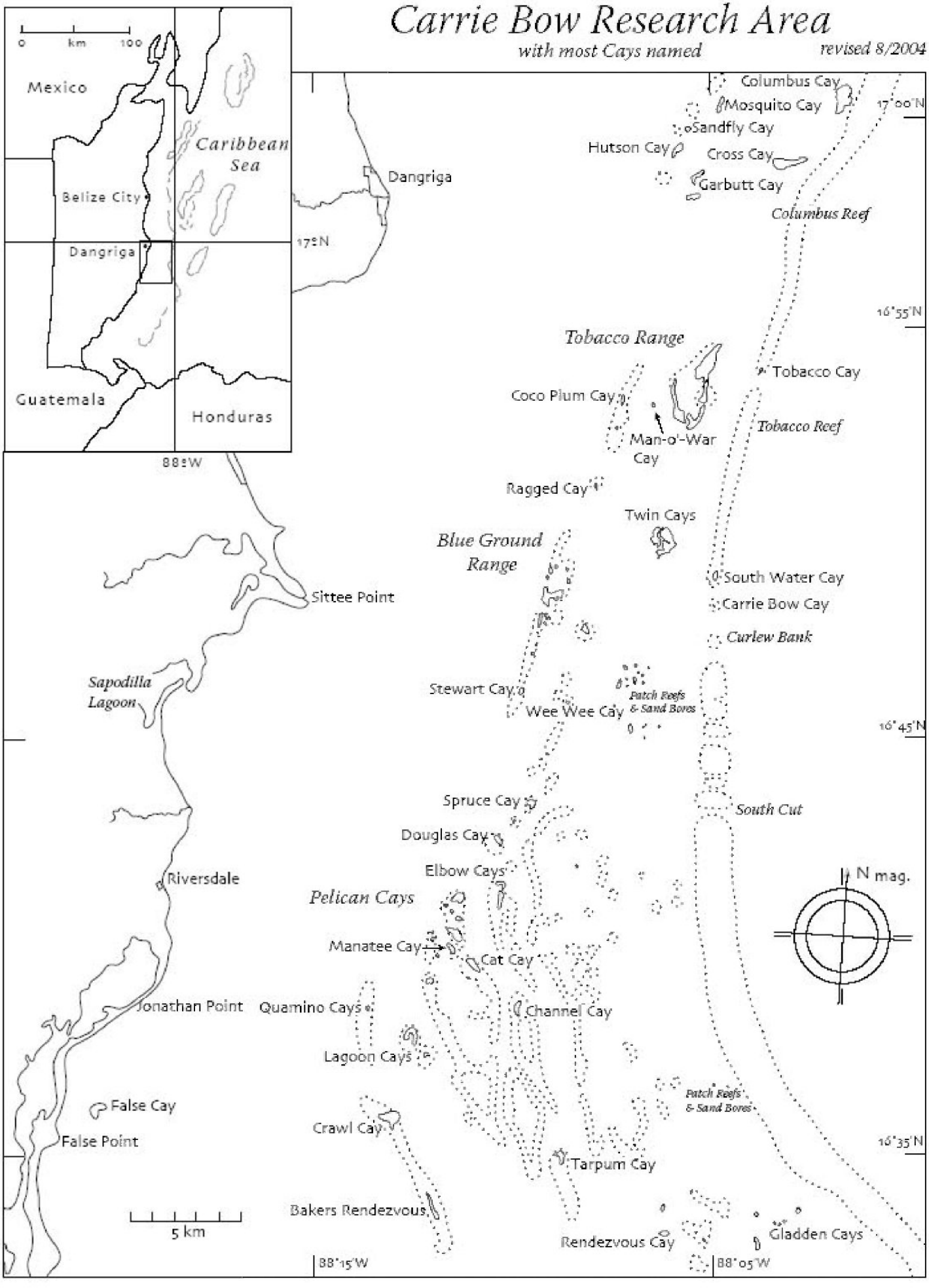
Smithsonian Institution

CCRE REPORTS

2002-2004

Caribbean Coral Reef Ecosystems • National Museum of Natural History

December, 2004


Carrie Bow Research Area
with most Cays named
revised 8/2004
0 km 100
Mexico
Caribbean Sea
Belize City
Dangriga
Guatemala
Honduras
88°W
17°N
Dangriga
Columbus Cay
Mosquito Cay
Sandfly Cay
Hutson Cay
Cross Cay
Garbutt Cay
Columbus Reef
17°00'N
16°55'N
Tobacco Range
Tobacco Cay
Coco Plum Cay
Man-o'-War Cay
Tobacco Reef
Ragged Cay
Twin Cays
Blue Ground Range
South Water Cay
Carrie Bow Cay
Curlew Bank
Sittee Point
Sapodilla Lagoon
Stewart Cay
Patch Reefs & Sand Bores
Wee Wee Cay
16°45'N
Spruce Cay
South Cut
Douglas Cay
Elbow Cays
Riversdale
Pelican Cays
N mag.
Manatee Cay
Cat Cay
Jonathan Point
Quamino Cays
Channel Cay
Lagoon Cays
Patch Reefs & Sand Bores
False Cay
Crawl Cay
16°35'N
False Point
Tarpum Cay
Bakers Rendezvous
Rendezvous Cay
Gladden Cays
5 km
88°15'W
88°05'W

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National Museum of Natural History
Caribbean Coral Reef Ecosystem Program
Washington, D. C. 20013-7012

December, 2004

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Flashbacks

1971 • National Museum of Natural History's I.G. Macintyre (geology & sedimentology), W. Adey, P. Kier, T. Waller (paleobiology), A. Dahl (botany), A. Antonius (postdoctoral fellow, invertebrate zoology), M. Rice, and K. Ruetzler (invertebrate zoology) found the program Investigations of Marine Shallow Water Ecosystems (IMSWE).

1972 • IMSWE search party identifies Carrie Bow Cay on the barrier reef of Belize as ideally located and affordable site for long-term, collaborative field research on tropical coastal ecosystems
• Establishment of principal reference transect across the Belize barrier reef just north of Carrie Bow Cay.

1974 • Hurricane Fifi destroys laboratory structures, uproots coconut trees, and reduces the surface area of Carrie Bow Cay by about one third, to 0.4 ha.

1975 • EXXON Corporation provides grant for study of the coral reef ecosystem at Carrie Bow Cay.
• Marine and terrestrial post-hurricane surveys.• Establishment of all-manual meteorological station.

1976 • Refinement and calibration of profiles and maps with the aid of vertical aerial photographs taken by Royal Signals Detachment helicopter • Introduction of aerial photography by helium balloon for community mapping
• Submersible tide recorder installed at Carrie Bow Cay concrete dock.

1977 • Field trip to Carrie Bow Cay by participants of the Third International Coral Reef Symposium.• Aerial and underwater surveys expanded to cover the entire barrier reef of Belize • Geology team drills first cores to determine reef history • EXXON's The Lamp publishes article on company-sponsored research at Carrie Bow Cay ("Where seaworms glow..").

1978 • Hurricane Greta destroys Carrie Bow Cay field station.

1979 • Post-hurricane survey and rebuilding of laboratory with several improvements • Count of participating scientists and of published scientific contributions both pass the 50 mark; 23 scientific institutions are now collaborating with NMNH.

1980 • EXXON Corporation funds new initiative: comprehensive study of a western Atlantic mangrove swamp ecosystem, now known as SWAMP (Smithsonian Western Atlantic Mangrove Program)
• Mapping of Twin Cays, principal site of SWAMP, by aerial photography and ground truthing.

1981 • Initiation of Art in a SWAMP project where scientific illustrators and scientists collaborate in analysis and pictorial rendition of mangrove communities in time and space • Employment of H. Edgerton underwater time-lapse camera with strobe light (on loan from the inventor) to record day-night activity in benthic communities
• Vibracoring at Twin Cays to determine internal structure and development.

1982 • Publication of The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, 1: Structure and Communities. Smithsonian Institution Press (K. Ruetzler & I.G. Macintyre, eds.). 1983 • New weather protected and enlarged seawater system for laboratory experiments installed on Carrie Bow Cay • Series of extremely low tides at noon time were observed to have catastrophic effects on reef and mangrove organisms.

1984 • First automated weather station installed at Twin Cays • Cooperation with Belize Government identifying coastal marine areas suitable for natural resource conservation • Busiest year since program start: 8 months continuing laboratory operation for 45 research staff.

1985 • First year of operation of Caribbean Coral Reef Ecosystems (CCRE), a new program of the National Museum of Natural History. It replaces the old IMSWE project and supplements the ongoing SWAMP program which is supported by a renewed annual grant by the EXXON Corporation.

1986 • Renovations on Carrie Bow Cay to accommodate dry-laboratory space, added living quarters, and boat, diving, and laboratory equipment • Mangrove vegetation map for Twin Cays completed • Published scientific contributions pass the number 200.

1987 • Record visitation of Carrie Bow laboratory, 120 total: 90 scientists and assistants; others dignitaries, including the Prime Minister of Belize, Smithsonian administrators, and media people working on documentaries and news-related productions • Continued facility renovation, including addition of solar photovoltaic system, large seawater tank, twofiberglass whalers, fluorescence microscope, and time-lapse video recorder with underwater camcorder.

1988 • Mangrove workshop for 37 EXXON-SWAMP scientists at Solomons, Maryland, entitled A Mangrove Ecosystem: Twin Cays, Belize.

1989 • Science as Art exhibit at the Smithsonian's S. Dillon Ripley Center displays scientifically important and aesthetically pleasing products from SWAMP mangrove research, such as community drawings, paintings, photographs, and sculpture-like epoxy casts of soft-bottom animal burrows • Vandalized and malfunctioning weather

station reconditioned and relocated to the Carrie Bow field laboratory • Mounting problems with anthropogenic stresses at research sites, such as heavy tourist visitation, garbage dumping, and clear-cutting mangrove trees.

1990 • CCRE-SWAMP program represented at first Caribbean Coastal Marine Productivity workshop, Jamaica, CARICOMP is a program for Caribbean-wide monitoring of environmental quality in reefs, mangroves, and seagrass meadows.

1991 • Belize Forestry Department helps stopping disturbances to SWAMP research sites. Belize Department of Natural Resources reviews legislation with intention of declaring Carrie Bow Cay - Twin Cays area protected research site • CCRE-SWAMP program staff participates in developing Belize Tropical Forestry Action Plan and helps designing Institute for Ecology to be based in Belmopan.

1992 • CCRE-SWAMP researchers produce video documentary on mangrove swamp biology • Unprecedented, severe problem with hydrozoan stings to snorkelers and divers in the Carrie Bow area traced tomicroscopic siphonophorans • CCRE-SWAMP staff and Belize Fisheries Department and Agriculture representatives conduct first workshop for Belize high-school teachers entitled Mangrove Conservation through Education • CCRE-SWAMP lecture series started in Belize City, co-hosted by Belize Audubon Society • CCRE officially joins the CARICOMP network and initiates monitoring program.

1993 • Belize Ministry of Natural Resources grants rights to Twin Cays for mangrove research • Launching of new 8 m (25 ft) research vessel Physalia, funded by a grant from the U. S. National Science Foundation, extends research radius over most of central and southern Belize • Ivan Goodbody pioneers surveys of Pelican Cays, a tunicate heaven at SSW of Carrie Bow.1994 • Start of collaborative surveys and experimental projects in the Pelican Cays • Pelican Cays workshop, co-hosted by Candy Feller (SERC), at Edgewater, Maryland.

1995 • Finalized lease with the Villanuevas of Placentia to southern portion of Northeast Cay, Pelican group, to establish a field base for future studies • Malcolm Spaulding develops plans for new integrated environmental sensing system with radio- telemetry linkto the University of Rhode Island's COASTMAP network.

1996 • Installation by Tom Opishinski of self-contained Endeco-YSI-Campbell monitoring station of meteorological and oceanographic parameters and hookup to Internet • Visit of field party from 8th International Coral Reef Symposium, Panamá.

1997 • Celebration of the 25th birthday of the Carrie Bow Marine Field Station • New U. S. National Science Foundation grant allows purchase of a second 8-m (25 ft) boat to back up the heavily used Physalia (under construction) • International team of seven expert systematists conduct workshop at Carrie Bow Cay to quantify the unusually high sponge diversity of the Pelican Cays • Number 500 reached of CCRE scientific contributions • Carrie Bow Field Station, including laboratories, weather station, kitchen, and living quarters is consumed by an accidental electric fire which was apparently sparked by a short in the wiring and aided by dry, termite-riddled lumber and strong northerly winds. Luckily, no-one was hurt.

1998 • Island clean-up and design for new field station completed. Construction work initiated but delayed by flooding and coastal erosion from hurricane Mitch • Completed editorial work on CD-ROM containing over 100 representative CCRE scientific papers that resulted from research at Carrie Bow Cay • Cosponsored Smithsonian (STRI) exhibit Our Reefs –Caribbean Connections in Belize City. Contributed large poster describing 25 years of CCRE coral reef research in Belize • Serious coral bleaching and die-off on reefs off Carrie Bow and Pelican Cays observed, partly caused by hurricane Mitch.

1999 • Rededication ceremony for the new Carrie Bow Marine Field Station, in August • BBC team (Bristol, UK) films segments for its Blue Planet TV series, including (with E. Duffy) eusocial shrimps living in sponges.

2000 • Publication of Natural History of Pelican Cays, Belize, in Atoll Research Bulletin (Macintyre & Ruetzler, eds, 2000) • Replacement of environmental monitoring station lost in the 1997 fire • Initiation of Twin Cays Biocomplexity Study funded by an NSF grant (to I. Feller & colleagues).

2001 • Completion of 3-room cottage over the eastern shore of Carrie Bow Cay • Hurricanes Michelle and Iris (October) barely miss Carrie Bow Cay, causing some damage to buildings and heavy beach erosion and devastate (Iris, in particular) large areas in southern Belize • Signing of MoU with Belize Fisheries Department officially acknowledging the Carrie Bow Marine Field Station as a nationally recognized laboratory • Publication of Golden (50-year anniversary) issue of Atoll Research Bulletin recognizing prominent coral reef scientists through their autobiographies, several of them participants in the CCRE Program.

2002 • Founding of the Smithsonian Marine Science Network (MSN), incorporating the CCRE Program and the Carrie Bow Marine Field Station • Number 600 reached of CCRE scientific contributions • Ranger Station established on southeast Twin Cays by Belize Fisheries Department to oversee South Water Cay Marine Reserve.

2003 • Cristián Samper, recently appointed director of the Smithsonian's Natural History Museum, visits the Carrie

Bow station in July, makes dives on the barrier reef, and snorkels in mangroves habitats • Hurricane Claudette threatens Carrie Bow (July) and necessitates temporary evacuation • Smithsonian Secretary Larry Small visits the Carrie Bow lab in December and dives on the reefs • Twin Cays Mangrove Biodiversity Conference is held at Ft. Pierce, Florida (December), convened by Klaus Ruetzler, Ilka Feller, and Ian Macintyre, and cosponsored by Valerie Paul of the Smithsonian Marine Station at Ft. Pierce.

2004 • CCRE Postdoctoral Fellowship established • Hurricane Ivan causes substantial coastal erosion of Carrie Bow Cay • Atoll Research Bulletin volume dedicated to Twin Cays Mangrove Biodiversity goes to press • Number 700 reached of CCRE scientific contributions • Carla Dietrich takes over from Michelle Nestlerode as CCRE research assistant • Addendum to MoU with Belize Fisheries Department signed, clarifying intellectual property rights and issues of bioprospecting • CCRE Program Administrator Marsha Sitnik (recently, administrative advisor) retires.

Introduction

During the past two-year period covered by this report, the CCRE Program gained momentum by becoming part of the latest Smithsonian research initiative, the Marine Science Network (MSN), officially approved by Undersecretary for Science David Evans in 2002. The Network links four coastal laboratories and long-term marine research sites in the western Atlantic Ocean along the east coast of North and Central America, and bridges the Panamanian isthmus from the Caribbean Sea to the Pacific Ocean (http://www.si.edu/marinescience): Smithsonian Environmental Research Center (SERC, Maryland), Smithsonian Marine Station at Ft. Pierce (SMSFP, Florida), CCRE's Carrie Bow Marine Field Station (Belize), and Smithsonian Tropical Research Institute (STRI, Panamá). For over thirty years, these facilities have provided unparalleled access to important coastal habitats such as estuaries, coral reefs, mangroves, sea grasses, and wetlands. Combined, they are uniquely positioned to support coordinated research and long-term monitoring in coastal ecosystems to increase our knowledge of biodiversity, ecological processes, and community dynamics, and of the effects of climate change, eutrophication, overfishing, and habitat destruction. For CCRE, the most notable benefit of the MSN association was the award of a 2-year postdoctoral fellowship, starting in 2004, dedicated to one of the program's missions.

In Belize, the formalization of the Southwater Cay Marine Reserve, which includes Carrie Bow Cay and most of the CCRE research area, was a big step toward protecting the southern barrier reef and its valuable fisheries resources. A ranger station was established at the southeastern point of Twin Cays which will help control illegal clear-cutting and habitat destruction in these mangrove islands.

Twin Cays was the central theme of a special CCRE symposium held at Ft. Pierce, Florida in December 2003. It was entitled The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change. The two-day colloquium was convened by Klaus Ruetzler (NMNH), Ilka Feller (SERC), and Ian Macintyre (NMNH), and co-hosted by Valerie Paul (SMS). It was attended by 35 study participants from the Smithsonian and collaborators from scientific institutions throughout the country. Talks, posters, and discussions centered on the systematics and ecology of microbes, algae, invertebrates, and fishes. Marine and terrestrial protozoan and invertebrate taxa were strongly represented, including foraminiferans, placozoans, sponges, sipunculan worms, crustaceans, insects, bryozoans, and ascidians. Other presentations were on the geological development of the mangroves, geomorphological changes over two decades, ecological impact of sediments, tidal flow, and anthropogenic stress, chemical defense mechanisms, scientific illustration of communities, and aspects of data management.

Important visitors to the Carrie Bow Marine Field Station were Smithsonian Secretary Larry Small (December 2003) and National Museum of Natural History Director Cristián Samper (July 2003). Both were enthusiastic scuba divers and (guided by Scientific Diving Officer Michael Lang) explored many of the reefs. They also participated in tours of several mangrove habitats.

Less appreciated but unavoidable visitors were four hurricanes, which prompted temporary evacuation of the Carrie Bow laboratory and caused substantial coastal erosion and some damage to the facilities: Hurricanes Michelle and Iris (October 2001), Claudette (July 2003), and Ivan (September 2004).

Acknowledgments

The Belize Fisheries Department hosted our research and we are grateful to Ms. Beverly Wade and Mr. James Azueta for collaborating in scientific and educational activities and issuing permits. The owners and staff of Pelican Beach Resort in Dangriga provided logistical support for our fieldwork; Therese and Tony Rath of Dangriga helped with local management, photography, and computer backup for our weather station. Numerous volunteer managers helped run the field station and assisted in research activities and we are indebted to them for their many efforts: Jerry and Sandy Alanko, Sam Benson, Earl David, Ed Hunt, Joel Leavitt, Dan Miller and Claudette DeCourley, Keith Parsons, Gary Peresta, Tom Pezzella, Bert Pfeiffer, and Craig Sherwood.

Back in Washington, we thank Vicky Macintyre for editorial work and Marty Joynt (Department of Zoology) for administrative advice and preparation of many documents. Marsha Sitnik helped prepare the wording of an addition (bioprospecting) to the Memorandum of Understanding with the Belize Fisheries Department. Michael Lang and Jennifer Dorton supervised and ran all aspects of scientific diving at Carrie Bow. We also thank the Smithsonian offices of the Undersecretary for Science and the Director of National Museum of Natural History for continued support and access to the Smithsonian Hunterdon Fund for part of our budget. A grant from the National Science Foundation for a biocomplexity study of the Twin Cays mangrove ecosystem (to Ilka Feller and colleagues, see projects below) greatly enlarged our scientific horizon and logistical capability. Last but not least, we thank Hans Pulpan, Fairbanks, for his enthusiasm and financial contribution.

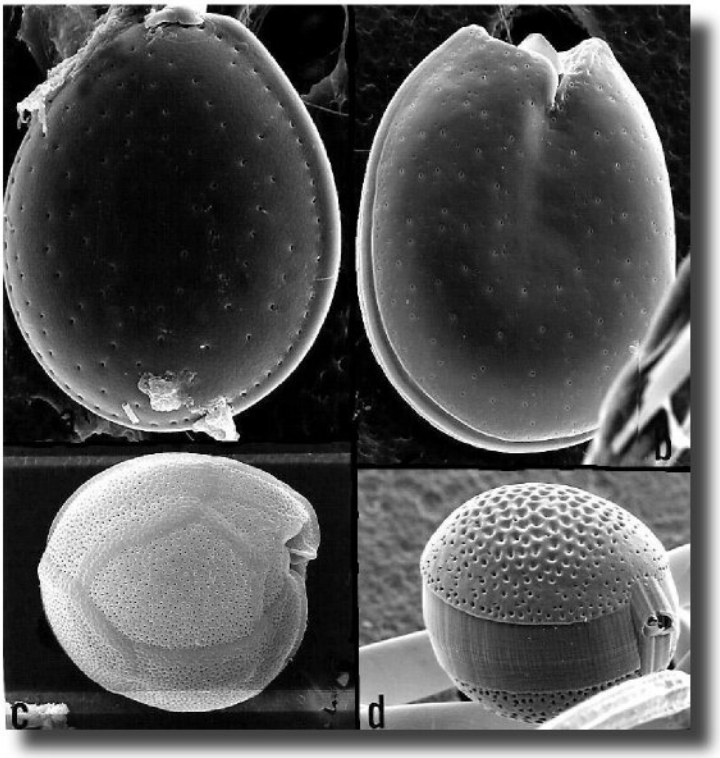
Research Projects

Biodiversity and its Links to the Ecosystem

Algae

Abundance and taxonomy of dinoflagellates in the naturally enriched lagoon of Douglas Cay

M. A. Faust



SEM photographs of benthic sand-dwelling dinoflagellates, *Prorocentrum arenarium, P. emarginatum, Gambierdiscus toxicus, Prorocentrum* sp. nov.

