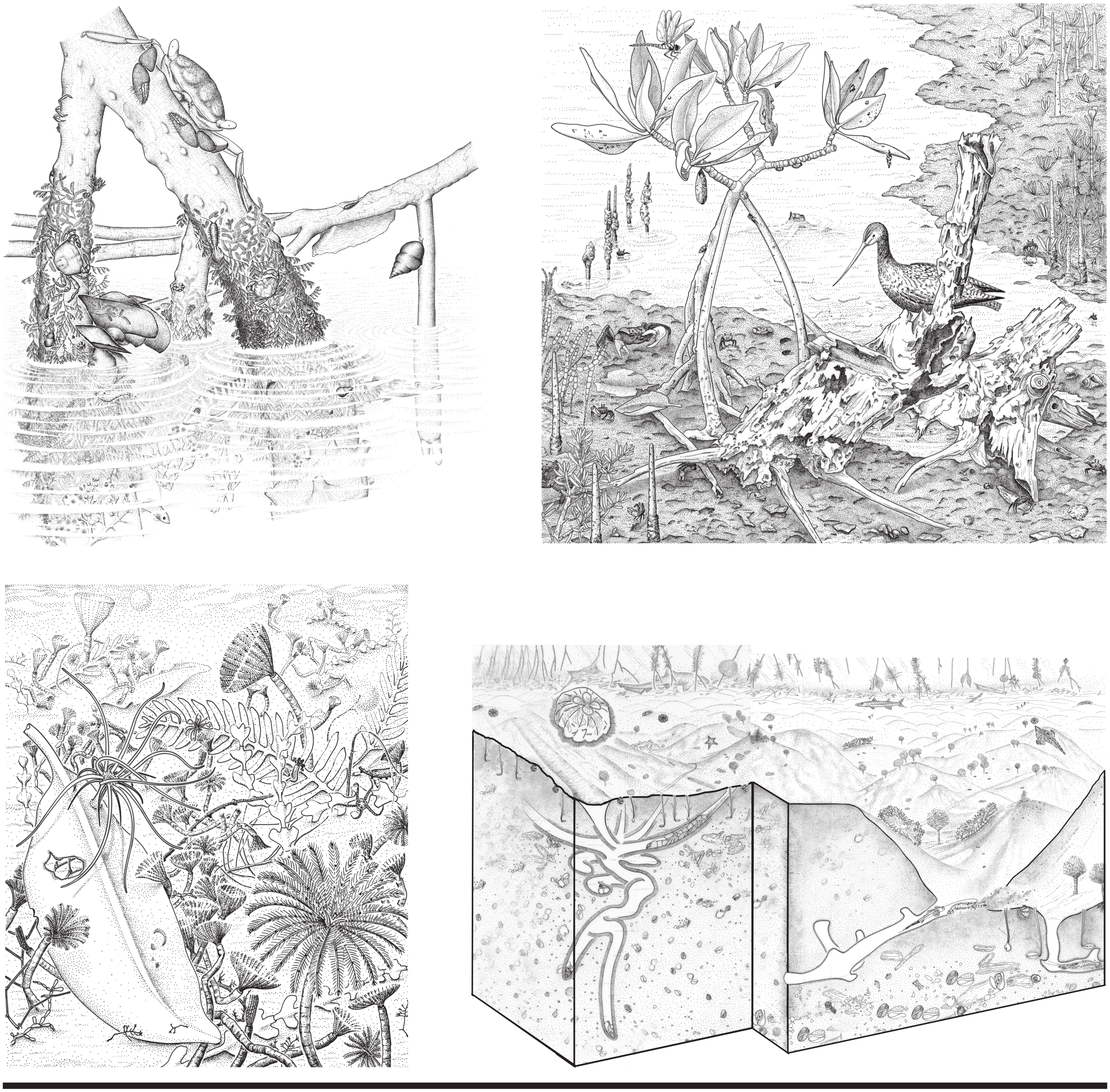


FIGURE 8. Examples of illustrations of mangrove swamp communities. Clockwise, from top left: characteristic intertidal red algal cover (*Bostrychietum*) on red-mangrove prop root, with mangrove oyster, mangrove crab, and periwinkle; tidal mudflat showing developed red-mangrove seedlings, black-mangrove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

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

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

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

In 1988 we held a workshop at the Calvert Marine Museum in Solomons, Maryland, to review the accomplishments and gaps in our research on the Twin Cays mangrove ecosystem. Close to 40 program participants summarized the progress of their work on internal structure, development over time, sedimentology, meteorology, hydrology, vegetation, productivity, nutrient cycling, temperature-salinity tolerance, and biodiversity of fauna and flora from microbes to amphibious fishes. The most obvious deficiencies were in oceanography, a number of important organism groups such as mollusks and fishes, and marine benthic and terrestrial ecology. One of the highlights was a report on a complementary team study of the Holocene geological history, peat composition, and terrestrial and marine vegetation of Tobacco Range, another large mangrove island about 3.5 km north of Twin Cays (Littler et al., 1995). This atoll-like range drew CCRE's attention when a large area of fractured and slumped fossil peat was discovered off its west shore.

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

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

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

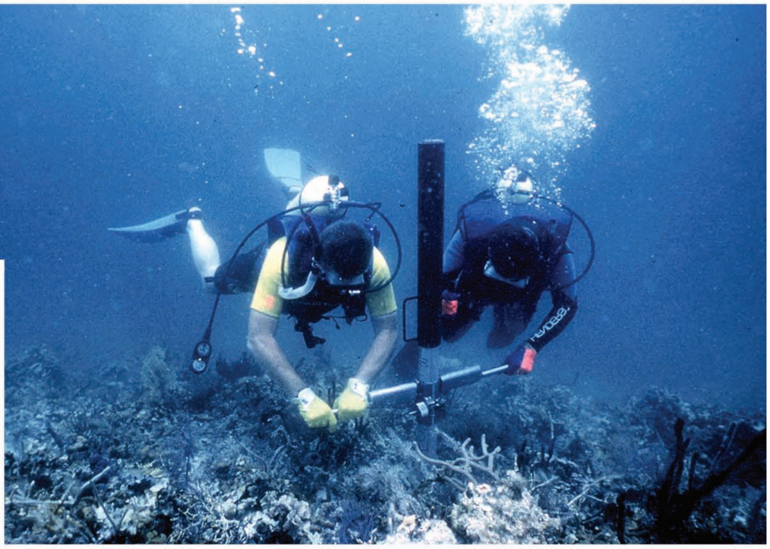
Side-tracked by the discovery of the Pelican Cays biodiversity hotspot (see the next section), the impact of a hurricane, and coral bleaching events, we were unable to convene another Twin Cays symposium until 2003. Meeting at the Smithsonian Marine Station in Fort Pierce, Florida, we found our mangrove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

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

PELICAN CAYS, BIODIVERSITY HOTSPOT

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

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



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

We were so impressed by the unusual diversity and ecological complexity of the Pelican Cays ecosystem that we asked the Belize Coastal Zone Management and Fisheries units to include the region in the South Water Cay MPA. Tony Rath (NaturaLight, Dangriga) and Jimmie Smith (Islands from the Sky, Houston, Texas) helped with aerial photography, Molly Ryan with mapping, and our research team along with outside collaborators addressed the new scientific perspectives (Macintyre and Rützler, 2000). Macintyre and his team, and Karen McKee (U.S. Geological Survey, Lafayette, Louisiana), spearheaded the study of geological underpinnings and vegetation history, Dan Urish (University of Rhode Island) and Tracy Villareal (University of Texas at Austin) the hydrography of the ponds, Thomas Shyka (National Oceanographic and Atmospheric Agency, Silver Spring, Maryland) the nutrient cycle and water flow patterns in the ponds, Steve Morton (Bigelow Laboratory, West Boothbay Harbor, Maine) and Maria Faust the phytoplankton, Mark and Diane Littler the marine algae and seagrasses, Susan Richardson (then at Yale University, New Haven, Connecticut) the epiphytic foraminiferans, Rützler and colleagues the sponges, Janie Wulff (then at Middlebury College, Vermont) sponge predation, Wolfgang Sterrer the gnathostomulids, Gordon Hendler (Natural History Museum, Los Angeles, California) the echinoderms, and Ivan Goodbody the tunicates. At the height of these investigations, we were able to introduce the spectacular coral communities of the cays to participants of the 8th International Coral Reef Symposium, along with other points of interests, such as community changes in the reef zones of the Carrie Bow reference transect over the past two decades (Macintyre and Aronson, 1997). The fishes of the Pelicans were investigated (just after the edited volume was published) by a team of ichthyologists led by our Museum's James Tyler and included former American Museum of Natural History curator (now retired) C. Lavett Smith (Smith et al., 2003). More recently, important suspension feeders that had not been covered by the earlier surveys, the bryozoans, were studied by our long-time collaborator Judith Winston of the Virginia Museum of Natural History (Winston, 2007).

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

A Memorable Year, 1997

In CCRE's 35-year history, 1997 stands out for its remarkable highs—and lows. Scientifically, many significant field projects were launched or carried to completion: investigations of coral bleaching, a new and unsettling phenomenon on the barrier reef (Aronson et al., 2000); ecophysiological analysis of periodic crustacean swarming among red-mangrove stilt roots (Buskey, 1998); a pioneering initiative to match poorly known fish larvae to the adults of the species, first by morphological means after rearing in the laboratory, later by DNA analyses (Baldwin and Smith, 2003); and a workshop on Caribbean sponge systematics with experts from five nations that led to a better understanding of the barrier-reef and mangrove poriferan fauna (Rützler et al., 2000). This was also the International Year of the Reef, and to celebrate the occasion we made every effort to share our enthusiasm for this unique environment with students and the general public through numerous lectures, poster sessions, and demonstrations, on site in Belize and back home at the National Museum of Natural History. To add to the festivities, our Carrie Bow field station, the logistical base and catalyst of our program, had reached the respectable age of 25 (1972–1997).

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

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

RESURGENCE AND BIOCOMPLEXITY

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

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

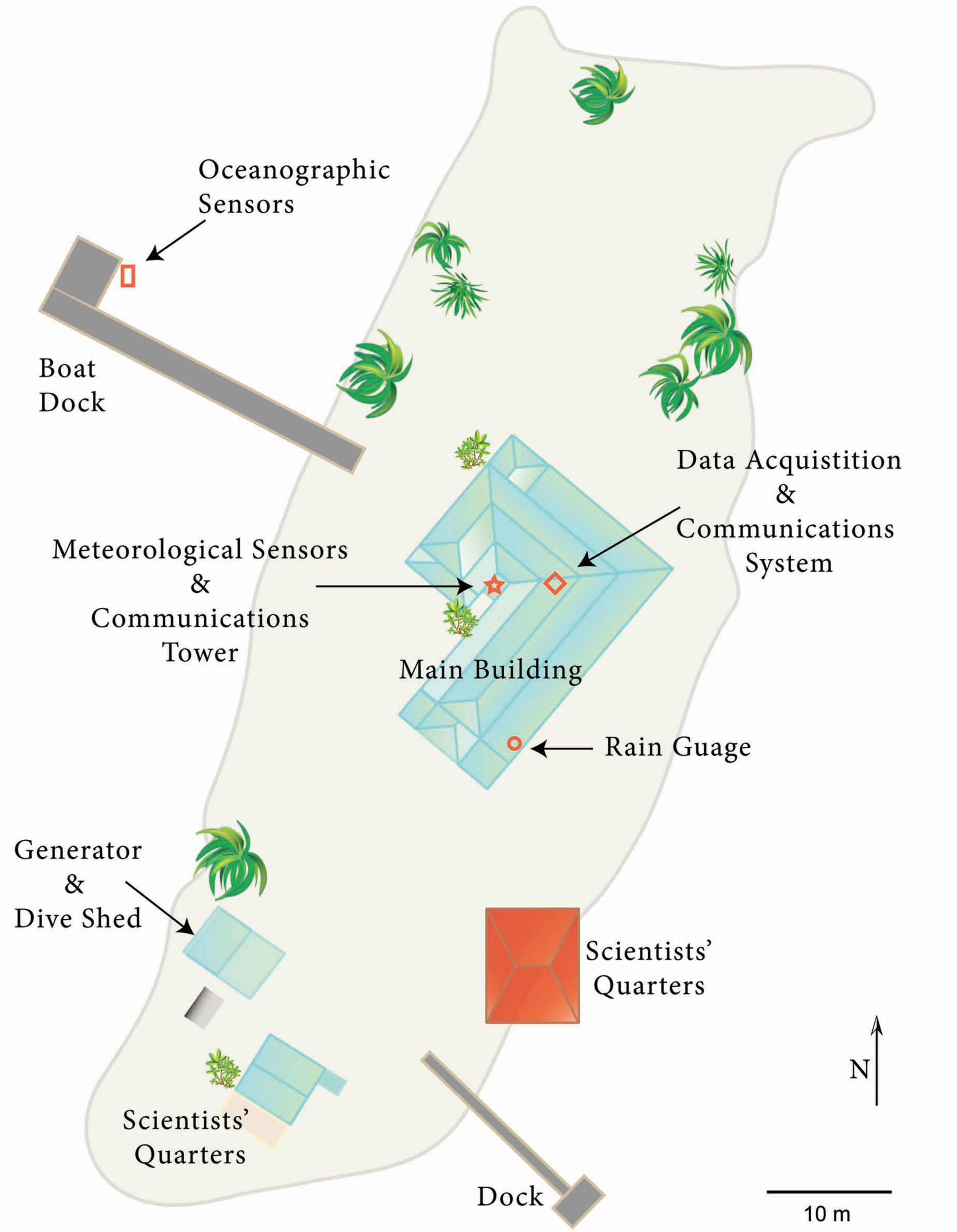


FIGURE 11. Map of Carrie Bow Cay (in 2000) identifying principal structures (number of coconut palms reduced for clarity).

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

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

CONCLUSION AND OUTLOOK

In 1972 a group of enthusiastic, like-minded young scientists embarked on a comprehensive, long-term field investigation of unprecedented dimensions for the Museum of Natural History. The team was unified in its belief that organisms had to be studied in their natural settings for a clear understanding of their features and role in their community (Figures 12, 13). Only then could a preserved museum collection aid in documenting the building blocks of an ecosystem. This approach was particularly true for coral reefs, which were all but inaccessible to scientists until scuba diving allowed in situ observations and experimental study. Similarly, it was essential to probe and sample substrata to better understand the structure of communities, present and past. The team directed its attention to the Caribbean because it is the Americas' tropical sea, to which our own nation is connected by weather, ocean currents, and marine resources, as well as by cultural and economic exchange.

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

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

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

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

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

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

ACKNOWLEDGMENTS

A program of this length would not have been possible without the help of countless supporters—too many to name individually. But all associated with us will know that they are being thanked because the spirit and camaraderie generated by our joint endeavor is unprecedented. No more than a handful of naysayers have attempted to slow our progress or dampen our enthusiasm—obviously without success. Above all, we are grateful to the Bowman family of Dangriga for leasing their Carrie Bow Cay to our program and for taking a serious interest in our work from the first day. The government of Belize, the Department of Fisheries in particular, hosted our scientific efforts and granted us necessary permits. Many of the people of Belize, from Dangriga Town in particular, helped us with logistics by sharing their knowledge of the country's coastal resources, their skilled and dedicated cooks, boatmen, carpenters, hotel services, and provisions. Back home, we received invaluable cooperation and support from scientific colleagues, private and federal funding sources, and Smithsonian staff from all levels of administration and science units, including the Natural History Museum's Director's Office, the Smithsonian Scientific Diving Program and its staff, and many of the Museum's research assistants, scientific illustrators, photographers, and collection managers. For my part, I could not have directed and inspired our program without the assistance of many dedicated collaborators: Mike Carpenter, CCRE operations manager; Marsha Sitnik, program administrator; and Kathleen Smith, Michelle Nestlerode, Martha Robbart, Robyn Spittle, and Carla Piantoni, research assistants.

Photographs and art in this contribution were contributed by Mike Carpenter, Chip Clark, Ilka Feller, Ron Larson, Kathy Larson, Sara Lewis, Diane Littler, Ian Macintyre, Vicky Macintyre, Julie Mount, Aaron O'Dea, Tom Opishinski, Mary Parrish, Laurie Penland, Carla Piantoni, Tony Rath, Mary Rice, Randi Rotjan, Klaus Ruetzler, Molly Kelly Ryan, Juan Sanchez, Kjell Sandved, Jimmie Smith, Kathleen Smith, Kay Vopel, all of whom are (or were at the time) affiliated with the Smithsonian Institution, and two undetermined photographers.

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LITERATURE CITED

Acosta, C. A., and M. J. Butler. 1997. Role of Mangrove Habitat as a Nursery for Juvenile Spiny Lobster, *Panulirus argus*, in Belize. *Marine and Freshwater Research*, 48:721–727.

Adey, W. H., and I. G. Macintyre. 1973. Crustose Coralline Algae: A Re-Evaluation in the Geological Sciences. *Geological Society of America Bulletin*, 84:883–904.

Antonius, A. 1982. "Coral Reef Pathology: A Review." In *The Reef and Man: Proceedings of the Fourth International Coral Reef Symposium*, Volume 2, pp. 3–6. Quezon City, Philippines : Marine Sciences Center, University of the Philippines.

Aronson, R. B. 1987. Predation on Fossil and Recent Ophiuroids. *Paleobiology*, 13(2):187–192.

Aronson, R. B., I. G. Macintyre, S. A. Lewis, and N. L. Hilbun. 2005. Emergent Zonation and Geographic Convergence of Coral Reefs. *Ecology,* 86:2586–2600.

Aronson, R. B., I. G. Macintyre, W. F. Precht, T. J. T. Murdoch, and C. M. Wapnick. 2002. The Expanding Scale of Species Turnover Events on Coral Reefs in Belize. *Ecological Monographs*, 72:233–249.

Aronson, R. B., W. F. Precht, I. G. Macintyre, and T. J. T. Murdoch. 2000. Coral Bleach-Out in Belize. *Nature (London)*, 405:36.

Baldwin, C., and D. Smith. 2003. Larval Gobiidae (Teleostei: Perciformes) of Carrie Bow Cay, Belize, Central America. *Bulletin of Marine Science*, 72:639–674.

Bowman, H. T. A. 1979. *Emerald Valley and Twinkling Town: My Autobiography.* Stone Haven, Stann Creek Valley, Belize: Author.

Buskey, E. J. 1998. Energetic Costs of Swarming Behavior for the Copepod *Dioithona oculata*. *Marine Biology*, 130:425–431.

Calder, D. R. 1991. Abundance and Distribution of Hydroids in a Mangrove Ecosystem at Twin Cays, Belize, Central America. *Hydrobiologia*, 216/217:221–228.

Carr, D., and J. Thorpe. 1961. *From the Cam to the Cays; the Story of the Cambridge Expedition to British Honduras 1959–60*. London: Putnam.

Cheeseman, J., and C. Lovelock. 2004. Photosynthetic Characteristics of Dwarf and Fringe *Rhizophora mangle* L. in a Belizean Mangrove. *Plant, Cell and Environment*, 27:769–780.

Cressey, R. 1981. *Parasitic Copepods from the Gulf of Mexico and Caribbean Sea, I:* Holomolochus *and* Novabomolochus. *Smithsonian Contributions to Zoology*, No. 339. Washington, D.C.: Smithsonian Institution Press.

Dahl, A. L. 1973. Surface Area in Ecological Analysis: Quantifications of Benthic Coral-Reef Algae. *Marine Biology*, 23:239–249.

Diaz, M. C., and B. B. Ward. 1997. Sponge-Mediated Nitrification in Tropical Benthic Communities. *Marine Ecological Progress Series*, 156:97–107.

Duffy, J. E. 1996. Eusociality in a Coral-Reef Shrimp. *Nature (London)*, 381:512–514.

Duran, S., and K. Rützler. 2006. Ecological Speciation in Caribbean Marine Sponges. *Molecular Phylogenetics and Evolution*, 40(1):292–297.

Dworschak, P. C., and J. Ott . 1993. Decapod Burrows in Mangrove-Channel and Back-Reef Environments at the Atlantic Barrier Reef, Belize. *Ichnos*, 2:277–290.

Erickson, A. A., I. C. Feller, V. P. Paul, L. M. Kwiatkowski, and W. Lee. 2008. Selection of an Omnivorous Diet by the Mangrove Tree Crab *Aratus pisonii* in Laboratory Experiments. *Journal of Sea Research*, 59:59–69.

Erpenbeck, D., S. Duran, K. Rützler, V. Paul, J. N. A. Hooper, and G. Wörheide. 2007. Towards a DNA Taxonomy of Caribbean Demosponges: A Gene Tree Reconstructed from Partial Mitochondrial COI Gene Sequences Supports Previous rDNA Phylogenies and Provides a New Perspective on the Systematics of Demospongiae. *Journal of the Marine Biological Association of the United Kingdom*, 87:1563–1570.

Erséus, C. 1988. Taxonomic Revision of the *Phallodrilus rectisetosus* Complex (Oligochaeta: Tubificidae). *Proceedings of the Biological Society of Washington*, 101(4):784–793.

Faust, M. A., and R. A. Gulledge. 1996. Associations of Microalgae and Meiofauna in Floating Detritus at a Mangrove Island, Twin Cays, Belize. *Journal of Experimental Marine Biology and Ecology*, 197:159–175.

Faust, M. A., and P. A. Tester. 2004. "Harmful Dinoflagellates in the Gulf Stream and Atlantic Barrier Coral Reef, Belize." In *Harmful Algae 2002. Proceedings of the Xth International Conference on Harmful Algae*, ed. K. A. Steidinger, J. H. Landsberg, C. R. Tomas, and G. A. Vargo, pp. 326–328. St. Petersburg, Fla.: Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO.

Feller, I. C. 1995. Effects of Nutrient Enrichment on Leaf Anatomy of Dwarf *Rhizophora mangle* (Red Mangrove). *Biotropica*, 28(1):13–22.

Feller, I. C., C. E. Lovelock, and K. L. McKee. 2007. Nutrient Addition Differentially Affects Ecological Processes of *Avicennia germinans* in Nitrogen vs. Phosphorus Limited Mangrove Ecosystems. *Ecosystems*, 10:347–359.

Feller, I. C., K. L. McKee, D. F. Whigham, and J. P. O'Neill. 2002. Nitrogen vs. Phosphorus Limitation across an Ecotonal Gradient in a Mangrove Forest. *Biogeochemistry*, 62:145–175.

Feller, I. C., D. F. Whigham, J. P. O'Neill, and K. L. McKee. 1999. Effects of Nutrient Enrichment on Within-Stand Cycling in a Mangrove Forest. *Ecology*, 80(7):2193–2205.

Ferrari, F., J. Fornshell, L. Ong, and J. W. Ambler. 2003. Diel Distribution of Copepods across a Channel of an Overwash Mangrove Island. *Hydrobiologia*, 477:1–13.

Ferraris, J. D. 1981. Oxygen Uptake with Acute Variation in Temperature and Salinity in Two Coral Reef Polychaetes. *Marine Ecology*, 2:159–168.

Ferraris, J. D., K. Fauchald, and B. Kensley. 1989. "Degrees of Fitness in Water and Ion Regulation in Alpheid, Polychaete, and Sipunculid Inhabitants of a Belizean Mangrove." In *Proceedings of the International Union of Physiological Sciences XVII*, p. 427. Helsinki: International Congress of Physiological Sciences.

Goodbody, I. G. 1995. Ascidian Communities in Southern Belize—A Problem in Diversity and Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5:355–358.

Graus, R. R., and I. G. Macintyre. 1976. Light Control of Growth Forms in Colonial Reef Corals: Computer Simulation. *Science*, 193:895–897.

———. 1989. The Zonation Patterns of Caribbean Coral Reefs as Controlled by Wave and Light Energy Input, Bathymetric Setting and Reef Morphology: Computer Simulation Experiments. *Coral Reefs*, 8:9–18.

Greer, J. E., and B. Kjerfve. 1982. "Water Currents Adjacent to Carrie Bow Cay, Belize." In *The Atlantic Barrier Ecosystems at Carrie Bow Cay, Belize, I: Structure and Communities*, ed. K. Rützler, and I. G. Macintyre, pp. 53–58. *Smithsonian Contributions to Marine Science*, No. 12. Washington, D.C.: Smithsonian Institution Press.

Hendler, G. 1982. Slow Flicks Show Star Tricks: Elapsed-Time Analysis of Basketstar (*Astrophyton muricatum*) Feeding Behavior. *Bulletin of Marine Science*, 32(4):909–918.

Kensley, B. 1984. *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, III: New Marine Isopoda. Smithsonian Contributions to Zoology*, No. 24. Washington, D.C.: Smithsonian Institution Press.

Kensley, B., and R. H. Gore. 1981. *Coralaxius abelei*, New Genus and New Species (Crustacea: Decapoda: Thalassinidea: Axiidae): A Coral-Inhabiting Shrimp from the Florida Keys and the Western Caribbean Sea. *Proceedings of the Biological Society of Washington*, 93:1277–1294.

Kier, P. M. 1975. *The Echinoids of Carrie Bow Cay, Belize. Smithsonian Contributions to Zoology*, No. 206. Washington, D.C.: Smithsonian Institution Press.

Kjerfve, B., K. Rützler, and G. H. Kierspe. 1982. "Tides at Carrie Bow Cay, Belize." In *The Atlantic Barrier Ecosystems at Carrie Bow Cay, Belize, I: Structure and Communities*, ed. K. Rützler, and I. G. Macintyre, pp. 47–52. *Smithsonian Contributions to Marine Science*, No. 12. Washington, D.C.: Smithsonian Institution Press.

Kohlmeyer, J. 1984. Tropical Marine Fungi. *Marine Ecology*, 5(4): 329–378.

Kokke, W. C. M. C., W. Fenical, C. Pak, and C. Djerassi. 1979. Minor and Trace Sterols in the Caribbean Sponge *Verongia cauliformis*. *Helvetica Chimica Acta*, 62:1310–1380.

Koltes, K. H., J. J. Tschirky, and I. C. Feller. 1998. "Carrie Bow Cay, Belize." In *Caribbean Coastal Marine Productivity (CARICOMP): Coral Reef, Seagrass, and Mangrove Site Characteristics*, ed. B. Kjerfve, pp. 79–94. Paris: UNESCO.

Kornicker, L. S., and A. C. Cohen. 1978. Dantyinae, a New Subfamily of Ostracoda (Myodocopina: Sarsiellidae). *Proceedings of the Biological Society of Washington*, 91(2):490–508.

Larson, R. J. 1979. Feeding in Coronate Medusae (Class Scyphozoa, Order Coronatae). *Marine Behaviour and Physiology*, 6:123–129.

Lewis, S. M. 1986. The Role of Herbivorous Fishes in the Organization of Tropical Reef Communities. *Ecological Monographs*, 56(3): 183–200.

Littler, D. S., and M. M. Littler. 1985. An Illustrated Marine Flora of the Pelican Cays, Belize. *Bulletin of the Biological Society of Washington*, 9:1–149.

Littler, M. M., D. S. Littler, and P. R. Taylor. 1983. Evolutionary Strategies in a Tropical Barrier Reef System: Functional-Form Groups of Marine Macroalgae. *Journal of Phycology*, 19:229–237.

Littler, M. M., I. G. Macintyre, and D. S. Littler, eds. 1995. Biology and Geology of Tobacco Range, Belize, Central America: A Mangrove System Containing Unique Fractured Peat Deposits. *Atoll Research Bulletin*, Nos. 426–431.

Lovelock, C. E., M. C. Ball, B. Choat, B. M. J. Engelbrecht, N. M. Holbrook, and I. C. Feller. 2006. Linking Physiological Processes with Mangrove Forest Structure: Phosphorus Deficiency Limits Canopy Development, Hydraulic Conductivity and Photosynthetic Carbon Gain in Dwarf *Rhizophora mangle*. *Plant, Cell and Environment*, 29:793–802.

Macintyre, I. G. 1975. A Diver-Operated Hydraulic Drill for Coring Submerged Substrates. *Atoll Research Bulletin*, 185:21–26.

———. 1984. Extensive Submarine Lithification in a Cave in the Belize Barrier Reef Platform. *Journal of Sedimentary Petrology*, 54: 221–235.

Macintyre, I. G., and R. B. Aronson. 1997. Field Guidebook to the Reefs of Belize. *Proceedings of the 8th International Coral Reef Symposium*, 1:203–222.

Macintyre, I. G., R. B. Burke, and R. Stuckenrath. 1981. Core Holes in the Puter Fore Reef off Carrie Bow Cay, Belize: A Key to the Holocene History of the Belizean Barrier Reef Complex. *Proceedings, Fourth International Coral Reef Symposium*, 1:567–574.

Macintyre, I. G., and K. Rützler, eds. 2000. Natural History of the Pelican Cays, Belize. *Atoll Research Bulletin*, Nos. 466–480.

Macintyre, I. G., K. Rützler, and I. C. Feller, eds. 2004a. The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change. *Atoll Research Bulletin*, Nos. 509–530.

Macintyre, I. G., S. V. Smith, and J. C. Zieman. 1974. Carbon Flux through a Coral-Reef Ecosystem: A Conceptual Model. *Journal of Geology*, 8:161–171.

Macintyre, I. G., M. A. Toscano, R. G. Lightly, and G. Bond. 2004b. Holocene History of the Mangrove Island of Twin Cays, Belize, Central America. *Atoll Research Bulletin*, 510:1–16.

McKee, K. L., I. Mendelssohn, and M. Hester. 1988. A Reexamination of Pore Water Sulfide Concentrations and Redox Potentials near the Aerial Roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany*, 75:1352–1359.

Miller, J. A., and I. G. Macintyre. 1977. *Field Guidebook to the Reefs of Belize*. Miami Beach, Fla.: Atlantic Reef Committee, University of Miami.

Modlin, R. F. 1987. Mysidacea from Shallow Water in the Vicinity of Carrie Bow Cay, Belize, with Description of Two New Species. *Journal of Crustacean Biology*, 7(1):106–121.

Morton, S. L., and M. A. Faust. 1997. Survey of Toxic Epiphytic Dinoflagellates from the Belizean Barrier Reef Ecosystem. *Bulletin of Marine Science*, 61(3):899–906.

Opishinski, T., M. L. Spaulding, K. Rützler, and M. Carpenter. 2001. "A Real Time Environmental Data Monitoring, Management and Analysis System for the Coral Reefs off the Coast of Belize." In *Proceedings, Oceans 2001 Conference, Nov. 5–8. Oceanic Engineering Society and Marine Technology Society*, Volume 2, pp. 1188–1197. Honolulu, Hawaii: IEEE.

Ott, J. A., and R. Novak. 1989. "Living at an Interface: Meiofauna at the Oxygen/Sulfide Boundary of Marine Sediments." In *Reproduction, Genetics and Distribution of Marine Organisms*, ed. J. S. Ryland, and P. A. Taylor, pp. 415–422. Denmark: Olsen and Olsen.

Ott, J. A., R. Novak, F. Schiemer, U. Hentschel, M. Nebelsick, and M. Polz. 1991. Tackling the Sulfide Gradient: A Novel Strategy Involving Marine Nematodes and Chemoautotrophic Ectosymbionts. *Marine Ecology*, 12(3):261–279.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science*, 301:955–958.

Pawson, D. L. 1976. Shallow-Water Sea Cucumbers (Echinodermata: Holothuroidea) from Carrie Bow Cay, Belize. *Proceedings of the Biological Society of Washington*, 89:369–382.

Robbart, M. L., P. Peckol, S. P. Scordilis, H. A. Curran, and J. Brown-Saracino. 2004. Population Recovery and Differential Heat Shock Protein Expression for the Corals *Agaricia agarites* and *A. tenuifolia* in Belize. *Marine Ecology Progress Series*, 283:151–160.

Rotjan, R. D., J. L. Dimond, D. J. Thornhill, B. Helmuth, J. J. Leichter, D. W. Kemp, and S. Lewis. 2006. Chronic Parrotfish Grazing Impedes Coral Recovery after Bleaching. *Coral Reefs*, 25: 361–368.

Rützler, K. 1975. The Role of Burrowing Sponges in Bio-Erosion. *Oecologia (Berlin)*, 19:203–216.

———. 1978a. "Sponges in Coral Reefs." In *Coral Reefs: Research Methods. Monographs on Oceanographic Methodology, No. 5*, ed. D. R. Stoddart and R. E. Johannes, pp. 299–313. Paris: UNESCO.

———. 1978b. "Photogrammetry of Reef Environments by Helium Balloon." In *Coral Reefs: Research Methods. Monographs on Oceanographic Methodology, No. 5*, ed. D. R. Stoddart and R. E. Johannes, pp. 45–52. Paris: UNESCO.

———. 1981. An Unusual Blue-Green Alga Symbiotic with Two New Species of *Ulosa* (Porifera: Hymeniacidonidae) from Carrie Bow Cay, Belize. *Marine Ecology*, 2:35–50.

———. 1988. Mangrove Sponge Disease Induced by Cyanobacterial Symbionts: Failure of a Primitive Immune System? *Diseases of Aquatic Organisms*, 5:143–149.

———. 2002. Impact of Crustose Clionid Sponges on Caribbean Reef Corals. *Acta Geologica Hispanica*, 37(1):61–72.

Rützler, K., M. C. Diaz, R. W. M. van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. Wulff. 2000. Diversity of Sponge Fauna in Mangrove Ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, 476:230–250.

Rützler, K., and I. C. Feller. 1988. Mangrove Swamp Communities: An Approach in Belize. *Oceanus*, 30(4):16–24.

———. 1996. Caribbean Mangrove Swamps. *Scientific American*, 274(3):70–75.

Rützler, K., and J. D. Ferraris. 1982. "Terrestrial Environment and Climate, Carrie Bow Cay, Belize." In *The Atlantic Barrier Ecosystems at Carrie Bow Cay, Belize, I: Structure and Communities*, ed. K. Rützler, and I. G. Macintyre, pp. 77–92. *Smithsonian Contributions to Marine Science*, No. 12. Washington, D.C.: Smithsonian Institution Press.

Rützler, K., J. D. Ferraris, and R. J. Larson. 1980. A New Plankton Sampler for Coral Reefs. *Marine Ecology*, 1:65–71.

Rützler, K., and I. G. Macintyre. 1978. Siliceous Sponge Spicules in Coral Reef Sediments. *Marine Biology*, 49:147–159.

———, eds. 1982. *The Atlantic Barrier Ecosystems at Carrie Bow Cay, Belize, I: Structure and Communities. Smithsonian Contributions to Marine Science*, No. 12. Washington, D.C.: Smithsonian Institution Press.

Rützler, K., D. L. Santavy, and A. Antonius. 1983. The Black Band Disease of Reef Corals, 3: Distribution, Ecology and Course of Disease. *Marine Ecology*, 4(4):329–358.

Rützler, K., and W. Sterrer. 1971. Oil Pollution: Damage Observed in Tropical Communities along the Atlantic Seaboard of Panama. *Bioscience*, 20:222–224.

Sebens, K. P., B. Helmuth, E. Carrington, and B. Aguis. 2003. Effects of Water Flow on Growth and Energetics of the Scleractinian Coral *Agaricia tenuifolia* in Belize. *Coral Reefs*, 22:35–47.

Signorovitch, A. Y., S. L. Dellaporta, and L. W. Buss. 2005. Molecular Signatures for Sex in the Placozoa. *Proceedings of the National Academy of Science of the United States of America*, 102(43):15518–15522.

Smith, C. L., J. C. Tyler, W. P. Davis, R. S. Jones, D. G. Smith, and C. C. Baldwin. 2003. Fishes of the Pelican Cays, Belize. *Atoll Research Bulletin*, 497:1–88.

Stoddart, D. R., F. R. Fosberg, and D. L. Spellman 1982. Cays of the Belize Barrier Reef and Lagoon. *Atoll Research Bulletin*, 256:1–74.

Stoddart, D. R., and R. E. Johannes, eds. 1978. *Coral Reefs: Research Methods. Monographs on Oceanographic Methodology, No. 5.* Paris: UNESCO.

Thomas, J. D., and J. L. Barnard. 1983. *The Platyischnopidae of America (Crustacea, Amphipoda). Smithsonian Contributions to Zoology*, No. 375. Washington, D.C.: Smithsonian Institution Press.

Urish, D. W. 1988. Freshwater on a Coral Island—Carrie Bow Cay. *Maritime, University of Rhode Island*, 32(3):4–6.

Vopel, K. C., G. Arlt, M. Pöhn, and J. Ott. 2002. Flow Microenvironment of Two Marine Peritrich Ciliates with Ectobiotic Chemoautotrophic Bacteria. *Aquatic Microbial Ecology*, 29:19–28.

Wainwright, P. 1988. Morphology and Ecology: The Functional Basis of Feeding Constraints in Caribbean Labrid Fishes. *Ecology*, 69:635–645.

Waller, T. R. 1980. *Scanning Electron Microscopy of Shell and Mantle in the Order Arcoidea (Mollusca: Bivalvia). Smithsonian Contributions to Zoology*, No. 313. Washington, D.C.: Smithsonian Institution Press.

Wilkinson, C. 1987. Interocean Differences in Size and Nutrition of Coral Reef Sponge Populations. *Science*, 236:1654–1657.

