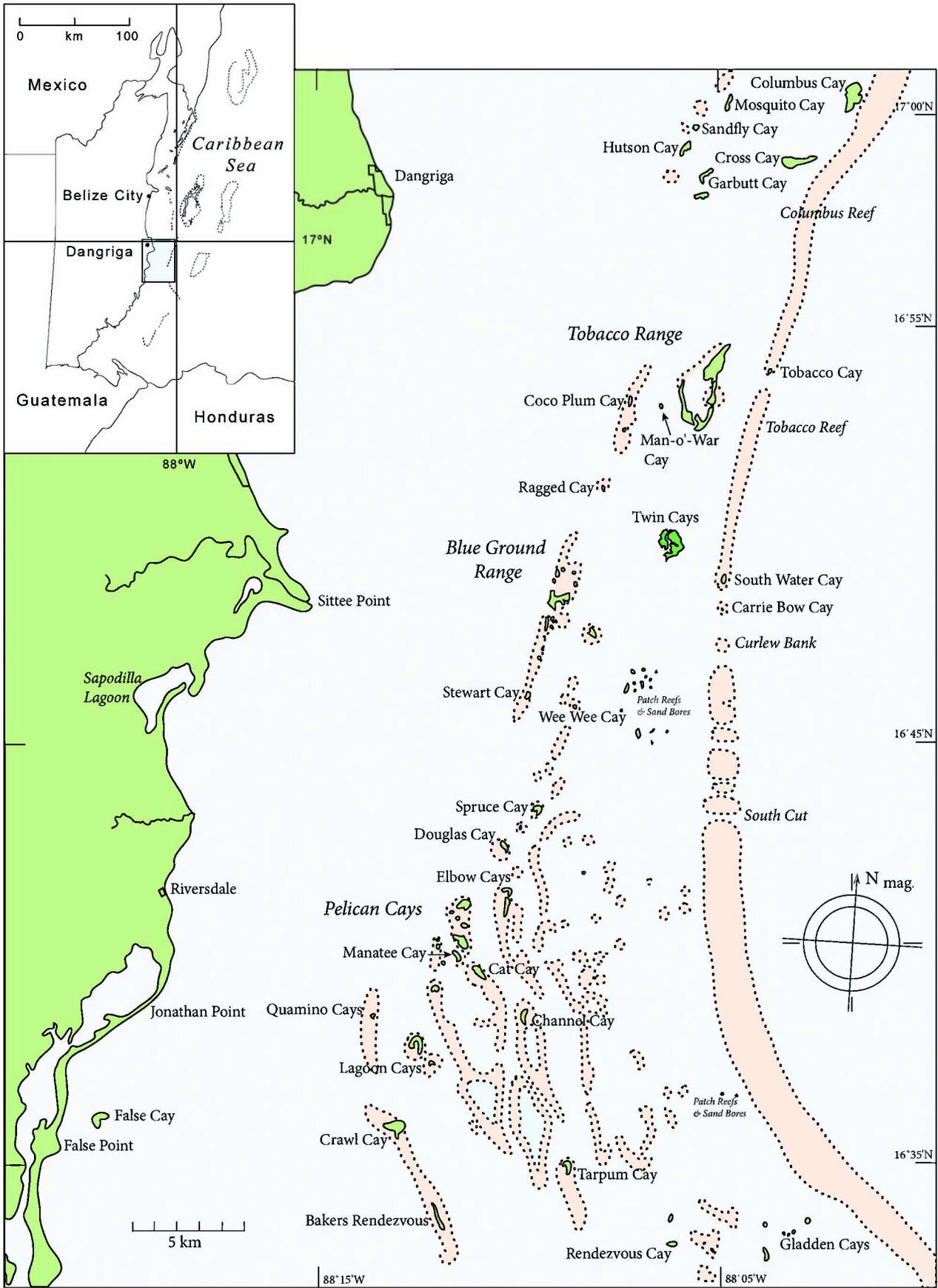


FIGURE 1. Map of research area in coastal Belize, Central America. The barrier reef and other reef tracts appear in pink.



FIGURE 2. The original Investigations of Marine Shallow-Water Ecosystems (IMSWE) survey team, the Belize barrier reef, and Carrie Bow facilities in the early 1970s. Upper left: The team included (left to right) Walter Adey, Arthur Dahl, Tom Waller, Klaus Ruetzler, and Arnfried Antonius (missing from the picture are Porter Kier, Ian Macintyre, and Mary Rice). Upper right: Belize barrier reef looking south, with South Water Cay in foreground and Carrie Bow Cay near center. Center left: Carrie Bow Cay looking southwest, with ocean-side reef flat in foreground. Center right: Carrie Bow facilities looking south, the Bowmans' "Big House" to the right and our lab building in the center. Lower left: Photographer Kjell Sandved working in the aquarium area. Lower right: Scientists in the lab are Anne Cohen (left) and Jim Thomas.

For the “lab,” we removed some of the cottage partitions that originally defined the bedroom space for the parents and three children, built a long bench along the oceanfront wall with a supply cabinet and photo table opposite it, and weatherproofed windows by inserting acrylic panes in the lower half to allow the wooden shutters to remain open under most weather conditions and thus let in more light. The sun gave us light for microscopy and photography, with a couple of small gasoline-driven generators doing the job whenever needed. We brought microscopes, cameras, some portable instruments, labware, and boating and dive gear from home but improvised on most additional laboratory or field needs. Our original IMSWE inflatable boat and 25 horsepower outboard engine were still in working order, supplemented by a similar inflatable recently added. A shortwave radio provided contact with Pelican Beach in Dangriga for ordering supplies, brought out once a week. A local cook prepared our meals and lived in a room under the big house; next to her was the simple residence of a native fisherman who served as caretaker and watchman, particularly when the island was deserted during the off-season. Our station manager was usually one of us, or one of our enthusiastic young museum technicians, or some other volunteer with technical know-how. When the lab was closed, all valuables were stored in high places (in case of storm floods), the windows shuttered, and the door padlocked and nailed to its frame. (“This,” the locals said, “does not keep the crooks out but keeps the honest people honest.”) During hurricane season, all major equipment was taken to Dangriga and stored in the Maya Hut behind Pelican Beach.

ANALYZING A COMPLEX ECOSYSTEM

THE EARLY YEARS

The program’s first targets were to map the reefs and other habitats near the field station, including Carrie Bow Cay itself, and to identify the key organisms in the communities (Figures 3, 4). Because the north–south-oriented barrier reef is the dominant feature separating the lagoon from open ocean, we established a transect perpendicular to its trend, originating well inside the lagoon in a seagrass bed 2 m deep; it then crossed the barrier-reef crest some 150 m north of Carrie Bow and extended due east across the reef and down the fore-reef slope to a depth of 30 m. This transect would become the baseline reference for all our topographic studies and future observations and experiments.

We also tried to develop some standard methods of sampling, extracting interstitial organisms, and determining biomass (Dahl, 1973; Macintyre, 1975; Rützler, 1978a). Because of the complexity of the reef framework (with its three-dimensional structure) and the diversity and size range of its inhabitants (which varied by at least three orders of magnitude), we had to modify many of the commonly used ecological methods to ensure compatible results.

Unable to employ self-contained recording instruments to monitor important environmental parameters, we established a manual routine for taking tide and temperature readings, and for observing solar radiation, wind speed and direction, precipitation, humidity, cloud cover, wave action, and turbidity with simple handheld devices. For specific projects, we measured salinity, oxygen concentration, pH values, water current speed, and submarine daylight with off-the-shelf instruments for which we built waterproof housings when necessary. These data, along with the first reef maps and results from transect surveys, were summarized in our 1975 progress report and distributed to program participants and supporters.

Many colleagues helped identify key organisms and determine biomass and spatial and temporal distribution (Adey and Macintyre, 1973; Kier, 1975; Pawson, 1976). Early on, we discovered unexpectedly high numbers of new species in almost all taxa, which was surprising because the Caribbean Sea is generally considered among the best-studied oceanic regions of the world. Using *in situ* methods, we identified and quantified environmental parameters such as light, water flow, and sediments making up the “microclimate” of particular organisms (Graus and Macintyre, 1976). We also investigated important associations and interactions between organisms, such as symbioses and space competition, predation, diets, and behavioral patterns. In addition, we measured primary production of benthic macroalgae and symbiotic microalgae, and growth and reproduction rates of reef-forming organisms, the first steps toward determining key metabolic processes (Macintyre et al., 1974).

