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

*D. Ross Robertson, John H. Christy, Rachel Collin, Richard G. Cooke, Luis D'Croz, Karl W. Kaufmann, Stanley Heckadon Moreno, Juan L. Maté, Aaron O'Dea, and Mark E. Torchin*

**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.

*D. Ross Robertson, John H. Christy, Rachel Collin, Richard G. Cooke, Luis D'Croz, Karl W. Kaufmann, Stanley Heckadon Moreno, Juan L. Maté, Aaron O'Dea, and Mark E. Torchin, Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Panama. Corresponding author: R. Robertson (drr@stri.org).* *Manuscript received 15 August 2008; accepted 20 April 2009.*

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

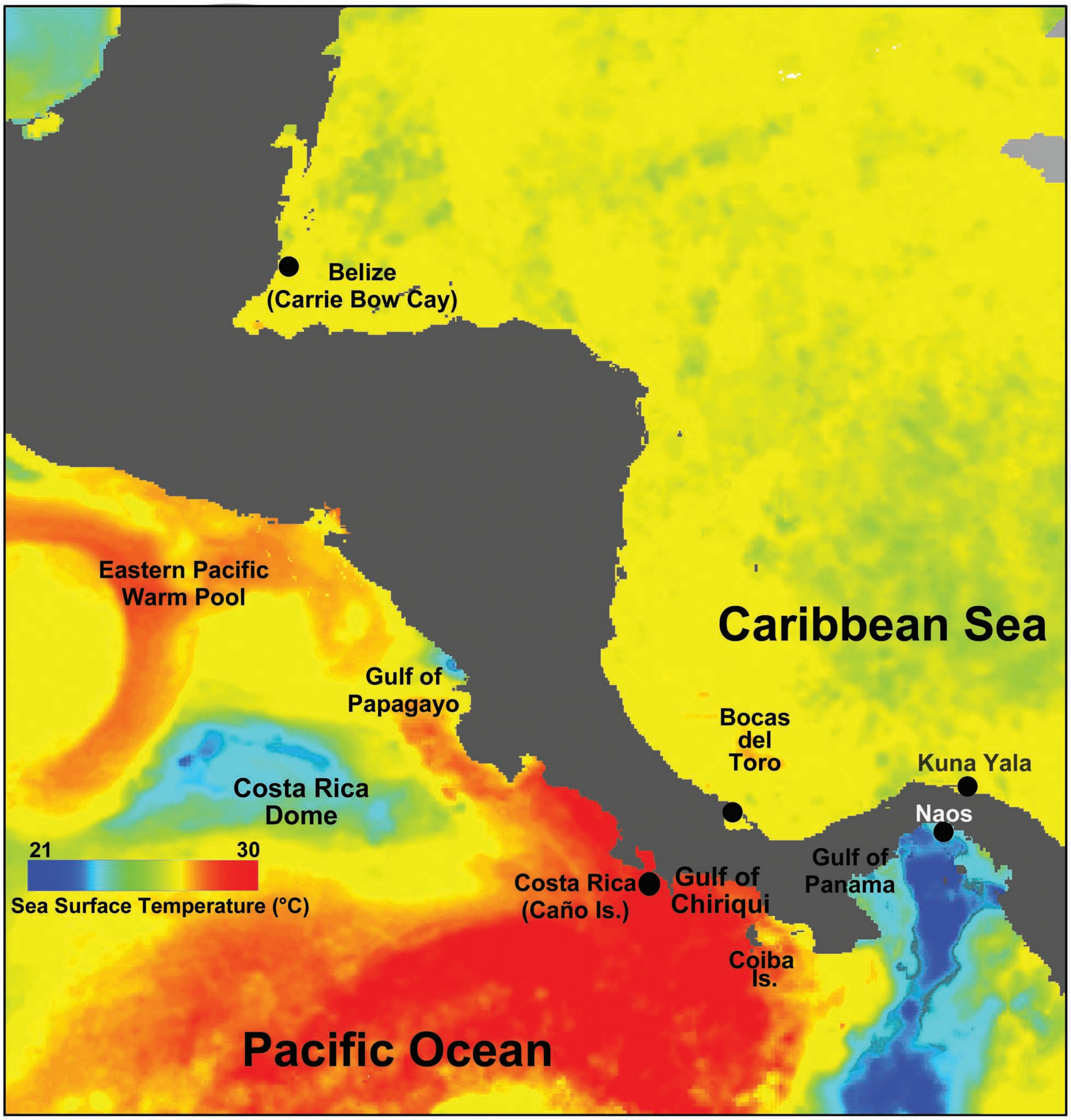


**FIGURE 1.** Temperature regimes on the Atlantic and Pacific coasts during the seasonal upwelling in the Gulf of Panama.