Winston, J. E. 1984. Shallow Water Bryozoans of Carrie Bow Cay, Belize. *American Museum Novitates*, 2799:1–38.

———. 2007. Diversity and Distribution of Bryozoans in the Pelican Cays, Belize, Central America. *Atoll Research Bulletin*, 546: 1–24.

Wulff, J. L. 2005. Trade-Offs in Resistance to Competitors and Predators, and Their Effects on the Diversity of Tropical Marine Sponges. *Journal of Animal Ecology*, 74:313–321.

The Smithsonian Tropical Research Institute: Marine Research, Education, and Conservation in Panama

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ABSTRACT. A grand geological experiment with a global reach to its biological impact, the formation of the isthmus of Panama between 15 and 3 million years ago split the tropical Interamerican Seaway into two and substantially changed the physical oceanography of each part. That event subjected the now-divided halves of the neotropical marine biota to new environmental conditions that forced each along a different evolutionary trajectory. For the past 45 years the Smithsonian Tropical Research Institute (STRI) marine sciences program has taken full advantage of this event by sponsoring research on a great diversity of topics relating to the evolutionary effects of the formation of the isthmus. That research, which has been supported by multiple laboratories on each coast and a series of research vessels, has produced more than 1,800 publications. Here we provide an overview of the environmental setting for marine research in Panama and an historical perspective to research by STRI's scientific staff at the different marine facilities.

INTRODUCTION

The unique geological history of Panama encourages a wider variety of research on tropical marine organisms than can be accomplished anywhere else in the world. The Central American Isthmus narrows in Panama to approximately 70 km, separating oceans that have very different oceanographic regimes and marine ecosystems. The formation of the central American isthmus, starting approximately 15 million years ago (Ma) and finishing in Panama about 3 Ma, had wide ramifications not only for the nature of the modern biological and geological world of the Americas but also for the entire global oceanic circulation. With the completion of this process the Gulf Stream strengthened, changing the Atlantic circulation. That change was soon followed by Northern Hemisphere glaciation, which in turn brought about a period of climate change in Africa that may have stimulated the origins of modern man. From a more local perspective, the completion of the isthmus set in motion a vast natural experiment: single populations of marine animals and plants were split and isolated in different and changing environments that forced their evolutionary divergence and fundamental changes in their biology.

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The Smithsonian Tropical Research Institute (STRI) marine research program in the Republic of Panama has taken full advantage of this globally significant geological event. In 1964 STRI established its first laboratories on the Pacific and Caribbean coasts within what then constituted the Panama Canal Zone. Since that time, marine research at STRI has expanded greatly and made major contributions to understanding of tropical marine biodiversity: the geological history of the isthmus and the development of environmental differences in the Caribbean and eastern Pacific, patterns of biodiversity in neotropical marine habitats, coral reef development, coral symbioses and diseases, the modes and tempo of species formation and diversification, evolutionary change within many groups of organisms relating to environmental differences on the two sides of the isthmus of Panama, and invasions by marine organisms facilitated by the Panama Canal and its shipping activity. To date marine research at STRI has resulted in more than 1,800 scientific publications; half of these have been produced by staff scientists and more than 200 published in high-profile journals such as *Science, Nature, Proceedings of the National Academy of Sciences of the United States of America, Proceedings of the Royal Society, American Naturalist, Evolution, Ecology,* and *Annual Review of Systematics and Ecology*.

In celebration of its role in coral reef research, the Smithsonian's 150th anniversary, and the International Year of the Reef, STRI hosted the Eighth International Coral Reef Symposium in Panama in 1996. This meeting brought 1,500 reef scientists and managers to Panama from around the world, resulting in the publication of a two-volume proceedings (Lessios and Macintyre, 1997), and an international traveling exhibit of coral reefs that is now resident at the Bocas del Toro Research Station.

Here we present an overview of the marine setting of Panama that clearly indicates its potential for research, and a historical summary of the diversity of marine studies conducted at the different STRI marine facilities. We then briefly outline STRI's marine education and outreach activities. Although this review focuses on the research activities of STRI's marine staff scientists, a strong fellowship program and a larger suite of visiting students and scientific collaborators have acted as substantial multipliers of STRI scientists' activities.

THE COASTAL OCEANOGRAPHIC SETTING OF THE ISTHMUS OF PANAMA

The emergence of the Isthmus of Panamá likely was the most crucial event for tropical marine ecosystems in the last 15 million years of earth's history. In Central America the marine environment experienced drastic changes in the two seas formed by the isthmus. As the isthmus approached closure, the Caribbean gradually became cut off from the eastward flow of Pacific water and became warmer, saltier (westward winds carried away evaporated moisture), and more oligotrophic. The Caribbean now is a relatively stable sea, with small fluctuations in temperature, relatively low tidal variation, and a relatively high salinity. Its relatively clear and nutrient-poor waters (D'Croz and Robertson, 1997; D'Croz et al., 2005; Collin et al., 2009) are ideal for the growth of coral reefs, and the wider Caribbean area ranks third behind the Indian Ocean and the Indo-West Pacific in terms of numbers of marine species. Annual rainfall is high on the Caribbean coast of Panama and follows the same basic seasonal pattern as on the lower-rainfall Pacific side of the isthmus (Kaufmann and Thompson, 2005). Relative to the Caribbean, the Tropical Eastern Pacific (TEP) exhibits much greater fluctuations in tides and temperature and has substantially lower salinity as a consquence of an area of very high rainfall along the Intertropical Convergence Zone. The TEP also has more and much larger areas of seasonal upwelling than the Caribbean. In addition, and in contrast to the Caribbean, the TEP also experiences strong longer-term variation in temperature and productivity from the influence of El Niño–Southern Oscillation Cycle (ENSO) events (D'Croz and O'Dea, 2009). Sea warming related to ENSO (which occurs at intervals of four to nine years) has drastic affects on coral reef development in the TEP. The direct marine effects of ENSO events in the tropical and warm temperate parts of the eastern Pacific are stronger than anywhere else in the world. Although coastal biological productivity is strongly related to benthic communities in the Caribbean, pelagic productivity and high availability of ocean-derived dissolved nutrients dominate the TEP, with high variability in those nutrient levels producing matching variability in the abundance of pelagic organisms (Miglietta et al., 2008). In Panama the nutrient-rich waters of its Pacific coast support commercial fisheries of major importance, fisheries that have no counterpart on the Caribbean coast.

The coastal marine communities of Panama are affected not only by inter-ocean differences in oceanography but also by marked local variation in shoreline environmental conditions along each coast. The Pacific shelf of Panama is wide and is divided, by the southward-projecting Azuero Peninsula, into two large areas, the (eastern) Gulf of Panama and the (western) Gulf of Chiriquí. The Gulf of Panama is subject to strong seasonal wind-driven upwelling, but the Gulf of Chiriquí is not (Figure 1; and see D'Croz and Robertson, 1997). In the latter Gulf, high mountains block the wind and prevent wind-induced upwelling (D'Croz and O'Dea, 2007). In contrast, the Caribbean coast of Panama is relatively straight and has a narrow continental shelf, except in the (western) Bocas del Toro Archipelago. Hydrological conditions vary substantially along the Caribbean coast, ranging from the nutrient- and plankton-poor waters in the (eastern) San Blas Archipelago, where river discharge is low and the influence of open ocean water is high (D'Croz et al., 1999), to the more turbid environments of the Bocas del Toro Archipelago, where rainfall and river discharge are higher as a result of the blockage of westward moisture flow by the highest mountains in Panama (D'Croz et al., 2005; Collin et al., 2009). Thus, Panama lays claim to having "four oceans," providing unique opportunities for

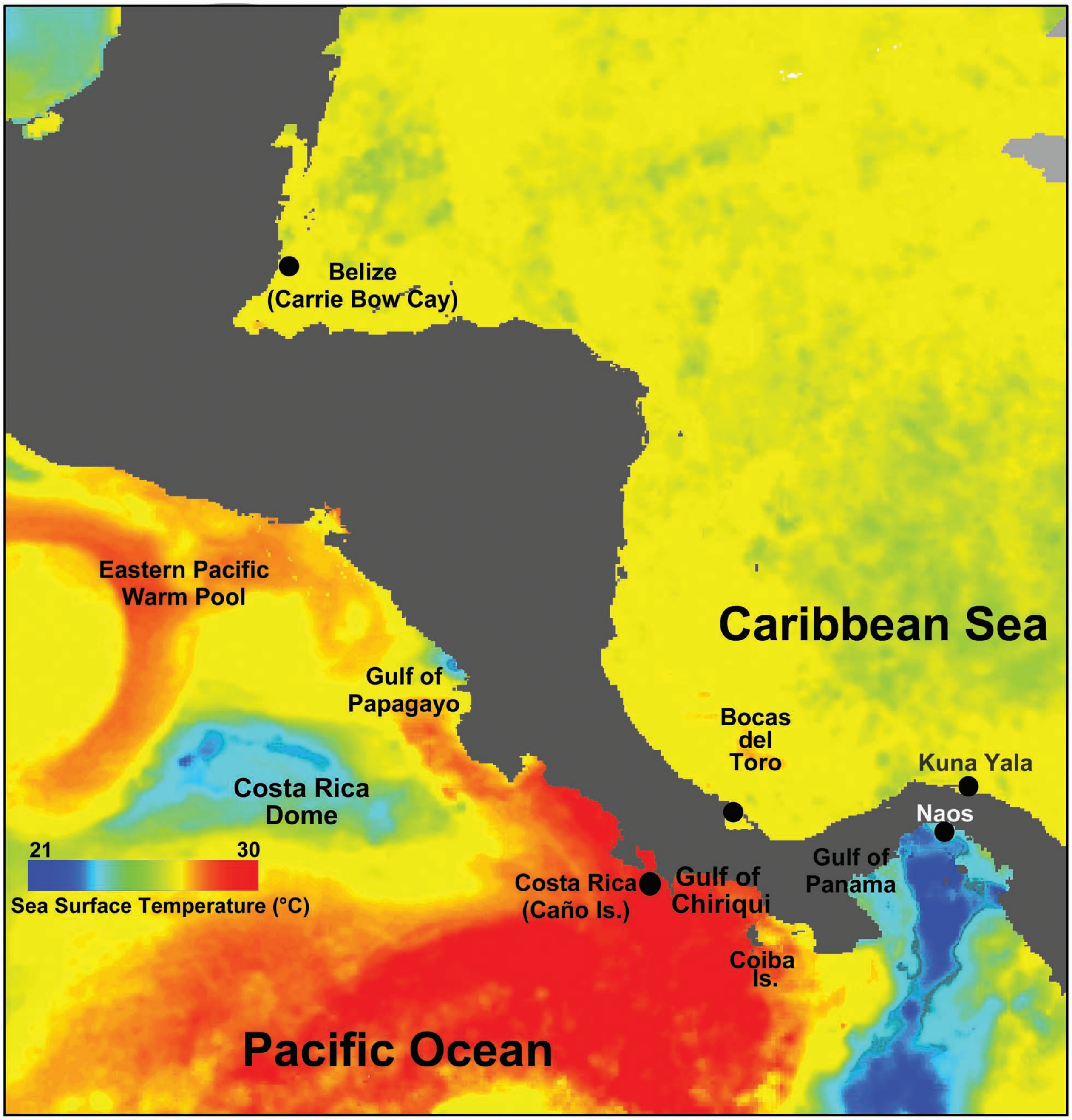

FIGURE 1. Temperature regimes on the Atlantic and Pacific coasts during the seasonal upwelling in the Gulf of Panama.

understanding how and why marine ecosystems vary and function as they do.

A HISTORICAL RESUME OF RESEARCH AT STRI MARINE FACILITIES

Marine research began at STRI in 1961with the doctoral work of STRI Director (Emeritus) Ira Rubinoff on trans-isthmian sister species of fishes (Rubinoff and Rubinoff, 1971), which led to STRI's first marine publication, based on work done near Punta Galeta (Rubinoff and Rubinoff, 1962). Since then the marine program has undergone exponential growth in its productivity. STRI currently operates two land facilities on the Caribbean coast of Panama, Punta Galeta Laboratory and Bocas del Toro Research Station, and two on the Pacific coast, Naos Island Laboratory complex and Rancheria Island field station. Between 1977 and 1997 STRI also operated a small, highly productive field station in the San Blas islands (Figure 2). In addition, STRI has maintained a series of small coastal research vessels that greatly expanded the geographic reach of its activities well beyond STRI's land facilities and, in fact, far beyond Panama.

MARINE ENVIRONMENTAL SCIENCES PROGRAM (MESP)

Monitoring the Physical Environment

In 1974, the Smithsonian Institution Tropical Environmental Sciences Program began monitoring physical environmental variables at Galeta, recording rainfall, wind speed and direction, solar radiation, reef flat water level, and air and water temperature hourly with automated equipment. Today, such physical data are recorded more frequently, automatically sent to a central processing facility via radio and internet, and added to a database that is available online at http://striweb.si.edu/esp/physical_monitoring/index_phy_mon.htm. Organization of physical data collection from Galeta has now been combined with that from Barro Colorado Island, Bocas del Toro, and several other sites, under the management of Karl Kaufmann. Recording of sea-surface temperature started at Galeta in 1988, and this monitoring now covers 33 shallow-water stations throughout the coastal waters on both coasts of Panama. Published summaries of the marine physical data include Meyer et al. (1974), Cubit et al. (1988), and Kaufmann and Thompson (2005). Physical environmental monitoring was conducted at the San Blas station from 1991 until its closure in 1998 and has been in progress at Bocas del Toro since 1999.

Monitoring the Biological Environment

The first phase of biological monitoring consisted of work done at Galeta that was stimulated by the two oil spills and formed part of their resultant studies. At San Blas, biological (plankton) monitoring co-occurred with the physical monitoring. At Bocas del Toro, biological monitoring that started in 1999 includes minor activity directed at seagrasses and mangroves in connection with CARICOMP. The major activity however, has been an expanding set of monitoring surveys of coral reefs by Hector Guzman, which now cover reefs scattered along both coasts of Panama (see http://striweb.si.edu/esp/mesp/reef_monitoring_intro.htm). This program developed from a survey of coral reefs in the general vicinity of Galeta made in 1985 (Guzman et al., 1991; and see also Guzman et al., 2008b).

GALETA POINT MARINE LABORATORY

The Galeta Point installation became a STRI laboratory in 1964 when a military building constructed in 1942 on a fringing reef flat was turned over to STRI, thanks to the efforts of Ira Rubinoff. From his research on inshore fishes in that area (Rubinoff and Rubinoff, 1962) Rubinoff recognized its value as an easily accessible Caribbean study site. By 1971 Galeta Point was STRI's primary marine research site, providing access to a fringing reef flat, seagrass beds, and mangroves within a few meters of a laboratory building, with housing in nearby Coco Solo. Early work emphasized the comparison of reefs on both sides of the isthmus (Glynn, 1972) and the geological structure and history of the reefs (Macintyre and Glynn, 1976). Fundamental insights into differences between the Caribbean and eastern Pacific at Panama also were developed by Chuck Birkeland (Birkeland, 1977) when, during his long-term residence at Galeta, he analyzed patterns of biomass accumulation on settling plates deployed on both sides of the isthmus.

Permanent monitoring of the biota at Galeta Point was started in 1970 by Chuck Birkeland, David Meyer, and Gordon Hendler to provide baseline data on a tropical Caribbean reef flat; this was done to determine the effect of the Witwater oil spill, which occurred in December 1968 about 5 km east of Galeta. Because no baseline data were available to determine effects of that spill on reef communities, the US Environmental Protection Agency provided funds to set up the study and to perform experiments testing susceptibility of corals to oil. Transects were established at both Galeta Point and Punta Paitilla on the

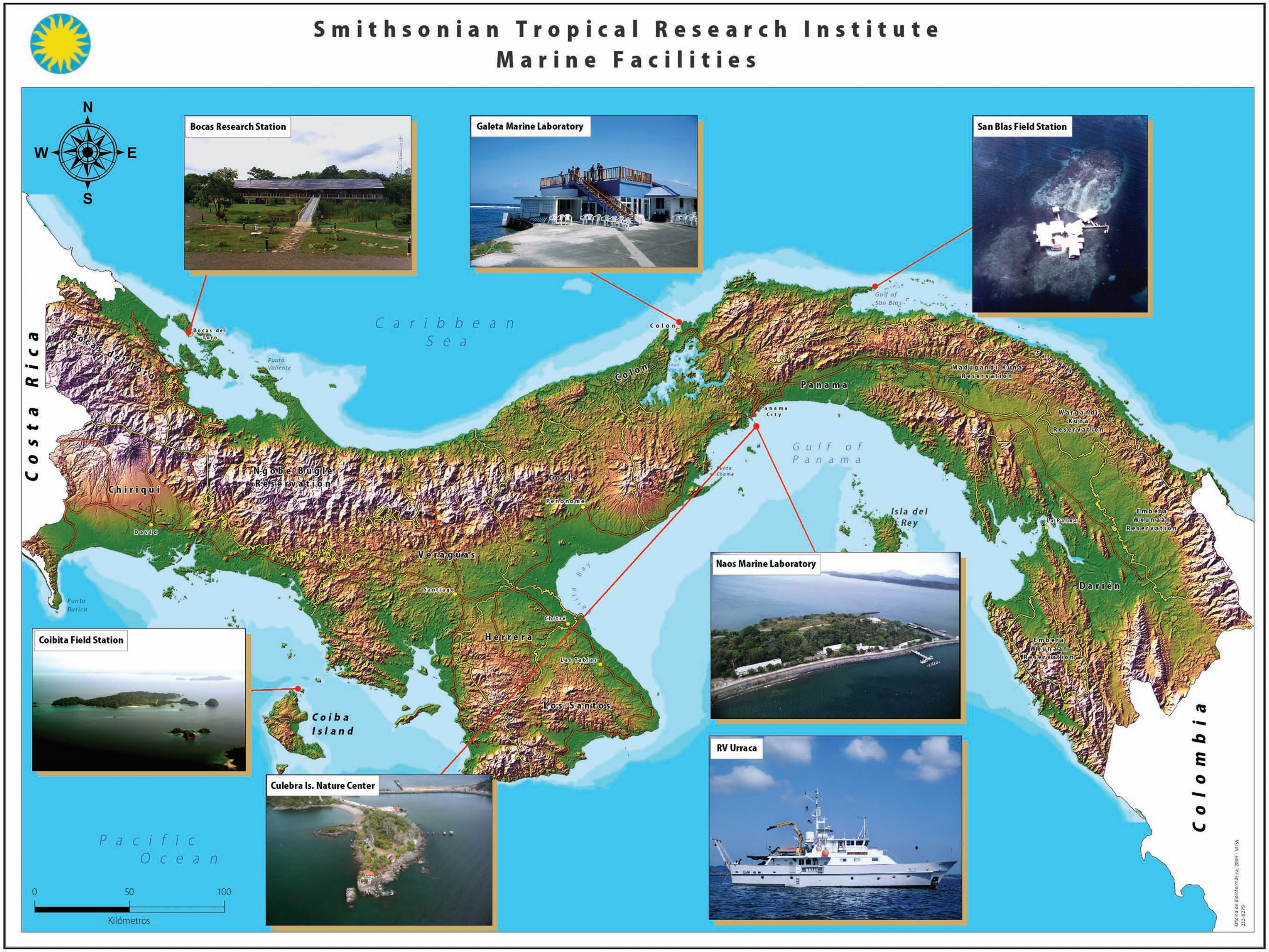

FIGURE 2. Map of Panama showing the distribution of Smithsonian Tropical Research Institute (STRI) marine facilities.

Pacific side to compare community structure, recruitment patterns, and the effect of oil on both communities (Birkeland et al., 1973).

In April 1986 a storage tank ruptured at an oil refinery about 4 km east of the laboratory, spilling 60,000–100,000 barrels of oil into the sea. The reef flat, grass beds, and mangroves around the Galeta laboratory were heavily oiled. This time a substantial amount of baseline data was available, thanks to the original transects set up by Birkeland, Meyer, and Hendler, whose monitoring had ended in 1982, and to the wider reef surveys in that area by Ernesto Weil. The Minerals Management Service of the U.S. Department of the Interior bestowed a 5 year grant to STRI to study the effects of the second oil spill in tropical areas (Keller and Jackson, 1993). That effort involved a considerable expansion of the types of data gathered, organisms studied, and habitats monitored over those in the first oil spill study. Subsequent to the second oil spill study the center of STRI research on coral reefs shifted first to San Blas then to Bocas del Toro. A long-term study (since 1988) of mangrove forest dynamics by Wayne Sousa (Sousa, 2007), occasional short-term projects, and physical environmental monitoring by MESP (see below) have continued at Galeta. The site also supports public education and outreach programs organized by Stanley Heckadon (see below). To date 315 publications include data obtained at Galeta laboratory, and the lab itself has produced 288 marine publications.

San Blas Field Station

The sparsely populated San Blas archipelago, in the autonomous Kuna Yala comarca, consists of several hundred sand cays scattered along the relatively sparsely populated eastern third of the Caribbean coast of Panama. The archipelago has the richest and most extensive development of coral reefs and associated fauna (including reef fishes) and flora in Caribbean Panama. Marine research sponsored by STRI began in San Blas in 1970, and research activity increased greatly in the late 1970s following the gradual construction by STRI from 1977 onward of a small field station that provided basic living accommodations and so allowed year-round research.

The San Blas field station, with its year-round access to a 15 km^2 area of rich reefs in calm, clear water, was the Caribbean base for many of STRI's comparative studies of the biology of closely related organisms on the Atlantic and Pacific sides of the Isthmus of Panama. Early research by STRI staff in San Blas included studies by STRI's founding director, Martin Moynihan, on the behavior of cephalopods (Moynihan, 1975; Moynihan and Rodaniche, 1982) and by Peter Glynn in the 1970s on coral reef development (Glynn, 1973). These investigations were followed by others on a broad range of organisms: Ross Robertson on the sexual patterns of labroid fishes, with Robert Warner (Warner et al., 1975; Robertson and Warner, 1978; Warner and Robertson 1978), and the recruitment dynamics and demography of reef-fishes (Robertson et al., 1999, 2005); Haris Lessios on the evolution and biology of echinoderms on the two coasts of the isthmus of Panama (Lessios, 1979, 1981, 2005); deputy director Eric Fischer on the sexual biology of simultaneously hermaphroditic groupers (Fischer, 1980, 1981; Fischer and Petersen, 1987); Nancy Knowlton on the biology and evolution of snapping shrimps and the reproductive biology, coral–algal symbioses, and evolution of corals (Rowan et al., 1997; Knowlton et al., 1977, 1992; Knowlton and Weigt, 1998); Jeremy Jackson on the comparative population and reproductive biology and evolutionary history of bryozoans on both sides of the Isthmus of Panama (O'Dea and Jackson, 2002; Dick et al., 2003; O'Dea et al., 2004); Luis D'Croz on comparative oceanographic conditions on the Caribbean and Pacific coasts of Panama (D'Croz and Robertson, 1997); and Hector Guzman on coral reef distribution and conservation (Andrefouet and Guzmán, 2005). During this period STRI also sponsored several anthropological projects on traditional Kuna society, acted as a conduit for international funding of Kuna marine management and conservation activities, and provide fellowships to Kuna University students.

The San Blas station provided essential support for projects on long-term ecological change on surrounding coral reefs. The combination of ease of access to shallow reefs, access as good as anywhere in the world, and the ability to do much work while on snorkel rather than scuba meant that it was possible to accumulate enormous data sets involving daily or shorter time period observations over months or years. These kinds of data are all too rarely available for tropical marine systems.

In early 1983 a Caribbean-wide mass die-off of an ecologically key organism on Caribbean reefs, the black sea urchin *Diadema antillarum*, began near San Blas and spread within the year throughout the entire Greater Caribbean. The year-round presence of biologists conducting long term studies of reef organisms at STRI's field station enabled the documentation of the start and spread of that event, which produced large, long-term effects on algal and coral growth on Caribbean coral reefs. Haris Lessios has followed the population and evolutionary consequences of that event for the urchin since it started (Lessios et al., 1984; Lessios, 2005). Year-round monitoring of reef-fish populations on reefs around that station over a 20 year period contributed key information to a meta-population study that documents a gradual Caribbean-wide decline in the overall abundance of reef fishes since the *Diadema* dieoff (Paddack et al., 2009). Long-term monitoring of climatic and oceanographic conditions by MESP enabled detailed examination of linkages between environmental dynamics and the dynamics of recruitment of pelagic larvae of reef-fishes (Robertson et al., 1999). In addition regular station visitors accumulated the world's only long-term data sets on gorgonians and sponges. The former work includes data on a combination of population dynamics and genetics of clone structure obtained by Howie Lasker and Mary-Alice Coffroth (Coffroth et al., 1992; Lasker, 1991; Lasker et al., 1996). The latter work includes data on the dynamics of sponge communities collected by Janie Wulff (Wulff, 1991, 1997).

Over the 20 years of its existence, research supported by the San Blas field station produced 363 publications on the biology of plants and animals living on the coral reefs around the station, at a peak annual operating cost of about US$100,000. The cheapness of this operation provides a startling example of how effective a small station can be for very little expense, so long as the necessary tools for field research are supplied: grass huts for living, rainwater for drinking and washing, communal kitchens, small boats, a scuba compressor, and, above all, field sites in calm clear water at the station's doorstep.

Local political events in this autonomously governed indigenous reserve led to the closure of the San Blas station in 1998. Although this closure terminated the activities of STRI staff scientists in that area for some time, several external researchers were able to make private arrangements to continue their work there. After the closure of the San Blas station the center of STRI's Caribbean research efforts moved to Bocas del Toro Province, at the opposite end of the Caribbean coast of Panama.

Bocas del Toro Research Station (BRS)

The Smithsonian Institution (SI) has a long history of terrestrial and geological research in Bocas del Toro Province. In the 1970s and 1980s Charles Handley of the Natural History Museum mounted a number of expeditions to the province to survey the mammal and bird fauna (Handley, 1993; Anderson and Handley, 2002). This phase was followed with ground-breaking geological work by STRI's deputy director, Anthony Coates. He used the rock outcrops in the province, which contain the most complete record of marine environments of the last 10 million years in the southern Caribbean, to help clarify events associated with the rise of the Isthmus of Panama (Collins et al., 1995; Collins and Coates, 1999; Coates et al., 2005).

In 1998 STRI purchased 6 hectares (ha) just outside the town of Bocas del Toro on Isla Colon. A dormitory was built on the site in 2001 and a modern, well-equipped laboratory in 2003. The BRS now houses 28 resident scientists and will soon add accommodation for 16 more. BRS can now host approximately 325 scientific visitors from more than 30 countries each year: 40% undergraduates, 25% graduate students, 10% postdoctoral fellows, and 25% researchers. About half the postdoctoral fellows and researchers are SI scientists. Research at the station has resulted in 201 scientific publications in the five years since its inauguration in 2003, with Rachel Collin as its director.

The BRS is now among the preeminent research stations in the Caribbean. It is better equipped and provides access to a larger diversity of habitats than almost any other research facility in that region. The wealth of natural diversity available near BRS combined with technical support facilities is reflected in the wide range of research projects that are conducted at the station. Significant research has focused on the coral bleaching response to stress and disease. These studies have shown that sugars are one of the most damaging components in pollution from rain runoff (Kline et al., 2006) and that coral disease is related to temperature stress. An SI fellow identified candidate genes that participate in coral's bleaching response to elevated temperature (DeSalvo et al., 2008). Research at the laboratory also has shown that some coral disease and death in the Caribbean results from a protozoan infection. Another strong line of research at the BRS is the investigation of the factors that lead to speciation in the marine environment. Groundbreaking work on hamlet fishes has shown that mate choice based on color pattern may drive divergence and that color patterns may evolve via aggressive mimicry, a previously undemonstrated mechanism of diversification (Puebla et al., 2007, 2008).

The BRS is also a local focus of taxonomic work and studies aimed at documenting marine biodiversity that were published in a special issue of the *Caribbean Journal of Science* dedicated to the marine environment and fauna of Bocas del Toro (Collin, 2005a, 2005b). Extensive work has been done there on the taxonomy of marine shrimps (Anker et al., 2008a, 2008b, 2008c). Bocas del Toro is a global hotspot of shrimp diversity and ranks within the top 10 sites in the world. More than 20 new shrimp species from Bocas del Toro have been described in the past five years. New species of other marine organisms, including snails, tunicates, sponges, flatworms, and meiofauna, have also been described on the basis of work at the BRS. As a result of these taxonomic and faunal studies, Bocas del Toro has the highest recorded tunicate diversity anywhere in the Caribbean and the third highest sponge diversity.

Other long-term projects based at BRS include studies focused on breeding success at major Caribbean turtle nesting beaches, the effects of noise pollution and tour boat operations on dolphin vocalization and behavior, effects of anthropogenic substrates, such as docks, on invasive tunicate abundance, effect of nutrient limitation on mangrove forest structure and diversity, emerging sponge diseases, and Caribbean-wide speciation in *Montastraea* corals caused by temporal shifts in spawning cycles.

Naos Island Laboratories

Naos is one of a cluster of four islands at the end of a 2 km long causeway at the Pacific entrance to the Panama Canal. STRI's first marine laboratory was established there in 1964 in an old military bunker and has since expanded to four buildings, three of them ex-US Navy buildings refurbished by STRI. This laboratory provides ready access to the upper bay of Panama with its extensive mangroves and a scattering of inshore islands, plus the coral reefs of the Perlas Archipelago, 50 km away. The laboratory complex, with a flow-through aquarium system, diving locker, small boat support, research vessel, and molecular laboratories, supports a wide range of research by all the marine scientific staff. Organismal studies based primarily at Naos cover or have covered the following topics: the Panama Canal as a hub for marine invasions, rocky intertidal community ecology, physiological ecology, behavioral ecology of intertidal organisms, coral reef development in the TEP, molecular evolution of marine organisms, life history evolution and evolution of mode of development, and marine zooarchaeology.

Panama as a Hub for Marine Invasions

Biological invasions are a potent force for change across the globe. Once established, introduced species can become numerically or functionally dominant, threatening native biodiversity and altering ecosystem processes. The flip side to the damage they cause is that introduced species can provide opportunities for insight as large-scale experiments to understand ecological and evolutionary processes. In marine and coastal environments, shipping is a major pathway for biological invasions and appears largely responsible for the recent dramatic increase in invasions.

Beginning with the studies of Hildebrand (1939) in the 1930s, followed by several investigations surrounding the potential problems associated with the construction of a sea-level Canal in Central America (Rubinoff, 1965, 1968; Rubinoff and Rubinoff, 1969), STRI has been central in evaluating the role of the Canal as a passageway for shorefishes. Interestingly, despite the Canal's 100 years of existence and the occurrence of approximately 1,500 species of marine and brackish-water fishes on the two coasts of Panama, only a handful of such species have successfully passed through the Panama canal and established populations in the "other" ocean. For example, only 8 species of such successful immigrants are known in the tropical eastern Pacific and only 3 have spread beyond the immediate confines of the Pacific entrance to the canal. Why are there so few successful invasions through a short, suitable corridor? Why do some invasions fail and others succeed? Panama and its canal have much to offer studies aimed at determining success or failure of invasions.

STRI is ideally situated to study marine and coastal invasions. Panama is one of the world's largest hubs for shipping. The Canal serves as an aquatic corridor connecting the Atlantic and Pacific Ocean basins, and ports on either side serve as hubs for international trade. Since its opening in 1914, approximately 800,000 ocean-going commercial vessels have passed through the Canal. Today, approximately 12,000 to 14,000 commercial ships transit the Canal annually (Ruiz et al., 2009). Moreover, Panama is initiating a major effort to expand shipping in the Canal by constructing additional locks on the Pacific and Atlantic coasts. Although the freshwaters of Lake Gatun, a large lake that constitutes the bulk of the canal, have strongly limited the inter-oceanic invasions of purely marine species, the new locks being added to the canal have the potential to increase the salinity of Gatun Lake and increase such interchange. With the Naos and Galeta marine laboratories strategically located at the Pacific and Atlantic entrances to the Canal, STRI is well positioned to continue to conduct a broad range of basic research on marine invasions.

In contrast to the limited exchange of fishes across the Isthmus, various introduced invertebrate species have been documented recently in the Canal, underscoring the fact that invasions are occurring. Some examples include a North American mud crab that has established a population in the Panama Canal expansion area (Roche and Torchin, 2007) and an invasive Japanese clam that reaches densities greater than 100 m^{-2} in the Canal, as well as an invasive snail that is known to host medically important trematode parasites. Although there are likely other such species, with few exceptions (Abele and Kim, 1989) invertebrate diversity of the Canal remains largely unexplored. Recently, STRI and SERC scientists teamed up to evaluate the role of the Canal in biological invasions and determine how patterns and processes driving invasions in tropical and temperate regions may differ.

Although the potential for invasions in Panama is likely to be high, with the exception of studies on fishes that have passed through the Canal in the past 40 to 50 years, we know surprisingly little about other coastal invasions that have resulted, and many established invasions probably have been overlooked (Miglietta and Lessios, 2009). With the current expansion of the Panama Canal, evaluating the importance of the Canal in regional and global invasions is arguably an imperative goal for the conservation of our coastal resources and an ideal opportunity to illuminate our understanding of biological invasions.

Rocky Intertidal Community Ecology

The rocky intertidal zone of the TEP appears to be largely bare rock, with very little macroalgal cover and few sessile invertebrates, which are not distributed in clear zones according to tidal height or wave exposure. The striking contrast between this system and those of temperate North America and Europe, which are well vegetated and have an abundance of invertebrates in regularly arranged zones, drew researchers such as Jane Lubchenco (currently director of the NOAA) and Bruce Menge to STRI in the late 1970s to seek an explanation. Their field exclusion experiments indicated that year-round predation and herbivory by a diverse community of highly mobile fishes, crabs, and mollusks forces their prey into refugia in cracks and under boulders and regulates directly, or indirectly, species interactions such that species capable of dominating space are kept in check (Menge and Lubchenco, 1981; Menge et al., 1986).

Physiological Ecology

The marine environment of the eastern Pacific is much more variable than that of the Caribbean, especially so during upwelling and in shallow-water and intertidal habitats. Temperatures in tidal pools at Naos range between approximately 18°C and more than 50°C. Jeffery Graham made contributions to basic understanding of how fishes and sea snakes contend with this and other physiological challenges in the TEP (Graham, 1970, 1971) and later investigated heat regulation in tunas (Graham, 1975). Ira Rubinoff, together with Graham and Panamanian cardiologist Jorge Motta, performed pioneering work on the temperature physiology and diving behavior and respiratory physiology of the neotropics' only sea snake species (Graham et al., 1971; Rubinoff et al., 1986).

Behavioral Ecology of Intertidal Animals

Marine behavioral and estuarine (soft-bottom) ecology has been the focus of long-term research programs by John Christy and his students on the reproductive ecology (larval release cycles in relation to predation risks; Morgan and Christy, 1995) and behavior (burrow ornaments as sexual signals; Christy et al., 2002) of intertidal crabs, particularly fiddler crabs. The latter reach their highest species diversity in the world on the Pacific coast of Central America (Sturmbauer et al., 1996). Christy recently completed five years of daily observations of the reproductive timing of a fiddler crab on Culebra beach, the results of which demonstrate that these crabs have a remarkable ability to track, on several time scales, complex variation in environmental conditions suitable for larval release. Research by Christy's lab on mechanisms of mate choice in fiddler crabs has shown that male courtship signals elicit responses in females that have been selected by predation, not because the signals lead to choice of the best male as a mate. This research has provided the best empirical support to date for the "sensory trap" mechanism of sexual signal evolution (Christy, 1995; Backwell et al., 2000, Kim et al., 2009). Together with work by terrestrial biologists at STRI, this research has made STRI a global center for the study of the evolution of sexual signals.

