



Peter W. Glynn with a new record of Indo-Pacific hydrocoral *Millepora exaesa* Forskål, discovered at Clipperton Atoll in April 1994 (Photo Gerald M. Wellington)

EASTERN PACIFIC CORAL REEFS: NEW REVELATIONS IN THE TWENTIETH CENTURY

BY

PETER W. GLYNN

INTRODUCTION

Ever since I entered the field of coral reef ecology, in the early 1960s, I have been intrigued by Darwin's (1842) and Dana's (1843, 1890) contention that, for reasons of cold water currents and upwellings, coral reefs should not (and do not) exist off western American shores. This idea was upheld by Vaughan (1919) and Crossland (1927), among others, almost 100 years later. However, Joubin's (1912) map of the coral reefs of the world, reprinted with additions by Wells (1957), shows coral reefs present on the Pacific coast of southern México, and along the coasts of El Salvador, Costa Rica, Panamá, Colombia, Ecuador, and northern Peru (Fig. 1). A coral reef is also shown at Cocos Island, but none is indicated in the Galápagos Islands. To my mind, this was clearly an interesting contradiction violating the dictum that coral reefs are confined to clear tropical waters of low organic productivity. This paradox stimulated one of my first aims upon reaching Panamá in 1967, that is, to determine if coral reefs — wave-resistant, geomorphologic structures that build the substratum on which they continue to grow — do in fact exist in the highly productive marine environment of Pacific Panamá. If coral reefs are found in eastern Pacific waters, then how are they distributed, what are their sizes, and when did they begin to accrete? Further, posing some ecological questions, what is their species composition, and how do various interactions, such as competition, grazing, predation, and symbiosis, regulate their community structure? This essay will explore the historical development of coral-reef studies in the eastern tropical Pacific, beginning in the late 1960s, from the perspective of someone who first observed reef-building corals in the Gulf of California in the early 1950s.

One of the strongest motivating factors in any scientific discipline is the excitement of discovery. The discovery of eastern Pacific coral reefs, their associated biota and diverse species interactions, has truly been an exhilarating experience for me. Many of the broad-ranging questions posed above have required extensive travel to remote areas. This has involved transporting field equipment on back roads, some mapped and some not, by foot and by a variety of watercraft that would never meet the safety requirements of the University National Oceanographic Laboratory Systems

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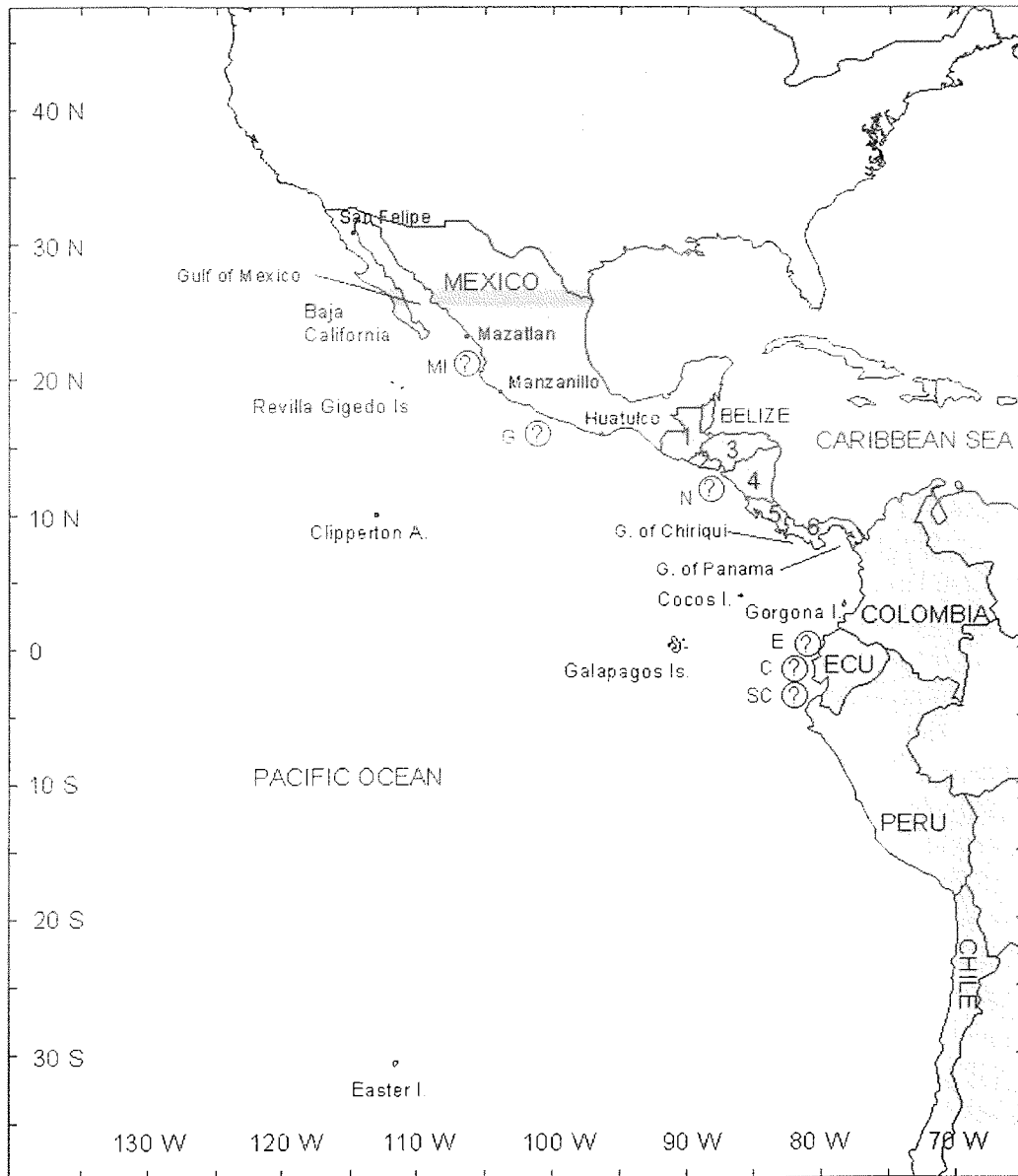


Figure 1. Locator map of the eastern Pacific. 1, Guatemala; 2, El Salvador; 3, Honduras; 4, Nicaragua; 5, Costa Rica; 6, Panamá. Question marks denote unexplored or relatively little studied areas: MI, Marias Islands; G, Guerrero state; N, Nicaragua; E, Las Esmeraldas; C, El Copé bank; SC, Santa Clara Island.

(UNOLS) National Science Foundation program. These excursions sometimes resulted in false starts, and unexpected, hazardous and amusing events that inevitably occur during field studies at remote sites. A few of these, which have contributed to the adventure of my work, are interlaced in the following narrative.

How did it all begin? My most vivid and cherished memories of first exploring and learning about marine life were with my great aunt, Dora Conrad, an eccentric but

lovable schoolmarm who gloried in explaining the ways of the natural world. During my preadolescent years, we tramped the hills, parks and beaches of southern California, where she extolled on the animal, vegetable and mineral worlds that unfolded before us. Since we both lived on Coronado Island, our walks became more focused on the shoreline. She was in great measure responsible for sparking my interest in marine life, which first led to making a shell collection, then to the collection and study of various plants, invertebrates and fishes. By the time I entered high school, my friends — John C. Elwell, Stephen E. Flynn, Marvin A. Nottingham, Charles Quinn, among others — and I began to make diving trips into México. As time went on my interests shifted more from spearfishing to exploring the panoply and interrelationships of marine life. I first observed living corals in the Gulf of California, in subtropical areas south of San Felipe, Baja California, and around San Carlos Bay and Tiburón Island. Our excursions eventually extended farther south into México, and to tropical areas around Mazatlán and Manzanillo. Stimulated by F. G. Walton Smith's book, *Atlantic Reef Corals* (1948), I traveled to Belize (formerly British Honduras) in 1959 to observe firsthand the largest coral-reef system in the Caribbean Sea. There I offered my diving services to a Mexican fishing crew in exchange for passage to the barrier reef. The three weeks of living and diving along the Belizean Barrier Reef left me with a lasting impression of the magnificence of the marine tropical world.

Two of my science teachers at Coronado High School — Curtis J. Yeagar in biology and Marvin Nottingham in chemistry — who recognized my interests encouraged me to continue studying in the natural sciences. In graduate school, at the Hopkins Marine Station of Stanford University, I was especially influenced by the high standards of scholarship and investigative pursuits of Arthur Giese, Cornelius van Niel, Lawrence Blinks, and Donald P. Abbott. Don Abbott was my doctoral adviser and mentor, greatly admired by me for his love and dedication to teaching and research (Fig. 2).



Figure 2. Three vertebrates contemplating the ways of intertidal invertebrates off the Hopkins Marine Station, Pacific Grove, California. Left to right: Donald P. Abbott, Peter W. Glynn, and Charles (Chuck) Baxter. Pete's (P. W. Glynn) Island is visible behind Chuck. July 20, 1977. (Photo C. Kitting)

Some experiences related to finding lodging form a vivid part of my memory of graduate school. During my field studies in Pacific Grove I inquired about renting the late Edward F. Rickett's Pacific Biological Laboratories. Steinbeck's colorful character "Doc," in his classic novel, *Cannery Row*, was in large measure fashioned from Ricketts, the marine biologist whom I greatly admired. I was shown through the living and laboratory spaces, still cluttered with papers and preserved specimens. I was allowed to keep one of Ed Rickett's desiccated tortoises, which I plucked from a large holding tank. Unfortunately, when I called the

following week to finalize a contract, I was told that another party had already offered a higher rent that I could not match. I did the next best thing, however, and let a room for \$25.00 per month above the Bear Flag bar and restaurant down the street. The clacking and whistling of the predawn freight train assured early morning rises for the summer low tides. While completing course requirements at the Stanford campus in Palo Alto I again began searching for convenient and low-cost accommodations. One afternoon after a seminar in Jordan Hall, the enormous labyrinthine biological sciences building, I wandered up a flight of stairs and discovered a little-known greenhouse loft. Off to one side was a vacant, low-ceiling room with a long desk, book shelves, sink, and electrical outlets. At first I tentatively occupied the desk, moved my books in, then an electric heating plate and coffee pot, sleeping bag and clothes, and presto, I had new accommodations. Early morning trips to the showers in the basement and my constant companions, the cooing pigeons nesting in the eaves, made this a most comfortable arrangement. After a few months my living situation was discovered by one of my distinguished committee members, shall we say Professor "Goodheart." Fortunately, he was sympathetic with my situation and allowed me to occupy this niche for the remainder of my tenure on the Stanford campus.