The primary goal of this project was to identify and quantify dinoflagellates in naturally enriched waters in Douglas Cay and control area outside the lagoon in oligothropic water. Assemblages of dinoflagellates exhibited different morphology, cell numbers and biodiversity. In Douglas Cay representing naturally enriched water, dinoflagellates were > 50 µm in size, cell shape discoid and highly sculptured, and cells were photosynthetic. Representative species include: three red tide forming species *Gonyaulax spinifera*, *Gonyaulax* sp. nov., and *Protoceratium spinulosum* all have highly ornamented cell surface, and tow toxins producing species *Prorocentrum mexicanum* & *Gambierdiscus toxicus*, and *Prorocentrum* sp. nov. Cell numbers ranged from 200 to 400 higher in Douglas Cay waters, and the mean chlorophylla a value was 5.01 µm/L while in the surroundings oligotrophic water mean chlorophyll a value was 0.3 µm/L. The dinoflagellate assemblages in outside waters were larger < 100 µm in size, cell shape more diverse and highly ornamented. Species were both photosynthetic: *Ceratium vultur* forming cell chains, *Ceratocorys horrida* ornamented with winged hypothecal spines with distal barbas, and *Ceratium horridum* with distinct curved horns; and heterotrophic species represented by round shaped *Diplopelta bomba*, a medium sized species with circular full body with extensive winged ribs of *Ornithocercus quadratus* that can have photosynthetic symbionts in its cingular chamber, and bloom forming *Protoperidium depressum.* Identification of dinoflagellates continues to asses their biodiversity in 48 collected samples.

Taxonomic diversity of symbiotic dinoflagellates in different environments

M. E. Warner

Several initial monitoring sites were established in order to record the type and population distribution of *Symbiodinium* spp (zooxanthellae) from several species of scleractinians and soft corals. A complete list of species sampled was provided to CCRE. Three primary sites were established in front of Carrie Bow Cay at 1 m (back reef lagoon), 8 m (fore reef), 16 m (top of outer ridge), and 25 m (outer slope). In addition to these sites, we sampled several species of scleractinians around the Pelican Cays in a haphazard survey pattern in shallow waters (1-3 m). At least three colonies were sampled for each species, with an approximately 1.5 cm core or branch fragment removed from each colony. Zooxanthellae were isolated on Carrie Bow Cay, placed in DNA preservation buffer, and stored at 4°C until transport back to the United States.

Ecology and experimental taxonomy of siphonalean green algae at Twin Cays

M. Littler & D. Littler

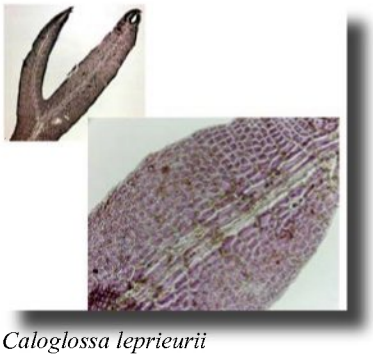
Siphonalean green algae (a highly diverse and taxonomically problematic group) dominate the standing stocks and productivity habitats within the Twin cays mangrove island ecosystem. For example, from one to a mixture of five species of *Avrainvillea* can dominate Twin Cays bays, ponds and lakes, with individuals expanding into large colonies. This common genus also occurs abundantly in virtually all calm-water back-reef habitats. The theoretical costs versus benefits of coloniality in marine animals and terres-

trial plants have received considerable attention. However, consideration of this phenomenon for marine plants is extremely limited. *Avrainvillea longicaulis* (f. *longicaulis*) is solitary in pristine back-reef environments with consistent wave action, but forms what appear to be clonal mounds, described as *A. longicaulis* f. *laxa*, in highly eutrophic and placid interior mangrove habitats. The "*laxa* form" appears uniquely adapted to utilizing flabellar stipes as subterranean rhizomes that spread laterally to produce large highly-productive mound-like colonies that overgrow seagrasses and understory macroalgae. We also observed what appears to be perennation in the back-reef "*longicaulis* form", where the only remains of lost blades are scars giving rise to newly forming blades from either the former stipes or columnar holdfasts. We showed that stipes and blades of the "*longicaulis* form" serve as expendable assimilators, with a major function of building a massive perennating/storage organ, the columnar holdfast, which a major function of building a total thallus. Additionally, we used a costs vs. benefits approach to test the hypothesis that the two remarkably different forms (i. e., f. *laxa* and f. *longicaulis*) are adaptative for their respective habitats. Replicated reciprocal transplant experiments, with appropriate transplant controls, for both forms showed (1) the induction of coloniality in individuals of f. *longicaulis* (under the presence of high nutrients and physically benign conditions) within calm interior mangrove ponds and (2) that large colonies of f. *laxa* transplanted to the back reef are susceptible to damage by only moderate wave surge and must develop a subterranean holdfast to survive, therein supporting our hypothesis concerning the cost/benefits of coloniality. In the back reef transplant study, physical disturbances (such as wave action and herbivory), as well as physiological stresses (such as epiphyte loading), result in disproportionate losses of the subterranean holdfast during more favorable conditions.

Avrainvillea longicaulis

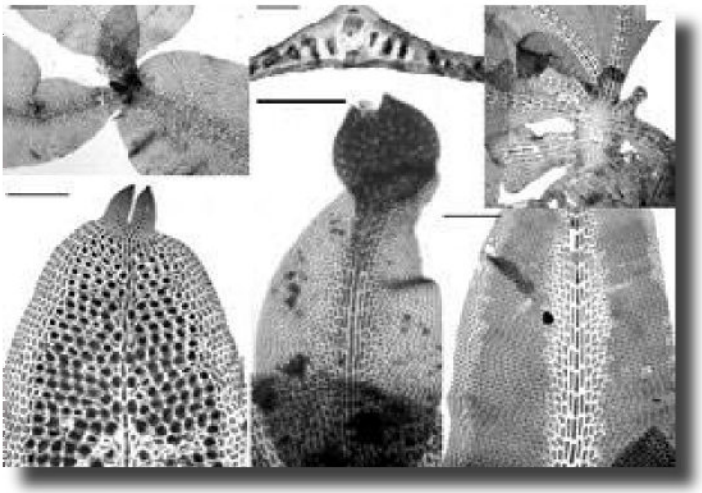
Characterization of bostrychietum mangrove algae based on morphological and molecular evidence: The red algal genus *Caloglossa* (Delesseriaceae, Ceramiales)

D. Krayesky & S. Fredericq



Caloglossa leprieurii

The euryhaline red algae genus *Caloglossa* (Harvey) G. Martens is a common member of the "Bostrychia-Caloglossa Association" in mangrove ecosystems, growing on pneumatophores or trunks of mangrove trees worlwide. Diagnostic features for separating species of *Caloglossa* pertain to branching pattern, rhizoidal pattern and position, number of cell rows around the nodes, and whether additional secondary blades are borne endogenously or adventitiously. Phylogenetic analyses inferred from chloroplast-encoded rbcL sequences of *Caloglossa* species from the western Atlantic, NW Gulf of Mexico, Pacific and Indian Ocean indicate that three distinct species go under the name *C. leprieruii* (Montagne) G. Martens (1869), the generitype described from French Guyana. The correct identity of *Caloglossa* from Twin Cays, Belize, awaits confirmation, but herbarium specimens examined to date indicate that lateral axes typically lack a primary adaxial cell row, and that rhizoids form a basal cortical pad. Because these features are also present in specimens from Guyana, Madagascar, Puerto Rico and Venezuela, Twin cays specimens may conform to true *C. leprieurii*, pending morphological and molecular examination of topotype material. A separate, undescribed species has been collected from black mangroves in Louisiana, and from Spartina salt marshes in Alabama, Virginia and Connecticut.



Caloglossa leprieurii: habit and sections of various plants.

Foraminiferans

Seasonal variation in the epiphytic foraminiferal biotas from *Thalassia* seagrass habitats at Twin Cays

S. L. Richardson

The epiphytic foraminiferal biotas living on the seagrass *Thalassia testudinum* were surveyed at four sites in the Twin Cays (Boston Bay, Sponge Haven, the Channel near the dock, and 'Cuda Cut) during June (wet season) and February (dry season). All epiphytic foraminiferans were censused on twelve blades (replicates) haphazardly collected from each site. A total of 15,455 individuals, comprising forty-one species were recorded. Diversity indices calculated were highest at the 'Cuda Cut site, lowest at Boston Bay and the Dock. Evenness was highest at Sponge Haven and lowest at the Dock site, reflecting the high dominance of the species *Rhizonubecula* sp. (68.24%) at the latter site. The most common species included: *Cornuspiramia antillarum* (multichambered, calcareous species with dendritic test), *Crithionina cushmani* (single-chambered species with test of agglutinated sponge spicules), *Flintia labiosa* (multichambered species with coiled, calcareous test), *Hemidiscella palabunda* (coiled, tubular species with agglutinated test), *Heterillina cribrostoma* (multichambered, calcareous species with coiled test), *Iridia diaphana* (single-chambered species with agglutinated test), *Planorbulina acervalis* (multichambered, calcareous species), *Rhizonubecularia* sp. (multichambered, calcareous species with irregularly dendritic test), *Rhizonubecularia adherens* (multichambered, calcareous species with dendritic test), and *Sorites dominicensis* (disk-shaped, multichambered, calcareous species with dinoflagellate endosymbionts).

Placozoa

Trichoplax adhaerens (Placozoa) diversity at Twin Cays

A. Y. Signorovitch & L. W. Buss

The phylum Placozoa comprises a group of benthic marine invertebrates that roughly resemble very large amoebae. Thought to be one of the earliest diverging phyla among the metazoa, placozoans have a relatively small genome size (~50Mb) and a simple body plan composed of four somatic cell types, no definite symmetry and a top-bottom polarity. Our lab at Yale University maintains clonal cultures of placozoans from the Caribbean. The life cycle of *Trichoplax adhaerens*, the sole member of the Phylum Placozoa, has remained unresolved for well over a century. Specifically, it is not known if the Placozoa possess a sexual phase in their life cycle. Our primary work with this group has focused on understanding its life cycle and mitochondrial genome diversity.

To this end, we surveyed almost the entire perimeter of Twin Cays for the presence of placozoans and sequenced sampled individuals at the mitochondrial 16S ribosomal DNA locus. Through this effort we discovered at least four very divergent clades of placozoans distributed around Twin Cays. Furthermore, no phylogeographic subdivision was detected, indicating that these clades are able to cohabit. Since the four clades are morphologically indistinguishable from one another at the level of the dissecting microscope, we have begun morphological and ultrastructural investigations of these clades using light and electron microscopy to determine if any clade-specific differences exist. This is the first study to survey for the presence, distribution and genetic diversity of placozoans in Twin Cays. With the first placozoan genome being sequenced next year, the animals collected at Twin Cays. This finding increases our understanding of placozoan systematics and suggests that inferences about the Phylum Placozoa must be based on observations of more than one *Trichoplax* clade.

Porifera

Barcoding sponges and testing the appetite of predators

S. Duran, M. Becerro & K. Rützler

More than 200 samples (of ca. 100 species) of sponges were collected for a pilot project that uses DNA analysis to aid and expedite the identification of species. Sponges present a significant challenge to systematists because they are extremely variable in phenotypic expression, a property that reflects adaptation to environmental influences and possibly evolutionary potential of a phylogenetically old group of organisms. We sampled in many habitats, including the fore reef, patch reefs, lagoon seagrass meadows, and mangroves of Twin and Pelican cays. We photographed the specimens in situ and close-up in the lab, and preserved them for DNA analysis as well as for conventional morphological and histological study. Many samples have already been sequenced at the Smithsonian Marine Station at Fort Pierce and comparative identification according to conventional taxonomy

is progress.

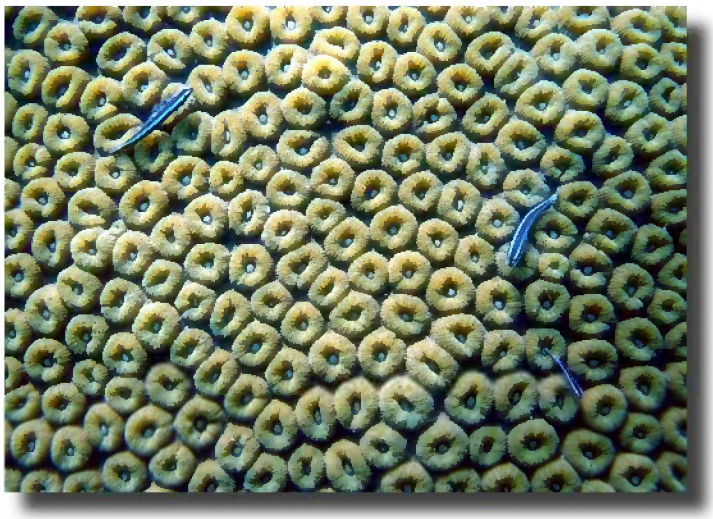
Some of us (MB, SD) also run a series of experiments to test chemical feeding deterrents (secondary metabolites) in sessile organisms against potential predators (see also Paul *et al.*, this report). In the lab, we offered the sea urchin *Didadema antillarum* a choice of artificial diets, with and without chemicals extracted from benthic organisms, and observed their responses. We offered the same choice to reef fishes in the field to identify potential predators. The results are being evaluated and will be published in the near future.

Mikel Becerro

Coral species boundaries: comparisons between Carrie Bow Cay and Panama for members of the *Montastraea annularis* complex

N. Knowlton, H. Fukami, D. Levitan & N. Budd

Members of the *Montastraea annularis* species complex (*M. annularis, M. faveolata,* and *M. franksi*) are the dominant reef builders of the Caribbean and have been so for millions of years. Despite their wide study by geologists and biologists, the nature of species boundaries in this group remains controversial. Many other coral species exhibit similar systematic ambiguities, and members of the *Montastraea annularis* complex represent a model system in this regard. Addressing the "species problem" in corals is important, not only for understanding their evolution (particularly the importance of hybridization), but also in the context of conservation (which depends on accurate species assignments). Our work has shown that in Panama, the three members of the species complex are clearly distinct in morphology, genetics, and reproductive isolation. In the Bahamas, in contrast, the species are hard to recognize by their colony morphologies, and show both genetic and morpholo



Montastrea sp.

gical overlaps. Reproductively, however, they show isolation comparable to that observed in Panama, and no typical F1 genotypes were observed. These results suggest that they have hybridized to some extent in this region, at least in the past, although the intrinsic barriers to gene flow are similar to those observed in Panama. These different sets of results from two ends of the range of these species lead logically to the question we wish to address in the research proposed here: How well isolated are the species in other geographic areas? The answer to this question is critical to an assessment of how commonly these coral hybridize. Because the

Bahamas lie outside the Caribbean and are thus somewhat isolated geographically, we hypothesize that Belize and Panama will be more similar in this regard than are Panama and the Bahamas. Our proposed experiments and observations at Carrie Bow Cay will allow us to test this hypothesis but because the coral spawning seasons occurs only following the full moon in August or September, results are not yet available at this time.

Platyhelminthes, Nemertea and Gnathostomulida

Systematics and biogeography of interstitial platyhelminth worms

S. Tyler & M. Hooge

We are describing species of Acoelomorpha and Catenuleda (Platyhelminthes) sampled from various sand habitats in the vicinity of Carrie Bow Cay to include them in our phylogenetic analyses of these taxa worldwide.

The biology of thiotrophic symbioses: Mouthless plathelminths and nematodes with microbial symbionts

J. Ott

Quantitative samples were taken from the sandbar extending from the north end of the island using cores with an area of 30 cm^2 and extracted by gently shaking with sea water in 1.5 l Erlenmeyer flasks and sieving through a 80µm mesh. Specimens of the large *Paracatenula* species were individually sorted under a dissecting scope. Fine sand was scraped together from the thin sediment cover overlying peat among the stilt roots of *Rhizophora mangle* at the west side of Twin Cays. Portions of the sand were placed into Erlenmeyer flask filled with a sodium sulfate solution in order to anesthetize the interstitial animals. The samples were then shaken, the supernatant then poured through a 80 µm sieve which was then placed in a petri dish with a few mm of sea water. After several hours most of the animals had crawled through the sieve and the small *Paracatenula* species could be collected after removing the sieve.

Single specimens of the large *Paracatenula* species were placed 2 ml seawater each containing thiosulfate at a concentration of 0, 2.5 and 5 mM. Photos and videos were taken on d Leica S6D stereo microscope with a Nikon Coolpix digital camera and a Panasonic single chip camera and recorded digitally. Specimens of all *Paracatenula* species were fixed in paraformaldehyde (for sulfur determinations and FISH), glutaraldehyde (for TEM) and 100% ethylalcohol (for sequencing). Dr. Wolfgang Sterrer (Bermuda Aquarium, Museum and Zoo) collaborated in all procedures and especially worked on the taxonomic identification and morphology of the *Paracatenula* species.

Three species of the genus *Paracatenula* were found. Two large species co-occur in the Carrie Bow Cay sandbar, *Paracatenula erato* Sterrer & Rieger 1974 and a species new to science, which will be described in a forthcoming publication. The third, smaller species was identified as *P. polyhymnia* Sterrer & Rieger 1974. It occurred in the fine sand from Twin Cays. *P. erato* has a slender, pointed rostrum Its symbiont containing region is ribbon shaped and can attain several mm in length. Due to its fragility, however, complete specimens are rarely found. Densities of *P. erato* were low at 30 to 100 specimen per m^2. The new species, *Paracatenula* n. sp., in contrast, has a larger finger-shaped rostrum and a more robust and massive rounded body. It is much more common, occurring in densities from 400 to 900 individuals per m^2. Due to its abundance and greater robustness this species was used for all experiments.

Densities of *P. polyhymnia* could not be assessed due to the sampling procedure which precluded coring. It was, however, abundant in the extracted samples.

Data from a previous visit to Carrie Bow Cay had suggested a active selection of thiosulfate enriched water over natural seawater. The experiments with different thiosulfate concentrations, however, did not show a difference in survival rate.

From the preserved specimens those preserved for sulfur determination have been sectioned for element analysis. The sections will be compared to those from marine turbellaria (*Macrostomum* sp.) without bacterial symbionts. Due to technical problems with the element analysis no results are available yet. Also the other preserved material still awaits further processing.

Unfortunately, no *Astomonema* specimens were found during the whole research period.

Papers and posters:

A manuscript on the identification of the symbionts in *Paracatenula polyhymnia* and *P.* n. sp. is in preparation.

Nemertean phylogenetics

J. Norenburg, M. Schwartz, C. Santos, J. Ferraris & B. Littman

We collected 117 specimens, representing 44 putative species, from a broad selection of habitats but most of the diversity was from rubble collected in five to 20 meters depth on the forereef and in the lagoon adjacent to CBC. Almost all are unknown or undescribed species. Some we had encountered on a previous trip but about 30 species were

new to us. As is usual, most species are represented by only one, two or three specimens and many of those lack gonads, which would be essential for taxonomic work. About 10 species have five or more specimens and we have started taxonomic work on these. We have sketches, detailed notes, and some sort of photographs for almost all species. These will migrate to the nemertean web site as appropriate parts of the site are developed. We have tissue samples for molecular data for almost all species, either a whole specimen or a piece taken from a single specimen. All other specimens were fixed for histology.

The molecular samples are the most important at this time, because they can be processed and yield useful information even when it is not practical to do definitive taxonomic work with other specimens. For instance, we have about 10 putative species or morphotypes that appear to be closely related and may actually be color morphs of each other. We don't think that this is likely for all of them but we have no way of knowing without doing a genetic analysis. This will tell us how to proceed with respect to anatomical and taxonomic study of these worms. We also collected several juveniles of Carcinonemertes from majid and xanthid crabs, not previously known as hosts. These worms live on crabs and eat their eggs and we are interested in discovering how widely distributed and how host-specific they are. Adult worms of different species can be almost impossible to distinguish; juveniles are impossible. However, the molecular data, eventually, can tell us who the worms are, whether they are undescribed species or known from other crab hosts. The caveat here is that the adult worms are tiny and the juveniles are microscopic; so that obtaining sufficient DNA is difficult and sometimes impossible. This work is underway.

Systematics and biogeography of Gnathostomulida and Catenulida

W. Sterrer

Gnathostomulida, a phylum of microscopic, interstitial marine worms, are well represented in detritus-rich sandy sediments that are usually found between coral reefs, seagrasses and mangroves. Of 25 species encountered in more than 100 sediment samples collected in southern Belize between 1974 and 2004, 18 species were found in the vicinity of Twin Cays.

Specimens of Gnathostomulida were collected for scanning electron microscopy analysis of jaw architecture (with M. V. Sorensen, University of Copenhagen), and for a comparative analysis of sperm and spermatogenesis (with S. Tyler and a graduate student , University of Maine). Four species of *Paracatenula*, a genus of mouthless marine Catenulida (Plathyhelmintes), were collected (*P. polyhymnia*, *P. erato*, *P. urania* and *P.* nov. sp.), in preparation for a paper on their occurrence in Belize, and their ecology and relationship with endosymbiotic chemoautrophic bacteria (with Jörg Ott, University of Vienna).

In addition, specimens of the anemone shrimp *Periclimenes pedersoni* were photographed and preserved, for a comparative study to determine the endemicity of the Bermudian species *P. anthophilus* (with A. J. Bruce, Queensland Museum, Brisbane).

Annelida

A study of polychaete diversity

K. Fauchald, G. Rouse & F. Pleijel

Two projects are being addressed, "Commensal polynoid polychaetes in the vicinity of Carrie Bow Cay" and "Upgrading the worms", studies linked to the development of an interactive regional key to polychaetes. First, variety of invertebrates, octocorals, sponges, mollusks and echinoderms were collected to study commensal scale worms. These samples provided many unusual and possibly new species and allowed the recording of detailed information about their relations with the host invertebrates, such as commensalism, food-parasitism, and other direct interactions. This purpose of this study is using the data in cladistic analysis and to determine possible dispersal modes and biogeographic consequences. Secondly, general collections of polychaetes from about 20 families were made to improve the quality of morphological information and data on the live organisms and their habitats. The objective is to create a set of well documented and illustrated data-bases leading to improved interactive keys.

Crustacea

Taxonomy and population structure of commensal leucothoid amphipods from the Belize Barrier Reef

J. D. Thomas & K. Klebba

In December of 2004 The PI and graduate student Kristine Klebba conducted work related to this project for 10 days in and around shallow reef habitats of Carrie Bow Cay. Collections and observations were carried out in three shallow water reef areas (<10 m depth); fore reef, mid-shelf patch reefs (Wee Wee Key, sand bores, and Blue Ground Range), and inner shelf patch reefs (Pelican Keys). Collections made at 35 stations produced 300+ specimens of commensal leucothoid amphipods. Material was returned to the PI's lab for taxonomic and genetic analyses. These initial collections were intended to provide an initial inventory of sponges and their leucothoid commensals.

Using specialized underwater collecting techniques a total of 21 sponges were sampled in-situ and in the lab. Ten species of leucothoid amphipods were documented from eleven sponge species. All the leucothoids are undescribed species. Digital photographs and color notes for all taxa were also recorded. This effort represents the first ever documentation of specific amphipod-host relationships in the Leucothoidae. It also demonstrates that fine-scale ecological structuring can be documented over relatively small geographic ranges. This information has significant implications for reef connectivity and resource management. The ability to identify such small-scale habitat patterns aptly demonstrates the importance of basic scientific inventory and assessment activities in providing information for the conservation and protection of the Belize reef systems.

