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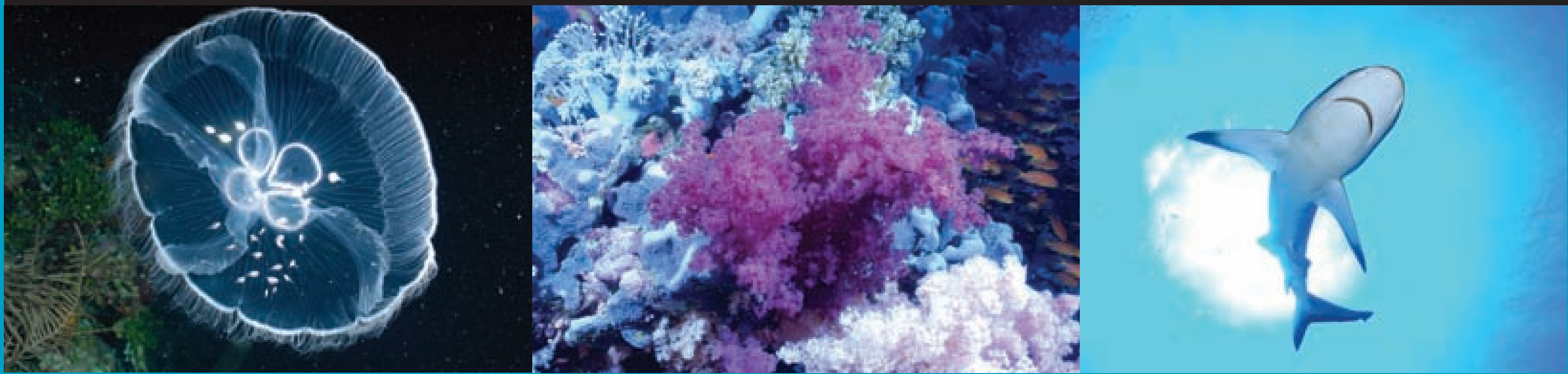

Proceedings of the Smithsonian Marine Science Symposium

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

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WASHINGTON D.C.
2009

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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Foreword

Nearly two-thirds of Earth's surface is covered by the ocean, a global system essential to all life. Impacts on one part of the ocean can have worldwide effects. The ocean moderates our climate, provides valuable resources, and produces at least half the oxygen we breathe: it makes our planet livable. We know little, however, about the physical, chemical, geological, and biological aspects of this crucial life support system.

The Smithsonian Institution, in efforts to increase knowledge about the ocean, has established a network of marine laboratories that monitors coastal habitats along a latitudinal gradient from the Chesapeake Bay through the Indian River Lagoon to the Mesoamerican barrier reef and on both sides of the Isthmus of Panama. The maintenance of long-term research projects and environmental monitoring is crucial to understanding changes that exceed in time the professional career of any given scientist. The information gained from such studies at stable sites enables scientists to differentiate between long-term changes and local or short-term environmental variations. Results contribute to our knowledge of systematics and ecology, physiology, behavioral sciences, geology, and paleoecology.

Our marine science universe comprises Smithsonian staff scientists and external collaborators and encourages the next generation of scientists, graduate students, and fellows. This symposium presents a Smithsonian-wide sample of marine science results.

Ira Rubinoff
Smithsonian Institution
Acting Under Secretary for Science, 2007–2008

Executive Summary

The results of the Smithsonian Marine Science Symposium, convened by the Marine Science Network on 15–16 November 2007 in Washington, D.C., are reported in 39 papers in this volume. These proceedings cover a wide range of marine research studies that demonstrate the breadth and diversity of science initiatives supported by the Smithsonian Marine Science Network. The first section treats an overview of the Smithsonian Marine Science Network established in 1998, and a brief background and history of multidisciplinary investigations spanning more than 37 years for each of the four 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 in this volume 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. The volume includes contributions on historical and geological aspects of coral reef and mangrove development; on biodiversity, developmental biology, and evolution (including molecular genetics) of sponges, cnidarians, sipunculan worms, crustaceans, and fishes; on ecology and population dynamics of algae, sponges, bryozoans, zooplankton, and miscellaneous invasive species; on environmental parameters, including pollutants, oceanographic factors, and hydrological regimes, and their effects on primary and secondary productivity, bleaching of symbiotic foraminiferans, benthic community structure, herbivory, development of toxic algal blooms, and land–sea connectivity in coastal habitats, that is, temperate bays and lagoons and tropical reefs and mangroves; and on conservation and education initiatives encompassing a range of organisms from sponges and corals to sea turtles, as well as communities such as tidal marshes, mangrove swamps, and coral reefs. As we prepare to face the challenges of rapidly accelerating biodiversity loss and global environmental stresses, particularly in highly vulnerable tropical shallow-water ecosystems such as reefs and mangroves, the focus of our scientific expertise on the member laboratories of the Marine Science Network has, during decades of documentation, established ecological standards that will help us monitor and evaluate future changes or trends and contribute to forthcoming education and conservation initiatives.

Michael A. Lang
Smithsonian Institution
Office of the Under Secretary for Science
April 2009

Introduction to the Smithsonian Marine Science Network

Michael A. Lang

ABSTRACT. The "Smithsonian Marine Science Symposium" contained more than 70 oral and poster presentations by Smithsonian scholars and collaborators and represented the first major dissemination of marine research results since the establishment of the Marine Science Network (MSN) in 1998. The MSN operates a unique array of laboratories and research vessels that spans the latitudinal gradient of the western Atlantic (Chesapeake Bay, Indian River Lagoon, Mesoamerican Barrier Reef, and Panamanian Coast) and crosses the isthmus of Panama. The Network is dedicated to understanding the rich biodiversity and complex ecosystem dynamics that sustain coastal processes and productivity. We study evolutionary, ecological, and environmental change in the ocean's coastal zones, increasing scientific knowledge of these environments and improving society's appreciation of the ocean's effect on our lives. Coastal environments are of immense economic and environmental importance and comprise 95% of the ocean's fisheries. Our coasts are the most densely populated and fastest growing communities in the USA. The MSN ensures integrated support of "Discovering and Understanding Life's Diversity," a core Smithsonian scientific mission. The MSN's goals are to ensure that the whole of the integrated Network is larger than the sum of its parts, leading to enhanced productivity through collaborative and comparative research, marine infrastructure development and support, professional training and outreach, and effective allocation of resources.

INTRODUCTION

The "Smithsonian Marine Science Symposium" was held 15–16 November 2007 to celebrate individual and long-term pan-institutional marine research, with a particular focus on highlights of the first ten years since the establishment of the Marine Science Network (MSN) in 1998. The symposium was convened by the Office of the Under Secretary for Science and represented the first gathering, of this magnitude, of Smithsonian marine scientists. The symposium presented marine research findings by Smithsonian scholars and their collaborators with emphasis on marine biodiversity, evolution, and speciation; biogeography, invasive species, and marine conservation, including life histories and microbial and behavioral ecology; and forces of ecological change in marine systems. The symposium carried on a tradition of Smithsonian marine science that began nearly 150 years ago and resulted in some of the world's foremost collections of marine specimens. More than 70 presentations

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and posters discussed results of marine research from the Chesapeake Bay, Indian River Lagoon and Florida Keys, the Mesoamerican Barrier Reef in Belize, the Atlantic and Pacific Coasts of the Isthmus of Panama, and other international research sites. Thirty-nine papers from this symposium are presented in this 38th volume of *Smithsonian Contributions to the Marine Sciences*, and additional marine education posters reside on http://www.si.edu/marinescience. Smithsonian speakers included marine research leaders, collaborators, and fellows from the Smithsonian Environmental Research Center, National Zoological Park, National Museum of Natural History, Smithsonian Marine Station at Fort Pierce, Caribbean Coral Reef Ecosystems Program, Smithsonian Tropical Research Institute, and the Office of the Under Secretary for Science.

The Smithsonian Institution operates a unique network of coastal laboratories and long-term research sites on the east coast of North and Central America that extends along the western Atlantic Ocean and bridges the Panamanian isthmus from the Caribbean Sea to the Pacific Ocean (Figure 1). Scientific diving supports a significant amount of Smithsonian marine research throughout the Network and internationally (Lang and Baldwin, 1996; Lang, 2007).

The Marine Science Network concept was developed in 1998 from the bottom up and has achieved the following important milestones:

1998: Formalization of a pan-institutional Smithsonian Marine Science Network initiated at two-day inaugural workshop at Smithsonian Environmental Research Center, with more than 50 Smithsonian Institution participants.
1999: Dedication of new Carrie Bow Cay Marine Field Station.
1999: Dedication of new Smithsonian Marine Station at Fort Pierce.
2000: MSN concept and infrastructure allocations approved by the Under Secretary for Science.
2001: Launch of the MSN website www.si.edu/marinescience.
2001: Annual MSN Calls for Proposals for infrastructure, marine research awards, and postdoctoral fellowships.
2003: Dedication of Bocas del Toro Marine Laboratory.
2006: Science Executive Committee review of Smithsonian marine science, including MSN.
2007: Formulation of Big Questions in Marine Science:
1. What are the major spatial and temporal patterns in distribution of biodiversity?
2. How does biodiversity, and the loss of biodiversity, affect the functioning of ecosystems?
3. How are humans changing the magnitude and distribution of biodiversity and what are the patterns and consequences?
2007: Smithsonian Marine Science Symposium.

The MSN is administered as a pan-institutional program through the Office of the Under Secretary for Science. It is governed by a seven-member Steering Committee composed of Michael Lang (Office of the Under Secretaray for Science), Anson Hines (Smithsonian Environmental Research Center), Eldredge Bermingham (Smithsonian Tropical Research Institute), Klaus Ruetzler (National Museum of Natural History), Robert Fleischer (National Zoological Park), Valerie Paul (Smithsonian Marine Station at Fort Pierce), and Phillip Taylor (National Science Foundation). Additional Smithsonian scientists participate by invitation in MSN research proposals and postdoctoral fellowship review panels, MSN symposia and workshop committees, and special projects. Support for MSN infrastructure, research, and postdoctoral fellowships is provided by the Office of the Under Secretary for Science's Johnson and Hunterdon Oceanographic Research Endowments.

There are four main unifying disciplinary themes to Smithsonian marine research: systematics, evolutionary biology, ecology, and geology. Biogeography is a key research element, linking systematics, ecology, and evolutionary biology. Mechanisms of biogeographic isolation are central elements in evolutionary theory, population dynamics, conservation biology, and patterns of biodiversity. Biogeographic patterns are crucial data in the determination of introduced and native species. Site-specific, long-term measurements of environmental variables allow for analysis of change over multiple time scales, which is necessary to detect patterns in typically complex ecological data. The Smithsonian Marine Science Network is uniquely positioned to monitor long-term change at its component sites. It has an extensive array of programs that address many of the most pressing environmental issues in marine ecosystems, including biological invasions, eutrophication, harmful species and parasites, plankton blooms and red tides, linkages among coastal ecosystems, global warming including sea-level rise, El Niño/La Niña effects, UV radiation impacts, habitat destruction, fisheries impacts, ecology of key habitats (estuaries, coral reefs, mangroves, seagrasses, wetlands), and biodiversity inventories.

The Smithsonian's marine education programs consist of public outreach and professional training. A series

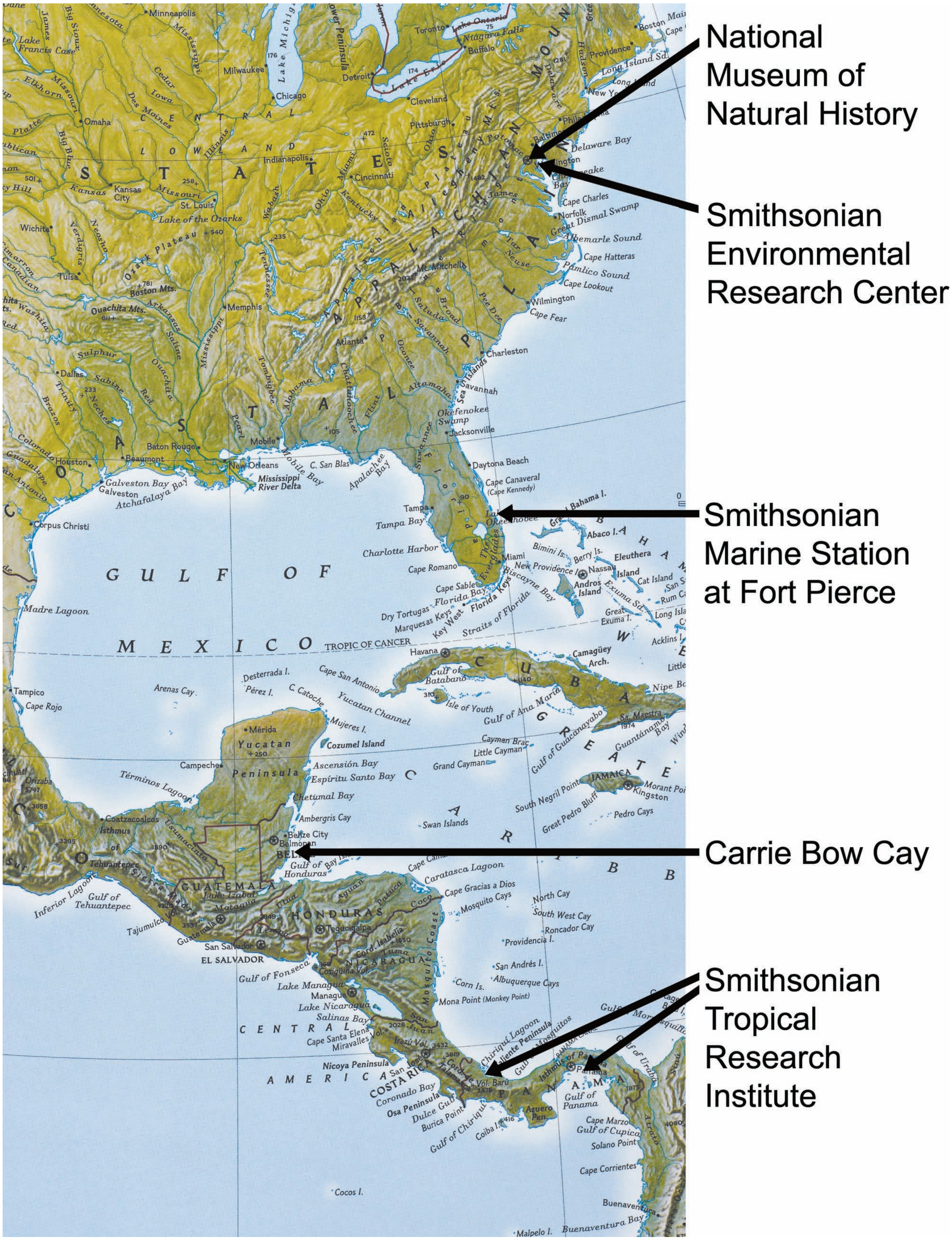

FIGURE 1. Map showing locations of the Smithsonian Marine Science Network members.

of these activities are aimed at promoting awareness and conservation of marine environments and at communicating the Smithsonian's research findings to the general public. By integrating research with education, the Smithsonian produces tomorrow's discoverers while pursuing today's discoveries. The public is engaged with interactive exhibits and scientists (e.g., the National Museum of Natural History's Sant Ocean Hall), symposia, popular books, lectures, and films about the marine environment. The Smithsonian Marine Science Network contributes to the public interest by disseminating novel environmental information around the globe. Its research helps build a solid foundation for informed decisions about environmental policy, natural resource management, and conservation.

Other recent coordinated Smithsonian marine science efforts of note are marine-terrestrial flora and fauna of Cayos Cochinos Archipelago, Honduras (Guzman, 1998), natural history of the Pelican Cays (Macintyre and Rützler, 2000), the Twin Cays mangrove ecosystem, Belize (Macintyre et al., 2004), and investigations of the marine fauna and environments of Bocas del Toro, Panama (Collin, 2005). Smithsonian taxonomic field guides and keys of algae, invertebrates, and fishes (Littler and Littler, 2000; Collin et al., 2005; Robertson, 2009) are valuable tools for biologists, divers, and fishermen alike.

Marine Science Network Mission and Vision

The MSN mission is dedicated to understanding the rich biodiversity and complex ecosystem dynamics that sustain coastal processes and productivity, and its vision is "to increase scientific knowledge of marine coastal environments and to improve society's appreciation of the ocean's effect on our lives."

Marine Science Network Goals

The MSN provides integrated support of "Discovering and Understanding Life's Diversity," a core scientific mission of the 2005–2010 Smithsonian Science Strategic Plan. The MSN ensures that the whole of the integrated Network is greater than the sum of its parts, leading to enhanced productivity through collaborative and comparative research facilitated by increased inter-unit coordination, marine infrastructure development and support, professional training and outreach, effective allocation of research funding, and transparent management, participation, and support for Smithsonian marine scientists through availability of shared resources and facility access.

SMITHSONIAN ENVIRONMENTAL RESEARCH CENTER (CHESAPEAKE BAY)

The Smithsonian Environmental Research Center (SERC) advances stewardship of the biosphere through interdisciplinary research and education. With a resident staff of more than 100 scientists, technicians, fellows, and students, SERC has experienced significant growth in the last few years. The SERC laboratories, educational facilities, and primary field sites are located 25 miles east of Washington, D.C., on the western shore of Chesapeake Bay. Its campus includes a growing complex of offices, laboratories, maintenance shops, a library, housing, and facilities for public programs. A dock, fleet of research vessels, dive locker, wet laboratory, aquarium room, and large fish-weir are used in support of estuarine research.