Upon nearing completion of my dissertation research, a study of the community structure and trophic interrelationships in a high intertidal assemblage, Don Abbott invited me into his office to discuss where I might like to teach. He laid out several letters from prominent, stateside universities, inquiring of the availability of recent graduates who might be interested in joining their faculties. Don was not surprised when I announced that I preferred to work in a tropical setting, and to take up an available teaching post at the University of Puerto Rico (Mayagüez) where I could investigate coral reefs. My wife, Carmen S. Glynn (Quiñones), who was born in southwestern Puerto Rico (Lajas), played no minor role in this decision. Don understood my desire to move to the tropics and offered his full support, for he too had an abiding interest in coral reefs, having lived for nearly five months in 1953 on Ifaluk Atoll in the Caroline Islands. He was part of a research team, including such other members as Marston Bates, Frederick (Ted) M. Bayer, and Joshua I. Tracey, charged with documenting the way of life of the Ifaluk people (Bates and Abbott, 1958).

The years spent in Puerto Rico (1960-1967), at the Institute of Marine Biology in Mayagüez and the Magueyes Island (La Parguera) field station, were pleasant and rewarding. There I began to develop an appreciation for the physical controls of reef development and the often subtle and complex biotic interactions regulating coral-community structure. Memories of 24- and 48-hour field exercises on offshore reefs with the Coral Reef Ecology class are still vivid and evoke a feeling of pedagogical accomplishment. At that time I also began reading the *Atoll Research Bulletin*, which supplied a diverse literature that helped to broaden an understanding of coral reef science in Puerto Rico, e.g., reef studies by J. W. Wells (1951) in the Marshall Islands, P. E. Cloud (1952) in the Gilbert Islands, and D. R. Stoddart (1962) in Belize. One of the star students in this course, Alina M. Szmant, has become a distinguished coral reef biologist. Juan A. Rivero and John E. Randall, successive directors of the Institute, offered invaluable support and encouragement during my employment at the University

of Puerto Rico. In 1967, I accepted a position with the Smithsonian Tropical Research Institute (STRI) in the Republic of Panamá. Upon leaving Puerto Rico, it was with sadness on the one hand, but with excitement on the other because I would be able to revisit tropical Pacific shores. A major research goal at STRI, strongly supported by successive directors Martin Moynihan and Ira Rubinoff, was to conduct comparative studies of the ecology, behavior, and evolution of marine species and communities on both Caribbean and Pacific shores.

EXPLORATION AND DISCOVERY

Equatorial Eastern Pacific

It seemed to me that information on the distribution of coral assemblages, their species composition, zonation, and extent of buildup under different environmental conditions was needed to help understand why reef development was not widespread in the eastern tropical Pacific. With my good friend and colleague, Robert H. Stewart, who had already begun surveying coral reefs in the Pearl Islands, I began a reconnaissance of coral reefs in the Gulf of Panamá. Coral specimens were collected, many of which were identified by J. Wyatt Durham. I was struck by the abundance of coral assemblages and coral reefs present on islands throughout the gulf. This was in stark contrast to Crossland's (1927) conclusion that coral reefs were absent from the upwelling Gulf of Panamá. To locate coral assemblages and reefs, I often flew with pilot friends along coastal areas during midday low-tidal exposures. Ira Rubinoff, Richard Rosenblatt, and others pursuing ichthyological studies suspected the presence of a rich fish fauna associated with corals in the nonupwelling Gulf of Chiriquí, western Panamá (Fig. 1). Ira arranged with the U.S. Navy an expedition to this remote and poorly known gulf in April 1970 aboard the LST *Traverse County*. In addition to the discovery of several new fish records and species, an interesting coral fauna and diverse assemblages of associated reef species were found. Several relatively well-developed coral reefs also were discovered, with distinct depth zones and thick framework structures. One of these, at the south end of Bahía Damas, Coiba Island, covers about 160 ha and may be the largest coral reef on the continental margin of the eastern Pacific (Glynn and Maté, 1997). Several coral-reef accumulations also were found along continental shorelines and, surprisingly, at the mouths of some large estuaries. Three species of hydrocorals, a taxon previously unknown in the eastern Pacific, were discovered on the Uva Island coral reef. Two of the hydrocorals belonged to central/western Pacific species, but one proved to be a new species endemic to the Gulf of Chiriquí (Weerdt and Glynn, 1991). Moderately large populations of the Crown-of-Thorns sea star, *Acanthaster planci* (Linnaeus), were found foraging on a variety of coral prey. Because of the prominent development and relatively high diversity of coral reefs in Chiriquí, a number of workers have been attracted to this region, including Charles Birkeland, Thomas F. Dana, Raymond C. Highsmith, Ian G. Macintyre, William A. Newman, John C. Ogden, James W. Porter, Robert H. Richmond, Ernesto Weil, and

Gerard (Jerry) M. Wellington. One of Tom Dana's (1975) studies, now considered a classic, proposed a model of long-distance dispersal from the central Pacific to explain the origin of eastern Pacific corals and coral reefs following Pleistocene extinctions. This hypothesis provoked caustic criticism from a few workers who held to a vicariance explanation for eastern Pacific coral origins (McCoy and Heck, 1976; Heck and McCoy, 1978). Some of my students have studied (and continue to study) coral reefs in Chiriquí as well, on one occasion establishing a temporary field laboratory with running seawater and various other amenities (Fig. 3).



Figure 3. Uva Island Beach Club, a temporary field laboratory, Gulf of Chiriquí, Panamá). Juan L. Maté and C. Mark Eakin (standing, left to right), David B. Smith, Peter W. Glynn, and José Manuel Gil Lasso (sitting, left to right). February 21, 1989. (Photo C. M. Eakin)

With information crossing my desk in the early 1970s of the existence of coral reefs in the Galápagos Islands, this seemed like the next logical place to investigate. The author of these findings, Jerry Wellington, located several coral-reef formations during an assessment of the marine resources of the Galápagos coastal environments. Thanks to grants from the Smithsonian Institution and the generosity of

Thomas J. Watson, Jr., we were able to embark on two research cruises in the Galápagos in 1975 and 1976. The research team in 1975 included John W. Wells, Charles (Chuck) Birkeland, Jerry, and myself (Figs. 4, 5, and 6). Working from the *M/Y Beagle III*, we surveyed several coral-reef sites from the southern sector of the archipelago to the northernmost islands of Darwin and Wolf. Upon completion of a second survey in 1976, aboard the *M/Y Palawan*, we had gained sufficient knowledge to publish a book on the corals and coral reefs of the Galápagos Islands (Glynn and Wellington, 1983). No fewer than six new species of azooxanthellate corals were named as a result of this work (Wells, 1982).

On our return trip to Panamá in 1975, John, Chuck, and I rented a car and drove up the Ecuadorean coast to examine a coral formation spotted earlier during an aerial overflight. It was high tide when we arrived at the beach near Machalilla and the object of our visit was located a few hundred meters offshore at Sucre Island. I spotted some fishermen down the beach with canoes and the stage was set for bartering. After considerable haggling, the best I could negotiate was a round trip to the island for the equivalent of about \$40. Chuck and I decided this was too high a price, so we donned our diving gear and started swimming toward Sucre Island. We were soon joined by a



Figure 4. En route to the *M/Y Beagle III* with a skiff full of gear, Academy Bay, Santa Cruz Island, Galápagos Islands. Fore to aft: John W. Wells, Peter W. Glynn, and Gerard M. Wellington. January 9, 1975. (Photo C. Birkeland)



Figure 5. Examining corals at the Urvina Bay uplift, Isabela Island, Galápagos Islands. Left to right: Peter W. Glynn, Gerard M. Wellington, and John W. Wells. January 15, 1975. (Photo C. Birkeland)



Figure 6. Discussing the day's activities in the salon of the *M/Y Beagle III*. Left to right: Charles Birkeland, John W. Wells, and Peter W. Glynn. January 22, 1975. (Photo G. M. Wellington)

so these remained with him as part of the final payoff. The Sucre Island coral formation turned out to be the first coral reef reported on the Ecuadorean coast and, at that time, the southernmost coral reef in the eastern Pacific.

Flying into and out of the Galápagos Islands in the 1970s was sometimes problematical and amusing in retrospect. On one occasion, Jerry and I were bumped from our flight when attempting to leave the islands after a research cruise. This

fisherman in his canoe who paddled alongside us. About halfway to the island, the price dropped to \$30, then to \$20, and finally to \$10 upon nearing the island and its fringing coral assemblages. By this time the fisherman realized we were serious and proceeded to help us collect corals during the remainder of the dive. By the end of the survey we were on friendly terms, and he told us of other coral formations in the area that he had seen while fishing. It had not escaped me that he was admiring my swim fins,

involved retracing our journey back to the Charles Darwin Research Station via overcrowded buses and a boat trip across Baltra Canal — a roundtrip journey that took up most of the day. We were again promised seats by the airline manager the next morning and I slipped him a \$20 bill to make certain we wouldn't be left behind. To our consternation, and to that of about 20 other souls standing on the tarmac, the plane was loaded, the doors shut, and it began to taxi down the runway. With engines whining, suddenly a door opened and the manager pointed to us, giving the sign that two more passengers were welcome aboard. With that, everyone started to run toward the plane juggling baggage the best they could. Jerry was quite athletic then (and is still), and was able to jump up to, and grasp, the opened doorway with a boost from my cupped hands. I then threw our bags to him, and grasped his down-stretched arm for the final lift into the plane — or so I thought. The other would-be passengers saw what we were doing and decided to take advantage of our human chain. One man grabbed my legs and another began to climb up my torso to reach the open door. I beckoned to Jerry on how to extricate myself from this predicament. Without hesitation, he instructed me to pummel and kick at the intruders until they fell away. This I did, Jerry quickly hoisted me up, the manager slammed the door shut, and off for the mainland we headed. On later visits to the Galápagos, I wondered if I might be spotted and “paid back” for this bravado.