Coral Reef Development in the Tropical Eastern Pacific (TEP)

Following the closure of the isthmus, different components of the tropical biota of the TEP reacted in different ways to resultant dramatic changes in the local marine environment. Most of the coral fauna was wiped out (~85% of the current, depauperate fauna is derived from Indo-Central Pacific immigrants), probably largely by extreme environmental fluctuations during ENSO events. Documentation of effects of environmental changes on coral reef development in that area has been the focus of 35 years of studies by Peter Glynn and his collaborators, not only in Panama but also further afield in the TEP in places such as the Galapagos (Glynn et al., 1979; Glynn and Wellington, 1983). STRI research on Panama's Pacific coral reefs began in the earlier 1970s, when, contrary to previous ideas, fully developed coral reefs were found in the Gulfs of Panama and Chiriquí (Glynn, 1972; Glynn et al., 1972; Glynn and Stewart, 1973). It also became evident that differences in reef growth in those gulfs were related to their different temperature regimes (Glynn and Stewart, 1973). Coral reefs in the Gulf of Panama are mainly confined to the warmer sides of the Pearl islands and grow at lower rates than reefs in the year-round warmth of the Gulf of Chiriquí (Glynn and Macintyre, 1977). The latter reefs grow at rates comparable to those on the Caribbean coast of Panama (Macintyre and Glynn, 1976), and corals in each gulf differ in their responses to temperature (D'Croz et al., 2001; Schloeder and D'Croz, 2004). A major thrust of work on TEP reefs has been to understand the effects of ENSO warming events on the survival and dynamics of reef ecosystems. Observations linked coral bleaching in Panama to high-temperature anomalies of the severe 1982–1983 ENSO (Glynn et al., 1988; Glynn and D'Croz, 1990; Glynn et al., 2001). Such bleaching led to region-wide mass coral mortality during the intense 1982–1983 and 1997–1998 ENSO events (Glynn, 1984; Glynn et al., 2001). Microcosm experiments at STRI confirmed that temperature stress produced bleaching and mass mortality of corals (Glynn and D'Croz, 1990) and that slow-growing massive species are more resistant than branching types to temperature-induced beaching (Huerkamp et al., 2001). There has been continuous monitoring of reef recovery since the mass coral mortality produced by the 1982–1983 ENSO, providing one of the longest term databases of this type in the world (Glynn, 1984, 1990; Glynn and Colgan, 1992; Glynn et al., 2001). Major efforts have also been made to investigate the reproductive ecology of corals, relating fecundity, spawning activity, and recruitment of surviving species to community recovery and reef resilience in Pacific Panama (Glynn et al., 1991, 1994, 1996, 2008; Colley et al., 2006; Manzello et al., 2008). Bleaching patterns have been related not only to the diversity of zooxanthellae symbionts of corals (Glynn et al., 2001) but also to coral genotypes (D'Croz and Maté, 2004), with both factors likely playing an important role in adaptive responses by corals to climate change. Research on corals in Pacific Panamá additionally involves the taxonomy and biogeography of gorgonian soft corals (Vargas et al., 2008; Guzman and Breedy, 2008).

Molecular Evolution of Marine Organisms

STRI has played a leading role in development of molecular techniques for studies of marine organisms, not only in relationship to trans-isthmian biology of neotropical taxa (reviewed by Lessios, 2008) but also in studying the global biogeography of pantropical groups. A 30 year history of such work, the longest in SI, began with studies of sea urchins by Haris Lessios (Lessios, 1979). That work, although centered at the molecular laboraties at Naos Laboratory, has relied on all other STRI marine facilities for collections and maintenance of live organisms. Since that start, molecular evolution studies at STRI have undergone explosive growth. Such studies include assessments of effects of the rise of the isthmus on the ecology and biology of neotropical organisms (Collin, 2003a) and patterns and processes involved in the evolutionary divergence of such taxa (Knowlton and Weigt, 1998; Hurt et al., 2009). Molecular studies also have led to the delineation of species boundaries in marine organisms (Knowlton, 2000) and understanding of global historical biogeography of pantropical groups (Lessios et al., 1999, 2001; Collin, 2003a, 2003b, 2005a; Quenoiville et al., 2004), invasions of the tropical Atlantic by Indo-Pacific taxa around southern Africa (Bowen et al., 2001; Rocha et al., 2005a), patterns of dispersal among different tropical biogeographic regions within the Atlantic (Lessios et al., 1999; Rocha et al., 2002, 2005b), physiological mechanisms involved in species formation (McCartney and Lessios, 2002; Zigler and Lessios, 2004), non-allopatric speciation within biogeographic regions (Rocha et al., 2005a; Puebla et al., 2007, 2008), patterns and processes involved in speciation of corals (Fukami et al., 2004), and the history of two-way transfers of species across the 4,000–7,000 km wide Eastern Pacific Barrier, the world's widest stretch of deep open ocean (Lessios and Robertson, 2006). Molecular evolution studies at STRI have produced 163 marine-themed publications to date.

Marine Archaeology: Historical Human Reliance on Marine Resources in Panama

Zooarchaeology has played an important role in STRI's anthropology program for the past 40 years (Linares and Ranere, 1980) through studies originated by Richard Cooke of pre-Columbian usage of marine resources in Panama, primarily in Panama Bay (Cooke, 1981). The expanding reference collection of 1,540 skeletons of 340 species of fishes and other organisms used in this research has also enhanced knowledge of the zoogeography of these organisms (Cooke and Jiménez, 2008b). This work has charted the time course of geographic changes in patterns of marine resource usage in Panama Bay. By 7,000–4,500 bp, humans on the shores of that bay exploited a wide variety of inshore marine resources, including more than

80 species of marine fishes (bony fishes, sharks, sawfish, sting rays) taken in a variety of different habitats (beaches, mangroves, estuaries, reefs, open water) using various methods (hook-and-line, nets, stationary wood-and-stone traps) (Cooke, 1992; Cooke and Jiménez, 2004, 2008a; Cooke et al., 2008). Other marine resources used include sea turtles, dolphins, manatees, and seabirds. The ritual importance of marine animals in pre-Columbian Panama is underlined by frequent images of sea turtles, fish, and marine invertebrates on pottery and goldwork (Linares, 1977; Cooke, 2004a, 2004b). Although currently there is no convincing zooarchaeological evidence for overfishing in pre-Columbian times in Panama, ongoing research in the Pearl Islands seems likely to identify pressures that produced changes to populations of mollusks and reef fish around individual islands. Intensive collection of colorful marine shells and marine birds for making ornaments likely led to local impacts on populations of these taxa.

Rancheria Island Field Station

Rancheria Island is situated in the center of the largest and best managed marine reserve in Panama: the Coiba National Park (and World Heritage Site) in the Gulf of Chiriqui. The park area has a long history of environmental protection (Coiba acted as a "free-range" prison island for almost 85 years) and hosts the largest area of coral reefs and richest [number of species] accumulation of corals on the entire continental shore of the TEP. A tiny, relatively undeveloped field station at Rancheria has supported research on coral reefs in the surrounding area by Peter Glynn and his collaborators (see above).

The Research Vessels

Four vessels were operated by STRI between 1970 and 2008: the 65-foot *Tethys* (1970–1972), the 45-foot RV *Stenella* (1972–1978), the 63-foot RV *Benjamin* (1978–1994), and the 96-foot RV *Urraca* from 1994 to 2008. None of those vessels was purpose built. The equipping of the *Urraca*, after its purchase, with an A-frame and oceanographic winch allowed intensive trawling and dredging activities (to depths of 250 m) and thus greatly extended the range of studies that could be supported beyond the previous emphasis on scuba-based research. These research vessels, and particularly the *Urraca*, enabled fieldwork in remote locations that lacked land bases for marine research and thus vastly extended the geographic reach of STRI biologists. The *Urraca* acted as such a base not only throughout Panama's territorial waters but also in localities as far afield as Clipperton Island (1,000 km west of Acapulco) in the Pacific (Robertson and Allen, 2008) and Honduras in the Caribbean (Guzman, 1998).

To date, 14 years service by the *Urraca* has produced 350 scientific publications. Research supported by the *Urraca* proved vital to the declaration of two large Marine Protected Areas (MPAs) on the Pacific coast of Panama, principally through the research activities of H. Guzman on coral diversity and conservation (see below). *Urraca* support of collecting along the entire Pacific coast of Panama, as well as Costa Rica, Clipperton and Cocos Islands (remote oceanic islands in the eastern Pacific), and El Salvador was essential for the development of the world's first online information system on a regional shorefish fauna (www.stri.org/sftep). In addition the *Urraca* provided extensive and extended support to the Panama Paleontology Program (see below) and for collecting fishes (Bermingham, Robertson), echinoderms (Lessios), soft corals (Guzman), and mollusks (Collin) for taxonomic and evolutionary studies, and hydrologic surveys (D'Croz).

HISTORICAL MARINE ECOLOGY: THE PANAMA PALEONTOLOGY PROJECT

STRI is unique in having an institutional marine program that includes both biology and geology, as well as a series of strong programs in various aspects of tropical terrestrial biology. Intellectual cross-fertilizations between scientists steeped in terrestrial and marine systems have maintained STRI as a place known for creative research.

The striking differences in environmental conditions and ecology from opposite sides of the Isthmus of Panama today, and their changes over time during Isthmus closure, provides marine paleontologists with a "natural experiment" with which to address, on an evolutionary and ecologically large scale, the impact of environmental change and genetic isolation on marine invertebrate faunas. In 1986 the Panama Paleontology Project (PPP) was initiated by Jeremy Jackson and Anthony Coates. Their aim was to survey coastal sediments of the isthmian area to establish if the fossil record were sufficiently complete to explore the evolutionary responses of marine communities to the gradual emergence of the Isthmus of Panama.

Stratigraphically complete Neogene deposits were soon discovered in the Panama Canal basin and Bocas del Toro, and excavations were subsequently extended to several other richly fossiliferous regions of Panama and Costa Rica, Venezuela, Ecuador, Jamaica, and the Dominican Republic. In addition, large-scale benthic surveys of modern shallow-water communities across the Caribbean and Tropical Eastern Pacific serve as a baseline for understanding biotic changes through geological time.

The PPP has so far involved more than 50 scientists from 20 institutions in seven countries and undertaken almost 40 expeditions to eight countries. The resultant collections comprise thousands of replicated samples and many millions of individual, quantitatively collected fossil specimens. The rigorous paleontological framework of the PPP presents evolutionary biologists with a unique view of 15 million years of life and environments in a tropical region. Using these samples and framework, the PPP has documented the environmental, lithologic, and biological changes in Isthmian nearshore marine habitats from 15 Ma to the present day, producing almost 200 publications to date (see http://www.fiu.edu/~collinsl/pppcon.html).

Placing igneous and sedimentary rock formations in sequence established a high-resolution stratigraphic system that was critical to effectively reconstruct patterns of biological change (Coates et al., 1992, 2005; Collins et al., 1996b; Collins and Coates, 1999). Aligned with taxonomic and paleoenvironmental analyses, these geological studies also permit reconstructions of land and water masses as the isthmus shoaled, providing dates of final closure that are essential for estimates of the timing of divergence of modern marine organisms (Collins et al., 1995; Coates and Obando, 1996) (Figure 3).

Data from PPP studies have revealed the following. (i) Faunal composition of Caribbean and Pacific fossil assemblages and the timing of paleoenvironmental change demonstrate that major cross-isthmian marine connections ceased approximately 3 Ma (Collins et al., 1995, 1996a; Coates et al., 2003, 2005; O'Dea et al., 2007a), consistent with dates from previous (non-PPP) oceanographic studies. (ii) Seasonal upwelling was strong in what is now the southwestern Caribbean (SWC) before isthmian closure, and constriction of the forming isthmus led to a rapid decline in upwelling intensity, resulting in a collapse in primary productivity from around 5 to 3 Ma (Collins, 1996). The increasing oligotrophy allowed reefal habitats to expand in the SWC while reducing the amount of filter-feeding molluscan habitat, and the cessation of upwelling also stabilized environments to modern-

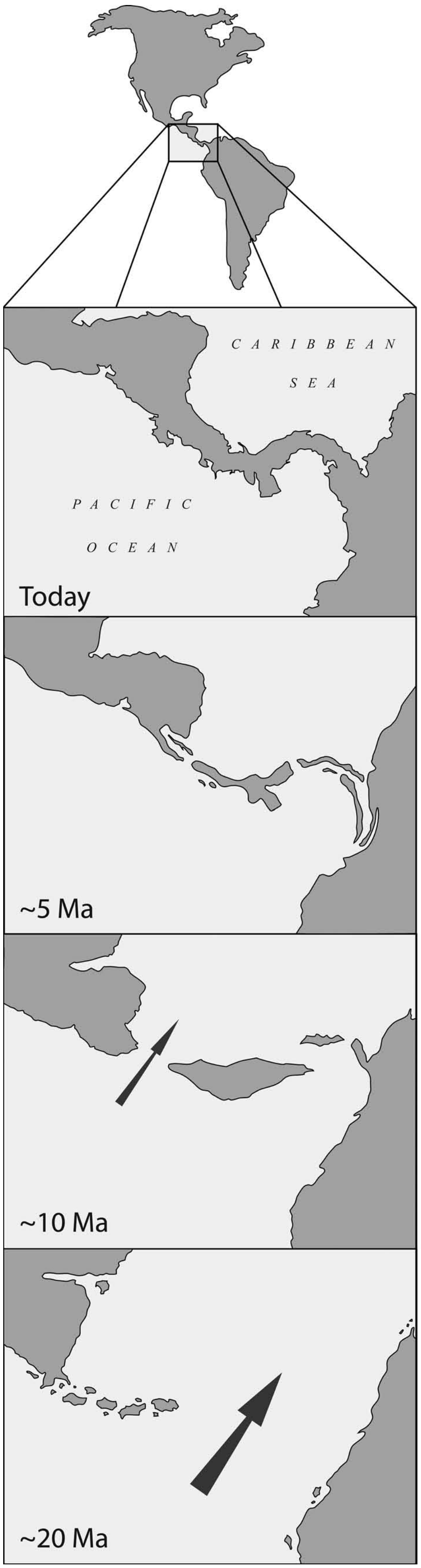

FIGURE 3. Formation of the Isthmus of Panama during the last 20 million years (Ma = million years ago). Arrows indicate direction of principal water flow through the Central American Seaway. (From O'Dea et al., 2007b.)

day conditions (O'Dea et al., 2007a; Jackson et al., 1999). Meanwhile, upwelling continued in what is now the TEP to the present day. (iii) A wide assortment of marine taxa experienced a major turnover in the now-SWC during the last 10 million years (Jackson et al., 1993; Jackson and Johnson, 2000; O'Dea et al., 2007a; Smith and Jackson, 2009). Origination of new species in all major groups of macroinvertebrates peaked at about 5–3 Ma, coincident with the formation of new habitat along the SWC coast of the Isthmus. (iv) From approximately 5–3 Ma the SWC remained connected to the TEP but coastal conditions became instable. This transition period saw most SWC faunas reach their peaks in diversity (Jackson and Johnson, 2000; Todd et al., 2002; Smith and Jackson, 2009). As old and new species coexisted in time, richness of most groups was around 30% to 60% higher than in the modern SWC. (v) Following isthmus closure and the birth of the modern-day Caribbean, a widespread extinction reduced numbers of gastropod, bivalve, coral, and bryozoan taxa by 30% to 95%. (vi) This massive extinction was strongly selective against nutriphilic taxa, indicating that the collapse in primary productivity was the causal mechanism. However, fine-scale environmental and community composition data reveal that extinction in most groups lagged well behind the shift to more oligotrophic conditions as the Isthmus closed (O'Dea et al., 2007a) (Figure 4). Time lags of this scale challenge the conventional wisdom that cause and effect have to be contemporaneous in macroevolution. (vii) Other ecological characteristics of organisms also shifted dramatically. Average coral colony and snail egg-size increased, larval durations of scallops decreased, and rates of clonality in free-living bryozoans declined dramatically. Ongoing field and laboratory work aims to analyze the fates and trajectories of clades that preserve modes of life, life histories, and feeding strategies in fossils within the rigorous framework provided by the PPP. This approach will help tease apart the drivers of macroevolutionary change in the neotropical seas (Jackson and Erwin, 2006).

MARINE EDUCATION AND OUTREACH

At the level of both the institution and the individual scientist, STRI, along with other SI bureaus, has become deeply involved in two global efforts connected with marine biodiversity: the Census of Marine Life (COML) and the Consortium for the Barcode of Life (CBOL). The COML aims to provide rapid and full documentation of marine biodiversity, while CBOL provides easy

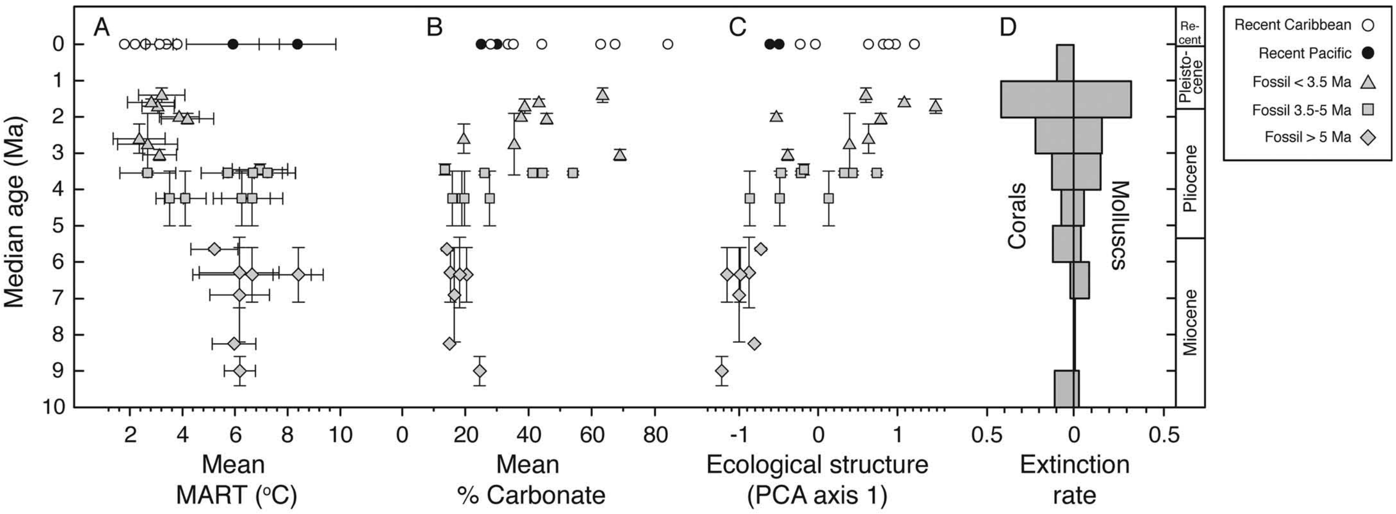

FIGURE 4. The sequence of environmental and ecological changes in the southwest Caribbean in response to the closure of the isthmus of Panama (Ma = million years ago). A. Upwelling intensity, as estimated by the mean annual range of temperature (MART), shifted rapidly from high values similar to the modern-day tropical eastern Pacific values to modern Caribbean values. B. Carbonate levels in sediments followed suit, with an increase in the Caribbean. C. Biotic assemblages shifted from mollusk-dominated to a mix of coral-, algae-, and mollusk-dominated communities (PCA = principal components analysis). D. Extinction rates of corals and mollusks peaked 1–2 million years after the environmental and ecological changes. (From O'Dea et al., 2007a.)

molecular means to confirm the identities of a broad array of species in both marine and terrestrial ecosystems. Substantial contributions of information on neotropical marine organisms have been made by STRI to both those efforts. Recently, the Encyclopedia of Life (EOL) began to make use of information generated by STRI scientists, and STRI also recently became part of the United States Geological Survey's Caribbean tsunami monitoring network.

Educational and outreach programs at STRI include a marine fellowship program for graduate students (worldwide, plus targeted to Latin America), hosting of K–12 school groups and teacher training (at Galeta Point Marine Laboratory and Bocas del Toro Research Station), conducting public seminars, responding to requests for information from Panamanian government entities, and supporting graduate student courses. The public marine education program at STRI consists of a series of activities aimed at promoting awareness and conservation of marine environments and communicating its research to the general public. Since 1992 the program has consisted of docent-led educational visits, seminars for teachers, and the development of educational materials (posters, newspapers and supplements, exhibits), and curricular materials for the classroom.

Culebra Island Education Center

The Punta Culebra Nature Center (PCNC) of STRI lies at the Pacific entrance to the Panama Canal immediately adjacent to the Naos Laboratory. For nearly a century, access to Culebra was restricted to U.S. military personnel, a practice that protected Culebra's shoreline organisms, which now exist in abundances not seen elsewhere in Panama Bay. The general health of the intertidal and shallow-water marine communities at Culebra makes the area especially attractive for research. Culebra has been a major research site for John Christy (since 1983), Mark Torchin (since 2004), and their students.

The PCNC relies on the support of the Smithsonian Foundation of Panama and international entities. The academic and public programs at Culebra encourage direct experiences with organisms in the local habitats and in touch pools. Exhibits promote environmental awareness, understanding, and conservation, emphasizing marine systems. Since it opened in 1996, 750,000 people have visited PCNC, with about 25,000 schoolchildren annually taking part in its educational program. The PCNC also fosters research on site, which allows visitors to see STRI scientists and students "in action."

Galeta Point Marine Laboratory

The education and outreach program at Galeta Laboratory was initiated by Stanley Hecakdon in 2000 to build bridges between research at Galeta on coral reefs, seagrass beds, and mangrove forests and the schools of Colon and wider Panama. The program seeks to motivate public interest on the importance of the sciences and the value of coastal tropical habitats, currently under severe threat because of a destructive style of economic development. Private donors have been vital to the success of this program, funding the construction of enhancements to Galeta buildings, a 300 m long mangrove boardwalk, and science equipment used by the program.

Attendance in the student education program climbed from 200 from an orphanage in nearby Colon in 2000 to a current 10,000 per year from all over Panama. These programs are hosted by 12 nature guides and 19 volunteers. Recently, the first live Internet broadcast was made from Galeta to elementary schools in New Jersey. The next step will be an online program to schools in Colon and, eventually, the rest of Panama. Galeta's public outreach program began in 2003 with the support of students from McGill University's "Panama Field Semester Studies." The first project was a socioeconomic study of a local fishing community, with fishermen then being trained in nature tourism to provide an alternative source of income. In 2006 Galeta began the Smithsonian Talk of the Month, at which STRI researchers share their work with the people of Colon. Teacher training aimed at raising the quality of science education in Colon started in 2007. To date 120 local elementary and high school teachers have been trained. Galeta laboratory also participates in a variety of community events: the yearly community beach cleanup; scientific and environmental fairs; and events such as Bio Diversity Day, World Mangrove Day, and Earth Day.

Bocas del Toro Research Station

The BRS has had active public programs, almost entirely funded by income from station fees, since the completion of the main laboratory building in 2003. Activities organized by the BRS for the general public include bimonthly public seminars given by researchers working at the station as well as weekly open houses and an annual Earth Day beach clean-up. In addition the Station opens its doors to the public during the annual Feria Ambiental weekend, at which environmental non-governmental organizations (NGOs) and governmental organizations from the region present information to the public, debate local conservation issues in a round-table format, and give public lectures on their projects. This Feria has proven to be highly successful, with representatives form organizations such as IUCN (International Union for Conservation of Nature) and The Nature Conservancy attending from Costa Rica and Panama City.

The BRS also has an active program working with local schools. School groups visit the station three days a week during the school year, and a biodiversity summer program is available for interested children on Isla Colon and Bastimentos. More than 1,000 children per year participate in these programs or, in more remote areas, receive visits from presenters of the public programs. Finally, the Station presents an annual teacher training workshop, which offers teachers development credit for learning about environmental issues and conservation.

The BRS is also active in undergraduate and graduate teaching. The station hosts undergraduate courses from 12 institutions from the USA, Colombia, Canada, and Germany and trains graduate students in the advanced Training in Tropical Taxonomy Program. This program aims to bring taxonomic experts and experts in training together in the field to provide hands-on training in taxonomy. This program focuses on groups for which taxonomic expertise is in immediate danger of disappearing. This program, the only one of its kind in the Neotropics, has so far trained 100 students from 30 countries and receives some funding from the National Science Foundation Pan-American Advanced Studies Institutes (NSF PASI) program as well as individual Assembling-the-Tree-of-Life grants.

The Online BRS Bilingual Biodiversity Database

The public face of the Bocas del Toro Research Station extends into cyberspace. The Online BRS Bilingual Biodiversity Database, available at http://biogeodb.stri.si.edu/bocas_database/?&lang=eng, has resulted from work at the BRS and now includes 6,000 species and 8,000 photos of organisms from Bocas del Toro province. This website is supplemented by printed identification guides to local organisms (Collin et al., 2005).

MARINE ZOOARCHAEOLOGY

The zooarchaeology reference collection at STRI is frequently used by students and researchers to identify archaeofaunal materials. Specimens are often loaned or donated to outside institutions. Panamanians have strong interests in their cultural heritage, and STRI zooarcheologists frequently give public lectures in Panama on the history of human–animal interactions in Panama and the relevance of zooarchaeology to tropical zoogeography and biodiversity. STRI's Bioinformatics office recently started work on an online database that will provide photographic, geographic, and biometric information on all identified zooarchaeological materials and specimens from Panamanian sites.

ONLINE INFORMATION SYSTEM ON TROPICAL EASTERN PACIFIC SHOREFISHES

This Shorefishes of the Tropical Eastern Pacific Online Information System (www.stri.org/sftep) exemplifies the Smithsonian's commitment to carrying information that its research generates to the widest possible audience. It provides free, public access to comprehensive information on the biology of almost 1,300 shorefish species. Systems such as these are useful for managers, biologists, students, and fishers wanting to identify fishes and obtain information about their biology. The information that systems such as this bring together allows comprehensive assessments of our level of knowledge about biodiversity (Zapata and Robertson, 2006) and regional geographic distribution of that diversity (Mora and Robertson, 2005; Robertson and Cramer, 2009).

MARINE CONSERVATION ACTIVITIES

The work that STRI biologists, notably Hector Guzmán, have done on organisms as diverse as corals, sea cucumbers (Guzman et al., 2003), conchs (Tewfik and Guzman, 2003), lobsters, and crabs (Guzman and Tewfik, 2004) has been instrumental in the establishment not only of management regulations for specific organisms but also of a large marine reserve on the Pacific coast of Panama: the Pearl Islands Special Managment Area in the Gulf of Panama (Guzman et al., 2008a). In addition, efforts by Todd Capson and research on corals by Hector Guzman (see Guzman et al., 2004) were instrumental in the declaration of Coiba National Park (where Rancheria Island is situated) as a World Heritage Site in 2005. In 2009 Panama's government established the Matumbal Reserve, a STRI-managed marine reserve that protects 34 ha of reefs, seagrass beds, and mangroves immediately adjacent to BRS. This reserve will ensure maintenance of the research potential of the station in an area of explosive tourism and developmental growth. During 2008–2009 STRI (primarily through the efforts of Juan Maté) has been involved with the recently completed development of a comprehensive zoning and management plan for Coiba Park and workshops aimed at informing government resource managers about the utility, methods, and needs of STRI's marine research activities.

The online information system on TEP shorefishes (see above) provided the primary database used in the first comprehensive IUCN Redlist Assessment of an entire regional shorefish fauna through workshops held in Costa Rica (2008) and Panama (2007). An equivalent information system encompassing more than 1,500 species of Greater Caribbean shorefishes, currently in production, will facilitate an equivalent Redlist assessment planned for the Greater Caribbean regional shorefish fauna.

Marine conservation activities by STRI staff also have a global and historical reach through the work of J. B. C. Jackson and colleagues on historical declines of coral reef growth and organisms induced by human activities, and the depletion of their marine resources, in the Caribbean area and throughout the rest of the tropics (Jackson, 1997, 2001; Jackson et al., 2001; Pandolfi et al., 2003, 2005; Pandolfi and Jackson, 2006).

BRS has been a member of CARICOMP (the Caribbean Coastal Marine Productivity Program) since 1997, contributing data to Caribbean-wide monitoring of seagrasses, corals, and mangroves (Collin, 2005a; Collin et al., 2009; Guzman et al., 2005). BRS also recently became part of a global IUCN program to assess the resilience of coral reefs worldwide. As part of this program, rapid assessments of the state of coral reefs at each site are linked to long-term monitoring of physical environmental data to predict the local response to future bleaching stress from elevated temperatures. Since 2000 STRI has also been involved with Conservation International, the United Nations Environmental Program, the International Union for the Conservation of Nature, and the governments of Panama, Costa Rica, Colombia, and Ecuador in an effort to develop the Eastern Tropical Pacific Seascape. This 2.1 million km^2 marine conservation area, in the equatorial part of the TEP, is based on a cluster of Marine Protected Areas, among them the Coiba National Park (see also Guzman et al., 2008a).

2008—A TIME OF TRANSITION

After 48 years and 1,800 publications the marine program, which remains an integral part of research at STRI, is undergoing rapid change. The year 2008 marked the end of an era, with the retirement of Ira Rubinoff and the succession of Eldredge Bermingham as STRI director. It also marked the start of a hiatus in the research vessel program, with the retirement of the RV *Urraca*, as its absence leaves a significant gap in research capability that STRI seeks to rapidly fill. The continuing development of the laboratory at Bocas del Toro will open up new opportunities for research. The development of a facility at Rancheria Island, and, perhaps, the Pearl Islands would greatly enhance accessibility of coral reefs and other marine habitats in the two largest nearshore archipelagos in the equatorial part of the eastern Pacific, archipelagos that to date have experienced relatively low impacts from economic development. STRI geologist Carlos Jaramillo is currently taking advantage of a unique event—major excavations to widen the Panama Canal—to clarify the history of the formation of the isthmus and thus help shed light on the history of changes in the neotropical marine ecosystems and the evolution of their organisms. In future STRI also will emphasize the development of tools that exploit the World Wide Web to enhance the diffusion of knowledge derived from its marine research, both through its own Bioinformatics office and through participation in global enterprises such as the Census of Marine Life, the Consortium for the Barcode of Life, and the Encyclopedia of Life. STRI's marine program will play an increasingly important role in efforts to understand the role of the oceans in global climate variability, interactions between terrestrial and marine ecosystems, and the response of marine ecosystems to climate change and more direct human-induced stresses.

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Scholarly Studies Program, the Women's Committee, the Hunterdon and Johnson Oceanographic Research Funds, and the Marine Science Network.

LITERATURE CITED

Abele, L. G., and W. Kim. 1989. The Decapod Crustaceans of the Panama Canal. *Smithsonian Contributions to Zoology*, 482:1–50.

Anderson, R. P., and C. O Handley Jr. 2002. Dwarfism in Insular Sloths: Biogeography, Selection, and Evolutionary Rate. *Evolution*, 56:1045–1058.

Andrefouet, S., and H. M. Guzman. 2005. Coral Reef Distribution, Status and Geomorphology: Biodiversity Rrelationship in Kuna Yala (San Blas) Archipelago, Caribbean Panama. *Coral Reefs*, 24:31–42.

Anker, A., C. Hurt, and N. Knowlton. 2008a. Revision of the *Alpheus cristulifrons* Species Complex (Crustacea: Decapoda: Alpheidae) with Description of a New Species from the Tropical Eastern Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 88:543–562.

———. 2008b. Revision of the *Alpheus formosus* Gibbes, 1850 Complex, with Redescription of *A. formosus* and Description of a New Species from the Tropical Western Atlantic (Crustacea: Decapoda: Alpheidae). *Zootaxa*, 1707:1–22.

———. 2008c. Revision of the *Alpheus websteri* Kingsley, 1880 Species Complex (Crustacea: Decapoda: Alpheidae), with Revalidation of *A. arenensis* (Chace, 1937). *Zootaxa*, 1694:51–68.

Backwell, P. R. Y., J. H. Christy, S. R. Telford, M. D. Jennions, and N. I. Passmore. 2000. Dishonest Signalling in a Fiddler Crab. *Proceedings of the Royal Society of London, B Biological Sciences*, 267:719–724.

Birkeland, C. 1977. The Importance of Rate of Biomass Accumulation in Early Successional Stages of Benthic Communities to the Survival of Coral Recruits. *Proceedings, Third International Symposium on Coral Reefs*, 1:16–21.

Birkeland, C., A. Alvarez Reimer, and J. R. Young. 1973. Effects of Oil on Tropical Shore Natural Communities in Panamá. Washington DC: Smithsonian Institution, Federal Water Quality Administration, U.S. Environmental Protection Agency.

Bowen, B. W., A. L. Bass, L. A. Rocha, W. S. Grant, and D. R. Robertson. 2001. Phylogeography of the Trumpetfishes (*Aulostomus*): Ring Species Complex on a Global Scale. *Evolution*, 55:1029–1039.

Christy, J. H. 1995. Mimicry, Mate Choice, and the Sensory Trap Hypothesis. *American Naturalist*, 146:171–181.

Christy, J. H., P. R. Y. Backwell, S. G. Goshima, and T. J. Kreuter. 2002. Sexual Selection for Structure Building by Courting Male Fiddler Crabs: An Experimental Study of Behavioral Mechanisms. *Behavioral Ecology*, 13:366–374.

Coates, A. G., M.-P. Aubry, W. A. Berggren, and L. S. Collins. 2003. Early Neogene History of the Central American Arc from Bocas del Toro, Western Panama. *Geological Society of America Bulletin*, 115:271–287.

Coates, A. G., J. B. C. Jackson, and L. S. Collins. 1992. Closure of the Isthmus of Panama: The Near-Shore Marine Record of Costa Rica and Western Panama. *Geological Society of America Bulletin*, 104:814–828.

Coates, A. G., D. F. McNeill, M. P. Aubry, W. A. Berggren, and L. S. Collins. 2005. An Introduction to the Geology of the Bocas del Toro Archipelago, Panama. *Caribbean Journal of Science*, 41:374–391.

Coates, A. G., and J. A. Obando. 1996. "The Geologic Evolution of the Central American Isthmus." In *Evolution and Environment in Tropical America*, ed. J. B. C. Jackson, A. F. Budd, and A. G. Coates, pp. 21–56. Chicago: The University of Chicago Press.

Coffroth, M. A., R. L. Lasker, M. E. Diamond, J. A. Bruenn, and E. Bermingham. 1992. DNA Fingerprints of a Gorgonian Coral: A Method for Detecting Clonal Structure in a Vegetative Species. *Marine Biology*, 114(2):317–325.

Colley, S. B., P. W. Glynn, A. S. May, and J. L. Maté. 2006. Species-Dependent Reproductive Responses of Eastern Pacific Corals to the 1997–98 ENSO event. *Proceedings of the 10th International Coral Reef Symposium*, 61–70.

Collin, R. 2003a. World-wide Patterns of Development in Calyptraeid Gastropods. *Marine Ecology Progress Series*, 247:103–122.

———. 2003b. Phylogenetic Relationships among Calyptraeid Gastropods and Their Implications for the Biogeography of Speciation. *Systematic Biology*, 52:618–640.

Collin, R., ed. 2005a. Marine Fauna and Environments of Bocas del Toro, Panama. *Caribbean Journal of Science*, 41:367–707.

Collin, R. 2005b. Ecological Monitoring and Biodiversity Surveys at the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. *Caribbean Journal of Science*, 41:367–373.

Collin, R., L. D'Croz, P. Góndola, and J. B. Del Rosario. 2009. "Climate and Hydrological Factors Affecting Variation in Chlorophyll Concentration and Water Clarity in the Bahia Almirante, Panama." In *Proceedings of the Smithsonian Marine Science Symposium*, ed. M. A. Lang, I. G. Macintyre, and K. Rützler, pp. 323–334. Smithsonian Contributions to the Marine Sciences, No. 38. Washington, D.C.: Smithsonian Institution Scholarly Press.

Collin, R., M. C. Diaz, J. L. Norenburg, R. M. Rocha, J. A. Sanchez, A. Schulz, M. L. Schwartz, and A. Valdes. 2005. Photographic Identification Guide to Some Common Marine Invertebrates of Bocas Del Toro, Panama. *Caribbean Journal of Science*, 41:638–707.

Collins, L. S. 1996. "Environmental Changes in Caribbean Shallow Waters Relative to the Closing Tropical American Seaway." In *Evolution and Environment in Tropical America*, ed. J. B. C. Jackson, A. F. Budd, and A. C. Coates, pp. 130–167. Chicago: University of Chicago Press.

Collins, L. S., A. F. Budd, and A. G. Coates. 1996a. Earliest Evolution Associated with Closure of the Tropical American Seaway. *Proceedings of the National Academy of Sciences of the United States of America*, 93:6069–6072.

Collins, L. S., and A. G. Coates, eds. 1999. *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*. Lawrence, Kans.: Allen Press.

Collins, L. S., A. G. Coates, W. A. Berggren, M.-P. Aubry, and J. Zhang. 1996b. The Late Miocene Panama Isthmian Strait. *Geology*, 24:687–690.

Collins, L. S., A. G. Coates, J. B. C. Jackson, and J. A. Obando. 1995. Timing and Rates of Emergence of the Limón and Bocas del Toro Basins: Caribbean Effects of Cocos Ridge Subduction? *Geological Society of America Special Paper*, 295:263–289.

Cooke, R. G. 1981. Los Hábitos Alimentarios de los Indígenas Precolombinos de Panamá. *Revista Medica de Panamá*, 6:65–89.

———. 1992. Prehistoric Nearshore and Littoral Fishing in the Eastern Ttropical Pacific: An Ichthyological Evaluation. *Journal of World Archaeology*, 6:1–49.

———. 2004a. "Observations on the Religious Content of the Animal Imagery of the 'Gran Coclé' Semiotic Tradition of Pre-Columbian Panama." In *Behaviour behind Bones. The Zooarchaeology of Ritual, Religion, Status and Identity*, ed. S. O'Day, W. van Neer, and A. Ervynck, pp. 114–127. Liverpool: Oxbow.

———. 2004b. "Rich, Poor, Shaman, Child: Animals, Rank, and Status in the 'Gran Coclé' Culture Area of Pre-Columbian Panama." In *Behaviour behind Bones. The Zooarchaeology of Ritual, Religion, Status and Identity*, ed. S. O'Day, W. van Neer, and A. Ervynck, pp. 271–284. Liverpool: Oxbow.

Cooke, R. G., and M. Jiménez. 2004. Teasing Out the Species in Diverse Archaeofaunas: Is It Worth the Effort? An Example from the Tropical Eastern Pacific. *Archaeofauna*, 13:19–35.