The greatest resource at SERC is its main research site on the Rhode River subestuary, which includes more than 1,072 ha of land and 26 km of undeveloped shoreline of the Chesapeake Bay. Since 1965, SERC's long-term studies have focused on the interactions among ecosystems in complex landscapes, tidal marshes, and estuaries. With the Rhode River site as its hub, SERC research radiates to sites around the world to address effects of global change, landscape ecology, coastal ecosystems, and population and community ecology. Much of SERC's comparative research across latitudes extends to the other sites of the MSN and includes studies of mangrove biocomplexity, invasive and native species biodiversity, estuarine food webs, land use impacts linked to water quality, carbon processing and global change, nutrient loading and low dissolved oxygen, ecosystem management of fisheries and crucial habitats, and life history patterns and evolution. Research at SERC focuses on five grand environmental challenges (Hines, 2009): (1) impacts of atmospheric change on climate, sea level, ultraviolet radiation, pollutant deposition, and carbon balance; (2) impacts of watershed nutrient discharges causing harmful algal blooms, depletion of oxygen, and destruction of submerged vegetation; (3) food web disruption by pollution and overfishing; (4) invasive species; and (5) landscape disturbance by agriculture and development.

Goals of SERC in marine education include professional training (interns, graduate students, postdoctoral fellows, and visiting scientists), teacher training, site visits and public programs, and distance learning.

NATIONAL ZOOLOGICAL PARK (WASHINGTON, D.C.)

The Smithsonian's National Zoological Park (NZP) was founded in 1889. Its mission is to provide leadership in animal care, science, education, and sustainability. Approximately 2,000 individuals of 400 different species constitute its animal collection. The NZP consists of a 163 acre urban park located in Rock Creek Park in northwest Washington, D.C., and the 3,200 acre Conservation and Research Center in Front Royal, Virginia, emphasizing reproductive physiology, analysis of habitat and species relationships, and the training of conservation scientists.

The National Zoological Park conducts international marine research on sea turtles and sea birds, ecology of bottlenose dolphins, Weddell seal lactation, life history and reproductive strategies of gray and harbor seals, nutritional ecology of sea otters, and cryopreservation of endangered coral species. Marine exhibits include the Seal and Sea Lion Pool and the Invertebrate Exhibit, which opened in 1987, where marine invertebrates comprise 75% of its live collections on display. The NZP's tools to inspire, train, and empower successive generations to care for the world's biological diversity are its exhibits, science, outreach, and education programs. Ultimately, efforts must be oriented toward protecting wildlife and other forms of biological diversity so that we, and future societies, continue to enjoy the incalculable benefits of our natural world.

NATIONAL MUSEUM OF NATURAL HISTORY (WASHINGTON, D.C.)

The National Museum of Natural History (NMNH) has a distinguished history of more than 150 years of sampling and collections-based research. Major collections represent algae and dinoflagellates, foraminifera, sponges, cnidarians, ctenophores, worms, crustaceans, mollusks, bryozoans, echinoderms, tunicates, fishes, marine reptiles, birds, and mammals), now numbering more than 33,000,000 specimens of plants and animals. Of approximately 2,415 families of marine invertebrates, nearly 67% are represented in the NMNH invertebrate collection, which is not limited solely to the diversity-rich tropics. The NMNH provides professional collection management services to the National Science Foundation United States Antarctic Program (USAP) and the international scientific community. A primary focus of this project is improving access to the collections through its cataloging (inventory) program (more than 900,000 USAP specimens) and loan program. More than 170,000 USAP specimens in 138 separate transactions were either lent or returned from loan between 1995 and the end of 2004, supporting the research efforts of scientists in 22 countries. Several hundred lots of archive samples from the Palmer Long-Term Ecological Research Program were also accessioned (Lemaitre et al., 2009).

The focus of marine science at NMNH addresses the diversity of marine life, where species occur, how they are related to each other, how marine diversity developed and how it is maintained, what are the human impacts on marine life, and how marine life-forms are used by people.

The Museum administers the Laboratories of Analytical Biology for state-of-the art molecular work and two marine field stations (Carrie Bow Cay, Belize, and Smithsonian Marine Station at Fort Pierce, Florida), member facilities of the MSN. Since 1966 the Museum has funded the *Atoll Research Bulletin*, which publishes research reports on the geology and ecology of islands and their adjacent coral reef and mangrove communities in tropical sites around the world.

The NMNH Ocean Initiative comprises the Sant Ocean Hall, the Ocean Web Portal, the Sant Chair in Marine Science, and interdisciplinary marine research at NMNH. Virtual access to the Museum's key marine collections is being created. The Initiative aims to train future generations of marine scientists and educate the public about, and raise awareness of, the importance of the ocean as a global system.

SMITHSONIAN MARINE STATION AT FORT PIERCE (FLORIDA)

The Smithsonian Institution has had a presence in Fort Pierce, Florida, since 1969 and was known then as the Fort Pierce Bureau. From 1969 to 1981, the Fort Pierce Bureau carried out studies including underwater oceanography with research submersibles, a survey of the Indian River Lagoon, coral reef research, and research on life histories of marine invertebrates, partly in collaboration with the newly formed Harbor Branch Foundation (now the Harbor Branch Oceanographic Institution at Florida Atlantic University). In 1981, the Fort Pierce Bureau was dissolved, and in its place the Smithsonian Marine Station at Link Port was formally recognized as an organizational unit under the auspices of the National Museum of Natural History. The Station took over the barge, acquired originally by the Smithsonian in 1973 from federal surplus, that was docked at the Harbor Branch campus. In 1996, the Smithsonian purchased, from the MacArthur Foundation, 8 acres of property 7 miles south near the Fort Pierce Inlet with easement access to the Indian River Lagoon. St. Lucie County enacted a 25 year lease of a county dock and adjacent land at a site on the inlet across from the Station, whose main building was completed and dedicated in 1999.

The Smithsonian Marine Station at Fort Pierce (SMSFP) is a marine science research center located on the Indian River Lagoon along 156 miles of Florida's central Atlantic coast. The Indian River Lagoon is a long, narrow, and shallow estuary adjacent to the Atlantic Ocean, separated by a strip of barrier islands. Biologists at SMSFP have the advantage of working just 20 miles from the Florida current, a stream of warm water from the Caribbean that moves northward past Florida's coastline as part of the larger, complex system of currents known as the Gulf Stream. The current carries with it many tropical marine organisms, allowing researchers to work at the interface of the Northern Hemisphere's tropical and temperate regions. Situated in a biogeographic transitional zone between the temperate and subtropical provinces, the SMSFP facility provides access to an extraordinary diversity of marine and estuarine species and to a variety of habitats, which include mangroves, salt marshes and sandy beaches, rocky intertidal substrates, seagrass beds, mud and sand flats, coral reefs, worm reefs, *Coquina* hard bottoms, deep coral rubble zones, shallow- to deep-water sandy plains, and the blue waters of the Gulf Stream.

The Marine Station supports and conducts scholarly research in the marine sciences, emphasizing studies of biodiversity, life histories, and ecology of marine organisms (Paul et al., 2009). The results of this research enable policy makers to make informed environmental decisions in guiding conservation and sustainable management of marine resources, as well as providing the basis for innovative applications in medicine, aquaculture, and the effective balance between development and conservation. For Smithsonian scientists, the SMSFP provides an important link with other MSN facilities in the tropics at the Smithsonian Tropical Research Institute (STRI) in Panama and Carrie Bow Cay in Belize and in the temperate region, the Smithsonian Environmental Research Center on the Chesapeake Bay.

The facilities at the Smithsonian Marine Station at Fort Pierce include an 8,000 square foot facility that houses a histology laboratory, an electron microscopy lab, a confocal microscope, a combination electrophoresis/DNA/chemistry laboratory, a photographic darkroom, flow-through seawater tables and aquaria, an industrial shop, and offices and laboratories for visiting scientists and fellowship recipients. The 39-foot R/V *Sunburst* and two smaller vessels are used for scientific diving, dredging, and trawling in the Indian River Lagoon, Continental Shelf, and Gulf Stream.

The Marine Station's educational efforts include postdoctoral fellows and interns, public events and lectures, school programs and public tours, a web site, the Indian River Lagoon Species Inventory, and the Marine Ecosystems Exhibit, which was established in 2001 with the following ecosystems on display: coral reef, seagrass, mangrove, hardbottom and nearshore habitats, and *Oculina* reef).

CARIBBEAN CORAL REEF ECOSYSTEMS PROGRAM (CARRIE BOW CAY, BELIZE)

Coral reefs are unique biogeological structures that thrive in clear, nutrient-poor (oligotrophic) tropical oceans and support a rich and diverse biological community. Reef systems are driven by the symbiosis between scleractinian corals and microscopic dinoflagellate algae (zooxanthellae) as their chief energy source. The largest, best developed, least polluted, and least commercially exploited coral reef in the Atlantic region is the Mesoamerican Barrier Reef in Belize. It is a complex of reefs, atolls, islands, oceanic mangroves, and seagrass meadows that extends over 160 km. For its unique characteristics and unperturbed condition, the Belize barrier reef has been declared a World Heritage Site.

In the early 1970s, Rützler et al. (2009) discovered the formidable qualities of the Belize (then British Honduras) barrier reef. After careful comparison with other locations in the western Caribbean, it was chosen as the site of an interdisciplinary long-term study of systematics, ecology, behavior, and evolution of reef organisms and the dynamics and historical development of reef communities (Rützler and Macintyre, 1982). Carrie Bow Cay, only three hours by plane and boat from Miami, was found to be the ideal logistical base because of its location on top of the barrier reef, only meters away from a variety of habitat types (reef flat, spur and groove, deep fore-reef slope, patch reefs, seagrass meadows, and mangroves), and its undisputed ownership by a Belizean family able to cater to all Smithsonian needs for lodging, food, local transportation, and contacts with government.

In 1985, as part of the U.S. Congress Caribbean Basin Initiative, the National Museum of Natural History received an increase to its budget base to continue and intensify study of Caribbean coral reef ecosystems. These funds allowed for the expansion of research facilities on

Carrie Bow Cay and the update of CCRE equipment. In the years since, CCRE has accomplished the following: amassed thousands of specimens of marine plants, invertebrates, and fishes, which are organized in an enormous database; assisted the government of Belize in shaping and justifying its coastal conservation policy; participated continuously in the Caribbean-wide reef monitoring network (CARICOMP); established the first meteorological oceanographic monitoring station in coastal Belize; and, above all, published well over 850 scientific papers in reviewed journals, as well as several books, doctoral dissertations, popular articles, and photo and video documentaries. Between 60 and 80 scientists use Carrie Bow Cay each year as a part of ongoing CCRE research.

The Carrie Bow Cay Laboratory serves primarily in support of SI marine scientists' research projects and their external collaborators. Seasonal hurricanes during the past 35 years could not destroy Carrie Bow Cay facilities to the extent that a devastating fire did in December 1997. Improved facilities now include dry and wet labs, housing, generator, compressor, small boats and scuba cylinders, and essential facilities such as solar power, a running-seawater system, and weather station.

CCRE's educational and outreach programs include its Belize teachers' mangrove workshops, publications, symposia, advisory consults with Belizean Ministries, and fellows and interns.

SMITHSONIAN TROPICAL RESEARCH INSTITUTE (REPUBLIC OF PANAMA)

The Smithsonian Tropical Research Institute's (STRI) marine research program in the Republic of Panama dates to 1964 when small laboratories were established on the Pacific and Caribbean coasts within the former Canal Zone. Today, STRI operates marine stations at Bocas del Toro and Galeta Point in the Caribbean and the Naos marine laboratory complex in the Pacific. Until 2008, the R/V *Urraca*, a 96 foot nearshore coastal oceanographic vessel, was outfitted with remotely operated vehicle, scientific diving, and dredging capabilities, and was operated under University National Oceanographic Laboratory System (UNOLS) research fleet standards.

At the Panama Canal, the Isthmus of Panama narrows to less than 100 km, separating oceans that are very different tropical marine ecosystems. The Caribbean is a relatively stable ocean, with small fluctuations in temperature and relatively low tidal variation. Its transparent, nutrient-poor waters are ideal for the growth of reefs, and it ranks just behind the Indian Ocean and the Indo-West Pacific in terms of numbers of marine species. The tropical eastern Pacific, in contrast, exhibits much greater fluctuations in tides and temperature, with seasonal upwelling locally and longer-term variation resulting from the El Niño southern oscillation cycle. Its more nutrient-rich waters support commercial fisheries of major importance. The creation of these two distinct marine realms by the rise of the Isthmus of Panama during the past 10 million years also contributed to the formation of the modern biological and geological world. During this interval, the Gulf Stream was established, the mammals of North America conquered a newly connected South America, the Ice Ages began, and modern man arose. The Isthmus played a major role in this history, and set in motion a fascinating natural experiment, as the animals and plants of the two oceans went their separate evolutionary ways.

There are also major differences within each ocean. In the Pacific, seasonal upwelling of nutrient-rich waters is strong in the Gulf of Panama, where trade winds blow freely across the Isthmus, but absent in the Gulf of Chiriqui, where the high terrain blocks these winds. The more stable conditions in the Gulf of Chiriqui support the best developed coral reefs in the tropical eastern Pacific. On the Caribbean side, the San Blas Archipelago is bathed in clear oceanic waters, whereas the reefs and mangroves of the enormous Chiriqui Lagoon of Bocas del Toro are enriched by runoff from the land. Thus, Panama can be considered a nation of four ocean types, providing unique opportunities for understanding how and why marine ecosystems function as they do.

Understanding the history and ecology of Panama's diverse marine environments has been a major theme of STRI's research over the past four decades (Robertson et al., 2009). Major programs include between-ocean comparisons of physical and biological oceanography, geological reconstruction of events leading up to and following the rise of the Isthmus, studies of marine biodiversity, and analyses of the vulnerability of marine habitats to natural and anthropogenic change. In celebration of STRI's role in coral reef research, the Smithsonian's 150th anniversary, and the International Year of the Reef, the Smithsonian hosted the Eighth International Coral Reef Symposium in Panama in 1996. This meeting brought 1,500 reef scientists and managers to Panama from around the world and resulted in the publication of a two-volume proceedings (Lessios and Macintyre, 1997) and an international traveling exhibit that has already brought STRI's marine discoveries to Miami, the District of Columbia, Honduras, and Jamaica.

The Marine Environmental Sciences Program (MESP) at STRI collects and analyzes fundamental oceanographic information that provides critical information for studies such as El Niño and coral bleaching. The Panama Paleontology Project in Bocas del Toro seeks to record the history of the divergence between the two oceans over the past 10 million years and the evolutionary response of marine organisms to these changes. Results from this project are the geological reconstruction of the closure of the Isthmus of Panama 3 million years ago and the discovery of a major extinction event in the Caribbean about 2 million years ago. Through a combination of molecular and paleontological information, STRI's molecular evolution program has developed a model system for determining the rate at which organisms diverge genetically through time (Panama molecular clock). This achievement allows for the phylogenetic reconstruction of marine life elsewhere in the world.

Educational programs within STRI include a marine fellowship program, school group visits (Culebra Nature Center, Galeta Point Marine Lab, Bocas del Toro Lab), public seminars, advisory consults with the Panamanian government, and graduate courses.

CONCLUSION

The Smithsonian Institution is unique among federal agencies, research organizations, and universities with its investment in comprehensive, long-term marine studies of crucial ecosystems at a latitudinal gradient of stable sites. Thousands of marine science publications provide results and data for synthesis and a new baseline for modeling and forecasting. Continued opportunities remain for many important marine organisms to be identified by conventional and molecular techniques and described. Deep reefs are becoming increasingly important as a focal area to understand how the reef system in toto functions and to quantify their physical, chemical, and biological contributions to the shallow reefs that we have studied for more than three decades (Lang and Smith, 2006). Life histories require further analysis to aid ecological understanding and fisheries management. Thirty-five-year multidisciplinary databases allow for early detection and evaluation of community changes, invertebrate diseases, invasive species, and recruitment caused by environmental degradation and catastrophic events.

The MSN continues to provide support for individual and pan-institutional collaborative research, postdoctoral marine science fellows, marine science staff and infrastructure support, marine outreach and education, and workshops and symposia: for example, Bocas del Toro taxonomy; coral reef management; mangrove ecology of Twin Cays, Belize; marine genetics; sea turtle conservation and population management; seagrass and mangrove ecosystems; neogastropod evolution; marine invasives of the Gulf of Mexico; and marine invasive species across latitudinal gradients. Outcomes of the integration of the Smithsonian marine facilities and programs since 1998 are the facilitated freedom of movement of scientists between units and the increased collaborations and co-authored publications. The MSN was highlighted as a model for pan-institutional Smithsonian programs by the Smithsonian Science Commission in 2003. The most likely keys to its success were the bottom-up development of the Network concept, starting with the Institution's staff scientists, and the availability of research funding through the Office of the Under Secretary for Science to enable marine research and postdoctoral fellowships.

The Smithsonian Marine Science Network and the Smithsonian Scientific Diving Program provide the facilities and support for the efficient conduct of marine research. The primary objective of the marine research effort is the advancement of science. The deliverable is mainly in the form of peer-reviewed publications for dissemination throughout the scientific community and to the public.

The importance of the MSN is its contribution to the knowledge of complex ecosystems including seagrasses, mangrove islands, bays, estuaries, and coral reefs, and the preservation of these precious resources by learning about their rich biodiversity, function, and interconnectedness. Only a long-term commitment will allow us to understand the dynamics of coastal processes and organisms, obtain the cooperation of the public, and educate a new generation.

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Land–Sea Interactions and Human Impacts in the Coastal Zone

Anson H. Hines

ABSTRACT. The Smithsonian Environmental Research Center (SERC) conducts research on land–sea interactions to understand natural processes and human impacts in linked ecosystems of the coastal zone. Coastal ecosystems support great biological productivity and are of immense ecological and economic importance. In addition, more than two-thirds of the human population resides in the coastal zone, where human activities cause chronic and acute disturbance of every habitat and marked degradation of ecological balance and productivity. The Chesapeake Bay and its Rhode River subestuary are used by SERC as model study systems to conduct long-term, intensive monitoring and experiments. Research at SERC focuses on five grand environmental challenges: (I) impacts of atmospheric change on climate, sea level, ultraviolet radiation, pollutant deposition, and carbon balance; (II) impacts of watershed nutrient discharges causing harmful algal blooms, depletion of oxygen, and destruction of submerged vegetation; (III) food web disruption by pollution and overfishing; (IV) invasive species; and (V) landscape disturbance by agriculture and development. Research by SERC on these grand challenges serves to advise policy and management from improved stewardship of coastal resources.