Some geologists and biologists collaborated in the study of geological processes such as the construction and destruction of the coral-reef framework and the calcification rates of corals, coralline algae, and other bioherms. Others studied physical and biological erosion and sediment production rates (Rützler, 1975), sediment sorting and colonization by meiofauna, and processes of recementation. Ian Macintyre initiated a drilling project with colleagues from the U.S. Geological Survey’s Energy Resource Division to learn about the historical development of the

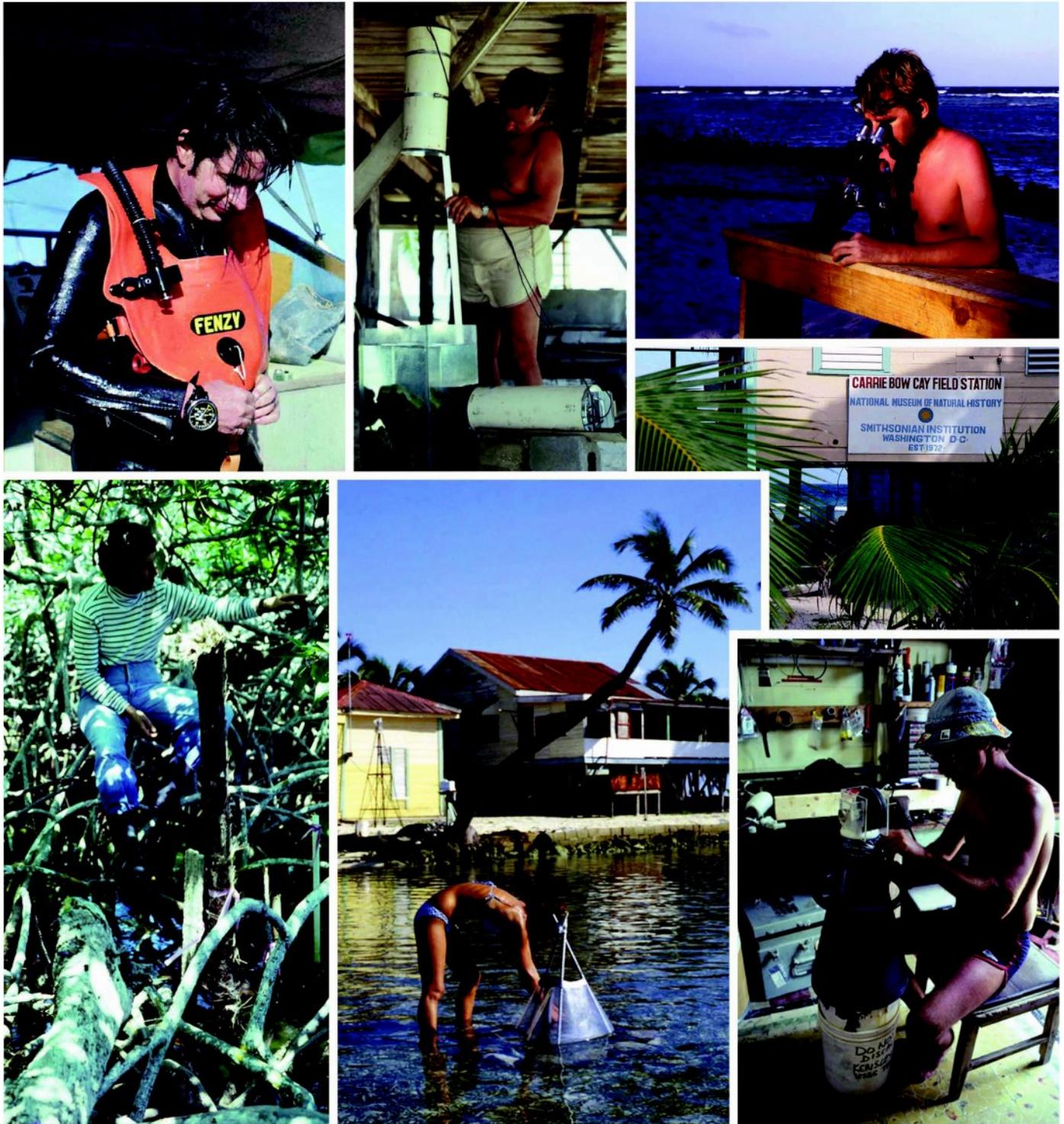


FIGURE 3. Some early program participants. Clockwise, from top left: Ian Macintyre about to enter the submarine Columbus Cay Cave; Arnfried Antonius setting up time-lapse camera for study of black band coral disease; Klaus Ruetzler catching the evening sun for a microscope examination; view of entrance of station; Mike Carpenter fixing an underwater viewer; Joan Ferraris measuring oxygen consumption of benthic community on the Carrie Bow reef flat; and Ilka Feller surveying red-mangrove insects at Twin Cays.

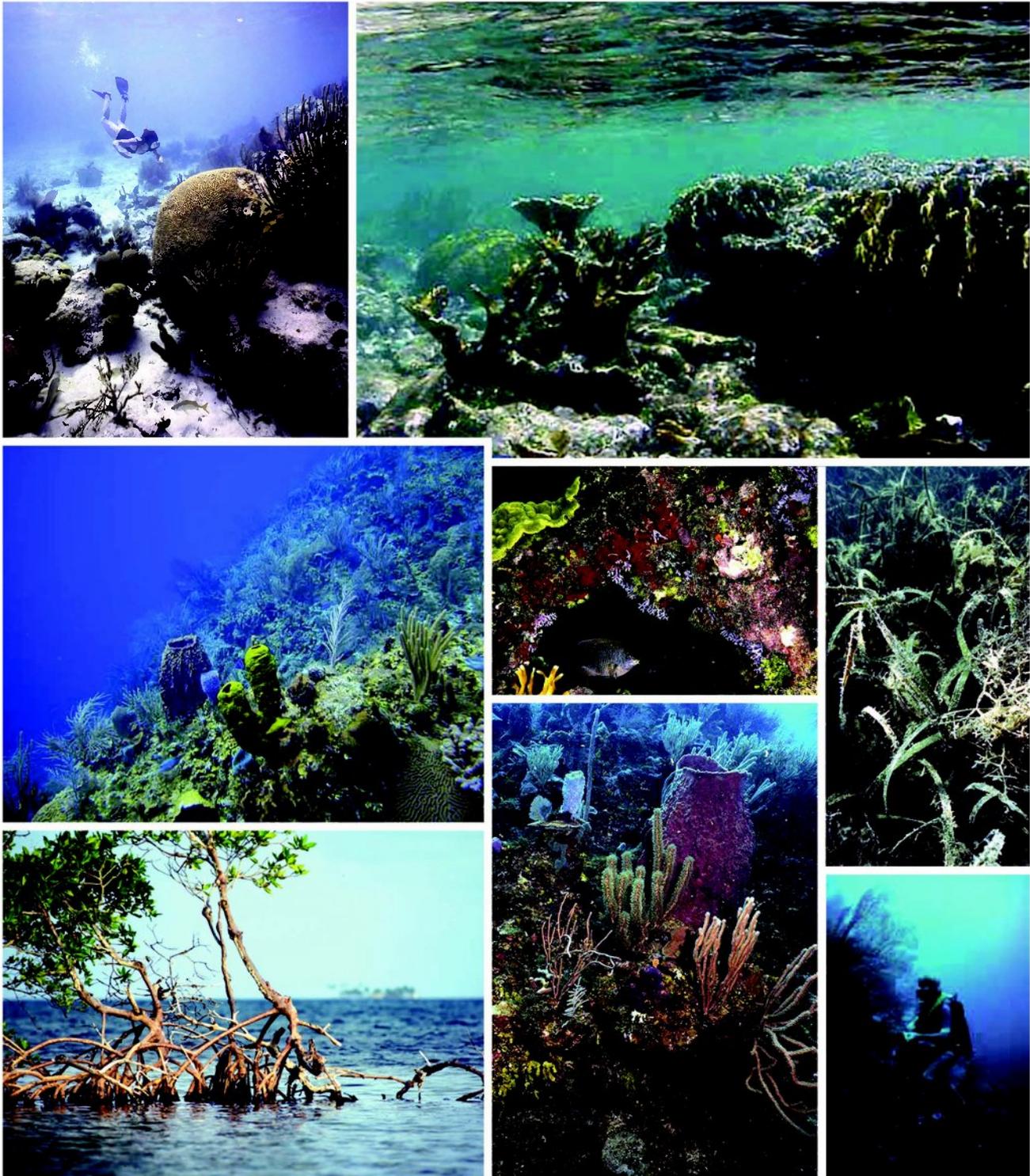


FIGURE 4. Principal marine habitats near Carrie Bow Cay. Top row: left, patch reef near the south tip of the island; right, barrier reef crest composed of elkhorn and fire coral (*Acropora*, *Millepora*). Middle row: left, outer fore-reef with corals, sponges, and gorgonians; center, small cave in the fore-reef framework; right, seagrass stand in the barrier-reef lagoon. Bottom row: left, red mangrove at Twin Cays, with Carrie Bow Cay in the background; center, gorgonian and barrel-sponge community on the outer fore-reef; right, diver on the fore-reef slope.

barrier reef. Cores from a series of holes yielded information on past community patterns and successions as well as the distribution of contemporaneous submarine cements within the reef structure (Macintyre et al., 1981).

Detailed maps and inventories of terrestrial plants on several Belizean cays, including Carrie Bow, from 1960, 1962, and 1972 (see Stoddart et al., 1982) aided in our observation of morphological and floral changes, particularly in relationship to the frequent hurricanes in the region. In 1974, only two years into our presence on Carrie Bow, Hurricane Fifi, which destroyed large coastal areas of Honduras, hit the barrier reef just south of our island. Although our reef habitats experienced only minor changes, primarily local breakdown of the framework and accumulation of rubble, most terrestrial life on Carrie Bow, particularly vascular plants, was killed by flooding—except for coconut trees, which suffered about a 20% loss (16 trees)—and there was severe coastal erosion. Upon remapping the island in the wake of this event, we noted some redepositing of beach sand and recolonization by plants through drift and windblown seeds.