One of my intrepid volunteer pilots, Dennis (Capt.) Cismowski, flew helicopters in the U.S. Army, helping me with reconnaissance flights in his spare time. Not only did Dennis assist me with aerial surveys in Panamá, Costa Rica and Colombia, but he was adroit at a variety of underwater tasks and also helped with in situ reef studies. Our automobile trip to Machalilla in 1975 allowed us to survey the central Ecuadorean coast, but there were rumors of coral reefs in the northern part of Ecuador, at Las Esmeraldas, near the Colombian border. I mentioned this to Dennis and he proposed that we fly to Ecuador from Panamá, cruising the coastline on the way. After obtaining permission to cross the Panamá/Colombia and Colombia/Ecuador international borders, with the assistance of the Smithsonian Institution and the U.S. State Department, we loaded our Cessna 172 with four scuba tanks and five jerricans of aviation fuel. We flew through some harrowing electric storms along the Choco coast and landed safely in Cali after a brief refueling stop in Buenaventura, Colombia. The administrator at the Cali airport claimed that our papers were not in order and demanded that we return to Panamá. I tried convincing him that we did have the necessary clearance, but he would not budge from his position. So we again refueled and took off, heading north to Panamá. When we reached a coastal mountain range, Dennis winked at me and said: “If you really want to go to Ecuador I can drop to just above tree level and no radar will be able to detect our progress.” I winked back and we were quickly heading south again. By the time we reached Tumaco, not far from the international border, we were running low on fuel. We buzzed the airfield, faking engine problems, were given a green light from the tower, and then landed. Our plane was immediately surrounded by armed Colombian soldiers. We were taken into custody and held at an army base for two days. The Cali airport administrator had radioed ahead that we would probably be heading south. We struck up a friendship with the Colombian lieutenant in charge of the garrison, who

allowed us to “escape” early one morning. As of this writing, Las Esmeraldas is still in need of study.

Before the 1980s, virtually nothing was known of the extent of coral-reef development along the Colombian Pacific coast. On our ill-fated flight to Tumaco, Dennis and I skirted Gorgona Island and spotted coral reefs on the east side of the island. A few years later (1979), I was invited by Henry von Prael to participate in the Sula III Expedition to Gorgona Island, organized to conduct inventories and studies of the marine and terrestrial biota of the island. Joining me was Peter Castro, one of my first students in Puerto Rico, who was on sabbatical leave (from California State Polytechnic University, Pomona) and working in my laboratory in Panamá. Between Henry, Felipe Guhl, and myself, we were able to characterize the coral fauna, assess corallivore activities, and complete reasonably detailed surveys of the distribution and geomorphology of the Gorgona Island coral reefs (Glynn et al., 1982). Peter Castro collected and described the decapod crustacean fauna living symbiotically among the branches of pocilloporid corals (Castro, 1982).

During our stay at Gorgona we were comfortably housed in the penal colony’s guest quarters and nourished by the prison’s finest cuisine. Admittedly, the green-colored needle fish was not my favorite breakfast fare, but the freshly baked bread was a delight. To obtain a bread roll required hard bartering with the inmates, some of whom were assigned to look after our needs. One evening I engaged “El Diablo,” one of our inmate helpers who was named for his Mephistophelean features, in a conversation to learn of the misdeed that landed him in prison. Many years ago, so the story went, he was an innocent lad fishing with a group of men in an estuary. They were dynamite-fishing, which was unlawful at the time. Suddenly a government patrol boat rounded the point. Everyone, save El Diablo, quickly jumped into the water and escaped by swimming into mangrove thickets. El Diablo didn’t know whether to flee or surrender; he panicked, compulsively lit a stick of dynamite, and threw it toward the approaching boat. He never revealed the full extent of the bodily harm done, but did say that he was resigned to remain in prison for the rest of his life.

In the late 1970s we conducted surveys along the Costa Rican coast, first by performing reconnaissance flights at midday low-tidal exposures to locate suspected coral assemblages, and then by traveling to sites by automobile and boat. These in situ inspections revealed the presence of numerous coral reefs from the southwestern sector of Costa Rica near Panamá to northwestern Costa Rica close to the Nicaraguan border. All of our survey work in Costa Rica was pleasant and productive except for one incident on the Santa Elena Peninsula near Nicaragua. Anastasio Somosa, the former president (dictator) of Nicaragua owned a ranch on this peninsula and at that time he still tried to lay claim to this territory. Further complicating events were the bands of Sandanista insurgents who were organizing raids in Nicaragua from sanctuaries in Costa Rica. On this occasion, in 1978, we were surveying areas in Santa Elena Bay by diving from a black inflatable. We were unaware that we were being watched by the crew of a Nicaraguan gunboat. When the gunboat suddenly accelerated and started heading directly toward us, we pulled anchor and made haste for the shallow end of the bay where our truck was parked. Fearing that we might be pursued by an armed landing

party, we quickly loaded the truck with our gear and departed the area in haste. My ventures into Costa Rica were not only beneficial on the research side, but also allowed me to meet several resident marine biologists, among whom Manuel M. Murillo, Jorge Cortés, and Hector Guzmán have figured importantly. Jorge was to become my first doctoral student at the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

Other Eastern Tropical Pacific Areas

More recently I have participated in field studies at Clipperton Atoll (1994), at Huatulco on the south coast of Mexico (1996, 1997), and at Easter Island (1999, 2000). For many years, the coral fauna and extent of reef development at Clipperton were largely unknown. Only tantalizing brief accounts and unpublished field notes were previously available (Allison, 1959; Hertlein and Emerson, 1957) on what is probably the largest coral-reef formation in the eastern Pacific region. Thanks to a grant from the National Geographic Society, J. E. N. (Charlie) Veron, Jerry Wellington, and I, among several other marine scientists, were able to join the Clipperton Expedition organized by John D. Jackson. Our 13-day study revealed that Clipperton contains a meager nine zooxanthellate coral species, of which only three or four have contributed importantly toward reef building. One of these, exhibiting an attractive plating morphology, was recently described by one of my current students and a colleague of his: *Porites arnaudi* Reyes Bonilla and Carricart Ganivet (2000). Since total live coral cover extends over 370 ha of bottom, to a depth of at least 80 m, this is the largest known coral reef in the eastern Pacific (Glynn et al., 1996). The next largest studied coral reef occurs at Coiba Island (Panamá), and covers 160 ha (Glynn and Maté, 1997).

En route to Clipperton, about 450 km SSW of the tip of Baja California, we visited three islands in the Revillagigedo Archipelago: San Benedicto, Clarion, and Roca Partida. Due to the sudden appearance of Barcena Volcano on San Benedicto Island, which received considerable local press in my home town (Coronado) when it was "born," during an explosive eruption on 1 August 1952, the extent of coral development on this island was uncertain. Barcena reached 300 m in elevation in only 12 days. Amazingly, six coral species were found at shallow depth along the basalt shoreline during our survey in 1994, and some of these corals formed abundant populations. One-meter-thick living pocilloporid fringing reefs were present at the north end of the island, suggesting rapid colonization and growth since the eruptive event. Growth rates of pocilloporid branches from 3 to 6 cm per year have been measured in the eastern Pacific (Glynn, 1977; Guzmán and Cortés, 1989), so a spurt in reef-framework accumulation of this magnitude is possible. Current studies in the Revillagigedo Islands, including Socorro Island, are being actively pursued by Mexican researchers (e.g., Reyes Bonilla and Carriquiry, 1994; Ketchum and Reyes Bonilla, 1997).

Palmer's (1928) brief and provocative account of the coral reefs of Huatulco was largely responsible for turning my attention to the southern coast of México. Like the gulfs of Panamá and Papagayo (Costa Rica), Huatulco lay within the upwelling Gulf of

Tehuantepec. Therefore, Palmer's mention of coral reefs was not surprising in light of their occurrence in other eastern Pacific upwelling centers. Initial surveys revealed the presence of 12 zooxanthellate coral species and 17 pocilloporid coral reefs, mostly in bays, ranging in depths from 2 to 14 m, and with framework buildups of 1 to 5 m (Glynn and Leyte Morales, 1997). Additional coral species records and new reefs are being discovered in this area as investigations proceed by workers at the Universidad del Mar, Oaxaca (Leyte Morales, 2001). A heightened interest in Pacific corals by Mexican workers in the 1990s has resulted in much new information regarding the reef-building scleractinian fauna and the distribution and environmental controls of reef development (e.g., Reyes Bonilla, 1993; Carriquiry and Reyes Bonilla, 1997; Ketchum and Reyes Bonilla, 1997; Reyes Bonilla and López Pérez, 1998). An area still in need of study, however, is the Mariás Islands, which lie northwest of Banderas Bay (Fig. 1, MI). A preliminary inspection of one of these islands, the northeast side of María Cleofas, has revealed the presence of a circular pocilloporid reef several km in circumference, possibly one of the largest coral reefs in the eastern Pacific (H. W. Chaney, pers. comm.). Since a penal colony is located in the Mariás Islands, it is difficult to obtain permission to work in this area. Finally, the Guerrero state coastline, a 300 km stretch from Acapulco to Zihuatanejo, is another relatively unstudied Mexican area.

Remaining Areas in Need of Study

Other eastern Pacific areas that are still in need of exploration are El Salvador, Nicaragua, and parts of the Ecuadorean coast. A recent survey of El Salvador by Héctor Guzmán, Jorge Cortés, and Juan Maté (29 March to 3 April 2001) failed to produce any corals. It is likely that turbulent seas and reduced visibility during this survey prevented a thorough search of favorable coral habitats. Another attempt should be made to investigate this area since local divers have observed corals here, notably offshore of Los Cóbano. The Farallones Islands in the Gulf of Fonseca (within Nicaraguan territory) may also be of interest because these islands are located in a more oceanic setting, of probably higher water quality, near the gulf entrance. The subtidal marine assemblages of the Esmeraldas coast of northern Ecuador are still largely unexplored since my failed attempt to reach this area in the late 1970s. The extensive shallow rocky platforms in this region may support coral communities. Ecuadorean fishermen have reported abundant massive corals further south on offshore banks, e.g., at El Copé off Libertad, and a coral reef at Santa Clara Island in the Gulf of Guayaquil.