INTRODUCTION

The coastal zone is of immense economic and environmental importance. More than 50% of the Earth's human population (3 billion people) resides in the coastal zone and relies on the goods and services of coastal ecosystems, and this number is expected to double by 2045 (Creel, 2003). Coastal communities are the most densely populated and fastest growing areas in the United States: 14 of the nation's largest 20 cities are in coastal locations; more than 50% of the U.S. population lives in 17% of the country's land, comprising coastal counties; this population concentration is expected increase to 70% within 25 years; and 23 of the 25 most densely populated counties encompass coastal cities and their surrounding sprawl (Crossett et al., 2004). The coastal environment includes the Earth's most biologically productive ecosystems, and this diverse environment includes unmeasured reserves of strategic minerals, oil and gas, and other nonliving resources. The coastal zone encompasses major hubs of global transportation and commerce and unparalleled opportunities for recreation and tourism, as well as the majority of fisheries and aquaculture industries. At the same time,

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these activities cause chronic and acute disturbance of every coastal habitat: overfishing has removed most large species at the top of the food web, and coastal waters receive most of the waste of urban centers and agricultural runoff of the coastal plain.

Research at the Smithsonian Environmental Research Center (SERC) focuses on land–sea interactions. Scientists at SERC study linked coastal ecosystems to understand natural processes and human impacts in the coastal zone. Ocean productivity is concentrated in the coastal fringe where nutrients run off the land and well up from the deep. The coastal environment includes the Earth's most biologically diverse ecosystems: estuaries, wetlands, mangroves, seagrasses, coral and oyster reefs, kelp forests, and pelagic upwelling areas. Bottom communities and water column processes of the photic zone are most tightly coupled in the nearshore shallows. Coastal waters comprise 95% of the oceans' fisheries. Thus, SERC research focuses on improved stewardship of these marine resources.

CHESAPEAKE BAY AND THE RHODE RIVER SUBESTUARY AS A MODEL SYSTEM

The Smithsonian Environmental Research Center utilizes the nation's largest estuary, Chesapeake Bay and its 177,000 km^2 watershed including six states and the District of Columbia (Figure 1), as its primary research landscape and main study site. In addition to SERC, this study area includes the Smithsonian's museum complex, zoological exhibits, and administrative offices. An area with a long American history of exploitation of coastal resources, the Chesapeake watershed is home to 17 million people, who are mostly concentrated in the urban centers and suburban sprawl of Baltimore, Washington, D.C., and Norfolk. Agriculture, particularly row crops, is the major land use of the Chesapeake watershed, and farming has been the major source of disturbance to the eastern deciduous forest for 400 years.

Established in 1965, SERC owns a unique 1,072 ha land holding for long-term descriptive and experimental studies of linked ecosystems in a model subestuary and subwatershed of Chesapeake Bay—the Rhode River, which is located 40 km east of Washington, D.C., and 10 km south of Annapolis, Maryland (Figure 2). The property at SERC includes cropland, forests in various successional stages, wetlands, and 26 km of undeveloped shoreline; this is the largest contiguous block of land dedicated to environmental research, science education, public access, and stewardship on the western shoreline of Chesapeake Bay. The 585 ha Rhode River subestuary is a shallow (maximum depth = 4 m), soft-bottom embayment in the lower mesohaline zone of the Bay. The facilities at SERC provide strategic support for research at the site and ready access to the rest of the Chesapeake watershed and estuary.

GRAND CHALLENGES OF COASTAL ENVIRONMENTAL RESEARCH

The purpose of this paper is to present examples that highlight SERC's coastal research on five grand environmental challenges. With data sets extending back to the 1970s and 1980s, SERC research monitors decadal-length changes to distinguish seasonal and annual fluctuations from long-term trends in the environment. Importantly, SERC research seeks to determine mechanistic understanding of the causes of change at multiple spatial scales ranging from global change to landscape, watershed, ecosystem, and community levels of organization. The land and long-term studies at SERC's Rhode River site afford multidisciplinary experimental analyses of mechanisms controlling ecological interactions. The research there addresses the grand challenges and advises environmental policy and management for improved stewardship of coastal resources.

Grand Challenge I: Impacts of Atmospheric Change

Human alterations of the atmosphere are causing rapid changes in climate, sea level, ultraviolet radiation, pollutant deposition, and ecosystem carbon balance. Research by SERC on the salt marshes of the Rhode River subestuary provides a good example of the ecological complexities of this challenge. B. G. Drake and colleagues have been conducting the world's longest running experimental manipulation of CO_2 on natural plant communities (1985 to present), which has been testing the effects of rising atmospheric CO_2 concentration in these salt marshes. The experiment measures response of the two dominant plant species at the site: *Spartina patens* and *Scirpus olneyi*. The experiment applied nine treatment combinations of three CO_2 levels in open-top chambers (ambient air at 340 ppm; elevated CO_2 at a twofold increase in concentration of 680 ppm; and a control treatment without chambers) crossed with types of patches (nearly monospecific *S. patens*; nearly monospecific *S. olneyi*; and patches with mixes of the two species) (Drake et al., 1989). Chambers were replaced exactly on replicate marked plots of the nine treatment

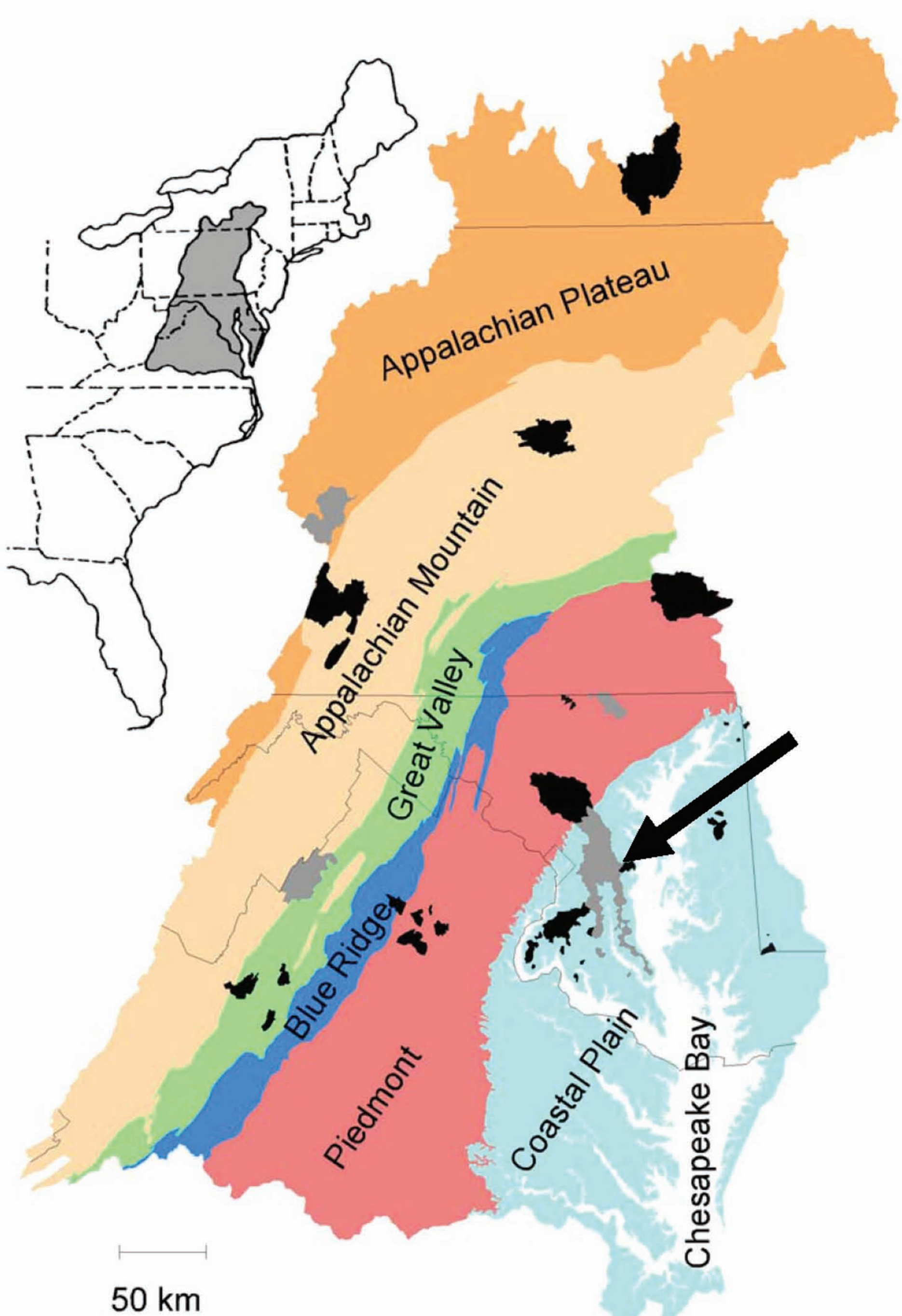

FIGURE 1. Map of Chesapeake Bay and its watershed with six physiographic provinces. Arrow indicates the location of the Smithsonian Environmental Research Center on the Rhode River subestuary and watershed. Darkened areas indicate 17 clusters of 500 subwatersheds that differed in land use and were monitored for stream discharges of nutrients.

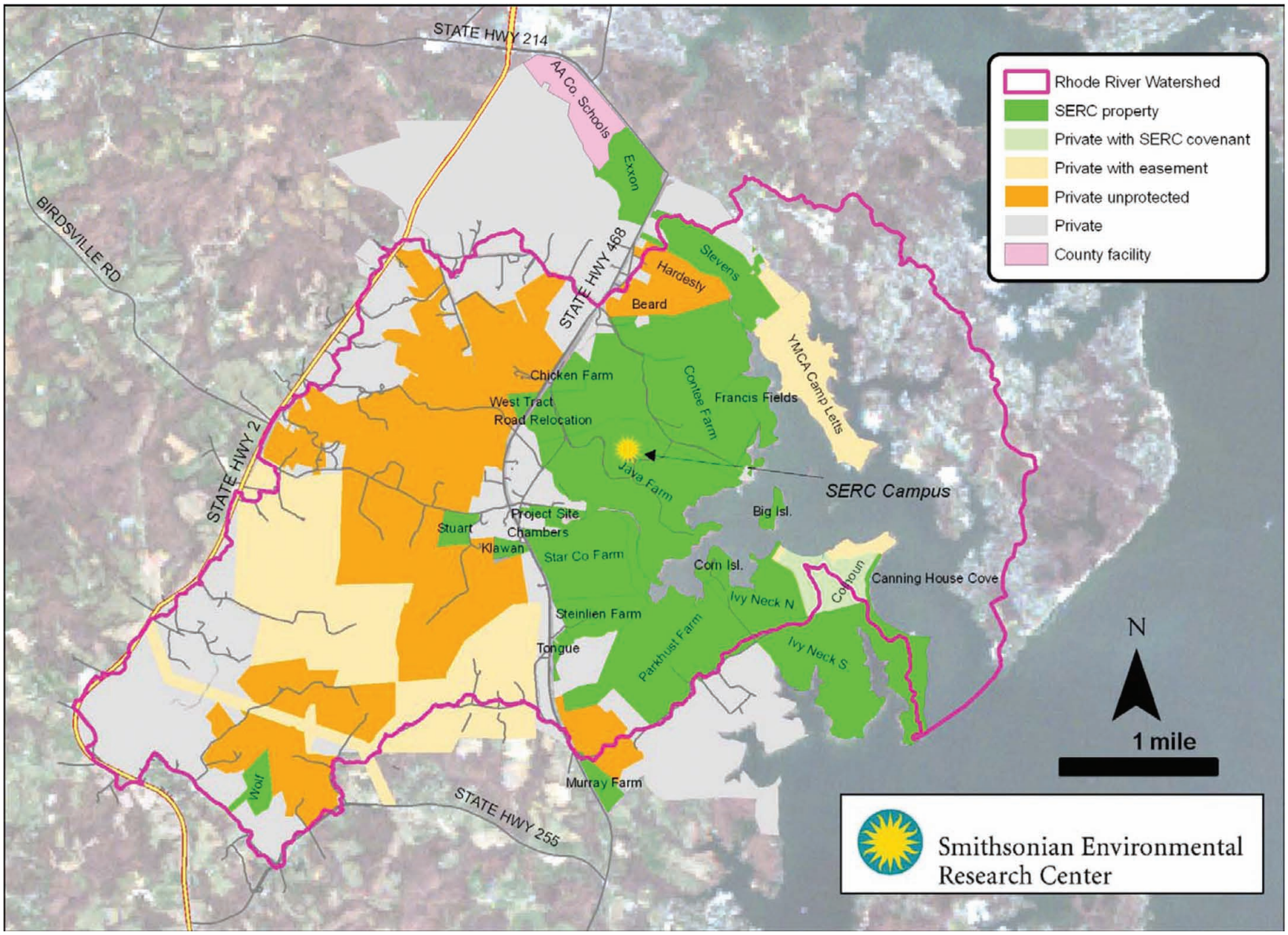

FIGURE 2. Map of land holdings (shaded green) of the Smithsonian Environmental Research Center (SERC) surrounding the Rhode River subestuary. Red outline shows the boundary of the watershed.

combinations for the duration of the growing season for the past 23 years (1995–2008). Photosynthesis and respiration were measured in each chamber during the growing season, and plant production was measured at the end of each season. As predicted, *Spartina patens* is a C_4 plant that responds weakly to rising CO_2, whereas growth and production were greatly stimulated in *Scirpus olneyi* as a C_3 plant (Drake and Rasse, 2003). However, the amount of stimulation of *S. olneyi* is significantly inversely dependent on salinity (i.e., water stress), with lower production in years of high salinities (i.e., low rainfall) (Rasse et al., 2005; and Figure 3).

Salt marsh research at SERC's Rhode River site also explores other ecosystem complexities. New research is tracking the fate of the carbon added by growth stimulation of the plants, which appears to be sequestered in the peat-forming roots of the salt marsh (Carney et al., 2007). Research conducted by J. P. Megonigal and colleagues at the same marsh study site compares effects of increased CO_2 interacting with nutrient additions to the marsh to determine whether peat accumulation is sufficient to keep up with rising sea level. Their initial results indicate that the peat accumulation is equivalent to the current rate of sea-level rise of approximately 3 mm year^{-2}, allowing the marsh to persist instead of becoming submerged. Additionally, a nonnative species, Phragmites australis, is rapidly invading the marsh site, similar to most others in the region (King et al., 2007); and its responses to the interaction of rising CO_2 and nutrients are unknown. The Chesapeake region has high levels of mercury deposition

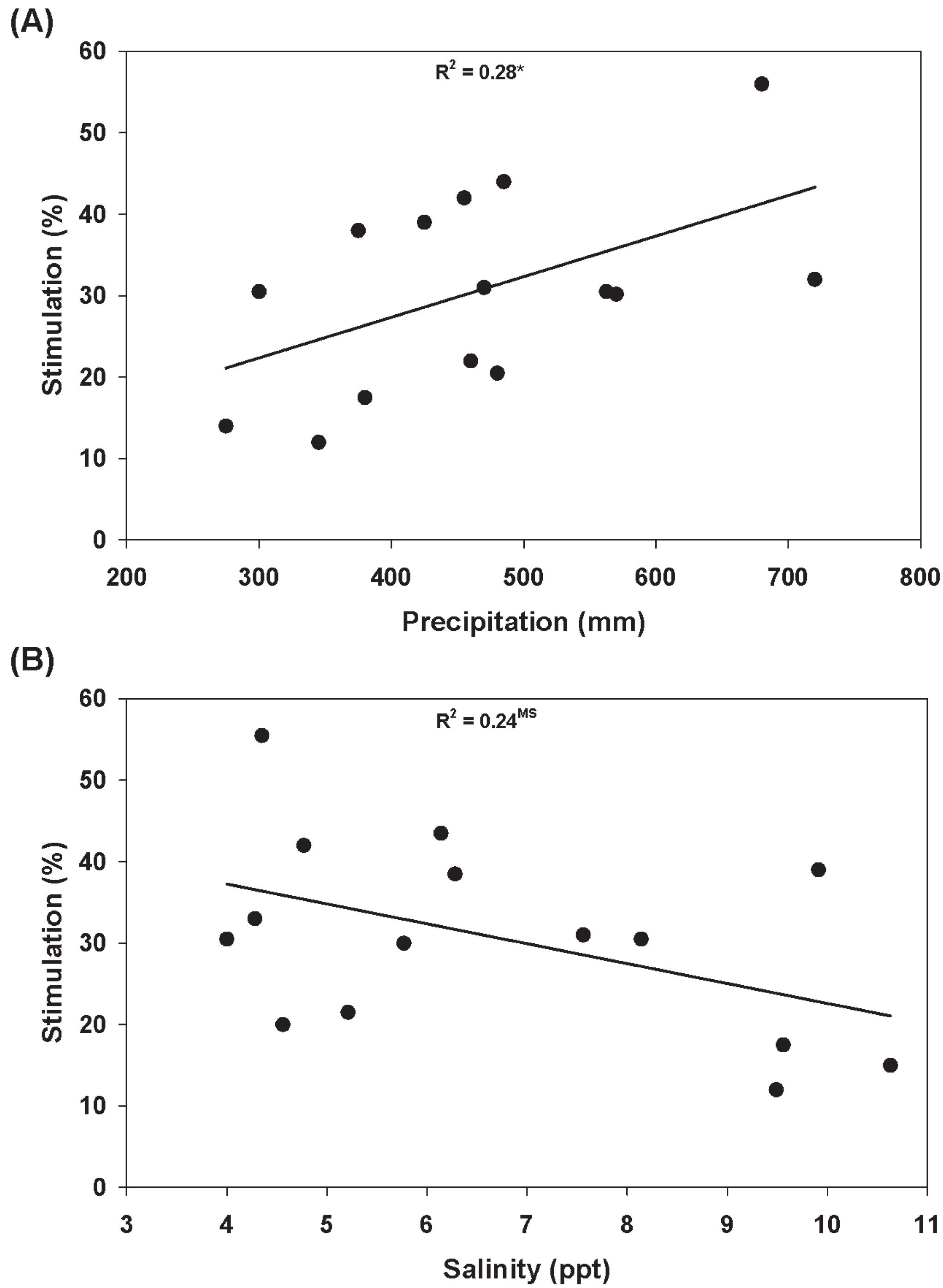

FIGURE 3. Effect of (A) precipitation and (B) salinity (ppt = parts per thousand) on the stimulation of photosynthesis by twofold increase in CO_2 concentration on the sedge *Scirpus olneyi* in open-top chambers placed on a salt marsh of the Rhode River subestuary during a 17-year period (1989–2003). (After Rasse et al., 2005.)

that is derived from coal-burning power plants. New work at the SERC salt marsh site shows that microbes rapidly activate the mercury (mercury-methylation) (Mitchell et al., 2008) deposited into marshes, thus feeding it into biological processes on the coastal food web (C. Mitchell and C. Gilmour, Smithsonian Environmental Research Center, 2008, personal communication).