GAINING MOMENTUM

Our venture took a significant step forward with the award, in 1975, of an annual grant by the Exxon Corporation from the company's public relations budget for Central America. Although relatively small, the funds nearly doubled our support and had no strings attached, except they were to be dedicated to Caribbean coral reef research. Added to this welcome development was a new and beneficial relationship with Captain Graham Thomas of the Royal Signals Detachment in Belize, a helicopter pilot detailed to support the training of British forces in jungle environments. Graham was able to equip his helicopter with an aerial camera and take vertical pictures of the Carrie Bow reefs that provided excellent photo coverage for a detailed mapping of the area's reef structures at a scale of 1:800 and to a depth of 10 m. This information constituted enormous progress over available nautical charts (with a scale of 1:125,000) that dated back to British surveys in the 1830s and were only partly updated in the 1940s. Even greater resolution in aerial mapping (but at the expense of areal coverage) was achieved by introducing a helium weather balloon equipped with a remotely operated camera. This technique (Rützler, 1978b), like several others devised by our team, was documented in a volume on coral reef research methodology sponsored by the United Nations Educational, Scientific and Cultural Organization (UNESCO) (Stoddart and Johannes, 1978).

In 1977, in association with the Third International Symposium on Coral Reefs in Miami, several of our team organized a well-received field trip to Belize, highlighted by a detailed field guide based on maps, transect data, and aerial and underwater habitat photographs emanating from the program (Miller and Macintyre, 1977). In short order, the program launched several new projects (Figure 5) to investigate the fate of siliceous skeletons in the calcium carbonate environment of the reef (Rützler and Macintyre, 1978), the feeding behavior of scyphomedusae (Larson, 1979), and the systematics of the unexpectedly diverse ostracod crustaceans (Kornicker and Cohen, 1978). Other innovative and pioneering work focused on the fine structure of bivalve anatomy as revealed through scanning electron microscopy (Waller, 1980) and, with collaborators from the Scripps Institution of Oceanography, on the chemistry of marine plant and invertebrate secondary metabolites that showed promise as antibiotics or other therapeutical substances (Kokke et al., 1979). By the end of 1978, more than 50 papers had been published or were in press to document the biology, ecology, and geology of the Belize barrier reef in the vicinity of Carrie Bow Cay.

The program's success appeared to be short lived, however: in late September 1978, Hurricane Greta passed across the Belize barrier reef just 6 km north of Carrie Bow. Four lives were lost in Dangriga, the citrus harvest in the valley to the west was destroyed, and there was heavy beach erosion at Pelican Beach Motel. Although no members of our group were on location because we had closed down for the season, part of our equipment was damaged when ocean storm surge and rain flooded the storage area. Storm waves from the east and strong backlashing winds from the northwest caused severe erosion of beach sand on Carrie Bow and wiped out some 30 coconut trees, the small house, and the outhouses. The ocean-side wall of the laboratory building also caved in, exposing equipment and supplies to saltwater spray. Following the storm, visibility in the usually very clear ocean water remained at less than 3 m for two weeks, most elkhorn (*Acropora palmata*) and fire coral (*Millepora complanata*) near the reef crest was reduced to rubble, and the salinity in the lagoon dropped from the usual 35‰ to 25‰.

Despite this setback, we decided to press our team and collaborators to complete work in progress and prepare a state-of-the-art summary of our accomplishments. The resulting volume (Rützler and Macintyre, 1982), later known as the Blue Book (for the color of the hard cover), became a platform for the next phase of investigations, as well as for raising funds. The first section presented a



FIGURE 5. A few examples of research activities of the 1970s to 1980s. Clockwise, from top left: boat operator Frank (Pelican Beach Resort) helps Ron Larson to lower plankton net from the stern of the boat; Ian Macintyre's group drill-coring down a sand groove on the fore-reef; Joan Ferraris (left) tending incubation chambers to measure temperature-salinity tolerance of invertebrates and Sara Lewis preparing aquaria for fish herbivory experiments; Sara measuring algal abundance in a quadrat frame on the reef flat; Klaus Ruetzler retrieving trace paper from tide recorder on Carrie Bow dock; Mark and Diane Littler's team assessing effects of nutrients on algal growth.

detailed overview of the physical and biological environment of our study site—its habitats and community structure, geological history, tides, water currents, climate, and terrestrial conditions—compiled by Ian Macintyre and myself and various outside collaborators, including Björn Kjerve (University of South Carolina, Columbia), Joan Ferraris (Mount Desert Island Biological Laboratory, Maine), and Eugene Shinn (U.S. Geological Survey, Miami). The next section focused on the benthic and planktonic communities—the carbonate microborers, micro- and macrobenthos, zooplankton, and the populations of a large submarine cave at nearby Columbus Cay—and their productivity. The principal collaborators were Joan Ferraris, Paul Hargraves (University of Rhode Island, Kingston), Jeffrey May (Rice University, Houston), and David Young (Department of the Navy, Mississippi). A section on biodiversity included many important groups of reef organisms, notably the algae and seagrasses (James Norris, NMNH), hydroids (Barry Spracklin, University of New Hampshire, Durham), medusae (Ronald Larson, a former NMNH technician who moved on to the University of Victoria, Columbia), stony corals (Stephen Cairns, NMNH), octocorals (Katie Muzik, postdoctoral fellow, NMNH), sipunculan worms (Mary Rice, NMNH), crustaceans and pycnogonids (Brian Kensley, Allan Child, NMNH), and echinoderms (Frederick Hotchkiss, postdoctoral fellow, NMNH; Bradford Macurda, Jr., University of Michigan, Ann Arbor). The most unusual discovery was that chironomid insect larvae, caught in emergence traps, are part of the offshore benthic community and live in fore-reef sand bottoms to depths of 30 m (Gernot Bretschko, Biological Station Lunz, Austria). A section on species interactions and responses to the environment addressed chemical defense in algae (James Norris), the life history and ecology of cnidarians (Ronald Larsen), growth patterns of reef corals (Richard Graus, NMNH), sponge–zoanthid associations (Sara Lewis, Duke University, Durham), bivalve larval settlement (Thomas Waller, NMNH), and resource partitioning in chaenopsid, coral-associated fishes (David Greenfield, Field Museum of Natural History, Chicago). The concluding chapter puts Carrie Bow Cay and its reefs in the larger context of the Belize barrier reef complex (contributed by Randolph Burke, North Dakota Geological Survey, Grand Forks, and David Stoddart).

Having overcome many of the start-up problems, including setbacks caused by the hurricanes, we forged ahead in the new decade with increasing productivity and innovation. CCRE members authored a number of important monographs and other reports on reef biodiversity. We started a series of papers on the fungi (Kohlmeyer,

1984) and algae (Littler and Littler, 1985); prepared analyses of several large crustacean groups, including parasitic copepods on fishes (Cressey, 1981), decapods (Kensley and Gore, 1981), isopods (Kensley, 1984), and amphipods (Thomas and Barnard, 1983); and published the first survey of local moss animals, bryozoans, by a colleague then at the American Museum of Natural History in New York (Winston, 1984).

We also conducted a series of day and night plankton tows over the fore-reef and over lagoon seagrass bottoms, which were surprisingly devoid of larval stages of some of the area's common animals, such as an assortment of cnidarians and sponges. We speculated that the larvae might be swimming close to or within the reef framework, where our boat-towed nets could not be operated, and decided to tow or push the plankton nets by hand, while swimming close to the bottom. Although more successful, this technique took time and effort to obtain sufficient samples. Eventually, we hit on the idea of building a stationary net supported by a frame that could be placed close to or among the coral heads or branches. For locations without strong directional currents, we added a waterproof electric motor with propeller and a flow meter to measure the volume of water that passed through the net. This setup ultimately produced excellent samples of great diversity considerably beyond the composition of plankton tows by boat (Rützler et al., 1980).

Having a small budget and intent on disturbing our study environment as little as possible, we sought creative field and laboratory techniques that would not require sophisticated instrumentation or climate control. In keeping with these goals, our colleague Sara Lewis, for one, completed the experimental fieldwork for her entire dissertation on fish herbivory on the Carrie Bow reef flat, just a few meters east of the lab building (Lewis, 1986). Some of our Museum's phycologists experimented with the influence of algal growth forms on herbivores at the same location (Littler et al., 1983). Ecophysiological work on temperature and salinity tolerance of polychaetes and other reef invertebrates was accomplished in situ and with simple, specially designed acrylic incubation chambers (Ferraris, 1981; Ferraris et al., 1989). Submarine cementation processes were determined experimentally in the karst cave habitat of Columbus Cay (Macintyre, 1984). Benefits of algal symbionts to sponge hosts were explored by in situ trials on a nearby patch reef (Rützler, 1981). And, with an innovative underwater time-lapse camera with strobe light borrowed from its inventor, Harald Edgerton at the Massachusetts Institute of Technology, we recorded several unattended day–night activities on the reef, including the

nocturnal feeding behavior of basket stars (*Astrophyton*) (Hendler, 1982).