———. 2008a. "Marine Catfish (Ariidae) of the Tropical Eastern Pacific: An Update Emphasizing Taxonomy, Zoogeography, and Interpretation of Pre-Columbian Fishing Practices." In *Archéologie du Poisson: 30 Ans d'Archéo -ichtyologie au CNRS*, ed. P. Béarez, S. Grouard, and B. Clavel, pp. 161–180. Antibes: Éditions APDCA.

———. 2008b. Pre-Columbian Use of Freshwater Fish in the Santa Maria Biogeographical Province, Panama. *Quaternary International*, 185:46–58.

Cooke, R. G., M. Jiménez, and A. J. Ranere. 2008. "Archaeozoology, Art, Documents, and the Life Assemblage." In *Case Studies in Environmental Archaeology, 2nd Edition,* ed. E. J. Reitz, C. M. Scarry, and S. J. Scudder, pp. 95–121. New York: Springer.

Cubit, J. D., R. C. Thompson, H. M. Caffey, and D. M. Windsor. 1988. *Hydrographic and Meterological Studies of a Caribbean Fringing Reef at Punta Galeta, Panamá: Hourly and Daily Variations for 1977–1985*. Washington, D.C.: Smithsonian Institution Press.

D'Croz, L., J. B. Del Rosario, and P. Góndola. 2005. The Effect of Freshwater Runoff on the Distribution of Dissolved Inorganic Nutrients and Plankton in the Bocas del Toro Archipelago, Caribbean Panama. *Caribbean Journal of Science*, 41:414–429.

D'Croz, L., and J. L. Maté. 2004. Experimental Responses to Elevated Water Temperature in Genotypes of the Reef Coral *Pocillopora damicornis* from Upwelling and Non-upwelling Environments in Panama. *Coral Reefs*, 23:473–483.

D'Croz, L, J. L. Maté, and J. E. Oke. 2001. Responses to Elevated Sea Water Temperature and UV Radiation in the Coral *Porites lobata* from Upwelling and Non-upwelling Environments in the Pacific Coast of Panama. *Bulletin of Marine Science*, 69:203–214.

D'Croz, L., and A. O'Dea. 2007. Variability in Upwelling along the Pacific Shelf of Panama and Implications for the Distribution of Nutrients and Chlorophyll. *Estuarine, Coastal, and Shelf Science*, 73:325–340.

———. 2009. "Nutrient and Chlorophyll Dynamics in Pacific Central America (Panama)." In *Proceedings of the Smithsonian Marine Science Symposium*, ed. M. A. Lang, I. G. Macintyre, and K. Rützler, pp. 335–344. Smithsonian Contributions to the Marine Sciences, No. 38. Washington, D.C.: Smithsonian Institution Scholarly Press.

D'Croz, L., and D. R. Robertson. 1997. Coastal Oceanographic Conditions Affecting Coral Reefs on Both Sides of the Isthmus of Panama. *Proceedings of the 8th International Coral Reef Symposium*, 2:2053–2058.

D'Croz, L., D. R. Robertson, and J. A. Martinez. 1999. Cross-Shelf Distribution of Nutrients, Plankton, and Fish Larvae in the San Blas Archipelago, Caribbean Panama. *Revista de Biología Tropical*, 47:203–215.

DeSalvo, M. K., C. R. Voolstra, S. Sunagawa, J. A. Schwarz, J. H. Stillman, M. A. Coffroth, A. M. Szmant, and M. Medina. 2008. Differential Gene Expression during Thermal Stress and Bleaching in the Caribbean Coral *Monastraea faveolata*. *Molecular Ecology*, 17:3952–3971.

Dick, M. H., A. Herrera-Cubilla, and J. B. C. Jackson. 2003. Molecular Phylogeny and Phylogeography of Free-Living Bryozoa (Cupuladriidae) from Both Sides of the Isthmus of Panama. *Molecular Phylogenetics and Evolution*, 27:355–371.

Fischer, E. A. 1980. Speciation in the Hamlets (Hypoplectrus: Serranidae): A Continuing Enigma. *Copeia*, 1980:649–659.

———. 1981. Sexual Allocation in a Simultaneously Hermaphroditic Coral Reef Fish. *American Naturalist*, 117:64–82.

Fischer, E. A., and C. W. Petersen. 1987. The Evolution of Sexual Patterns in the Seabasses. *Bioscience*, 37:482–489.

Fukami, H., A. F. Budd, D. R. Levitan, J. A. Jara, R. Kersanach, and N. Knowlton. 2004. Geographic Differences in Species Boundaries among Members of the *Montastraea annularis* Complex Based on Molecular and Morphological markers. *Evolution*, 58:324–337.

Glynn, P. W. 1972. "Observations on the Ecology of the Caribbean and Pacific Coasts of Panama." In *The Panamic Biota: Some Observations Prior to Sea Level Canal*, ed. M. L. Jones. *Bulletin of the Biological Society of Washington*, 2:13–30.

———. 1973. "Aspects of the Ecology of Coral Reefs in the Western Atlantic Region." In *Biology and Geology of Coral Reefs*, ed. O. A. Jones and R. Endean, pp. 271–324. New York: Academic Press.

———. 1984. Widespread Coral Mortality and the 1982–83 El Nino Warming Event. *Environmental Conservation*, 11:133–146.

———. 1990. "Coral Mortality and Disturbances to Coral Reefs in the Tropical Eastern Pacific." In *Global Ecological Consequences of the 1982–1983 El Niño-Southern Oscillation*, ed. P. W. Glynn, pp. 55–126. Amsterdam: Elsevier.

Glynn, P. W., and M. W. Colgan. 1992. Sporadic Disturbances in Fluctuating Coral Reef Environments: El Niño and Coral Reef Development in the Eastern Pacific. *American Zoologist*, 32:707–718.

Glynn, P. W., S. B. Colley, C. M. Eakin, D. B. Smith, J. N. Cortes, N. J. Gassman, H. Guzman, J. B. Del Rosario, and J. S. Feingold. 1994. Reef Coral Reproduction in the Eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). II. Poritidae. *Marine Biology*, 118:191–208.

Glynn, P. W., S. B. Colley, N. J. Gassman, K. Black, K Cortez, J. Nunez, and J. L. Maté. 1996. Reef Coral Reproduction in the Eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). III. Agariciidae (*Pavona gigantea* and *Gardineroseris planulata*). *Marine Biology*, 125:579–601.

Glynn, P. W., S. B. Colley, J. L. Maté, J. Cortés, H. M. Guzmán, R. L. Bailey, J. S. Feingold, and I. C. Enochs. 2008. Reproductive Ecology of the Azooxanthellate Coral *Tubastraea coccinea* in the Equatorial Eastern Pacific: Part V. Dendrophylliidae. *Marine Biology*, 153:529–544.

Glynn, P. W., J. Cortés, H. M. Guzmán, and R. H. Richmond. 1988. El Niño (1982–83)-Associated Coral Mortality and Relationship to Sea Surface Temperature Deviations in the Tropical Eastern Pacific. *Proceedings of 6th International Coral Reef Symposium*, 3:237–243.

Glynn, P. W., and L. D'Croz. 1990. Experimental Evidence for High Temperature Stress as the Cause of El Niño-Coincident Mortality. *Coral Reefs*, 8:181–191.

Glynn, P. W., N. J. Gassman, C. M. Eakin, J. Cortés, D. B. Smith, and H.M. Guzmán. 1991. Reef Coral Reproduction in the Eastern Pacific: Costa Rica, Panamá, and Galápagos Islands (Ecuador). I. Pocilloporidae. *Marine Biology*, 109:355–368.

Glynn, P. W., and I. G. Macintyre. 1977. Growth Rate and Age of Coral Reefs of the Pacific Coast of Panama. *Proceedings of 3rd International Coral Reef Symposium*, 2:251–259.

Glynn, P. W., J. L. Maté, A. C. Baker, and M. O. Calderon. 2001. Coral Bleaching and Mortality in Panama and Ecuador During the 1997–1998 El Niño-Southern Oscillation Event: Spatial/Temporal Patterns and Comparisons with the 1982–1983 Event. *Bulletin of Marine Science*, 69:79–110.

Glynn, P. W., and R. H. Stewart. 1973. Distribution of Coral Reefs in the Pearl Islands (Gulf of Panama) in Relation to Thermal Conditions. *Limnology and Oceanography*, 18:367–379.

Glynn, P. W., R. H. Stewart, and J. E. McCosker. 1972. Pacific Coral Reefs of Panama: Structure, Distribution and Predators. *Geologischen Rundschau*, 61:483–519.

Glynn, P. W., and G. M.Wellington. 1983. *Corals and Coral Reefs of the Galapagos Islands*. Berkeley: University of California Press.

Glynn, P. W., G. M. Wellington, and C. Birkeland, C. 1979. Coral Reef Growth in the Galapagos: Limitation by Sea Urchins. *Science*, 203:47–48.

Graham, J. B. 1970. Temperature Sensitivity of Two Species of Inter-tidal Fishes. *Copeia*, 1970:49–56.

———. 1971. Temperature Tolerances of Some Closely Related Tropical Atlantic and Pacific Fish Species. *Science*, 172:861–863.

———. 1975. Heat Exchange in Yellow Fin (*Thunnus albacares*) and Skipjack (*Katsuwonus pelamis*) Tunas and the Adaptive Significance of Elevated Body Temperatures in Scombrid Fishes. *Fishery Bulletin*, 73:219–229.

Graham, J. B., I. Rubinoff, and M. K. Hecht. 1971. Temperature Physiology of the Sea Snake *Pelamis platurus*: An Index of Its Colonization Potential in the Atlantic Ocean. *Proceedings of the National Academy of Sciences of the United States of America*, 68:1360–1363.

Guzmán, H. M., ed. 1998. Marine-Terrestrial Flora and Fauna of Cayos Cochinos Archipelago, Honduras. *Revista Biologia Tropical Supplement)*, 46:1–200.

Guzman, H. M., P. A. G. Barnes, C. E. Lovelock, and I. C. Feller. 2005. A Site Description of the CARICOMP Mangrove, Seagrass and Coral Reef Sites in Bocas del Toro, Panama. *Caribbean Journal of Science*, 41:430–440.

Guzman, H. M., S. L. Benfield, O. Breedy, and J. M. Mair. 2008a. Broadening Reef Protection across the Marine Conservation Corridor of the Eastern Tropical Pacific: Distribution and Diversity of Reefs in Las Perlas Archipelago, Panama. *Environmental Conservation*, 35:46–54.

Guzman, H. M., and O. Breedy. 2008. *Leptogorgia christiae* (Octocorallia: Gorgoniidae): A New Shallow Water Gorgonian from Pacific Panama. *Journal of the Marine Biological Association*, 88:719–722.

Guzman, H. M., R. Cipriani, and J. B. C. Jackson. 2008b. Historical Decline in Coral Reef Growth after the Panama Canal. *Ambio*, 37:342–346.

Guzman, H. M., C. A. Guevara, and O. Breedy. 2004. Distribution, Diversity, and Conservation of Coral Reefs and Coral Communities in the Largest Marine Protected Area of Pacific Panama (Coiba Island). *Environmental Conservation*, 3:111–121.

Guzman, H. M., C. A. Guevara, and I. C. Hernandez. 2003. Reproductive Cycle of Two Commercial Species of Sea Cucumber (Echinodermata: Holothuroidea) from Caribbean Panama. *Marine Biology*, 142:271–279.

Guzman, H. M., J. B. C. Jackson, and E. Weil. 1991. Short-Term Ecological Consequences of a Major Oil Spill on Panamanian Subtidal Reef Corals. *Coral Reefs*, 10:1–12.

Guzman, H. M., and A. Tewfik. 2004. Population Characteristics and Co-occurrence of Three Exploited Decapods (*Panulirus argus*, *P. guttatus*, *Mithrax spinosissimus*) in Bocas del Toro, Panama. *Journal of Shellfish Research*, 23:575–580.

Handley, C. 1993. "Conservación de la Fauna y Flora en las Islas de Bocas del Toro." In *Agenda Ecológica y Social para Bocas del Toro*, ed. S. Heckadon-Moreno, pp. 43–48. Panama: Paseo Pantera and Smithsonian Tropical Research Institute.

Hildebrand, S. F. 1939. The Panama Canal as a Passageway for Fishes, with Lists and Remarks on the Fishes and Invertebrates Observed. *Zoologica*, 24:15–45.

Hueerkamp, C., P. W. Glynn, L. D'Croz, J. L. Maté, and S. B. Colley. 2001. Bleaching and Recovery of Five Eastern Pacific Corals in an El Niño-Related Temperature Experiment. *Bulletin of Marine Science*, 69:215–236.

Hurt, C., A. Anker, and N. Knowlton. 2009. A Multilocus Test of Simultaneous Divergence across the Isthmus of Panama Using Snapping Shrimp in the Genus *Alpheus*. *Evolution*, 63:514–530.

Jackson, J. B. C. 1997. Reefs since Columbus. *Coral Reefs*, 16(Suppl.): S23–S32.

———. 2001. What Was Natural in the Coastal Oceans? *Proceedings of the National Academy of Sciences of the United States of America*, 98:5411–5418.

Jackson, J. B. C., and D. H. Erwin. 2006. What Can We Learn about Ecology and Evolution from the Fossil Record? *Trends in Ecology and Evolution*, 21:322–328.

Jackson, J. B. C., and K.G. Johnson. 2000. Life in the Last Few Million Years. *Paleobiology*, 26:221–235.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. G. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. M. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, 293:629–637.

Jackson, J. B. C., J. A. Todd, H. Fortunato, and P. Jung. 1999. "Diversity and Assemblages of Neogene Caribbean Mollusca of Lower Central America." In *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*, ed. L. S. Collins and A. G. Coates, pp. 193–230. Lawrence, Kans.: Allen Press.

Kaufmann, K., and R. C. Thompson. 2005. Water temperature variation and the meteorological and hydrographic environment of Bocas del Toro, Panama. *Caribbean Journal of Science,* 41:392-413.

Keller, B. D., and J. B. C. Jackson, eds. 1993. *Long-Term Assessment of the Oil Spill at Bahía Las Minas, Panama: Synthesis Report*. OCS Study MMS 93-0047. New Orleans: U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office.

Kim, T. W., J. H. Christy, S. Dennenmoser, and J. C. Choe. 2009. The Strength of a Female Mate Preference Increases with Predation Risk. *Proceedings of the Royal Society B Biological Sciences*, 276:775–780.

Kline, D. I., N. M. Kuntz, M. Breitbart, N. Knowlton, and F. Rohwer. 2006. Role of Elevated Organic Carbon and Microbial Activity in Coral Mortality. *Marine Ecology Progress Series*, 314:119–125.

Knowlton, N. 2000. Molecular Genetic Analyses of Species Boundaries in the Sea. *Hydrobiologia*, 420:73–90.

Knowlton, N., J. L. Mate, H. M. Guzman, R. Rowan, and J. Jara. 1997. Direct Evidence for Reproductive Isolation among the Three Species of the *Montastraea annularis* Complex in Central America (Panama and Honduras). *Marine Biology*, 127:705–711.

Knowlton, N., and L. A. Weigt. 1998. New Dates and New Rates for Divergence across the Isthmus of Panama. *Proceedings of the Royal Society (London) Series B Biological Sciences*, 265:2257–2263.

Knowlton, N., E. Weil, L. A. Weigt, and H. M. Guzman. 1992. Sibling Species in *Montastraea annularis*, Coral Bleaching and the Coral Climate Record. *Science*, 255:330–333.

Lasker, H. R. 1991. Population Growth of a Gorgonian Coral: Equilibrium and Non-equilibrium Sensitivity to Changes in Life History Variables. *Oecologia (Berlin)*, 86:503–509.

Lasker, H. R., D. A. Brazeau, J. Calderon, M. A. Coffroth, R. Coma, and K. Kim. 1996. In Situ Rates of Fertilization among Broadcast Spawning Gorgonian Corals. *Biological Bulletin*, 190:45–55.

Lessios, H. A. 1979. Use of Panamanian Sea Urchins to Test the Molecular Clock. *Nature (London)*, 280:599–601.

———. 1981. Reproductive Periodicity of the Echinoids *Diadema* and *Echinometra* of the Two Coasts of Panama. *Journal of Experimental Marine Biology and Ecology*, 50:47–61.

———. 2005. *Diadema antillarum* Populations in Panama Twenty Years Following Mass Mortality. *Coral Reefs*, 24:125–127.

———. 2008. The Great American Schism: Divergence of Marine Organisms after the Rise of the Central American Isthmus. *Annual Review of Ecology and Systematics*, 39:63–91.

Lessios, H. A., B. D. Kessing, and J. S. Pearse. 2001. Population Structure and Speciation in Tropical Seas: Global Phylogeography of the Sea Urchin *Diadema*. *Evolution*, 55:955–975.

Lessios, H. A., B. D. Kessing, D. R. Robertson, and G. Paulay. 1999. Phylogeography of the Pantropical Sea Urchin *Eucidaris* in Relation to Land Barriers and Ocean Currents. *Evolution*, 53:806–817.

Lessios, H. A., and I. G. Macintyre, eds. 1997. *Proceedings of the 8th International Coral Reef Symposium,* Volumes 1 and 2. Smithsonian Tropical Research Institute, Republic of Panama.

Lessios, H. A., and D. R. Robertson. 2006. Crossing the Impassable: Genetic Connections in 20 Reef Fishes across the Eastern Pacific Barrier. *Proceedings of the Royal Society (London) B Biological Sciences*, 273:2201–2208.

Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of *Diadema* Mass Mortality Throughout the Caribbean. *Science*, 226:335–337.

Linares, O. F. 1977. "Ecology and the Arts in Ancient Panama: On the Development of Rank and Symbolism in the Central Provinces." In *Studies in Precolumbian Art and Archaeology*, Volume 17. Washington, D.C.: Dumbarton Oaks,

Linares, O. F, and A. J. Ranere, eds. 1980. *Adaptive Radiations in Prehistoric Panama. Peabody Museum Monographs No 5*. Cambridge: Harvard University Press.

Macintyre, I. G., and P. W. Glynn. 1976. Evolution of Modern Caribbean Fringing Reef, Galeta Point, Panama. *American Association of Petroleum Geologists Bulletin*, 60:1054–1072.

Manzello, D. P., J. A. Kleypas, D. A. Budd, C. M. Eakin, P. W. Glynn, and C. Langdon. 2008. Poorly Cemented Coral Reefs of the Eastern Tropical Pacific: Possible Insights into Reef Development in a high-CO_2 World. *Proceedings of the National Academy of Sciences of the United States of America*, 105:10450–10455.

McCartney, M. A., and H. A. Lessios. 2002. Quantitative Analysis of Gametic Incompatibility between Closely Related Species of Neotropical Sea Urchins. *Biological Bulletin*, 202:166–181.

Menge, B. A., and J. Lubchenco. 1981. Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients. *Ecological Monographs*, 51:429–450.

Menge, B. A., J. Lubchenco, L. R. Ashkenas, and F. Ramsey. 1986. Experimental Separation of Effects of Consumers on Sessile Prey in the Low Zone of a Rocky Shore in the Bay of Panama: Direct and Indirect Consequences of Food Web Complexity. *Journal of Experimental Marine Biology And Ecology*, 100:225–269.

Meyer, D. L., C. M. Birkeland, and G. Hendler. 1974. "Environmental Sciences Program Marine Studies, Galeta Point." In *Environmental Monitoring and Baseline Data*, ed. D. M. Windsor, pp. 273–409. Washington, D.C.: Smithsonian Institution Environmental Sciences Program.

Miglietta, M. P., and H. A. Lessios. 2009. A Silent Invasion. *Biological Invasions*, 11:825–834.

Miglietta, M. P., M. Rossi, and R. Collin. 2008. Hydromedusa Blooms and Upwelling Events in the Bay of Panama, Tropical East Pacific. *Journal of Plankton Research*, 30:783–793.

Mora, C., and D. R. Robertson. 2005. Causes of Latitudinal Gradients in Species Richness: A Test with the Endemic Shorefishes of the Tropical Eastern Pacific. *Ecology*, 86:1771–1782.

Morgan, S. G., and J. H. Christy. 1995. Adaptive Significance of the Timing of Larval Release by Crabs. *American Naturalist*, 145:457–479.

Moynihan, M. H. 1975. Conservatism of Displays and Comparable Stereotyped Patterns among Cephalopods. In *Function and Evolution in Behavior*, ed. G. Baerends, C. Beer, and A. Manning, pp. 276–291. Oxford: Clarendon Press.

Moynihan, M. H., and A. Rodaniche. 1982. The Behavior and Natural History of the Caribbean Reef Squid, *Sepioteuthis sepioidea*. Berlin: Verlag Paul Parey.

O'Dea, A., A. Herrera-Cubilla; H. M. Fortunato, and J. B.C. Jackson. 2004. Life History Variation in Cupuladriid Bryozoans from Either Side of the Isthmus of Panama. *Marine Ecology Progress Series*, 280:145–161.

O'Dea, A., and J. B. C. Jackson. 2002. Bryozoan Growth Mirrors Contrasting Seasonal Regimes across the Isthmus of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 185:77–94.

O'Dea, A. A., J. B. C. Jackson, H. Fortunato, J. Travis Smith, L. D'Croz, K. G. Johnson, and J. A. Todd. 2007a. Environmental Change Preceded Caribbean Extinction by 2 Million Years. *Proceedings of the National Academy of Sciences of the United States of America*, 104:5501–5506.

O'Dea, A., F. Rodriguez, C. DeGracia, and A.G. Coates. 2007b. La Paleontología Marina en el Istmo de Panamá. *Canto Rodado*, 2:149–179.

Paddack, M. J., C. Aguilar, R. S. Appeldoorn, J. Beets, E. W. Burkett, P. M. Chittaro, K. Clarke, R. Esteves, A. C. Fonseca, G. E. Forrester, A. M. Friedlander, J. García-Sais, G. González-Sansón, L. K. B. Jordan, D. McClellan, M. W. Miller, P. Molloy, P. J. Mumby, I. Nagelkerken, M. Nemeth, R. Navas-Camacho, J. Pitt, N. V. C. Polunin, M. C. Reyes-Nivia, D. R. Robertson, A. R. Ramírez, E. Salas, S. R. Smith, R. E. Spieler, M. A. Steele, I. D. Williams, C. Wormald, A. R. Watkinson, J. Reynolds, and I. M. Coté. 2009. Recent Caribbean-wide Declines in Reef Fish Abundance. *Current Biology*, 19:1–6.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hugues, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H Newman, G. Paredes, R. R. Warner, and J. B.C. Jackson. 2003. Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science*, 301:955–958.

Pandolfi, J. M., and J. B.C. Jackson. 2006. Ecological Persistence Interrupted in Caribbean Coral Reefs. *Ecology Letters*, 9:818–826.

Pandolfi, J. M., J. B.C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Ogden, H. P. Possingham, and E. Sala. 2005. Are U.S. Coral Reefs on the Slippery Slope to Slime? *Science*, 307:1725–1726.

Puebla, O., E. Bermingham, and F. Guichard. 2008. Population Genetic Analyses of *Hypoplectrus* Coral Reef Fishes Provide Evidence That Local Processes Are Operating during the Early Stages of Marine Adaptive Radiations. *Molecular Ecology*, 17:1405–1415.

Puebla, O., E. Bermingham, F. Guichard, and E. Whiteman. 2007. Colour Pattern as a Single Trait Driving Speciation in *Hypoplectrus* Coral Reef Fishes? *Proceedings of the Royal Society (London) B Biological Sciences*, 274:1265–1271.

Quenouille, B., E. Bermingham, and S. Planes. 2004. Molecular Systematics of the Damselfishes (Teleostei: Pomacentridae): Bayesian Phylogenetic Analyses of Mitochondrial and Nuclear DNA Sequences. *Molecular Phylogenetics and Evolution*, 31:66–88.

Robertson, D. R., J. D. Ackerman, J. H. Choat, J. M. Posada, and J. Pitt. 2005. Ocean Surgeonfish *Acanthurus bahianus*. I. The Geography of Demography. *Marine Ecology Progress Series*, 295:229–244.

Robertson, D. R., and G. R. Allen. 2008. Shorefishes of the Tropical Eastern Pacific Online Information System. www.stri.org/sftep.

Robertson, D. R., and K. Cramer. 2009. Marine Shore-fishes and Biogeographic Subdivisions of the Tropical Eastern Pacific. *Marine Ecology Progress Series*, 380(1):1–17.

Robertson, D. R., S. Swearer, K. Kaufmann, and E. B. Brothers. 1999. Settlement vs. Environmental Dynamics in a Pelagic Spawning Reef Fish in Caribbean Panama. *Ecological Monographs*, 69:195–218.

Robertson, D. R., and R. R. Warner. 1978. Sexual Patterns in the Labroid Fishes of the Western Caribbean, II: The Parrotfishes (Scaridae). *Smithsonian Contributions to Zoology*, 255:1–25.

Rocha, L. A., L. Anna, D. Bass, D. R. Robertson, and B. W. Bowen. 2002. Adult Habitat Preferences, Larval Dispersal, and the Comparative Phylogeography of Three Atlantic Surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, 11:243–251.

Rocha, L. A., D. R. Robertson, C. R. Rocha, J. L. Van Tassell, M. T. Craig, and B. W. Bowen. 2005a. Recent Invasion of the Tropical Atlantic by an Indo-Pacific coral reef fish. *Molecular Ecology*, 14:3921–3928.

Rocha, L. A., D. R. Robertson, J. Roman, and B. W. Bowen. 2005b. Ecological Speciation in Tropical Reef Fishes. *Proceedings of the Royal Society (London) B Biological Sciences*, 272:573–579.

Roche, D. G., and M. E. Torchin. 2007. Established Population of the North American Harris Mud Crab, *Rhithropanopeus harrisii* (Gould 1841) (Crustacea: Brachyura: Xanthidae) in the Panama Canal. *Aquatic Invasions*, 2:155–161.

Rowan, R., N. Knowlton, A. Baker, and J. Jara. 1997. Landscape Ecology of Algal Symbionts Creates Variation in Episodes of Coral Bleaching. *Nature (London)*, 388:265–269.

Rubinoff, I. 1965. Mixing Oceans and Species. *Natural History*, 74:69–72.

———. 1968. Central American Sea Level Canal: Possible Biological Effects. *Science*, 161:857–861.

Rubinoff, I., J. B. Graham, and J. Motta. 1986. Diving of the Sea Snake *Pelamis platurus* in the Gulf of Panamá. I. Dive Depth and Duration. *Marine Biology*, 91:181–191.

Rubinoff, I., and R. W. Rubinoff. 1962. New Records on Inshore Fishes from the Atlantic Coast of Panama. *Breviora*, 1962:1–7.

Rubinoff, R. W., and I. Rubinoff. 1969. Observations on Migration of a Marine Goby Through the Panama Canal. *Copeia*, 1969:395–397.

———. 1971. Geographic and Reproductive Isolation in Atlantic and Pacific Populations of Panamanian *Bathygobius*. *Evolution* 25:88–97.

Ruiz, G. M., M. E. Torchin, and K. Grant. 2009. “Using the Panama Canal to Test Predictions about Tropical Marine Invasions.” In *Proceedings of the Smithsonian Marine Science Symposium*, ed. M. A. Lang, I. G. Macintyre, and K. Rützler, pp. 291–299. Smithsonian Contributions to the Marine Sciences, No. 38. Washington, D.C.: Smithsonian Institution Scholarly Press.

Schloeder, C., and L. D’Croz. 2004. Responses of Massive and Branching Coral Species to the Combined Effects of Water Temperature and Nitrate Enrichment. *Journal of Experimental Marine Biology and Ecology*, 313:255–268.

Smith, J. T., and J. B. C. Jackson. 2009. Ecology of Extreme Faunal Turnover of Tropical American scallops. *Paleobiology*, 35:77–93.

Sousa, W. P. 2007. Mangrove Forest Structure and Dynamics, Punta Galeta, Panama. *Bulletin of the Ecological Society of America*, 88:46–49.

Sturmbauer, C., J. Levington, and J. H. Christy. 1996. Molecular Phylogeny of Fiddler Crabs: Test of the Hypothesis of Increasing Behavioral Complexity in Evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 93:10855–10857.

Tewfik, A., and H. M. Guzman. 2003. Shallow-Water Distribution and Population Characteristics of *Strombus gigas* and *S. costatus* (Gastropoda Strombidae) in Bocas del Toro, Panama. *Journal of Shellfish Research*, 22:789–794.

Todd, J. A., J. B. C. Jackson, K. G. Johnson, H. M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The Ecology of Extinction: Molluscan Feeding and Faunal Turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London, B Biological Sciences*, 269:571–577.

Vargas, S., H. M. Guzman, and O. Breedy. 2008. Distribution Patterns of the Genus *Pacifigorgia* (Octocorallia: Gorgoniidae): Track Compatibility Analysis and Parsimony Analysis of Endemicity. *Journal of Biogeography*, 35:241–247.

Warner, R. R., and D. R. Robertson. 1978. Sexual Patterns in the Labroid Fishes of the Western Caribbean. I. The Wrasses (Labridae). *Smithsonian Contributions to Zoology*, 254:1-27.

Warner, R. R., D. R. Robertson, and E. G. Leigh Jr. 1975. Sex Change and Sexual Selection. *Science*, 190:633–638.

Wulff, J. L. 1991. Asexual Fragmentation, Genotype Success, and Population Dynamics of Erect Branching Sponges. *Journal of Experimental Marine Biology and Ecology*, 149:227–247.

———. 1997. Mutualism among Species of Coral Reef Sponges. *Ecology*, 78:146–159.

Zapata, F., and D. R. Robertson. 2006. How Many Shore-Fish Species Are There in the Tropical Eastern Pacific? *Journal of Biogeography*, 34:38–51.

Zigler, K. S., and H. A. Lessios. 2004. Speciation on the Coasts of the New World: Phylogeography and the Evolution of Bindin in the Sea Urchin Genus *Lytechinus*. *Evolution*, 58:1225–1241.

Protandric Simultaneous Hermaphroditism Is a Conserved Trait in *Lysmata* (Caridea: Lysmatidae): Implications for the Evolution of Hermaphroditism in the Genus

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ABSTRACT. Shrimps from the genus *Lysmata* are unusual because of their peculiar sexual system. Individuals in a population first reproduce as males, to change later in life to functional simultaneous hermaphrodites. The evolutionary origin of this sexual system, called protandric simultaneous hermaphroditism (PSH), is a longstanding question overdue for consideration. A previously proposed "historical contingency" hypothesis suggested that PSH evolved in the tropics from an ancestral protandric species of *Lysmata* that became socially monogamous and symbiotic with sea anemones. The restricted probability of encountering mating partners by shrimps because of their association with their hosts would have favored PSH. Here, I first provide evidence that PSH is a fixed trait within the genus. Second, I examine whether the historical contingency hypothesis appropriately explains the origin of PSH in the genus. Using anatomical observations and laboratory experiments combined, I demonstrate that two shrimps from the genus *Lysmata*, *L. galapagensis* and *L. boggessi*, feature PSH. Study of museum specimens suggests that nine other species of *Lysmata* are protandric simultaneous hermaphrodites. The foregoing information indicates that PSH represents a fixed trait in the genus *Lysmata*. Ancestral character state reconstruction using Bayesian inference allowed testing whether the ancestral *Lysmata* featured a symbiotic lifestyle and a socially monogamous mating system, as proposed by the historical contingency hypothesis. In agreement with this hypothesis, analysis indicated that the most common recent ancestor of *Lysmata* was most likely socially monogamous. However, the ancestral lifestyle was equally likely to be free-living or symbiotic. Thus, the present study provides partial support for the historical contingency hypothesis. Studies on the sexual system and lifestyle of more species and development of a more robust phylogeny are needed to reveal the evolutionary origin of PSH in the genus *Lysmata*.

INTRODUCTION

In decapod crustaceans, the greatest diversity of sexual systems is found in the infraorder Caridea. Most caridean shrimps are gonochoric, with individuals in a population producing only male or female gametes during their entire life. Well-studied examples include *Rhynchocinetes typus* (Correa et al., 2000), *Hippolyte obliquimanus* (Terossi et al., 2008), *Pontonia margarita* (Baeza, 2008a), and *Hippolyte williamsi* (Espinoza-Fuenzalida et al., 2008). The second most common sexual system is protandry. In at least 31 species of shrimps, individuals in a population reproduce first as males and change to females later in life

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(Bauer, 2000). Although several variants of protandry have been reported (e.g., protandry with primary females in *Crangon crangon*; Schatte and Saborowski, 2006), no study has reported protogyny (changing sex from female to male) among shrimps. Most recently, a particular variant of simultaneous hermaphroditism, that is, adolescent protandry sensu Ghiselin (1974), protandric cosexuality sensu Policansky (1982), or protandric simultaneous hermaphroditism (PSH) sensu Bauer (2000), has been described for shrimps from the genera *Lysmata* (Baeza et al., 2008) and *Exhippolysmata* (Kagwade, 1982; Braga et al., 2009). It must be noticed that a recently developed molecular phylogeny for *Lysmata* and other related genera demonstrated that the genus *Exhippolysmata* represents a derived group of shrimps within the genus *Lysmata* (Baeza et al., 2009). Thus, species of *Exhippolysmata* are treated here as members of the genus *Lysmata*.

In protandric simultaneous hermaphroditic shrimps, juveniles consistently mature as functional male individuals (also called male-phase [MP] shrimps; Bauer and Holt, 1998) bearing typical caridean male characters (i.e., coupling hoods and appendix masculina on the first and second pleopods, respectively) (Bauer and Holt, 1998; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008). These functional males later attain female sexual function and develop into functional simultaneous hermaphrodites (hereafter, hermaphrodites; but also called female-phase [FP] shrimps; Bauer and Holt, 1998). Resembling females of caridean gonochoric species, hermaphrodites mate as females shortly after molting, spawn oocytes to an abdominal chamber where fertilization takes place, and brood their embryos for relatively long periods of time (e.g., 10–15 days in *Lysmata wurdemanni*; Baeza, 2006). These hermaphrodites retain testicular tissue, male ducts, and gonopores and thus have the ability to reproduce as both male and female (Bauer and Holt, 1998). After becoming hermaphrodites, individuals do not revert to males (Baeza, 2007a), and no self-fertilization has been demonstrated (Bauer and Holt, 1998; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008).

So far, the various studies on the sexual biology of shrimps from the genus *Lysmata* suggest that all species exhibit PSH. Protandric simultaneous hermaphroditism is suspected to be a fixed trait in the genus. Nonetheless, additional information from more species is needed to confirm this notion. In turn, other life history traits differ within these two genera. Shrimps have been reported to inhabit the shallow subtidal and intertidal of subtropical and tropical rocky and coral reefs around the world. Some species of *Lysmata* live in groups, others are solitary, while some species are socially monogamous (pair-living; e.g., *L. grabhami* (Gordon, 1935)) (Wirtz, 1997). Several species with an inconspicuous coloration dwell freely among rocks in temperate zones, while other more colorful species inhabit tropical sponges (*L. pederseni* Rhyne and Lin, 2006) (Rhyne and Lin, 2006). Other strikingly brilliant species clean fishes (*L. amboinensis* (De Man, 1888)) (Limbaugh et al., 1961). Species from this genus represent ideal candidates to explore the role of ecological conditions in explaining evolutionary innovations in the marine environment (see Baeza and Thiel, 2007).

Recent studies have examined various aspects of the biology of various *Lysmata* and *Exhippolysmata* shrimps (Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008; Lopez-Greco et al., 2009). Furthermore, shrimps from the genera *Lysmata* and *Exhippolysmata* are currently being used as models in evolutionary biology and behavioral ecology because of their peculiar sexual system (Baeza and Bauer, 2004; Baeza, 2006, 2007a, 2007b, 2007c). In spite of the increasing knowledge regarding the behavior and ecology of several species of *Lysmata*, the evolutionary origins of PSH in the genus remain uncertain. Although recent studies have shown that the variety of lifestyles of *Lysmata* is greater than originally recognized (Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008), an emerging dichotomy in social organization and ecology was noted in initial studies. One group of species (named "Crowd" species by Bauer, 2000) was described as inhabiting warm subtropical environments, occurring as dense aggregations in their refuges, and exhibiting no specialized fish-cleaning behavior (i.e., *L. californica*: Bauer and Newman, 2004; *L. wurdemanni*: Baeza, 2006). A second group (named "Pair" species by Bauer, 2000) was described as mostly tropical, occurring at low densities in the subtidal, and dwelling as socially monogamous pairs on sea anemones used as spots for fish-cleaning activities (i.e., *L. grabhami*: Wirtz, 1997; *L. amboinensis*: Fiedler, 1998). Based on this initial dichotomy, Bauer (2000) proposed that PSH evolved in the tropics from an ancestral symbiotic protandric species of *Lysmata* that became a specialized fish cleaner. Restricted mobility of individuals resulting from their association with the host and, hence, reduced probability of encountering mating partners would have favored PSH (also see Bauer, 2006). Under such a scenario, the "Crowd" warm temperate species that do not exhibit specialized cleaning behaviors would have evolved from tropical species with specialized cleaning behaviors and more complex mating systems (Bauer, 2006). A recent phylogeny developed for the genus found no support for Bauer's hypothesis because socially monogamous species presented a more derived position than gregarious species (Baeza et al., 2009). However, no formal testing of Bauer's ideas was conducted. Current advances in ancestral character state reconstruction using Bayesian inference (Pagel et al., 2004) make it possible to test whether the ancestral *Lysmata* featured a symbiotic lifestyle and a socially monogamous mating system, as proposed by Bauer (2000).