Taxonomic Studies: Literature analysis and collections studies established the Belize commensal leucothoids as undescribed species. Nine of the undescribed leucothoid taxa have been illustrated, and inked plates are in the process of being returned for proofing. SEM work has commenced with preliminary analysis of three of the morphotypes. These results support the main premise of the proposed research; that taxonomic and ecological diversity in commensal leucothoid amphipods is greatly underestimated. Currently, *Leucothoe spinicarpa* is the only species of leucothoid amphipod reported from the western Atlantic Ocean. In reality, *L. spinicarpa* is a "catch-all" species complex. Finally, a *Leucothoe* database has been completed and is available on the PI's website.

Ecological Studies: Preliminary data indicate what appear to be three distinct distribution patterns of commensal leucothoids in the Belize region. Barrier reef, mid-shelf, and inner shelf reefs appear to have characteristic species occurrence patterns of commensal leucothoids. Whether this is a result of the amphipods' association with particular host sponges, or somehow reflects other ecological distribution factors requires further investigation.

Genetic Analysis: To date, genetic analysis has been carried out in Leucothoe "morphotype 3" commonly found in the tube sponge *Callyspongia vagifalis* in both Belize and Florida. Variations in a 422 bp segment of the mitochondrial cytochrome oxidase subunit I (COI) gene were used to infer patterns of gene flow among six geographic locations between the southeast coast of Florida and Belize. A total of 42 haplotypes were identified from 171 animals sampled. Gene flow was low among South Florida locations [17%]. Belize populations were genetically distinct from all Florida populations. A summary of this research was presented at the International Cgral Reef Symposium in Okinawa, July 2004.

Diversity of decapod crustaceans from Twin Cays, Pelican Cays, Carrie Bow Cay and adjacent intertidal to shallow subtidal waters

D. Felder, R. Lemaitre, R. Robles & J. Stake

Collections were focused on and immediately around Carrie Bow, Twin Cays, and shoals along S. Water Cay. Extensive collections of decapods (along with ancillary collections of stomatopods) were obtained toward production of the regional checklist which, as proposed, continues work begun by D. L. Felder and R. Manning in the early 1980's; the 2002 trip contributed extensively to a collections of color photographs for potential use in production of a regional guidebook to the decapod crustaceans, in an anticipated collaborative effort between D. L. Felder and R. Lemaitre. Over 1000 decapods crustacean photographs were taken by DLF in the present effort, a few samples of which are here attached. Other project elements proposed by DLF included the obtaining of genetic samples and larval stages for selected groups of burrowing thalassinideans (with associates) and porcellanids under study; all objectives were met. Likewise, all project elements proposed by RL and CT

were met, as extensive collections of *Iridopagurus* were obtained for use in fresh dissection studies of gross anatomy and preservation for use in subsequent microscopy. These were essential to their on-going investigations of structure, function and phylogenetic significance of hermit crab sexual tubes. During the 2002 trip, access to sites other than those in very close proximity to Carrie Bow was very limited by the theft of the laboratory small boats and outboard motors just prior to our arrival, and the undependability of the arranged alternative. However, work in the immediate vicinity of the lab was productive, nonetheless.

The return to Carrie Bow in 2003 provided an opportunity to add substantively to these holdings, obtain additional color photographs, and supplement holdings of previously collected species with alcohol-preserved materials needed for mtDNA sequencing. It also provided an opportunity to survey the decapods of the Twin Cays area for preparation of a field guide to common decapods, and materials will be applied toward resolving a number of systematic problems among the Alpheidae, Callianassidae, Axianassidae, Porcellanidae, Diogenidae, Paguridae, Portunidae, and Xanthoidea, all of which are currently under study by a combination of morphological, genetic, and developmental techniques.

Echinodermata

Survey of Belizean echinoderms

G. Hendler

Echinoderms were surveyed at seven localities that had been studied during the 1980s and last in 1997, including Carrie Bow Cay, Elbow, Fisherman's, and Lagoon cays, Baker's Rendez-vous, and East Cut reef. Echinoderms were also extracted from 13 quantitative samples of *Halimeda*. Marked changes in the composition of the echinoderm fauna were anticipated, in connection with the recent, widespread mortality of Belizean reef corals, especially agariciids, and heavy siltation of lagoonal reef slopes. Preliminary presence/absence results for three localities (see appendix below), comparing data for 1997 and 2003, suggest that species composition is largely unchanged. However, the absence of *Ophioderma appressum* at Lagoon Cay, may be an important indicator, as it had been a widely occurring species at most localities in the past. At this point, results are anecdotal and quite preliminary. The sea star *Oreaster reticulatus* appeared to be more common than in past years, and individuals of the brittle star *Ophiolepis impressa* were generally small, suggesting that there may have been a widespread recruitment of that species during the past six years. A thorough analysis of the samples is still required, and continued monitoring would be useful to delineate major long-term changes or lack thereof.

Urochordata

Diversity and distribution of ascidians at Twin Cays

I. Goodbody

Thirty-one species of ascidian in nine Families have been recorded from Twin Cays during ten years of study. Twin Cays is the type locality for three of these species. Colony forming species, notably hose in the families Didemnidae, Polycitoridae and Perophoridae predominate over solitary species which are poorly represented. The distribution in Twin Cays and habitat requirements of these different species are considered and the composition of the fauna is compared with that of other well documented mangrove environments in the Caribbean Basin. It is suggested that several other species of ascidian may colonise Twin Cays in years to come if the environment alters significantly. Notable among these are two species of *Ecteinascidia* which have breeding populations within a few kilometers distance from Twin Cays.

Pisces

Molecular and morphological identification of the larvae of Caribbean reef fishes

C. C. Baldwin & L. Weigt, with D. G. Smith & J. H. Mounts

The identities of pelagic larval stages constitute the largest gap in our knowledge of the coral-reef fish fauna of the Caribbean Sea. Research during the past decade has resulted in the identification of numerous larvae of coral-reef fishes from Belize. This success is largely due to the development and refinement of field methods for rearing to an identifiable size living fish larvae collected in a moored plankton net. Existing field methods will continue to result in the identification of new larval types; however, the methods are time consuming, and less progress has been made in identifying larvae of many groups than satisfactory. It is therefore desirable and logical to augment current identification methods with modern techniques for genetic identification. We started developing a database of mitochondrial DNA sequences for adults of shorefish species from Belize and Panama, a genetic identification method for larvae designed to target species-level identification. Then we collected specimens (5-6 specimens of each species to account

for population variation) for tissue samples. Tissues were amplified and sequenced (16S or 12S, or both, cytochrome b, and a portion of the "D-loop"). Primers are being designed to amplify all taxa of interest to ultimately produce agarose gel patterns attributable to a species. Genetic identification of an unknown larva through PCR/RFLP could involve multiple steps, depending on the taxonomic level to which a larva can be identified (usually family) prior to beginning the genetic analysis.

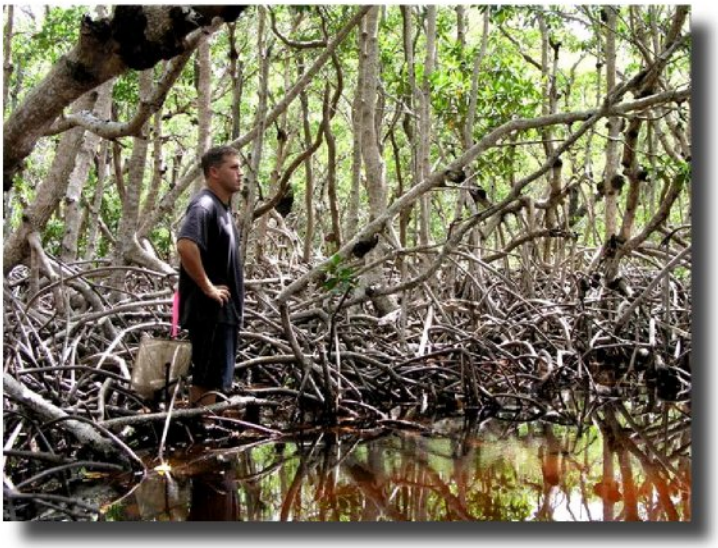
Rypticus sp..

The mangrove fish communities of Belizean mangrove cays

S. Taylor, W. P. Davis, C. McIvor & E. Reyier

In 2003 we completed a preliminary survey of fishes utilizing the mangroves of the Belize cays during a high-water period, focusing on Twin Cays. A combination of trapping, netting and visual surveys was used to determine which species were : 1) found in the prop-root or canopy of the red mangrove 'fringe' 2) found in the 'transition' zone mangroves, internal ponds, creeks and flats, 'dwarf' reds or sinkholes. Over 80 species of fish were documented, along with several commercially important macro-crustaceans. In addition, we compared fish visual census data at two sites on Twin Cays in red mangrove fringe adjacent to areas were mangroves are being cut with intact habitat. Over 80 samples (teleosts, crustaceans) were also processed for future isotope analysis. Another sampling event during a low-water period would provide valuable comparative data.

In 2004 we have completed a second survey (September 15-30, 2004) survey of fishes utilizing the mangroves of the Belize cays, with a focus on Twin Cays. We have used the same methodology as the first survey (trapping, netting and visual surveys) to determine relative species compositions in differing mangrove habitats and have expanded upon preliminary surveys comparing fish assemblages/densities in shoreline areas where mangroves have been cut vs. un-cut shorelines. In addition, we have provided numerous further vertebrate/invertebrate samples for stable isotope analysis (by others) for the Trophic Network Analysis proposed for Twin Cays. Water levels during the sampling period were seasonally high, and we now have thoroughly sampled this seasonal high-water period. A comparable low-water sampling episode would provide valuable comparative data.



Eric Reyier pensively surveys a 'sinkhole' in the Belize Cays for fishes

We have continued with the same methodology and gear-types. We completed 611 trap-nights with Gee traps, collecting 2,080 fishes (22 species) and 661 crustaceans (at least several species, yet to be identified). Some interesting comparisons between collections in cut vs. un-cut areas of Papa Gabriels may be made when data analysis is complete. In addition, we are documenting significant water quality differences between cut and un-cut locales. We completed 10 over-night sets of the fyke net, which collected 986 fishes and 60 crustaceans. Throw-trap collections (n=40) captured an additional 85 fishes and 24 crustaceans.

We have continued with the visual census survey of mangrove shorelines subject to cutting vs. uncut. We completed four surveys (2 each on east and west Twin Cays) at the same sites censused previously. Our data for this survey confirm what was observed in 2003: density of non-schooling fishes is 3.3 times higher along un-cut shorelines than along cut shorelines. Differences are even more marked for schooling species. Species diversity was also significantly higher along un-cut shorelines. We conducted additional visual surveys at other locales around Twin Cays, Peter Douglas Cay and the Pelican Cays. Between our captured specimens and species identified in visual surveys, we have now confirmed at least 110 species of fish present within mangrove systems of the Belize Cays, and addition of 34 species since the 2003 survey.

Processed samples for stable isotope analysis were submitted to Marilyn Fogel for inclusion in the data for the Trophic Network Analysis for Twin Cays. Eight-four fish and invertebrate samples representing 27 species were forwarded for this analysis.

During this visit, we were unable to make contact with Mr. Godwin Humes (Fisheries Department, Belize), who was absent from Twin Cays during our tenure. We had anticipated working further with him.

Chaenopsid blenny systematic and ecological research

J. Tyler & D. Tyler

Three years of ichthyological surveys in the Pelican Cays came to an end in 2001, and the results of the survey were published in Smith *et al.*(2003), in the most recent issue of the Atoll Research Bulletin, and the description of one of the new species (a chaenopsid) collected during the survey was published in Tyler and Hastings (2004). The CCRE proposal of 2003 by Tyler and Smith for a two year program of further work on fish distributions in the Pelicans fared poorly in peer review, and that proposed work will not be undertaken, so the results of the Pelican Cays fish survey remains the progress report.

The work by J. and D. Tyler on chaenopsid blennies around Carrie Bow Cay over the years has resulted in the descriptions of several new species of this group of hole-dwelling blennies and improved knowledge of their behavioral ecology: Smith *et al.* (1998), Tyler and Hastings (2004), Tyler and Tyler (1997, 1999)

On the basis of our previous work around Carrie Bow, we know that there is one additional undescribed species of the genus *Emblemariopsis* in shallow water around the lab. We have collected single specimens, both males, of it on two occasions in the coral heads to the north of the lab, incidental to our work on *E. pricei* and *E. ruetzleri*. The new species is in the group of species of *Emblemariopsis* having 13 pectoral-fin rays and an orbital cirrus. It differs from the other species in having a long and lobed orbital cirrus and in having males with only a moderately dark head and a relatively plain body.

The two specimens of the new species were collected in dead parts of coral heads at the north end of Carrie Bow just inside the reef crest on the south side of the channel between Carrie Bow and South Water cays. These two locations are in slightly higher energy waters than the many places just 20-30 meters or more inside the crest closer to Carrie Bow where we have studied *E. pricei* and *E. ruetzleri* in some detail over the years.

To properly describe the new species of *Emblemariopsis*, which we suspect is the last one to be described from the shallow water immediately around Carrie Bow, we propose to use quinaldine to collect additional specimens of it using scuba, especially at the coral heads just inside the reef crest to the north of the lab. We also will concentrate on finding females, probably in the algal turf of the heads. The locations at which we collect the additional specimens will help us delineate how the habitat of the new species differs from that of the two other better- known species of *Emblemariopsis* at Carrie Bow: *E. pricei* (holes in live coral, in a wide variety of moderate energy water locations and types of coral, mound and branched), and *E. ruetzleri* (holes in dead areas of mound corals only, and mostly just to the north of the lab, in moderate energy water). We will also make comparisons to the habitat of *E. dianae* from well south of Carrie Bow (holes in dead areas of mound corals only, in low energy lagoonal waters from Wee Wee to the Pelicans). We have over the years sampled chaenopsid blennies extensively enough around Carrie Bow to believe that the new species is confined to just inside the reef crest to the north of the lab, but we will do additional sampling elsewhere around the lab to check on the validity of this assumption.

We will also try to collect the burrows of the new species to determine its hole preference. We know that *E. pricei* is usually found in holes made by serpulid worms (*Spirobranchus*), whereas *E. ruetzleri* and *E. dianae* are usually found in holes made by vermetid mollusks (*Dendropoma* and *Petaloconchus*). It will be of interest to find if the type of hole occupied by the new species is of worm versus mollusk origin (and of what genus), or of something different.

Depending on how successful we are in finding numerous burrows of the new species, we will try to mark the holes (of burrows not collected for identification of origin) from which specimens have been removed and re-examine these hole on subsequent days to determine if the holes are rapidly re-colonized by the new species or by other chaenopsids. This information will be compared with that available on the rate on recolonization (summarized in Tyler and Hastings (2004) for the three species of *Emblemariopsis* mentioned above.

Quantitative assessment of herbivorous reef fish populations near Carrie Bow Cay: Comparison of 1982 and 2004

P. Wainwright & D. Bellwood

In July of 2004 I visited Carrie Bow Cay with a my colleague David Bellwood and we conducted a quantitative survey of the abundance of herbivorous reef fish on the Belizean barrier reef, repeating a study that was conducted over 20 years ago (Lewis and Wainwright, 1985). I will report more fully on this project in a future report but I wanted to give the basic findings here. In July of 2004 we used the same methods as Lewis and Wainwright (1985) to measure parrotfish and surgeonfish abundance in the major reef zones on the Belizean barrier reef. We swam tape transects, counting all fish in these families 1.0 m on either side of a 50 m tape. Four passes were swum per transect and eight transects were swum for each of four reef zones. We found no significant change in the abundance (or species composition) of the herbivore guild in a comparison of the 2004 and 1983 data. It appears, that while the Belizean reef is fished with regularity and moderate intensity, and although there have

been some stressors acting on the reef in recent years, nevertheless the populations of herbivorous fishes have remained unchanged over the past 20 years. This is an encouraging sign given the concern over global coral reef declines and may indicate that even moderate protection can make a big difference to populations of reef fishes.

Cryptotomus sp.

The demography of reef-fishes at Carrie Bow Cay, Belize.

R. Robertson & J. H. Choat

Our sampling in the vicinity of CBC in September/October 2002 represents an expansion of our study of geographic variation in the demography of Caribbean reef fishes in relation to latitude and fishing pressure. The site that provides the best contrast for comparison of the results of the Belize sampling is the Los Roques archipelago off the north coast of Venezuela. Los Roques is a national park that possesses a largely intact reef fish fauna due to effective protection and rigorous control of fishing. This is limited to lobsters and deep-water line fishing, with both trapfishing and spearfishing being banned. In contrast there are no controls evident on fin-fish fisheries in the vicinity of CBC.

Los Roques has an abundance of the largest and most spectacular members of the Caribbean reef fish fauna, including the three largest species of parrotfishes *Scarus guacamaia*, *Scarus coelestinus* and *Scarus coeruleus*. These species are locally extinct on many Caribbean reefs, due largely to their susceptibility to spearfishing. Large predatory reef fishes that have been heavily impacted by fishing elsewhere in the Caribbean also are abundant at Los Roques. These include snappers (such as the schoolmaster *Lutjanus apodus,* the yellowtail snapper *L. chrysurus*, and the grey snapper *L griseus*), groupers, and the Hogfish *Lachnolaimus maximus*. During expeditions to Los Roques in 2000 and 2002 and CBC in 2002, immediately after work at Los Roques, we made population samples of a number of those species as part of a program to examine variation in their size, growth, population age-structure and longevity at seven sites scattered between Bermuda and Panama. Otoliths of those individuals currently are being processed at JHC's laboratory in Australia.

During our two weeks at CBC we saw no more than 3 small individuals of each of the three *Scarus* species mentioned above (as opposed to hundreds of large individuals of all three at Los Roques during an equivalent period). The three snappers were also much less abundant at CBC than at Los Roques. To illustrate some of the differences we observed we provide comparisons of three species important to Caribbean fisheries that we sampled at Los Roques and Belize. These were the schoolmaster snapper, (*L.apodus*) the grey snapper, (*L.griseus*) and the hogfish (*L.maximus*). These figures clearly indicate effects of fishing at Belize. At Belize the samples were dominated by small individuals with an average size of less than 30 cm FL with no individuals reaching a size of 45 cm. In contrast the Los Roques population had a large size class that contained individuals in excess of 50 cm FL that was absent in Belize. A similar pattern is present in grey snappers and hogfish. In each of these species the obvious effect of fishing pressure is to remove the larger individuals from the population. These trends were confirmed by underwater counts. The differences were very obvious in the case of the two snappers in which large aggregations of hundreds of large individuals of both species were observed at Los Roques. At Belize we saw them in aggregations of up to several dozen, dominated by small individuals.

Analysis of the otoliths of one species included in the Belize sampling, *Acanthurus bahianus*, has been completed and a manuscript on demographic variation at 10 sites between 32N and 23S is in preparation.

Lutjanus apodus

Acanthurus bahianus

Paleobiology and Microevolution

Study of the recent history of the lagoonal reefs in the Rhomboid Cays, Belize

I. G. Macintyre & R. B. Aronson

A total of 15 cores were collected that helped us complete our shallow-water study in which we are documenting the intrinsically controlled shallowing-upward shift in reef communities from *Acropora cervicornis* to *Porites divaricata* and *Millepora* spp. We also completed a study of the preservation of the uppermost *Agaricia tenuifolia* layer on the shallow slopes of these reefs, six years after the 1998 mass mortality of this community caused by bleaching and after our coring sites were exposed to the heavy seas of Hurricane Mitch in 1998 and Hurricane Iris in 2001. Hurricane Iris, a category four storm that passed directly through the southern portion of our study area, was particularly likely to have disrupted the preservation of the *Agaricia* layer, but in fact we found that the layer had remained intact at 11 out of 12 coring sites. In addition, Aronson completed four damselfish-population surveys (a spin-off from our project) in the fore reef off Carrie Bow Cay and Tobacco Reef and Macintyre took digital underwater photographs of coral and reef structures for the CCRE program's image collection.

Sedimentary patterns and geological history of Twin Cays

I. G. Macintyre & M. A. Toscano

In 1982 we carried out an initial survey of the sea floor in and around Twin Cays. A total of five marine facies were identified. In addition 120 sediment samples indicated that the sediments associated with these facies are dominantly *Halimeda* grains with lesser amounts of mollusks and foraminifera. Mud-rich areas are mostly limited to low-energy areas in the channels and the deeper offshore locations. Seventeen vibracores collected along north/south and east/west transects indicated that the two mangrove islands have been formed by accumulations of mangrove peat and carbonate sediment that are almost nine m thick. Mangrove communities were established on a Pleistocene limestone substrate about 8,000 calendar years ago and kept pace with the late Holocene transgressing seas. At several stages, lagoonal sands invaded the mangrove communities and commonly were subsequently overgrown by the mangroves. Seven core holes drilled around the perimeter of Twin Cays penetrated the upper 1.58 m of the Pleistocene limestone. Despite extensive subaerial alteration, the cores reveal both a branching *Porites* facies and a *Thalassia*/sediment facies. X-ray diffraction analyses indicate that all of the limestone has altered to calcite. The overall pattern consists of a mottled chalky limestone with numerous rhizolith tubules, which are scattered throughout a dense partially leached limestone. Over 70,000 years of subaerial exposure of this limestone has resulted in an extensive diagenetic alteration assisted by roots from a terrestrial plant system.

Reticulate evolution in Caribbean reef sponges? A multi-dataset approach to explain high diversity of the genus *Agelas*

F. J. Parra-Velandia, S. Zea & R. W. M. van Soest

Agelas conifera octopus form

The genus *Agelas* (Porifera, Demospongiae, Agelasidae) is an interesting group of closely related tropical sponges, whose extraordinary morphological similarity contrasts with a yet uncertain phylogenetic relationship with other groups of demosponges. Its great diversity in the Caribbean Sea (14 species, vs. eight species in the Indo-Pacific) and the existence of geographically distinct morphotypes in several species, has led us to hypothesize the occurrence of a Caribbean radiation of the genus during the Neogene, possibly related to the closing of the isthmus of Panama and the subsequent changes in sea-level during the glaciations of the northern hemisphere. To test these hypotheses, we undertook an extensive sampling in several localities throughout the Caribbean, to obtain morphological, biochemical and molecular data to reconstruct the phylogeny of the genus and associate the branching events with Neogene history. In this paper, we present the taxonomic description of the species existing in the Southern Caribbean and a preliminary cladogram based on morphological characters. Samples were obtained from several localities in Venezuela, the continental coast of Colombia, the San Andrés and Old Providence Archipelago (Colombia) in the SW Caribbean, and from Belize. Specimens were observed and photographed *in situ*

and fragments of them collected. From the fraction fixed in 96 % ethanol, to be used in the morphological analysis, clean spicule mounts were made, as well as dehydrated and stained thick sections mounts for microscopical examination of the skeleton. Seven species were collected and described: *Agelas clathrodes*, *A. citrina*, *A. conifera*, *A. dispar* (brown morphotype, orange morphotype), *A. sceptrum*, *A. sventres* and *A. wiedenmayeri*. While most species show a rather constant morphology throughout the sampled localities, there is a strong geographical as well as local variation in *A. conifera*. In this species in some areas there are locally unique morphotypes, but in others there are two or three morphotypes coexisting sympatrically. The latter is indicative of the existence of more than one species or of a complex of species. The morphotypes of *A. dispar* are morphologically quite distinct and do not coexist within the same geographical area in the Southern Caribbean. However, their sympatric occurrence in The Bahamas indicate that they are different species. Morphological characters are now being analyzed and polarized to reconstruct the internal phylogeny of the group.