During reef surveys in the early phase of our program, we were already seeing a number of dead or damaged corals with no clear sign of the common physical impacts related to storms or boat anchors. Our postdoctoral fellow Arnfried Antonius pioneered these observations at Carrie Bow and elsewhere in the Caribbean, as well as in the Indo-Pacific (Antonius, 1982). One notable feature of many of these flagging corals was a black line between live coral tissue and recently dead (white) skeleton. During collaborative studies, we determined that the black band consisted of a mat of entangled filamentous cyanobacteria, with a number of associated microbes, and that the photosynthetic bacteria had an appetite for coral tissue, thereby causing what has been called “black band disease” (Rützler et al., 1983).

OCEANIC MANGROVE SWAMPS

Anyone looking through our 1982 “Blue Book” will notice that mangroves are barely mentioned, except for a few remarks about Twin Cays, a mangrove island in the lagoon just over 3 km northwest of Carrie Bow (Figure 6). This lack should not be taken as a sign of little interest. CCRE workers have in fact been highly impressed by the relatively clear (for a swamp) water in the tidal channels and the rich flora and fauna, particularly the sponges, covering the stilt roots of red mangrove (*Rhizophora mangle*).

On an earlier visit to a very similar mangrove island, East Bimini in the Bahamas, I had been so struck by its subtidal diversity that it seemed an ideal community for multidisciplinary study. The “discovery” of Twin Cays during the early 1980s rekindled this interest, and coincidentally our Exxon supporters indicated that they wanted to diversify their generosity in Central America beyond coral reef research. We therefore submitted a new proposal to their open competition for the comprehensive study of a Caribbean mangrove ecosystem at Twin Cays. A factor in our favor was that oil pollution caused by tanker ballast-water discharge or wrecks was affecting Caribbean beaches and reefs at that time. Indeed, a colleague and I had studied the effect of such an oil spill at Galeta Island, Caribbean Panama, a decade earlier and found that the subtidal reef corals were barely affected by the spill but that the oil slick had caused severe damage to the nearby intertidal mangrove community (Rützler and Sterrer, 1971). Our proposal won another five years of research grants, and we named our initiative SWAMP (Smithsonian Western Atlantic Mangrove Program). This

support was supplemented by internal grants for specific purposes, notably Fluid Research Funds travel awards, a Scholarly Studies grant for mangrove research, a Smithsonian Associates Women’s Committee award for scientific illustration, W. R. Bacon Scholarships (for external collaborators), Seidell Funds for library enhancements, and National Science Foundation grants to outside collaborators (who were to some extent also supported by their home institutions).

Because mangroves are tidal communities with terrestrial, intertidal, and subtidal components, we could expand our fields of interest, adapt our methods to the new environment, and add a number of disciplines to our study that are not usually applicable in the subtidal reef environment (Rützler and Feller, 1988; Figure 7). With a wider biodiversity horizon, we could now conduct surveys of microbes, fungi, algae, sponges and their endofauna, polychaetes, crustaceans, echinoderms, and bryozoans. We were fortunate to have a rare expert on the quantitatively important ascidian tunicates join us at this time, Ivan Goodbody of the University of the West Indies, Jamaica. Our team also explored the geological history of the mangrove by coring through massive peat accumulations and dating the different horizons and also initiated terrestrial studies of the mangrove’s lichens, insects, spiders, reptiles, and birds.

An important first step was to explore and map Twin Cays and name the many bays, ponds, creeks, mud flats, and lakes and give them coordinates (before Global Positioning System [GPS] devices were available) that would allow us to relocate research sites. We also wanted to garner more interest in the mangrove ecosystem, but because swamps tend to be viewed as undesirable environments, it took considerable effort to win over our sponsors, local hosts, and even many colleagues. Good photography was a decided help, but even the best pictures convey but a tiny segment of a process in nature, although they are absolutely necessary for documenting shapes, expressions, or colors, of course. To depict the entirety of, say, an animal–plant association, we needed to capture the obvious and the hidden, the large and the small (in proper detail and perspective), and the dynamics of day versus night—in a word, we needed to combine art with science. We did just that in a new project called Art in a SWAMP (Figure 8). The lead artist was Ilka (“Candy”) Feller, a contract illustrator at the time with vast experience in the fields of botany and entomology, having worked with numerous colleagues in those departments in our Museum over many years. Candy not only employed her artistic talent in the illustration of mangrove communities, but she was so captivated by the entire ecosystem that she resumed academic studies (after



FIGURE 6. Twin Cays mangrove habitats. Clockwise, from top left: the island viewed southwest toward Carrie Bow Cay and the barrier reef; mangrove fringe lining the Main Channel; sponge clusters in one of the tidal channels supported by red-mangrove stilt roots; diverse community of sponges and ascidians on a root substrate; a newly discovered and described sponge (genus *Haliclona*) anchored on and in the mangrove-peat bank that lines many channels; juvenile barracuda hiding among mangrove roots; a snorkeler exploring Hidden Creek, which connects a shallow mangrove lake with the open Main Channel.



FIGURE 7. (*facing page*) Examples of projects initiated at Twin Cays. Clockwise, from top left: mapping and exploring team landing on the western shore; our weather station erected in a large tidal mud flat; scientific illustrator Mary Parrish sketching mangrove communities; Molly Ryan photographing community samples returned to the lab at Carrie Bow for one of her scientific illustrations; student volunteer helping to collect specimens; ichthyologists Will Davis and C. Lavett Smith comparing catches; Ilka Feller measuring salinity in Hidden Lake, the location of one of her mangrove fertilization and growth experiments; Ian Macintyre, with Ilka, dissecting termite nest during an exploration of the mangrove's interior.

having raised two daughters), completed a dissertation on the Twin Cays mangrove, and became one of the foremost mangrove ecologists working on communities between Florida and Brazil and as far away as Australia and New Zealand. Other artists on the project were Mary Parrish, first a staff member in my department and now illustrator in the Department of Paleobiology; Molly Kelly Ryan, Invertebrate Zoology staff illustrator; and Jennifer Biggers, then my contract research assistant and illustrator. This team, along with Paleobiology's Ian Macintyre, Natural History Museum photographer Chip Clark, Invertebrate Zoology technician Mike Carpenter, and several more associates and volunteers engaged in detailed surveys and mapping of Twin Cays geomorphology and in analysis and graphic reconstruction of habitats and communities, ranging from epiphytic sponges to intertidal algae–invertebrate associations to red mangrove–insect interactions, and an entire mudflat population (Rützler and Feller, 1996).

Our growing familiarity with mangrove organisms raised a number of significant ecological and behavioral questions concerning the composition and ecology of floating cyanobacterial mats (addressed by Maria Faust in the Department of Botany; Faust and Gullede, 1996) and herbivory in macroalgal communities (investigated by Mark and Diane Littler and colleagues; e.g., Littler et al., 1983). A rare immune disease was discovered in a sponge (Rützler, 1988) in which the usually beneficial microbial symbionts turn against their host. The dynamics and behavioral patterns of swarming copepod crustaceans among mangrove roots were investigated by Frank Ferrari, Invertebrate Zoology, and colleagues (Buskey, 1998; Ferrari et al., 2003). Also, new work was done on invertebrates living in complex burrows in the sediment substrata of mangrove channels (Dworschak and Ott, 1993), and on the importance of mangroves for the recruitment and protection of commercial species such as spiny lobster (Acosta and Butler, 1997). In research on another puzzling question—the role of sponge cyanobacterial symbionts in both mangrove and reef nutrient cycling—it was shown that nitrogen fixing by bacteriosponges is indeed an important input to the community (Diaz and Ward, 1997). With the

new emphasis on the biology of the Twin Cays mangrove, Ian Macintyre applied geological techniques over several years to reveal its biological history: using a portable vibracore, he mapped and carbon-dated the subsurface layering of peat, sand, and rubble, all the way to Pleistocene level (Macintyre et al., 2004b).

As our financial situation improved, we were able to address the bothersome problem of coping without automated instrumentation for continuous monitoring of basic meteorological and oceanographic parameters. Up to then we had documented the tidal regime at Carrie Bow Cay with a pressure sensor (Kjerfve et al., 1982) and relied on various borrowed or leased instruments to meet the needs of specific projects for monitoring water currents, temperature, solar radiation precipitation, or wind (Greer and Kjerfve, 1982; Rützler and Ferraris, 1982). None of these improvised methods provided long-term, reliable records even if we were on site. With the help of contract engineer George Hagerman, we adapted a leased Anderaa (Bergen, Norway) automatic weather station for our purposes and installed it on a massive, elevated wood platform in an extended tidal mud flat to the north of Twin Cays. This setup provided us with continuous data for several years until it became outdated and fell victim to vandalism.

CARIBBEAN CORAL REEF ECOSYSTEMS: A BREAKTHROUGH

In the early 1980s, Richard Fiske, then Director of the National Museum of Natural History, asked for proposals that would interest our sponsors in the U.S. Congress, who at that point appeared to favor the expansion of promising research already in progress. To our surprise, the Museum received an increase to its budget base for the study of Caribbean Coral Reef Ecosystems beginning in 1985. Modeled on the IMSWE-SWAMP initiatives, the CCRE program encompassed reef, mangrove, seagrass, and plankton communities, with a primary focus on the Carrie Bow Cay region.