Here, I provide evidence that PSH is a fixed trait within the genus *Lysmata* (including *Exhippolysmata*), as suspected by previous studies (see Bauer, 2000; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008). For this purpose, I examined the sexual system of two shrimps from the genus, *L. galapagensis* Schmitt, 1924 and *L. boggessi* Rhyne and Lin, 2006, using anatomical observations and laboratory experiments. I also examined specimens from another nine species deposited at the National Museum of Natural History (NMNH), Washington, D.C. The information altogether strongly suggests that PSH is a conserved trait within the genus *Lysmata*. My second goal was to examine Bauer's (2000) hypothesis regarding the evolution of PSH in *Lysmata*. I tested whether the ancestral *Lysmata* was socially monogamous (1) and strictly symbiotic with, for example, sea anemones (2), as proposed by this author. To accomplish this second goal, a review of the literature on the socioecology of *Lysmata* was conducted. Next, the lifestyle of shrimps was mapped onto the phylogeny of the genus, and the likelihood of specific traits to occur at particular ancestral nodes in the phylogeny was tested.

METHODS

Collection and Maintenance of Shrimps

Individuals from the two studied species were collected between February and August, 2006, at different localities in Panama and Florida, USA. Individuals from *L. boggessi* were collected at night during low tides from seagrass beds at Madelaine Key (27°38′51.87″N, 82°42′56.50″W), Fort De Soto National Park, Florida. Specimens from *L. galapagensis* were collected from Islas Secas (7°58′37.54″N, 82°02′18.02″W), Gulf of Chiriqui, Panama. Immediately after collection, specimens were transported to the R/V Urraca and then to the Naos Marine Laboratories, Panama (*L. galapaguensis*) or directly to the Smithsonian Marine Research Station at Fort Pierce, Florida (*L. boggessi*). Individuals were maintained in 15–70 L aquaria at a water temperature of 22°–33°C and 34–36 ppt salinity and were fed every other day with shrimp pellets before being selected for dissections or experiments.

Dissections

Observations on reproductive anatomy were conducted as in Baeza (2008b) in a total of six specimens of each species, three presumptive males (3.6–3.8 and 4.0–4.6 mm carapace length [CL] in *Lysmata galapagensis* and *L. boggessi*, respectively) and three presumptive hermaphrodites that were brooding embryos (4.4–5.1 and 6.5–5.6 mm CL in *Lysmata galapagensis* and *L. boggessi*, respectively). First, the presence or absence of male gonopores on the coxae of the fifth pereiopods was recorded for each individual. Individuals with male gonopores (all) had sperm collected from the ejaculatory ducts using short electric shocks that results in the ejection of a spermatophore (as noted in Baeza, 2006, 2007c). Each individual was then dissected to extract the gonad for examination under the stereomicroscope. Finally, the first and second pleopods were dissected and the presence or absence of appendices internae and masculinae, respectively, were recorded. Specimens were defined as males or hermaphrodites by the presence (males) or absence (hermaphrodites) of coupling hooks (cincinnuli) and appendices masculinae on the endopods of the first and second pleopods, respectively (see Baeza, 2007c, 2008b).

Experiments

Three experiments, as described in Baeza et al. (2008) and Baeza (2008b), were conducted to determine the sexual system of the three species under study. In summary, the different experiments determined whether (1) brooding shrimps (reproducing as females) were capable of mating as males, (2) brooding shrimps were capable of self-fertilization, and (3) males were capable of becoming hermaphrodites with time (see Results). In the first experiment (*n* = 5), pairs of brooding shrimps were maintained in 21 L aquaria. In the second experiment, five brooding shrimp were each maintained alone. In the third experiment (n = 5), pairs of males (small nonbrooding shrimp with no externally visible female gonads and visible cincinnuli and appendices masculinae) were maintained separately in 21 L aquaria for at least 50 days. Individuals were examined daily for hatching of the embryos, the presence of exuvia from molting, development of mature oocytes in the gonad (visible through the carapace), and spawning of a new batch of eggs. The development of any newly spawned embryos was examined in detail after four days of spawning.

Following the rationale developed by Baeza et al. (2008), if in the first experiment ovigerous shrimps that paired together produced normally developing broods, then it was inferred that either the other ovigerous shrimp in the aquarium acted as a male to inseminate its partner, or that the shrimp was capable of self-fertilization. If in the second experiment shrimps in isolation failed to successfully produce and brood developing eggs, then the possibility of self-fertilization was eliminated. If in the third experiment individuals identified as males at the beginning of the experiment developed the ovarian portion of the ovotestis and produced eggs, then I inferred that male shrimps mature as hermaphrodites (see Baeza et al., 2008).

Population Structure, Sex Ratio, and Abundance

Information on the abundance, population structure, and sex ratio (males to hermaphrodites) of each species was collected from the field. The carapace length (CL) and number of shrimps of each sexual phase and each species captured during the different samplings were recorded. The sampling effort (total number of hours spent collecting shrimps) was calculated for each sampling event. Relative abundance of shrimps was estimated by dividing the sample abundance (number of shrimps captured) by the sampling effort.

Museum Specimens

Specimens from nine different species of *Lysmata* deposited at the Collection of Crustaceans, National Museum of Natural History (NMNH; Smithsonian Institution, Washington, D.C.) were examined. Dissection of specimens pertaining to the collection was not possible because only a few individuals were available from several of the examined species and many of the specimens were part of the type series used to describe the species. Therefore, the identification of males and hermaphrodites was mostly based on external morphological characters (see foregoing). When identifying sexual phases, particular attention was given to the presence of male gonopores at the base of the coxae of the fifth pair of pereiopods in brooding shrimps as a likely indicator of simultaneous hermaphroditism (see Results).

Testing the Historical Contingency Hypothesis

To examine whether the historical contingency hypothesis proposed by Bauer (2000) appropriately explains the origins of PSH in shrimps from the genus *Lysmata*, the lifestyle (in terms of the propensity to develop symbiotic partnerships and natural group size) was reconstructed using BayesTraits (Pagel and Meade, 2006; available at www.evolution.rdg.ac.uk).

A pruned set of sequences (from the 16S mitochondrial gene) recently published by Baeza et al. (2009) was used to generate a phylogenetic hypothesis for the group on which to reconstruct the evolution of lifestyles in shrimps. The sequences pertained to 20 species of *Lysmata* and *Exhippolysmata* plus 3 other species (*Merguia rhizophorae*, *Hippolyte williamsi*, and *H. inermis*) used to root the trees during the initial phylogenetic analysis. The set of aligned sequences was first imported to BayesPhylogenies (Pagel et al., 2004) to obtain a Bayesian posterior distribution of phylogenetic trees. Metropolis coupled–Markov chain–Monte Carlo analyses were conducted using a GTR + I (invariant) + G (gamma) model of nucleotide substitution. The analysis was run on two different simultaneous chains. A total of 6,000,000 iterations were conducted, and sampling was performed every 100th tree. The last 1,000 posterior probability trees generated by BayesPhylogenies were then imported to BayesTraits. The submodule MultiState in BayesTraits uses Markov chain Monte Carlo (MCMC) methods to infer values of traits (that adopt a finite number of discrete states) at ancestral nodes of phylogenies. Additionally, this method permits testing for particular ancestral characters at specific nodes taking phylogenetic uncertainty into account (Pagel et al., 2004).

The two traits here analyzed have three states each. For group size, the states were (1) aggregations (including swarms), (2) small groups, and (3) pair-living (social monogamy). The three character states used for describing the symbiotic propensity of different shrimp species were (1) free-living, (2) facultative associate (with different moray eel species, such as *L. californica* and *L. seticaudata*; with sea anemones, such as *L. ankeri*), and (3) strictly symbiotic with either sponges (e.g., *L. pederseni*) or sea anemones (*L. amboinensis, L. grabhami*). Information on the lifestyle of each species was obtained by direct observation of shrimps in nature (personal observations), from the literature (see literature review), or from both sources.

During the analysis, a reversible-jump MCMC search was used with two independent chains that were run for 6,000,000 iterations with a burn-in of 50,000. I choose the prior distribution of the parameters in the model with the option Hyperprior (see Pagel et al., 2004), seeding an exponential distribution from uniform on the interval 0.0 to 30 and a rate deviation of 18. These values were selected considering preliminary runs and were used to keep the acceptance rate at approximately 0.3, as recommended by Pagel et al. (2004). Character states at internal nodes were reconstructed using the most recent common ancestor method. I tested hypotheses about particular character states at specific nodes when comparing the MCMC run-in which the node was “fossilized” (constrained) to one state versus an alternative. The command *Fossil* allows testing whether a particular state is “significantly” more likely at a specific node than an alternative state. For each tested character, the same set of conditions (prior distribution, burn-in) as used in the ancestral character state reconstructions already described were used. However, the MCMC was run 5 times for each trait state tested, and a total of 100,000,000 iterations were conducted. Bayes factors were calculated as the difference between the highest harmonic mean of the marginal likelihood from the five MCMC runs for each state (Pagel et al., 2004). The strength of support for one model over another was measured using the scale from Kass and Raftery (1995).

RESULTS

DISSECTIONS

Dissections demonstrated that all shrimps (brooding or nonbrooding) from the two species had male gonopores at the coxae of the fifth pair of pereiopods (Figure 1A). Female gonopores at the coxae of the third pair of pereiopods were more difficult to reliably observe. From all shrimps (brooding or nonbrooding), sperm cells shaped in the form of an inverted umbrella were retrieved from the male gonopores by electroshocks (Figure 1A,B). Dissections of the gonads from small shrimps not brooding embryos (presumptive males) demonstrated the presence of an ovotestes (Figure 1C) with an undeveloped anterior female portion full of immature oocytes (lacking coloration) (Figure 1D) and a posterior male gonad containing sperm cells with the same morphology as the sperm retrieved from the gonopores (see Figure 1B). Gonads dissected from brooding (presumptive hermaphrodites) shrimps also had ovotestes, but with a large ovarian portion full of mature oocytes and a relatively small posterior testicular portion with sperm (Figure 1E). In both brooding and nonbrooding shrimps, vas deferentia and oviducts extended laterally from the testicular and ovarian portions, respectively (Figure 1C,E).

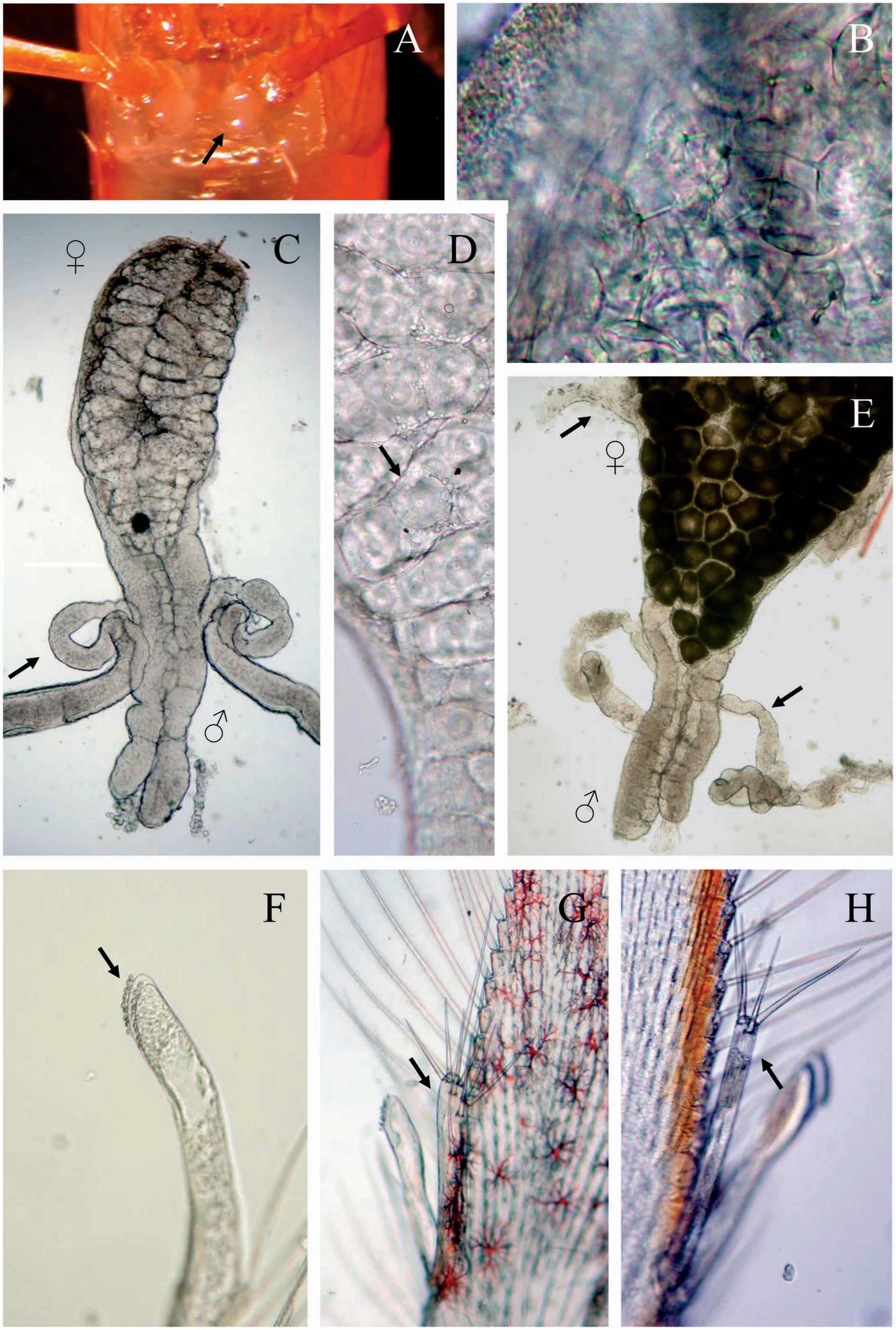
Shrimps brooding embryos invariably lacked cincinnuli and appendices masculinae in the endopod of the first and second pereiopods, respectively. In contrast, appendices masculinae bearing relatively long spines and numerous cincinnuli were observed in the second and first pleopods, respectively, of nonbrooding shrimps (Figure 1F–H). Some minor differences between the two species were noticed regarding the relative length and number of spines borne by the appendix masculinae; in *L. boggessi*, the spines were more numerous and longer than those of *L. galapagensis* (Figure 1G,H). Overall, all the anatomical differences observed between brooding and nonbrooding shrimps indicate that the populations of all the *Lysmata* species studied herein are indeed composed of males and hermaphrodites.

EXPERIMENTS

When two brooding individuals (presumed hermaphrodites) were paired, all individuals in the two species examined successfully hatched their embryos as larvae, molted, and spawned a new batch of oocytes below the abdomen. The oocytes remained attached to the pleopods and showed embryonic development as embryos (i.e., early blastulae formation) after three days. This embryological development suggests the ability of the other hermaphrodites in the same aquarium to reproduce as males or, alternatively, the possibility of selfing by the hermaphrodites acting as females. However, none of the 10 hermaphrodites (5 of each species) maintained in isolation from conspecifics successfully reared their embryos to larvae. These solitary shrimps molted and spawned oocytes to beneath the abdomen. However, the oocytes invariably disappeared from the pleopods within a few days after spawning. Overall, the observations from these first two experiments strongly suggest that brooding hermaphrodites do not have the capability of self-fertilization. Therefore, brooding shrimps (hermaphrodites) maintained in pairs indeed acted as males and fertilized eggs when their partners molted and reproduced as females.

In the experiment conducted to determine whether males mature as hermaphrodites later in life, all six males of *L. galapagensis* turned into simultaneous hermaphrodites within four months. Males showed signs of ovarian maturation during intermolt periods. When the gonad was full of large green (vitellogenic) oocytes, the male shrimps molted into hermaphrodites. Most probably, these shrimps mated as females shortly after molting for the first time in their lifetime because the spawned embryos beneath the abdomen were observed developing normally several days after spawning.

In contrast to *L. galapagensis*, all six male shrimps from *L. boggessi* died of unknown reasons within the first month of the experiment. However, observations on three males of *L. boggessi* in the maintenance aquaria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indicated that they turn into hermaphrodites before four months. This change of sexual phase was accomplished after a single month, as observed in *L galapagensis*. Thus, it may be concluded that *L. galapagensis* and *L. boggessi* are protandric simultaneous hermaphrodites, incapable of self-fertilization.

POPULATION STRUCTURE, SEX RATIO, AND ABUNDANCE

Abundances of *L. galapagensis* and *L. boggessi* at the different sampling locations were high and low, with a mean of 2.79 and 0.317 individuals collected per minute per sampling period, respectively. In the two species, population was biased toward males. The ratio of males to total shrimps collected during the sampling period was 0.024 and 0.16 for *L. galapagensis* and *L. boggessi*, respectively. The range of body size registered for males varied from 1.9 to 3.8 and from 3.13 to 5.75 mm CL in *L. galapagensis* and *L. boggessi*, respectively. Hermaphrodites ranged in size between 4.1 and 5.1 and 5.63 and 6.5 mm CL in *L. galapagensis* and *L. boggessi*, respectively (Figure 2).

MUSEUM SPECIMENS

A variable number of specimens from *L. anchisteus*, *L. argentopunctata*, *L. chica*, *L. kuekenthali*, *L. moorei*, *L. philippinensis*, *L. rathbunae*, *L. trisetacea*, and *L. vittata* were available at the NMNH. Small shrimps in each species appear to be males as they have cincinnuli and appendices masculinae in the second and first pleopod, respectively. In turn, shrimps brooding embryos (the great majority of them above average size) invariably lacked cincinnuli and appendices masculinae in the endopod of the first and second pereiopods, respectively. This last observation suggests they were hermaphrodites. It was not possible to detect transitional individuals in these species because no dissections were possible and gonad condition was not easily observed. The carapace of formaldehyde- and alcohol-fixed specimens is not translucent as it is in living or recently preserved specimens. Also, shrimps less than 3.0 mm CL were not sexed because of the risk of inflicting damage. For all species examined except *L. anchisteus*, *L. argentopunctata*, and *L. philippinensis*, a relatively large sample of specimens was available. The size–frequency distribution of the different species strongly resembled that of the two species studied above, with small shrimps resembling males and large shrimps resembling hermaphrodites (Figure 3). Observations of the coxae of the fifth pair of pereiopods of the largest brooding shrimps in each species demonstrated the presence of male gonopores. Overall, the distribution of the sexes across size classes and the limited observations on the external male and female anatomy suggest that all these other *Lysmata* shrimps are protandric simultaneous hermaphrodites.

FIGURE 1. (*facing page*) *Lysmata galapagensis* and *Lysmata boggessi*: anatomical and morphological differences between males and hermaphrodites. A, spermatophore (arrow) retrieved from gonopores of hermaphrodite (*L. boggessi*); B, sperm from male (*L. galapagensis*); C, ovotestes from male (anterior female and male portions on top and bottom, respectively; arrow points at left vas deferentia) (*L. galapagensis*); D, close-up of female gonad portion in male (arrow points at immature oocyte) (*L. boggessi*); E, ovotestes from dissected hermaphrodite (anterior female and male portions on the top and bottom, respectively; top and bottom arrows point at right oviduct and left vas deferentia, respectively) (*L. galapagensis*); F, endopod of first pleopod in male (arrow points at cincinulli) (*L. galapagensis*); G, endopod of second pleopod in male (arrow points at appendix masculina) (*L. galapagensis*); H, endopod of second pleopod in male (arrow points at appendix masculina) (*L. boggessi*).

LITERATURE REVIEW

The literature review of the 41 species of *Lysmata* (including *Exhippolysmata*) described to date revealed that the geographic and bathymetric distribution, coloration, and habitat of these species are relatively well known. Shrimps from the genus *Lysmata* occur in tropical, subtropical, and temperate waters around the world and can be found among rocks or fossilized coral, live coral, seagrass blades, on muddy and shell bottoms, or associated with sponges or sea anemones in the intertidal or subtidal to 360 m depth. Most species have an inconspicuous coloration (red striped, translucent reddish with reddish flagella on both pairs of antenna). Only 4 species are reported as featuring a striking color pattern (contrasting body colors, bright white flagella on both antenna). This dichotomy in coloration was previously noticed by Bauer (2000). *Lysmata splendida*, one of the 4 species with a brilliant coloration, most probably is a cleaner shrimp. However, nothing is known about its reaction to fish and its propensity to clean them. Similarly, information regarding the degree of specialization of the cleaning behavior is unknown for most of the species (Table 1).

Information on the socioecology and sexual system is, in general, poorly known. Information on lifestyle

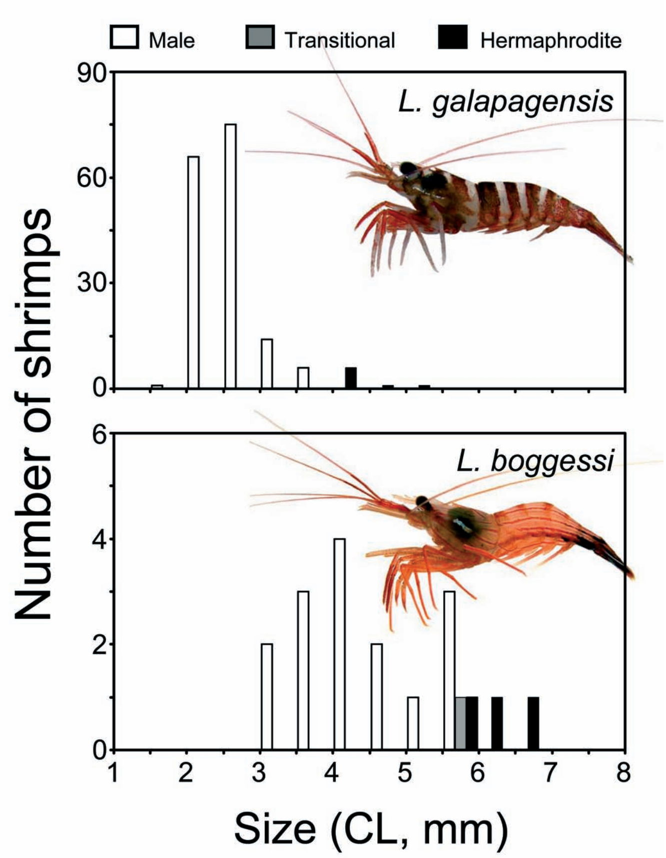

FIGURE 2. *Lysmata galapagensis* and *L. boggessi* population structure (n = 178 and 22 shrimps, respectively, from *L. galapagensis* and *L. boggessi*; CL = carapace length).

(socioecological attributes) is available only for 18 of the 41 described species. Of these, 7 species live in crowds (aggregations), 7 species live in small groups, 3 species live in pairs (i.e., they are socially monogamous), and 1 species is reported as living in extremely large aggregations (in swarms; *Exhippolysmata oplophoroides*). Demonstration of PSH using a combination of experimental, morphological, and anatomical findings and population structure is available for 12 species. A strong indication of PSH exists for another 10 species. Although the information is incomplete (PSH has been reported for a total of 22 species, or 54% of the described species), this review clearly demonstrates that the lifestyle and socioecology of shrimps from this genus are more complex than originally thought and further confirms the idea that PSH is a fixed trait in the genus *Lysmata* (including *Exhippolysmata*).

Testing the Historical Contingency Hypothesis

The 50% majority-rule consensus tree obtained during the initial phylogenetic analysis confirms the existence of the three natural clades (tropical-American, cosmopolitan, and cleaner) noticed previously by Baeza et al. (2009). However, one important difference between the present consensus tree and that previously published is that *L. olavoi* is not supported as the most basal species within the genus. This difference between trees might (1) be an effect of the different set of species used for the phylogenetic analysis or (2) perhaps have occurred because the different software programs used for phylogenetic inference function with different algorithms. On the other hand, the monophyly of *Lysmata* is well supported in this new tree, with a 100% posterior probability (Figure 4; Baeza et al., 2009: fig. 1).

The lifestyle of shrimps mapped onto the consensus tree indicated that the most recent common ancestor of the species pertaining to the neotropical and cosmopolitan clades was gregarious. In contrast, the ancestor of the species comprising the cleaner clade most probably was socially monogamous (see Figure 4). On average, the node of the most common recent ancestor of all *Lysmata* species is reconstructed to be in state 2 (social monogamy) with 80% of certainty. The degree of certainty varied from tree to tree but was generally high, as indicated by the low standard deviation of this value (SD = 0.03, calculated from 2,000,000 iterations using 1 of 1,000 randomly sampled posterior probability distribution trees at each iteration). The largest harmonic log-likelihood obtained from five independent runs when the node was fossilized to state 0 and 2 was –22.309507 and –20.865237, respectively. The almost three log-unit improvement in likelihood (Bayes factor = 2.89) of the model when the node was fossilized to state 2 represents evidence that the ancestral lifestyle of Lysmata was social monogamy.

With regard to the propensity for developing symbiotic interrelationships, the reconstructions suggest that the ancestor of the neotropical and cosmopolitan clades most probably had a free-living lifestyle and did not develop any symbiotic partnership with other macroinvertebrates. It should be noticed that the degree of certainty of these two inferences is relatively low, as indicated by the large standard deviations of the distribution of the character (see Figure 4). Also, the reconstructions indicate that, with a probability of 0.46 ± 0.20 or 0.41 ± 0.18, either facultative partnerships or strict symbiosis,

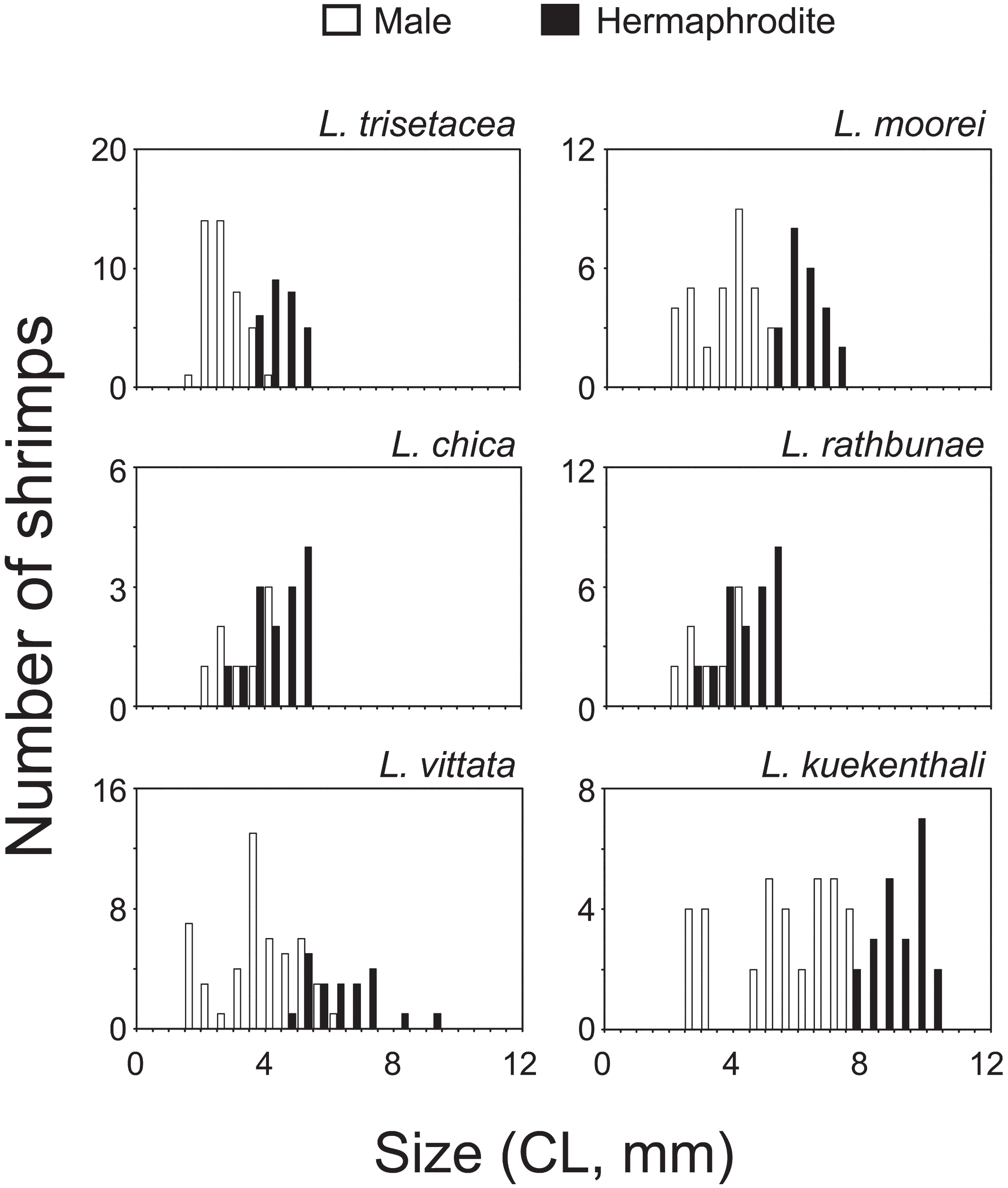

FIGURE 3. *Lysmata* spp. Population structure of selected species from the National Museum of Natural History (n = 71, 56, 22, 31, 70, and 57 shrimps from *L. trisetacea*, *L. moorei*, *L. chica*, *L. rathbunae*, *L. vittata*, and *L. kuekenthali*, respectively).

respectively, was the ancestral state of the genus *Lysmata*. The improvement in the likelihood of the model (Bayes factor = 1.51) when the node was fossilized to state 2 (strict symbiosis) was low compared to when the node was fossilized to state 0 (free-living). Therefore, there is no evidence indicating that symbiosis is significantly more likely than a free-living lifestyle in the ancestral *Lysmata*.

Overall, the present ancestral character state reconstruction provides partial support for Bauer's (2000) hypothesis about the evolution of PSH in shrimps from the genus *Lysmata*.

TABLE 1. Diversity of lifestyles and sociobiology in shrimps from the genera *Exhippolysmata* and *Lysmata*. A question mark (?) indicates data not available.

Species	Geographic distribution	Bathymetric distribution (m) [a]	Habitat [b]	Latitude	Lifestyle	Coloration	Cleaning behavior [c]	Sexual system (SS) [d]	Evidence used forSS [e]	References [f]
E. ensirostris	Indo-Pacific	I & S	?	Tropical	?	?	?	PSH?	E,M	1,10,13
E. hastatoides	W. Africa	12–48	?	Tropical	?	?	?	?	?	1
E. oplophoroides	W. Atlantic	7–27	R	Subtropical	Swarms	?	?	PSH	D,M,P	1,4,14
E. tugelae	South Africa	22–48	?	Subtropical	?	?	?	?	?	1
L. amboinensis	Red Sea, Indo-Pacific	S	S	Tropical	Pairs	Brilliant	S	PSH	E	1,15,26
L. anchisteus	Caribbean	0–3	R,M	Tropical	?	?	?	?	?	1,3
L. ankeri	Caribbean	0–2	S,C	Tropical	Groups	Dull	U	PSH	D,E,M,P	27
L. argentopunctata	E. Pacific	0–35	R,C	Tropical	?	Dull	?	?	?	2
L. bahia	W. Atlantic	I	F	Subtropical	Groups	Dull	U	PSH	D,E,M,P	16
L. boggessi	Caribbean	0–2	S,R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	29
L. californica	E. Pacific	I & S	R,S	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,2,17
L. chica	Galapagos	I & S	R,C	Tropical	?	Dull	?	?	?	2
L. debelius	Indo-Pacific	10–28	R,S	Tropical	Pairs	Brilliant	S	PSH	?	1,11,26
L. galapagensis	E. Tropical Pacific	0–2	R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,2,29
L. grabhami	Caribbean, Atlantic	Subtidal <55	S	Tropical	Pairs	Brilliant	S	PSH	D,M	1,3,18,26
L. gracilirostris	E. Tropical Pacific	0–138	R	Tropical	?	Dull	U	PSH?	M	2,27
L. hochi	Caribbean	I	F	Tropical	Groups	Dull	U	PSH	D,E,M,P	19
L. intermedia	Caribbean, Atlantic	0–22	A,R,C	Tropical	Groups	Dull	U	PSH	D,E,M,P	1,3,16
L. kempi	Burma	37	?	Tropical	?	?	?	?	?	1
L. kuekenthali	Red Sea, Indo-Pacific, South Africa	0–11	?	Tropical	?	Dull	?	PSH	?	1,10,27, 29
L. moorei	Caribbean, W. Atlantic	I	R,F	Tropical	Groups	Dull	U	PSH?	M	1,9,27
L. morelandi	New Zealand	I & S	R	Temperate	?	?	?	?	?	1
L. multiscissa	Djibouti, Africa	?	?	Tropical	?	?	?	?	?	1
L. nayaritensis	E. Pacific	I & S	R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	2,20
L. nilita	Mediterranean, E. Atlantic	?	?	Subtropical	?	Dull	?	PSH	E,M	1,21
L. olavoi	Azores and Savage Is.	135–360	?	Tropical	?	Dull	?	PSH?	M	1,6,28
L. pederseni	Caribbean	S	S	Tropical	Groups	Dull	U	PSH	D,E,M,P	22,27
L. philippinensis	Philippines	267	?	Tropical	?	?	?	?	?	1
L. porteri	Juan Fernandez, E. Pacific	0–12	R	Subtropical, temperate	?	?	?	?	?	1
L. rafa	Caribbean	I & S	R	Tropical	Groups	Dull	U	PSH	D,E,M	22,27
L. rathbunae	Caribbean	13–119	?	Tropical	?	Dull	?	PSH?	M,P	1,3,23

continued

L. seticaudata	Mediterranean, E. Atlantic, Black Sea	I,S	R,S	Subtropical	Crowd	Dull	U	PSH	D,E,M,P	1,21,24
L. stenolepsis	Cape Verde	150–275	?	Tropical	?	?	?	?	?	1,7
L. striata	Caribbean	I	R,M	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,25,27
L. splendida	Indo-Pacific	6–35	W,C	Tropical	?	Brilliant	?	?	?	12
L. ternatensis	Djibouti, Indonesia	<62	Sa	Tropical	?	Dull	?	?	?	1
L. trisetacea	Red Sea, New Zealand	0–150	R,C	Tropical	?	?	?	?	?	1,2
L. uncicornis	NW Africa	4–5	R	Subtropical	?	Dull	?	?	?	1,8
L. vittata	Indo-Pacific, Australia, E. Africa	0–54	A	Tropical	?	?	?	?	?	1,5
L. wurdemanni	Caribbean, E. Atlantic, Gulf of Mexico	0–30	R,J	Subtropical	Crowd	Dull	U	PSH	D,E,M,P	1,3,26,27
L. zacae	Indo-Pacific	?	?	?	?	?	?	?	?	1

[a] I = intertidal; S = subtidal; numbers refer to depth in meters.

[b] A = associated with algae; S = symbiont (with moray eels in the case of *L. californica* and *L. seticaudata*); Sa = coarse sand; R = rocky bottoms and/or rubble; C = among corals; F = fossilized coral terraces; J = jetties; M = mud; W = caverns, on reef roof walls.

[c] S = specialized; U = unspecialized.

[d] PSH = protandric simultaneous hermaphroditism.

[e] D = dissections; E = experiments; M = morphology; P = population structure.

[f] References: 1, Chace, 1997; 2, Wicksten, 2000; 3, Chace, 1972; 4, Williams, 1984; 5, Kemp, 1914; 6, Fransen, 1991; 7, Crosnier and Forest, 1973; 8, Holthuis and Maurin, 1952; 9, Rathbun, 1906; 10, Holthuis, 1948; 11, Bruce, 1983; 12, Burukovsky, 2000; 13, Kagwade, 1982; 14, Braga et al., 2009; 15, Fiedler, 1998; 16, Baeza, 2008b; 17, Bauer and Newman, 2004; 18, Wirtz, 1997; 19, Baeza and Anker, 2008; 20, Baeza et al., 2008; 21, d'Udekem d'Acoz, 2002; 22, Rhyne and Anker, 2007; 23, Rhyne and Lin, 2006; 24, Dohrn and Holthuis, 1950; 25, Anker et al., unpublished; 26, Bauer, 2000; 27, unpublished observations; 28, Fransen, personal communication; 29, this study.

DISCUSSION

The present study suggests that the sexual system in shrimps from the genus *Lysmata* (including *Exhippolysmata*) represents a fixed trait. Anatomical observations, behavioral experiments, and field samples demonstrated that the 2 species studied here are protandric simultaneous hermaphrodites, as reported for all other *Lysmata* species (Table 1). Size–frequency distributions and additional but limited anatomical observations of museum specimens further suggest that at least 9 other species are protandric simultaneous hermaphrodites. Including the information generated in the present study, PSH has been reported for a total of 22 species, or 54% of the 41 species described worldwide.