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

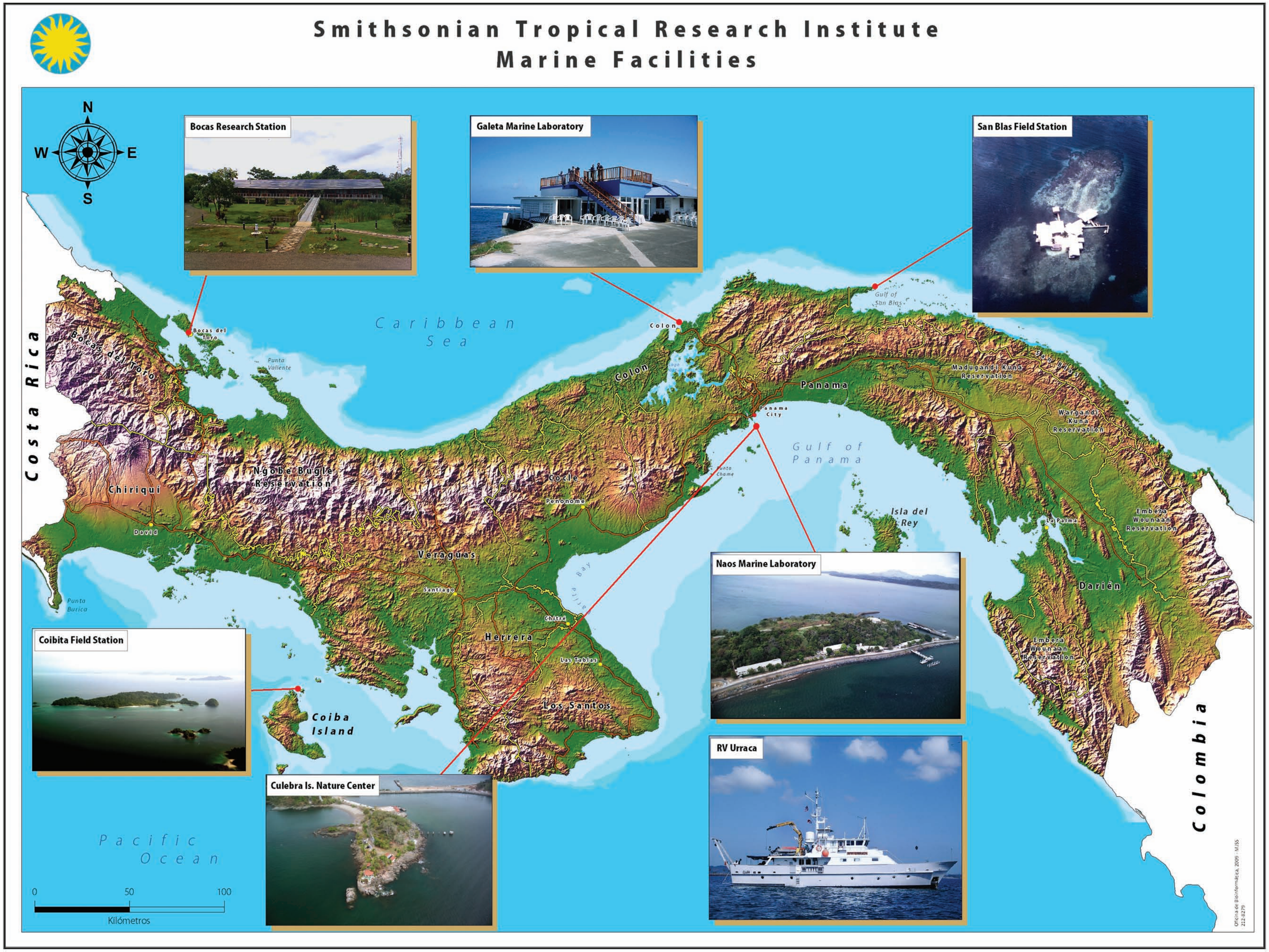


FIGURE 2. Map of Panama showing the distribution of Smithsonian Tropical Research Institute (STRI) marine facilities.