Phenotypic plasticity and morphological integration in branching modular organisms: intra-specific analysis of *Pseudopterogorgia bipinnata* at Carrie Bow Cay, Belize

J. A. Sánchez

An important question in the study of evolution is whether organisms' characters are independent of each other or behave and evolve as integrated modules or systems. In modular colonial organisms, which form by the repetition of identical units, their emergent forms are usually complex networks. Colony form in these taxa is a consequence of modular (polyp) replication, and if there is a tight integration (e.g., pleiotropy or linkage disequilibrium) among modular and supra-modular traits (e.g., polyp aperture, inter-polyp spacing, branch thickness, internode, and branch length), then changes at the module level may lead to changes in colony architecture. Alternatively different groups of traits may evolve semi-independently (or conditionally independent) if different developmental mechanisms co-occur, which has not been considered in the past. It has been found that all characters exhibited associations with each other, a multivariate analysis, correcting for semi-independence, showed the strongest integration among the colony level (network) characters. This is the first quantitative demonstration that branching characters within colonial organisms are independent of characters of the modules (Sánchez and Lasker, Proc. Roy. Soc. B, in press). Although it is expected that this patterns occurs at the intraspecific level it is unknown if that really occurs. This study focus on the evolution of branching at the intraspecific level, which requires the study of population genetics of a species. The goals are to study the phenotypic plasticity of its branching patterns to examine two aspects (1) the morphologic integration of traits and (2) to determine the reaction norm of the many phenotypes against environmental conditions. For those purposes, I am using four polymorphic microsatellite loci, mitochondrial, and nuclear DNA sequences of the population present at Carrie Bow Cay, Belize. My preliminary findings suggest that the morphologic integration found interspecies is also present in populations of *P. bipinnata*. Even more interesting, although the change of the phenotype seems independent of genotype, the phenotypes present themselves somewhat discretely from the presence of overlapping zones, where two phenotypes are found side-to-side sharing the same environment. This explains why this species has been considered three species until now (*P. kallos, P. bipinnata, and P. antillarum*) but the genetics show they are clearly the same interbreeding species. Of further need of investigation, the phenotypes present in the extremes of the environmental boundaries seem to develop their phenotype forms according to maternal inheritance. Since the species is a brooder, newly developed colonies may spend substantial time on their mothers' surface, thus potentially being subject to specific developmental "signals" that may determinate phenotype, which could explain the presence of overlapping phenotypes in their marginal environments.

Population structure and biogeography of the coral banded shrimp, *Stenopus hispidus*

W. Browne

Stenopus hispidus

The species appears to have a pantropical distribution based on morphological description and possesses a benthic adult reproductive phase coupled with a pelagic larval phase. We (collaboration with Nik Schizas at the University of Puerto Rico) are currently sequencing several *S. hispidus* genes (CO1, ITS-1, 12S, and cytb) from material I collected at Carrie Bow Cay, STRI-Panama, Oahu, and Puerto Rico (through Nik). My most recent sampling suggests that juvenile *S. hispidus* is commonly settling at depths in excess of 10 m along outer reef walls, while larger reproductive adults predominate in the shallows and less exposed inner reefs. I am hopeful that the sequencing data will take us a step beyond general gene flow information supporting connections between populations, and perhaps pointing toward an interpretable recruitment pattern at the local level. With respect to this developing story, sampling at Carrie Bow has thus far only been in the inner reef shallows and during snorkeling along mangrove fringes (and thus restricted to reproductive adults). If the sequencing data support my observations, I would like to sample the outer reef spur and groove faces adjacent to Carrie Bow (particularly if the genetic data suggest a local recruitment pattern among our other sampled populations).

Molecular phylogenetics and phylogeography of sipunculan worms

A. Schulze & M. E. Rice

During our stay at Carrie Bow Cay from April 16-30, 2003 we collected sipunculan worms at 16 stations in the vicinity of Carrie Bow Cay, Southwater Cay, Twin Cays, Curlew Reef and Sand Bores. Two types of habitat were sampled: 1. Coral rubble from intertidal to 20 m depth and 2. Mangrove and *Thalassia* rootmats. We found a total of thirteen sipunculan species, covering eight of the currently recognized seventeen genera, and five of the six families. Collected specimens were sorted according to species and usually kept alive for several days in order to observe possible spawning. Most of the specimens were eventually fixed in 95% Ethanol for molecular studies. Some samples were preserved in 2.5% glutaraldehyde for electron microscopy.

Furthermore, we performed two plankton tows on the east side of Carrie Bow Cay parallel to the reef crest. Sipunculan larvae were abundant in the plankton samples, with at least six larval types present. Larval samples were sent to Lee Weigt at the Laboratory of Analytical Biology at the Smithsonian Institution in Washington DC. We are planning to identify the larvae using molecular sequence data which can be compared to our molecular database of adult sipunculans.

Brittlestar, *Amphipholis squamata*, in the tropics: independent Indo-Pacific origins of two Atlantic lineages with secondary contact?

H. A. Lessios, R. Sponer & M. S. Roy

Dispersal of organisms determines the extent of spread of genomic combinations, and thus of any adaptations. In marine organisms, dispersal is usually accomplished through the broadcasting of larvae or by a vagile adult phase. Some marine species, however, lack these means of invading new habitats and of maintaining genetic contact between their populations. The expectation is that they have restricted distributions or consist of species complexes, each limited to a small geographic area. One exception is *Amphipholis squamata*, a small brittle star that broods its young within the maternal body cavity. Even though neither the adult nor the juveniles have any obvious means of dispersing, *A. squamata* has a cosmopolitan distribution. Research on this species has uncovered unexpected biogeographic patterns and evolutionary histories which are at the center of our investigation the Caribbean. The most striking result of the preliminary DNA analysis is the existence of two genetically divergent clades among Western Atlantic specimens. In a haplotype network, the two Atlantic clades are located at the two extreme ends, each connecting separately to haplotypes of Indo-Pacific populations. This pattern could indicate that the clades did not originate in the Atlantic, but rather arose independently from an ancestral Indo-Pacific population. There is no indication that the two Atlantic clades of *A. squamata* are morphologically differentiated, which is not

surprising, given that ancient cryptic species of the complex display extreme morphological stasis. Future collecting of *A. squamata* specimens will be from algal turfs and coral rubble in Panama, Belize, Florida, the Dominican Republic, Barbados, Trinidad and Curacao will add to our data and help test our hypothesis that mechanisms other than adult benthic dispersal (an extremely slow method) must exist; possibly rafting on algae and drifting debris.

Amphipholis squamata with one of five baby brittlestars

Developmental systematics: synthesizing developmental and phylogenetic information in the Malacostraca (Crustacea)

N. Patel & W. Browne

One former and two current members of Nipam Patel's laboratory (William Browne, Courtney Babbit, and Danielle Liubicich), from the Department of Integrative Biology, University of California, Berkeley, collected and processed crustacean embryos from several locations near Carrie Bow Cay. Research in Nipam Patel's lab focuses on both embryonic development and the evolution of developmental genes and genetic pathways within arthropods (with a heavy emphasis on crustacean embryogenesis). The principal collection sites for the 2003 visit included Twin Bay located on the south-west tip of West Twin Cay, Hidden Creek on the south end of East Twin Cay, Ctenophore Ridge located at the south tip of Manatee Cay (Pelican Cay), and a night plankton tow one half mile east of the barrier reef off Carrie Bow Cay. For this particular field collection our primary aim was to fill developmental gaps in our embryonic series for the basal malacostracan, *Paranebalia belizensis,* and the swarming mysid *Mysidium columbiae.*

Each day consisited of one to two trips to Twin Cay. During each trip we secured *Halimeda* containing *Paranebalia* in buckets and *Mysidium* in plastic bags from along the overhanging mangroves in Twin Bay and Hidden Creek. The animals were then transported back to the field station and maintained in flow through tanks. Our embryonic development gap was determined to be between 1AM-6AM for *Mysidium columbiae*. We made several overnight timed collections from the *Mysidium columbiae* maintained in the flow through system.

Throughout days and nights, we sorted and fixed individual lots of *Paranebalia belizensis*, cumacean (*Vauthamsonia minor*), and tanaidacean embryos for specified periods of time in a phosphate buffered saline solution containing 3.7% formaldehyde (followed by storage in methanol). This treatment permits us to assay whole intact embryos for gene expression patterns at multiple levels (both gene transcription (RNA) and gene products (protein)). For many of these lots we also stored additional animals directly in 95% ethanol to facilitate both the isolation of genomic DNA and mRNA. The collection of these embryos was essential for the phylogenetic analysis of embryonic change in the Malacostraca (C. Babbitt, Ph.D thesis in progress).

Our fixation methods for crustacean species other than *Mysidium*, due to the structure of the egg shell and multiple embryonic membranes, requires individual dissections during fixation to allow our fixative to penetrate the embryos. The dissecting scopes were indispensable for this process. For all new species collected, material was obtained for the purposes of accurate species identification (adult females/males), assay of gene expression (embryos), and performing gene cloning (whole adult females/males, dissected adult female tissue, and embryos).

During our 2001 visit we had scouted potential new collections sites at Pelican Cays. This year in a major new development for our continuing work on Peracaridian taxa we returned to a submerged ridge (Ctenophore Ridge) at the south tip of Manatee Cay. This area is somewhat sheltered from open water by Cat Cay to the east, however, there is a strong upwelling current which brings large numbers of Ctenophores to the surface (Nipam Patel commented on large numbers of Ctenophores in the Pelican Cays area in JUN 1997, we returned and scouted this ridge in SEP 2001). The vast majority of the Ctenophore swarms are composed of *Mnemiopsis*, with some *Beroe*. Approximately 10-15% of the *Mnemioposis* individuals were observed carrying an associated pelagic hyperiid amphipod. These amphipods (along with their hosts) are easily collected by hand and two collection trips were made to gather sufficient material for a species ID and to begin the process of cloning of genes thought to be required for the development of the amphipod brain and nervous system (Browne, NSF postdoctoral grant DBI-0310269). A number of these amphipods were kept at the station for several days for observation. They appear to have a non-parasitic relationship with their *Mnemiopsis* hosts and appeared to clean the host surface at regular intervals. Both the adult, juvenile, and embryonic stages of the

amphipod have the same transparent optical properties of the *Mnemiopsis* ctenophore host. The embryos themselves have what appears to be a large lipid. The embryos themselves have what appears to be a large lipid droplet sequestered within their yolk. During the first few early cell cleavage events this droplet is compartmentalized to one side of the egg (the transparent quality of the embryo precluded observation of cell cleavage plans by light microscopy). Later in development the droplet is observed sequestered in the developing midgut. As the midgut begins actively digesting yolk reserves, the droplet was observed breaking down in the digestive ceacum and anterior region of the developing midgut. I am very interested in following the early cleavage stages in this amphipod and this should be possible on a return visit with the use of the station compound microscope (camera would be used for documentation) and injected DiI membrane markers.

Due to time constraints we executed only a single night plankton tow off the barrier reef one half mile east of Carrie Bow Cay utilizing the station plankton net and large skiff. To ensure safety we reconnoitered our plankton tow course, as well as ingress/ egress routes to the Carrie Bow dock, during daylight by recording several GPS waypoints for accurate night navigation. The tow was successful in recovering several species of Hyperiid amphipods that will be used in molecular phylogenetic analyses. Limited sampling, however, requires that a more systematic program of multiple night plankton tows be instituted for the purpose of obtaining larger numbers of these particular pelagic Hyperiid amphipod species.

The large and diverse number of crustacean embryos we were able to collect, dissect, and fix will provide exciting information useful in extending our studies of embryonic development, genetic evolution, and morphological diversity in these malacostracan species. The principal aims of the field collection were achieved as well as, again introducing new and valuable material into our continuing studies of embryonic development and morphological evolution within the Malacostraca.

Neurogenesis, brain development, and developmental systematics in the Amphipoda (Crustacea: Malacostraca: Peracarida)

W. Browne, M. Martindale & E. Seaver

During this field period we aimed at obtaining more specimens of the leptostracan *Paranebalia belizensis* and a *Mnemiopsis*-associated hyperiid amphipod, first collected in 2003. We also located and collected additional crustacean taxa useful for population genetics, molecular genetic, and developmental studies, such as Belizean populations of *Parhyale hawaiensis*, *Stenopus hispidus*, and representative gammarid and hyperiid amphipod species, isopod species, and stomatopod species. The continuing focus of our studies is understanding some of the mechanisms driving gene expression and gene function that play important roles in the development and evolution within Amphipoda and related malacostracan crustacean. The evaluation and interpretation of differences and similarities found within and between the resulting developmental and genetic data sets requires a reliable systematic framework. A systematic and phylogenetic approach to these comparative studies enhances our ability to identify specific questions regarding developmental mechanism changes that appears relevant to evolutionary change within malacostracan crustaceans.

Molecular systematics of a marine species flock, Caribbean hamlets

E. Bermingham, O. Puebla & Liz Whiteman

Hamlets are an ideal model system to study the incipient stages of speciation in marine fishes. Evolution in this group has been extremely rapid and is associated with the development of striking color pattern and behavioral differences among the 12 recognized species. Color pattern distinctions that define "morphospecies" are maintained across the Caribbean, and in the face of syntopic distribution patterns that can yield as many as six species in a single area of reef. For this project, we made behavioral observations of hamlets during their crepuscular spawning to quantify assortative mating in two locations, over four different time periods. In addition, members of spawning pairs were caught with hand nets, fin-clipped, and marked. In year one in Bocas del Toro we established aquaria, and undertook pair choice experiments with captive fish. The fin clips are being used a source of DNA, which in turn will permit mtDNA and microsatellite analysis. Our lab has significant experience with DNA sequence and microsatellite analysis and we have already developed more than 20 hamlet microsatellite markers that will be used to establish the genetics of hamlet mating associations.

In 2004 two sites were considered, Bocas del Toro (Panama) and Carrie Bow Cay (Belize), taking advantage of Smithsonian Institution facilities in each location.

Genetics. One hundred and seventy-one samples representing 5 color morphs have been collected in Bocas del Toro, and 158 individuals representing 6 morphospecies in the vicinity of Carrie Bow Cay, Belize. Five new microsatellite loci have been developed in addition to the 5 previous existing loci (McCartney *et al.* 2003). A locus developed for the Hawaiian grouper *Epiniphelus quernus* (Rivera *et al.* 2003) was also successfully amplified and analyzed with Hypoplectrus samples. DNA extractions have been performed for 96 samples from Bocas del Toro and Belize. These samples are being genotyped at the 11 microsatellite

loci at the time this proposal is being written.

Ecology. Hamlet species densities were estimated at both sites using a combination of line transects and timed roving searches. Habitat assessments through standard line transects and digital habitat imaging were also performed to test the extent to which morph frequencies can be explained by habitat, and broad fish censuses were conducted to test the hypothesis of aggressive mimicry (Thresher 1978). 4x100m transects were performed in Bocas del Toro and Belize in

Caribbean Hamlet

three different habitats (reef/sand upper edge, dense shallow reef and deep patchy reef) in order to i) test specifically for ecological differences between *H. unicolor* and *H. puella/H. nigricans* and ii) capture rare species in the transects.

Behavior. Ten dusk dives were performed in Bocas and two in Belize to observe hamlet spawning and record the association of morphospecies during the act of spawning.

Color analysis. Underwater pictures of all species were taken at both sites in an effort to make a detailed coloranalysis and compare color variation to genetic variation.

Reproductive and Developmental Biology

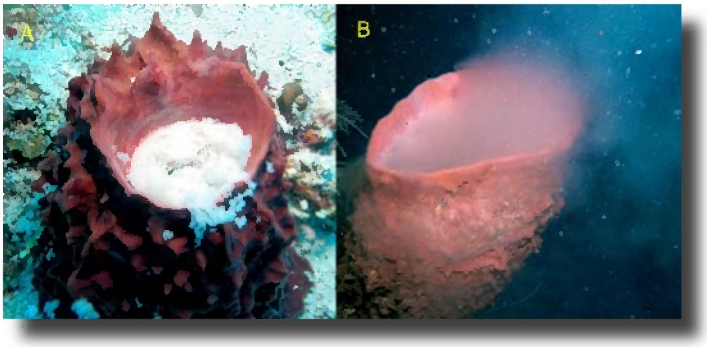
Spawning of the giant barrel sponge *Xestospongia muta* in Belize

R. Ritson-Williams, M. A. Becerro & V. J. Paul

On March 30, 2004 we observed the giant barrel sponge *Xestospongia muta* broadcast spawning at the barrier reef, south of Carrie Bow Cay, Belize. *X. muta* was observed on the inner reef slope (10-20m depth) and on the fore reef slope (15- >60m), but only individuals on the fore reef slope below 20m were observed spawning. Spawning of *X. muta* was synchronous, involving numerous male and female specimens of various sizes. Spawning had already started at 8 am and continued until at least 9 am. Eggs were negatively buoyant being accumulated in the sponge atrium and scattered on the benthos around the sponge. Sperm was positively buoyant and left a "cloud" in the water column. We dove further south along the reef on March 28 & 31 and did not observe *X. muta* spawning (we did not dive on March 29).

Even though sponges are a major component of Caribbean coral reefs little is known about the timing of their spawning. In Curaçao the sponge *Neofibularia nolitangere* is known to synchronously spawn in the afternoon of October and November three days after the full moon. Further studies are necessary to determine what factors trigger/control spawning in *X. muta*.

(*From a Reef Sites article in Coral Reefs, in press (2004); courtesy Raphael Ritson Williams*)



An investigation of the developmental mechanisms controlling zooid arrangement and identity in the *Siphonophora*

C. Dunn

My research seeks to elucidate the developmental mechanisms by which Siphonophores, a group of pelagic colonial Hydrozoans, are able to precisely order polyps and medusae along their linear stem in a repeating, species-specific pattern. Siphonophores are difficult to obtain as they are fragile and usually present only in oceanic waters far from the coast. Carrie Bow Cay affords a unique opportunity to investigate siphonophores because they can be collected beyond the reef crest in "blue water" and brought back to the lab for detailed study.

It was with this goal that I spent three weeks at Carrie Bow Cay in July- August, 2002. The year before *Agalma okeni*, a species that I work with frequently, had been readily available. It was not found in 2002, but several specimens of *Stephanophyes superba*, a single *Nanomia bijuga*, and a single *Diphyes dispar* were collected. The growth zones of these species are particularly difficult to work with because of their small size, precluding the types of developmental investigations I was hoping to make, but I was able to ob-

serve other relevant features of their morphology. The most important of these is the exact order of polyps and medusae along their stem. When Siphonophores were not available I continued with other ancillary projects begun the previous year. The most important of these was collecting several more strains of *Trichoplax adhaerens*, an enigmatic animal with a very simple type of organization. This will facilitate genetic studies (completed by other investigators) that seek to determine if sexual reproduction is a part of the *Trichoplax* lifecycle. I also collected several strains of *Vallicula multiformis*, a benthic ctenophore that is found on mangrove roots. These are in stable culture and their asexual reproduction is under investigation by Leo Buss.

Cassiopea sp.

Larval development of *Ophiostigma isocanthum*

G. Hendler

In 2003, *Ophiostigma isocanthum*, a common Caribbean ophiuroid, was spawned and reared in the laboratory for the first time. It is one of a suite of small brittle star species that occurs in profusion in calcareous algae and other nursery habitats. New information on its rapid larval development clarifies the reason for its previously unexplained abundance, particularly in mangrove cay lagoons with restricted water circulation. Its eggs sink and develop into short-lived, non-feeding pluteus larvae that tend to swim near the bottom of the culture container. Its development is abbreviated. The larvae complete metamorphosis in less than a week. They have just two (rather than eight) larval arms, a modification previously described in only two other ophiuroid species. The material collected has already been examined using DIC microscopy and SEM, and several remarkable morphological features of the ophioplutei will be extremely useful for understanding the diversity of ophiuroid development.

Burrowing brittlestars, amphiurids and *Ophiopsila* are challenging to study because they remain hidden from view. That difficulty was overcome by examining amphiurids in narrow "ant colony" aquaria. Preliminary results, which were filmed in 2004 at the Carrie Bow Cay laboratory using a basic MINI-DV recorder, suggested that behavior of the species is controlled by the ambient light level. Animals remain densely coiled in a knot-like posture during the day and when illuminated at night, but hold several of their arms into the water in the dark. Even more interesting, a dye-tracer experiment suggested that their ciliated "spines" transport water inside the artificial "burrow". This indicates that the modified spines can create a respiratory current that enables *Ophiopsila* to occupy burrows in hypoxic sediment, even during the day when it appears to be immobile. Other observations suggest that the exceptionally long, prehensile tube feet are used for suspension feeding at night.

The species *Sigsbeia conifera*, which occurs in Belizean spur and groove habitats, represents a rare example of a "primitive" brittle star that broods embryos and young. Based on specimens collected, I found that its broods consist of embryos at different stages of development. I still wish to collect and dissect enough specimens of *Sigsbeia* to discover the nature of its early, informative, developmental stages. Making collections at different times of the year will improve the possibility of finding embryos at the right stage of development.

Crustacean embryonic development

W. E. Browne

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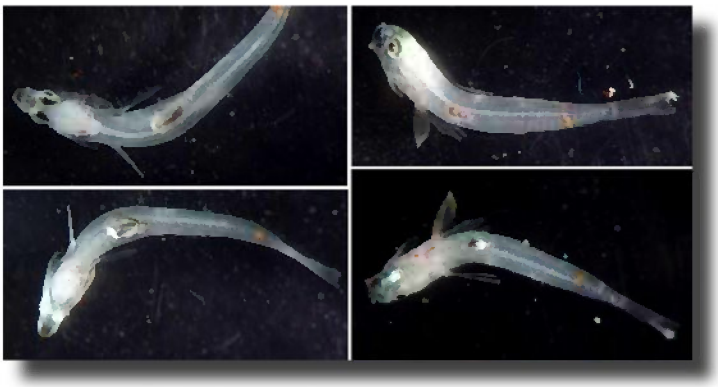
A comparison of morphological features, rates of endochondral ossification, and gonad ontogeny among larval and post-metamorphic stages of Caribbean teleost species

K. S. Cole

The following collections were made according to our objectives: Eggs of several common species of gobies in the genus *Coryphopterus*, and two species of damselfish common to Belizian waters, *Abudefduf saxatilus* (the sergeant major) and *Stegastes dorsopunicans* (the dusky damselfish); we reared the larvae and observed early larval species-specific morphological features. Newly settled individuals of several common goby species, including *Coryphopterus eidolon*, *C. dicrus*, *Lophogobius cyprinoides* and *Gobiosoma xanthiprora*. Based on these, we were able to characterize species-specific morphological traits associated with and aid in the species identification of pre-settlement larval stages.