Grand Challenge II: Impacts of Nutrient Loading

Over-enrichment of coastal waters with nutrients causes harmful algal blooms, depletion of oxygen, and destruction of submerged vegetation. Eutrophication in Chesapeake Bay and many other coastal systems is causing "dead zones" of anoxic and hypoxic waters along deeper bottom areas. A major focus of the restoration efforts of the Environmental Protection Agency's Chesapeake Bay Program has been to reduce nutrient loading by phosphorus and nitrogen runoff into the Bay. Long-term watershed and estuarine water quality monitoring by SERC at the Rhode River site and throughout Chesapeake Bay shows the dynamic interactions of stream discharge, nutrient inputs, and plankton responses affecting oxygen levels.

Watershed nutrient discharge occurs primarily in storm events and is related to both geologic position (e.g., Piedmont or Coastal Plain provinces of the Chesapeake watershed) and land use, especially development and agriculture (Figure 4). Plankton productivity is much higher in years with high runoff, which leads to plankton blooms (Figure 5). Long-term monitoring from 1986 to 2004 shows that water clarity (Secchi disc depth) and near-bottom oxygen levels have declined significantly in the Rhode River subestuary (Figure 6). Although oxygen levels at SERC's long-term monitoring station in the shallow edge of the Bay generally do not fall below alarming levels of approximately 6 ppm, oxygen levels in the deeper mainstem of the Bay drop to very low levels (Hagy et al., 2004) and occasionally spill into the mouth of the Rhode River, killing benthic organisms (A. Hines, personal observations).

With the decline in water clarity, light levels are not sufficient to support growth of seagrasses and other submerged aquatic vegetation, which had largely disappeared from the Rhode River subestuary and much of Chesapeake Bay by the early 1970s. These structured ecosystems are important nursery habitats for fish and crabs in coastal systems such as Chesapeake Bay. Recent SERC research

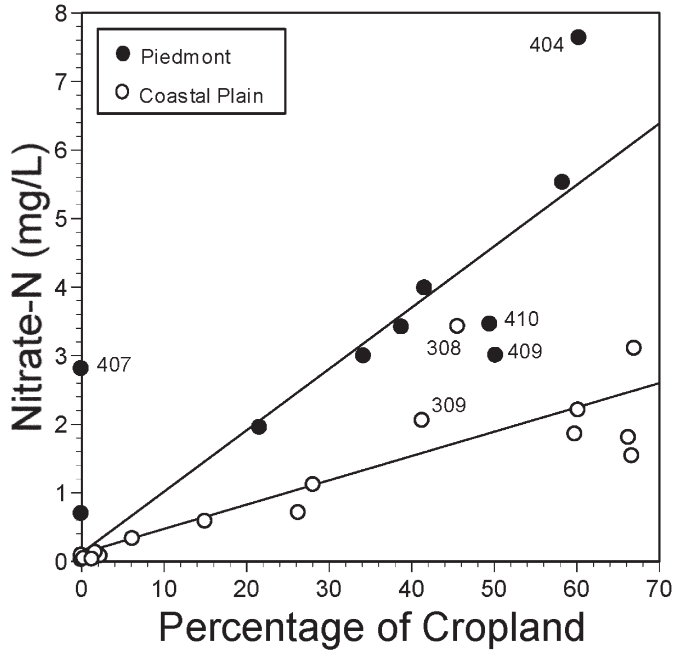

FIGURE 4. Effects of cropland on stream discharge of nitrogen for watersheds in the Piedmont and Coastal Plain physiographic provinces of Chesapeake Bay (see Figure 1). Nitrogen is shown as nitrate concentration on the *y*-axis; cropland is shown as a percentage of land use of the subwatershed area on the *x*-axis. (After Jordan et al., 1997.)

emphasizes the linkage of submerged aquatic vegetation to watershed characteristics (Li et al., 2007).

Grand Challenge III: Food Web Disruption by Pollution and Overfishing

Pollution and overfishing result in severe disruptions of coastal food webs (Jackson et al., 2001). The combined effects of low dissolved oxygen and loss of submerged aquatic vegetation comprise much of the major impact of pollution in coastal systems such as Chesapeake Bay. However, inputs of mercury and other toxic chemicals also markedly affect the food web as they become concentrated at its upper levels, often causing serious effects on seafood that affect human health (Krabbenhoft et al., 2007). Impacts of overfishing and habitat loss have resulted in the loss of sustainable stocks for nearly every fishery species in Chesapeake Bay and in nearly every coastal system worldwide. After a century of intense exploitation, disease, and ecosystem impacts, oysters, as the Bay's most productive

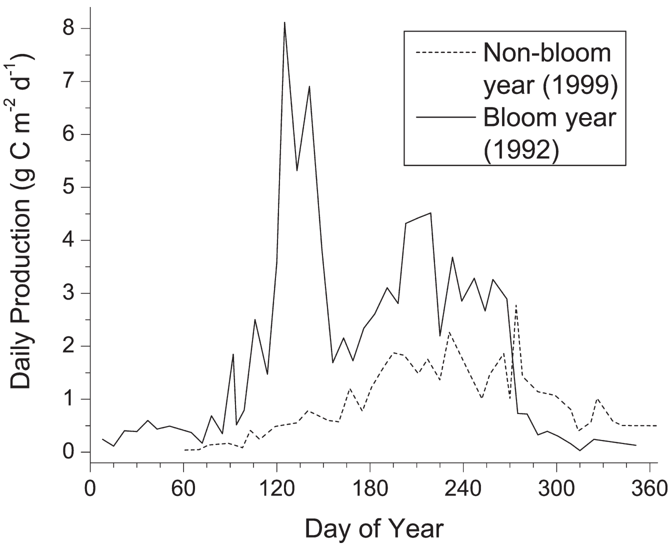

FIGURE 5. Comparison of carbon production in the Rhode River subestuary during two years, one with and one without a spring plankton bloom, which is mainly regulated by variation in spring precipitation and watershed discharge. (After Gallegos and Jordan, 1997.)

fishery historically, are now at only 1% of their biomass in 1900 (Rothschild et al., 1994). Eutrophication and overfishing act as multiple stressors on coastal food webs, and management's too narrow focus on single factors may have adverse consequences for restoring ecosystem health and fishery production (Breitburg et al., 2009).

Blue crabs are the remaining major lucrative fishery in the upper Bay, but the blue crab stock has also declined by 60% since 1991 (CBSAC, 2008). Research by SERC at the Rhode River subestuary provides the most detailed analysis of blue crab ecology available (Hines, 2007). Nearly 30 years of SERC experiments show that blue crabs are the dominant predator on benthic communities in the estuary, and their foraging limits abundance and species composition of infaunal invertebrates as well as causing major bioturbation of the upper 10 cm of sediments (Hines et al., 1990). Long-term monitoring of fish and blue crabs throughout the Rhode River subestuary shows the marked seasonal and annual variations in population abundance (Figure 7), as blue crabs migrate from the nursery habitat and become inactive below 9°C in winter. Annual variation in recruitment into the Rhode River causes more than a 10-fold fluctuation in abundance, with obvious variation in effects of predation on infaunal invertebrates. Many upper Chesapeake Bay nursery habitats now appear to be below carrying capacity for juvenile blue crabs (Hines et al., 2008). Recent SERC blue crab research has focused on de-

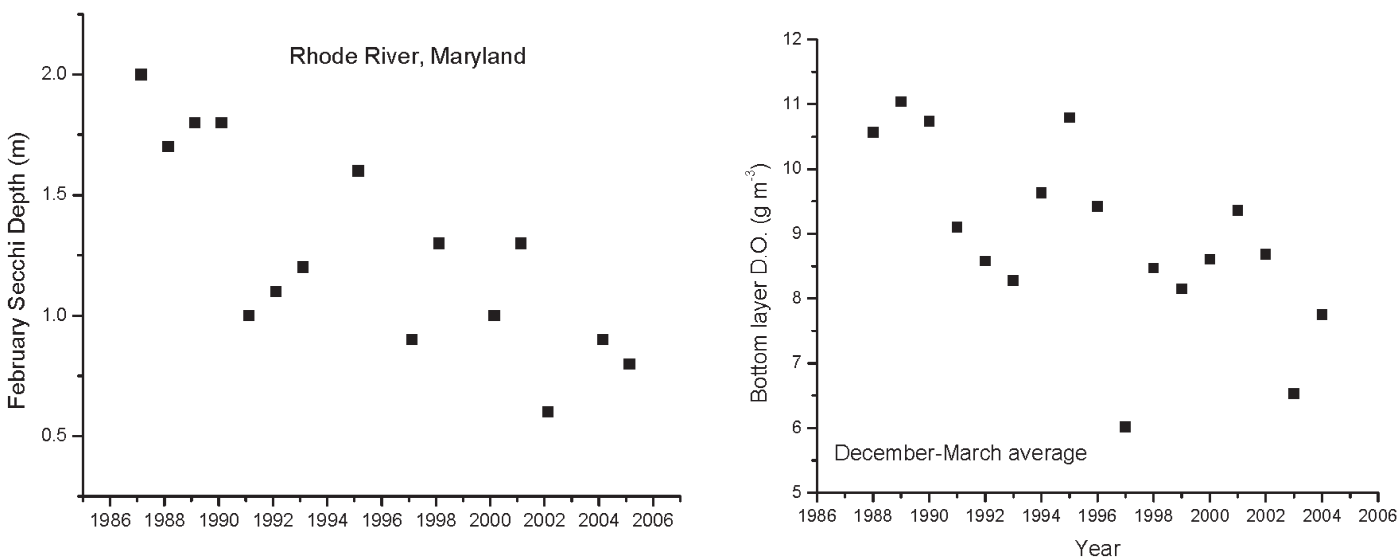

FIGURE 6. Long-term trends in water clarity as determined by Secchi (disk) depth (left) and in oxygen concentration (D.O. = dissolved oxygen; right) in the Rhode River subestuary. (Figure courtesy of C. Gallegos.)

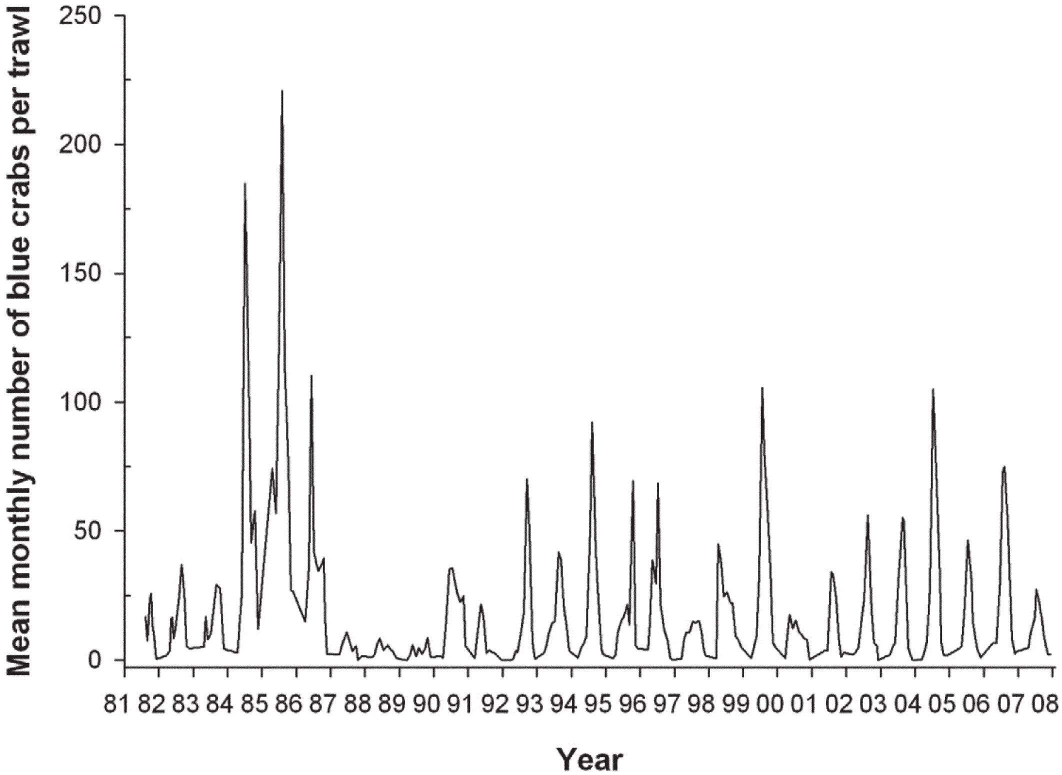

FIGURE 7. Seasonal and annual variation in abundance of blue crabs caught in 3 m otter trawls in the Rhode River subestuary. Abundance is the monthly mean of three trawls at each of three permanent stations within the estuary.

veloping innovative approaches to restoring the blue crab population in the Bay, especially by testing the feasibility of releasing hatchery-reared juvenile blue crabs into nursery areas such as the Rhode River (Hines et al., 2008).

Grand Challenge IV: Invasive Species

Invasions of nonindigenous species are drastically altering biodiversity, structure, and function of coastal ecosystems (Ruiz et al., 2000). The largest, most comprehensive research program on marine invasive species in the USA is conducted by SERC. Rates of invasion into coastal ecosystems are increasing markedly as a result of a wide range of human-mediated vectors, but most importantly as a result of shipping, both ballast water discharge and hull fouling (Ruiz et al., 2000). The SERC database for invasive species (NEMESIS) documents more than 500 invasive species of invertebrates, algae, and fish in North American coastal waters. For Chesapeake Bay approximately 176 species are documented as established invasions (Figure 8). Invasions are dynamic and ongoing in Chesapeake Bay, as indicated by recent records of Chinese mitten crabs (Ruiz et al., 2006). Many species are having large but poorly understood impacts in Chesapeake ecosystems, such as the salt marsh reed *Phragmites australis* (King et al., 2007).

Grand Challenge V: Landscape Disturbance by Agriculture and Development

Agriculture and urbanization are causing widespread modifications of landscape structure. Researchers at SERC recently analyzed various indicators of estuarine habitat quality for 31 Chesapeake subwatersheds that differed in five categories of land use composition: forest, agriculture, developed, mixed agriculture, and mixed developed (Figure 9). These land uses have profound effects on estuarine habitat quality because they increase stormwater runoff and loading of nutrients. Nitrogen discharge into subestuaries of

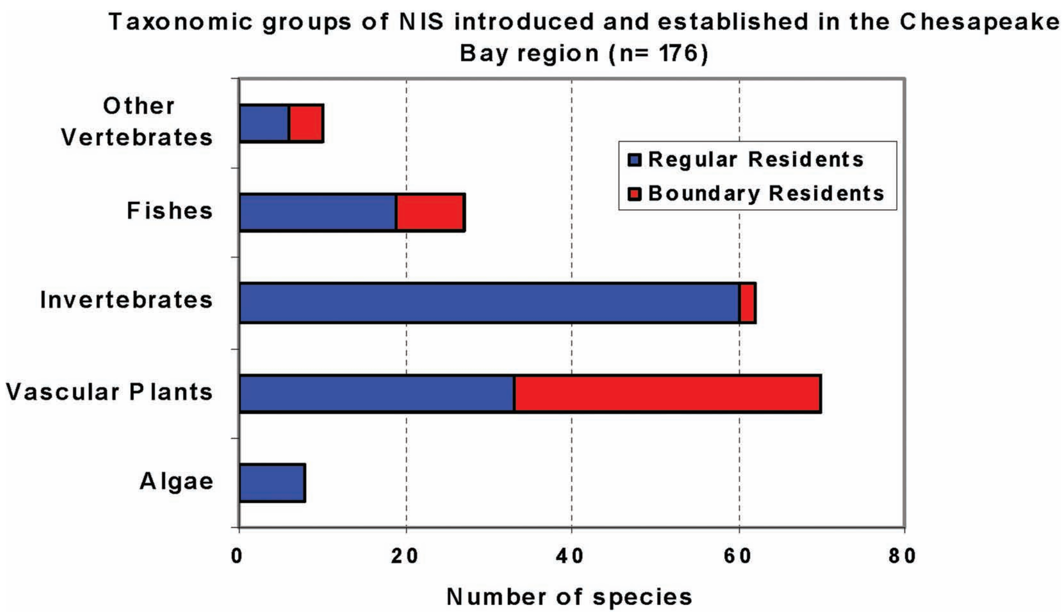

FIGURE 8. Numbers of invasive species documented for algae, vascular plants, invertebrates, fishes, and other vertebrates (total number = 176 species) in Chesapeake Bay. Regular residents are species living in habitats below tidal influence; boundary residents are species primarily living either above the intertidal zone or in nontidal freshwater and that occasionally move into tidal portions of the Bay. (NIS = noninvasive species.)

agricultural and developed watersheds was high in both wet and dry years, but in dry years it was high only in developed watersheds, which continue to have high human water use regardless of rainfall (Figure 10) (Brooks et al., 2006). Land use also has marked effects on levels of toxic chemicals in the food webs of the subestuaries. Level of polychlorinated biphenyls (PCBs) was highly correlated with percentage of developed lands on the subwatershed (Figure 11).