The well-conserved sexual system in *Lysmata* contrasts with that reported for other genera from the closely related family Hippolytidae. For instance, two different genera of Hippolytidae shrimps, *Thor* and *Hippolyte*, are known to contain both gonochoric and strict sequentially hermaphroditic species (Espinosa-Fuenzalida et al., 2008, and references therein). The reasons for PSH to be fixed in *Lysmata* are not clear, especially when considering the diversity of environments inhabited by these species (see Table 1). Different habitats with varying degrees of structural complexity, seasonality, and predation regimes should favor different sexual systems. For instance, the rather heterogeneous environment (i.e., seagrass beds, seaweed meadows) in which the gregarious *L. boggessi* and *L. wurdemanni* occur is expected to favor sequential hermaphroditism over PSH. In these complex environments, male mating success most likely decreases with increasing body size because small body size is expected to increase searching ability and, ultimately, male mating success when encounter rate among conspecifics is high (Baeza and Thiel, 2007). This small-male advantage together with the well-reported exponential relationship between fecundity and body size in female shrimps is expected to favor strict protandry over simultaneous hermaphroditism in these species (Charnov, 1982).

On the other hand, hermaphroditic shrimps are known to experience brooding constraints (e.g., *L. wurdemanni*; Baeza, 2007c), a condition that theoretically favors simultaneous hermaphroditism (see Charnov, 1982, and references therein). Similarly, in socially monogamous *Lysmata* (e.g., *L. grabhami*; Wirtz, 1997), infrequent encounter rates among conspecifics should be favoring strict simultaneous hermaphroditism over PSH. It should pay (in term of fitness) for each individual in a pair to reproduce both as male and female as soon as possible during their lifetime because this strategy increases reproductive success through both sperm donation to the partner and female reproduction. Thus, an early male phase in these socially monogamous species should not be adaptive. On the other hand, differing costs between the sex functions might explain the existence of an early male phase before the simultaneously hermaphroditic phase in these monogamous species. The relatively large energetic and temporal costs of producing ova might delay maturation of the female function, resulting in a functional adolescent male phase previous to the simultaneously hermaphroditic phase (see Baeza, 2006). Additional studies in gregarious and socially monogamous cleaner shrimp species should improve our understanding about the conditions favoring PSH under a social monogamous mating system in *Lysmata*.

The literature review conducted herein indicates that the diversity of lifestyles in the genus is greater than previously recognized. Initial studies reported a distribution for the genus restricted to tropical-subtropical waters. The present review suggests that shrimps also inhabit cold temperate environments. *Lysmata porteri* is reported from southern Chile, and *L. morelandi* inhabits New Zealand (see Table 1). Because *Exhippolysmata* spp. represents a derived group of *Lysmata*, the deep water environment represents another environment colonized by the species in this group (see Baeza et al., 2009). Also, the dichotomy in social organization ("Crowd" versus "Pair" species) noted in initial studies (Bauer, 2000) is not supported. In addition to tropical pair-living and temperate gregarious species, the present review indicates other species forming swarms (extremely large aggregations) in temperate deep water soft-bottom environments (i.e., *E. oplophoroides*) or living in small groups in the tropical or subtropical intertidal that might or not associate with sea anemones (*L. ankeri*; Table 1). The possibility of an adaptive radiation in this group of shrimps is currently being explored. The rather unusual sex allocation pattern of this shrimps might represent the key innovation allowing species in these two genera to colonize and persist in environments where species with conventional sexual systems might fail.

The ancestral character state reconstruction analysis conducted in this study provides partial support for Bauer's (2000) hypothesis about the evolution of PSH in *Lysmata*. The analysis suggested that the ancestral *Lysmata* shrimp lived as socially monogamous pairs either facultatively associated to other macroinvertebrates or featuring a strictly symbiotic lifestyle (with sea anemones, for example). The free-living condition of several species pertaining to the cosmopolitan and neotropical clades is likely to be derived according to the present analysis. PSH might have

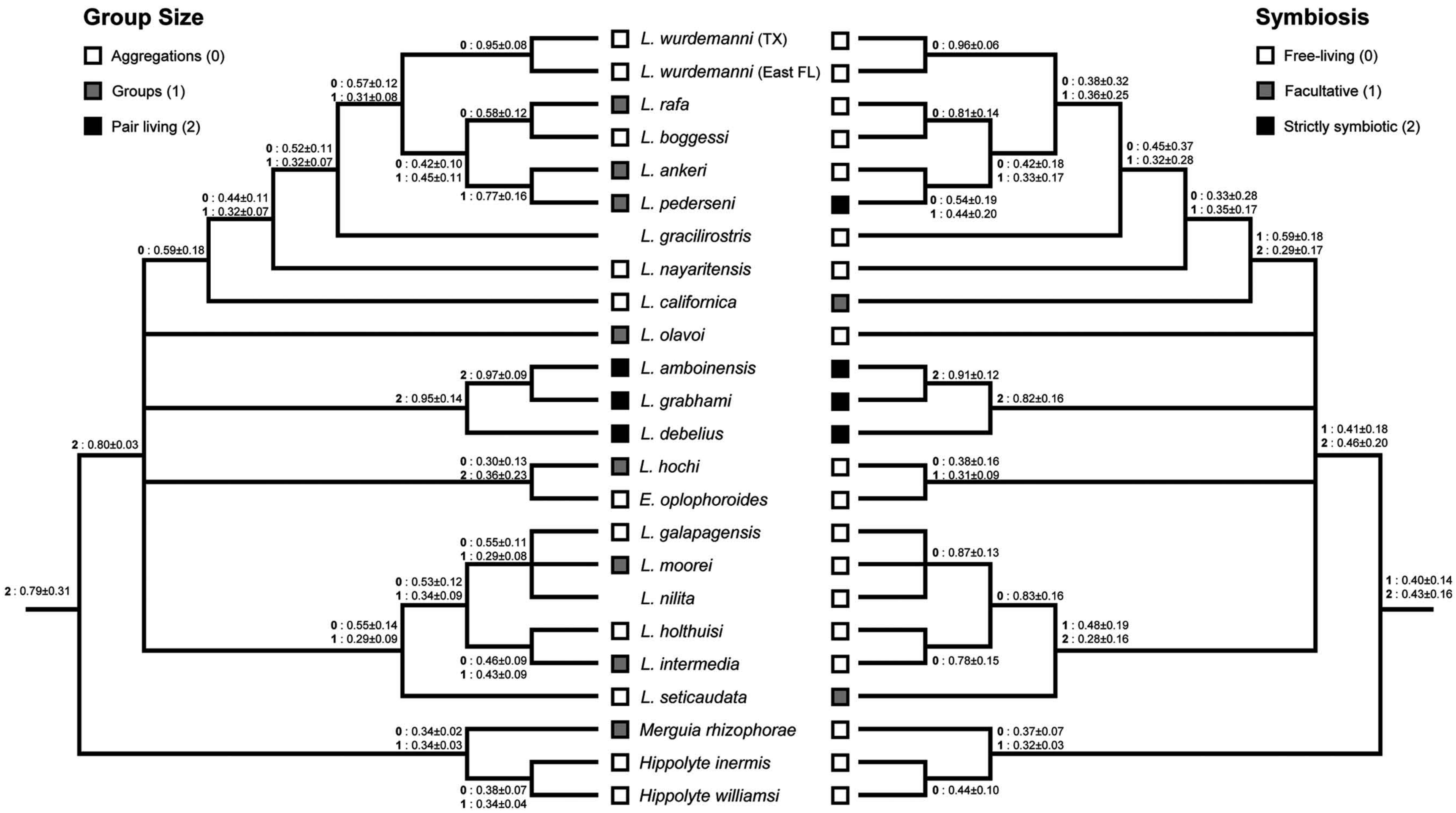

FIGURE 4. A 50% majority-rule consensus tree obtained using Bayesian inference phylogenetic methods showing the posterior densities of the reconstructed ancestral states (symbiosis and group size) at different nodes. For each node, the posterior probability for group size (left tree) and symbiosis (right tree) obtained when reconstructing the ancestral state of the most recent common ancestor to different clades in each tree is shown.

evolved in the tropics from an ancestral protandric species of *Lysmata* that became a specialized fish cleaner, as suggested by Bauer (2000). Restricted mobility of individuals resulting from their association with the host, and, hence, the reduced probability of encountering mating partners, would have favored PSH (Bauer, 2000) (see foregoing for further details about this hypothesis). Nonetheless, the inferences about ancestral character states from the present analysis need to be considered with caution. Indeed, the present analysis did not support an ancestral symbiotic condition as significantly more likely than a free-living condition. Also, several internal nodes in the phylogenetic tree were not well supported by the Bayesian analysis of phylogenetic inference (see Baeza et al., 2009). This low support for internal nodes, together with the breadth of the posterior distributions of the character inferred for these nodes, means that other alternative routes to the evolution and maintenance of this peculiar sexual system in *Lysmata* cannot be ruled out.

Among alternative historical scenarios (to that proposed by Bauer, 2000), PSH might well have evolved from a strict simultaneous hermaphrodite or even from a strict gonochoric free-living ancestor inhabiting tropical environments. The evolution of PSH from an ancestral strictly simultaneous hermaphroditic condition has been reported previously for the worm *Ophryotrocha diadema*, one of the few other marine invertebrates in which PSH has been demonstrated (Dahlgren et al., 2001). Acting together with the conditions favoring simultaneous hermaphroditism (i.e., low abundance), sex-dependent energetic costs might have favored an early maturation of the male reproductive function compared to that of the female function in the ancestral free-living shrimp (regardless of its sexual system), ultimately resulting in the evolution of PSH as we observe it today in *Lysmata* (and *Exhippolysmata*). Similarly, brooding constraints experienced by hermaphroditic shrimps might have favored the retention of the male function later in life. If the space for brooding embryos in the abdomen becomes saturated, allocation of energy to sperm production is expected to maximize fitness. This argument is similar to that of Ghiselin (1987) to explain apparent protogynous simultaneous hermaphroditism in chitons. In some species of polyplacophorans, individuals brood eggs along the side of the body. Early in life, they reproduce strictly as females until they reach a size at which the space in which they brood is saturated. At that point, the same individuals start producing sperm while they are brooding. Brooding constraints have been previously reported for at least one species of *Lysmata* (*L. wurdemanni*; Baeza, 2006). New studies are needed to confirm whether brood constraints are common in the genus.

In the scenarios depicted here, we should expect that, in a phylogeny of the group, "tropical–low abundance" species would have a more basal position than the "Pair" and "Crowd" species ("Pair" and "Crowd" sensu Bauer, 2000). The rather complex mating system (social monogamy) and specialized fish-cleaning behavior of the "Pair" species most probably evolved from "tropical–low abundance" species without complex cleaning behavior and with rather simple mating systems (i.e., without long-lasting associations between mating partners), as appears to be the case for most shrimps from the closely related family Hippolytidae. The unresolved position of the different natural clades with respect to each other in the current phylogeny (see also Baeza et al., 2009) constrain testing this last hypothesis against Bauer's (2000) ideas. Future studies attempting to resolve the natural relationships among species of *Lysmata*, *Exhippolysmata*, and other related taxa together with the detailed examination of their sexual system should allow explaining the origin of simultaneous hermaphroditism in shrimps from the genus *Lysmata*.

Last, it is worth mentioning one of the main assumptions of the present analysis. PSH was treated as a singular innovation only originating in the genus *Lysmata* (which contains *Exhippolysmata*), as initially suggested by Bauer (2000). To the best of my knowledge, shrimps from the genus *Merguia*, apparently the sister group to *Lysmata*, seem to have a gonochoric sexual system. However, this observation needs experimental confirmation. Most importantly, future studies need to test for the existence of protandric simultaneous hermaphroditism in members from other closely related genera (i.e., *Mimocaris*, *Parahippolyte*, *Merguia*, *Merhippolyte*). These studies might reveal that PSH is not a singularity. Indeed, PSH has independently evolved in the past at least four other times outside the Caridea. In addition to *Lysmata* shrimps, PSH has been confirmed in the polychaete worm *Ophryotrocha diadema* (Premoli and Sella, 1995), the land snail *Achatina fulica* (Tomiyama, 1996), the tunicate *Pyura chilensis* (Manríquez and Castilla, 2005), and the symbiotic barnacle *Chelonibia patula* (Crisp, 1983). If simultaneous hermaphroditism turns out not to be a singularity in shrimps from the families Hippolytidae and Lysmatidae, then it should be possible to explore the environmental conditions that favor this unique sexual system in shrimps.

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LITERATURE CITED

Baeza, J. A. 2006. Testing Three Models on the Adaptive Significance of Protandric Simultaneous Hermaphroditism in a Marine Shrimp. *Evolution*, 60:1840–1850.

———. 2007a. Male Mating Opportunities Affect Sex Allocation in a Protandric Simultaneous Hermaphroditic Marine Shrimp. *Behavioral Ecology and Sociobiology*, 61:365–370.

———. 2007b. No Effect of Group Size on Sex Allocation in a Protandric-Simultaneous Hermaphroditic Shrimp. *Journal of the Marine Biological Association of the United Kingdom*, 87:1169–1174.

———. 2007c. Sex Allocation in a Simultaneously Hermaphroditic Marine Shrimp. *Evolution*, 61:2360–2373.

———. 2008a. Social Monogamy in the Shrimp *Pontonia margarita*, a Symbiont of *Pinctada mazatlantica*, in the Tropical Eastern Pacific Coast. *Marine Biology*, 153:387–395.

———. 2008b. Protandric Simultaneous Hermaphroditism in the Shrimps *Lysmata bahia* and *L. intermedia*. *Invertebrate Biology*, 127:181–188.

Baeza, J. A., and A. Anker. 2008. *Lysmata hochi* n. sp., a New Species of Hermaphroditic Shrimp from the Southern Caribbean. *Journal of Crustacean Biology*, 28:148–155.

Baeza, J. A., and R. T. Bauer. 2004. Experimental Test of Social Mediation of Sex Change in a Protandric Sequential Hermaphrodite; The Marine Shrimp *Lysmata wurdemanni* (Crustacea: Caridea). *Behavioral Ecology and Sociobiology*, 55:544–550.

Baeza, J. A., J. Reitz, and R. Collin. 2008. Protandric Simultaneous Hermaphroditism and Sex Ratio in the Shrimp *Lysmata nayaritensis*. *Journal of Natural History*, 41:2843–2850.

Baeza, J. A., C. D. Schubart, P. Zillner, S. Fuentes, and R. T. Bauer. 2009. Molecular Phylogeny of Shrimps from the Genus *Lysmata* (Caridea: Lysmatidae): The Evolutionary Origins of Protandric Simultaneous Hermaphroditism and Pair-Living. *Biological Journal of the Linnaean Society,* 96:415–424.

Baeza, J. A., and M. Thiel. 2007. "The Mating System of Symbiotic Crustaceans: A Conceptual Model Based on Optimality and Ecological Constraints." In *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms*, ed. J. E. Duffy and M. Thiel, pp. 250–267. Oxford, UK: Oxford University Press.

Bauer, R. T. 2000. Simultaneous Hermaphroditism in Caridean Shrimps: A Unique and Puzzling Sexual System in the Decapoda. *Journal of Crustacean Biology*, 20(Spec. No. 2):116–128.

———. 2006. Same Sexual System but Variable Sociobiology: Evolution of Protandric Simultaneous Hermaphroditism in *Lysmata* Shrimps. *Integrative and Comparative Biology*, 46:430–438.

Bauer, R. T., and G. J. Holt. 1998. Simultaneous Hermaphroditism in the Marine Shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae): An Undescribed Sexual System in the Decapod Crustacea. *Marine Biology*, 132:223–235.

Bauer, R. T., and W. A. Newman. 2004. Protandric Simultaneous Hermaphroditism in the Marine Shrimp *Lysmata californica* (Caridea: Hippolytidae). *Journal of Crustacean Biology*, 24:131–139.

Braga, A. A., L. S. López-Greco, D. C. Santos, and A. Fransozo. 2009. Morphological Evidence for Protandric Simultaneous Hermaphroditism in the Caridean *Exhippolysmata oplophoroides*. *Journal of Crustacean Biology*, 29:34–41.

Bruce, A. J. 1983. *Lysmata debelius*, New Species, a New Hippolytid Shrimp from the Philippines. *Revue Francaise d'Aquariologie et Herpetologie*, 4:115–120.

Burukovsky, R. N. 2000. *Lysmata splendida* sp. nov., a New Species of Shrimp from the Maldives (Crustacea: Decapoda: Hippolytidae). *Senckenbergiana Maritime*, 30:223–227.

Chace, F. A. Jr. 1972. *The Shrimps of the Smithsonian–Bredin Caribbean Expeditions with a Summary of the West Indian Shallow-Water Species*. Smithsonian Contributions to Zoology, No. 98. Washington, D.C.: Smithsonian Institution Press.

———. 1997. *The Caridean Shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae*. Smithsonian Contributions to Zoology, No. 587. Washington, D.C.: Smithsonian Institution Press.

Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton: Princeton University Press.

Correa, C., J. A. Baeza, E. Dupré, I. A. Hinojosa, and M. Thiel. 2000. Mating Behavior and Fertilization Success of Three Ontogenetic Stages of Male Rock Shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *Journal of Crustacean Biology*, 20:628–640.

Crisp, D. J. 1983. *Chelonobia patula* (Ranzani), a Pointer to the Evolution of the Complemental Male. *Marine Biology Letters*, 4: 281–294.

Crosnier, A., and J. Forest. 1973. "Les Crevettes Profondes de l'Atlantique Oriental Tropical." In *Faune Tropicale 19*. Paris: O.R.S.T.O.M.

Dahlgren, T. G., B. Åkesson, C. Schander, K. M. Halanych, and P. Sundberg. 2001. Molecular Phylogeny of the Model Annelid *Ophryotrocha*. *Biological Bulletin*, 201:193–203.

Dohrn, P. F. R., and L. B. Holthuis. 1950. *Lysmata nilita*, a New Species of Prawn (Crustacea Decapoda) from the Western Mediterranean. *Pubblicazioni della Stazione Zoologica di Napoli*, 22:339–347.

d'Udekem d'Acoz, C. 2002. *Lysmata seticaudata* (Risso, 1816) and *L. nilita* Dohrn and Holthuis, 1950 Are Protandrous Simultaneous Hermaphrodites (Decapoda, Caridea, Hippolytidae). *Crustaceana*, 75:1149–1152.

Espinoza-Fuenzalida, N. L., M. Thiel, E. Dupre, and J.A. Baeza. 2008. Is *Hippolyte williamsi* Gonochoric or Hermaphroditic? A Multi-Approach Study and a Review of Sexual Systems in *Hippolyte* Shrimps. *Marine Biology*, 155:623–635.

Fiedler, G. C. 1998. Functional, Simultaneous Hermaphroditism in Female-Phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae). *Pacific Science*, 52:161–169.

Fransen, C. H. J. M. 1991. *Lysmata olavoi*, a New Shrimp of the Family Hippolytidae (Decapoda, Caridea) from the Eastern Atlantic Ocean. *Arquipelago-Life Marine Sciences*, 9:63–73.

Ghiselin, M. T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.

———. 1987. "Evolutionary Aspects of Marine Invertebrate Reproduction." In *Reproduction of Marine Invertebrates: General Aspects: Seeking Unity in Diversity*. Volume 9, ed. A. C. Giese, J. S. Pearse, and V. B. Pearse, pp. 609–665. Pacific Grove, Calif.: The Boxwood Press.

Holthuis, L. B. 1948. Note on Some Crustacea Decapoda Natantia from Suriname. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C, Biological and Medical Sciences*, 51:1104–1113.

Holthuis, L. B., and C. Maurin. 1952. Note sur *Lysmata uncicornis* nov. spec. et sur deux autres espèces intéressantes de crustacés décapodes macroures de la côte Atlantique du Maroc. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 55:197–202.

Kagwade, P. V. 1982. The Hermaphrodite Prawn *Hippolysmata ensirostris* Kemp. *Indian Journal of Fisheries*, 28:189–194.

Kass, R. E., and A. E. Raftery. 1995. Bayes Factors. *Journal of the American Statistical Association*, 90:773–795.

Kemp, S. 1914. Notes on Crustacea Decapoda in the Indian Museum, V. Hippolytidae. *Records of the Indian Museum*, 10:81–129.

Limbaugh, C., H. Pederson, and F. A. Chace, Jr. 1961. Shrimps That Clean Fishes. *Bulletin of Marine Science*, 11:237–57.

Manríquez, P. H., and J. C. Castilla. 2005. Self-Fertilization as an Alternative Mode of Reproduction in the Solitary Tunicate *Pyura chilensis*. *Marine Ecology Progress Series*, 305:113–125.

Pagel, M., and A. Meade. 2006. Bayesian Analysis of Correlated Evolution of Discrete Characters by Reversible-Jump Markov Chain Monte Carlo. *The American Naturalist*, 167:808–825.

Pagel, M., A. Meade, and D. Barker. 2004. Bayesian Estimation of Ancestral Character States on Phylogenies. *Systematic Biology*, 53:673–684.

Policansky, D. 1982. Sex Change in Plants and Animals. *Annual Review of Ecology and Systematics*, 13:417–495.

Premoli, M. C., and G. Sella. 1995. Sex Economy in Benthic Polychaetes. *Ethology, Ecology, and Evolution*, 7:27–48.

Rathbun, M. J. 1906. South American Crustacea. *Revista Chilena de Historia Natural*, 11:45–50.

Rhyne, A. L., and A. Anker. 2007. *Lysmata rafa*, a New Species of Peppermint Shrimp (Crustacea, Caridea, Hippolytidae) from the Subtropical Western Atlantic. *Helgoland Marine Research*, 61:291–296, doi:10.1007/s10152-007-0077-4.

Rhyne, A. L., and J. Lin. 2006. A Western Atlantic Peppermint Shrimp Complex: Re-Description of *Lysmata wurdemanni*, Description of Four New Species, and Remarks on *Lysmata rathbunae* (Crustacea: Decapoda: Hippolytidae). *Bulletin of Marine Science*, 79:165–204.

Schatte, J., and R. Saborowski. 2006. Change of External Sexual Characteristics During Consecutive Moults in *Crangon crangon* L. *Helgoland Marine Research*, 60:70–73, doi:10.1007/s10152-005-0013-4.

Terossi, M., L. S. López-Greco, and F. L. Mantelatto. 2008. *Hippolyte obliquimanus* (Decapoda: Caridea: Hippolytidae): A Gonochoric or Hermaphroditic Shrimp Species? *Marine Biology*, 154:127–135.

Tomiyama, K. 1996. Mate-Choice Criteria in a Protandrous Simultaneously Hermaphroditic Land Snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae). *Journal of Molluscan Studies*, 62:101–111.

Wicksten, M. K. 2000. The Species of *Lysmata* (Caridea: Hippolytidae) from the Eastern Pacific Ocean. *Amphipacifica*, 2:3–22.

Williams, A. B. 1984. *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Washington, D.C.: Smithsonian Institution Press.

Wirtz, P. 1997. Crustacean Symbionts of the Sea Anemone *Telmatactis cricoides* at Madeira and the Canary Islands. *Journal of Zoology*, 242:799–811.

Reconciling Genetic Lineages with Species in Western Atlantic *Coryphopterus* (Teleostei: Gobiidae)

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ABSTRACT. Species identification of western Atlantic *Coryphopterus* can be problematic because some of the species are morphologically similar, there is confusing morphological variation within some species, no taxonomic key includes all currently recognized species, and the validity of some species is questionable. The most recently published keys do not include *Coryphopterus tortugae* or *C. venezuelae*, the validity of which as distinct from *C. glaucofraenum* has been questioned. Neighbor-joining trees derived from mitochondrial cytochrome *c* oxidase I (COI) sequences (DNA barcoding) were used to determine the number of genetically distinct lineages of *Coryphopterus* from collections made off Belize, Curacao, and Florida. Additional specimens for genetic and morphological analysis were obtained from Panama, Venezuela, and the Bahamas. Subsequent comparative analysis of preserved voucher specimens from which DNA was extracted and digital color photographs of those specimens taken before preservation yielded, in most cases, sufficient morphological information to separate the genetic lineages. Species identification of the lineages was then determined based on review of original and subsequent descriptions of *Coryphopterus* species and examination of museum specimens, including some type material. Many museum specimens are misidentified. Twelve species of *Coryphopterus* are herein recognized in the western Atlantic and Caribbean: *C. alloides*, *C. dicrus*, *C. eidolon*, *C. glaucofraenum*, *C. hyalinus*, *C. kuna*, *C. lipernes*, *C. personatus*, *C. punctipectophorus*, *C. thrix*, *C. tortugae*, and *C. venezuelae*. *Coryphopterus bol* Victor, 2008 is a synonym of *C. venezuelae* (Cervigón, 1966). Although genetically distinct, *C. glaucofraenum* and some specimens of *C. venezuelae* are extremely similar and cannot be separated on the basis of morphology 100% of the time. Comments on the identification of each *Coryphopterus* species and a revised key to western Atlantic species are provided.

INTRODUCTION

To provide specific identifications of larvae of Caribbean reef fishes at Carrie Bow Cay, Belize, a small coral-fringed island on the Belizean Barrier Reef (16°48.5′N, 88°05′W), we have been matching larvae to adults through DNA barcoding (mitochondrial cytochrome c oxidase I [COI] sequences). In addition to greatly increasing our success rate of identifying larvae, DNA barcoding is also providing a method of checking existing species-level classifications by revealing the numbers of distinct genetic lineages within genera.

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Attempts to identify Belizean *Coryphopterus* species using the most recently published keys (Böhlke and Robins, 1960, 1962; Böhlke and Chaplin, 1968; Murdy, 2002) proved problematic for certain species. None of those keys includes *C. tortugae* (Jordan) or *C. venezuelae* Cervigón, presumably because the validity of both species as distinct from *C. glaucofraenum* Gill has been questioned (e.g., Böhlke and Robins, 1960; Cervigón, 1966; Thacker and Cole, 2002). Longley and Hildebrand (1941) and Böhlke and Robins (1960) considered *C. tortugae* (Jordan; type locality, Dry Tortugas, Florida) a synonym of *C. glaucofraenum* Gill. Garzón-Ferreira and Acero (1990) redescribed *C. tortugae* as distinct based on new collections from the Colombian Caribbean. Thacker and Cole (2002) acknowledged the latter work but did not recognize *C. tortugae* in their phylogenetic analysis of *Coryphopterus* species. Victor (2008) recognized *C. tortugae* as distinct from *C. glaucofraenum* and identified what he considered a cryptic new species within Garzón-Ferreira and Acero's (1990) *C. tortugae*, which he named *Coryphopterus bol*. Cervigón (1994) elevated *C. venezuelae* from a subspecies of *C. glaucofraenum* to a distinct species, but it was not included in Murdy's (2002) key or Thacker and Cole's (2002) and Victor's (2008) molecular phylogenies of *Coryphopterus* species.

Another problem with identification of western Caribbean *Coryphopterus* is that stated distributions of many species are conflicting, and some do not include the western Caribbean. Greenfield and Johnson (1999) identified nine species of *Coryphopterus* from Belize (all of the 12 recognized herein except for *C. venezuelae*, *C. punctipectophorus*, and the recently described *C. kuna* (Victor, 2007)). Murdy (2002) listed only *C. alloides*, *C. dicrus*, *C. glaucofraenum*, *C. hyalinus*, *C. lipernes*, and *C. personatus* as having ranges that include Central America, western Caribbean, or Caribbean. A search for reef-associated species in Belize in FishBase (www.fishbase.org) returned only *C. alloides*, *C. eidolon*, *C. glaucofraenum*, and *C. personatus*.

The purposes of this paper are to assess the number of valid *Coryphopterus* species known from the western Atlantic and to provide comments on the identification of, and a revised key to, those species based on results of DNA barcoding, subsequent examination of voucher specimens and color photographs of them, examination of museum specimens, and reference to original and other descriptions of the species. A neotype for *C. glaucofraenum* is designated because the location of Gill's (1863) holotype is unknown.

METHODS

Depending on the locality, fish specimens were collected using the fish anesthetic quinaldine sulfate or rotenone. Specimens were measured to the nearest 0.5 mm, photographed with a Fujifilm FinePix 3 digital camera to record color patterns, sampled for genetic analysis, and then preserved as vouchers. Tissue sampling for molecular work involved removing a muscle biopsy, eye, or caudal body portion (depending on size) and storage in saturated salt buffer (Seutin et al., 1990). Genomic DNA was extracted from up to approximately 20 mg minced preserved tissue via an automated phenol:chloroform extraction on the Autogenprep965 (Autogen, Holliston, MA) using the mouse tail tissue protocol with a final elution volume of 50 μL. For polymerase chain reaction (PCR), 1 μL of this genomic DNA is used in a 10 μL reaction with 0.5 U Bioline (BioLine USA, Boston, MA) Taq polymerase, 0.4 μL 50 mM $MgCl_2$, 1 μL 10× buffer, 0.5 μL 10 mM deoxyribonucleotide triphosphate (dNTP), and 0.3 μL 10 μM each primer FISH-BCL (5′-TCAACYAATCAYAAAGATATYGGCAC) and FISH-BCH (5′-TAAACTTCAGGGTGACCAAAAAATCA). The thermal cycler program for PCR was 1 cycle of 5 min at 95°C; 35 cycles of 30 s at 95°C, 30 s at 52°C, and 45 s at 72°C; 1 cycle of 5 min at 72°C; and a hold at 10°C. The PCR products were purified with Exosap-IT (USB, Cleveland, OH) using 2 μL 0.2× enzyme and incubated for 30 min at 37°C. The reaction was then inactivated for 20 min at 80°C. Sequencing reactions were performed using 1 μL of this purified PCR product in a 10 μL reaction containing 0.5 μL primer, 1.75 μL BigDye buffer, and 0.5 μL BigDye (ABI, Foster City, CA) and run in the thermal cycler for 30 cycles of 30 s at 95°C, 30 s at 50°C, 4 min at 60°C, and then held at 10°C. These sequencing reactions were purified using Millipore Sephadex plates (MAHVN-4550; Millipore, Billerica, MA) per manufacturer's instructions and stored dry until analyzed. Sequencing reactions were analyzed on an ABI 3730XL automated DNA sequencer, and sequence trace files were exported into Sequencher 4.7 (GeneCodes, Ann Arbor, MI). Using the Sequencher program, ends were trimmed from the raw sequences until the first and last 10 bases contained fewer than 5 base calls with a confidence score (phred score) lower than 30. After trimming, forward and reverse sequences for each specimen were assembled, each assembled contig was examined and edited by hand, and each sequence was checked for stop codons. Finally the consensus sequence from each contig was aligned and exported in a nexus format. Neighbor-joining trees (Saitou and Nei, 1987) and distance matrices were generated using Paup*4.1 (Swofford, 2002) on an analysis of Kimura 2-parameter (K2P) distances (Kimura, 1980).

MATERIAL

The *Coryphopterus* material examined is listed in the Appendix (Table A.1). This table includes the voucher specimens represented in the neighbor-joining tree (Figure 1), as well as non-voucher specimens collected as part of this or other projects. Most specimens examined genetically for this chapter are juveniles or adults, except those of *C. kuna*; that species is represented in our samples only by larvae. For most specimens analyzed genetically, a digital color photograph of the specimen taken before dissection and preservation is housed at the Smithsonian Institution. Cytochrome *c* oxidase I (COI) sequences for specimens analyzed genetically are deposited in GenBank (accession numbers GQ367306–GQ367475). Genetic information for several specimens collected in the Bahamas was not available in time for inclusion in the neighbor-joining tree, but identifications of those specimens based on that information are discussed in the text.

RESULTS

Twelve distinct genetic lineages of *Coryphopterus* are present in our material (see Figure 1). One of those lineages, a single specimen identified as *C. alloides* from Curacao is under additional investigation and is not discussed further here. Tissue samples of *C. punctipectophorus* were not available for genetic analysis. The other lineages, from top to bottom in Figure 1, are *C. lipernes*, *C. hyalinus*, *C. personatus*, *C. tortugae*, *C. glaucofraenum*, *C. venezuelae*, *C. dicrus*, *C. thrix*, *C. eidolon*, *C. alloides*, and *C. kuna*. Comments on the identification of each lineage, as well as *C. punctipectophorus*, are provided below. The COI sequence of *Coryphopterus bol* Victor, 2008 (PR SIO0869, fig. 1 [SIO = Scripps Institution of Oceanography]) is part of the *C. venezuelae clade*, and the synonymy of that species is discussed below. Intra- and interspecific differences in percent sequence divergence for COI for all species are provided in Table 1. We have not plotted distribution maps of *Coryphopterus* species because our samples are from a limited number of locations, and historical confusion about the identification of some species precluded our relying on geographic information based on museum catalogues. Based on extensive recent collecting throughout the Caribbean, Ross Robertson (Smithsonian Tropical Research Institute, personal communication, 8 June 2009) and James Van Tassell are providing distribution maps of *Coryphopterus* species in their *Shorefishes of the Greater Caribbean* CD, expected to be released in 2009.

Coryphopterus lipernes **Böhlke and Robins, 1962**

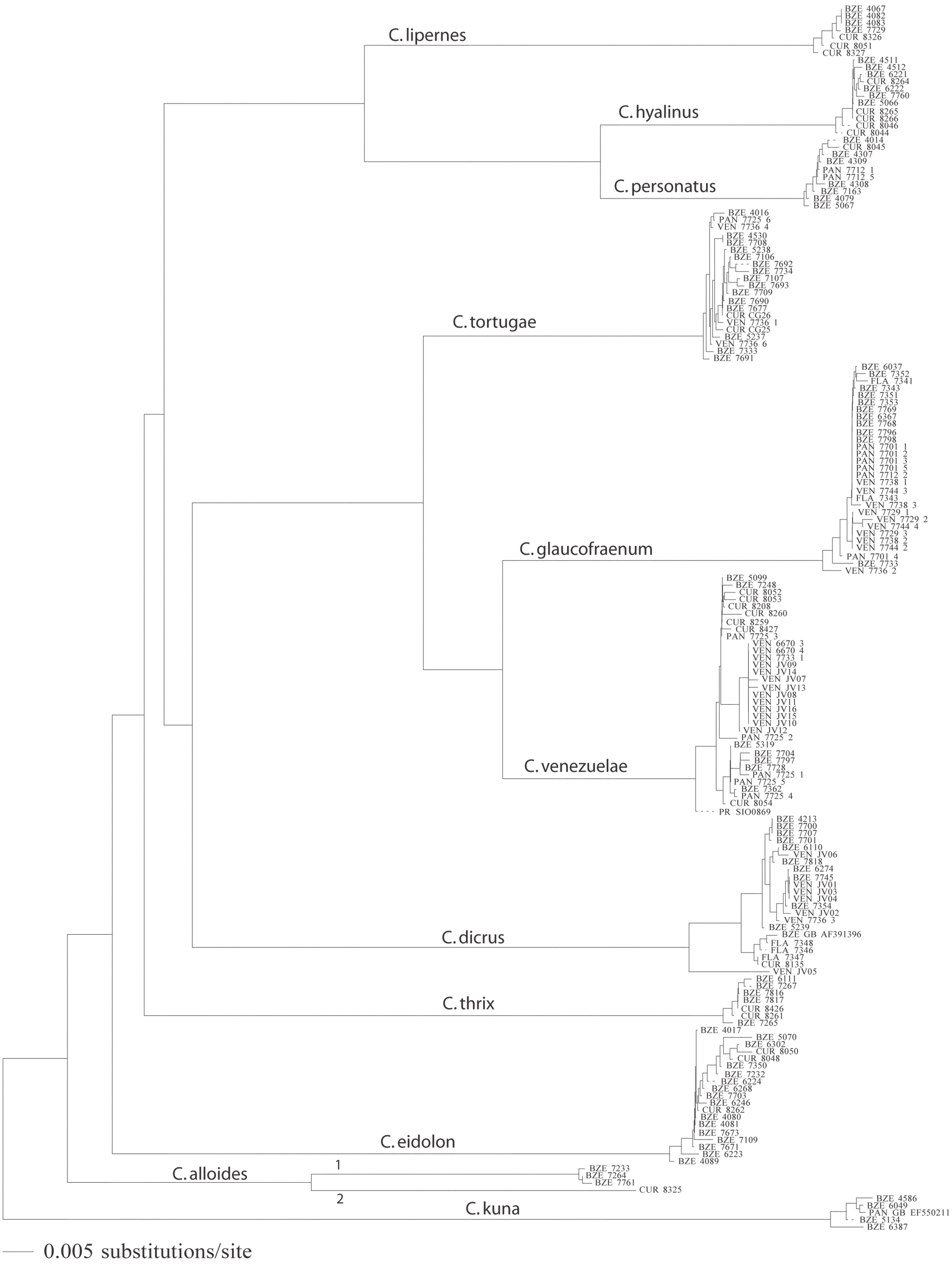
FIGURE 2

Our specimens of *C. lipernes* from Belize and Curacao form a close genetic clade. Identification of *C. lipernes* presents no problems: It is distinguished from all *Coryphopterus* species except *C. hyalinus* and *C. personatus* by the presence of black pigment surrounding the anus; from *C. hyalinus* by the presence of a single (vs. two) anterior interorbital pore; and from *C. personatus* by color pattern (see Figure 2). We did not make fin-ray counts for *C. lipernes*, but according to Böhlke and Robins (1962), *C. lipernes* also differs from *C. personatus* in having 10 (vs. 11) second dorsal- and anal-fin elements. Murdy (2002) distinguished *C. lipernes* and *C. personatus* from *C. hyalinus* by the presence of two pores between the eyes (vs. three), but as noted by Böhlke and Robins (1962), there is one *anterior* interorbital pore in *C. lipernes* and *C. personatus* and two in *C. hyalinus*.