Exploratory studies were recently (1999, 2000) initiated at Easter Island, an isolated coral outpost in the southeastern Pacific. This area is of interest because of its hypothesized biogeographic link with the far eastern Pacific. It is possible that Easter Island has served as a stepping stone during the migration of corals and reef-associated species from the easternmost Polynesian Islands into the equatorial eastern Pacific. Of the 11 currently recognized zooxanthellate corals, two species are predominant: *Pocillopora verrucosa* (Ellis and Solander) and *Porites lobata* Dana. Incipient reef frameworks are 2 to 7 m in vertical relief in some areas, e.g. on the northeastern insular

shelf that is sheltered from high wave assault (Hubbard, pers. comm.; Glynn et al., in press).

A central Pacific area that may share a link with the eastern Pacific is the Line Islands, an island chain located immediately north of the equator and centered about 1,600 km south of the Hawaiian Islands. These islands lie astride the North Equatorial Counter Current and may represent a source area for propagules traveling toward the east as proposed by Tom Dana (1975). Jerry Wellington and I are now planning a research trip to the Line Islands to study the ecology, morphology, and genetic structure of suspected scleractinian coral migrants.

CORAL BIOLOGY AND ECOLOGY

From the exploratory work outlined above and more focused studies, our understanding of eastern Pacific coral-reef biology and ecology has been greatly broadened in recent years. I offer here a thumbnail sketch of some of these recent advances, emphasizing findings that serve to characterize eastern Pacific reef-coral communities. In the following, I comment briefly on: (a) the nature of eastern Pacific coral reefs and their general community structure, (b) the dynamics of coral population abundances, (c) coral growth, (d) feeding relationships, (e) bioerosion, (f) coral reproduction, (g) disturbances, (h) zooxanthella symbiont diversity, and (i) coral population modeling.

Eastern Pacific Coral Reefs, a Profile

It quickly became evident from the surveys conducted in Central and South America that structural coral reefs were abundant in many areas of the eastern Pacific, albeit small in size, patchily distributed, and generally present at shallow depths. The established prevalence of coral reefs supports Durham (1947, 1966) and Squires (1959), who maintained that coral reefs were present along the Pacific coast of the Americas. Even though most of these reefs are developed at shallow depths, they seldom break the surface and are visible for only short periods during extreme low tidal exposures. Unlike coral reefs in other provinces, eastern Pacific reefs are best developed in protected bays or along coastal areas not subject to intense wave assault. The most prevalent taxa contributing to reef frameworks belong to species of *Pocillopora*, which form vertically elongate, interlocking, and highly porous structures. Since these reefs contain sparse amounts of binding crustose coralline algae and exhibit minimal submarine cementation, this may in large part explain why they are not developed on exposed coastlines. In upwelling areas, the best reef development also tends to occur on the sheltered sides of islands, oriented away from the strongest effects of upwelling (Glynn and Stewart, 1973). An additional interesting feature of most eastern Pacific reefs is that they are monogeneric in composition, constructed dominantly of one or only a few species. In addition to *Pocillopora* spp., some reef assemblages contain massive corals such as *Porites lobata*, *Pavona* spp., and *Gardineroseris planulata*

(Dana). See Guzmán and Cortés (1993), Cortés (1997), and Glynn (2001) for succinct overviews of the nature of eastern Pacific coral reefs.

Like having a favorite book, coral reef biologists often have a favorite reef. My favorite reef is the Uva Island reef in the nonupwelling Gulf of Chiriquí, which has been under constant study since 1970 (Figs. 7 and 8). Why? Because it has offered up so many answers to a long list of research questions. It also supports a high diversity of



Figure 7. Bird's eye view of the Uva Island study reef, Gulf of Chiriquí, Panamá during a midday low tidal exposure. February 8, 1989. (Photo C. M. Eakin)

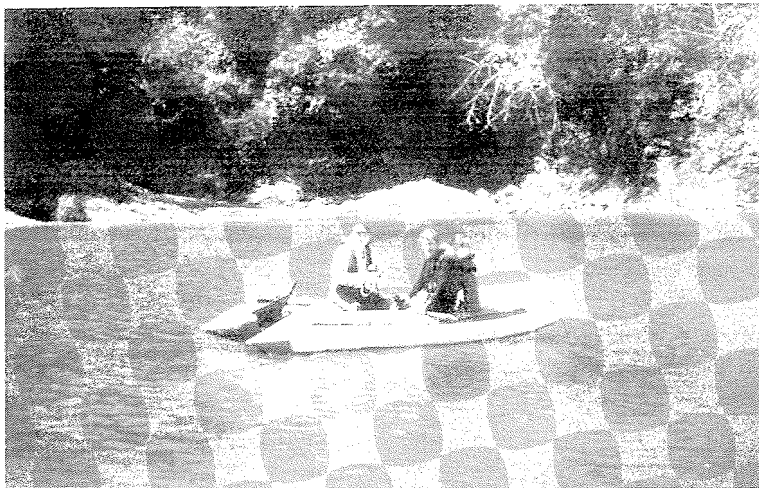


Figure 8. Peter W. Glynn and Ian G. Macintyre preparing for a dive at the Uva Island study reef. February 22, 1989.

reef-associated organisms and is located in a beautiful embayment of a heavily forested, uninhabited island with a waterfall spilling onto a pebble beach. Adding to the excitement of our studies, elasmobranch sightings were common at the Uva Island reef in the 1970s. These included mostly white-tip sharks, bull sharks, and numerous manta rays. As many as a half dozen manta rays could be seen wheeling along the reef front where they were grazing on zooplankton.

Occasionally they became an annoyance by swimming into our float lines that marked study sites and dragging them seaward beyond the reef. These graceful animals, and the sharks, are now rarely seen. I must relate a bizarre encounter with one of these mantas, a behavioral maneuver I have not heard repeated.

One morning I was deeply engaged in a task that required close attention to the bottom. Although it was a sunny day, the light from above would momentarily dim as if from a passing cloud. After two or three such incidents, I looked toward Aníbal, my diving partner. He motioned for me to look overhead. I had attracted a large manta, with a four-meter wing span, that was hovering above. I disengaged from my work and began

to watch the manta that was moving ever closer. It moved close enough for me to touch its mouth. It then began to press against me (I was wearing a black wet suit) and to envelop me with its wings, curling them around my body. When I observed a pair of claspers and realized that this was a male, perhaps in a precopulatory mode, I gently tapped it on the head with my dive knife. After a few additional taps, the manta moved back and slowly swam away.

Coral Population Abundances

With the discovery of new zooxanthellate coral records and new species in the eastern Pacific during the past few decades, generic and species diversity have increased from 5 to 10, and from 10 to 40+, respectively (compare Figs. 48 and 50 in Veron, 1995, with Table 1 in Glynn and Ault, 2000; Reyes Bonilla, in press). Some new records are instantly recognizable, such as the occurrence of hydrocorals or fire corals (*Millepora* spp.) in the Gulf of Chiriquí, Panamá. When I first observed these corals at the Uva Island reef in 1970 — and this was not difficult because they were everywhere — it was immediately obvious that they represented new species records because fire corals had not been previously reported from the eastern Pacific region. Upon further study, it was found that three species of *Millepora* were present on the Uva reef and elsewhere in the Gulf of Chiriquí. Two of these, *Millepora intricata* Milne Edwards and *Millepora platyphylla* Hemprich and Ehrenberg, are well known throughout the Indo-Pacific region. One of the fire corals proved to be a new species, first recognized by the late Prof. Dr. H. Boschma from specimens that I sent to him. All known colonies of this unnamed species bleached and died during the 1982-83 El Niño event. Realizing the importance of this mortality event, and not wanting the species to slip into oblivion — to become an anonymous or “centinelan extinction” (Wilson, 1992) — I invited Walentina (Wallie) H. de Weerd, one of Prof. Boschma’s disciples, to accompany me to Chiriquí to observe and collect additional dead colonies to describe the species. This we did (Weerd and Glynn, 1991), and the then presumed extinct new species became known as *Millepora boschmai* Weerd and Glynn. Since this disappearance of a reef-building coral species was the first ever — no other coral was known to have become extinct in recent times — it was reported in the journal *Science* (Glynn and Weerd, 1991). Five live colonies were rediscovered about a year later, on the north side of Uva Island (Glynn and Feingold, 1992). This site was subsequently christened Lazarus Cove by Mark Eakin. I was both elated to learn that *M. boschmai* was still alive and chagrined in having to retract the high profile claim of an extinction. The lesson learned: one must exercise extreme caution in announcing a species extinction in the marine environment, especially for a subtidal species capable of larval dispersal. Postscript: the five live colonies of *M. boschmai* again bleached and died during the 1997-98 El Niño-Southern Oscillation (ENSO) event. Thorough searches in Lazarus Cove and other likely habitats (as of March 2001) have failed to disclose any living colonies.

Extreme fluctuations in population abundances have been documented for several eastern Pacific zooxanthellate corals. The vulnerability of a high proportion of

the coral fauna can be appreciated from the following: (a) 15 of 41 species are known from only 1 or 2 localities; (b) many consist of small populations (< 100 colonies per site); and (c) 9 species have experienced recent local-to-regional scale extinctions (Glynn, 1997; Glynn and Ault, 2000). Some of my colleagues have grouched that it is difficult to follow the population status of particular species from my publications. This is true, and it is no less difficult for me in light of the rapidly changing abundances that are observed between censuses. Coral population structure at many localities is indeed dynamic.