Adults and various-sized immatures of Caribbean gobies in the genera *Gobiosoma*, *Gnatholepis*, *Lophogobius*, *Nes* and *Priolepis* for histological examination in the hole laboratory and comparison of gonad ontogeny patterns and identifcation of ontogenetic differences between species exhibiting hermaphroditic and non-hermaphroditic sexual patterns. In addition, we collected miscellaneous fish larvae in order to compare the relative degree of skeletal bone formation among species characterized as having a low, moderate or high activity post-metamorphic lifestyle.



Early stage of *Gnatholepis thompsoni*

The high frequency of males in the twin cays population of *Rivulus marmoratus* (Pisces: Rivulidae) has a genetic basis

B. J. Turner, W. P. Davis, D. S. Taylor, B. Jarrett & M. Fisher

Data from a two-generation "common garden" experiment strongly suggest that the production of males at relatively high frequency in the Twin Cays (TC) population of the mangrove killifish *Rivulus marmoratus* has a genetic basis. Most other populations of this unique self-fertilizing vertebrate are composed almost entirely of hermaphrodites, and their major mode of reproduction is essentially obligate self-fertilization. They usually consist of arrays of many homozygous clones that can be distinguished by DNA fingerprinting techniques. In the laboratory, males can be induced in stocks derived from these populations by a variety of temperature manipulations, but "spontaneous" males are rare. In contrast, all the hermaphrodites collected from the TC population have been multilocus heterozygotes by direct progeny tests. Males comprise about 20 – 30% of the animals in this population, and this high frequency of males has persisted for over a decade. Male x hermaphrodite matings are apparently a major component of the breeding system in the TC population; i.e., the population is essentially androdioecious. To our knowledge, this breeding system has not been previously reported in vertebrates. Spontaneous production of males at ordinary laboratory temperatures (26 C) occurs at high frequency in TC lines, and many lines have been lost because they produced no hermaphrodites at all. Transitions from functioning adult hermaphrodites to males have also been observed for the first time. Our data show that elevated male production in TC lines persists for at least two generations in the laboratory, while lines derived from the Belize mainland produce far fewer males under identical culture conditions. A convincing combination of molecular and circumstantial evidence argues that the TC population is not basal or ancestral to others. Therefore, its breeding system is likely the result of a virtually unprecedented evolutionary transition from ancestral selfing to outcrossing (in the form of androdioecy) even though much theory argues that such transitions usually cannot occur.

Gonad ontogeny in gobiid fishes and distinctive morphological features of early post-hatching and post-settlement stages for several species of Caribbean gobies and damselfish

K. S. Cole

This project had three objectives. The first was to collect demersal eggs of several goby and damselfish species and subsequently hatch and rear larvae to identify species-specific larval morphological traits, as a contribution to the growing database (Baldwin, Johnson and Smith CCRE contributions and reports) of larval fish identification for the western Atlantic. The second was to collect newly settled individuals of these same species so as to characterize species-specific metamorphosis traits. The third goal was to collect immatures and adults of several goby species of unknown sexual pattern to determine which species are hermaphroditic and compare gonad ontogeny patterns for hermaphroditic and non-hermaphroditic species.

This project was delayed for several years due to the re-building of the Carrie Bow Cay facilities and subsequent schedule conflicts on the P.I.'s part. In November of 2002, a two-week visit was made to Carrie Bow by myself and a diving assistant. However, within a few days of our arrival, the theft of all station boats greatly reduced our allowable diving program. Following the recovery of one of the boats, several collection dives were made on the drop off and at Pelican Cays, two sites targeted for goby collections for the gonad onotogeny portion of the project. However, assorted problems with insecure anchorage at the drop off (limited anchor and rope supplies) and sites requiring on long range trips (which left the station with no boat), limited the ability

to collect many specimens, or to do the repeat-diving necessary to identify spawning sites, necessary for the goals of this project. A second trip was made in late May 2003. However, once again, diving was limited, this time, due to sinus problems.

In addition to the proposed goals of the project, I was also interested in determining if rates of mineralization of larval skeletal elements (i.e. endochondral ossification) among bony fishes varies according to post-metamorphic lifestyles and swimming modes. As a preliminary exploration of this topic, a modified plankton net was taken down on both the November 2002 and May 2003 trip and deployed as a standing collecting net off the fore reef pier. This was done to determine if : (i) fish larval collections could relatively easily be made; and (ii) if resulting larval collections produced a diversity of identifiable (to family) fish taxa for both sedentary, moderately mobile and highly active lifestyles. Fish larvae very close to metamorphosis were collected on both trips, with the majority being collected on nights leading up to the new moon. In addition, collected larval specimens included gobies, blennies, eels and flatfishes (relatively sedentary lifestyle); damselfishes and cardinalfishes (moderately active lifestyle) and bonefish and jacks (high activity lifestyle). Preliminary clearing and counterstaining of some specimens in each lifestyle category supported the hypothesis that more active post-metamorphic lifestyles, which result in higher bone-loading through more rapid or sustained body musculature contractions, are associated with earlier and more extensive development of endochondral bone during the later larval stages.

Ecology, Population Dynamics, and Ecophysiology

Species-specific PAM microscopy of tropical microalgae

T. A. Villareal

Tropical microalgae are exposed to high light levels and exist in nutrient-poor seas. These conditions are known to enhance photoinhibition and depress photosynthesis in phytoplankton. However, investigations on individual species may show very different patterns and suggest that species-specific responses may vary. Active fluorescence systems coupled to microscopes have the capability of directly measuring photosynthetic capacity of individual species. Previous work at Carrie Bow Cay on the giant diatom *Ethmodiscus* indicated that it has extremely high tolerance to light, a rapid recovery from the quenching mechanisms that siphon off excess photosynthetic energy, and an unusual pattern of fluorescence response when assayed in the PAM (pulse amplitude modulation) fluorometer. It lacks a typical daily cycle of yield (Fv:Fm) that was found in other diatom species (*Hemiaulus* spp.) from the same net tows. These patterns, first discovered in field material, are now being explored under more controlled experimental conditions.

Quantification of microzooplankton community grazing and growth in a mangrove creek

E. J. Buskey

The microzooplankton of mangrove creeks in Belize are dominated by protozoa including ciliates and heterotrophic dinoflagellates. A large fraction of the phytoplankton is typically in the < 10 um size category, and therefore enters the food web primarily through protozoan grazers rather than being directly grazed on by crustacean zooplankton. Previous studies have shown that copepods in these mangroves channels feed primarily on protozoa rather than phytoplankton. Grazing of microzooplankton on phytoplankton was measured using a modification of the seawater dilution method. Results from these grazing experiments show that, depending on the microzooplankton community present, anywhere from 32-95% (mean 68%) of phytoplankton standing stock was consumed daily by protozoa in the mangrove creeks. This is consistent with studies performed in other environments. These studies also estimate the growth rate of the phytoplankton, and show that phytoplankton populations more than double each day, more than compensating for the grazing of the protozoa

Chemical defenses in coral reef macroalgae and cyanobacteria

V. J. Paul

The principal objective of this research is to determine the impact of chemical compounds in algae and cyanobacteria on grazers, and thus the importance of these chemicals in determining distribution and abundance of this food resource.

During the first year we were able to compare the susceptibility of a variety of seaweeds to herbivory by natural assemblages of reef fishes and the sea urchin *Diadema antillarum.* We brought collections of seaweeds and cyanobacteria that were unpalatable back to the Smithsonian Marine Station and extracted these with organic (1:1 ethyl acetate:methanol) and aqueous (1:1 ethanol:water) solvents.

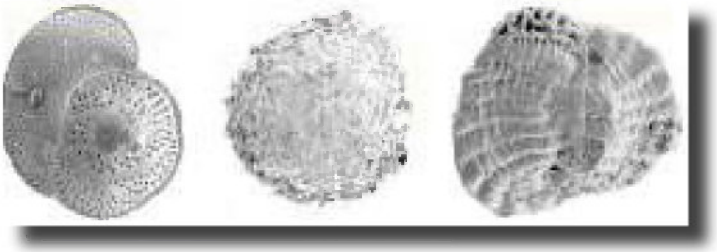
During the second year we tested these extracts in field feeding assays toward natural assemblages of reef fishes and in aquaria toward the sea urchin *Diadema antillarum* to better understand chemical defenses of these algae. The significance of this work and results are summarized below.

Marine algae and cyanobacteria are important competitors for space in tropical reef habitats. Of increasing concern on coral reefs worldwide is the overgrowth of corals by macroalgae and benthic cyanobacteria resulting, in some cases, in algae becoming abundant in formerly coral-dominated habitats. Species that have proliferated in reef habitats include *Dictyota* spp., *Lobophora variegata*, *Halimeda* spp., and occasionally cyanobacteria. Many of these species are known to be chemically defended against generalist herbivores. To determine the relative palatability of a variety of macroalgae and cyanobacteria we conducted multiple choice feeding assays with natural assemblages of reef fishes and the sea urchin *Diadema antillarum* at Carrie Bow Cay field station in Belize during April 2003 and 2004.

Most of the cyanobacteria and some of the macroalgae were not readily consumed by reef fishes, which is consistent with previous observations on Pacific reefs. There was considerable variation in the susceptibility of different species of *Dictyota*, *Halimeda*, and *Caulerpa* to herbivory. Intraspecific differences in algal susceptibility to reef fish were observed between shallow and deep water forms of *Stypopodium zonale* and between ruffled and decumbent forms of *Lobophora variegata*. Unlike the herbivorous fishes, urchins did not distinguish between shallow and deep forms of *S. zonale* and between the two morphologies of *L. variegata*. In general, *Diadema antillarum* individuals were less discriminating in their algal preferences than reef fishes and consumed some of almost all species offered to them. They consumed large amounts of the red algae *Trichogloea* sp. and *Liagora* cf. *albicans* and the cyanobacterium *Schizothrix* sp., which were avoided by fishes. They also consumed some of *Stypopodium zonale* and *Lyngbya majuscula*, which fishes did not eat. The fish were deterred by *S. zonale* and *Taonia* sp. extracts, while the urchins readily consumed them. Both the fish and the urchins were deterred by the extracts of *Laurencia poiteaui* and *L. microcladia*. These observations support the hypothesis that herbivorous reef fishes and D. antillarum have different algal preferences (often driven by chemical defenses), and therefore, they can have a differential effect on macroalgal community composition. The die-off of *D. antillarum* has led to proliferation of brown algae which herbivorous fishes do not consume. Fish and urchins can control a mixed community of algae on Caribbean reefs better than either one alone.

Ecology of epiphytic foraminiferans from seagrass habitats

S. L. Richardson



Samples of the seagrass *Thalassia testudinum* were collected from nine sites in June 2001 (Carrie Bow Cay, Twin Cays, Man O'War Cay, Cat Cay, and Manatee Cay) and again in February 2002 (Carrie Bow Cay, Twin Cays, Man O'War Cay, Tobacco Range lagoon (new), Cat Cay, and Manatee Cay). Sites were selected from both open waters, and in close proximity to mangroves. Twelve seagrass blades were surveyed from each site for live individuals of epiphytic Foraminiferans. Live individuals were identified to species, and counted. Statistical analysis of the data collected in June 2001 has revealed distinct differences in species composition, species richness, and population densities between the samples collected in open-water sites and those collected in mangrove habitats (lagoons and channels). A total of 43 species were identified from all sites, species richness at each site ranged from S=5 (Cat Cay) to S=31 ('Cuda Cut), and the total number of individuals ranged from N=105 (Cat Cay) to N= 4302 (Twin Cays Dock). Cluster analysis of the data set yielded two distinct clusters: mangrove sites *vs.* open-water sites. Preliminary analysis of the data collected for some of the sites surveyed during the dry season in February 2002 (Boston Bay, Sponge Haven, Man O'War Cay, Carrie Bow Cay, and Cat Cay), indicates that for most sites, the epiphytic foram populations are approximately half of what they were in June 2001, during the wet season. Species richness and blade surface areas remain almost the same, although species dominance (as reflected in higher evenness indices) appears to be lower during the dry season relative to wet season. The exception to this trend was seen at Man O'War Cay where the total number of individuals was 2.5 times higher in February 2002 (N=4888) than in June 2001 (N=1962). This observation is potentially explained by a higher nutrient input into the surrounding seagrass beds during the breeding season of the nesting colony magnificent frigate birds that resides on Man O'War Cay. The higher population densities and higher dominance values (lower evenness indices) observed in samples collected from mangrove habitats during June 2001, are interpreted as a response to an influx of mangrove-derived nutrients during the wet season.

Several hundred specimens of the epiphytic species *Sorites dominicensis* were collected from the Twin Cays in February 2002, and measured in order to construct growth

curves and a horizontal (or static) life table. *S. dominicensis* is seen to have a Type III survivorship curve which is characteristic of many marine invertebrates with high juvenile mortalities. These results are similar to growth and survivorship curves generated for *S. dominicensis* populations living in the Indian River Lagoon, FL, and the Florida Keys.

Microbial dynamics in the lagoon at Douglas Cay (Atlantic Coral Reef off Belize, Central America)

R. J. Chróst

The major objective of project 2002 was to measure dynamics of: 1) number of bacterial communities and the percentage of metabolically active cells, 2) bacterial biomass production, 3) turnover rate of bacterial biomass, and 4) DOC concentration in an inner lagoon at Douglas Cay and outside open water during dinoflagellates development (dominant species: *Gonyaulax polygramma, G. grindleyi, Protoceratium reticulatum, Prorocentrum mexicanum, P. emarginatum*).

Bacteria in water of inner lagoon at Douglas Cay were 8-27 times more abundant in comparison to open seawater outside the cay. An interesting observation was that bacterial numbers markedly increased in both sampling sites just after the heavy rain (May 21).

The concentration of standing-stock bulk DOC available for bacterial metabolism was very similar in both environments. This may suggest rapid DOC degradation and its turnover at Douglas Cay inner lagoon because it would be hard to believe that water enrichment processes caused by pelicans feeding activity and runoff from the mangrove island did not increase DOC level. Similar concentrations of DOC in Douglas Cay lagoon and outside open seawater can only result when input rates of DOC are balanced by equal rates of DOC microbial degradation.

Bacterial communities in an inner lagoon in Douglas Cay had higher metabolic activities than micro -organisms grown in open seawater. High metabolic activity of heterotrophic bacteria and probably higher availability of organic substrates in the DOC pool for their metabolism resulted in very high rates of bacterial biomass production in water samples from an inner lagoon at Douglas Cay in comparison to open seawater samples.

Turnover time of produced biomass in water samples from an inner lagoon at Douglas Cay was significantly shorter than in open seawater indicating that large portion of bacterial biomass was rapidly consumed by higher trophic levels (e.g. Protozoans and microsooplankton).

Turnover time of bacterial biomass in water of inner lagoon at Douglas Cay did not vary strongly during the study period and fluctuated between 8.7 and 14.9 hours. There were observed very dynamic variations in turnover time of bacterial biomass in samples from outside open seawater (from 9.19 to 80.21 hours). Interesting observation was that in samples taken just after a heavy rain from outside open seawater turnover time of bacterial biomass significantly shortened from ca. 56 to nine hours and then elongated again to 70 hours.

These results illustrate that microbial, especially heterotrophic bacterial, activity and metabolism of "internal eutrophication sources" at Douglas Cay are extremely highly significant ecophysiological processes that control organic matter and inorganic nutrients levels in this environment and therefore directly regulate the degree of water eutrophication. Thus microbial activity plays a crucial role in functioning of these types of subtropical environments.

Synergistic effects of physically and biologically induced H_2S flux – implications for the evolution of chemoautotrophic ectosymbioses

K. C. Vopel & D. Thistle

Kay C. Vopel

This project belongs to a series of studies that aims to understand the making of a ectosymbiosis between chemoautotrophic bacteria and the sessile ciliate *Zoothamnium niveum*. The conspicuous large colonies of *Z. niveum* live in densities of more than 1000 mP-2P on vertical walls of peat-banks that border coves and channels of red mangrove (*Rhizophora mangle*) islands of the barrier reef off Dangriga, Belize. The feather-shaped colonies are composed of polymorphic zooids attached to a branched stalk and can be up to 15 mm long. Coccoid and rod̃shaped sulphide oxidising bacteria cover all but the most basal parts of the colonies as a single layer. Their white appearance is indicative of intracellular sulphur globules that are associated with the oxida-

tion of sulphur compounds. We conducted in situ time-series measurements of O_2 and H_2S at high spatial resolution using fast responding underwater microelectrodes (Unisense, Denmark). Flow velocity and hydrostatic pressure were measured simultaneously for the duration of the experiment. Unidirectional flow was applied to ciliate colonies in situ using a water pump. Data suggest that the supply of H_2S and O_2 to the *Z. niveum* symbiosis results from the synergistic effects of two advective transport processes - the pulsing release of H_2S from the rootlet conduits and the ciliate-generated current.

Population dynamics and productivity of red-mangrove sponges

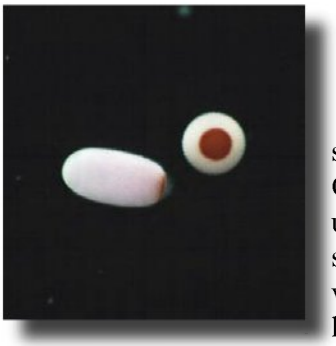
C. Díaz & K. Rützler

Haliclona nov. sp.

Sponges represent a dominant component of epibiont communities in Caribbean mangrove ecosystems but their composition, abundance, dynamics, and ecological role remains little known. Studies have shown that sponge species composition on red mangrove (*Rhizophora mangle*) aerial roots may be unique for a particular lagoon, creek, or island, reflecting environmental or historical differences between sites. Furthermore, sponges, through their association with microbes, are mediating non-animal metabolisms, such as nitrification, at important rates in this ecosystem. A comparative study of the structure and dynamics of poriferan epibionts on mangrove aerial roots was recently initiated at three Caribbean localities: Twin and Pelicans cays in Belize, Bocas del Toro, Panamá, and Margarita Island, Venezuela. Analyses of seasonal and long-term changes in sponge diversity and relative abundance will elucidate the effects of environmental parameters and help identify indicators of mangrove community health.

Larval ecology and adult distribution of mangrove sponges

K. Rützler



More than 70 species of sponges are found at Twin Cays. Twenty of these may be undescribed and are still under study. Surveys and experiments with settling plates show that horizontal distribution is primarily determined by substrate availability and water flow; vertical zonation also by tidal signature, light and sediment exposure, and space competition. Where favorable conditions are combined, the sponge biomass to substrate ratio reaches record values. A few species are uniquely adapted to withstand adverse conditions, such as burial in mud and temperature-salinity extremes. Sponge larvae are poor swimmers and stay mobile for only a few days. Laboratory experiments show that they switch from positive to negative phototaxis only hours after their release. In situ they stay and settle near parent populations and along the path of strong currents. Most environmental conditions suitable for sponge growth found in Caribbean mangroves exist also in tidal forest in the Indo-Pacific but the large tidal fluctuations in that region preclude sponge growth by daily exposure of stable substrates to air.

Population recovery and differential heat shock protein expression for the corals *Agaricia agaricites* and *A. tenuifolia* in Belize

M. L. Robbart, P. Peckol, S. P. Scordilis, H. Allen Curran & J. Brown-Saracino

Over recent decades, coral reefs worldwide have experienced severe sea-surface temperature (SST) anomalies. Associated with an El Niño-Southern Oscillation (ENSO) event of 1997–1998, nearly 100% mortality of the space-dominant coral *Agaricia tenuifolia* was reported at several shelf lagoonal sites of the Belize barrier reef system; a less abundant congener, *A. agaricites*, had lower mortality rates. We assessed *A. agaricites* and *A. tenuifolia* populations at coral reef ridges in the south-central sector of the Belize shelf lagoon and forereef sites to document recovery following the 1998 ENSO event and subsequent passage of Hurricane Mitch. To investigate the difference in heat stress tolerance

between the 2 species, heat shock protein (HSP) expression was examined in the laboratory under ambient (28°C) and elevated (+6°C) temperatures. Populations of *A. agaricites* and *A. tenuifolia* surveyed at forereef sites in 1999 showed after effects from the 2 disturbances (partial colony mortality was ~23 and 30% for *A. agaricites* and *A. tenuifolia,* respectively), but partial mortality declined by 2001. At reef ridge sites, *A. tenuifolia* exhibited 75 to 95% partial colony mortality in 1999 compared to 18% in the less abundant *A. agaricites*. We measured a significant increase in percentage live cover at ridge sites for both *Agaricia* species from 1999 to 2001, except at Tunicate Ridge; at this site, which has restricted water flow, live *A. tenuifolia* cover remained low (~10%) 3.5 yr after the 1998 warming event, due in part to high sponge cover (>75%). Immunoblotting results indicated that *A. agaricites* had twice as much HSC 70 (16.9 µg cm–2) as *A. tenuifolia* (8.7 µg cm–2) at ambient temperatures and 6× as much under the +6°C treatment. In addition to the inducible response by *A. agaricites*, this species expressed HSP 90, whereas *A. tenuifolia* did not. The distinctive patterns of population recovery and HSP expression suggest that *A. tenuifolia* has a lesser ability to produce HSPs for protection against environmental stress than *A. agaricites*. Such differences in resilience to large-scale environmental disturbances such as intermittent ENSO episodes may drive a dramatic change in coral species abundance patterns.

Agaricia tennifolia

Environmental and physiological determinants of species dominance on the Belizean barrier reef

B. Helmuth, K. P. Sebens, E. Carrington, J. Leichter & L. Johnson

Our project focuses on the coupled effects of temperature, water flow, and light in driving the physiological performance of three key species of coral, *Agaricia tenuifolia*, *Acropora cervicornis*, and *Porites divaricata*. These three species comprise the competitive dominants on much of the Belizean barrier reef, and differences in their physiological responses to the environment may determine their relative rankings in a competitive hierarchy. Our work over the last year has taken a two-pronged approach, monitoring environmental variables at multiple sites near Carrie Bow Cay and the Pelican Cays, and measuring physiological responses by corals under controlled laboratory conditions.

Environmental monitoring

Since March 2000, a series of temperature loggers (Onset Water Temp Pro) has been deployed on the fore and back reefs surrounding Carrie Bow Cay, and at sites at Cat, Manatee and Channel Cays. Loggers are programmed to record average temperatures at ten minute intervals with an accuracy of < 0.3°C, and have been deployed at depths ranging from just subsurface to 40m. These loggers have been recording continuously since their deployment, and have provided us with a detailed, temporally- and spatially-high-resolution view of thermal characteristics of the waters around several sites in Belize.