Coryphopterus hyalinus **Böhlke and Robins, 1962**

FIGURE 2

The validity of *C. hyalinus* as distinct from *C. personatus* has been questioned (e.g., Smith et al., 2003), but the two are genetically distinct (see Figure 1, Table 1). Of the *Coryphopterus* gobies with a black ring of pigment around the anus (*C. hyalinus*, *C. personatus*, and *C. lipernes*), *C. hyalinus* is the only one with two anterior interorbital pores (Böhlke and Robins, 1962; Böhlke and Chaplin, 1968). Because head pores can be difficult to see in fresh material (considerably easier to see in preserved specimens), separation of *C. hyalinus* and *C. personatus* in the field can be difficult. We have observed no consistent differences in pigmentation in fresh or preserved specimens of the two species, but we often collect *C. hyalinus* in deeper water than *C. personatus*.


C. lipernes
BZE 4067
BZE 4082
BZE 4083
BZE 7729
CUR 8326
CUR 8051
CUR 8327
BZE 4511
BZE 4512
BZE 6221
CUR 8264
BZE 6222
BZE 7760
BZE 5066
C. hyalinus
CUR 8265
CUR 8266
CUR 8046
CUR 8044
BZE 4014
CUR 8045
BZE 4307
BZE 4309
PAN 7712 1
PAN 7712 5
BZE 4308
C. personatus
BZE 7163
BZE 4079
BZE 5067
BZE 4016
PAN 7725 6
VEN 7736 4
BZE 4530
BZE 7708
BZE 5238
BZE 7106
BZE 7692
BZE 7734
BZE 7107
BZE 7693
BZE 7709
BZE 7690
BZE 7677
CUR CG26
C. tortugae
VEN 7736 1
CUR CG25
BZE 5237
VEN 7736 6
BZE 7333
BZE 7691
BZE 6037
BZE 7352
FLA 7341
BZE 7343
BZE 7351
BZE 7353
BZE 7769
BZE 6367
BZE 7768
BZE 7796
BZE 7798
PAN 7701 1
PAN 7701 2
PAN 7701 3
PAN 7701 5
PAN 7712 2
VEN 7738 1
VEN 7744 3
FLA 7343
VEN 7738 3
VEN 7729 1
VEN 7729 2
VEN 7744 4
VEN 7729 3
VEN 7738 2
VEN 7744 2
C. glaucofraenum
PAN 7701 4
BZE 7733
VEN 7736 2
BZE 5099
BZE 7248
CUR 8052
CUR 8053
CUR 8208
CUR 8260
CUR 8259
CUR 8427
PAN 7725 3
VEN 6670 3
VEN 6670 4
VEN 7733 1
VEN JV09
VEN JV14
VEN JV07
VEN JV13
VEN JV08
VEN JV11
VEN JV16
VEN JV15
VEN JV10
VEN JV12
PAN 7725 2
BZE 5319
BZE 7704
BZE 7797
BZE 7728
PAN 7725 1
C. venezuelae
PAN 7725 5
BZE 7362
PAN 7725 4
CUR 8054
PR SIO0869
BZE 4213
BZE 7700
BZE 7707
BZE 7701
BZE 6110
VEN JV06
BZE 7818
BZE 6274
BZE 7745
VEN JV01
VEN JV03
VEN JV04
BZE 7354
VEN JV02
VEN 7736 3
BZE 5239
C. dicrus
BZE GB AF391396
FLA 7348
FLA 7346
FLA 7347
CUR 8135
VEN JV05
BZE 6111
BZE 7267
BZE 7816
BZE 7817
C. thrix
CUR 8426
CUR 8261
BZE 7265
BZE 4017
BZE 5070
BZE 6302
CUR 8050
CUR 8048
BZE 7350
BZE 7232
BZE 6224
BZE 6268
BZE 7703
BZE 6246
CUR 8262
BZE 4080
BZE 4081
BZE 7673
BZE 7109
C. eidolon
BZE 7671
BZE 6223
BZE 4089
1
C. alloides
BZE 7233
BZE 7264
BZE 7761
CUR 8325
2
C. kuna
BZE 4586
BZE 6049
PAN GB EF550211
BZE 5134
BZE 6387
0.005 substitutions/site

Coryphopterus personatus (Jordan and Thompson, 1905)

FIGURE 2

Identification of *C. personatus* also presents no problems using published keys. It can be distinguished from *C. hyalinus* by the presence of a single interorbital pore and from *C. lipernes* by pigment pattern (see Figure 2). According to Böhlke and Robins (1962), *C. personatus* also can be separated from *C. lipernes* by having 11 (vs. 10) total elements in the second dorsal and anal fins.

Coryphopterus tortugae (Jordan, 1904)

FIGURE 3

Longley and Hildebrand (1941) and Böhlke and Robins (1960) considered *C. tortugae* (Jordan: type locality, Dry Tortugas, Florida) to be a synonym of *C. glaucofraenum* Gill. Garzón-Ferreira and Acero (1990) redescribed *C. tortugae* as distinct based on new collections from the Colombian Caribbean. Victor (2008) concurred with Garzón-Ferreira and Acero's (1990) recognition of *C. tortugae* but noted that their Santa Marta specimens constitute a distinct species, which he described as *C. bol*. As noted below (see "Synonymy of *Coryphopterus bol*"), *C. bol* appears to be a synonym of *C. venezuelae*.

We had initially identified all specimens of the *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* clades as *C. glaucofraenum* using published keys (Böhlke and Robins, 1960; Böhlke and Chaplin, 1968; Murdy, 2002). However, those specimens separate into three well-defined lineages based on COI sequences. Specimens in one of those lineages are usually paler than those of the other two and almost always have a central bar of basicaudal pigment (vs. usually two spots or a dumbbell- or C-shaped marking), characters described by Garzón-Ferreira and Acero (1990) as diagnostic for *C. tortugae*. Böhlke and Robins (1960), who considered *C. tortugae* to be a pallid form of *C. glaucofraenum*, noted that the pigment markings along the side of the body are round (upper row) or vertically elongate (lower row) versus X-shaped as in *C. glaucofraenum*, usually a consistent feature in our specimens of *C. tortugae*. The pigment spots in the lower row of markings along the side of the body in *C. tortugae* are usually vertically elongate (crescents or some part of an X), but they are rarely distinct X-shaped markings. If some of the anterior markings do resemble X's (Figure 3D), the height of each X is considerably smaller than the height of the X's in *C. glaucofraenum* and, when present, in *C. venezuelae* (half or less of eye diameter in *C. tortugae*, approximately three-quarters of or equal to eye diameter in the other two species). The pigment spots in the lower row also are not rounded, as they are in pale specimens of *C. venezuelae*.

We have not found the basicaudal pigment to be a reliable character for separating *C. tortugae* from *C. glaucofraenum* and *C. venezuelae*, as all three species may have a central bar of pigment; however, *C. tortugae* does not have two distinct spots in any of our material, so if that feature is present in a specimen, it is not *C. tortugae*. *Coryphopterus tortugae* shares with *C. glaucofraenum* and *C. venezuelae* the presence of a distinct dark blotch or triangle behind the eye above the opercle and with *C. glaucofraenum* the absence of a pigment spot on the lower portion of the pectoral-fin base. Garzón-Ferreira and Acero's (1990) redescription of *C. tortugae* did not mention the absence of this spot, presumably because the Santa Marta specimens included in their description do have the spot and appear to be *C. venezuelae* (see "Synonymy of *Coryphopterus bol*," below). Our investigations indicate that the absence of this pigment spot on the pectoral-fin base, along with the presence of vertically elongate versus round pigment spots in the lower row of markings on the body, is significant in separating *C. tortugae* from pale specimens of *C. venezuelae*. Examination of photographs of the holotype of *Ctenogobius tortugae* (SU 8363) confirms that there is no pigment on the lower portion of the pectoral-fin base.

Coryphopterus tortugae is most easily separated from all other *Coryphopterus* by the following combination of characters: a dark blotch or triangle of pigment above the opercle is present; large X-shape markings on the side of the body and a spot on the lower pectoral-fin base are absent; at least some of the pigment markings in the lower row along the side of the body are vertically elongate or crescent shaped; and the overall coloring is pale.

Coryphopterus glaucofraenum Gill, 1864

FIGURE 4

The location of the single type specimen upon which Gill described *C. glaucofraenum* is unknown (Eschmeyer, 2008). Böhlke and Robins (1960:108–109) described

FIGURE 1. (*facing page*) Neighbor-joining tree derived from cytochrome *c* oxidase I sequences showing genetically distinct lineages of western Atlantic *Coryphopterus*.

TABLE 1. Average (and range) Kimura two-parameter distance summary for *Coryphopterus* species based on cytochrome *c* oxidase I (COI) sequences of individuals represented in the neighbor-joining tree in Figure 1. Intraspecific averages are shown in bold; n/a = data not available.

***Coryphopterus* sp.**	***lipernes* (*n* = 7)**	***hyalinus* (*n* = 11)**	***personatus* (*n* = 10)**	***tortugae* (*n* = 21)**	***glaucofraenum* (*n* = 29)**	***venezuelae* (*n* = 33)**	***dicrus* (*n* = 22)**	***thrix* (*n* = 7)**	***eidolon* (*n* = 19)**	***alloides* *1* (*n* = 3)**	***alloides* 2 (*n* = 1)**	***kuna* (*n* = 5)**
lipernes	**0.13%** (0.00–0.35)	–	–	–	–	–	–	–	–	–	–	–
hyalinus	14.88% (14.21–15.40)	**0.06%** (0.00–0.31)	–	–	–	–	–	–	–	–	–	–
personatus	15.66% (15.10–16.03)	7.14% (6.79–7.65)	**0.14%** (0.00–0.46)	–	–	–	–	–	–	–	–	–
tortugae	19.60% (18.65–20.23)	21.14% (20.64–21.82)	20.08% (19.46–21.02)	**0.20%** (0.00–0.61)	–	–	–	–	–	–	–	–
glaucofraenum	20.71% (19.49–21.20)	21.68% (20.61–22.44)	21.50% (20.48–22.30)	12.07% (11.07–12.99)	**0.19%** (0.00–0.92)	–	–	–	–	–	–	–
venezuelae	21.37% (19.27–22.13)	20.86% (19.59–21.69)	20.12% (18.58–21.18)	9.84% (8.10–10.77)	9.51% (8.59–10.21)	**0.53%** (0.00–1.24)	–	–	–	–	–	–
dicrus	21.72% (20.10–22.56)	19.68% (18.61–20.37)	19.03% (18.30–19.94)	17.53% (16.59–18.07)	20.65% (19.82–21.32)	18.28% (16.46–19.00)	**0.61%** (0.00–2.82)	–	–	–	–	–
thrix	21.86% (20.85–22.69)	21.10% (20.11–22.44)	19.70% (19.19–20.48)	19.00% (18.43–19.63)	21.03% (20.30–21.54)	19.30% (17.61–20.12)	21.30% (20.74-21.84)	**0.11%** (0.00–0.48)	–	–	–	–
eidolon	25.16% (24.45–26.19)	19.19% (18.19–20.11)	17.92% (17.12–18.82)	19.74% (18.34–21.42)	23.17% (21.98–25.04)	18.72% (16.75–20.36)	19.39% (18.69–20.87)	19.54% (18.96–20.41)	**0.24%** (0.00–0.99)	–	–	–
alloides 1	22.13% (21.53–22.53)	17.90% (17.09–18.64)	18.16% (17.69–18.93)	19.44% (18.79–20.14)	21.69% (20.98–22.48)	18.62% (17.67–19.70)	18.15% (17.52–19.03)	20.39% (19.91–21.18)	18.06% (17.28–19.08)	**0.21%** (0.16–0.31)	–	–
alloides 2	21.15 (21.02–21.68)	17.75% (17.62–17.96)	19.27% (19.04–19.94)	21.73% (21.38–22.18)	21.30% (21.04–21.81)	19.68% (18.58–20.23)	17.11% (16.70–17.80)	19.16% (19.10–19.38)	19.34% (18.82–19.90)	9.68% (9.48–9.88)	**n/a** n/a	–
kuna	26.41 (25.59–27.00)	23.22% (22.62–23.65)	25.70% (24.86–26.37)	25.51% (24.58–26.27)	27.87% (26.79–28.53)	25.78% (24.48–26.64)	24.91% (23.36–25.57)	25.63% (24.96–26.27)	25.54% (24.61–26.20)	23.30% (22.77–23.65)	23.97% (23.59–24.30)	**0.57%** (0.15–1.24)

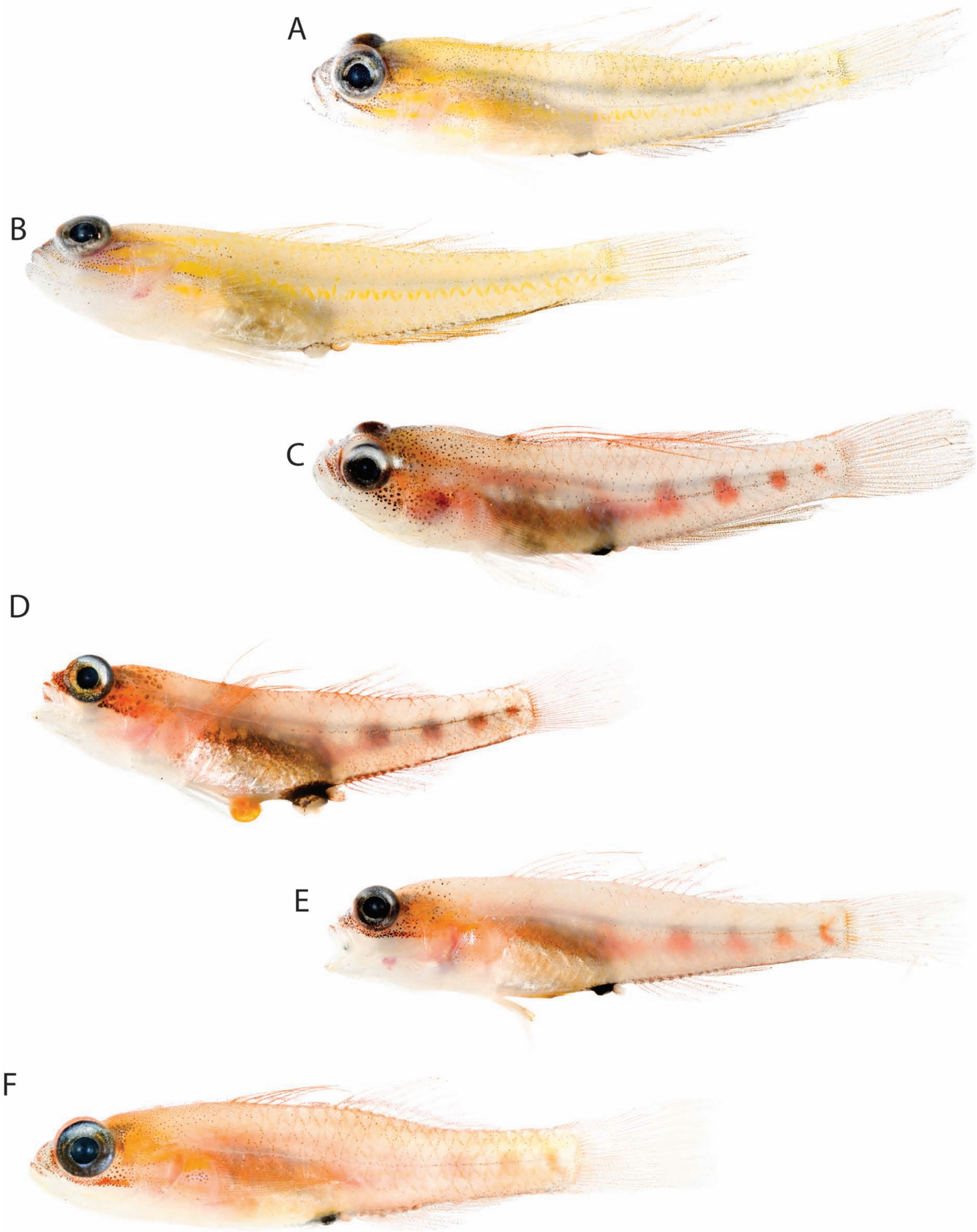


FIGURE 2. *Coryphopterus lipernes*: A, Curacao, 20 mm SL, DNA 8326, USNM 394896; B, Curacao, 21 mm SL, DNA 8051, USNM 394895. *Coryphopterus hyalinus*: C, Curacao, 20 mm SL, DNA 8044, USNM 394890; D, Curacao, 17 mm SL, DNA 8265, USNM 294889. *Coryphopterus personatus*: E, Curacao, 21 mm SL, DNA 8045, USNM 294897; F, Belize, 15 mm SL, DNA 7163, USNM 394742.

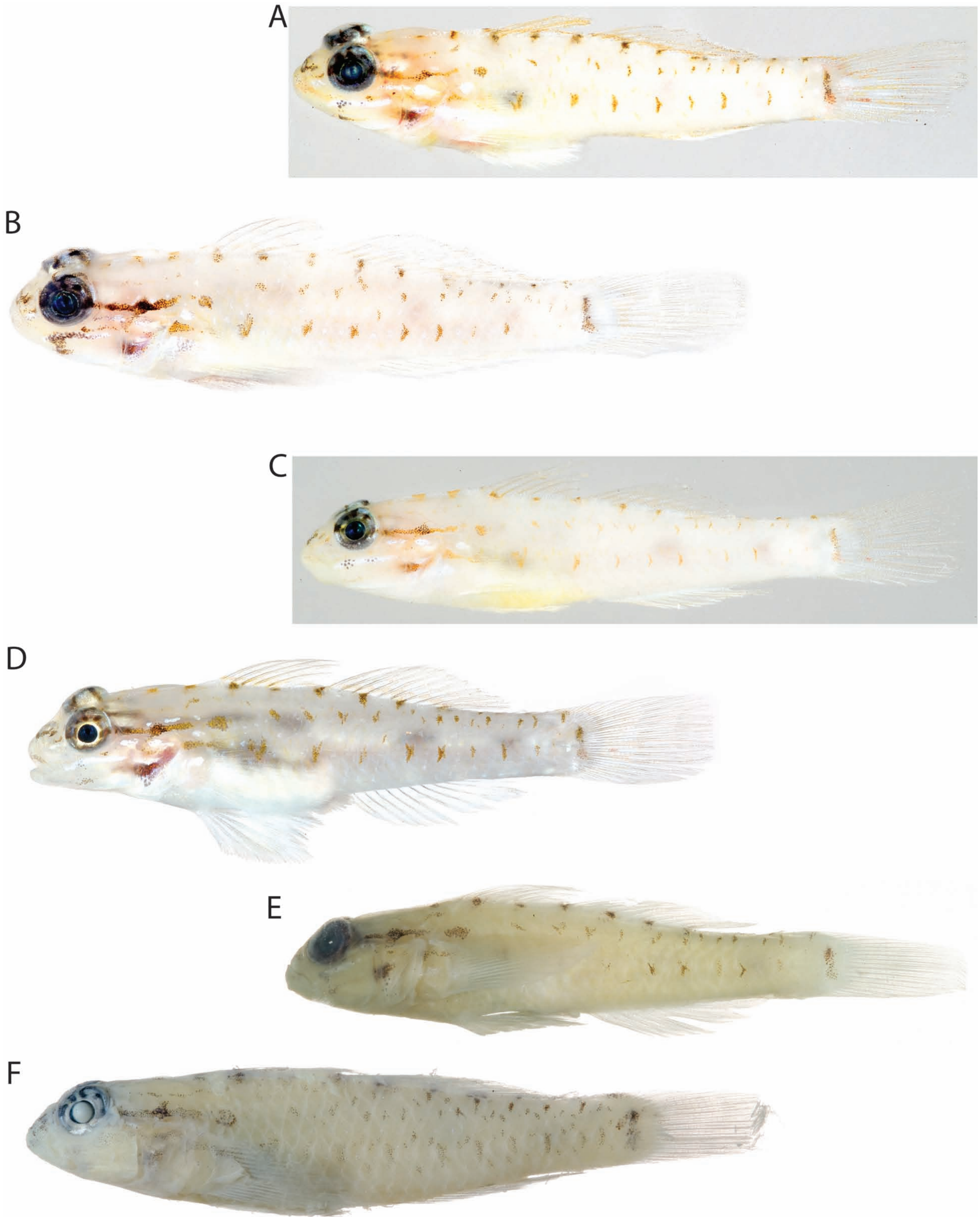


FIGURE 3. *Coryphopterus tortugae*: A, Belize, 25 mm SL, DNA 7333, USNM 394744; B, Belize, 34 mm SL, DNA 5237, USNM 394743; C, Belize, 36 mm SL, DNA 7107, USNM 394733; D, Belize, 40 mm SL, DNA 4530, USNM 394730; E, Belize, 40 mm SL, DNA 4530, USNM 394730, preserved; F, Venezuela, 37 mm SL, DNA 7736 4, AMNH 247340, alcohol preserved.

two forms of *C. glaucofraenum*: "[D]ark inshore form (typical *glaucofraenum*)" and"[P]allid white-sand form." Specimens in our genetic clade identified as *C. glaucofraenum* match the Böhlke and Robins (1960) "typical *glaucofraenum*," an identification supported by the fact that the pallid form is now recognized as *C. tortugae*. Below (see "Designation of Neotype for *Coryphopterus glaucofraenum*") we select a neotype for *C. glaucofraenum* Gill.

In our material, adult *C. glaucofraenum* can always be separated from *C. tortugae* by having at least some large, well-formed X-shaped markings along the side of the body. It can almost always be separated from *C. venezuelae* by lacking a prominent dark marking on the lower portion of the pectoral-fin base and sometimes by having 10 total anal-fin elements. Rarely, *C. glaucofraenum* has a dark pectoral-fin base that includes pigment on the lower portion (Figure 4G), and *C. venezuelae* may have 9–11 anal-fin elements, 10 being the typical count in our material (Table 2). *Coryphopterus glaucofraenum* usually can be separated from both *C. tortugae* and *C. venezuelae* by the shape of the pigment marking above the opercle: a two-peaked blotch in *C. glaucofraenum*, and a triangular or rounded blotch in *C. tortugae* and *C. venezuelae*.

If a specimen has a two-peaked blotch of pigment above the opercle, has at least some large (height approximately three-quarters of or equal to diameter of eye) X-shaped markings along the side of the body, has 10 anal-fin elements, and lacks pigment on the lower portion of the pectoral-fin base, it is unquestionably *C. glaucofraenum*.

***Coryphopterus venezuelae* (Cervigón, 1966)**

FIGURE 5

The most recent keys to western Atlantic *Coryphopterus* (Böhlke and Robins, 1960, 1962; Böhlke and Chaplin, 1968; Murdy 2002) do not include *C. venezuelae*, originally described as a subspecies of *C. glaucofraenum* by Cervigón (1966), but recognized as a separate species by Cervigón (1994) and known at the time only from Venezuela. In the *Coryphopterus* material from the northeast coast of Venezuela that we examined are specimens that are clearly *C. venezuelae* based on Cervigón's (1966, 1994) descriptions: most notably the presence of 11 second dorsal- and anal-fin elements, a dark blotch of pigment on the lower portion of the pectoral-fin base, and two dark spots on the base of the caudal fin (e.g., Figure 5D herein). However, those Venezuelan specimens are part of a clade based on COI analysis (see Figure 1) that includes specimens from Venezuela, Curacao, Panama, Belize, Puerto Rico, and the Bahamas (the last not shown on the tree) that usually have 10 second dorsal- and anal-fin elements and various patterns of pigment on the base of the caudal fin, including a central bar, two spots joined by a bar, and a C-shaped blotch (Figure 5A–C,E). The Venezuelan specimens on the tree (Figure 1), including two that have 10 second dorsal- and anal-fin elements (VEN 7733 1 and VEN JV12), cluster within the *C. venezuelae* clade, but the genetic distance between the Venezuelan specimens and other members of the clade is only 0.41% to 0.85%. This distance is extremely small relative to the genetic distance between the *C. venezuelae* clade and other species on the tree (9.51%–20.86%; see Table 1), suggesting that the individuals in this clade represent a single species. Corroborating the identification of the clade as Cervigón's *C. venezuelae* is the presence in all individuals in the clade of a dark spot on the lower portion of the pectoral-fin base. Among western Atlantic *Coryphopterus*, only *C. punctipectophorus* and *C. dicrus* have a prominent pigment spot on the lower portion of the pectoral-fin base: *C. punctipectophorus* is not known from the Caribbean, and it differs morphologically from *C. venezuelae* in, among other features, lacking a dark blotch of pigment behind the eye above the opercle; in *C. dicrus*, there is also a prominent spot of equal size on the dorsal portion of the pectoral base that is lacking in *C. venezuelae* (which may have a slash of pigment but never a well-defined dorsal spot equal in size and intensity to the lower spot); *C. dicrus* also lacks the dark pigment behind the eye above the opercle and lacks a pelvic frenum (both present in *C. venezuelae*).

Our data thus suggest that *C. venezuelae* is a much more widespread species than previously recognized, and fin-ray counts alone are not sufficient in diagnosing the species. Cervigón (1994) believed that the presence of 10 second dorsal- and anal-fin elements in *C. glaucofraenum* distinguished it from *C. venezuelae*. In his material of the latter, all specimens had 11 second dorsal-fin elements and most had 11 anal-fin elements (two had 10). Most of our specimens of *C. glaucofraenum* have 10 second dorsal- and anal-fin elements, but two specimens have 11 second dorsal-fin elements, and two have 9 anal-fin elements (see Table 2). Both 10 and 11 second dorsal- and anal-fin elements are common in specimens in our *C. venezuelae* clade (Table 3), although we found 11 in both fins only in some of our material from Venezuela. It is significant that one of the *C. venezuelae* specimens from Venezuela that has 10 elements in both fins was caught in the same sample as

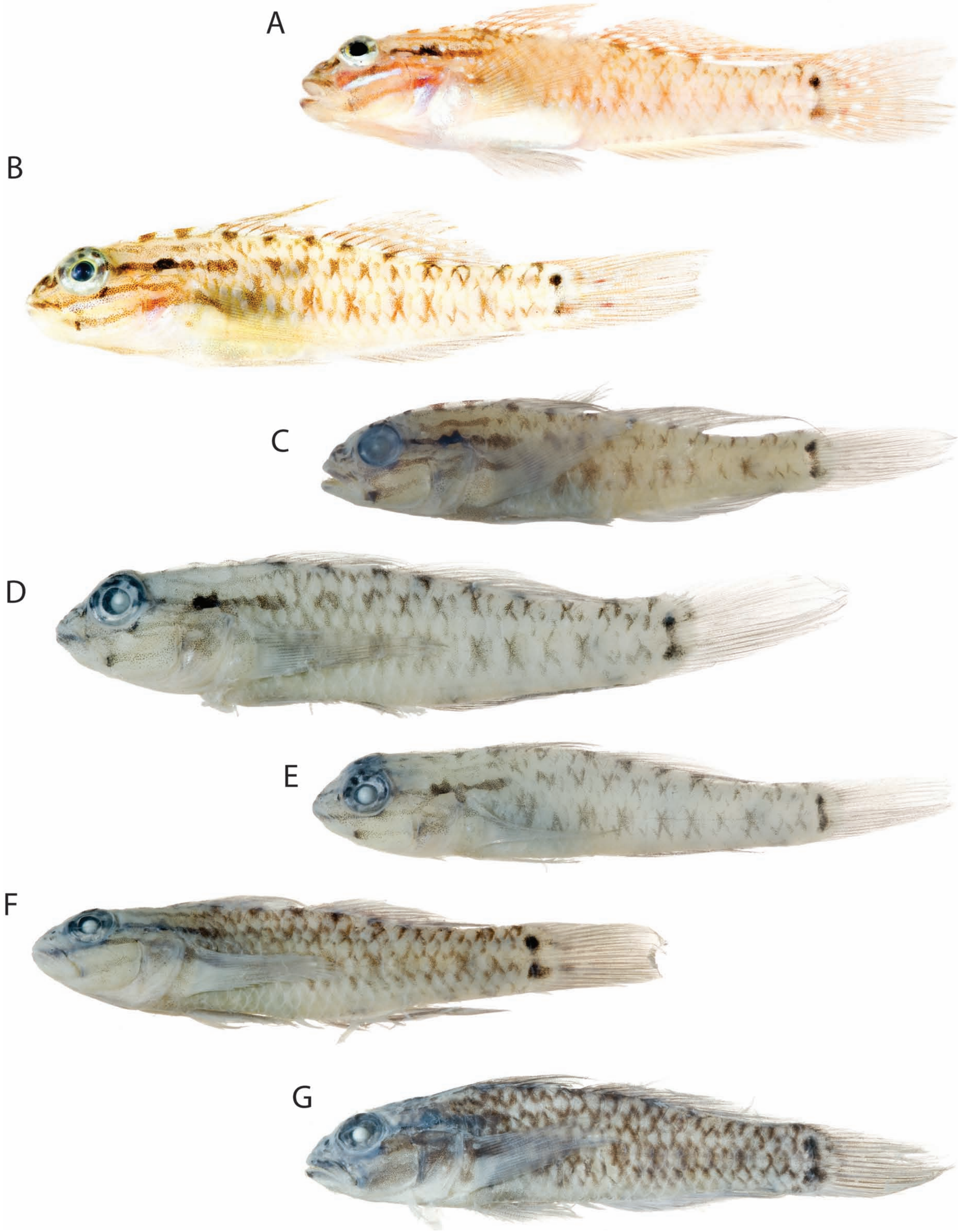


FIGURE 4. *Coryphopterus glaucofraenum*: A, Belize, 44 mm SL, DNA 6367; B, Belize, 25 mm SL, DNA 7352, USNM 394354; C, Belize, 35 mm SL, DNA 7351, USNM 394353, preserved; D, Venezuela, 31 mm SL, DNA 7744 2, AMNH 247339, alcohol preserved; E, Venezuela, 27 mm SL, DNA 7744 3, AMNH 247339, alcohol preserved; F, Panama, 34 mm SL, DNA 7712 2, AMNH 247335, alcohol preserved; G, Panama, 37 mm SL, DNA 7701 1, AMNH 247334, alcohol preserved.

several with 11 in both fins. There is thus more variability in numbers of second dorsal- and anal-fin elements than Cervigón indicated, and those fin-ray counts are of value in separating *C. glaucofraenum* and *C. venezuelae* only when 11 elements are present in both fins—a condition we have not observed in *C. glaucofraenum*, which may have 11 second dorsal-fin elements but no more than 10 anal-fin elements (see Table 2).

If a specimen has a dark blotch or triangle of pigment above the opercle, 11 second dorsal-fin *and* 11 anal-fin elements, and a prominent pigment spot on the lower portion of the pectoral-fin base, it is *C. venezuelae*.

If a specimen has those features and has 10 second dorsal- and anal-fin elements, it is usually *C. venezuelae* but could be *C. glaucofraenum*: as noted under "*Coryphopterus glaucofraenum*," rarely specimens of that species may have pigment on the ventral portion of the pectoral-fin base. The shape of the pigment marking above the opercle (with two peaks in *C. glaucofraenum*, a single triangular or rounded blotch in *C. venezuelae*; see "*Coryphopterus glaucofraenum*") will frequently resolve the species identification.

There are two distinct forms of *C. venezuelae* in terms of body pigment: one has at least some large X-shaped markings in the ventral row of markings similar to those of *C. glaucofraenum* (Figure 5B,D,E); the other is a much paler form, and the ventral pigment markings along the side of the body are usually fairly small, somewhat circular blotches (Figure 5A,C). Both forms, including the palest specimens, have a pigment spot on the lower pectoral-fin base, but this spot may be composed primarily of yellow chromatophores versus melanophores in pale specimens. The less-pigmented form is most easily confused with *C. tortugae*, but some of the pigment spots in the ventral row of *C. venezuelae* are usually more circular than the vertically elongate ones of *C. tortugae*. Additionally, none of our specimens of *C. tortugae* has a spot of pigment (yellow or black) on the ventral portion of the pectoral-fin base. Although unusually divergent intraspecifically in patterns of pigmentation (see Figure 5) relative to, for example, the very similar patterns between species such as *C. personatus* and *C. hyalinus*, the two forms of *C. venezuelae* form a tight genetic clade (intraspecific variation, 0.53%; see Figure 1, Table 1). The different pigment patterns do not correspond to different fin-ray counts, as we have observed 10 and 11 second dorsal- and anal-fin elements in both forms. For example, note the similar patterns of pigmentation in a specimen of *C. venezuelae* from Venezuela (Figure 5D) that has 11 second dorsal- and anal-fin elements and a specimen of *C. venezuelae* from Panama (Figure 5E) that has 10 second dorsal- and anal-fin elements. Furthermore, the differences are not attributable to sexual dimorphism or geography, but they could reflect differences in local habitat. Some specimens of *C. venezuelae* collected in mangrove areas tend to be dark, and those collected in reef areas pale, although we note that a dark form was collected on a reef off Panama (Figure 5E).

There is some correlation with size: the pale form of *C. venezuelae* is more common among small specimens (<30 mm standard length [SL]), and the form with prominent X-shaped markings is more common among larger specimens (>40 mm SL). Adults of the pale form of *C. venezuelae* (e.g., Figure 5A) look remarkably similar to juveniles (e.g., see Figure 7C). There is also a trend toward increasing depth of the head and anterior body in larger specimens. Similar differences in body shape and pigment with increasing size are evident in *C. glaucofraenum* (compare the juvenile in Figure 7B with adults in Figure 4). Possibly in *C. venezuelae*, growth is not always accompanied by a transformation in pigment and body depth, and adults retain more of the juvenile features. More investigation is needed to determine the relationships in *C. venezuelae* among pigment pattern, body shape, size, maturity, and local habitat. Cervigón (1966, 1994) did not illustrate any of his type specimens of *C. venezuelae*, but we obtained digital photographs of two of his paratypes (MOBR-P-0867 [Museo Oceanológico Hermano Benigno Román, Venezuela]; one is shown in Figure 6). The holotype is not in good condition (J. C. Capelo, MOBR, personal communication, 4 July 2008). The pigment of the paratypes most closely resembles that in Figure 5D herein: a triangular to rounded mark above the opercle, a roughly circular dark spot on the ventral pectoral-fin base, and two basicaudal spots joined by a light dusky bar. There is some evidence of X-shaped markings on the side of the body, but the body pigment is mostly faded. Cervigón (1966, 1994) did not mention X-shaped markings in his descriptions; rather, he noted that there are three longitudinal rows of dark spots.

TABLE 2. Frequency distributions of numbers of second dorsal-fin and anal-fin elements in two species of *Coryphopterus*.