Another enigmatic occurrence has involved the appearance, and sudden disappearance, of *Acropora valida* Dana at Gorgona Island, Colombia (Prahl and Mejía, 1985). The “curse of *Acropora*,” as it has become known, is a haunting malediction not soon to be forgotten. It started as a remarkable discovery and ended in terrible tragedies. Sightings of *Acropora* off western American shores had been rumored for many years, but never substantiated. Then on 8 September 1983, three colonies of *Acropora valida* were discovered by Angela Mejía, one of Henry von Prahl’s students, at Gorgona Island, Colombia. The publication of this discovery created quite a stir among the cadre of eastern Pacific cora-reef workers. Many questions concerning these corals were being asked and follow-up studies planned. Sadly, Angela suffered a severe motorcycle accident in 1988, which totally beclouded her memory of this remarkable find. Then in 1989, Henry von Prahl, the remaining link to the discovery, fatefully boarded an Avianca flight from Bogotá to Cali on which he and all others perished in a midair explosion, the pusillanimous act of a terrorist. *Acropora* colonies have not been found subsequently at Gorgona Island or anywhere else in the eastern Pacific. To this day, some superstitious-leaning workers are both hopeful and fearful of making such a discovery.

A final example of an extremely rare species is *Siderastrea glynni*, named in my honor by Ann (Nancy) Budd and Héctor Guzmán (Fig. 9). This species was found at Urabá Island in Panamá Bay, and the only known population consisted of just five colonies (Budd and Guzmán, 1994).



Figure 9. Live colony of *Siderastrea glynni*, about 11 cm in diameter, in an aquarium. March 16, 1993. (Photo C. M. Eakin)

Since the condition of these colonies began to deteriorate during the 1997-98 ENSO event, displaying bleaching and tissue loss, Héctor transported four of the remaining colonies to Naos Island. Here they are being cared for, and are showing signs of recovery, in aquaria of the Smithsonian Tropical Research Institute. Following the discovery of this species, extensive surveys in presumably suitable habitats have failed to reveal additional populations. What is the origin of this species? Are there

source populations elsewhere (locally or distant), perhaps in unexpected habitats? Are the five colonies survivors of a large population, now destined to extinction? This is a sample of the questions raised by this puzzling discovery.

Coral Growth

Once it was established that coral reefs were widespread in the eastern Pacific, the next task was to measure the growth rates of a variety of reef-building species to determine if these were comparable with coral growth elsewhere in the central and western Pacific where reefs are better developed. Pocilloporid corals, the chief reef builders, were found to have vertical skeletal extension rates of 3 to 6 cm yr⁻¹ (Glynn and Stewart, 1973; Glynn, 1977). During periods of moderate upwelling, coral growth was considerably less, around 1 to 2 cm yr⁻¹, and growth ceased altogether at temperatures of 18°C or lower. Massive corals typically grow more slowly than branching species, and the mean outward-growing skeletons of different massive species range from about 0.8 to 1.7 cm yr⁻¹ (Glynn and Wellington, 1983; Guzmán and Cortés, 1989). The general conclusion emerging from these studies is that eastern Pacific corals are capable of rapid growth and that their growth rates are approximately equivalent to those of similar or identical species in the central and western Pacific.

Feeding Relationships

As Birkeland (1977) noted in his study of coral recruitment in relation to competition with other benthic organisms — such as algae, sponges, bryozoans, barnacles, and tunicates — slow-growing corals do not compete well with other fast-growing taxa in nutrient-rich environments. Selective grazing by fishes and invertebrates, if sufficient, can tip this balance in favor of corals by removing potentially superior competitors that would otherwise overgrow the corals. Beyond Birkeland's early study in the Gulf of Panamá, no additional work has been carried out in the eastern Pacific on the quantitative relations between grazing pressure and coral recruitment.

Another aspect of feeding ecology relating to animals that feed on the living tissues of corals (corallivores) has received considerable attention, perhaps because of the unusual numbers of these consumers on eastern Pacific reefs. These range from micropredators, roughly equivalent to parasites, to macroconsumers that are capable of digesting all tissues from sizable coral colonies. The variety of corallivores that have been studied are species of gastropods, crustaceans, echinoderms, and fishes (Glynn, 1982a; Guzmán, 1988).

Acanthaster planci (Linnaeus), a large sea star that feeds almost exclusively on corals, occurs from the Gulf of California to Colombia (Malpelo Island) and Ecuador (northern Galápagos Islands). Usually, only single individuals are occasionally seen at the latter two localities, suggesting a transient existence in its southernmost range. Moderately large numbers (20 to 30 inds ha⁻¹) are sometimes observed on reefs in the Gulf of Chiriquí, but population outbreaks — on the scale observed at several central and western Pacific reefs (100s to 1000s inds ha⁻¹) — have not been reported in the eastern Pacific. A clue to how the numbers of this sea star might be controlled came from frequent sightings of particular shrimp and worms with *Acanthaster*. Careful observations revealed that the harlequin shrimp *Hymenocera picta* Dana and the amphinomid polychaete worm *Pherecardia striata* (Kinberg) were actually attacking



Figure 10. The harlequin shrimp, *Hymenocera picta*, attacking the crown-of-thorns sea star *Acanthaster planci* on the Uva Island reef, 3 m depth. Shown is one of a ♂/♀ male pair that was following the sea star for several days and removing its organs (hepatic caeca and gonads). December 19, 1982

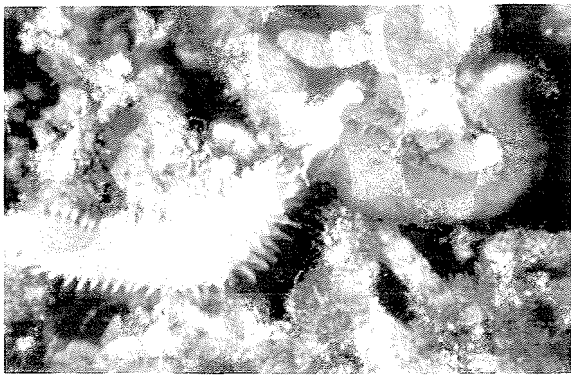
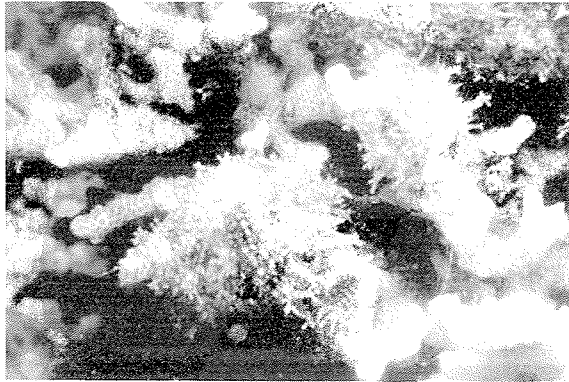


Figure 11. A scavenging polychaete worm (*Pherecardia striata*) feeding on the dismembered arm of a sea star, Uva Island reef, Panamá, 2 m depth. December 19, 1982

Acanthaster, in lilliputian style (Glynn, 1982b). The ~3-cm-long shrimp, usually a female-male pair bond, typically rides on the upper surface of ~30-cm-diameter sea stars (Fig. 10). I have spent hours to days following individual *Acanthaster* under attack by these shrimp. By means of their sharp chelae, the shrimp pick and tear at the sea star's body until breaking through to the organs within. They then remove and feed on hepatic caeca, gonads, and various other soft parts. Then enter the 5- to 10-cm-long worms (Fig. 11), which come streaming out of the porous reef — upwards of 200 to 400 inds m⁻² (Glynn, 1984a). The worms crawl into the sea star through the incisions made by the shrimp. The worms also consume the sea star's soft parts, reaching virtually all internal recesses. These attacks cause slow death, from a few to several days, but occur so frequently they would seem to exercise an important control on adult sea star numbers.

Other intriguing feeding relationships — involving ovulid gastropod and pufferfish corallivores, and crustacean guards and damselfishes

that repel corallivores and grazing fishes — have offered a rich source of material for documenting the intricacies of some of the biotic interactions affecting coral-community structure. The gastropod corallivore *Jenneria pustulata* (Lightfoot) can sometimes attain high local abundances where it can consume all of the tissues of large colonies of *Pocillopora* (Glynn, 1984b). *Jenneria* is truly a beautiful animal, and one cannot help but imagine that its polyp-like mantle extensions and black-encircled, orange shell pustules are not somehow involved in mimicking its coral prey (Fig. 12). A variety of fishes feed on *Jenneria*, at least when it can be detected. The tenacity with which crustacean guards (*Trapezia* spp. and *Alpheus lottini* Guérin) defend their coral hosts from *Acanthaster* attacks, and their repertoire of defensive strategies (Fig. 13), are nothing short of amazing (Glynn, 1983). The guards can even detect an approaching



Acanthaster by means of waterborne chemical cues and ready themselves for a defensive attack by scurrying along the outermost colony branches (Glynn, 1980). A variety of field observations

Figure 12. *Jemmeria pustulata*, an ovulid gastropod corallivore stripping the tissues from *Pocillopora damicornis* at night on a coral reef in the Secas Islands, Gulf of Chiriquí, Panamá, 5-m depth. July 19, 1981.