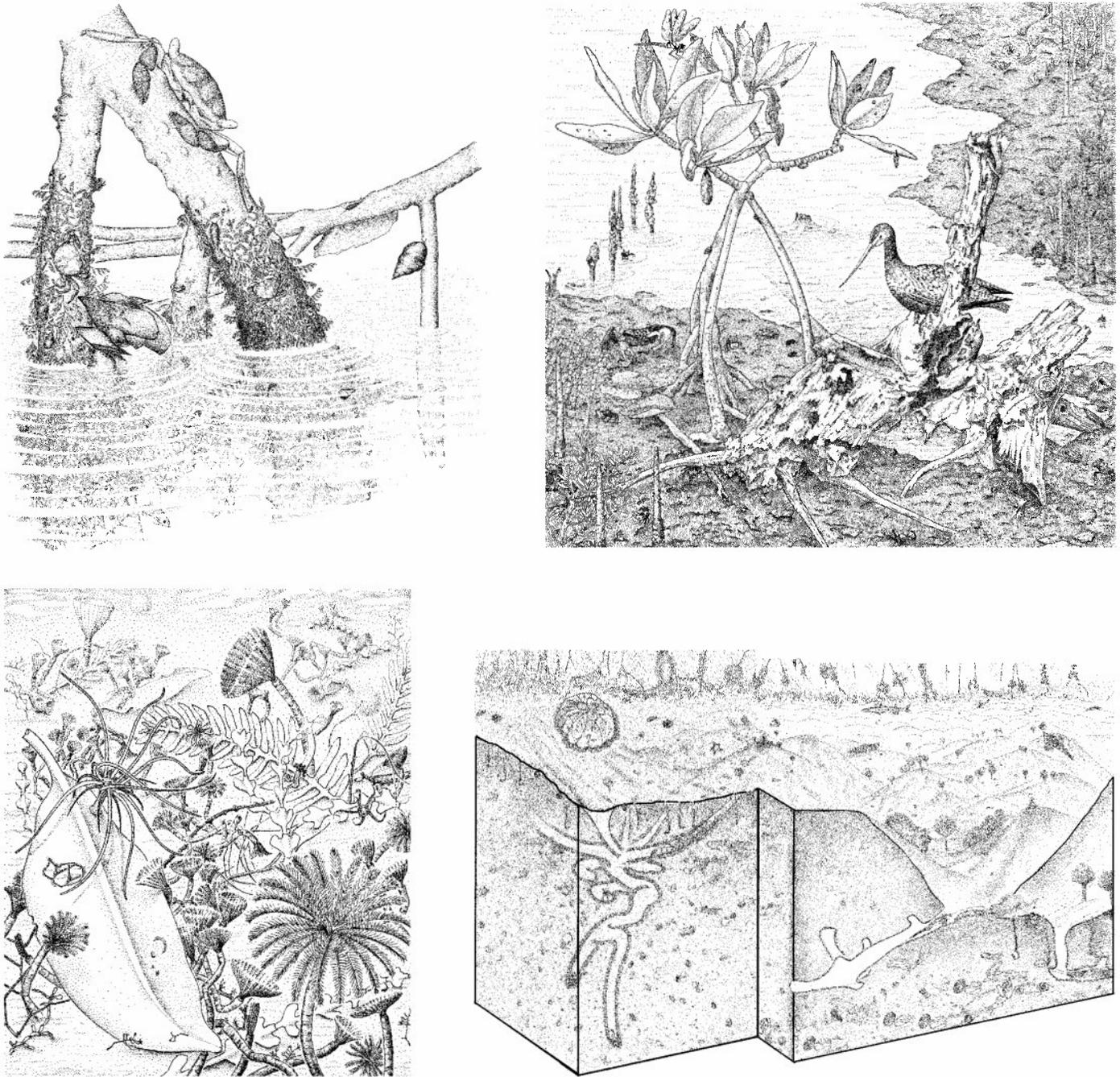


FIGURE 8. Examples of illustrations of mangrove swamp communities. Clockwise, from top left: characteristic intertidal red algal cover (*Bostrychietum*) on red-mangrove prop root, with mangrove oyster, mangrove crab, and periwinkle; tidal mudflat showing developed red-mangrove seedlings, black-mangrove pneumatophores, driftwood, and a marbled godwit; cut-away view of mangrove channel bottom showing characteristic benthic organisms including decapod burrowers; close-up of peat-bottom community with algae, fallen mangrove leaves, sea anemone, and sabellid tube worms.

Under a new administrative structure approved by Director Fiske, CCRE would be governed by a steering committee chaired by me and composed of representatives of different departments and disciplines, including outside advisers. Marsha Sitnik, who worked with all the Museum's interdepartmental biodiversity initiatives, became program administrator. Now we could afford the important position of operations manager, filled by Mike Carpenter, who serves as field station logistics director and has trained and supervised our volunteer station managers, each of whom typically spends three to six weeks at Carrie Bow Cay.

The new funding allowed us to lease all of Carrie Bow Cay year round and remodel the big house for much-needed dry-lab space for instruments, a library, computer, and additional living accommodations. We built a separate, sound-insulated compressor-generator shed, added propane gas refrigerators to kitchen and labs, and improved radio-communication and other safety features for boating and diving. New equipment included microscopes, balances, centrifuge, and other analytical equipment. We also upgraded our weather station with real-time data access and connected it with the Belize Meteorological Office, which had no offshore monitoring facility. Even more important, we had a modest budget for travel stipends to attract outside collaborators to work on organisms or disciplines not covered by Smithsonian staff scientists.

At the end of the first CCRE program year, our publication list exceeded 200 entries. Several of the projects mentioned earlier were continued or completed and new ones begun with like-minded colleagues whose expertise filled the gaps in our experience. To name a few of these projects, some focused on the control of reef zonation by light and wave energy (Graus and Macintyre, 1989), the taxonomy and ecology of hydroids (Calder, 1991), oligochaete worms (Erséus, 1988), mysid crustaceans (Modlin, 1987), and ascidians (Goodbody, 1995); the predation and feeding ecology of sponges (Wilkinson, 1987), echinoderms (Aronson, 1987), and fishes (Wainwright, 1988); the ecophysiology of invertebrate-bacterial symbiosis supporting life in hydrogen sulfide environments (Ott and Novak, 1989; Ott et al., 1991) and mangrove-tree metabolism (McKee et al., 1988); and island groundwater hydrology (Urish, 1988).

In 1988 we held a workshop at the Calvert Marine Museum in Solomons, Maryland, to review the accomplishments and gaps in our research on the Twin Cays mangrove ecosystem. Close to 40 program participants summarized the progress of their work on internal structure, development over time, sedimentology, meteorology,

hydrology, vegetation, productivity, nutrient cycling, temperature-salinity tolerance, and biodiversity of fauna and flora from microbes to amphibious fishes. The most obvious deficiencies were in oceanography, a number of important organism groups such as mollusks and fishes, and marine benthic and terrestrial ecology. One of the highlights was a report on a complementary team study of the Holocene geological history, peat composition, and terrestrial and marine vegetation of Tobacco Range, another large mangrove island about 3.5 km north of Twin Cays (Littler et al., 1995). This atoll-like range drew CCRE's attention when a large area of fractured and slumped fossil peat was discovered off its west shore.

At a subsequent planning workshop in Jamaica, CCRE established a protocol for studies at Twin Cays and Carrie Bow Cay. This initiative, called Caribbean Coastal Marine Productivity (CARICOMP), calls for simple but universally applicable methodologies in the monitoring of major oceanographic parameters and health of the Caribbean's principal communities. To this end, we established representative plots and transects in mangrove, seagrass meadow, and fore-reef, which are being evaluated yearly for changes in structure and productivity, while climatic factors are determined on a weekly basis (Koltes et al., 1998).

As our scientific drawing and photography of swamp communities gained scientific importance and aesthetic value, we were invited to display some of this work to the public at the Smithsonian's S. Dillon Ripley Center in an exhibition titled "Science as Art." It included a video documentary on mangrove swamp biology, produced in collaboration with colleagues from the University of Vienna (Joerg Ott and Alexander Bochdansky). The video also served as a teaching aid in an annual educational workshop for Belize high school teachers, conducted by Candy Feller and Marsha Sitnik in collaboration with the Belize Fisheries and Forestry departments and titled "Mangrove Conservation through Education." This was a timely workshop, indeed: our research area at Twin Cays was showing the first signs of anthropogenic stress in response to tourist visitation, garbage dumping, vandalism (of our weather station and boat dock), and the clear-cutting of mangrove trees to gain land for development. These developments had a particularly adverse impact on Candy and her colleagues, whose work on mangrove plant ecology required extended undisturbed natural conditions to single out parameters (nutrients, in particular) that enhance or impede growth (Feller, 1995; Feller et al., 1999). Fortunately, at our urging, Belize's Forestry and Natural Resources Departments helped slow the disturbances and started work on a conservation plan for the South Water

Cay Marine Protected Area (MPA) that would include Carrie Bow and Twin Cays.