In addition to effects on the watershed, development of the shoreline has large impacts on coastal ecosystems. Research by SERC in the Rhode River shows that the shallowest fringe of the subestuary serves as a critical refuge habitat for juvenile fishes and crabs to avoid larger predators, which are restricted to deeper water (Ruiz et al., 1993; Hines and Ruiz, 1995). Coarse woody debris from forested shores also plays a valuable role as structural habitat and refuge from predators (Everett and Ruiz, 1993). As development results in cutting down the riparian forest and hardening the shoreline with bulkheads and riprap to prevent erosion, water depth at the shoreline increases and the source of woody debris is lost. With the loss of functional refuge in the nearshore shallows, juvenile fish and crabs become increasingly accessible to predators.

CONCLUSION

The decadal data sets generated by SERC for the linked ecosystems of the Rhode River and Chesapeake Bay clearly show the importance of sustaining long-term, intensive studies to distinguish natural variation and trends of human impacts. The rate of change associated with human impacts is increasing markedly as the effects of global change become manifest and as the human population of the watershed continues to grow rapidly, with another 50% increase predicted in the next 25 to 50 years. The interactive effects of these multiple stressors require much more research to define improved management solutions to restore and sustain these resources. Scientists at SERC also extend studies of the large-scale systems of the Rhode River and Chesapeake Bay through comparative studies with other coastal areas, especially latitudinal comparisons of systems in the Smithsonian Marine Science Network along the western Atlantic. Although each site has its idiosyncratic traits, the common impacts of the grand challenges of atmospheric change, nutrient loading, food web disruption by pollution and overfishing, invasive species, and land development are all manifested pervasively in the linked ecosystems throughout the coastal zone.

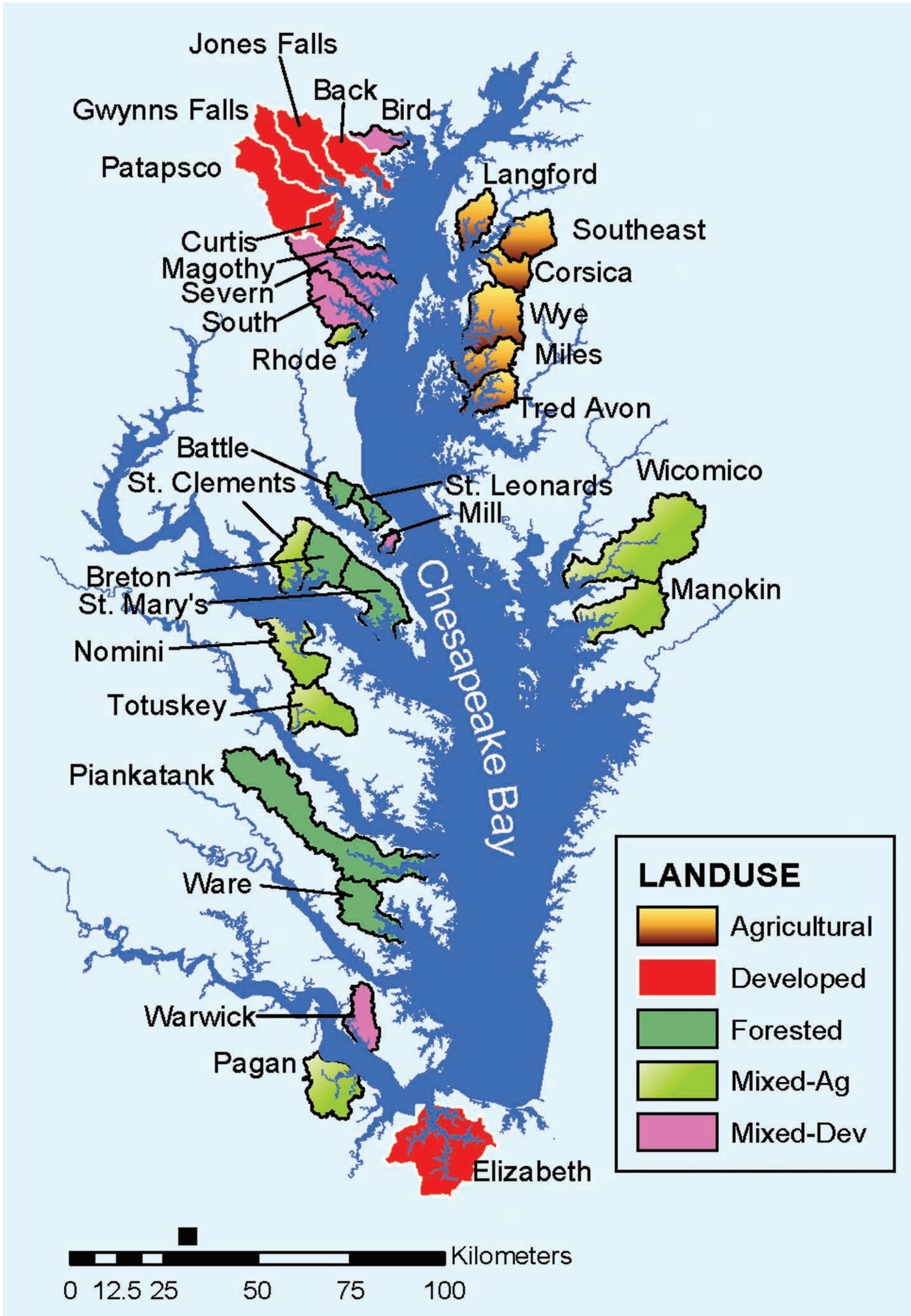

FIGURE 9. Map of 31 subwatersheds of Chesapeake Bay that were sampled for effects of land use on estuarine habitats. Watersheds were categorized in the five predominant categories shown: forest, agriculture, developed, mixed-agriculture, and mixed-developed.

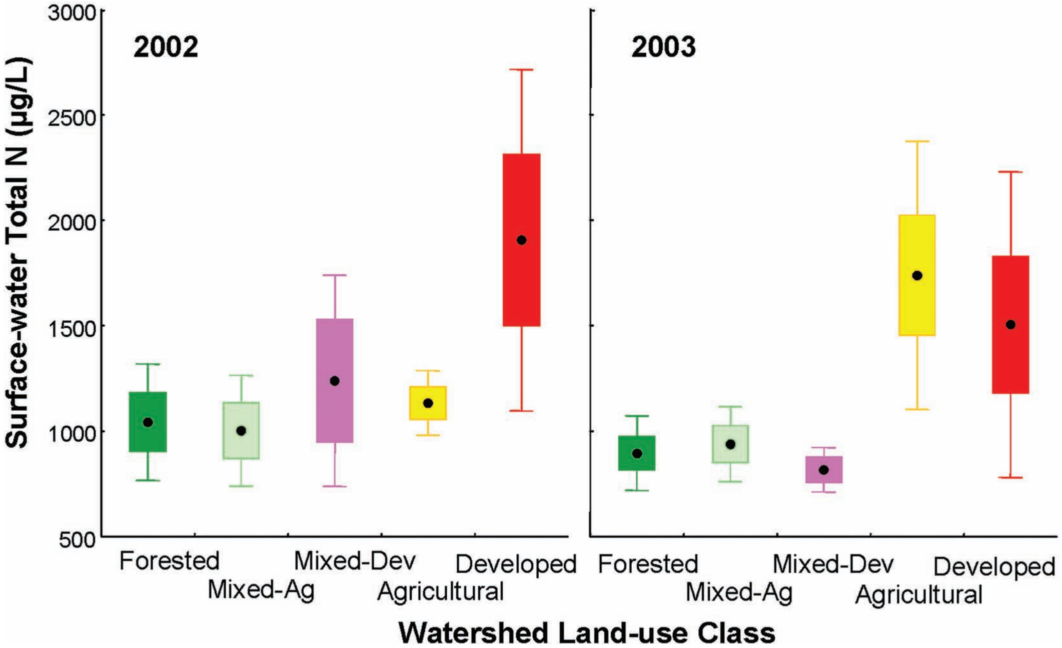

FIGURE 10. Effect of land use on nitrogen discharge from watersheds in the five land use categories shown in Figure 9. Stream surface discharges are compared among land use categories between a dry year with record low rainfall (2002, left) and a wet year (2003, right) with high rainfall. (After Brooks et al., 2006.)

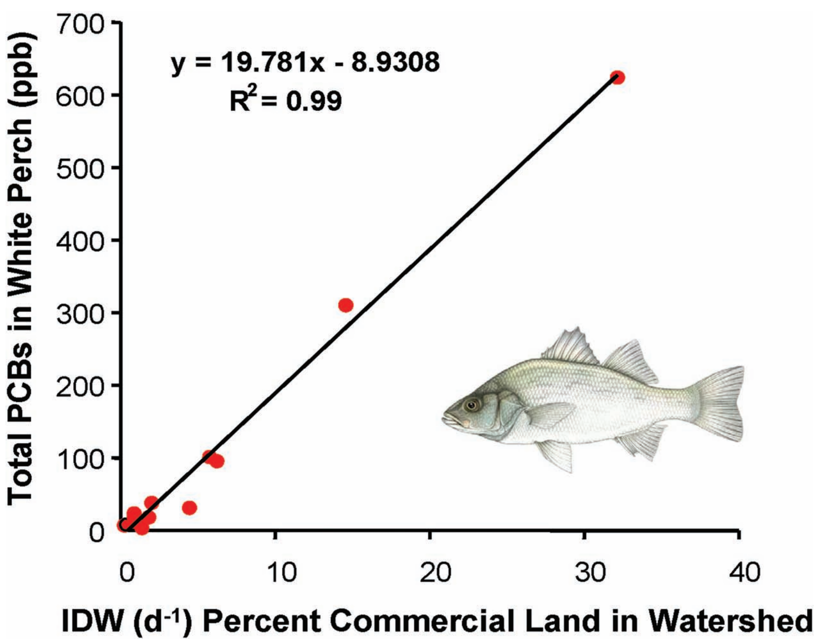

FIGURE 11. Concentration of toxic polychlorinated biphenyls (PCBs) in white perch (*Morone americana*) sampled from Chesapeake subestuaries with watersheds of varying percentages of commercially developed land use (IDW = inverse distance weighted). Watersheds sampled are shown in Figure 9. (After King et al., 2004.)

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Smithsonian Marine Station at Fort Pierce: Thirty-Eight Years of Research on the Marine Biodiversity of Florida

Valerie J. Paul, Julianne Piraino, and Laura Diederick

ABSTRACT. The Smithsonian Marine Station at Fort Pierce, located on South Hutchinson Island in Fort Pierce, Florida, has had an ongoing program in the marine sciences since the early 1970s. Funded by a private trust from J. Seward Johnson, Sr., to the Smithsonian, the marine program has supported the research of Smithsonian scientists and their associates, postdoctoral fellows, resident scientists, and the operations of the station, including a small support staff. The station is administered by the National Museum of Natural History as a facility for research dedicated to the marine sciences. The Smithsonian Marine Station at Fort Pierce has developed a strong, broadly based research program focusing on ecology, evolution, systematics, and life histories of marine organisms. Ongoing studies address important issues in biodiversity, including global climate change, invasive species, harmful algal blooms, larval ecology, and evolutionary developmental biology.

INTRODUCTION

The Smithsonian Marine Station at Fort Pierce (SMS) is dedicated to studying the rich diversity of marine life of the Indian River Lagoon and Florida coast. In sharing its findings with the scientific community, resource managers, and the general public, the Marine Station promotes the conservation and stewardship of Florida's vast marine resources. Research activities focus on the Smithsonian Institution's core scientific emphasis of discovering and understanding life's diversity. Although most research projects focus on biodiversity, life histories, and ecology of marine and estuarine organisms, complementary studies of physical and chemical processes related to the marine environment are also part of the Station's investigations. The insights gained by the research conducted at SMS are widely disseminated through scientific publications (more than 780 to date; see complete listing on the Station's website www.sms.si.edu), scientific and public presentations, popular articles, and the media, thus contributing to the broader mission of the Smithsonian Institution for the "increase and diffusion of knowledge."

The Smithsonian's presence in Fort Pierce, Florida, began in 1969 through an association with Edwin Link, an inventor and engineer who was involved at that time in the design of research submersibles, and J. Seward Johnson, Sr.,

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founder of the Harbor Branch Foundation, now known as the Harbor Branch Oceanographic Institute (HBOI) at Florida Atlantic University (Figure 1). In late 1969, the Smithsonian was given two trust funds through the generosity of J. Seward Johnson, Sr., for the development and maintenance of a submersible (then under construction) and for research in underwater oceanography. At its completion in 1971, the submersible, the Johnson Sea-Link I, was donated to the Smithsonian. In 1973, after a tragic accident in the Johnson Sea-Link in which two men died, the Smithsonian transferred ownership of the submersible to Harbor Branch. Following the transfer of the submersible, the Smithsonian's marine research program in Fort Pierce continued to be supported by income from both trust funds, then later, after certain legal resolutions, by one of the two funds, designated as the Hunterdon Fund. The Smithsonian carried out its activities in Fort Pierce on the grounds of the Harbor Branch Foundation (Link Port) under the auspices of the Fort Pierce Bureau, a unit administered directly by the Office of the Secretary and then later by the Assistant Secretary for Science. In March 1981 this Bureau was dissolved as an organizational entity, and the administrative responsibility for the Smithsonian research programs at Link Port was transferred to the Director of the National Museum of Natural History (NMNH). The organization was then retitled by the Secretary of the Smithsonian as the Smithsonian Marine Station at Link Port. At the time of the transfer of administrative responsibility, the directive from the Office of the Assistant Secretary for Science was that a strong research program in marine science should be established and that the program should be open to all marine scientists in the Smithsonian Institution. In response, Richard Fiske, then Director of NMNH, established an inter-unit advisory committee, appointing Catherine Kerby, his administrative assistant, as chair of the committee, and Mary Rice, Department of Invertebrate Zoology (on assignment to the Fort Pierce Bureau), as director of the facility and research programs at Link Port. Rice held this position until her retirement in 2002, at which time Valerie Paul was selected as her successor.

The Smithsonian Marine Station at Link Port was initially set up with a small on-site staff and well-equipped laboratories and field facilities to provide opportunities for Smithsonian scientists and their colleagues to conduct field research in a highly diverse subtropical marine environ-

FIGURE 1. J. Seward Johnson, Sr. (left), and inventor Edwin Link were instrumental in providing funding and submersibles for the Smithsonian's marine research program in Fort Pierce, Florida.

ment. This plan gave Museum scientists the opportunity to extend and broaden their research from museum collections to field studies in such areas as behavior, ecology, physiology, and life histories. Moreover, it provided the opportunity for all Smithsonian marine scientists to carry out comparative studies of the diverse ecosystems and biota within the Fort Pierce vicinity and peninsular Florida and, most importantly, to establish long-term databases and to conduct long-term studies. An important component of the plan was to include postdoctoral fellows, both to complement the research of Smithsonian scientists and to contribute to training of future generations of marine scientists. In addition, by serving many Smithsonian scientists (as opposed to a few resident scientists), the program was conceived to yield maximum productivity of high-quality modern science and to be the most equitable and effective use of available funds.

For the first 18 years the Smithsonian Marine Station at Link Port used a vintage WW II barge as a floating laboratory docked at Harbor Branch (Figure 2) as the base of operations for its highly successful research program, which was carried out primarily by visiting scientists from the Smithsonian, their colleagues, and postdoctoral fellows. Restrictions imposed by the space and structural limitations of the barge for many research activities as well as its high maintenance requirements led the Smithsonian to pursue plans for a land-based laboratory.

In May 1999 these plans were realized when, with the approval of J. Seward Johnson, Jr., and a signed Memo of Understanding, the Smithsonian Marine Station relocated to an 8 acre site acquired from the MacArthur Foundation near the Fort Pierce Inlet, 7 miles south of Harbor Branch. At this time the official name of the station was changed to the Smithsonian Marine Station at Fort Pierce. The move was made into a newly constructed 8,000 square foot building with offices and laboratories for visiting scientists, resident staff and postdoctoral researchers, general-use laboratories for chemistry, microscopy, and molecular research (Figures 3, 4), and a wet laboratory supplied by a small seawater system. In March 2003, a 2,400 square foot storage building was completed. The building includes a workshop and storage for scientific supplies, scuba equipment, and other marine research equipment. In April 2004 a research dock was completed on the Indian River Lagoon, which is accessible by an easement on adjacent property. A flow-through seawater building was

FIGURE 2. A retired World War II Army barge was remodeled to include two levels of offices and laboratories for use by the Smithsonian Marine Station scientists from the early 1970s to 1999.

FIGURE 3. This aerial view shows the location of the Smithsonian Marine Station on the Fort Pierce Inlet of the Indian River Lagoon in Florida.

added to the campus in August 2005. The relocation to the new research building and campus provided the opportunity for the Smithsonian Marine Station to increase and strengthen the breadth and diversity of its research as well as to establish new collaborative interactions. The move also made it possible to expand the Station's educational mission, initiating new cooperative ventures in education and public outreach.