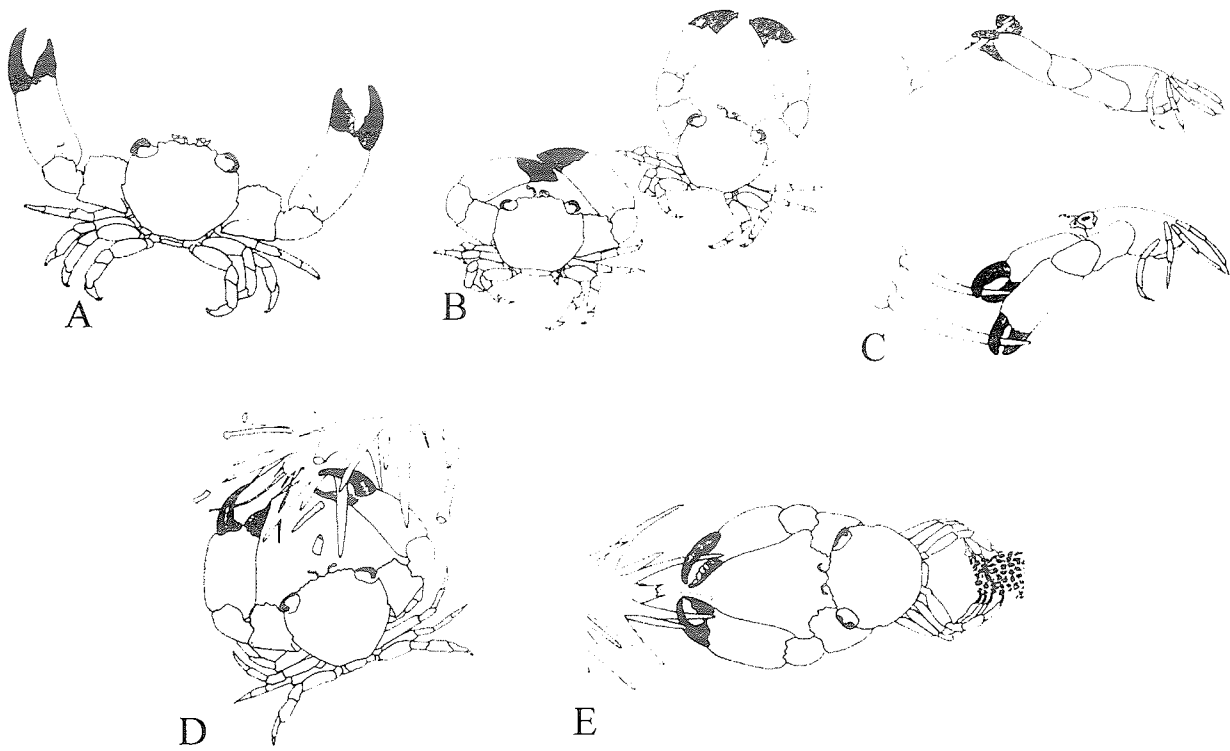


Figure 13. Defensive behaviors of a *Trapezia* crab guard directed toward the crown-of-thorns sea star. (A) startle display; (B) pushing; (C) up-down jerking of sea star; (D) pinching and clipping of sea star's spines and tube feet; (E) resisting retreat of sea star (modified after Glynn, 1983).



and experiments have been performed to document these behaviors (Fig. 14).

Figure 14. Peter W. Glynn investigating the responses of crustacean guards to a model Crown-of-Thorns sea star and the 'juices' of a living sea star, Uva Island study reef. January 14, 1980.

Bioerosion

In 1980, Ray Highsmith published an insightful paper relating bioerosion to areas of high nutrients and plankton primary productivity. This relationship was based primarily on a correlation of sites of varying productivity with the numbers of boring bivalves in coral skeletons. He ranked the eastern Pacific as the coral-reef region most severely affected by bioerosion. Basically, because most bioeroders prosper in high nutrient environments with high concentrations of plankton, their growth and abundance overwhelm corals that generally do well in less productive settings. Several studies have substantiated this pattern and have quantified the high rates of reef erosion, not only by internal bioeroders (e.g., cyanobacteria, sponges, worms, and bivalves), but also by external bioeroders (e.g., crustaceans, mollusks, echinoderms, and fishes). Bioerosion accelerates in dead corals, rapidly weakening and reducing the size and integrity of limestone skeletons. This sort of damage often leads to frustration when attempting to secure a complete core from an old coral colony (see below, Coral and Reef Growth History). The bases of such colonies, with the earliest (and oldest) growth records, are often riddled with bioeroders or are completely missing.

Galápagos Islands coral reefs that suffered 95 to 99% mortality during the 1982-83 El Niño warming event were attacked continually by large numbers of the blunt-spined sea urchin *Eucidaris galapagensis* Döderlein. This sea urchin feeds on algae that colonize the dead coral skeletons and, in the process, its sharp-cutting teeth erode the dead coral surfaces. It was disheartening to witness the relentless breakdown and disappearance of the Galápagos reefs in less than 20 years following the El Niño disturbance (Glynn, 1994; Reaka-Kudla et al., 1996). Erosion of the Uva Island reef in Panamá following coral mortality in 1982-83 was not so dramatic as in the Galápagos, but nonetheless substantial, particularly in certain reef zones (Eakin, 1996). In Panamá, the most influential surface bioeroder is *Diadema mexicanum* A. Agassiz, the black-spined sea urchin. Reef-base zones with low abundances of damselfish are especially susceptible to sea urchin erosion, whose numbers commonly exceeded 50 inds m⁻². Damselfishes cultivate algal lawns and remove sea urchin competitors from their territories, thereby protecting portions of the reef frame (Eakin, 1987, 1988; Glynn, 1988). Eakin's (1996) CaCO₃ budget for the 2.5 ha Uva reef revealed an average net erosion rate of 4,800 kg yr⁻¹ in the mid-1990s, compared with a net deposition of 8,600 kg yr⁻¹ prior to the 1982-83 El Niño event. An updated model suggests the Uva reef is still in an erosional mode, but that extreme La Niña-related low-tidal coral mortalities in 1989 and 1993 had a greater influence on reef erosion than coral mortalities resulting from the 1997-98 ENSO bleaching event (Eakin, 2001).

Thus, Highsmith's (1980) contention that rates of bioerosion are elevated in high nutrient/primary productivity environments is still valid, but these rates are accelerated during periods of high coral mortality resulting from a variety of disturbances such as El Niño warming and low sea-level stands.

Coral Reproduction

Many hundreds, if not thousands, of human hours have been devoted to the study of coral reproduction by my research team. The first in-depth study by Bob Richmond (1985) failed to detect planulation in colonies of *Pocillopora damicornis* monitored weekly in Panamá for nearly a year. Central and western Pacific populations of this species are highly fecund, releasing larvae monthly throughout the year. Because of the apparent absence of spawning (planulae or gametes) in eastern Pacific *P. damicornis*, Bob concluded that these populations were essentially asexual and had evolved life-history characteristics favoring clonality. Bob further argued that these isolated “sterile” populations would occasionally receive sexual larval recruits by long-distance dispersal, especially during El Niño years when west-to-east flowing currents increase in volume and rate (Richmond, 1990).

Continuing studies in Costa Rica, Panamá, and the Galápagos Islands have revealed high levels of gamete production in *P. damicornis* and all other reef-building coral species studied to date (Glynn et al., 1991, 1994, 1996, 2000). Only *Porites panamensis* releases planula larvae, with most, and perhaps all, of the remaining zooxanthellate species spawning gametes. While *P. damicornis* is highly fecund, producing large numbers of mature eggs and sperm at these locations, we have never observed this species spawning. As of this writing, only three eastern Pacific species have been observed spawning gametes, namely, *Pavona gigantea*, *Pavona varians*, and *Pavona* sp. a. The latter species, closely related to *P. varians*, is presently being named (Glynn et al., 2001). Histological studies of several other species have revealed mature gametes in abundance, but no sign of planula larvae. Late one sunny afternoon in the Galápagos Islands, near full moon during a peak high tide, several colonies of *P. gigantea* were observed shedding clouds of eggs and sperm. Upon revisiting this population in the following and subsequent years, under virtually identical conditions, no additional spawning was observed.

Over the years, we have scheduled diving teams to watch for spawning on the Uva Island coral reef at all times of the day and night, performing late-night and early-morning observations. Meal times have been partly to blame for not detecting spawning sooner in two coral species. After a full day of diving-related work, none of us was interested in coaxing the ship’s cook to schedule dinner later than about 1800, at sunset or a little later. Also, if a night dive was planned, it was better to eat early to allow time for one’s stomach to settle. As it turned out, we continually missed the spawning of *Pavona* sp. a, which occurred shortly after sunset, at peak high tide a few days following the full moon. Then we were chagrined to learn that breakfast had interfered with observing spawning in *Pavona varians*, again near peak high tide a few days following full moon, but just before sunrise. It turns out that this 12-hour spawning separation prevents these sibling species from hybridizing. This difference in the timing of spawning serves as a clear-cut trait to help distinguish between these closely related species.

While these studies are contributing to our base of knowledge, there is still a plethora of unanswered questions associated with the reproductive biology of corals.

For example, more information is needed concerning spawning behavior and its relationship with water-column microscale mixing processes, lunar periodicity, the seasonality of spawning, fecundity, and the length of larval lives and their dispersal capabilities. Virtually nothing is known of the reproductive biology of eastern Pacific hydrocorals (*Millepora* spp.), the most sensitive of all reef-building species to ENSO warming disturbances. A big mystery is the discrepancy between the high level of sexual activity in many species and their typically low recruitment success. What is occurring between the time of mature gamete production and recruitment? Our histological studies show no gamete resorption. It is therefore reasonable to assume that spawning most likely occurs? Is mortality high in the water column before settlement, or are early benthic stages being killed before recruitment? The answers to these questions are crucial for an understanding of coral-community development and the capacity for recovery following various sorts of disturbances.

Disturbances

Cool currents and local upwellings, long believed to be the leading limiting factors affecting coral growth, are now recognized to be but two of numerous conditions that can influence eastern Pacific reef development. The two major temperate current systems that limit the northern and southern migration of reef-building corals are the California Current off the west coast of Baja California and the Peru Coastal Current near the Peru-Ecuadorean border, respectively. As has been amply demonstrated, however, the three major upwelling centers — the Gulfs of Tehuantepec, Papagayo, and Panamá — do support abundant coral populations and reef development.

Since ENSO disturbances, including primary and secondary effects, were not recognized until the dislocations documented during and following the 1982-83 ENSO, the realization of the multifarious effects of this natural perturbation could be regarded as the most important revelation of the twentieth century concerning impacts to coral reefs. Mechanically induced mortalities of corals and reef associates by storms and increased wave assault are more likely during ENSO activity (Robinson, 1985; Lirman et al., 2001). The immediate effects of El Niño warming (i.e., the loss of zooxanthellae leading to coral bleaching and mortality) may be followed by several longer-term secondary effects such as: (a) increased emigration and mortality of obligate coral crustacean symbionts (Glynn et al., 1985); (b) the disruption of live-coral barriers that prevent *Acanthaster* from entering and feeding on patches of preferred prey (Glynn, 1985); (c) predator concentration on surviving corals (Glynn, 1990; Guzmán and Cortés, 1992); (d) interference with coral reproduction and reduced recruitment (Glynn et al., 2000); and (e) the invasion of dead coral patches by echinoids and damselfishes that interfere with coral regeneration and perhaps larval settlement (Wellington, 1982; Glynn, 1990). Other effects that can interfere with corals are related to La Niña or the ENSO cool phase, such as (a) dinoflagellate blooms (Guzmán et al., 1990); (b) extreme low tidal exposures (Eakin et al., 1989; 2001); (c) stressful upwelling events (Glynn and D'Croz, 1990); and (d) the proliferation of macroalgae that compete with, and sometimes overgrow, corals (Glynn and Maté, 1997).