Side-tracked by the discovery of the Pelican Cays biodiversity hotspot (see the next section), the impact of a hurricane, and coral bleaching events, we were unable to convene another Twin Cays symposium until 2003. Meeting at the Smithsonian Marine Station in Fort Pierce, Florida, we found our mangrove program had accumulated enough scientific results not only to fill a volume of multidisciplinary papers but also to demonstrate changes in the structure of the ecosystem over a span of two decades (Macintyre et al., 2004a). Articles on geological history and sedimentary conditions were spearheaded by Ian Macintyre and those on aquatic ecology by Rützler and colleagues. Other contributions covered a wide range of topics: changes in the mangrove landscape, documented through aerial and satellite imagery by Wilfrid Rodriguez and Ilka Feller at the Smithsonian Environmental Research Center; marine botany, investigated by Maria Faust and the Littler team; Foraminifera, by Susan Richardson of the Smithsonian Marine Science Network (MSN); symbiotic ciliates, by Joerg Ott; sponge ecology, by Cristina Diaz (then an MSN Fellow with me) and Janie Wulff (now at the Florida State University, Tallahassee); and two very different worm groups, the interstitial gnathostomulids by Wolfgang Sterrer (Natural History Museum, Bermuda), and the burrowing sipunculans, by Anja Schulze, postdoctoral fellow, and Mary Rice, emeritus scientist, both at SMS, Ft. Pierce, Florida (Mary is also the founding director of that laboratory). William Browne (University of Hawaii, Honolulu) summarized years of genetic and developmental research on mangrove crustaceans, Judith Winston her work on bryozoans, and Ivan Goodbody his observations on ascidian diversity. Years of genetic research at Twin Cays on a highly unusual amphibious fish, the mangrove rivulus, was summarized by Scott Taylor and his collaborators, and terrestrial biology received a welcome boost from observations by Seabird McKeon (then at SERC) and Stephen Mitten (University

of Missouri, St. Louis, now based in Belize). Energy flow was also examined in a paper on nutrients derived from microbial mats by Samantha Joye (University of Georgia, Athens), and another on the planktonic food web by Edward Buskey (University of Texas at Austin). To round out the reports, Mary Parrish explained the important role of scientific field illustration—a collaboration between scientist and artist—in analyzing and explaining mangrove communities.

CCRE's recent accomplishments also include two far-reaching initiatives. The first, begun by collaborator Emmett Duffy from the Virginia Institute of Marine Science (Gloucester Point), is a study of the systematics and ecology of snapping shrimp (Alpheidae) that live in reef sponges with a large interior cavity system, such as the genus *Agelas*. As the work progressed with various specialists and graduate students coming on board, alpheids were found to have much more genetic diversity and ecological complexity than previously thought. Another discovery, a first among marine life, was that these crustaceans have the same advanced social structure (eusociality) as some well-studied terrestrial animals, such as termites (Duffy, 1996). Second, a logistical breakthrough, made possible through our collaboration with colleagues at the University of Rhode Island, was the development of a new integrated environmental sensing system with a radio-telemetry link to the Internet (Opishinski et al., 2001).

PELICAN CAYS, BIODIVERSITY HOTSPOT

In the early 1990s, our neighbors on Wee Wee Cay, Paul and Mary Shave, alerted us to another amazing ecosystem: the Pelican Cays (16°59.8'N, 88°11.5'W), a biologically rich mangrove island group less than 20 m south-southwest of our Carrie Bow station (Figure 9). We now had an 8 m boat, more substantial than any before, that could take us there in about an hour. Ivan Goodbody, the first to visit the Pelicans on the rumor of an

FIGURE 9. (*facing page*) The Pelican Cays “mangreef.” Clockwise, from top left: aerial photograph of Cat Cay showing mangrove, reef ridges, and deep lagoons (Manatee Cay, left, and Fisherman’s Cay are in the background); diver swimming over coral (*Agaricia*) below the canopy of a red-mangrove tree; Rich Aronson and Ian Macintyre operating a hand corer to retrieve subbottom coral and other deposits; close-up of ascidian (*Clavellina*)–sponge (*Monanchora*, *Spirastrella*) community, enveloped by brittle star arms, on Manatee Cay mangrove root; Klaus Ruetzler sampling sponges (*Aphysina*) in a marine pond on Fisherman’s Cay; Coral Ridge (*Agaricia*, *Palythoa*) with sponges (*Chondrilla*) at Cat Cay lagoon entrance (sponge-covered mangrove roots in background).



ascidian paradise there, found the area teeming with ascidians—and much more. Many of us followed in short order, eager to investigate the Pelicans' atoll-like reef, an elongate north–south-oriented structure measuring almost 10×3 km and studded with about a dozen mangrove cays on its northern rim. Most of the islands enclose deep circular ponds that support and protect a diverse community of marine plants and sessile filter feeders—particularly sponges and ascidians—flourishing on red-mangrove stilt roots and peat banks. A wealth of other invertebrates and fishes live just below the tide line, a mix of reef and mangrove organisms, some species previously seen only in much deeper water on the barrier fore-reef, although the Pelican Cays are situated deep inside the barrier-reef lagoon, halfway between the reef and the mainland.

We were so impressed by the unusual diversity and ecological complexity of the Pelican Cays ecosystem that we asked the Belize Coastal Zone Management and Fisheries units to include the region in the South Water Cay MPA. Tony Rath (NaturalLight, Dangriga) and Jimmie Smith (Islands from the Sky, Houston, Texas) helped with aerial photography, Molly Ryan with mapping, and our research team along with outside collaborators addressed the new scientific perspectives (Macintyre and Rützler, 2000). Macintyre and his team, and Karen McKee (U.S. Geological Survey, Lafayette, Louisiana), spearheaded the study of geological underpinnings and vegetation history, Dan Urish (University of Rhode Island) and Tracy Villareal (University of Texas at Austin) the hydrography of the ponds, Thomas Shyka (National Oceanographic and Atmospheric Agency, Silver Spring, Maryland) the nutrient cycle and water flow patterns in the ponds, Steve Morton (Bigelow Laboratory, West Boothbay Harbor, Maine) and Maria Faust the phytoplankton, Mark and Diane Littler the marine algae and seagrasses, Susan Richardson (then at Yale University, New Haven, Connecticut) the epiphytic foraminiferans, Rützler and colleagues the sponges, Janie Wulff (then at Middlebury College, Vermont) sponge predation, Wolfgang Sterrer the gnathostomulids, Gordon Hendler (Natural History Museum, Los Angeles, California) the echinoderms, and Ivan Goodbody the tunicates. At the height of these investigations, we were able to introduce the spectacular coral communities of the cays to participants of the 8th International Coral Reef Symposium, along with other points of interests, such as community changes in the reef zones of the Carrie Bow reference transect over the past two decades (Macintyre and Aronson, 1997). The fishes of the Pelicans were investigated (just after the edited volume was published) by a team of ichthyologists led by our Muse-

um's James Tyler and included former American Museum of Natural History curator (now retired) C. Lavett Smith (Smith et al., 2003). More recently, important suspension feeders that had not been covered by the earlier surveys, the bryozoans, were studied by our long-time collaborator Judith Winston of the Virginia Museum of Natural History (Winston, 2007).

Although still uncertain of the causes of this archipelago's unusually high biodiversity, CCRE researchers saw ample evidence of its fragility and warned of the irreparable harm that could come to its delicate communities from careless visitors or water warming during long periods of calm (as observed in course of some hurricanes). Little did we know that our concerns would soon prove to be well founded. In the course of a number of routine survey flights over the reef, we noted disturbing signs of land “development” on several of the Pelican islands, subsequently confirmed by ground-truthing: we found large areas of mangrove clear-cut and bottom sediments near the cays dredged to obtain fill material on which homes and resorts could be built. We reported our observations to the authorities because by that time the cays were already part of the South Water Cay MPA and mangrove cutting was illegal without a special permit. At the time of this writing, the activities have stopped and are under investigation by the government of Belize. Unfortunately, a great natural treasure has been severely damaged, without any clear sense of whether and how soon a recovery will be possible.

A MEMORABLE YEAR, 1997

In CCRE's 35-year history, 1997 stands out for its remarkable highs—and lows. Scientifically, many significant field projects were launched or carried to completion: investigations of coral bleaching, a new and unsettling phenomenon on the barrier reef (Aronson et al., 2000); ecophysiological analysis of periodic crustacean swarming among red-mangrove stilt roots (Buskey, 1998); a pioneering initiative to match poorly known fish larvae to the adults of the species, first by morphological means after rearing in the laboratory, later by DNA analyses (Baldwin and Smith, 2003); and a workshop on Caribbean sponge systematics with experts from five nations that led to a better understanding of the barrier-reef and mangrove poriferan fauna (Rützler et al., 2000). This was also the International Year of the Reef, and to celebrate the occasion we made every effort to share our enthusiasm for this unique environment with students and the general public through numerous lectures, poster sessions, and demon-

strations, on site in Belize and back home at the National Museum of Natural History. To add to the festivities, our Carrie Bow field station, the logistical base and catalyst of our program, had reached the respectable age of 25 (1972–1997).

But the Gods of the Sea must have had other plans for this venerable facility. On 6 December 1997 an accidental fire broke out, aided by old, termite-riddled lumber and fanned by a strong northerly wind. Most of the station was reduced to ashes—laboratory, kitchen, living quarters, even wooden vats filled with water, all except a small cottage and the generator hut, which were isolated on the south end of the island. The blaze destroyed much valuable equipment, including microscopes, balances, solar system, weather station, and the contents of the library. As a result, little fieldwork could be done in the following year, although we did investigate the fire's damage to the island (20 or more coconut trees were lost) and the impact of recent complete flooding (which caused substantial coastal erosion). Two other points of interest were the impact on the reef after being subjected to stormy seas with waves up to 6 m and to an extensive calm period with shallow-water warming that appeared to precipitate the bleaching and death of large numbers of corals.