Results at the Carrie Bow Cay site have shown that while there appears to be no sharply defined thermocline in the water column on the fore reef, water temperatures can vary by 3°C or more on a daily basis, particularly in shallow water. Temperatures above 31°C are not uncommon, especially in areas with restricted water flow. Data also indicate an unusual pattern of thermal variability due to the interaction of surface heating with the tidal regime. In water <5 m depth, corals often experience a diurnal pattern in thermal exposure as surface radiation heats the shallow water, with peaks regularly occurring at 2 PM. In slightly deeper water (5 –10 m), the pattern becomes semidiurnal as the lowering tide brings the heated surface waters to the corals. As a result, depending on the timing of the tides, temperatures spikes at these depths can often occur at night when the coral is respiring but not photosynthesizing. We have also previously shown that water flow regularly varies over this same depth gradient, as, obviously, does light. This unique set of thermal conditions therefore represents an excellent opportunity to measure the coupled effects of temperature and water flow on both zooxanthellar photosynthesis as well as on coral respiration, and ultimately, to examine the physiological responses to flow, light and temperature of four major competitors for space on the reef.

A key result of our preliminary database is the observation that temperature, light and water flow patterns can change over much smaller spatial and temporal scales than anticipated, and that these parameters are not always coupled. For example, we have identified regions with high light, low flow and high temperature (Cat Cay shallow); high light, high flow and low temperature (Carrie Bow Cay shallow), and low light, high temperature and low water flow (Channel Cay deep), etc. These regions will provide a means

of nondestructively testing the predictions generated by our controlled experiments.

Physiological effects of water motion, temperature and fluctuating environments

Previous work has shown that increasing water motion can have significant effects on levels of photosynthesis by zooxanthellae and respiration rates of coral tissue, through its effect on oxygen and/or bicarbonate flux. Work conducted by our team on *Agaricia tenuifolia* (Sebens *et al.*, 2003) has shown that in stark contrast to other species tested to date, photosynthetic capacity of zooxanthellae in this coral appears to be relatively insensitive to flow. However, respiration is significantly affected by flow, as in other species. We interpret these results as an indication of the ability of *A. tenuifolia* to inhabit very poor environmental conditions including very low flow speeds, a result consistent with levels of flow observed and predicted inside aggregations. By creating limiting conditions of light and flow within aggregations, this species may be able to effectively exclude competitors less able to physiologically contend with these extreme conditions.

Data collected during July 2002 also suggest that respiration and photosynthesis by *Agaricia tenuifolia* may change with temperature, and with the duration of exposure. We found significant increases in respiration by coral tissue with increased temperature, and significant decreases in photosynthesis, but only after exposures of 48 h. or more. Preliminary evidence collected from other species suggests that *Acropora* and *Porites* also exhibit responses to temperature increases, and that of the three species *Acropora* appears the least able to physiologically acclimate.

High frequency variability in the thermal regimes of the Belizean Barrier reef: implications for coral physiology and reserve design

B. Helmuth, K. P. Sebens, E. Carrington, J. Leichter & L. Johnson

Coral bleaching is strongly correlated with elevated water temperature, and remote sensing (R/S) techniques have emerged as an effective means of estimating large-scale patterns of coral mortality. However, because R/S techniques are capable of recording only sea surface temperature (SST), their effectiveness at estimating temperatures at depths relevant to corals has yet to be fully tested. We deployed arrays of temperature recorders from surface to 40 m depths on the back-reef and fore-reef slopes of Carrie Bow Cay, as well as at several sites in the Pelican Cays. Instruments recorded water temperatures at intervals of 10-15 min. and at resolutions of ~0.15-0.3°C. We used time series analysis to quantitatively describe high frequency variability in thermal signals at each depth and at each site, and compared these signals to those obtained from surface temperature measurements. Strong diurnal periodicity associated with solar heating was evident in shallow waters <10 m, while semidiurnal periodicity associated with internal tidal forcing was observed at deeper depths. Thus, the thermal regimes experienced by corals is strongly site and depth specific, and is unlikely to be predictable solely on the basis of sea surface temperatures.

We measured the likely physiological consequences of these rapid changes in seawater temperature to coral physiological performance using both respirometry (oxygen production and uptake) techniques, as well as with a Pulse Amplitude Modulated Fluorometer. The effects of short-term (20-minute) exposures to elevated temperature varied by species. Net photosynthesis was dramatically reduced in *Acropora cervicornis*, but was unaffected in *Agaricia tenuifolia* and *Porites divaricata*. However, respiration rates of *P. divaricata* significantly decreased with increasing temperature. Photosynthesis by both *A. cervicornis* and *A. tenuifolia* significantly decreased after exposure to elevated temperatures after approximately nine hours (~semidiurnal variability).

Thus, corals do show physiological responses to high frequency changes in temperature, but these responses vary from species to species. Significantly, these temperature changes are unlikely to be predictable on the basis of surface temperatures alone. Changes in water column thermal stratification with changing climate may lead to complex alterations in the mechanisms controlling subsurface thermal regimes. Time series analysis of in situ records of water temperature provides a means of quantitatively comparing thermal regimes across space and through time, and emphasizes high levels of heterogeneity in temperatures experienced by corals in the field.

The physiological ecology and taxonomic diversity of symbiotic dinoflagellates in different environments: Understanding the influence of physical and biological factors on symbiont population distributions

M. E. Warner

We performed extensive analyses of photosynthetic performance at the four Carrie Bow Cay sites in a subset of coral species: *Siderastrea radians* (1 m only), *Porites astreoides*, *Porites porites* (1 and 8 m only), *Diploria strigosa*, *Diploria labyrinthiformis*, *Montastraea annularis*, *Montastraea cavernosa*, *Montastraea faveolata*, *Stephanocoenia intercepta*, *Siderastrea siderea*, and *Agaricia lamarki* (20 m

only). Several corals were also marked with two inch stainless steel numbered tags or four inch rubber cattle tags in order to rapidly find the same colonies for future repeated sampling work. Photosynthetic measurements were made using a submersible PAM fluorometer in order to record the dark and light acclimated quantum yields of photosystem II over several days. In order to record maximum photosynthetic activity, samples were compared between time points at sunrise (5:30 6:30) and mid-day (11:00-12:00) peak irradiance determined by a cosine PAR sensor at the surface of the water by the marine station. Several of these measurements were repeated on different days due to variable cloud cover and storm activity during the first four days of our work period. Lastly, a subset of corals (n=4 / species) were sampled and transplanted from 25 m to the top of the outer ridge (16 m) and secured to concrete blocks with marine epoxy. This brief transplantation experiment was designed to investigate the immediate affects of an irradiance spike on the photobiology of the algae under a slightly more realistic transplant scheme (e.g. as opposed to moving corals from 25 m to 2 m), as well as to investigate the possibility of changes in symbiont populations after a longer period (several months) following transplantation. Data analyses thus far has shown that there are some significant differences in the capacity of photoprotection between different species at each depth on a diel cycle, and we expect our molecular work will confirm that this may correlate to different algal types between these respective host corals. DNA extractions from our sample collections (over 200 independent samples) are now 80% complete and we have begun our analyses by denaturing gradient gel electrophoresis (DGGE) in order to determine the correct molecular lineage for each algal sample. We anticipate that the all data will be processed prior to our requested next trip to Carrie Bow in order to sample from the same locations to test for seasonal variability in photosynthetic performance and algal population distributions.

Diploria strigosa

Roles of predators, physical disturbance, and competition in development of contrasting sponge faunas

J. Wulff

Spongivorous predators prevent the usual Caribbean mangrove sponge species from inhabiting the Pelican Cay mangroves by consuming them, and the usual mangrove species prevent the typical reef sponge species from inhabiting Twin Cays by growing faster and smothering them. A comparison of specific growth rates (i.e., standardized by initial volume) among small pieces cut from reef sponge species growing on mangrove roots in the Pelicans (i.e., the controls for these experiments) and small pieces (of comparable sizes, between two and 10 cm^3 to control for size-specific growth rates) of the same species grown on the reef they inhabit in Panama, reveals that these sponge species (except for the unusual *Desmapsamma anchorata*) grow significantly faster on mangrove roots. The mangrove roots are a superior environment, probably nutritionally as well as physically, and yet these species are normally prevented from growing in this habitat. This suggests a trade-off between growth rate and predator resistance. When all growth rates are compared in the form of specific growth rates it is clear that the reef sponges grow quite slowly (with the exception of the very fast growing weedy and parasitic species, *Desmapsamma anchorata*), the readily consumed mangrove species grow very much faster, and the less readily consumed mangrove species grow at intermediate rates. Survival and growth rate would be predicted to be related in a system in which competition for space is the chief determinant of survival. When survival and growth rate are plotted against each other for these 12 sponge species, two very different relationships between these variables can be seen. Separating the reef species from the mangrove species, makes it readily apparent that the mangrove species do show this relationship of survival to growth rate, exactly as predicted. The reef sponges do not, and all have very similar low growth rates (except *D. anchorata*), just as predicted if a variety of processes control survival. The difference in diversity between these two sets of mangrove cays may also reflect these differences in what processes influence survival. In the competition-influenced system, diversity is relatively low (57 species) whereas the system in which a variety of processes may play roles has 2.6 times the number of species (147). This relationship is, of course, not demonstrated to be causal by this study, but does address current community ecology theory in an intriguing way.

UV sensitivity of ophiocomid brittle stars

G. Hendler

This was a continuation of studies carried out at CBC on color-change and photosensitivity of *Ophiocoma* species. The objective was to determine whether darkly pigmented *Ophiocoma wendtii* or pale colored *Ophiocoma pumila* is better able to withstand the damaging effects of UV irradiation. Experimental individuals were held in shallow aquaria with flowing seawater. The containers were either covered with transparent, UV-opaque plastic, or with transparent, UV-transmitting plastic. *Ophiocoma pumila* began to autotomize its arms within 24 h and to die, before *O. wendtii* were affected. It appeared likely, however, that the responses of both species could have been influenced by temperature stress. Despite the continuous seawater flow, daily maximum temperatures in the aquaria reached several degrees above ambient seawater temperatures. It will be necessary to control for temperature in future experiments.

Ecology of the *Montastraea "annularis"* species complex at the barrier reef complex, Carrie Bow Cay

J. Pandolfi

While originally considered a generalist, modern *Montastraea "annularis"* sensu lato, long thought to represent one species, was shown to consists of a complex of at least three sympatric species in shallow- to mid-reef depths in Central America that differ in overall colony shape and the shape of the growing edge. The purpose of this field season was to go back to some of the original localities where variation in *M. "annularis"* was documented, with a new perspective on species differences to document ecological distribution of each of the three purported species of the *M. "annularis"* species complex. We sampled along 25 additional (to previous) transects at three sites, Tobacco Reef, Carrie Bow Cay, and Curlew Cay; and at each site at five or six water depths (habitats).

Establishing a monitoring site on the Belizean barrier Reef at Rendezvous Cay

I. G. Macintyre

For one week (April 19-26, 2002) I joined the Cambridge University Team to establish survey markers off Rendezvous Cay. This area became a classic reef survey site following the very detailed mapping of the shallow-water reef communities here during the 1959-1960 Cambridge Expedition. The four original Cambridge team members were John Thorpe, Will Warham, Paul Bregazzi, and David Stoddart. This team arrived a week ahead of me to map the island and mark the two transect lines.

My assignment was to drill 19 mm diameter holes to a depth of 20 cm into hard substrate with an underwater pneumatic drill operated from a SCUBA tank. Then 61 cm length stainless steel rods were inserted into the holes and fixed in place with Adhesive Reef Epoxy. The steel rods were fitted with shackles to allow the attachment of survey lines. A total of seven rods were placed along two transect lines, which extended from the shallow fore-reef to the back-reef lagoon.

After the installation of the rods Will Warham completed a photographic survey along a nylon line attached to the rods. Overall coral cover in 2002 (12.2 %) had deceased considerably compared with that recorded in 1960 (39.5 %), especially on the leeward side of the reef. This and future surveys will be contributed to the Carribean-wide CARICOMP reef monitoring system.

Melanie McField of the World Wildlife Fund's Mesoamerican Reef Program joined us for one day to take GPS readings at each of the survey-rod sites.

Continuing monitoring of this historically important site will be carried out by M. McField and the Belize Coastal Zone Management Institute.

Long-term changes in coral community composition at two scales on the barrier reef complex, Carrie Bow Cay

J. Pandolfi

One of the important first steps in understanding the ecology of coral reef communities is to examine how taxonomic composition and diversity vary over different spatial

and temporal scales. In 2001, I serendipitously located quadrats that had been laid down and photographed in 1986 by Ann Budd, University of Iowa. These were part of a study where she had emplaced 12 quadrats at four different habitats around Carrie Bow Cay, Curlew Cay, and Southwater Cay. Photographs of these quadrats provide unique information for understanding changes on the reef over a 15-year interval. Not only that, but Budd also has coral abundance data from transects she censused near the quadrats. This provided an opportunity to look at ecological changes on reefs over two scales: the 1-m2 quadrat and the 30-m transect. We photographed 12 1-m2 quadrats, haphazardly placed, at each of the same four sites. Photos were shot as four quadrants of each quadrat, resulting in 192 photos (four sites x 12 quadrats x four quadrants). These photos give a measure of the variability in coral species composition that can be directly compared to those obtained from the 1986 quadrats. The results will provide us with fundamental information on the long-term ecological dynamics of coral reefs over multiple scales, and may help to resolve the paradox of ecological chaos at small spatial and temporal scales versus community predictability at larger ones.

Invasive species in marine ecosystems: Analysis of fouling and wood-boring communities

A. H. Hines, G. M. Ruiz, K. Rützler, B. Tunberg & D. G. Smith

The extent and significance of nonindigenous species (NIS) invasions in coastal marine ecosystems have become increasingly evident in recent years, but we currently lack the necessary data to evaluate spatial and temporal patterns of marine invasions. Past work has identified many apparent patterns of invasion among coastal systems; however, these data derive primarily from literature-based syntheses rather than standardized, quantitative, and contemporary field surveys. We set out to test the following hypotheses: The number of established non-indigenous species decreases with increasing latitude; the rate of spread of non-indigenous species is related to life history characteristics; the rate of new invasions is associated with intensity of vectors (e.g., shipping) and will decline with increasingly effective management efforts; nonindigenous species do not respond to the same biogeographic boundaries in invaded regions as native species. We have started to employ standardized "settling plates" and wooden blocks in high salinities at several sites, including Panama, Belize, Florida, and the Chesapeake Bay, and will process the developing fouling and wood-boring communities under the direction of systematists for each taxonomic group after several months of exposure.

The ecology of *Batis maritima* in mangrove ecosystems with varying nutrient limitations

D. Whigham, I. Feller, C. Lovelock & J. T. A. Verhoeven

Batis maritima L. (Bataceae) is a widespread low-growing and clonal perennial plant of neotropical, subtropical, and temperate wetlands. *Batis* is often the dominant low growing species in mangroves and appears to grow best in high-salinity, open-canopy habitats. In high-salinity habitats, it has a low stature and reproduces by clonal propagation of horizontally growing branches. In shaded habitats, plants are taller and clonal propagation by horizontal branch formation does not occur. In open habitats, individuals are shorter and the horizontal branching pattern is limited to the edges of salt pans. *Batis* shoots in all habitats are capable of rooting when they come into contact with the substrate, which is a second clonal growth pattern. We are investigating *Batis maritima* at Twin Cays, Belize, and Ft. Pierce Florida, particularly the effects of nutrient availability on its growth rate and form. At the Belize site, we are testing the hypotheses that *Batis'* growth is N- and P- limited, and at the Florida site, that N is limiting. Our investigations include *Batis maritima*'s impact on the recruitment of black mangrove, a mangrove with small seedlings, and its nutrient quality which may influence patterns of insect herbivory, a phenomenon that has not previously been investigated for understory species in mangroves.

Development of food web models for mangrove channels with aggregated populations

J. W. Ambler & T. Gregg

The main focus of the research trip in 2002 was to measure the contribution of phytoplankton to ecosystem metabolism in the Lair Channel on East Twin Cay. Our results suggest that floating algal mats, which lift off the bottom of the Lair Channel in the late afternoon, contribute significantly to the primary production of the Lair Channel. Our ecosystem metabolism data includes dawn and dusk measurements of dissolved oxygen to determine NPP (dawn to dusk difference) and community respiration (dusk to dawn decrease); and experimental runs with a floating dome to measure a transfer coefficient for dissolved oxygen between the water surface and the overlaying air. In addition, we have a fifteen day time series of dissolved oxygen measured at four depths at dusk to observe trends in ecosystem NPP. On days when dissolved oxygen concentrations were high-

est, they were usually highest at 1.5 m, the depth closest to the bottom where the algal mats occurred. During several days, dissolved oxygen was lowest at the surface, which correlated with surface inhibition of phytoplankton observed from our light dark bottle experiments. This time series will be helpful in interpreting our dawn-dusk ecosystem metabolism measurements and also in planning the placement of in situ YSI sondes, which can measure dissolved oxygen and other variable for several days. Temperature and salinity were relatively stable during the 15 day time series, although several storms passed through.

Batis maritima

Observation of swarms of *Dioithona oculata* in the fore reef by SCUBA was another objective we accomplished during this field trip. Five dives were performed under CCRE permission to dive to 30 ft., and two dives were performed through IZE at deeper depths. Several search strategies were employed during the CCRE dives: zigzag search up and down spurs, swam length of channel on southern edge of fore reef, and swam at 25 ft. along the fore reef. During these dives, no dioithonan swarms were observed although mysids were observed regularly. For the deeper IZE dives, we swam along the dropoff along the reef south of CBC. During one of these dives, dioithonan swarms were so dense that the water was cloudy and visibility was markedly reduced. This environment was completely different from the protected mangrove channels where we have observed smaller, denser swarms.

Mangrove forest classification and change in Twin Cays

W. Rodriguez & C. Feller

Classification of tropical ecosystems using remotely sensed images help us update the status of land cover and land use and are an effective medium to quantify forest spatio-temporal changes caused by natural or anthropogenic causes. In this project, we have used aerial photography from January 2003, with 1-m spatial resolution and three bands in the visible region of the light spectrum, to classify the present status of mangrove forests in Twin Cays, an intertidal mangrove island located in the Belizean Reef ecosystem. Ground truth, ancillary oblique aerial photos, and intimate knowledge of the mangrove system helped us distinguish 29 thematic categories that reflect mangrove species, growth status, and anthropogenic disturbance in the island. To quantify overall changes during approximately two decades in the main three mangrove species (red, black, white) in Twin Cays we are using aerial photography from 1986 and 2003, and satellite imagery from the Ikonos sensor for years 2001 and 2003. Image pre-processing consisted of radiometric and geometric corrections prior to classification and change-detection analysis. For geometric correction of both aerial photos, we used the image-to-image registration method, in which Ikonos 2001 data was used as the base image. All images were georeferenced to the UTM coordinate system and spatial resolution was maintained at one meter. To avoid mis-registration problems, the root-mean-square (RMS) error between scene co-registrations was maintained at +/- 0.5 pixels. Accuracy assessments for classification and change detection are part of the ongoing analysis. All data have been integrated into a geographic information system used for storage, update, and subsequent geographic analysis.

Species Interaction and Behavior

Adaptive value of aggregative behavior to zooplankton

E. J. Buskey

In the mangrove prop root habitat of Twin Cays and along the barrier reef of Carrie Bow Cay in Belize there are several excellent examples of aggregative behavior in zooplankton including the swarming behavior of the copepods *Dioithona oculata* and *Acartia spinata*, and the shoaling and schooling behavior of the mysid *Mysidium columbiae*. The primary adaptive advantages of aggregative behavior in zooplankton are thought to be one) reduced dispersion by currents (Buskey *et al.* 1996, Buskey 1998 a,b), 2) increasing encounter rates with potential mates (Ambler *et al.* 1996, Buskey 1998) and 3) enhanced defenses against visual predators (e.g. O'Brien and Ritz 1988). A recent provocative study by Ritz (2000) suggests a fourth potential advantage: that schooling behavior in mysids confers a hydrodynamic advantage and allows for energy conservation compared to solitary behavior. My past studies have focused primarily on verifying the first two proposed adaptive advantages of

aggregative behavior. This year I focused my studies on predator avoidance behavior by copepod swarms and mysid schools, and the possible energetic advantages of schooling behavior in mysids.

I. *High speed video studies of copepod and mysid escape behavior*

Using high speed video and computerized motion analysis techniques, we quantified the escape responses of copepod swarms and mysid schools to both simulated and natural predators. During a previous trip to CCRE in April 2002, we began detailed kinetic studies of the escape behaviors of mangrove mysids using a portable high speed video system that is capable of capturing images at 1000 frames per second. We completed this study during 2004 and quantified numerous rapid "tail flip" escape jumps by the mysids which reaching peak speeds of over 1000 mm/s and initial accelerations of over 300 m/s^2. We also examined the escape behavior of a swarm-forming copepod species from the barrier reef of Belize, *Acartia spinata*. This species has impressive escape reactions to hydrodynamics disturbances, with escape jumps of over 600 mm/s and a response latency of less than 4 m. These copepods are capable of remaining within swarms under turbulent conditions found along the reef. In laboratory studies we found that small scale turbulence reduces the sensitivity of these copepods to hydrodynamic disturbances, making them more vulnerable to predators. Swarm formation under turbulent conditions may produce a confusion effect for visual predators which would offset their reduced ability to detect the approach of predators using hydrodynamic signals.

II. *Measurement of respiration rates of individual, aggregated and schooling mysids.*

This year (2004) I also examined the hypothesis of a metabolic advantage to schooling behavior in *Mysidium columbiae*. A study by Ritz (2000) had proprosed a large metabolic advantage to schooling behavior in mysids and euphausiids. I have measured the metabolic cost of swimming behavior in these mysids in a past study (Buskey 1998b) so it was a straightforward exercise to adapt these methods to address the hypothesis of metabolic atvantage to mysid schooling behavior. We did find a significant decrease in metabolic rates of schooling mysids compared to solitary or randomly oriented individuals, although the decrease in was not as large as that proposed by Ritz (2000).