Another type of seriously degrading impact to coral reefs worldwide — i.e., sedimentation and eutrophication — is increasingly observed in the eastern Pacific. This is especially true at low-latitude coastal areas with high rainfall. Rampant clear-cutting, with little or no concern for land management, has transformed verdant forests and mangrove shores to croplands, pasturage, aquaculture ponds, and urban sprawl. Two of my former students, Jorge Cortés and Bernardo Vargas Ángel, have documented this kind of damage to coral reefs in Costa Rica and Colombia, respectively. Several reef scientists attending the Eighth International Coral Reef Symposium in Panamá in 1996 were reminded of how a damaged watershed can have far-reaching effects on coral reefs. Rainfall was excessive a few weeks before a post-symposium field trip to coral reefs in the Gulf of Chiriquí, an outing I helped arrange to showcase our study reefs to a cadre of international reef researchers. Unfortunately, a period of heavy rainfall before the excursion caused extensive soil erosion and river runoff with silt-laden plumes extending over most of the continental shelf. Our field trip was literally a washout with water visibility often ranging between only 30 to 100 cm.

Sadly, poor land use in coastal areas has greatly diminished three high-diversity ecosystems: lowland rainforests, mangrove shores, and coral reefs. It is becoming increasingly difficult to swim over pristine coral reefs and to hear howler monkeys and squawking parrots in the adjacent forest. Some additional disturbances to coral reefs and environmental concerns, mainly related to human activities, are addressed below (see, *The Future of Eastern Pacific Coral Reefs*).

Zooxanthellae Diversity

Molecular genetic studies have revealed that scleractinian corals harbor a diversity of algal symbiont taxa (Rowan and Powers, 1991; Rowan and Knowlton, 1995; Baker and Rowan, 1997; Rowan, 1998; Baker, 1999). Some intriguing patterns of bleaching resistance in relation to symbiont distribution in scleractinian corals have been recently documented. For example, in Caribbean *Montastraea*, much of the intraspecific variation in response to a natural bleaching event in 1995 was explained by the distribution of symbiont taxa (Rowan et al., 1997). Additionally, one of four symbiont taxa identified in Panamanian *Pocillopora* spp., a member of *Symbiodinium* clade *D*, was especially resistant to bleaching caused by elevated temperature and high irradiance stress during the 1997-98 El Niño warming event (Baker, 1999; Glynn et al., 2001). In contrast, the hydrocoral *Millepora intricata* is often the first to bleach during periods of high-temperature stress, and suffers high rates of mortality. In Panamá, *Millepora* hosts unusual symbionts (*Symbiodinium* clade *A*), which have not to date been documented in scleractinian corals from the far eastern Pacific (*Symbiodinium* clade *A*), an observation that is intriguing in the context of its bleaching susceptibility (Baker, 1999).

Some workers have suggested that bleaching may provide corals with a mechanism for the removal of sensitive symbionts and replacement by more resistant alternatives (Rowan and Powers, 1991; Buddemeier and Fautin, 1993). This stress response — termed the “adaptive bleaching hypothesis” — remains controversial, partly

for want of direct empirical investigation (but see Baker, 2001). Certainly, some colonies with resistant symbionts fared better during the 1997-98 El Niño than colonies without. However, it is not clear whether bleached corals that contained susceptible symbionts, but still managed to survive, have shown any change in their symbiont communities since recovering from the bleaching event.

Coral Population Modeling

With the availability of long-term data on various aspects of a coral population (namely, growth, recruitment, predation, El Niño-related mortality, and recovery), Peggy Fong and I have developed a dynamic simulation model of the abundance and size structure of *Gardineroseris planulata* on the Uva Island coral reef (Fong and Glynn, 1998). Results of this initial simulation effort demonstrated that predation by *Acanthaster planci* was of overwhelming importance to coral population structure on the Uva reef due to both stronger effects of predation (larger transitions) and the frequency of predation (yearly) compared with ENSO (episodically) disturbances. This model was modified for use at the regional scale to incorporate diverse environmental settings of temperature and predation in nonupwelling and upwelling areas of Panamá and the Galápagos Islands (Fong and Glynn, 2000). Results of the regional model suggest that ENSO impacts can be accurately predicted by the rate of temperature change in an area during an ENSO event. Validation of model predictions in upwelling and nonupwelling environments during the 1997-98 El Niño event is encouraging and signals an understanding of the critical processes that regulate coral population structure (Fong and Glynn, 2001). As we continue to gain confidence in this effort, we plan to expand the modeling to include multiple coral species populations and other aspects, such as nutrient availability, algal/coral competition, and herbivore grazing effects.

One problem inherent in studies of coral-reef ecology is that most reefs have been studied over relatively short ecological time scales (Jackson, 1997), while many processes controlling coral population and community dynamics occur over much longer periods. Simulation modeling is one tool that can be used to synthesize knowledge of processes investigated on ecological time scales in order to develop predictions on a longer time scale (Ebenhöh, 1994; Jørgensen, 1994). The effects of ENSO events in the tropical eastern Pacific have been studied over a relatively long time (~30 years) compared with ecological studies in many other reef systems (Connell, 1997). These data provide a unique opportunity to develop simulation models that can be used to predict the condition of coral populations, communities, and ecosystems in the future.

CORAL AND REEF GROWTH HISTORY

Since many of the newly found eastern Pacific reefs were well developed, some exhibiting vertical thicknesses of several meters, we began to wonder how old they might be. We started to investigate this question by core drilling, using the same

underwater hydraulic drill, assembled by Ian Macintyre, that worked so effectively on Caribbean coral reefs. However, due to the large number of cavities and fragile structure of pocilloporid reefs, which are the main reef types present in Panamá, we found that the drill usually fell rapidly through the coral framework without retaining sufficient material for study. Occasionally we encountered a massive coral species near the reef basement, which could be dated to reveal the age of one small section of the reef. These preliminary efforts disclosed maximum reef ages of 4,500 to 5,600 years BP and vertical framework thicknesses of 10 to 13 m (Glynn and Macintyre, 1977). Jorge Cortés, my first doctoral student, core-drilled a poritid reef in Costa Rica (Cortés et al., 1994), which also revealed a comparable age (4,000-5,500 years) and vertical buildup (4-10 m). These measurements compared reasonably well with the ages, vertical buildups and rates of CaCO_3 production in other coral-reef regions (see Table 24 in Glynn and Wellington, 1983).

In order to develop a sense of the extent of pocilloporid reef development under different environmental settings and over larger areas, we began to probe these reefs with iron pipes, an idea suggested by Ian Macintyre. We utilized sections of black iron pipe of high carbon content, fitted with stainless steel bits. These were driven into reefs with a sledge hammer, and by rotating the drill string with clamps outfitted with handles. This probing was generally timed to take advantage of low tides, so that some of the work could be completed on drying reef flats or in waist-deep water. Aníbal Velarde, my steadfast assistant at STRI, did much to advance this work. On one occasion, by brandishing a pipe and sledge hammer, he averted an imminent mugging while we were probing a reef on Pedro Gonzalez Island, Pearl Islands. Our pipe sections and probing tools thus served not only the drilling work, but protection from hooligans as well.

After acquiring a sense of the time over which reef growth has occurred, and the rate of limestone accretion, it became of interest to gain some knowledge of the relationship between reef-growth history and the environmental setting of particular eastern tropical Pacific sites. An approach that would allow the investigation of this subject was the discipline of sclerochronology, which had its beginnings in a pioneering study by John Wells (1963). Work on this topic in the eastern Pacific was initiated mainly by my colleagues and me in Panamá, Costa Rica, and the Galápagos Islands. We began by core-drilling and dissecting the aragonitic skeletons of massive corals, many ranging in age from about 100 to 365+ years (Fig. 15). By determining the chronology of interannual growth records and skeletal hiatuses, it has been possible to identify periods of accelerated, retarded, and interrupted coral growth. Armed with the necessary analytical tools to measure certain chemical tracers incorporated into the lattice structure of aragonitic skeletons (e.g., O and C isotopes, trace metals such as Mn and Cd, and fulvic and humic acids), my co-workers have been able to relate periods of coral growth with environmental change. For example, analysis of oxygen isotopic fractionation has allowed the identification of past ENSO events (Carriquiry et al., 1988; Druffel et al., 1990; Wellington and Dunbar, 1995). Additionally, stable oxygen isotopic

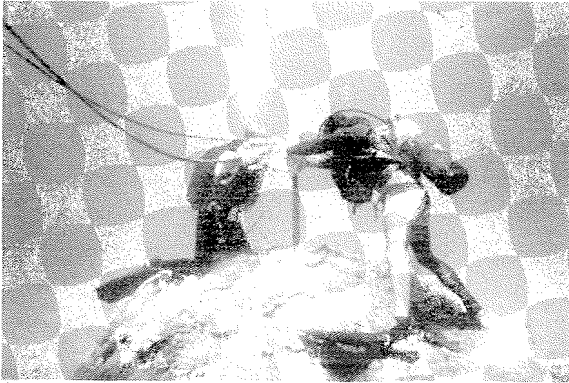


Figure 15. Core drilling a large colony of *Porites lobata*, Secas Islands, Gulf of Chiriquí, Panamá. Left to right: Peter W. Glynn and Anibal Velarde. July 23, 1984.

convergence zone (Linsley et al., 1994). While such paleoclimate studies help advance our understanding of the environmental bounds of reef growth, the extent of these investigations in the eastern Pacific is confined by a generally poor fossil record and high rates of bioerosion following coral death.