In the struggle to understand life, how its diversity has come about, and the current rapid loss of biodiversity on a global scale, the Smithsonian Marine Station is positioned as are few laboratories in the world to study this exceptional diversity from an array of environments. The Smithsonian Marine Station is located on the Fort Pierce Inlet of the Indian River Lagoon (IRL) (see Figure 3), an estuary extending along one-third the length of the east coast of Florida. The IRL is widely recognized as one of the most diverse estuaries in North America, and it has been designated an estuary of national significance by the Environmental Protection Agency. The Marine Station's unique location on the Fort Pierce Inlet puts it in a prime position to access oceanic waters and to sample organisms from the Florida Current and other offshore habitats. This region of Florida's coast, characterized as a transitional zone where temperate and tropical waters overlap, offers access to a great variety of habitats and an extraordinary diversity of species. To the south of Fort Pierce, within a few hours of travel, are Florida Bay and the Florida Keys, the only living tropical coral reefs in the continental United States.

Specialized equipment and instrumentation at the Smithsonian Marine Station include temperature-controlled aquaria and incubators, equipment for preparing tissues for light and electron microscopy, an ultracold freezer, equipment for electrophoresis, a thermocycler for DNA amplification, high performance liquid chromatographs, a gas chromatograph/mass spectrometer, and a UV-visual spectrophotometer. For microscopic studies, equipment is available for light, epi-fluorescent, and Nomarski microscopy, time-lapse and normal-speed cinematography, photomicrography, video recording and editing, inverted microscopy, scanning and transmission electron microscopy (Figure 5), and confocal laser scanning microscopy.

Confocal laser scanning microscopy (CLSM) has become an increasingly important tool in modern environmental microbiology, larval ecology, developmental biology, and biochemistry. CLSM involves the use of a light microscope, laser light sources, a computer, and special software to image a series of in-focus optical sections through thick specimens. The specimens, which can be live or fixed, are stained with fluorescent dyes that highlight specific structures when excited by the lasers. Once the stacks of two-dimensional (2-D) images are collected, the computer software constructs spectacular, information-rich, three-dimensional (3-D) images that yield a wealth of information. In June 2008, the Smithsonian Marine Station acquired a Zeiss LSM510 confocal system that is already providing data in the cutting-edge studies of Postdoctoral

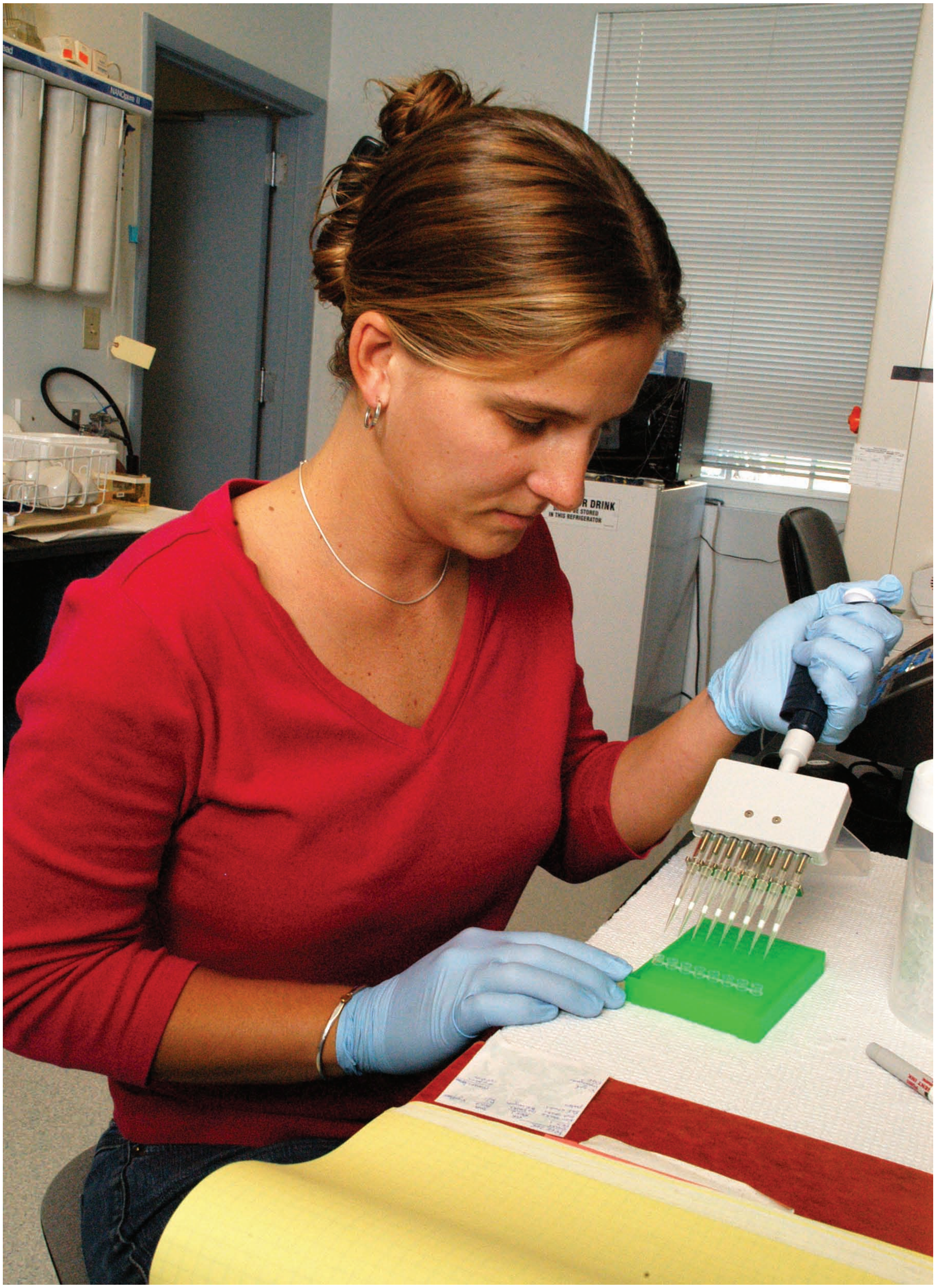


FIGURE 4. Smithsonian Marine Science Network Postdoctoral Fellow Koty Sharp uses molecular methods to determine the diversity of bacteria associated with corals.

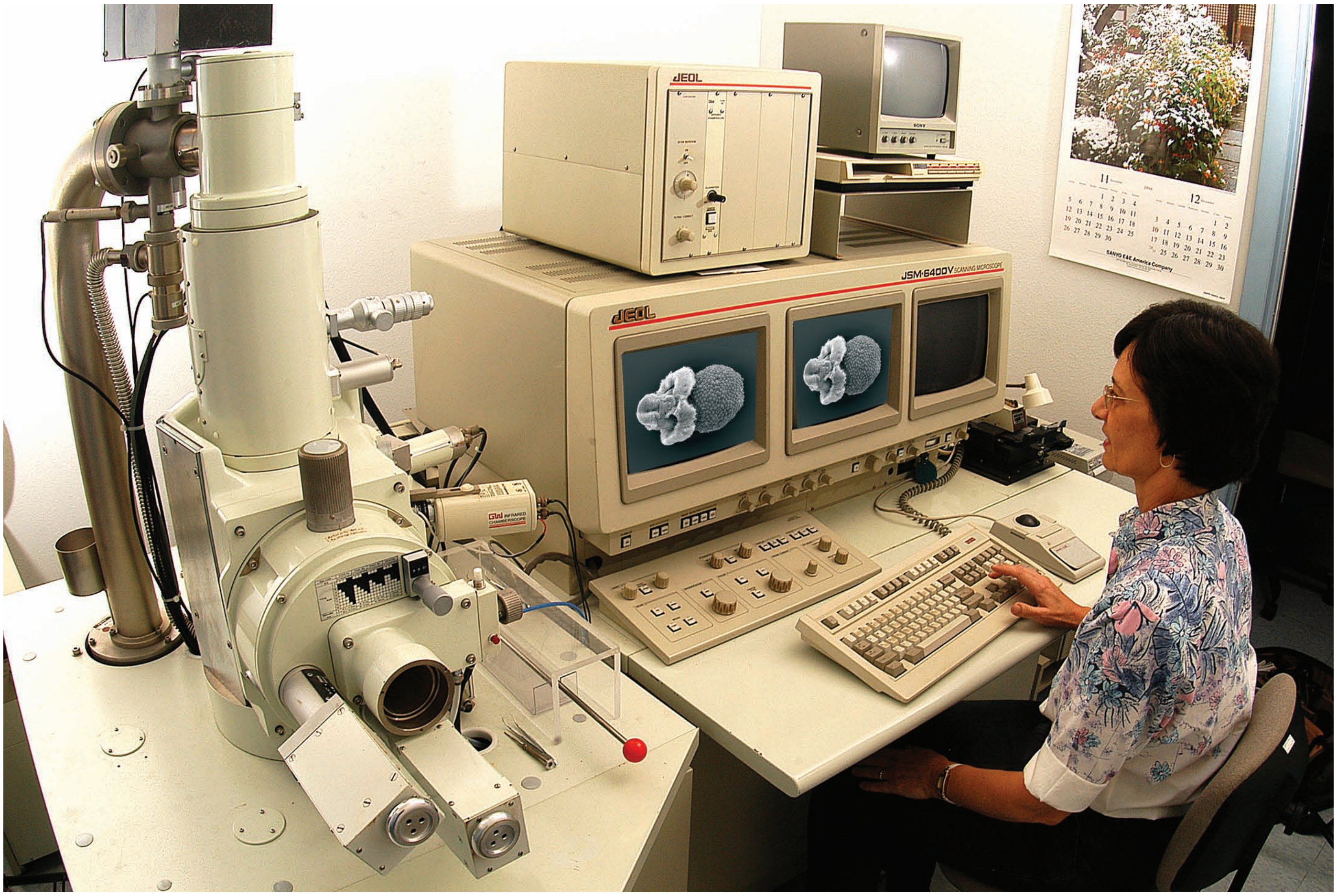


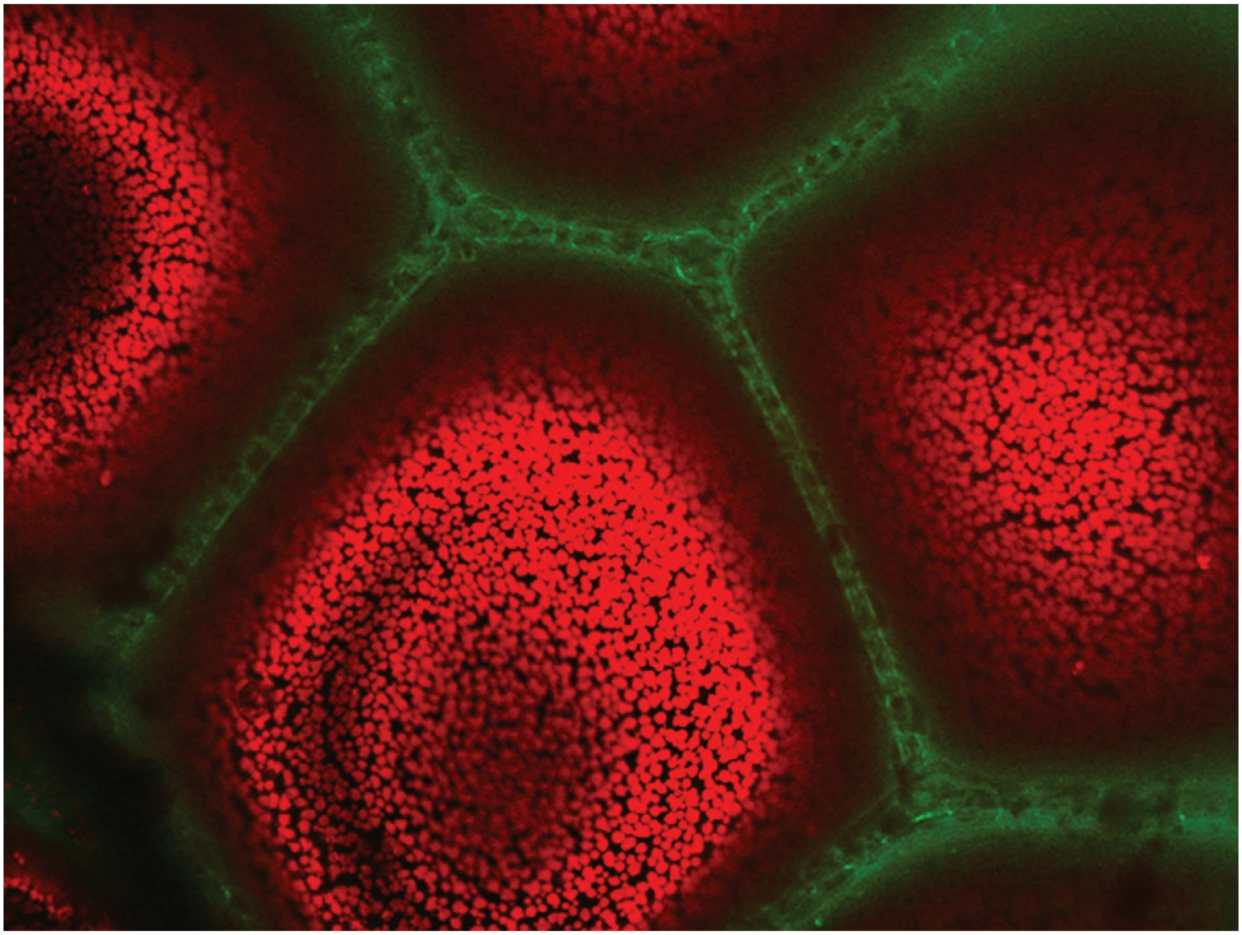
FIGURE 5. Julie Piraino, Laboratory Manager, examines the larva of a sipunculan worm on the scanning electron microscope.

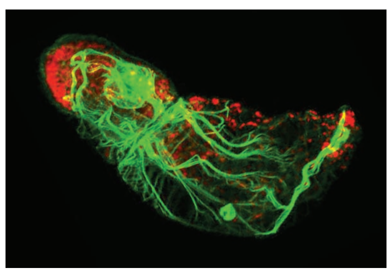
Fellow Koty Sharp on the presence and transmission of bacteria in corals, and in research conducted by Postdoctoral Fellow Kate Rawlinson on the fate of individual cells in the development of embryos of polyclad flatworms. This new microscope will greatly increase the capabilities of Smithsonian marine scientists to conduct probe-based subcellular studies in biochemistry, microbiology, and developmental biology (Figure 6).

The Marine Station owns four boats for use in field studies: a 17 foot Boston Whaler and a 21 foot Carolina Skiff for work in the shallow waters of the IRL, a 21 foot center-console boat to access nearshore waters, and a 39 foot vessel, the R/V *Sunburst*, for offshore research activities. These vessels provide access to the diverse marine and estuarine environments in the vicinity of SMS. The excellent location, facilities, instrumentation, and skilled staff of the Smithsonian Marine Station facilitate research on many diverse topics in marine biology and marine biodiversity.

RESEARCH ACTIVITIES

The Smithsonian Marine Station at Fort Pierce is an important contributor to the marine research and collections at the National Museum of Natural History. It provides a vital link between tropical and temperate ecosystems in a coastal network of marine research stations known as the Smithsonian Marine Science Network. The Marine Science Network (MSN) is an array of laboratories spanning the western Atlantic coastal zone and across the Isthmus of Panama, facilitating long-term interdisciplinary, comparative research among MSN sites, including the Smithsonian Environmental Research Center (SERC)





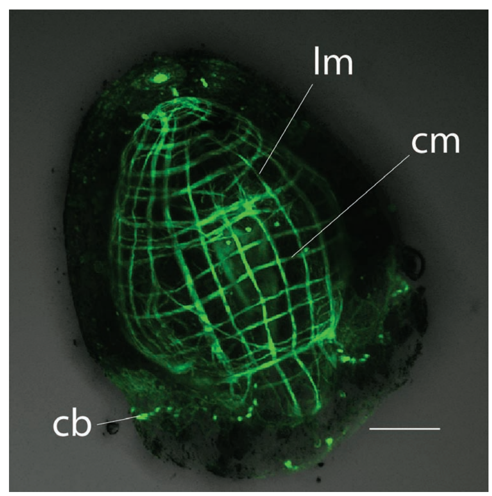


FIGURE 6. Left: Confocal microscopy captures an oxidative burst reaction by the green alga *Dictyosphaeria cavernosa* following exposure to the fungus *Lindra thalassiae*. An oxidative burst is an explosive production of reactive oxygen species (hydrogen peroxide is an example) intended to act as first defense against invading pathogens. Middle: Confocal image shows development of musculature and nervous system in a larva of a sipunculan worm. Right: Confocal laser scanning micrograph of the musculature of a Müller's larva of the flatworm *Cycloporus variegatus*. Phalloidin staining shows circular and longitudinal muscles (cm, lm, respectively) and the ciliary band (cb). Scale = 30 μm.

in Maryland, the Carrie Bow Cay Marine Field Station in Belize, and the Smithsonian Tropical Research Institute (STRI) in Panama.

Research at SMS continues to be carried out by Smithsonian scientists from various units within the Institution along with their colleagues from other national and international institutions, as well as by resident SMS scientists, postdoctoral fellows, and graduate students (Figure 7). Ongoing research programs by resident scientists at the Smithsonian Marine Station involve coral reef research,

FIGURE 7. Visiting Scientist Anastasia Mayorova (kneeling) collects sipunculan worms with the assistance of Mary Rice, Director Emeritus of SMS (left), and Research Technician Woody Lee.

monitoring that is supporting restoration of the Florida Everglades, harmful algal blooms, marine natural products, and invertebrate larval life histories, evolution, and development. The Smithsonian Marine Station promotes the education of emerging scientists by offering pre- and postdoctoral research fellowships and supporting the work of student interns. Examples of ongoing research activities are discussed below.