Flow microenvironment of two marine peritrich ciliates with ectobiotic chemoautotrophic bacteria

K. Vopel, C. H. Reick, G. Arlt, M. Pöhn & J. A. Ott

The flow microenvironment of two marine peritrich ciliates, *Vorticella* sp. and *Zoothamnium niveum*, with ectobiotic sulfur bacteria was studied with frame-by-frame analyses of video sequences and a microsensor for fluid velocity. Both species populate the chemocline above H_2S releasing mangrove peat. *Vorticella* sp. moves the surrounding seawater up to a horizontal and vertical distance of at least 400 µm with a maximum flow velocity of 18 mm s–1 close to its peristomial edge. The feather-shaped colonies of *Z. niveum* generate a unidirectional flow of seawater passing the colony perpendicular to the stalk; the convex side of the feather faces upstream. The flow velocity increased exponentially towards the colony, up to 11 mm s–1 at a distance of 100 µm. Contraction of the stalk forces the zooids of *Vorticella* sp. and *Z. niveum* towards the substrate at a high velocity of 71 and 520 mm s–1, respectively. During contraction of *Vorticella* sp., only little seawater is dragged along towards the surface to which the ciliates are attached whereas the contraction of *Z. niveum* resulted in a clear increase in the velocity of the seawater both surrounding the colony and above the substrate. Extension of the species proceeds 700 to 1000 times more slowly than contraction, and the surrounding seawater sticks to the cells and therefore is dragged along. The measurements given here support our earlier data indicating the importance of the feeding current for the bacteria-ciliate association, i.e. the cilia beat drives H_2S- and O_2-containing seawater toward the zooid at high velocity and thus, supports the growth of the ectobiotic sulfide-oxidizing bacteria. Rapid movement, shrinkage (*Vorticella* sp.) and bunching (*Z. niveum*) of the zooids during stalk contraction apparently cause sufficient shear stress to abrade ectobiotic bacteria that, once suspended, could enter the feeding currents.

Zoothamiun niveum (Ciliophora, Peritrichida). Feather-shaped colonies grouped around "miniature vents" at the surface of vertical overhanging mangrove peat walls. The white appearance of their ectobiotic bacteria is caused by cellular inclusion of elemental sulfur

Wave-induced venting sustains chemoautotrophic ectosymbiosis

K. Vopel

A symbiosis between the sessile ciliate *Zoothamnium niveum* and ectobiotic sulphur bacteria was discovered in coves of mangrove islands off the Belize coast (Ott, 1998 #645, Bauer-Nebelsick, 1996 #546). The stalked colonies of *Z. niveum* grow on vertical peat walls around the opening of small conduits created by the microbial decomposition of mangrove-rootlets. Here we show how the combined effects of ciliate behaviour and wave-generated boundary-layer flow generate a pulsing supply of H_2S and O_2 to the ectobiotic bacteria and, thus, facilitate symbiotic growth. We present evidence that flow-ciliate interactions generate oscillating pressure gradients that cause a pulsing exchange of the conduits deoxygenated, H_2S-containing void. The conduits are charged with H_2S by diffusion from the decomposing tissue of the rootlets during periods of low flow speed due to flow reversal. During these times, the feeding current of the zooids transports oxygenated seawater toward the ectobiotic bacteria. In contrast at high flow speed, the conduits void is discharged, drawn along the colonies, and transported toward the ectobiotic bacteria. By growing on the surface of the zooids that is against a rapid and constant current of alternately deoxygenated and H_2S containing and fully oxygenated seawater the ectobiotic bacteria overcome diffusion limitations of substrate supply.

Life cycle and interactions in a thiotrophic symbioses between *Zoothamnium niveum* (Ciliophora, Oligohymenophora) and chemoautotrophic sulfide oxidizing bacteria

C. Rinke, B. Pflugfelder, R. Lee & K. S. Nies

We were able to collect and fix sufficient samples of *Zoothamnium niveum* from the mangrove island Twin Cays for in situ analyses including scanning electron microscopy (SEM), transmission electron microscopy (TEM), and fluorescence in situ hybridization (FISH). Samples for molecular analysis (PCR, cloning and sequenzing) were collected and shock frozen in liquid nitrogen for analysis at the laboratory of the University of Vienna. Overall more than 2000 ciliates could be fixed or frozen for further analysis.

Our next goal was to compare *in situ* collections of the symbiosis with specimens growing in an artificial system. Therefore we installed and tested a flow through respirometry system in the laboratory to control water chemistry, flow rate and water temperature, and to test the optimal conditions of sulfide and oxygen concentrations to cultivate the symbioses. We were able - for the first time in thiotrophic symbiosis research - to successfully maintain a symbiosis in an artificial system over the whole generation time of the host, including asexual reproduction leading to new organisms. This breakthrough allows us to study the life cycle of host and symbionts in detail under controlled conditions and provides a valuable tool to investigate the interactions between the two partners.

The conducted research operations were mainly applied simultaneously, whereby Bettina Pflugfelder and Christian Rinke focused on the collection of the specimens and various fixations and Ray Lee and Katherine Susan Nice performed the cultivation of ciliates in the flow trough respirometry system,

The successful cultivation allows furthermore that the symbiosis could be maintained under various stress conditions within the flow through respiratory system for future analysis to observe changes of growth and reproduction rate of the host, symbiont density, symbiont specificity and macromolecular composition of the symbionts.

Maintenance and specificity in the *Zoothamnium niveum* symbiosis–facing stress

C. Rinke & D. Yost

Denise Yost

Zoothamnium niveum (Ciliophora, Oligohymenophora) from Twin Cays is obligatorily covered with a white bacterial coat, symbiotic, sulfide-oxidizing chemolithoautotrophs. Recently we were able to maintain the compound organism in our flow through respiratory system (FTRS) by controlling and altering the water chemistry over the whole generation time, including asexual reproduction of the host leading to new organisms. This breakthrough allowed us to study the life cycle of the host and the symbiont in detail under controlled conditions and provided a

valuable tool to investigate the interactions between the two partners. Furthermore, the symbioses could be exposed to stress conditions created in the FTRS and detailed analyses of changes in specificity and maintenance of the symbiotic association could be documented. Under suboptimal chemical conditions (lack or insufficient oxygen supply; lack or insufficient hydrogen sulfide supply) survival rate of the symbiosis decreases. Growth rate and physiological activity of the symbionts and symbiont density decrease; and growth rate of the host colony and swarmer production decrease. The above mentioned stress conditions also lead to increase of non-symbiotic microbial fouling.

The biology of thiotrophic symbioses: habitat finding and directional movement in protists and flatworms associated with symbiotic sulfur oxidizing bacteria

J. Ott

Motile macrozooids (swarmers) of *Zoothamnium niveum* were obtained from colonies collected on the peat wall of a tidal channel at Twin Cays. Colonies were removed from the peat and kept in petri dishes where they release swarmers within a few hours. Batches of 20 swarmers were collected and introduced in chambers made of acryl glass tubes (diameter 20 mm, length 50 mm, wall thickness 5 mm). The chambers were sealed on both ends with a dialysis membrane. The chambers were then kept in

the darkness either in oxygen saturated water (flow through system of the aquarium), in anoxic water (bubbled with nitrogen gas, and in sulfidic water (buried in a bucket containing sulfidic sand, sulfide concentration approximately 300-500 µM in the pore water). Swarmers were allowed to settle on the wall of the tube and on the gas permeable membrane, where a gradient of oxygen and sulfide was expected to form in the nitrogen and sulfide treatments. Swarmers settled randomly in both the oxygen and the nitrogen treatment, but significantly preferred to settle on the membrane or the tube area closer than 10 mm from the membrane. This pattern suggests that the swarmers use sulfide rather than low oxygen as a cue for settlement

Influence of competition, predation, mutualism, and physical environment on sponge diversity on reefs and in mangroves

J. Wulff

Differences in diversity and species composition of sponges on Twin Cays *vs*. Pelican Cays mangrove roots appear to reflect differences in the relative importance of competition and predation in determining which sponge species inhabit the roots. In the Pelicans, spongivorous fishes may help to maintain exceptionally high sponge diversity by preferentially consuming fast-growing typical mangrove species. By contrast, in Twin Cays, competition is more important in determining which species are successful. Diversity is consequently lower, as expected in a system in which competitive dominants eliminate some species. Complexity is added by differences in sponge diversity and species composition among sites at Twin Cays. Predation does not appear to be a factor at Twin Cays, and so I have begun to investigate other factors that might cause diversity and species differences among sites, especially recruitment and abiotic parameters. Could site-specific patterns of sponge species composition have arisen by chance and be maintained by limited larval dispersal? Or do physical/chemical factors that differ from site to site favor particular sets of species? To see if abiotic factors cause the lower diversity in Hidden Creek, I transplanted species that are missing in Hidden Creek from Sponge Haven to Hidden Creek. The first recruitment data demonstrate that post-recruitment processes must play roles in determining species composition on Hidden Creek roots. The next step is to measure growth rates for more of the

species, as competition appears to be mediated primarily by relative growth rates of neighboring sponges. The possibility of elimination of sponge species from a system by overgrowth begs the question: Why does overgrowth result in mutual benefit in some systems and in elimination in others?

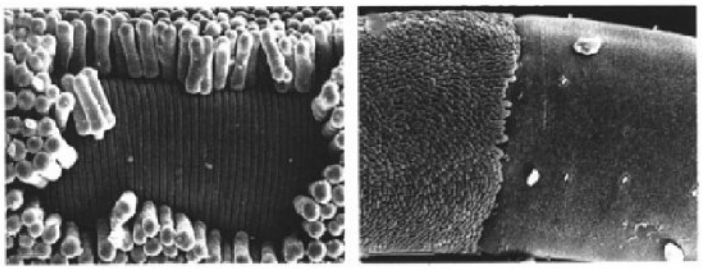
Partners adhesion mechanisms in the *Laxus oneistus* – bacteria symbiosis

S. Bulgheresi

A whole set of evidences presented in our previous proposals pointed to *Laxus oneistus* mannose-specific lectins as being the best candidates for enabling this nematode to associate with its bacterial symbionts. Our present goal is therefore the identification of these sugar-binding proteins.

During a four weeks period in March 2003 we collected approximately 10, 000 *L. oneistus* individuals from a shallow sandbar at CBC. Because we are undertaking both a homology approach and a biochemical one, part of the material was used to construct a phage cDNA library - to be screened by means of degenerate primers - and part to purify mannose- binding lectins by affinity chromatography.

The construction of the library is still under way, while three mannose-binding proteins are currently being analysed by MALDI-TOF Mass Spectrometry in order to gain protein sequence information.



The free-living nematode *Laxus oneistus* (Desmodoridae, Stilbonematinae) covered by its characteristic mono-specific bacterial coat

A taxi for symbionts: the flatworm *Paracatenula erato* as a vehicle for thiotrophic chemosynthetic bacteria

J. Ott

In April 2002, sampling of flatworms on a shallow sandbar at the north end of Carrie Bow Cay using cores , extraction by elutriation, maintenance of the worms under various conditions (seawater, seawater with sodium thiosulfate added, artificial sulfide producing systems), choice experiments in which the worms were tested whether they could distinguish between normal seawater and water containing reduced sulfur species thus being able to actively find sulfur sources for their symbiotic bacteria.

Worms were not as abundant as in the previous year, probably as a result of disturbance of the sandbar by two hurricanes which had passed CBC in the previous year. We could, however, find and photograph extremely large specimen with over 5 mm in length. These large specimens break easily and only a fraction of these injured worms survive for more than a day. The amount of animals for experiments was therefore limited and it was not possible to execute the complete program as stated in the proposal.

Choice experiments were conducted with freshly collected worms and those which had been kept in pure seawater or thiosulfate over night. Worms could choose between normal seawater and seawater containing 1mM sodium thiosulfate offered in concentric chambers connected by holes. Initial experiments showed that the worms had a "centrifugal" tendency and in absence of a gradient would end up in the outer chamber within a few hours when placed in the central chamber and would remain in the outer chamber when placed there. All experiments were therefore conducted by placing the worms in the central chamber and comparing the times it took the worms to reach the outer chamber.

There was no difference between the behavior of freshly collected worms and those that had been kept overnight, regardless of treatment.

Worms moved significantly faster from seawater in the central chamber into the outer chamber when the latter contained thiosulfate rather than normal seawater. In the reverse experiment (thiosulfate in the inner, seawater in the outer chamber) the worms moved slower than with no gradient, however the difference was not significant.

A set of experiments using Pasteur pipettes closed at one end with agar containing sodium sulfide (500µM) and filled with sea water into which the worms were introduced failed because the worms when reaching the sulfidic end stopped moving and died.

In addition, specimens of both *Paracatenula erato,* the stilbonematid *Robbea hypermnestra* and the ciliate *Zoothamnium niveum* were collected and preserved for verification of the molecular identification of their symbionts by fluorescent in-situ hybridization (FISH). The FISH procedure has already been successfully carried out in the Vienna laboratory

The coral-killing alga *Metapeyssonelia corallepida* in the reefs of Carrie Bow Cay, Belize

G. Rebitsch & A. Antonius

Epizoism is a relative new threat to coral health. Coral reefs around Carrie Bow Cay, Belize, Central America were investigated in 1972 (Antonius 1973) and resurveyed in 1997 (Antonius & Ballesteros 1998). A rather epizootic occurrence of various benthic organisms overgrowing living coral attracted the attention of the scientists. The investigations showed increasing threats of Cyanophyta, Rhodophyta, Phaeophyta (*Lobophora variegata*) and Porifera (for example *Cliona caribbea*) overgrowing living corals (Antonius & Ballesteros, 1998).

One of the most frequently encountered species during the observations in the Caribbean Sea was a member of the family Peyssonneliaceae (Antonius, 1999). It was found to be a species of *Metapeyssonnelia*, a genus described by Boudouresque et al (1976) from the Mediterranean Sea and formerly considered to be monospecific. *M.corallepida* can overgrow and kill corals (PEY-Syndrome).

Some questions about occurrence and distribution of PEY remain, such as the reasons for the patchy occurrence of the disease, its ecology, the way it overgrows corals, and related problems.

We attempted to elucidate the ecology and anatomy of *Metapeyssonnelia corallepida* and to evaluate the threat it poses to coral reefs, especially around Carrie Bow Cay, Belize, Central America.

Our results indicated that skeletal morphology of *M.complanata* altered in between the different research areas. Colonies in the lagoon were delicate and fragile. Small colonies were exposed, distributed in the seagrass. 49 colonies of *M. complanata* were countered. Not even one colony was infected with *M. corallepida*. The average coral size is 1,98, which corresponds a S-Colony.

In the fore reef as well as in the back reef *M. complanata* colonies were massive, upright and foliose. In the back reef 76 colonies were countered, therefore 55 corals were infected with *M. corallepida* (72%)(Fig.10). Average coral size in all five research areas is 3, which corresponds a M-coral. The coverage of the infected colonies with *M. corallepida* is between 0-50% and the average coverage is 12,5%. Corals with different sizes are diverse infected with the PEY-Syndrome. S-colonies were infected by 61%, M-colonies by 74%, L-colonies by 79% and XL-colonies are infected even by100% with the algae.

118 colonies of *M. complanata* were countered at the fore reef, therefore 85 (72%) corals with different grades of coverage with *M.corallepida*.

Coral size averages 3,2, which corresponds a *M-coral*. The coverage with the algae is between 0-60%, coverage averages 15,6%. Here different coral sizes are also infected with different grades of *M. corallepida*. 42% of S-colonies were infected by PEY, 52% of M-colonies, 100% of L-colonies and 89% of XL-colonies.

In conclusion, corals in the fore reef region have the largest average size and the highest average coverage (15,6%) with PEY-Syndrome; 72% of the corals in the back reef and in the for reef are infected with *M. corallepida;* corals of the lagoon are not infected at all (0%).

Differential coral mortality due to parrotfish attack: why all colonies are not equal

R. Rotjan & S. M. Lewis

Parrotfish are traditionally classified as herbivorous fishes, worldwide. Yet, while parrotfish eat mostly algae, it is also well known that some parrotfish species dedicate a small portion of their diet to live coral. This small dietary deviation for parrotfish may be a more major event for the coral, as predation scars are highly conspicuous and can range from a few bites to total colony destruction. In 2003 we investigated predation intensity and associated mortality of *Porites astreoides* coral due to parrotfish *Sparisoma viride* feeding. Using transect and census field methods, we determined that 15.9% of *P. astreoides* colonies on the Carrie Bow Cay (CBC) backreef within a 22000 ft^2 area died due to predation by *S. viride* and that 3.5% of live *P. astreoides* colonies within that area had fresh (not colonized by algae) predation scars, but with remaining live tissue. Thus, almost 20% of these corals are affected by parrotfish predation, suggesting that predation might be a selective pressure for coral response. We assessed coral response by sampling colonies with and without predation scars for differences in nutritional quality and defensive characteristics. We also confirmed previously recorded CBC data from Littler and Littler showing that predation intensity is highest within 10 m of the reef crest, which anecdotally corresponds to the densest aggregation of *S. viride* initial and terminal phase individuals. The high level of predation impact, coupled with the proximity of predation intensity to the reef crest, surprisingly does not correlate with size of predation scars. Of the corals with predation scars, there is large variation in the predation area per colony.

We began to explore hypotheses for why some cor-

als are more susceptible to predation than others. We investigated nutritional quality and defensive characteristics of colonies, as well as correlation with their associated biota. Although these data are still being analyzed in the lab, we found that in many cases (~60%), parrotfish are targeting corals with skeletal holes from associated macroborers, such as endolithic barnacles or serpulid polychaete worms. Barnacle distribution does not show a significant correlation with predation patterns, whereas polychaete distribution shows a highly significant correlation. Further, live polychaete densities increase further from the reef crest, where predation is less intense. Thus, it appears that associated coral macroborers directly influence predation choices by *S. viride*.

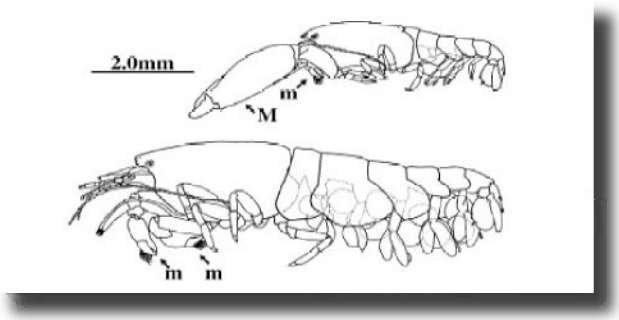
In 2004 we examined three important unresolved aspects of coral predation: whether parrotfish coral predators are choosing specific coral prey colonies based on nutritional quality, lowered defenses, or associated biota; whether corals change their nutritional quality or defensive characters in response to parrotfish or butterflyfish predation; and whether various scleractinian coral species can survive predation bouts of varying intensity. We addressed these questions using a combination of observational and experimental manipulations that are now being evalued.

Sara Lewis' experiment and Randi Rotjan in the field.

Cooperation, conflict, and communication among eusocial shrimps (*Synalpheus*)

E. Duffy

Over the last decade or so, our studies of sponge-dwelling snapping shrimps (genus *Synalpheus*) at Carrie Bow Cay have clarified the practical taxonomy, phylogenetic relationships, host associations, ecology, and social behavior of these intriguing crustaceans. The advances in taxonomy and classification of *Synalpheus* paved the way for developing a model system for comparative analysis of several general problems in evolutionary ecology. Having developed effective methods for maintaining and observing colonies of individually marked shrimps in living sponges in the lab, our research centered on detailed behavioral observations for testing hypotheses on the evolution of eusociality in these animals. These observations focussed on conflict among colony members, conflict between residents and intruders to the colony, cooperative defense against intruders, and the role of communication via "mass snapping" in mediating cooperative defense.



Morphological transformation of the queen in *Synalpheus filidigitus*. Top: a smaller female (carapace length = 1.81 mm) from a colony of four individuals; this specimen carried a single egg, and a normally developed major chela (M), or snapping claw. Bottom: the largest female found in our collection (carapace length = 3.13 mm), from a colony of 121 individuals. This specimen carried 29 eggs and bore two minor chelae (m). Note the enlarged abdomen, and replacement of the major chela by a second minor-type chela (m) in the larger queen. Both specimens drawn to same scale. (Duffy, 2003)

Processes across Ecosystems

Measurement, recording, and Web-based data distribution of environmental parameters

T. Opishinski, K. Rützler & M. Carpenter

A new computer with Internet connection was installed at Dangriga which receives radio-transmitted data from the Carrie Bow environmental monitoring station and transmits them to the Smithsonian at Washington, DC. Weather conditions (wind speed/direction, rainfall rate/accumulation, air temperature, relative humidity, atmospheric pressure and solar radiation) and the physical properties of the seawater (water level, turbidity, dissolved oxygen, water temperature, pH, conductivity/salinity) are measured automatically, every 15 minutes, by the system. All accumulated datasets were periodically uploaded to the Web. The ongoing efforts to provide reliable meteorological and oceanographic data and to improve the accessibility to the data have led to a number of successes. First, there was a dramatic increase in the number of researchers, environmental managers and government agencies using the data to complement their work. Second, the data are accessed by the National Weather Service of Belize and weather conditions for Carrie Bow Cay are provided in the daily forecast. And third,

the Belize Coastal Zone Management used the wind data to justify natural damage to a building structure in an insurance claim. Environmental conditions are now posted to the Internet in real time. Immediate access allows monitoring the system's performance without visiting the site, and improving and prioritizing maintenance. Try it at HTUhttp://web8.si.edu/belizeUTH and select Environmental Data Archives from the table of contents.

CARICOMP Program at Carrie Bow Cay

K. Koltes & J. Tschirky

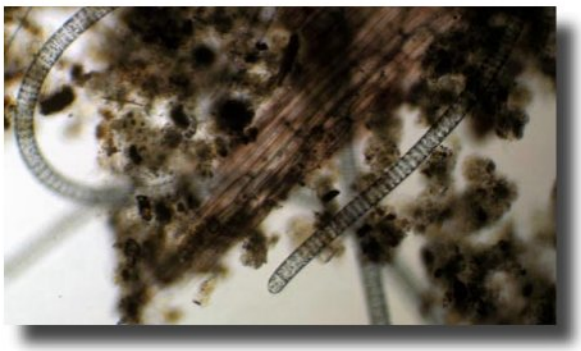
The Caribbean Coastal Marine Productivity (CARICOMP) Program is a regional scientific effort to study land-sea interaction processes, to monitor change, and to provide scientific information for management of the coastal resources in the wider Caribbean region. CARICOMP provides long-term, standardized, synoptic monitoring data critical to understanding the productivity, structure, and function of the three important coastal ecosystems in the region: coral reefs, mangroves, and seagrasses. Established in 1990, the network has grown to include over 30 sites with varying degrees of participation. Data collection at Carrie Bow Cay began in 1994. The 10+ year record of oceanographic measurements at Carrie Bow Cay now represents the longest continuous dataset, particularly of water temperatures, on the Mesoamerican Barrier Reef. Several significant weather events have been captured in the meteorological and oceanographic records, including the El Niño of 1998 and the passage of a number of hurricanes, as well as anomalies associated with more typical weather events. The data have been used to groundtruth remotely-sensed sea surface temperatures and to validate meteorological data generated by the fully-automated weather station.

Biological monitoring has documented the decline of reefs and other habitats that have suffered major natural impacts in recent years: high sea temperatures (with bleaching) in 1995 and 1998, and hurricanes in 1998 (Mitch), 2000 (Keith) and 2001 (Iris and Michelle) which, in addition to high wave action, brought massive freshwater runoff with high turbidity. These events contributed to a significant loss of coral cover in the CARICOMP transects, from about 19% in 1994 to about 7% in 2002, and a nearly 30% drop in rugosity over the same period. All scleractinian coral species have declined in abundance, with the possible exception of *Colpophyllia natans*. Among the gorgonians, populations of sea rods are stable, feathers have decreased, while fans are recovering (from aspergillosis or hurricane loss). No large changes were detected at the seagrass sites, except for slight summer/winter variations.