	No. of second dorsal-fin elements		No. of anal-fin elements		
Species	**10**	**11**	**9**	**10**	**11**
C. glaucofraenum	22	2	2	20	—
C. venezuelae	20	13	1	22	11

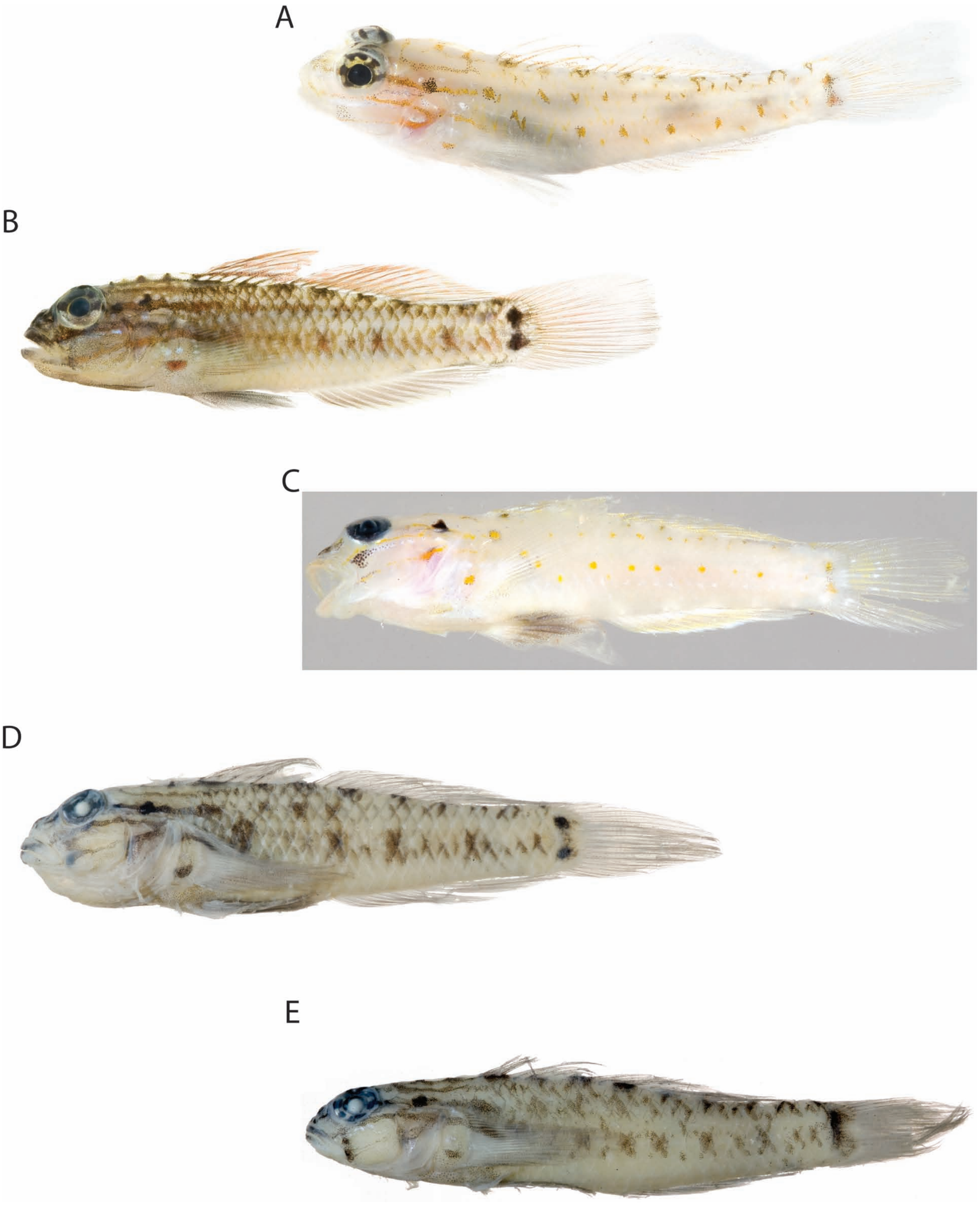


FIGURE 5. *Coryphopterus venezuelae*: A, Curacao, 29 mm SL, DNA 8260, USNM 394740; B, Venezuela, 54.4 mm SL, no DNA, Photo No. 1907 VT-05-530, photo by J. V. Tassell and D. R. Robertson; C, Belize, 35 mm SL, DNA 7248, USNM 394736; D, Venezuela, 50 mm SL, DNA JV15, AMNH 247345, alcohol preserved; E, Panama, 42.5 mm SL, DNA 7725-1, AMNH 247341, alcohol preserved.

Synonymy of *Coryphopterus bol*

Victor (2008) described *Coryphopterus bol* as a species that heretofore had been masquerading under *C. tortugae* (e.g., Garzón-Ferreira and Acero 1990:107, fig. 1A, Santa Marta specimens). We believe that Victor (2008) was correct in recognizing that the Santa Marta specimens are not *C. tortugae*, but our investigation indicates that they are *C. venezuelae*. The COI sequence that Victor (2008) provided for the new species (from the holotype from Puerto Rico) places it solidly with our *C. venezuelae* clade (PR SIO 0869, fig. 1). The average genetic distance between *C. bol* and individuals of *C. venezuelae* is 0.38% (range, 0.00%–0.85%) and, for comparison, the average genetic distance between the holotype of *C. bol* and the next most closely related clade (*C. tortugae*) is more than 20-fold greater, or 8.47% (range, 8.10%–9.21%). Diagnostic features of Victor's (2008:4) *C. bol* include 10 second dorsal- and anal-fin elements; 19 pectoral-fin rays; pelvic fins fully joined and with a distinct frenum; a prominent, dark, upward-pointed triangular marking on the stripe behind the eye; a discrete blotch of small melanophores on the lower third of the pectoral fin base; and a basicaudal marking that resembles a thick "C." The combination of the triangular marking on the stripe behind the eye above the opercle, the pigment blotch on the lower portion of the pectoral-fin base, and 10 second dorsal- and anal-fin elements matches most of our *C. venezuelae* specimens. Victor (2008) distinguished his new species from *C. venezuelae* based on the presence of 11 second dorsal- and anal-fin elements in *C. venezuelae*, but, as noted above (also see Table 2), specimens matching Cervigón's *C. venezuelae* based on the pre-pectoral pigment may have 10 or 11 second dorsal- and anal-fin elements.

Coryphopterus bol also matches *C. venezuelae* in number of pectoral-fin rays (19 in *C. bol*, 61% of specimens with 19 in Cervigón's [1994] *C. venezuelae* material), pelvic-fin morphology, and other pigment. For example, the basicaudal mark in *C. venezuelae* may be C-shaped, but it ranges in our material from two separate spots to a central bar of pigment (some examples are shown in Figure 5). The basicaudal pigment is also somewhat variable in the type material of *C. bol* (Victor, 2008:fig. 1). Two of the type specimens of *C. bol* most closely resemble the pale form of *C. venezuelae*; that is, the form with round spots on a relatively slender body (holotype and a 32.1-mm SL paratype). Two paratypes (24.5 and 29 mm SL) are darker and have at least some X-shaped markings. None of Victor's type material is larger than 32 mm SL, and, as noted under *C. venezuelae*, above, most of our dark, deeper-bodied specimens of *C. venezuelae* are >40 mm SL.

TABLE 3. Frequency distributions of the combinations of second dorsal-fin and anal-fin elements in *Coryphopterus venezuelae* by country.

	No. of second dorsal-fin elements / anal-fin elements				
Country	**10/9**	**10/10**	**10/11**	**11/10**	**11/11**
Belize	—	2	—	—	—
Curacao	1	11	1	1	—
Panama	—	6	1	—	—
Venezuela	—	2	—	1	9
Puerto Rico	—	1[a]	—	—	—

[a] Holotype of *Coryphopterus bol*.

In summary, one cannot distinguish *C. bol* and *C. venezuelae* on the basis of numbers of second dorsal- and anal-fin elements because there is more variation in those counts than previously reported. One might argue that specimens from Venezuela that have 11 elements in both the second dorsal and anal fins and heavy pigment with X-shape markings are *C. venezuelae* and that everything else in our *C. venezuelae* clade is *C. bol*. However, some specimens with those features, except with 10 elements in the second dorsal and anal fins, were taken in the same station off Venezuela as those with 11 elements (AMNH 247345 [American Museum of Natural History]), so would one identify the former as *C. venezuelae* or *C. bol*? Species identification of specimens with 11/10 or 10/11 second dorsal-/anal-fin elements also would be nebulous, as would species identification of dark forms with 10/10 but otherwise virtually identical to those with 11/11 (e.g., Figure 5D,E). Variation in COI among all specimens in the *C. venezuelae* clade is well within typical intraspecific levels for the genus. However, even if COI is masking recent divergence within the clade, there is a diagnostic morphological feature for the clade: a conspicuous spot or blotch of pigment on the lower pectoral-fin base; in combination with a triangular or circular blotch of pigment behind the eye above the opercle, this character is unique to *C. venezuelae*. The more common presence of 11 second dorsal- and anal-fin elements in some Venezuelan specimens may best be interpreted as regional variation. Known currently from Belize, Panama, Curacao, Venezuela, the Bahamas, the U.S. Virgin Islands, Puerto Rico, Saba, and Brazil, *C. venezuelae* appears to be a widespread species. It is misidentified in the USNM (U.S. National Museum;

FIGURE 6. Paratype of *Coryphopterus venezuelae*, MOBR-P-0867, 42 mm SL (length estimated from ruler included with original photograph; this is likely Cervigón's 41.2 mm SL paratype).

i.e., National Museum of Natural History, Smithsonian Institution)—and likely other museum collections—as *C. glaucofraenum* or *C. tortugae*.

Key Notes for *C. tortugae, C. glaucofraenum,* and *C. venezuelae*

Juveniles (Figure 7), and occasionally adults, of *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* may lack the black marking or triangle above the opercle, or it is not as dark as other pigment in the stripe posterior to the eye. As we have used this feature in the "Revised Key to Western Atlantic *Coryphopterus*" (see below) to separate *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* from other species, absence of this feature in specimens of any of those species could present identification problems. If there are well-defined X's of pigment along the sides of the body (*C. glaucofraenum* and some *C. venezuelae*) or the basicaudal pigment comprises two spots or a dumbbell-shaped marking (most *C. glaucofraenum* and some *C. venezuelae*), users of the key should follow the option in the couplet that indicates the dark marking is present above the opercle (4b). If a specimen lacks the dark pigment spot above the opercle, has 11 second dorsal- and anal-fin rays, and has a prominent dark blotch on the lower portion of the pectoral-fin base, it can only be *C. venezuelae*. *Coryphopterus punctipectophorus* is similar in lacking the pigment spot above the opercle and having 11 second dorsal-fin elements, but it has 10 anal-fin elements (Springer, 1960). Furthermore, geography will currently separate those two species: *C. venezuelae* occurs in the Caribbean, and *C. punctipectophorus* is known only from the Gulf of Mexico and off the southeastern USA.

Coryphopterus dicrus Böhlke and Robins, 1960

FIGURE 8

Numerous features, in combination, separate *C. dicrus* from other western Atlantic *Coryphopterus*, including the following: no black ring of pigment around anus; no distinct dark spot behind eye above opercle; anal-fin elements 10; pelvic frenum absent; pectoral-fin base with two prominent dark spots of equal intensity, one above the other; and sides of body freckled with scattered large and smaller pigment blotches. The last two characters are the quickest way to make the identification. The only other species that usually have pigment dorsally *and* ventrally on the pectoral-fin base are *C. venezuelae* and *C. thrix*, but the dorsal pigment on the pectoral-fin base in *C. venezuelae*, when present, is a slash versus a spot, and the dorsal pigment on the pectoral-fin base in *C. thrix* is usually much more pronounced than the ventral marking. Additionally, both species have a pelvic frenum, which is lacking in *C. dicrus*.

Coryphopterus thrix Böhlke and Robins, 1960

FIGURE 8

Coryphopterus thrix is the only western Atlantic species of *Coryphopterus* that lacks black pigment around the anus *and* has the second dorsal-fin spine elongated into a filament. If the spine is broken, however, the species is still identifiable by the combination of features presented in the key, most notably the absence of a distinctive pigment blotch above the opercle, presence of a conspicuous dark blotch on the dorsal portion of the pectoral-fin base, and presence of a pelvic frenum.

Coryphopterus alloides Böhlke and Robins, 1960

FIGURE 9

Distinguishing features of *C. alloides* include having a low anal-fin count (8–9 total elements), a dark blotch of pigment on the lower portion of the membrane between the second and third dorsal spines, and the pelvic fins almost completely separate. Only *C. kuna*, among the *Coryphopterus* species lacking a black ring of pigment around the anus, has as few as 9 anal-fin elements, but that species has 9 second dorsal-fin elements and 15 pectoral rays (vs. usually 10 and 16–17, respectively, in *C. alloides*). *Coryphopterus kuna* may have a stripe and distal flag of pigment on the first dorsal fin, but it never has the pigment blotch on the lower portion of the first dorsal fin characteristic of *C. alloides*. The living color pattern of *C. alloides* is also distinctive: the head and anterior portion of the body bear a considerable amount of orange pigment, whereas the posterior portion of the body is yellow. An apparently cryptic species related to but genetically distinct from *C. alloides* and known only from Curacao is currently under investigation.

Key Note

In some preserved specimens of *C. alloides*, there are melanophores above the opercle that may lead the user of the key to select "4b. Distinct black blotch or triangle behind eye above opercle . . ." However, this pigment is never as consolidated and prominent in *C. alloides* as in

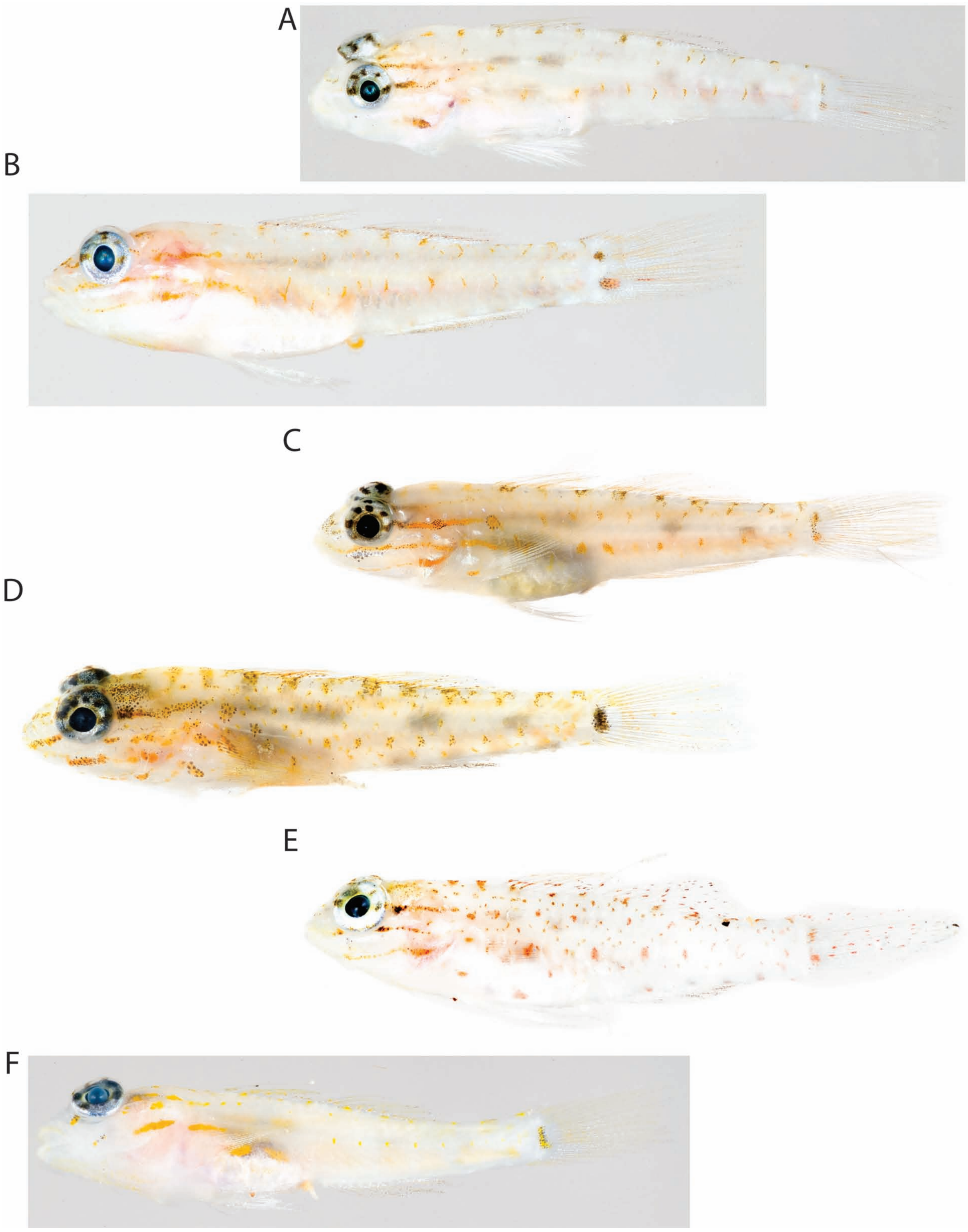


FIGURE 7. *Coryphopterus* juveniles: A, *C. tortugae*, Belize, 20 mm SL, DNA 7693, USNM 394800; B, *C. glaucofraenum*, Belize, 17 mm SL, DNA 7769, USNM 394793; C, *Coryphopterus venezuelae*, Belize, 17 mm SL, DNA 7728, USNM 394881, D, *Coryphopterus thrix*, Curacao, 16 mm SL, DNA 8261, USNM 394760; E, *Coryphopterus dicrus*, Belize, 13 mm SL, DNA 6110, USNM 394779. F, *Coryphopterus eidolon*, Belize, 18 mm SL, DNA 6223, USNM 394788.

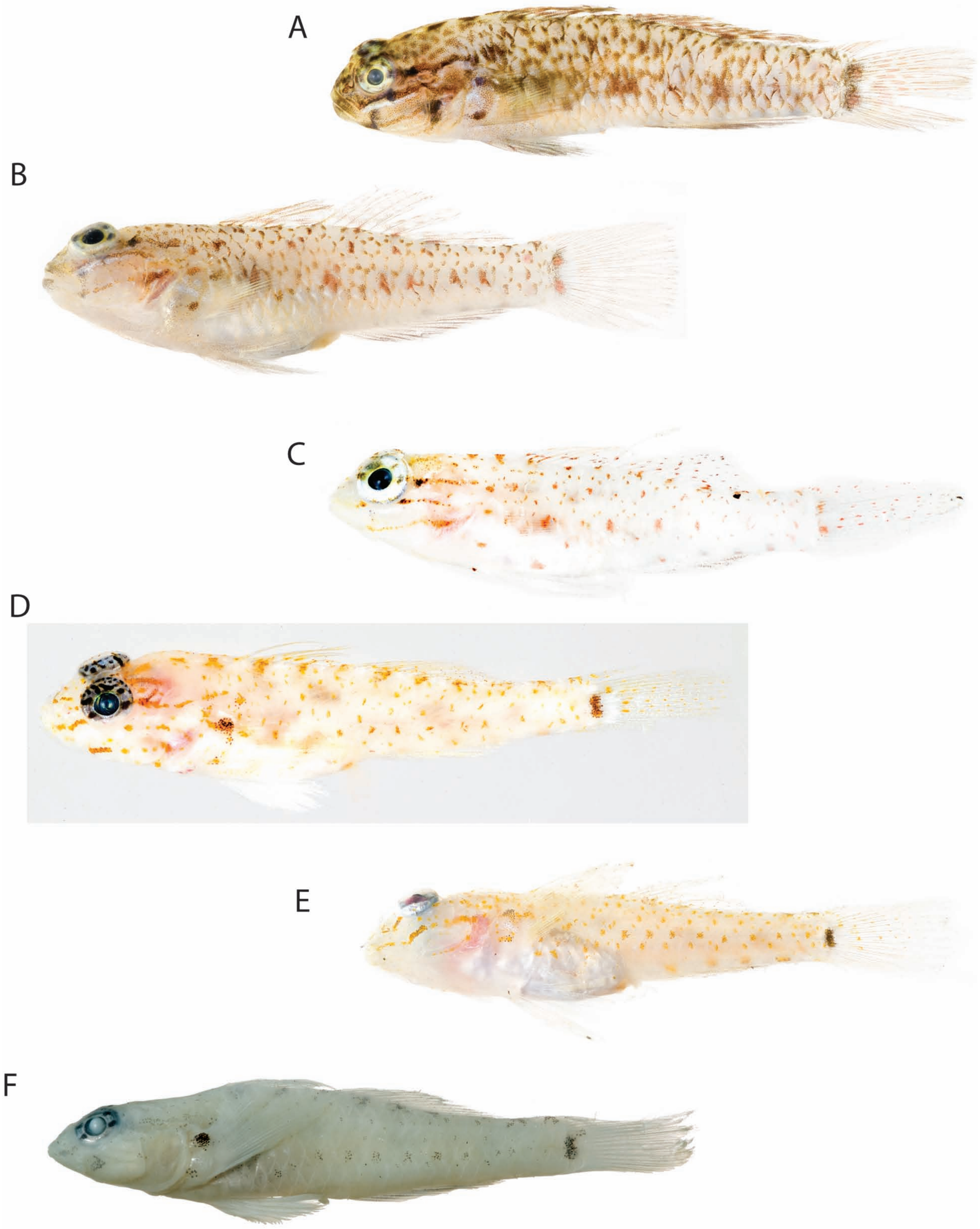


FIGURE 8. *Coryphopterus dicrus*: A, Florida, 38 mm SL, DNA 7348, USNM 394345; B, Curacao, 30 mm SL, DNA 8135, USNM 394747; C, Belize, 13 mm SL, DNA 6110, USNM 394779. *Coryphopterus thrix*: D, Belize, 23.5 mm SL, DNA 7816, USNM 394914; E, Curacao, 23 mm SL, DNA 8426, USNM 394761; F, Venezuela, AMNH 244983, 26 mm SL, alcohol preserved, no DNA.

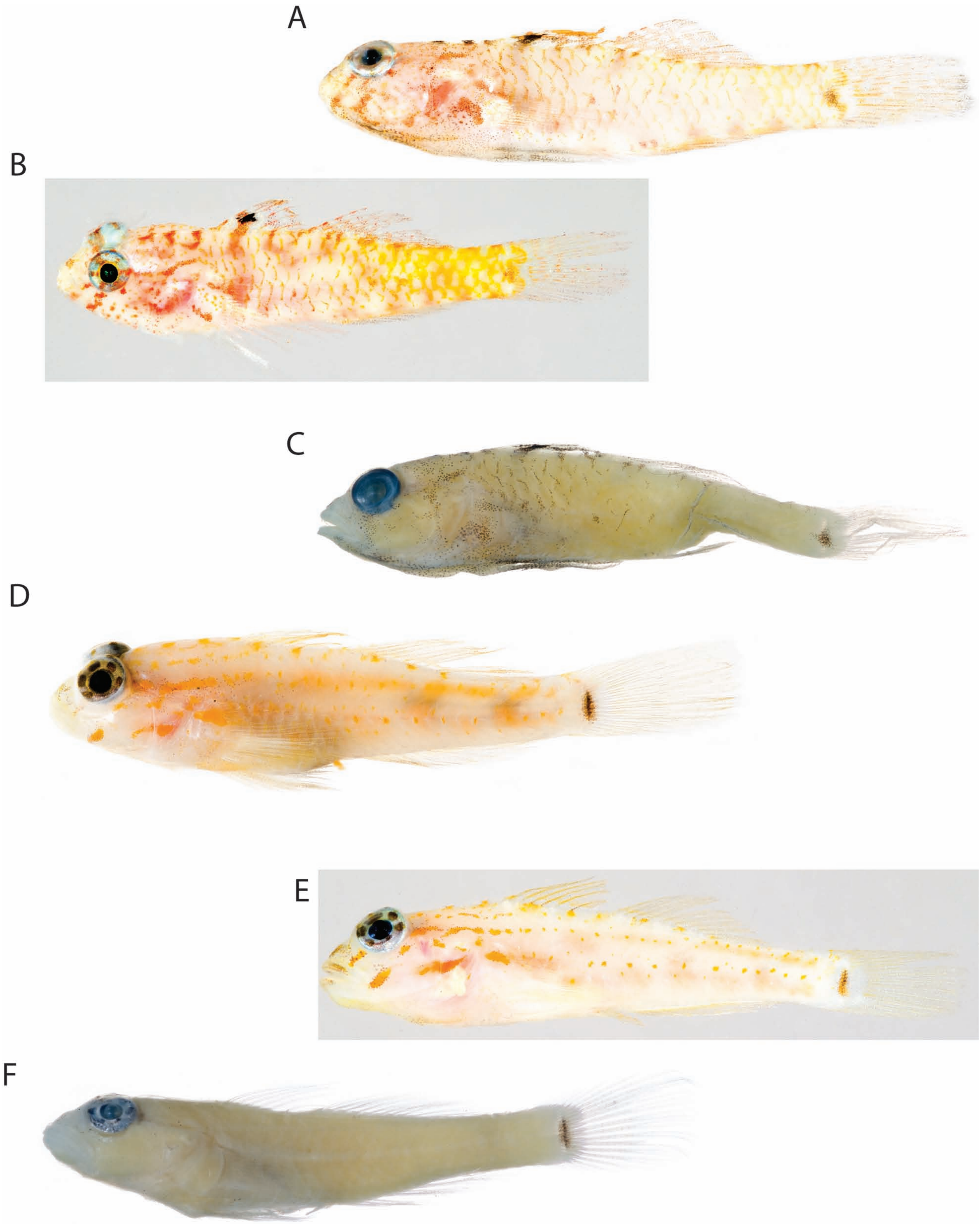


FIGURE 9. *Coryphopterus alloides*: A, Belize, 24 mm SL, DNA 7233, USNM 394754; B, Belize, 19 mm SL, DNA 7264, USNM 394755; C, Belize, 24 mm SL, preserved, DNA 7233, USNM 394754. *C. eidolon*: D, Curacao, 38 mm SL, DNA 8050, USNM 394885; E, Belize, 34 mm SL, DNA 7109, USNM 394752; F, Belize, 33 mm SL, preserved, DNA 5070, USNM 394750.

C. tortugae, *C. glaucofraenum*, and *C. venezuelae*; furthermore, *C. alloides* lacks a pelvic frenum, a conspicuous feature in the other three species.

***Coryphopterus eidolon* Böhlke and Robins, 1960**

FIGURE 9

Pigment, except for basicaudal and scattered small body melanophores, is yellow, which disappears during preservation, typically rendering this a very pale goby. In life there is a yellow stripe behind the eye bordered by small melanophores that remain in preserved specimens after the color fades. There are no dark markings above the opercle, on the pectoral-fin base, or on the first dorsal fin. The absence of distinctive markings (other than the basicaudal mark) is the easiest way to recognize *C. eidolon*, a very abundant species in many of our samples, particularly from Belize and Curacao.

***Coryphopterus kuna* Victor, 2007**

FIGURE 10

Baldwin and Smith (2003) described *Coryphopterus* B larvae from Belize as likely belonging to an unidentified species based on the low second dorsal- and anal-fin counts (9 in both fins) and low pectoral-fin count (15). Victor (2007) described *C. kuna*, which has the low fin-ray counts of the *Coryphopterus* B larvae, as a new species from off Panama. Incorporation of the COI sequence published in the original description of *C. kuna* into our analysis revealed that *Coryphopterus* B larvae are *C. kuna*. This species is distinctive in typically having 9 second dorsal- and anal-fin elements, as well as a low pectoral-ray count of 15 (found elsewhere only in *C. personatus* and *C. hyalinus*). Apparently a small fish—the adult male holotype is 17.1 mm SL—*C. kuna* has little dark pigment: numerous small spots on the pelvic fin of the holotype, a few scattered small spots on the sides of the body, no markings on the pectoral-fin base, and no basicaudal spot. It lacks a pelvic frenum.

***Coryphopterus punctipectophorus* Springer, 1960**

FIGURE 10

Coryphopterus punctipectophorus is similar to *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* in having three rows of pigment spots along the side of the body, but it differs from those species in lacking a dark blotch or triangle behind the head above the opercle. It is most similar to *C. venezuelae* in having a prominent dark spot on the lower portion of the pectoral-fin base, and juvenile (and occasionally adult) specimens of *C. venezuelae* that lack the pigment blotch above the opercle will typically key to *C. punctipectophorus* based on the ventral pigment spot on the pectoral-fin base. Like *C. venezuelae*, *C. punctipectophorus* was originally described as having 11 second dorsal-fin elements, but as noted above (see *C. venezuelae*), the former has 10 or 11 second dorsal elements. The "dusky light buff" pigment spots along the dorsal contour and "coral pink" spots along the sides of the body in fresh material of *C. punctipectophorus* (Springer, 1960:240; see Figure 10B,E herein) apparently fade in preserved material (see Figure 10D). The known distribution of *C. punctipectophorus* includes both coasts of Florida, the Gulf of Mexico (including the southern Gulf where it meets the Caribbean), and South Carolina. It apparently inhabits deeper water than some *Coryphopterus* species: the type material was collected at 62 and 120 feet. It has not been reported from the Caribbean. We have not collected *C. punctipectophorus*, and fresh material of the species was not available for inclusion in our genetic analysis. Thacker and Cole's (2002) *C. punctipectophorus* from Belize (GenBank Accession No. AF391396) is *C. dicrus*, based on incorporation of their COI sequence into our data set.

REVISED KEY TO THE WESTERN ATLANTIC SPECIES OF *CORYPHOPTERUS*

1a. Black ring of pigment surrounding anus 2
1b. Black ring around anus absent 4
2a. One interorbital pore anteriorly 3
2b. Two interorbital pores anteriorly . . . . ***Coryphopterus hyalinus***
3a. Second dorsal and anal fins each typically with 11 total elements; head with some orange pigment in life; body translucent, with several squares or rectangles of pale orange pigment internally; preserved specimens lacking conspicuous postorbital stripes of melanophores but with "mask" of pigment around eye . . . . ***Coryphopterus personatus***

(continued on p. 130)

REVISED KEY TO THE WESTERN ATLANTIC SPECIES OF *CORYPHOPTERUS* (*continued*)

3b. Second dorsal and anal fins typically with 10 total elements; head and body predominantly yellow in life; a dusky internal stripe along posterior section of vertebral column; preserved specimens with postorbital stripes of melanophores and scattered spots over entire body . . . . **_Coryphopterus lipernes_**

4a. No distinct black blotch behind eye above opercle in adults; pigment above opercle, if present, no larger or darker than other markings behind eye; pelvic frenum present or absent (see "Key Note" for *C. alloides* in text). ***5***

4b. Distinct black blotch or triangle behind eye above opercle in adults, blotch usually larger and darker than other pigment in stripe behind eye; pelvic frenum present (see "Key Notes for *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae*" in text) 10

5a. Anal-fin elements 8–9 (usually 9), pectoral-fin rays 15–17, pelvic frenum absent ***6***

5b. Anal-fin elements 10–11, pectoral-fin rays 17–20, pelvic frenum present or absent ***7***

6a. Second dorsal and anal fins each with 9 elements; pectoral-fin rays 15; pelvic fins fully joined; first dorsal fin with stripe of black pigment; in life, head and body with orange spots and blotches and sometimes with flag of dark pigment on 1st–3rd dorsal spines . . . .**_Coryphopterus kuna_**

6b. Second dorsal fin with 10 elements, anal fin with 9 (rarely 8); pectoral-fin rays 16–17; pelvic fins almost completely separate; black blotch or bar between 2nd and 3rd dorsal spines; head and anterior body mottled orange in freshly caught specimens, posterior body mottled yellow . . . . **_Coryphopterus alloides_**

7a. Pectoral-fin base with two prominent dark spots of equal intensity, one *dorsally* and one *ventrally*; upper spot usually with swath of melanophores extending posteriorly onto pectoral-fin rays; sides of body freckled with scattered large and smaller blotches of melanophores (blotches associated with coral, tan, yellow pigment in life); pelvic frenum absent . . . . **_Coryphopterus dicrus_**

7b. Pectoral-fin base not with two prominent dark spots (or, if two spots present, upper spot more intense); sides of body with few dark markings (with few to many yellow spots in life) or with three rows of light markings (coral pink/orange in life); pelvic frenum present. ***8***

8a. Pectoral-fin base without prominent dark markings but sometimes with a few to many scattered melanophores; sides of body with few if any dark markings (with yellow spots in life) except for basicaudal spot. . . . . .**_Coryphopterus eidolon_**

8b. Pectoral-fin base with prominent markings; sides of body with or without numerous dark markings ***9***

9a. Pectoral-fin base with distinct pigment spot *dorsally*, spot usually dark above, diffuse below, often with dots trailing ventrally; ventral dots coalescing into a separate spot in some specimens (ventral spot, if present, less intense than dorsal spot); second dorsal-fin elements 9–10; second dorsal spine filamentous . . . .**_Coryphopterus thrix_**

9b. Pectoral-fin base with prominent dark spot or blotch only on *ventral* portion; second dorsal-fin elements 11; second dorsal spine not filamentous. . . . . **_Coryphopterus punctipectophorus_**

10a. Body usually pale, pigment primarily comprising three rows of markings on side of body; lower row comprising small, mostly vertically elongate markings, some of which may be crescent shaped or some part of an X-shape but rarely well-defined X's; if X-shaped markings present, their height is considerably shorter than eye diameter; pigment marking above opercle usually a triangle, and basicaudal pigment usually a central bar . . . . **_Coryphopterus tortugae_**

10b. Body heavily pigmented or pale but without vertically elongate or crescent-shaped markings in ventral row of pigment on side of body; height of X-shaped markings, if present, three-quarters of or equal to diameter of eye; pigment marking above opercle triangular, rounded, or with two peaks; basicaudal pigment comprising two separate spots, two spots connected by a line of pigment and resembling a dumbbell, a central bar, or a C-shaped marking. ***11***

11a. Pigment on pectoral-fin base variable but always with dark spot or rectangular-shaped blotch ventrally (may be associated with bright yellow pigment in life); one or two additional bars, blotches, or concentrations of pigment sometimes present dorsally; three rows of dark markings on side of body, some in lower row large, X-shaped markings in heavily pigmented specimens, small, circular blotches in paler specimens; pigment marking above the opercle triangular or round . . . . **_Coryphopterus venezuelae_**

11b. Pectoral-fin base rarely with prominent dark marking ventrally, although melanophores may form one to three light to moderate concentrations on base; body with three rows of dark markings, most of those in the lower row large, distinctive X-shaped markings; pigment marking above opercle usually with two well-defined peaks . . . .**_Coryphopterus glaucofraenum_**

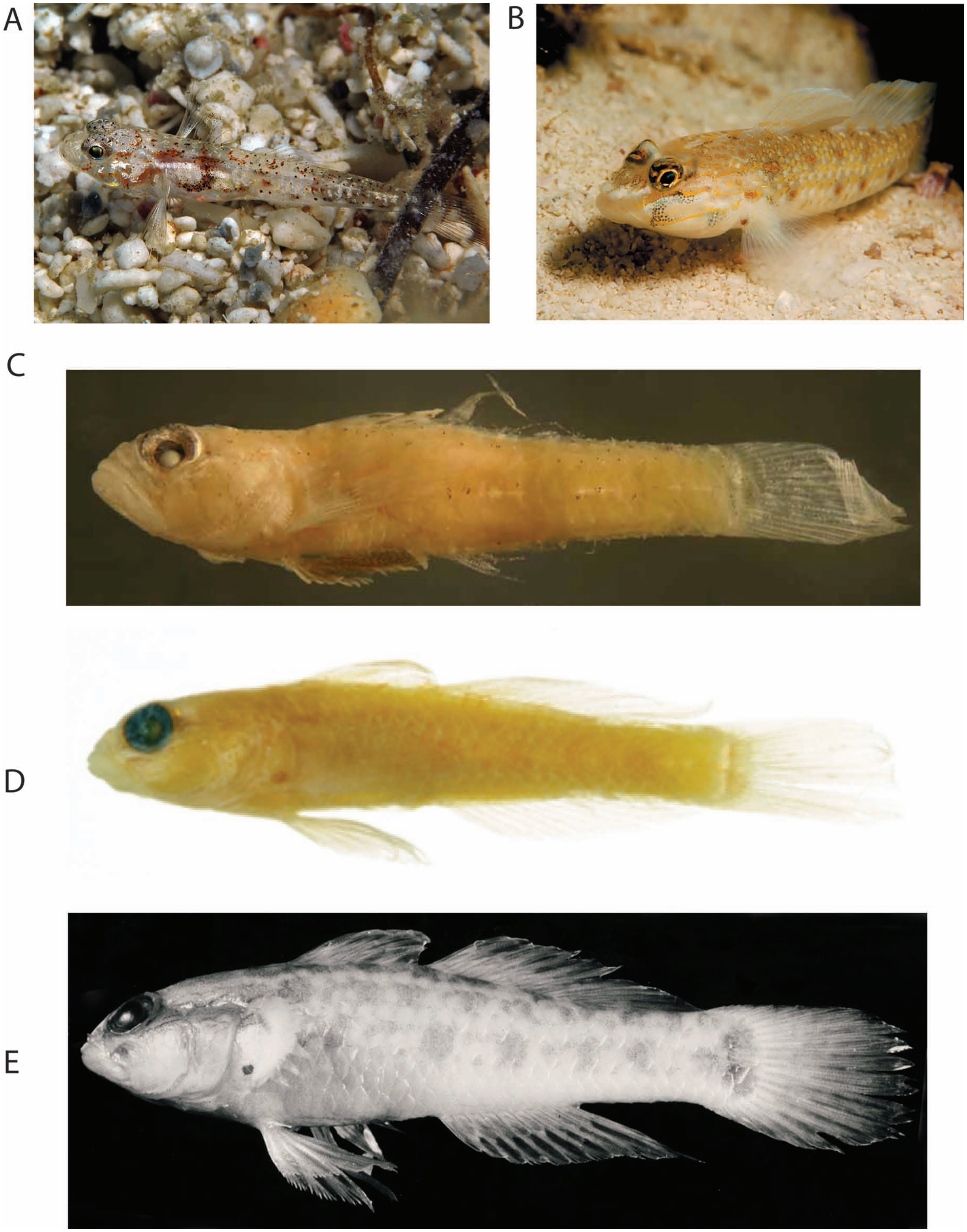


FIGURE 10. A, *Coryphopterus kuna*, San Andres, Colombian Caribbean (photo by Keri Wilk, ReefNet Inc.); B, *Coryphopterus punctipectophorus*, Holbox Island, Mexico (photo by Hilario Itriago); C, *Coryphopterus kuna*, Panama, 17.1 mm SL, holotype, SIO-07-5, preserved, DNA GB EF55021 (reproduced from B. Victor, 2007, fig. 1A, *Zootaxa* 1526:53); D, *Coryphopterus punctipectophorus*, South Carolina, 28 mm SL, USNM 315530, preserved, no DNA; E, *Coryphopterus punctipectophorus*, Florida, Gulf of Mexico, 42 mm SL, holotype, ANSP 90103, preserved, no DNA.