At this juncture, we gave serious consideration to terminating the CCRE program at this location—but not for long. Buoyed by the positive spirit of the Bowman family (and some insurance payback) and the talent of a young Cuban-trained architect, Hedel Gongora, we designed a new field laboratory to take the place of the old main house. It was built by local carpenters with lumber from pine forest in the west of the country, complete with wet lab, dry lab, library, running seawater system, workshop, and kitchen (Figures 10, 11). The facility was rededicated as the Carrie Bow Marine Field Station in August 1999, with more than 100 visitors in attendance to celebrate the occasion, including local fishermen, cooks, the Minister of Environment, the U.S. ambassador to Belize, scientists, and representatives of all major conservation societies. Over the next two years, we added one cottage for living quarters and rebuilt the one spared by the fire. With generous donations from a number of U.S. companies and individuals, we replaced and improved most laboratory equipment and instrumentation, and Tom Opishinski installed a new meteorological-oceanographic monitoring station enhanced by COASTMAP software (donated by the University of Rhode Island). By the beginning of 2000, CCRE was back on its feet, functioning as a year-round scientific program.

RESURGENCE AND BIOCOMPLEXITY

With a renovated field station, CCRE's scientific momentum took off once again, with new scientific opportunities as well as challenges. Nearly 80 scientific staff resumed field research disrupted by the fire or initiated new projects. A number centered on the sad effects of environmental stress or degradation on delicate but essential reef-building corals. To aid in the understanding of possible coral revival, Ken Sebens (then at the University of Maryland) and colleagues evaluated the benefit of water currents for the growth of the reef-building shallow-water coral *Agaricia*, which has been adversely affected by extended calm periods during hurricanes (Sebens et al., 2003). A parallel ecophysiological study found different tolerances to elevated temperature among species of *Agaricia* and speculated that their abundance may therefore vary with environmental disturbance (Robbart et al., 2004). However, corals that have survived such events may have their recovery impeded by the grazing of parrotfish, which are otherwise considered beneficial to the health of reefs (Rotjan et al., 2006). According to a series of investigations on predators and competitors of reef and mangrove sponges, these aggressors help defense mechanisms in sponges evolve (Wulff, 2005). In another sponge study, we concluded that encrusting excavating sponges have a competitive edge over reef corals weakened by elevated temperatures: the sponges can undermine the weakened opponent as well as displace its living tissue (Rützler, 2002). Assessments by Rich Aronson (Dauphin Island Sea Lab, Alabama), with collaborators, showed alarming recent changes in the composition of reef-building coral species as a result of stress and disease (Aronson et al., 2002, 2005), while John Pandolfi (then, Paleobiology) identified trends responsible for the decline of coral-reef ecosystems worldwide (Pandolfi et al., 2003). A discovery with harmful implications for human consumption of seafood (ciguatera poisoning) was the increase in toxic dinoflagellate algal blooms in our area (Faust and Tester, 2004), a phenomenon attributed to increased nutrient levels in lagoon waters, earlier considered a potential threat (Morton and Faust, 1997). On a more positive note, studies by Ana Signorovitch (then a graduate student at Yale University) applying innovative molecular methods to the enigmatic *Trichoplax* in the one-species phylum Placozoa found considerable genetic diversity there as well as signs of sexual reproduction (Signorovitch et al., 2005). Using a new approach to sponge systematics from the cytochrome oxidase subunit 1 gene tree, Sandra Duran (postdoctoral



FIGURE 10. New Carrie Bow Marine Field Station (2000) and Biocomplexity Program. Top row: left, aerial view of Carrie Bow Cay looking north (see details on map, Figure 11); right upper, the island with laboratory and living facilities as seen from the barrier reef (open-ocean side) and, image immediately below, view from the dock (lagoon side). Center row: left, flow-through seawater system photographed from the storage tank above; center, dock-mounted oceanographic sensors; right, view of upper-level dry lab. Bottom row: Starting the Twin Cays Biocomplexity Program on mangrove nutrient cycle: left, Ilka Feller with experimental enclosure in a tidal mudflat surrounded by black mangrove; right, subtidal bacterial mat with decaying mangrove leaves, an early stage in the cycle.

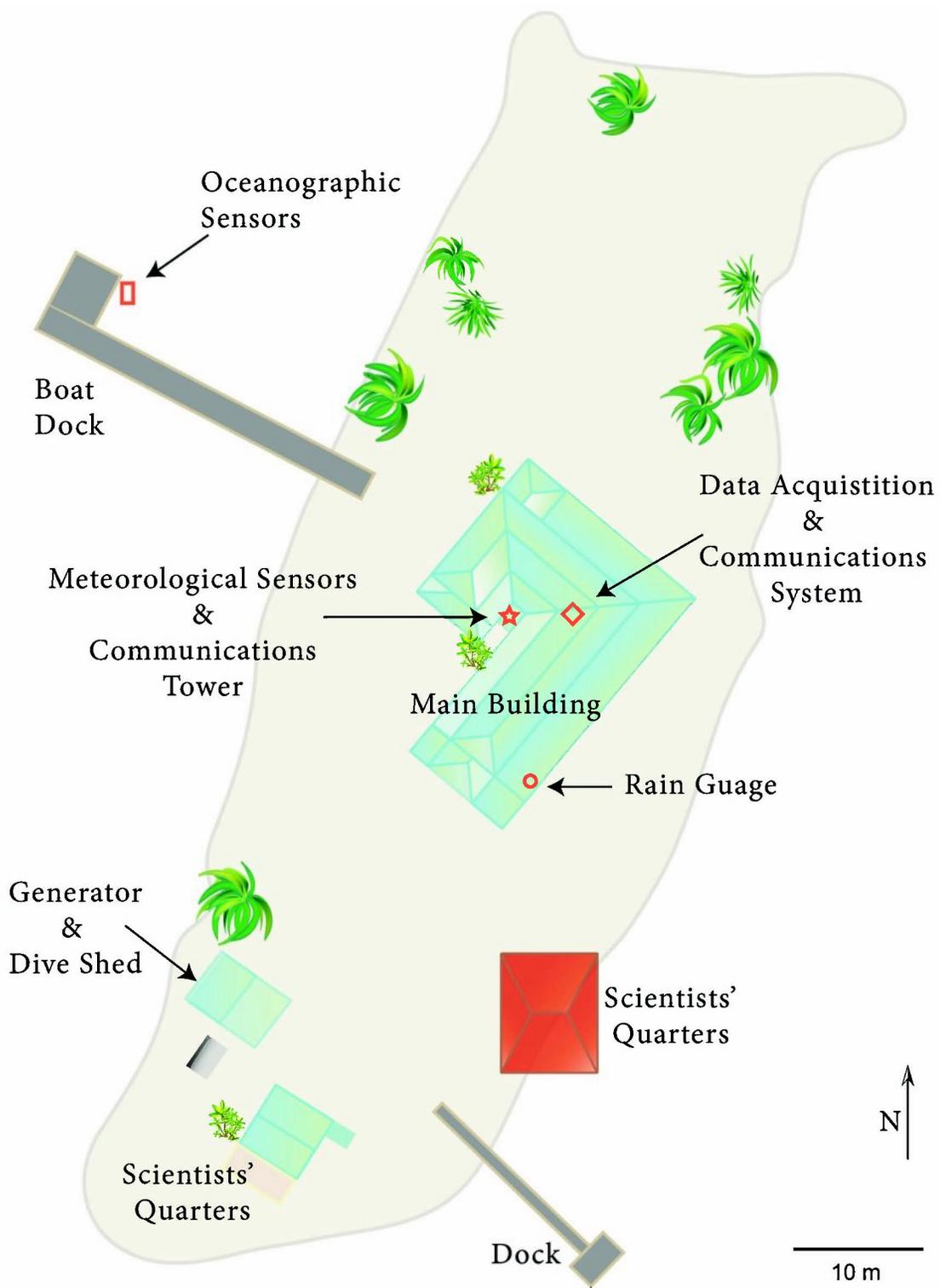


FIGURE 11. Map of Carrie Bow Cay (in 2000) identifying principal structures (number of coconut palms reduced for clarity).

fellow with Valerie Paul at SMS, Ft. Pierce) uncovered important information on rDNA phylogenies and an interesting case of ecological speciation wherein populations from reefs and mangroves in close vicinity were genetically more distant than those from similar habitats separated by thousands of kilometers (Duran and Rützel, 2006; Erpenbeck et al., 2007).