Microbial mats: important sources of nitrogen and carbon in mangrove ecosystems

S. Joye & R. Lee

Microbial mats are a common but poorly studied component of the Twin Cays ecosystem. Microbial mats support high rates of primary production and are sites of rapid elemental cycling. A diverse array of microbial mat communities, dominated by filamentous or heterocystous cyanobacteria, purple sulfur bacteria, and heterotrophic bacteria were observed on Twin Cays. We quantified daily rates of carbon fixation, nitrogen fixation and denitrification using a variety of techniques, including rate assays with specific metabolic inhibitors, microelectrodes, and stable isotope tracers. Sediment chlorophyll concentrations and pore water nutrient concentrations illustrated high photosynthetic biomass in surface sediments and reduced conditions at depth. In the presence of added nitrate, denitrification rates exceeded nitrogen fixation rates by orders of magnitude. However, at in situ nitrate concentrations, nitrogen fixation dominated the diel N cycle. Primary production rates were high (up to 45 mmol $C/m_2/d$ and 35 mmol $O_2/m_2/h$ gross) across different mat types. Microbial mats account for a significant amount of primary production and N input via nitrogen fixation, and may serve as an important component of the food web.



Tidal influence on the growth of a mangrove forest, Twin Cays West Island

D. W. Urish, R. Wright, W. Rodriguez & I. C. Feller

The primary goal of this ongoing study at Twin Cays' West Island is to determine how natural and anthropogenic hydrologic conditions influence changes in flow channels and vegetation growth in an inter-tidal tropical mangrove island. Approximately ten years ago the natural mangrove forest was greatly altered by the cutting of survey swaths in many locations across the island. Hydrologic studies done over the past year in comparison with studies done ten years ago indicate that cutting has caused significant changes on the inter-tidal movements within the mangrove forest. In particular, a much more dense mangrove growth has taken place along the new flow channels created by the survey swaths. It appears also that channels boundaries have changed, with particular note that the more vigorous growth appears to have encouraged sediment deposition. Detailed topography/bathymetry mapping and a dye flow study to examine flow patterns were accomplished. This establishes a base line with which to measure changes. Over the past year a geodatabase was developed for the island, which includes dye-flow runs, topographic/bathymetric contours, monitoring stations, island boundaries, and registration and rectification of aerial photography taken in 1986 and 2003. Key island points were located with the Global Positioning System (GPS) and geo-referenced into the maps. The on-going hydrologic work is coordinated closely with the Mangrove Biocomplexity Project. In collaboration with this work, 12 automated water-level and water-temperature monitoring stations were installed in January 2003 at key locations on West Island. These stations, in conjunction with the automated climatological data collection system at Carrie Bow Cay, will give a continuous record of the island's hydrologic system. The identification of categories of the mangrove cover by growth and species characteristics on Twin Cays has just been accomplished.

Candy Feller downloading water level data logger.

Trophic interactions within the planktonic food web in mangrove channels of Twin Cays

E. J. Buskey

The tidal channels of mangrove islands such as Twin Cays, Belize support a productive and diverse microplankton assemblage. In turn, this microplankton community supports large populations of endemic mesozooplankton species that form dense aggregations in the prop-root environment along the margins of these channels. The growth rate of the phytoplankton community and the grazing rate of the heterotrophic microzooplankton community were measured using the seawater dilution method. In separate experiments, the grazing rate of the swarm-forming copepod Dioithona oculata on natural microplankton assemblages was measured during both 24-hour and 12-hour (day/night) incubations. Chlorophyll concentrations in the natural plankton assemblages used in these experiments ranged ca. 1–11 µg Chl a per liter. Dinoflagellate populations typically ranged ca. 17–50 cells per ml, with heterotrophic dinoflagellates generally exceeding autotrophic forms in abundance. Ciliates were the second most abundant form of heterotrophic microzooplankton, with populations ranging from 1–15 cells per ml. Results of the dilution experiments indicate that during the study period, phytoplankton growth exceeded microzooplankton grazing in all experiments. Grazing experiments with *Dioithona oculata* carried out over a 24-hour period indicated that copepod ingestion rates were highest on ciliates and autotrophic dinoflagellates, and that copepod populations are capable of grazing a large fraction of the protozoan population each day. These experiments suggest that protozoan populations in mangrove channels are under "top-down" control by copepod grazing, rather than being limited from the "bottom-up" by food availability. The 12 hour incubation experiments indicated that there were no consistent diurnal changes in feeding rates. Since these copepods form high density swarms during the day, competition for food within swarms must be intense.

Patterns of nutrient limitation in three Caribbean mangrove ecosystems

I. C. Feller, C. Lovelock, D. Whigham & K. L. McKee

Nutrient over-enrichment of the coastal zone is recognized as one of the major threats to marine environments worldwide. However, little is known about what types of changes might be expected to occur in response to the process of eutrophication of mangrove wetlands, which are often immediately next to oligotrophic, but highly diverse, marine ecosystems. The objectives of this study are to determine

the patterns of nutrient limitation across mangrove forests in the Caribbean and the effects of nutrient availability on plant growth, within-plant nutrient conservation mechanisms, litter turnover rates, soil chemistry, and primary consumption. We proposed to test the following hypotheses: Increased availability of a limiting nutrient will change nutrient conservation patterns in mangrove forests (mangrove ecosystems will become more "leaky" as a result of eutrophication of the coastal zone); nutrient cycling patterns are open in early stages of mangrove succession and closed with ecosystem development (early successional mangrove forests will be more "leaky" than the mature, undisturbed stands); and following disturbance, regenerating forests tightly conserve nutrients (successional forests retain a maximum amount of their nutrients and have potential for greater net primary productivity than mature forests). We are comparing plant growth, nutrient cycling processes, and animal-plant interactions in response to nutrient enrichment in mangrove forests at Twin Cays, Indian River Lagoon, and Bocas del Toro. At each site, we use fertilization experiments set up along transects subdivided into zones (i.e., fringe, transition, dwarf, landward), based on a tree-height gradient. Identical biological, physical, and chemical measurements were made at all sites, including forest composition and structure and soil chemistry (e.g., pH, redox potentials, salinity, sulfide levels, and nutrient concentration). Data from these experiments will be compared to each other and to similar on-going fertilization experiments in mangrove forests in the Indo-West Pacific. These experiments are fundamental to understanding the global impact of eutrophication on mangrove systems.

Impact of nutrient availability on mangrove forest structure and tree function

C. E. Lovelock, M. C. Ball & I. C. Feller

Structural heterogeneity of mangrove forests is high, and results in a wide diversity of habitats for flora and fauna. We assessed forest structure and plant function over the variation in tree height occurring in the mangroves of Twin Cays, Belize, and investigated how changes in nutrient availability, imposed by a long-term fertilization experiment, influenced forest structure and plant function. Forest structure, measured as leaf area index (LAI, m^2 leaf area per m^2 ground area), was greatest in tall fringing forest and lowest in dwarf stands. Fertilization of dwarf stands with phosphorus (P) for six years resulted in similar LAI to that observed in tall fringing forests. The change from the dwarf habit, to trees which resemble fringe forest when fertilized with P, was associated with a greater capacity to conduct water through stems, larger xylem vessels, and higher photosynthetic rates. Increases in the capacity of stems to conduct water (larger xylem vessel diameters) are necessary requirements for attaining high levels of transpiration and plant productivity. We predict that enrichment of mangroves forests with P will increase forest productivity, but reduce the structural diversity of heterogeneous mangrove forests.

Search for annamox activity in oligotrophic mangrove soil and sediment

P. Megonigal

This project is an extension of research by the I.C. Feller Biocomplexity group who determined that that the decomposition of a cellulose standard material (cotton strip) is phosphorus-limited in all plant communities at Twin Cays, which suggests that the microbial community is uniformly P-limited. This result contrasts with the observation that trees in the fringe areas are nitrogen-limited while dwarf trees are P-limited. Based on these observations of differential nutrient limitation for plants and microbes, we measured soil microbial biomass in Feller's Twin Cays fertilization transects to determine the effects of different nutrient additions on soil microbial communities. We hypothesized that microbial biomass will increase under P addition, but not under N addition, relative to control conditions.

Microbial biomass in coarse (<1 mm) and fine (<250 μm) soil was determined by the chloroform fumigation-incubation procedure. In the coarse fraction, there were no significant differences in microbial biomass between soils from different fertilization treatments or vegetation zones. In the fine fraction, there was no difference between soils from the two vegetation zones. However, nitrogen fertilization resulted in a significant decrease in microbial biomass compared to both the P or control treatments. Future fieldwork will be designed to shed light on the apparent inconsistencies between the earlier and the present studies.

Linking function and structure across environmental gradients in three Caribbean mangrove forests

C. E. Lovelock, I. C. Feller & M. C. Ball

The growth of mangrove trees in response to gradients in nutrient availability varies both among sites and over environments within sites. This study investigated the underlying physiological processes that result in the observed complex patterns of nutrient limitations in mangrove tree growth across three of the Marine Science Network (MSN) sites. We used a combination of field and laboratory tech-

niques to examine how nutrient availability interacts with high levels of salinity, inundation and low soil redox potentials to generate observed patterns in forest structure. Our aim is to provide a predictive understanding of the response of different tree species to concurrent variations in nutrient availability, salinity, and inundation by understanding the underlying physiological processes limiting growth. Understanding these interactions allows us to predict changes in mangrove forest structure along tidally maintained gradients in salinity and inundation, and with cultural eutrophication. Our work is ongoing and focused at Bocas del Toro, Panama, Twin Cays, Belize, and Ft. Pierce, Florida.

Mangrove channel network model: assessment of prop root epibiont and bottom epifaunal biomass in the Lair and Main channels of Twin Cays

U. M. Scharler

Extensive populations of particle feeders inhabit the prop root habitat of mangrove channels which occur between mangrove islands in the lagoon behind the Belize barrier reef. Food sources for the particle feeders include detritus, phytoplankton, bacteria and microzooplankton. In order to study the contribution of the various food sources to the food web, two channel environments at Twin Cays were analyzed. A food web model is being built based on estimates for biomass of the major species, and estimates of their rates of respiration, ingestion, and production, referenced to area and time. Quantification of the biomass of prop root organisms and the channel floor epifauna was initiated and expressed as g dry weight per m^2 channel floor.

Mangrove Biocomplexity

I. C. Feller & colleagues

In Year Four of the biocomplexity project, we compared experiments at Twin Cays, Belize, Bocas del Toro, Panama, and Ft. Pierce, Florida (Smithsonian Marine Science Network). Although growth of dwarf mangrove forests at Twin Cays and Bocas del Toro was P-limited, N enrichment had a significant effect on patterns of growth and biomass distribution. These results contrast with an experiment in the Indian River Lagoon, Ft. Pierce, where growth was N-limited. Although results differed by site and species, addition of either N or P altered the allocation of biomass to leaves versus stems. At all sites, the highest ratio of leaf area to total biomass occurred in the control trees, which suggests that under nutrient limiting conditions resource allocation to leaf area was maximized. Nutrient enrichment altered patterns of nutrient uptake and internal dynamics. Comparison of P- versus N-limited sites also suggested that salt tolerance in some mangrove species varies depending on nutrient availability and the nature of nutrient limitation in the environment.

K. McKee compared below-ground production of mangroves at Twin Cays with sites in Panama (Bocas del Toro), Australia (Port Douglas, Hinchinbrook, and Townsville), and New Zealand (Waikapoa). Mangroves growing on peat had higher rates of below-ground production than those growing on mineral substrates. Below-ground production varied with hydrology and tree physiography, increasing from dwarf to riverine stands. Root production by mangroves growing on peat was P-limited, but those on mineral soil did not respond to nutrient addition. Below-ground response to nutrients did not parallel above-ground response. Nutrient limitation of root production was secondary to flooding stress. Fine root production increased P *vs.* N acquisition.

S. Joye, R. Lee, & B. Porubsky measured nutrient cycling rates and processes at Twin Cays. Every dwarf mangrove sediment examined had a diverse array of laminated microbial mat organisms including diatoms, coccoidal and filamentous cyanobacteria, and purple and green sulfur bacteria from mm to cm in depth. Their surveys found that primary photosynthetic organisms are present and active in these mats. Diel patterns of nitrogen fixation and denitrification were observed in all forest types, with some sites exhibiting day-time maxima and other sites exhibiting night-time maxima. Primary production rates and photosynthetic biomass are variable across Twin Cays, but relatively constant throughout the year. Rates of nitrogen fixation and denitrification were variable among sites and seasons. The patterns of N input in the dwarf zones via activity in microbial mats may contribute to the larger, ecosystem scale patterns of nutrient limitation observed in trees.

M. Fogel, with *S. MacDonald & V. Brenneis* collected and analyzed samples from Twin Cays for isotopic and elemental composition to understand trophic connections in the mangrove and to assist in the development of a network-analysis model. They found that in dwarf zones, if microbial and algal floc was extensive, the micro- and meiofauna were almost totally dependent on this food source for both C and N. In transition zones, often the driest, mangrove C and N were used almost exclusively by small invertebrates. The diets of animals living in fringe zones depended upon the proximity to seagrass beds or open ocean waters.

M. Jacobson's laboratory examined the biogeochemical cycling of nutrients (nitrogen and phosphorus), carbon, sulfur and oxygen at Twin Cays. They measured pore water respiration calibrated with total CO_2 analysis, nitrate reduction, and other geochemical measures to describe

the response of sediment microbial processes to tree height and fertilization. These values are being compared with enzyme ratio measures to determine the degree of limitation associated with zone and fertilization.

M. Frischer examined microbial activity and bacterial biomass, activity, and community structure. He found that bacterial biomass was not significantly affected by location, sediment depth, or fertilization treatment during the dry season. However, bacterial biomass was lower during the dry season compared to wet season. Microbial activity was highest in the fringe zone at all depths. Respiration rates from the transition zone were significantly enhanced by N fertilization. However, P fertilization generally had little effect except in surface sediments. Fertilization had little effect on respiration rates of microbes associated with decomposing leaves. Respiration rates associated with wood was approximately half that of leaves and six times the rate associated with peat samples. The species richness of eubacterial communities (determined by using molecular techniques) was not affected by fertilization. However, the similarity between bacterial communities decreased proportionally with geographic separation in both horizontal (tree zone) and vertical (depth) directions. Fungi appear to be the initial colonizers and are replaced by bacteria as leaf decomposers. Microbial diversity and community structure indicated that mangrove microbial communities were most directly influenced by physical/chemical factors and indirectly influenced by the growth of the dominant macrophyte, mangrove trees.

C. Shearer & J. P. Schmit focused on microbial community structure and fungi in sediment. They found that species richness and abundance of fungi in sediments were influenced by their location along the tree-height gradient. Fungal diversity in the fringe was greater than in the transition or dwarf zones, but there were no differences between the transition and dwarf zones. There was no significant difference in fungal diversity in sediments related to nutrient treatment or depth, although there is a trend for higher fungal species in the N-fertilized transects. In leaves, fungi were most diverse early in the decay process. As decay continued, fungal diversity declined but bacterial abundance increased, indicating a shift in the decomposer community. In wood, fungi diversity was strongly influenced by nutrient addition.

J.Cheeseman examined plant physiological responses and focused on gas exchange and chlorophyll fluorescence to provide fundamental data on mangrove physiological responses to differences in nutrient availability across environmental gradients. He found that regardless of their location within the Twin Cays system, *Rhizophora mangle* leaves contain approximately 20% of their dry weight as proanthocyanidins (condensed tannins) and another 20% as flavonoids. During senescence, flavanol glycosides decreased in abundance. These changes may be important in order to prevent the build-up of undigestible litter and to speed up turnover of nutrients.

C. Lovelock & M. Ball established that hydraulic conductance and architecture differed across the tree height gradient at Twin Cays, and that fertilization with N and P affected the hydraulic conductance of plants, with P limited dwarf trees showing a doubling of conductance when fertilized, compared to control trees. Hydraulic architecture was also sensitive to fertilization. Responses of hydraulic conductance and architecture closely correlate with growth enhancements and lead to the hypothesis that nutrient limitations are in some way limiting water transport in these P-limited mangrove forests. Leaf water potentials, measured with a Wescor System, did not reveal differences among nutrient treatments, but largely followed salinity gradients both within and among sites.

I. Feller, with *A. Chamberlain & S. McKeon*, characterized communities of primary consumers and measured the effects of tissue quality on herbivory. Damage by leaf chewers varied by zone but not by nutrient treatment. The lowest levels occurred in the dwarf trees and the highest in the fringe. Herbivory also varied by functional feeding groups. *Aratus pisonii*, the mangrove tree crab, was the dominant leaf chewer. Leaf damage varied by zone but not by nutrient treatment. *Ecdytolopha sp.*, a specialist borer in apical buds of *R. mangle*, caused a loss of yield that also varied among zones but not nutrient treatment levels. In contrast, herbivory by *Marmara sp.*, a microlepidopteran tissue miner, was altered by nutrient treatment but not by zone.

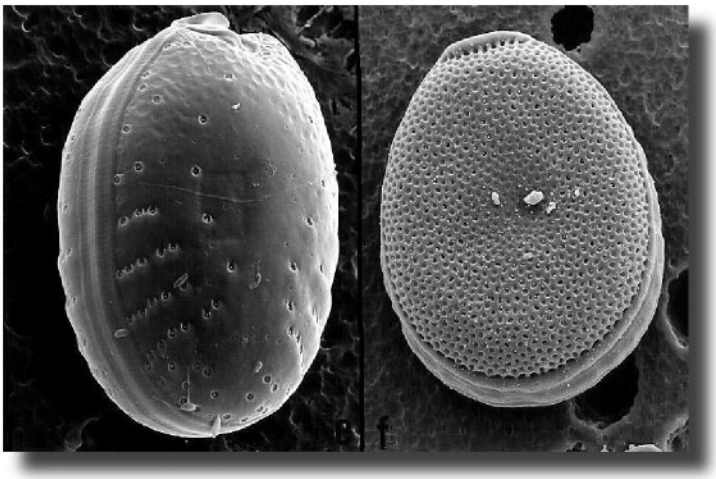
K. McKee & T. Martinez studied rates and patterns of elevation change, vertical accretion, subsidence, peat composition, and stratigraphy at Twin Cays. Surface elevation change rates varied between zones. Addition of N to dwarf trees accelerated elevation loss, whereas addition of P to dwarf trees altered elevation change pattern from loss to a gain. Nutrient addition did not alter root or peat decomposition rates, but fine roots were more refractory than coarse roots. Root mortality rates were negatively correlated with elevation change. Together, root production and mortality explained 90% of the variation in surface elevation change at Twin Cays. These results demonstrate that at Twin Cays, the more productive mangrove stands are keeping pace with sea-level rise, but areas with sparse or no mangroves are collapsing. Addition of nutrients will have complex effects on ability of this mangrove system to accommodate sea-level rise.

R. Ulanowicz & U. Scharler integrated field observations and used network analysis to model the trophic interrelationships among the major components of the mangrove community at Twin Cays. During Year 3, they related the demands of consumers to the supplies of prey items through a program that estimates the dietary proportions according to biomass, trophic topology, and physiological demands. In Year Four, they created a new algorithm that distributed flow among the availabilities and requirements of the species on a

uniform basis ("liquid-filling" routine). They concluded that there was no statistical difference between either of these methods of estimation and estimated networks. An algorithm to automatically update the magnitudes of the least-inference estimates according to the observed isotopic ratios of respective predators and prey is now operational and awaiting application on the forthcoming network estimates and accumulated isotopic ratios.

Effect of excessive dissolved nutrients (eutrophication) on phytoplankton and benthic microalgal blooms over near-reef mangrove and seagrass communities

M. Faust



SEM photographs of benthic sand-dwelling species from South Cay. *Prorocentrum rathymum* (left) and *P. hoffmannianum*

Twin Cays, near the center of the Belizean barrier reef complex, have a rich dinoflagellate and microalgal population. Benthic dinoflagellates are the most abundant group of microalgae in this detritus-driven mangrove ecosystem. I have determined the population structure and ecology of 54 species in floating detritus, and plankton at three sites: The Lair, Boston Bay and Main Channel. Here, the microscopic food web organisms are the primary producers and the meiofauna primary consumers within the system. I also found numerous potential ciguatoxigenic organisms as part of the mangrove microscopic food web that been implicated in tropical fish-born human diseases. My studies illustrate that mangroves are ideal habitats for the development of benthic assemblages of harmful and red-tide forming dinoflagellates, not recognized before, and possible sites of origin for ciguatera outbreaks world-wide. The effects of household waste on the biodiversity of the organisms in protected embayments are illustrated the first time. While dinoflagellates have little economic value, indirectly they may signal change in the health of an undisturbed aquatic ecosystem. The effects may lag for many years behind their initial causes, a challenge in understanding change in ecosystems.

A nutrient oasis in an oligotrophic sea: a model of natural eutrophication

R. J. Chróst, M. A. Faust & P. A. Tester

The principal goal of the fieldwork was to better understand how natural eutrophication alters nutrient and carbon flows in a tropical ecosystem and how those changes alter the structure of the food web and the habitat for ciguatoxic dinoflagellates. For this purpose, we investigated the eutrophic lagoon at Douglas Cay and compared it to the Lair at Twin Cays as control. These two systems provided data on physical-biological coupling, phytoplankton biomass, productivity, and nutrient dynamics that allow prediction of consequences of nutrient enrichment of oligotrophic waters. We found that in "floating muck" (a microbial mat), nutrients and carbon are being similarly recycled in both, the eutrophic Douglas Cay and the control-system Lair. However, the presence of a larger nutrient pool at Douglas Cay results in increased aquatic productivity via the flow of carbon through the bacteria and microscopic eukariotes in the food web. The shifts in nutrients and carbon flow result in different microbial community structure, growth of phytoplankton populations, and food composition for heterotrophs. We also continued to isolate toxic, ciguatera-causing dinoflagellates to provide culture material for development of a molecular probe.

Communities and environment of aquatic habitats at Twin Cays

K. Rützler & C. Díaz

Over the past 20 years, the rich fauna and flora of Twin Cays off southern Belize had been explored by CCRE collaborators and compared with coral and turtle-grass habitats of the surrounding Belize lagoon and nearby mangroves and reefs. Among the many subtidal habitats found in these cays, some 20 stations were visited to re-examine composition of plankton and benthos, topography of sediment and peat bottoms, and parameters that determine distribution of organisms, particularly the sessile benthos. The principal objective of this survey was to determine changes over time and to establish a baseline to be published with collaborators Ilka Feller, Ivan Goodbody, and Ian Macintyre. The results of this work are in press in a dedicated volume of Atoll Research Bulletin

Recent Publications

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