Marine Biodiversity

The Smithsonian Marine Station has long had a central focus on documenting biodiversity of marine life in the most diverse coastal waters of the continental United States. NMNH invertebrate zoologist David Pawson has discovered and documented echinoderms (sea urchins, sand dollars, sea cucumbers) in shallow and deep waters of Florida for more than 25 years (Hendler et al., 1995). He has found sand dollars that are probably hybrids between two species in the offshore waters of Fort Pierce. Other groups of organisms that have been well studied by NMNH researchers for many decades include the marine algae (Mark and Diane Littler), foraminifera (Marty Buzas), crustaceans (Rafael Lemaitre and colleagues), deep- and shallow-water mollusks (Jerry Harasewych and Ellen Strong), and meiofaunal organisms (animals less than 1 mm in size that live in sand and sediments) (Jon Norenburg and coworkers). Additionally, many SMS scientists, including former director Mary Rice, have focused on understanding the diversity and distribution of larval forms of different groups of marine invertebrates. These larval stages are morphologically and ecologically very different from adult life stages and are extremely important for the transport and propagation of marine species, sometimes over long distances (Figure 8). Tuck Hines and Richard Osman (SERC) have also studied recruitment patterns and larval ecology for a variety of invertebrate larval forms in the IRL. A few examples of the many biodiversity studies conducted at SMS are highlighted below.

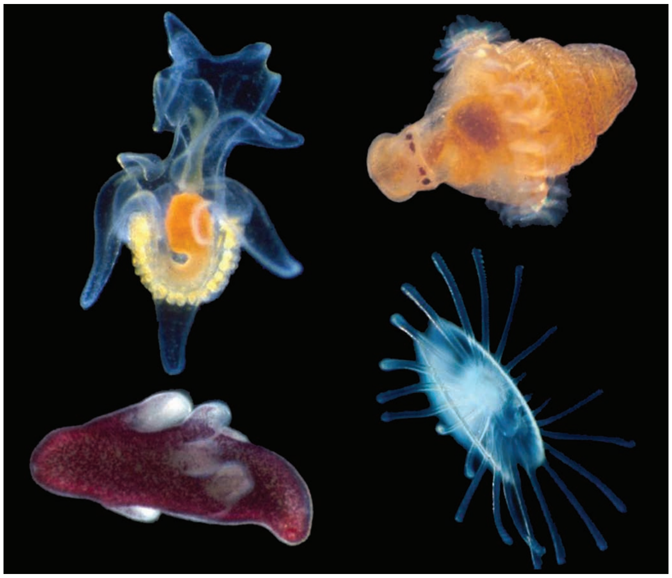


FIGURE 8. Examples of marine invertebrates, the larval development of which has been studied by Mary Rice and colleagues at SMS for more than 30 years. Organisms shown here, clockwise from upper left, are a starfish brachiolarian larva, a sipunculan pelagosphera larva, a brachiopod larva, and a flatworm Muller's larva.

With much of their research focused on ecology, physiology, and pollution-oriented work, Mark and Diane Littler observed a growing need for an easier means for field scientists and resource managers to identify the diverse and abundant marine algal species in the field. They have published user-friendly field guides, including the award-winning book *Caribbean Reef Plants* (Littler and Littler, 2000), with much of their laboratory and field research based at SMS. More recently, with co-author M. Dennis Hanisak (Harbor Branch Oceanographic Institute), they published *Submersed Plants of the Indian River Lagoon: A Floristic Inventory and Field Guide* (Littler et al., 2008), a book rich with photography and illustrations depicting the taxonomy and distributional patterns of more than 250 species of submersed plants in the Indian River Lagoon. The book was based on six years of field and laboratory work along the central east coast of Florida.

D. Wayne Coats, a protistan ecologist at the Smithsonian Environmental Research Center, has worked on the biology and ecology of free-living and symbiotic protists for 20 years. His work has enabled comparisons between the Chesapeake Bay and Indian River Lagoon estuaries and provided enhanced understanding of how eukaryotic microbes influence the structure of marine food webs (Snoeyenbos-West et al., 2004). Much of Coats' work at SMS has considered the biodiversity and trophic biology of protists living in coastal waters of Florida or associated with local marine fauna. He has shown parasitism of planktonic ciliates in the Indian River Lagoon to be a major pathway for recycling material within the microbial loop. Coats and his graduate students have also shown that many free-living photosynthetic dinoflagellates have the ability to feed on ciliate protozoa. Although ingestion rates are typically low, the high densities attained by red-tide dinoflagellates in the Indian River Lagoon and Chesapeake Bay make their ability to ingest ciliates an important microbial food web interaction. Feeding on ciliates and other protists may help sustain blooms when nutrient resources for photosynthesis are limited. Coats and his colleagues have also revealed a rich and poorly known ciliate fauna associated with the respiratory tract of bottle-nosed dolphins and other cetaceans (Ma et al., 2006). Previously reported to be parasitic, these ciliates appear not to directly impact the health of animals held in captivity. Through his work at SMS, Coats has helped define the significance of protists within the marine ecosystem. In some instances, these protists compete directly with zooplankton for food resources, thus limiting the upward movement of energy and matter in the food web. In other instances, they can recycle biomass not readily grazed by zooplankton, thus repackaging it in a form that can move more readily through the food web.

Mary Rice, former director of SMS, established a program of life history studies more than 30 years ago involving numerous postdoctoral fellows and visiting scientists who have worked on a variety of marine invertebrates. Her research has focused on an enigmatic group of marine worms known as sipunculans. Presumably a primitive group related to annelids and mollusks, sipunculans are unique in their complete lack of segmentation and single unpaired ventral nerve cord. One of several objectives of her studies has been the use of developmental studies to understand phylogenetic affinities both within the group and with other spiralian phyla (Schulze and Rice, 2009). Other objectives have been comparative studies of reproductive biology and ecology of shallow-water and deep-sea species, an investigation of the biology of oceanic larvae, including their metamorphosis and their role in species distribution, and a systematic survey of the Sipuncula of Florida and the Caribbean.

In studies of reproductive biology, comparative information was gathered for numerous species on gametogenesis, spawning, egg sizes, egg maturation, fertilization, and reproductive seasonality (Rice, 1989). Year-long observations of reproductive activity in *Phascolion cryptum*, a small species inhabiting discarded gastropod shells in the subtidal waters of the Indian River Lagoon, revealed that—in contrast to temperate species—animals were reproductive throughout the year. A collaborative ultrastructural study of spermiogenesis was also conducted. The most abundant sipunculan of the Indian River Lagoon, this species was recorded in densities up to 2,000 to 3,000 per square meter. No longer found in these densities, the population has declined for reasons unknown (Rice et al., 1983).

Studies of larval biology by Rice and collaborators have concentrated on the oceanic pelagosphera larvae of sipunculans that occur in abundance in the Florida Current, a component of the Gulf Stream System that flows along the edge of the Continental Shelf offshore from Fort Pierce. Reported in warm water currents throughout the world's oceans, these larvae are known to be long lived, existing in the larval stage for 6 to 7 months, and hence to have the potential for widespread species dispersal (Rice, 1981). Continuing for more than three decades, the studies have included descriptions of the various larval morphotypes through light and scanning microscopy, as well as an investigation of factors inducing metamorphosis and the identification of species by rearing larvae to adulthood. Several of the larvae were identified by rearing, surviving in the laboratory for periods of 3 to 26 years as adults. In more recent collaborative studies (with Postdoctoral Fellow Anja Schulze and staff of the NMNH Laboratory of Analytical Biology), genomic analysis, comparing larval and known adult sequences, was utilized to identify additional larval types. These analyses suggested the presence of two cryptic species, characterized by morphologically similar adults but different larval types.

Jon Norenburg (NMNH), together with students, postdoctoral fellows, and collaborators, has been and is focused on discovering nemertean diversity in Florida and using that diversity to address broader questions. In short visits over the course of 20 years they have collected as many as 70 putative species, primarily from the shoreline and shallow coastal waters, from a region with 24 previously known species. Many of the additional species are potential range extensions that await confirmation with specimens from type locales, especially those in southern Brazil, which is the nearest subtropical nemertean fauna that also is well documented. There also are tantalizing preliminary data for close genetic links with European species (Maslakova and Norenburg, 2008). New species have been named, and another 10 to 15 potential new species await additional specimens or genetic work. Most nemerteans have few to no external diagnostics to characterize and discriminate species unambiguously. Almost all the species collected in Florida by Norenburg and coworkers in the past 15 years were processed with genetic work in mind, which will resolve some questions of identity and yield realistic estimates of true diversity and contribute important samples for studying diversification of the phylum (Thollesson and Norenburg, 2003). That effort in Florida is an important component of two global-scale nemertean projects headed by Norenburg: (1) diversity and coevolution of the specialized, ectosymbiotic carcinonemertid worms with their decapod crustacean hosts (mostly crabs), and (2) phylogeny and biogeography of *Ototyphlonemertes*, which are specialized and miniaturized worms occupying the aqueous pore space in coarse sediments, such as coarse sand beaches and in high-current subtidal habitats. Norenburg's study of nemerteans in Florida has contributed important original observations about developmental biology of nemerteans, and one species in particular has revolutionized our understanding of nemertean evolution (Maslakova et al., 2004).

Carole Baldwin and Lee Weigt from the National Museum of Natural History are studying fish diversity, including larval fishes, through DNA barcoding methods. Fish taxonomists have traditionally classified fishes based on morphological features that can be seen and described. However, many families of fishes, such as parrotfishes and gobies, have members that look so similar they are virtually indistinguishable without examining the genetic material. Baldwin and her research team have now cataloged more than 200 species (from more than 1,000 specimens) from the Indian River Lagoon. Processing involved identifying and measuring each fish, photographing its live coloration, taking a tissue sample for DNA analysis, and preserving the rest of the specimen as a voucher for NMNH archival collections. Tissue samples from each specimen were used to create a DNA barcode, which is unique to the individual fish species and can be used for identification purposes. Not only will this work be important for establishing a database of genetic information for fishes of the Indian River Lagoon, it will greatly increase our understanding of shorefish diversity. The overall goal of the work is to provide a new, more realistic estimate of species diversity in the Caribbean, Florida, and adjacent areas. Having amassed DNA extractions from fishes from a variety of taxa and from multiple localities in the tropical Atlantic, the investigators can now examine interspecific phylogenetic relationships to investigate patterns of speciation and potential patterns of morphological divergence accompanying speciation.

Important reasons often cited for understanding biological diversity are the possible benefits these species might yield as foods, medicines, or for other human uses. Valerie Paul, Director of SMS, and members of her research group investigate the chemical diversity of marine organisms by studying marine natural products, small molecules produced as chemical signals or as toxins or chemical defenses. Members of Paul's research team isolate and characterize natural products from Florida's marine life (seaweeds and invertebrates) and have discovered compounds that have never previously been found in nature. A current area of interest for her research group is the biodiversity and chemical diversity of benthic marine Cyanobacteria. Through collaborations with medicinal chemists, they are actively investigating the beneficial uses of these compounds for treatment of human diseases such as cancer and bacterial infections.

Marine Ecology

Valerie Paul studies marine plant–animal interactions in coral reef habitats. Coral reefs in Florida and throughout the world are declining, in part the consequence of shifts from coral- to algal-dominated communities. Paul and members of her research team study grazing by reef fishes and sea urchins and the effects of herbivory on coral reef community structure (Paul et al., 2007). They have found that chemical defenses of marine algae allow some well-defended marine plants to dominate on coral reefs despite grazing pressure. Key to the recovery of coral reefs is the successful recruitment of coral larvae to become juvenile and eventually adult corals (Ritson-Williams et al., 2009). Paul's research group and their collaborators examine positive and negative interactions between coral larvae and the marine algae that dominate coral reef habitats. Some of the same species of algae that are chemically protected from grazers can inhibit the settlement of coral larvae, thus preventing the successful recovery of coral reefs.

Algae are an essential part of marine ecosystems and when maintained in balance can provide food, shelter, oxygen, and more to millions of organisms, including people. But some algae can produce harmful toxins and, under certain conditions, can grow out of control. These so-called harmful algal blooms have been increasing in frequency and severity along the world's coastlines. NMNH scientist Maria Faust has been investigating the types of planktonic harmful algae, often called red tides, which occur along Florida's east coast (Faust and Tester, 2004). Valerie Paul, NMNH Statistician Lee-Ann Hayek, and Postdoctoral Fellows Karen Arthur and Kate Semon have been studying formation of blooms of marine cyanobacteria in Florida's estuaries and coral reefs and trying to elucidate environmental factors that contribute to bloom formation (Paul et al., 2005). Increased nutrients from land-based sources, such as runoff from fertilizers and sewage treatment plants, may help to fuel some of these algal blooms. The biological and biochemical diversity of harmful algae is the subject of ongoing research, which has led to the discovery of novel toxins produced by these cyanobacteria.

Estuaries and coasts around the world are approaching critical levels of degradation, and the southern Indian River Lagoon is no exception. Large-scale, collaborative efforts are underway to restore biodiversity and the vital ecological functions these ecosystems provide. Bjorn Tunberg and members of his benthic ecology research team at SMS are involved in one of the most ambitious of these projects, the Comprehensive Everglades Restoration Plan (CERP). Extensive modifications to the southern IRL watershed over the past 100 years have decreased the system's ability to store water and have increased nutrient-rich stormwater runoff. The CERP plan, under the direction of the South Florida Water Management District and the U.S. Army Corps of Engineers, aims to restore wetlands and build water storage basins to improve estuarine health. Tunberg and his team established a benthic monitoring program five years ago to provide a baseline data set of species distribution and abundance in the sediments of the Indian River Lagoon. This team is acquiring quarterly data that will allow them to detect and predict long-term changes in the benthic communities throughout the central and southern Indian River Lagoon.

The location of the Smithsonian Marine Station on the Indian River Lagoon for 37 years has allowed Smithsonian researchers to establish long-term and intensive research projects that are valuable in understanding and assessing marine biodiversity. Long-term biological monitoring is most effectively carried out on organisms with high densities, many species, short generation times, quick responses to changes in environmental variables, and a long history of extensive study on a worldwide basis. The benthic foraminifera fit these requirements, and their populations have been monitored in the Indian River Lagoon for more than 30 years by Marty Buzas (NMNH).

At one station near the Harbor Branch Oceanographic Institute, monthly replicate sampling of foraminifera living in the sediment has been carried out since 1977. These data indicate significant differences between seasons, as well as among years, but no overall increase or decrease over a longer time span. The spatial distribution of the foraminifera forms an environmental mosaic of patches whose densities change with time. This newly discovered phenomenon was termed pulsating patches (Buzas et al., 2002; Buzas and Hayek, 2005). At the St. Lucie Inlet, observations were made in 1975–1976 and again 30 years later in 2005. Species richness had greatly declined over 30 years, and the community structure of the foraminifera in this area was completely destroyed (Hayek and Buzas, 2006). Monitoring at this Inlet during 2007–2008 has shown that species richness has increased; however, except for the abundant species, the fauna does not contain the same species as it did 30 years ago. Monitoring efforts are continuing, and Buzas and Hayek have also begun a coring program to determine the effects of both natural and anthropogenic effects on community changes during the past 150 years.

Candy Feller, Dennis Whigham, coworkers from the Smithsonian Environmental Research Center (SERC), and national and international collaborators have conducted long-term studies of the mangrove ecosystems of the Indian River Lagoon. The overall goal of this project is to collect hydrological, nutrient, microbial, and vegetation data in support of their long-term ecological studies of factors that control the structure and function of mangrove ecosystems (Figure 9, top). Feller has continued a study of how nutrient enrichment affects the mangrove communities along the Atlantic coast of Florida for the past 10 years. Fertilization experiments designed to enrich nitrogen (N) and phosphorus (P) in sediments have shown that black mangrove forests in Florida are nitrogen limited. When nitrogen was added in the IRL, the black mangroves grew out of their dwarf form (Feller et al., 2003). Addition of N also affected internal dynamics of N and P, caused increases in rates of photosynthesis, and altered patterns of herbivory (Lovelock and Feller, 2003). These findings contrast with results for mangrove forests in Belize and Panama where the seaward fringe was N-limited but the dwarf zone was P-limited. Their studies have demonstrated that patterns of nutrient limitation in mangrove ecosystems are complex, that not all processes respond similarly to the same nutrient, and that similar habitats are not limited by the same nutrient when different mangrove forests are compared (Lovelock et al., 2006; Feller et al., 2007).

Feller and her colleagues have also studied the effects of the 2004 hurricanes Frances and Jeanne on the mangrove communities (Figure 9, bottom). Over the past 4 years they have continued to monitor and quantify the recovery of the mangroves, documenting tree height, leaf area index, mangrove type, mangrove defoliation and recovery, hydrology, and salinity. Damage to the mangroves was higher in the fringe and transition zones than in the dwarf zone. The N-fertilized trees sustained significantly higher damage than controls in all zones and have been slower to recover. After 2.5 years, the leaf area index (LAI) of P-fertilized and control trees was equal to pre-storm levels, whereas +N trees were less than 90% recovered. LAI again decreased dramatically in January 2007, presumably as the result of an intense 2 year drought in Florida.

Dennis Whigham and colleagues from the University of Utrecht, The Netherlands Institute for Ecology–Centre for Limnology, and the University of South Florida are determining the relationships between the structure and productivity of different mangrove habitat types and hydrological processes and nitrogen cycling, including characteristics of the microbial community associated with nitrogen cycling. Their hydrological studies have shown that there is no evidence of freshwater input from groundwater into their study site and that the groundwater chemistry is primarily influenced by evapotranspiration. Subsequently, salt pans and dwarf mangrove communities develop in areas that are characterized by hypersaline conditions associated with evapotranspiraton. Growth rates are lower in the salt pan and dwarf mangrove habitats, and preliminary results indicate that the microbial community in those habitats differs from other habitats.