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-

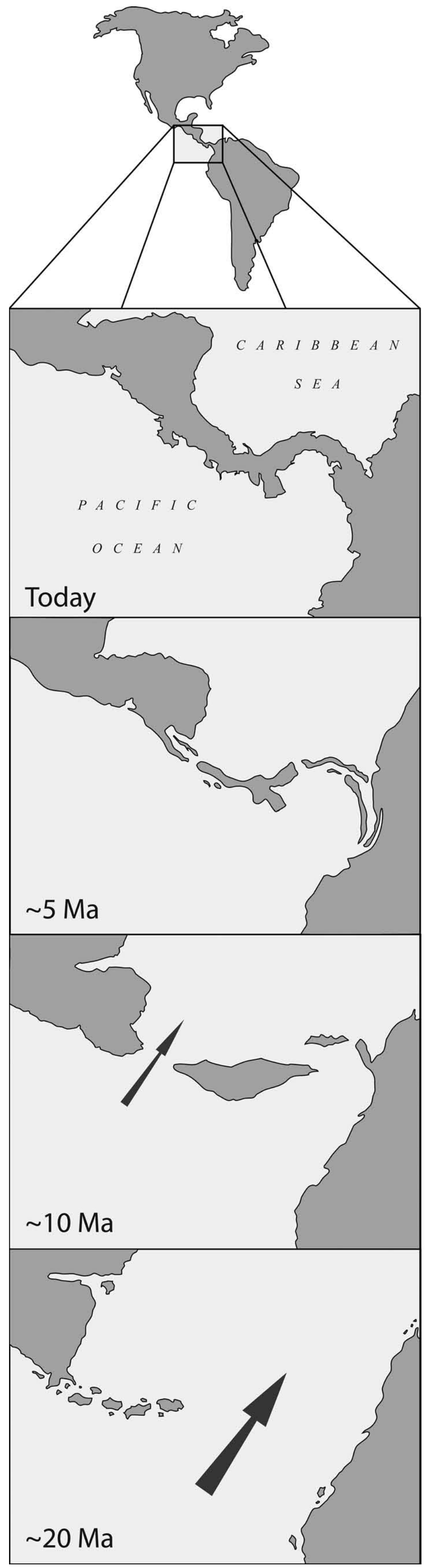


**FIGURE 3.** Formation of the Isthmus of Panama during the last 20 million years (Ma = million years ago). Arrows indicate direction of principal water flow through the Central American Seaway. (From O'Dea et al., 2007b.)

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

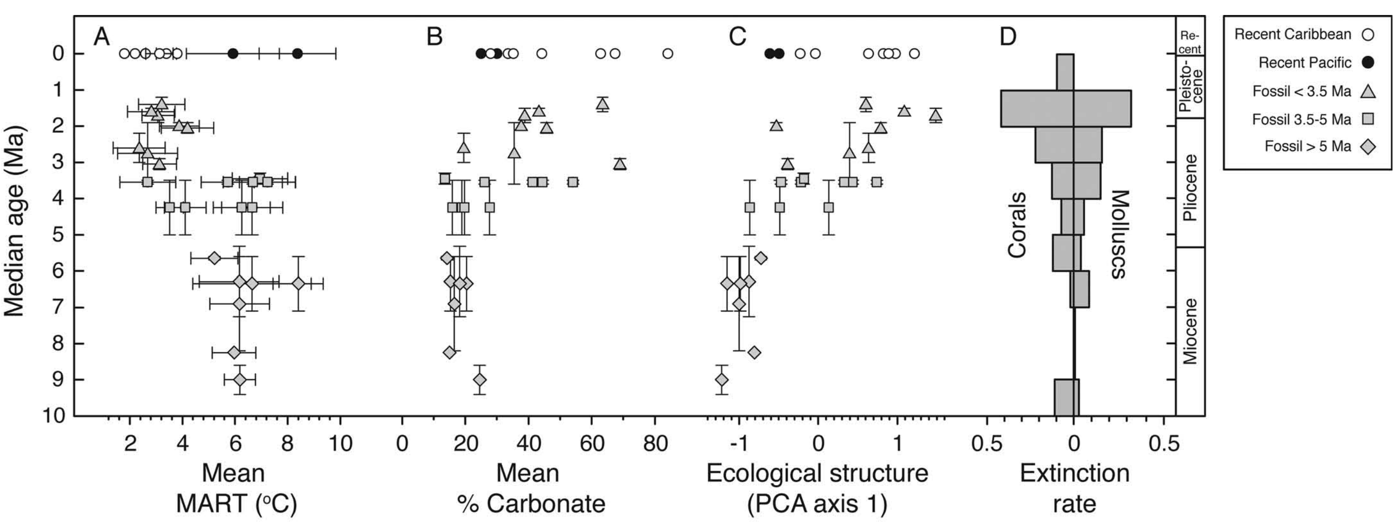


**FIGURE 4.** The sequence of environmental and ecological changes in the southwest Caribbean in response to the closure of the isthmus of Panama (Ma = million years ago). A. Upwelling intensity, as estimated by the mean annual range of temperature (MART), shifted rapidly from high values similar to 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.

### ACKNOWLEDGMENTS

STRI's marine program thanks Panama for its cooperation in hosting STRI, and for the long-term support of the Panamanian government entities that manage marine resources and marine reserves and cooperate with STRI's research activities (the Autoridad Maritima de Panamá, the Autoridad Nacional del Ambiente, and the Autoridad de los Recursos Acuaticos de Panamá). Many local and international donors have contributed generously to the development of STRI facilities and to its education and research programs, notably D. Cofrin, F. Hoch, P. Peck, K. and E. Himmelfarb, the Upton Trust, and the Fundación Smithsonian de Panamá. Marine science at STRI also has benefitted immensely over the years from grants made by the National Science Foundation, the Secretaría Nacional de Ciencia Tecnología de Panamá (SENACYT), Conservation International, the Darwin Initiative, the Nature Conservancy, the National Geographic Society, and various Smithsonian entities: the

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.