One breakthrough during this period was the five-year multidisciplinary “Mangrove Biocomplexity Study at Twin Cays: Microbial and Nutrient Controls,” funded by the National Science Foundation and headed by Ilka Feller, with nine collaborators from outside institutions (see Figure 10). Several important contributions to an understanding of nutrient production, cycling, limitation, effects on organisms, and related ecophysiological phenomena have already been published (Feller et al., 2002, 2007; Lovelock et al., 2006; Cheeseman and Lovelock, 2004), but many more are expected in the near future now that the fieldwork phase of the Biocomplexity Program has come to a conclusion. One surprising discovery, in a complementary project by CCRE post-doctoral fellow Amy Erickson, was that the intertidal tree crab *Aratus*, long thought to be a mangrove leaf eater, actually prefers an animal diet if given a choice (Erickson et al., 2008). Another important finding, by a group from the University of Vienna, related to the microenvironment of sessile ciliates growing on mangrove peat banks and associated with chemoautotrophic bacteria coating their surface. By analyzing motion behavior of the ciliate and measuring microelectrodes in situ, scientists could show that the hydrogen sulfide required by the symbionts seeped into the boundary layer between the peat surface and oxygenated water column (Vopel et al., 2002).

CONCLUSION AND OUTLOOK

In 1972 a group of enthusiastic, like-minded young scientists embarked on a comprehensive, long-term field investigation of unprecedented dimensions for the Museum of Natural History. The team was unified in its belief that organisms had to be studied in their natural settings for a clear understanding of their features and role in their community (Figures 12, 13). Only then could a preserved museum collection aid in documenting the building blocks of an ecosystem. This approach was particularly true for coral reefs, which were all but inaccessible to scientists until scuba diving allowed in situ observations and experimental study. Similarly, it was essential to probe and sam-

ple substrata to better understand the structure of communities, present and past. The team directed its attention to the Caribbean because it is the Americas’ tropical sea, to which our own nation is connected by weather, ocean currents, and marine resources, as well as by cultural and economic exchange.

In the beginning, we were convinced that together, and with the cooperation of selected specialized collaborators, we could pierce most of the secrets of a functioning coral reef in little more than a decade and generate models for predicting future trends. It did not take long for the restrictions of space, limits of available talents, and chronic shortage of funds to show us how naïve we were. Besides, as all scientists know, every resolved problem opens up new questions. Nevertheless, we can look back on over a third of a century of substantial progress, with more than 800 research papers in print and many more under way, all focused on a particular reef ecosystem and covering a significant time span. Our investigators addressed a vast array of subjects: biodiversity, from microbe to mammal; the geological and sedimentological setting and its developmental history; the physical and chemical factor regime; developmental biology, genetics, food chains, nutrient production, and cycling; behavior, competition, predation, and disease; and fisheries and conservation. We produced an impressive database that a new generation of motivated researchers can build upon with the benefit of technical advancements such as molecular analysis, which should shed further light on eutrophication, climate change, and other stress factors responsible for the increasing occurrence of algal blooms and devastating invertebrate diseases. These topics and more will need our full attention to help guide resource management and conservation efforts—and, above all, to preserve the aesthetic and economic value of the world’s reefs.

Over the past few years our program has once again come up against a number of hurdles. Financial shortages in the Natural History Museum’s budget have eroded our funding, while staff has been reduced and not replaced, leaving our scientific and management capabilities somewhat shaky. However, some of the slack was picked up by endowed funds, and our field station became part of the Smithsonian-wide Marine Science Network, joining the ranks of our “big brothers,” the Environmental Research Center at Chesapeake Bay, the Marine Station in Florida, and the Tropical Research Institute in Panama.

It is gratifying to find that half the papers in this volume of the *Smithsonian Contributions to Marine Science* series emanated from our CCRE program and the Carrie Bow Marine Field Station. The scientific advances



FIGURE 12. Examples of recent projects conducted at Carrie Bow. Top row: left, diver sampling fish larvae in situ, a project on larval rearing and molecular identification headed by Carole Baldwin and Lee Weigt; right, Juan Sanchez setting up in situ experiment for study of gorgonian ecology and growth. Middle row: left, Randi Rotjan recording fish bites on coral (*Porites*) on the reef shallows (inset below: larval fish [*Rypticus*] reared by the Baldwin team in the Carrie Bow seawater system to develop characteristics used in identification of adults); center, colonial ciliates (*Zoothamnium*), barely 15 mm tall, with bacterial ectobiont, dwell on mangrove peat and are studied by Joerg Ott's group; right, collaborator Kay Vopel measuring the microclimate surrounding *Zoothamnium*, primarily the oxygen versus hydrogen sulfide balance. Bottom row: left, Klaus Ruetzler recording progress of an excavating encrusting sponge (*Cliona*) that competes with temperature-stressed coral (*Diploria*) (center); right, new records of sponge disease are exemplified by this specimen (*Callyspongia*).

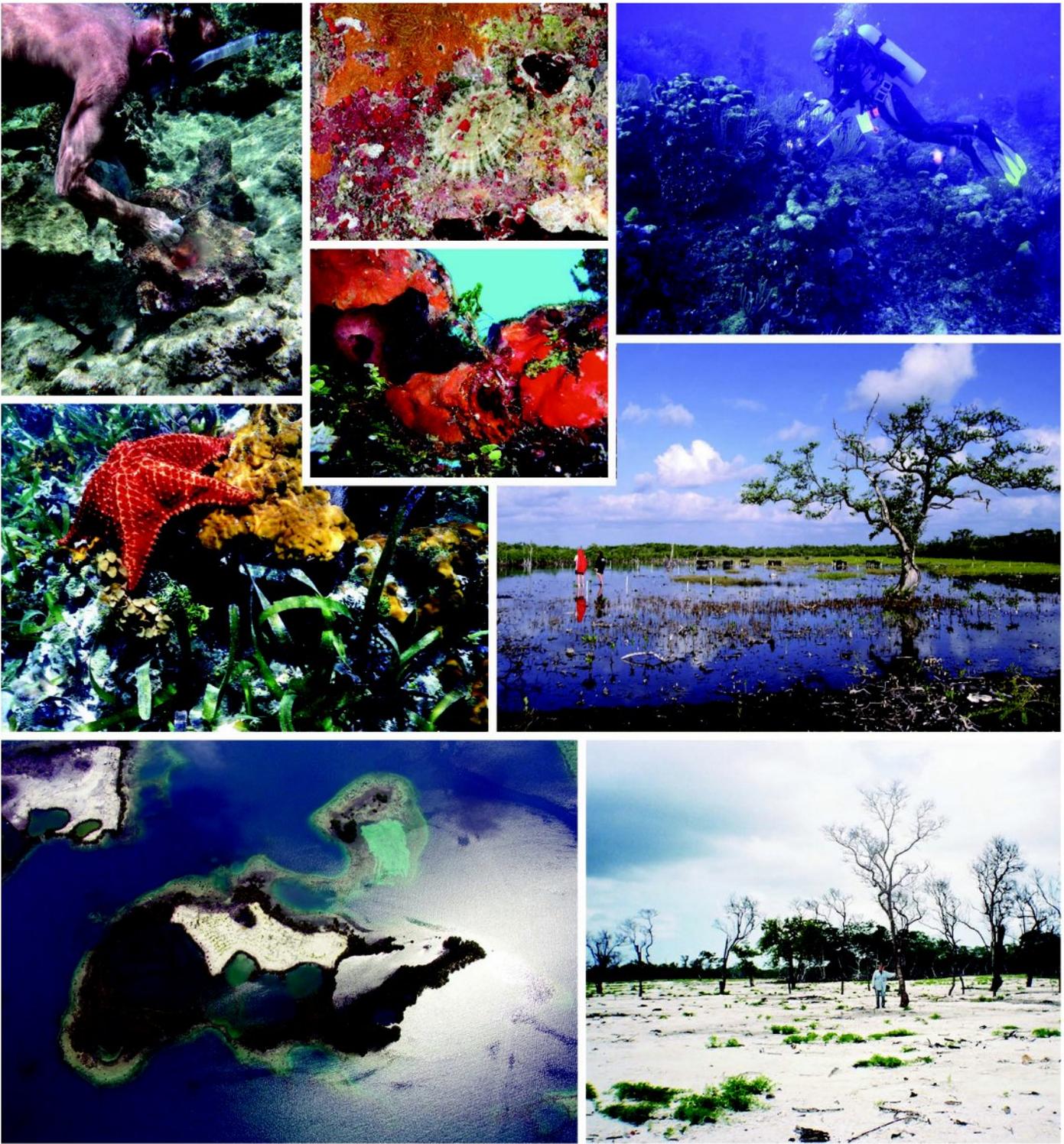


FIGURE 13. Research in progress and unanticipated new opportunities. Top row: left, Klaus Ruetzler initiated (with Carla Piantoni) a study of cryptic and cave-dwelling reef communities in shallow-water (center, upper photo) and deep-water (center, lower photo) habitats with little or no light exposure; right, Laurie Penland assists recording cave fauna using a digital HD video camera. Middle row: left, water warming during hurricanes killed many shallow-water corals in the Pelican Cays, which became overgrown by sponges (*Chondrilla*) that benefit starfish (*Oreaster*) as a source of food, thus starting a new ecological cycle; right, clear-cutting of mangrove and filling in resulting tidal flats with coral sand for “land development” started here at Twin Cays in the 1990s and continued at the Pelican Cays. Bottom row: left, Manatee Cay shown in 2008; right, this environmental disaster, recently stopped by the government of Belize, offers opportunities to study parameters of recovery of stressed and depleted marine and terrestrial communities.

achieved through CCRE research indicate that our decisions and actions over the years have blazed a fertile trail for the future of our science.

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