The studies described above document the morphological, genetic, and biochemical diversity of Florida's marine life. Collectively, these biodiversity and ecological studies and investigations of long-term changes in Florida's coastal waters, including the Indian River Lagoon, mangrove ecosystems in Florida, and coral reef habitats of southeast Florida and the Florida Keys, give us the background essential to document changes in biodiversity resulting from human and climatic impacts on Florida's coastal environments.

EDUCATION AND OUTREACH

As a resource for educators, students, researchers, and the public, the Marine Station maintains a species inventory of plants and animals in the Indian River Lagoon. The Indian River Lagoon Species Inventory website (www.sms.si.edu/IRLspec) is continually expanding and now includes more than 3,000 species with many photographs and scientific references. In addition to individual species

FIGURE 9. Top: From front to back, Smithsonian Marine Station graduate fellow Juliane Vogt (University of Dresden), postdoctoral fellow Cyril Piou, and volunteer Rainer Feller explore the mangrove at Hutchinson Island, Florida, looking for light gaps. Bottom: Sharon Ewe (on left) and Anne Chamberlain examine damage to the mangroves at Hutchinson Island, Florida, immediately after Hurricane Jeanne.

reports that give habitat, distribution, life history, population biology, physical tolerance, and community ecology information, the database includes information on non-native and endangered, threatened, and special-status species. An electronic companion publication to the Species Inventory is the Field Guide to the Indian River Lagoon (www.sms.si.edu/IRLfieldguide). Both projects have been supported by the Indian River Lagoon National Estuary Program administered by the St. Johns River Water Management District. Features such as an interactive glossary, enhanced indexing, and links to other relevant websites add to the educational value of these websites.

The Smithsonian Marine Ecosystems Exhibit in the St. Lucie County Marine Center celebrated its seventh anniversary in August 2008. Administered by the Smithsonian Marine Station, the exhibit showcases the Caribbean coral reef ecosystem that was a popular exhibit at the National Museum of Natural History for more than 20 years and the first living model of an Atlantic coral reef ecosystem available for public viewing. Through an outpouring of local interest and support, the exhibit was transferred to Fort Pierce to a building constructed and maintained by St. Lucie County for the sole purpose of housing this educational attraction. At the Ecosystems Exhibit, visitors are invited to explore six Florida marine habitats and learn about the complexity and importance of these ecosystems (Figure 10). The largest aquarium houses a Caribbean coral reef display. Additional aquaria depict a seagrass bed, red mangrove coastline, estuarine and nearshore habitats, and a deep-water *Oculina* coral reef. Smaller aquarium displays highlight single species of interest, and a touch tank offers visitors personal interaction with various local invertebrates, such as horseshoe crabs, sea urchins, sea cucumbers, and peppermint shrimp.

This public aquarium is unlike any other, providing an accurate representation of the underwater worlds of the Indian River Lagoon and Atlantic Ocean. Although these waters are a common sight to many coastal Florida residents, few have experienced the unsurpassed diversity of life just below their surface. By highlighting this diversity and displaying local ecosystems as complex communities of organisms interacting in their environments, the Exhibit aims to provide the public with a better understanding of the fragile coastal ecosystems of the Indian River Lagoon and the surrounding area, including the impacts people have on them.

The Smithsonian Marine Ecosystems Exhibit is a field trip destination for thousands of school-aged children each year (Figure 11). Although some choose a self-guided visit, most participate in one of several structured programs facilitated by Education staff members. Program options are age- and grade-appropriate and are structured in compliance with Florida's Sunshine State Standards. Activities include scavenger hunts, water quality experiments, food web and energy transfer studies, simulated benthic sampling, and field experiences in the Indian River Lagoon.

In 2005, education staff at the Exhibit began offering community and visitor programs. Ranging from informative breakfast programs to sleepovers and summer camps, the new programs target traditional visitor groups in new ways, providing more focused and in-depth learning experiences for those interested in taking advantage of the many resources the Smithsonian has to offer. The enthusiastic response from the community has resulted in continual additions to the events calendar.

In addition to being a physical destination for the local community, the Ecosystems Exhibit has also established itself as a valuable resource for local schools and community organizations that do not have the means to travel. Education staff provides classroom outreach programs, bringing the wonders of the underwater world to hundreds of students each school year. Education staff members have also developed Resource Loan Kits for area teachers to borrow for in-classroom use for a two-week time period. The Exhibit website also hosts three webcams that provide live feeds to three of the Exhibit's displays. Online visitors have alternate, unparalleled views into the seagrass and coral reef model ecosystems, as well as through the lens of a laboratory microscope. Future plans include the development of online curricula and activities based on observations made via the webcams.

LOOKING TO THE FUTURE

During the past 37 years the Smithsonian Marine Station at Fort Pierce has developed a strong, broadly based program in marine biodiversity research focusing on systematics, ecology, and life histories of marine organisms. With nearly four decades of research along the IRL, the Smithsonian Marine Station has been able to establish long-term and intensive research projects that are valuable in understanding and assessing marine biodiversity as well as the changes in biodiversity occurring on a global scale. As a result of its excellent location, modern facilities, and experienced staff, the Marine Station is well positioned to continue to address important research topics including global climate change, invasive species, harmful algal blooms, systematics, larval ecology, and evolutionary developmental biology.

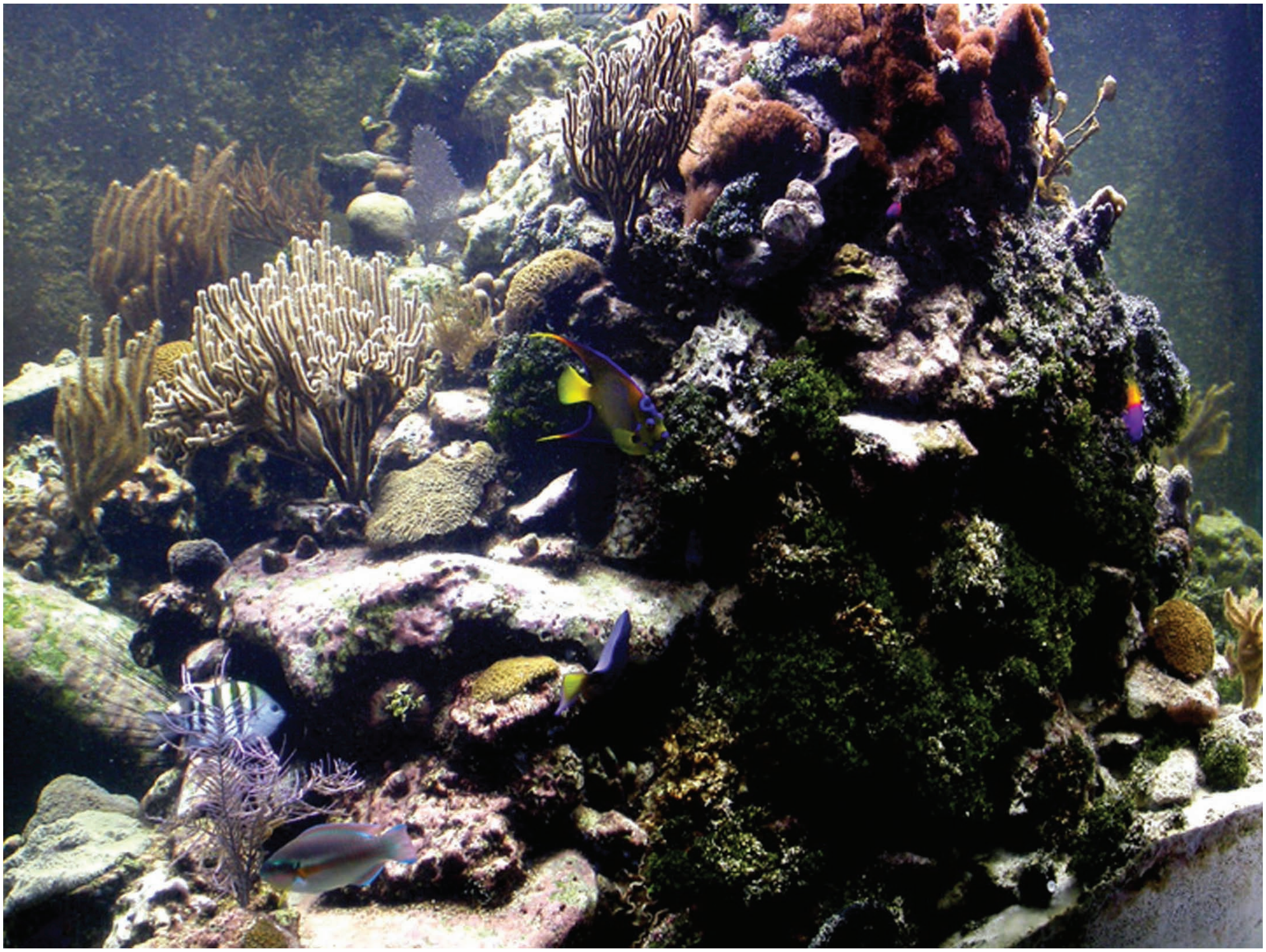


FIGURE 10. The coral reef at the Smithsonian Marine Ecosystems Exhibit.

The Smithsonian Marine Ecosystems Exhibit makes the work of Smithsonian marine researchers accessible to a broad, non-scientific audience. The living displays capture the dynamic quality of natural ecosystems, and the educational offerings are a reflection of the same. Programs, displays, and live exhibits are constantly changing, evolving, and taking on new life, providing a foundation to ensure the Exhibit's future in an ever-changing community.

Acknowledgments

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FIGURE 11. Top: A young girl takes a closer look at the inhabitants of the seagrass ecosystem. Bottom: Excited children view the nearshore reef ecosystem.

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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 km^2 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 actuopaleontologist (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 Caribbean. 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°48′N, 88°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 morphology: 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 m^2 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.

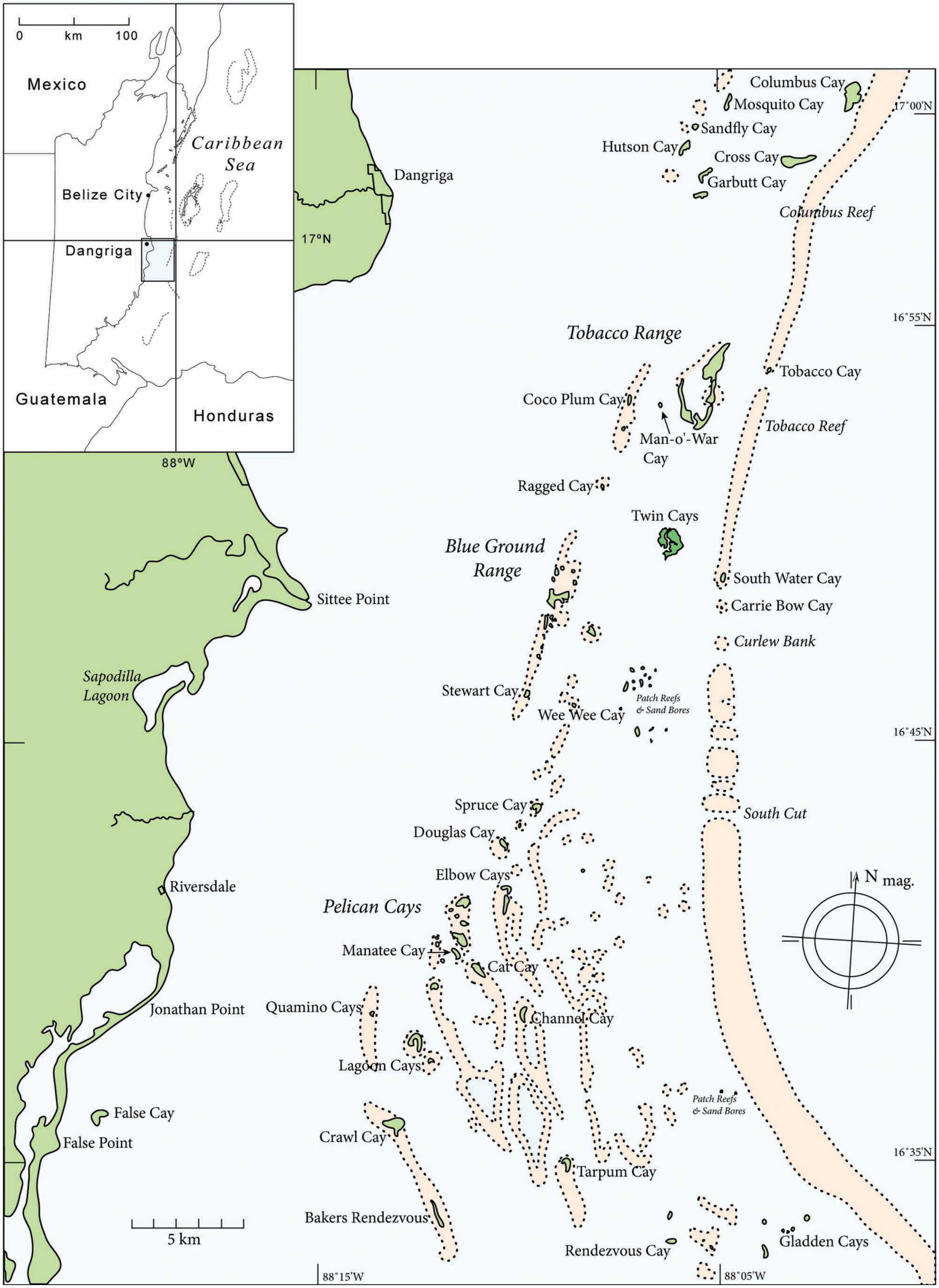

FIGURE 1. Map of research area in coastal Belize, Central America. The barrier reef and other reef tracts appear in pink.

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

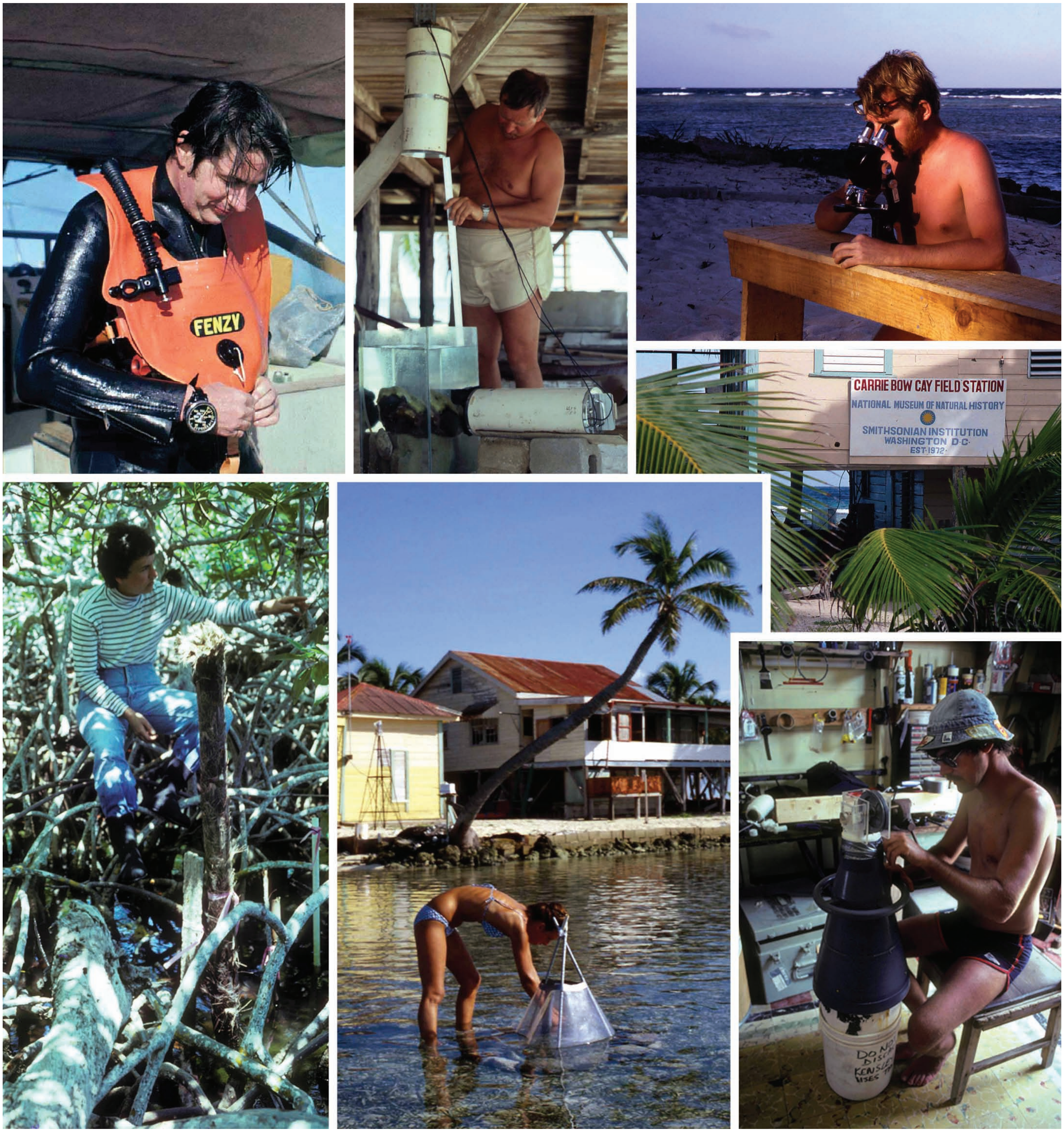

FIGURE 3. Some early program participants. Clockwise, from top left: Ian Macintyre about to enter the submarine Colombus Cay Cave; Arnfried Antonius setting up time-lapse camera for study of black band coral disease; Klaus Ruetzler catching the evening sun for a microscope examination; view of entrance 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, Colombia), 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, Colombia), 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 Randolf 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 Gulledge, 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.