Another approach that can reveal information on the developmental history of coral communities involves a detailed examination of reef sediments. We have obtained sediments from the Uva reef by air lifting and from push cores (Fig. 16). One must

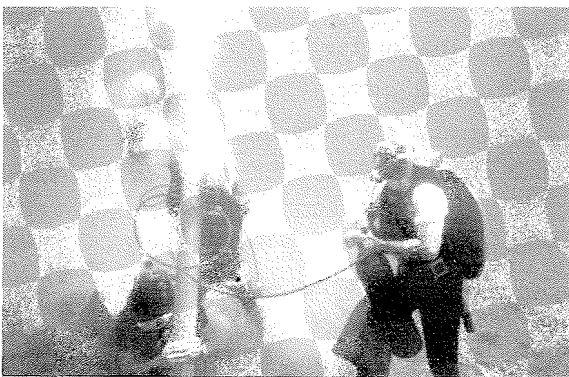


Figure 16. Air-lifting sediments at the Uva Island study reef, Gulf of Chiriquí, Panamá. Left to right: Peter W. Glynn, Anibal Velarde, and Aaron Yedid. July 18, 1984.

exercise caution that the reef sites selected for study have not been subject to violent storms or burrowing organisms, both factors that could disrupt the sequence of sedimentary strata. The C-14 dating of carbonate sediments from the Uva reef have not shown any time reversals, suggesting minimal mixing of shallow and deep sediment layers. Sediments obtained from 2.5 m depth ranged from 1,645±300 to 3,830±300 years in age. The *Acanthaster* skeletal remains throughout the sedimentary strata are equal in abundance to the sea star remains found in surface sediments. This suggests the presence of low-to-moderate *Acanthaster* abundances (15-30 inds) on the Uva reef during the past ~4,000 years.

signatures in a 365+-year-old Galápagos coral have permitted detection of the Little Ice Age, revealing low sea temperatures during the early 1600s and early 1800s (Dunbar et al., 1994). Further, specific geochemical indicators can also provide information on variations in salinity, rainfall, river outflow (Dunbar et al., 1994; Linsley et al., 1994), upwelling and nutrient availability (Shen and Sanford, 1990; Shen et al., 1992), the timing of volcanic eruptions (Shen et al., 1991), and shifts in the position of the intertropical

convergence zone (Linsley et al., 1994). While such paleoclimate studies help advance our understanding of the environmental bounds of reef growth, the extent of these investigations in the eastern Pacific is confined by a generally poor fossil record and high rates of bioerosion following coral death.

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ENTER EL NIÑO

After accepting a position at the Rosenstiel School of Marine and Atmospheric Science (University of Miami), I arranged a research cruise to revisit study sites in the Gulf of Chiriquí in March 1983. In anticipation of moving to Florida, I began making plans to return to coral reef studies in the western Atlantic. Therefore, before leaving Panamá I thought it would be appropriate to sample, perhaps for the last time, some Pacific reef sites that had been under continuous study since the early 1970s. Much to my astonishment, the Uva Island coral reef appeared to have been brushed by a snowfall. All corals were bleached bone white. Surveys on other coral reefs in Panamá, including both nonupwelling and upwelling environments, revealed the same severe bleaching effects. Corals began dying and by the end of the disturbance event, just a few weeks later, overall mortality in Panamá amounted to 75 to 85% of the total live cover. Several of my colleagues in Costa Rica, Colombia, and the Galápagos Islands were notified of this mass bleaching event and asked if anything similar had been observed in their study areas. It was soon realized that this coral bleaching and mortality disturbance was regional in scale, occurring throughout the eastern equatorial Pacific. Coral mortality was greatest in the Galápagos Islands, with 95 to 97% overall mortality.

Initially I was uncertain about the cause(s) of this unprecedented bleaching event. Before learning of its widespread extent, I thought it might have been a result of human pollution, possibly by pesticides. In the summer of 1983, while coral bleaching and mortality were still in progress, I was scheduled to participate in the Coral Reef Population Biology course offered by the Hawaii Institute of Marine Biology. Armed with underwater photographs of the bleaching event and observations of the immediate responses of corals and other reef associates, I presented this information to the summer class. During the lively discussion that followed, Paul L. Jokiel asked if we had considered elevated sea temperatures as a possible causative agent of bleaching. Since the disturbance was taking place during the 1982-83 El Niño event, which was accompanied by high sea-temperature anomalies, this seemed like a reasonable lead to investigate. An analysis of the timing, spatial extent, and rate of increase of sea-surface temperature anomalies showed a remarkably close correspondence with the patterns and severity of coral mortality (Glynn, 1984c; Glynn et al., 1988). These findings prompted an experimental study by Luis D'Croz and me, designed to assess the effects of slightly elevated water temperature on coral vitality and survivorship. It was found that controlled temperatures, mimicking the warming and duration that occurred during the El Niño event, also promoted coral bleaching and death, thus validating the field observations (Glynn and D'Croz, 1990). For this publication, Luis and I received the Best Paper Award for volume 8 (1990) of the journal *Coral Reefs*.

Large-scale bleaching and mortality can have important effects at the ecosystem level. Since coral reefs are built dominantly by zooxanthellate corals (calcareous algae play a minor role on most eastern Pacific reefs), and the high biotic diversity of reefs is largely a result of the shelter and trophic resources they offer, the reduction in abundance of these foundation species can have notable cascading effects. Of the

several secondary disturbances that followed the high coral mortality in 1982-83, the continued bioerosion of dead corals was perhaps the most serious. Sea urchins and fishes grazing on the algal cover of dead corals and internal bioeroders, such as sponges and bivalves, converted dead reef surfaces to sediment. This led to the complete elimination of reef structures in the Galápagos Islands (Glynn, 1994; Reaka-Kudla et al., 1996) and to the destruction of large sections of reefs along coastal Ecuador (Glynn, in press), in Panamá (Eakin, 1996), and at Cocos Island, Costa Rica (Guzmán and Cortés, 1992). Long-term secondary effects such as bioerosion, loss of firm surfaces for coral settlement, corallivores, and phase shifts to algal-dominated communities were considered earlier in more detail (see Disturbances).

Since the first documented coral-bleaching event of 1982-83, several others associated with ENSO warming have been reported with varying effects at other localities in the eastern Pacific in 1986-87, 1991-92, 1995, and, most recently, in 1997-98. It is plausible that repeated El Niño disturbances during the recent geologic past have limited coral community diversity and the development and persistence of significant reef structures in the eastern Pacific (Glynn and Colgan, 1992). Of greater concern is the possibility that eastern Pacific warming disturbances are a harbinger of change toward a greenhouse world that could affect coral reefs globally.

While nominees are never privy to the discussions that decide awards, I suspect that my research into the causes and consequences of widespread El Niño-induced coral disturbances played a pivotal role in receiving the Charles Darwin Medal in 1992, the most prestigious honor bestowed by the International Society for Reef Studies.

THE FUTURE OF EASTERN PACIFIC CORAL REEFS

Until the ENSO impacts of the last two decades, it was generally held that eastern Pacific coral reefs were threatened mostly by anthropogenic activities against a background of localized natural disturbances. Diverse human-related disturbances have been associated with declines in coral abundance and the degradation of whole reefs. As noted earlier, deforestation and soil erosion were perhaps responsible for the greatest damage to reefs in Costa Rica, Colombia, and Panamá. Other types of damage in México, mainland Ecuador, the Galápagos Islands, and the aforementioned countries have resulted from coastal construction projects, destructive fishing, the collection of corals for sale as curios, boat groundings, anchor damage, and the release of contaminants (such as oil, detergents, and pesticides) in reef areas. Adverse natural disturbances, as noted earlier, include ENSO warming events, low tidal exposures, tectonic events (resulting in coastal uplift and landslides), hurricanes, and a variety of biotic effects such as bioerosion and predation. I have personally observed the negative effects of the majority of these various sources of disturbance, with increasing frequency in recent years.

Coral bleaching and mortality resulting from ENSO-related elevated temperatures appear to be greater on offshore than on nearshore coral reefs in the equatorial eastern Pacific (Macintyre et al., 1992; Glynn et al., 2001). If this pattern is

substantiated by continuing studies, it will be even more urgent that nearshore coral assemblages be protected from human disturbances, which are more likely near mainland population centers. Such inshore areas could serve as refugia for some species that might suffer higher mortalities in more offshore settings. With 22 existing and 6 proposed marine-protected areas with coral assemblages and/or coral reefs in the eastern tropical Pacific (the majority of these are located in nearshore environments), several Latin American governments now recognize the importance of conserving natural resources and safeguarding high-diversity coastal ecosystems (Glynn, 2001).

Some incidences of human-induced damage have resulted from ill-advised good intentions. One such example occurred on a popular snorkeling reef at Huatulco, México. Since dive boats frequently visited this reef and indiscriminantly dropped anchors on live corals, an effort was made to position mooring lines along the reef edge to prevent anchor damage. Unfortunately, the placement of concrete blocks for fastening the mooring lines was not properly supervised and these were dropped directly onto the living coral framework, causing extensive localized damage.

Every now and again during my tenure at STRI (Panamá), the monstrous proposal of constructing a sea-level canal would raise its ugly head. This usually occurred during drought years when freshwater supplies became low, thus threatening the operation of the Panama Canal locks. Unless properly barriered, a sea-level canal would allow the movement of marine organisms, including predators, toxic species, parasites, and pathogens, from one ocean to the other. Since the two tropical seas have been separated for over 3 to 3.5 million years, allowing for substantial evolutionary divergence, the sudden rejoining of biotas would likely result in unpredictable biotic impacts. In light of the many environmental and economic problems that followed in the wake of previous large-scale ecological changes, such as construction of the Aswan Dam and the Suez and Welland Canals, the U.S. National Academy of Sciences Committee on the Ecology of the Interoceanic Canal considered an unrestricted breaching of the Panamic Isthmus by a sea-level canal totally unacceptable (Newman, 1972). It will be necessary to revive this important recommendation in the face of future threats.

Even if effective biotic barriers are in place, there are other ways that accidental or intentional introductions can occur, and all of these should be guarded against with vigilance. For example, exotic species can be introduced accidentally via ship's ballast water or from fouling communities, and in association with species intended for aquaculture or stock enhancement. Unfortunately, deliberate introductions have been made by some tropical aquarium enthusiasts who have released live, nonnative species into both Caribbean and Pacific reef waters. And even the scientific community is not exempt from such poor judgment. I won't mention names, but one of my colleagues once purposely introduced Indo-Pacific coral and molluscan reef species onto a Caribbean reef and another colleague suggested that it would be interesting to release the predatory sea star *Acanthaster* onto Caribbean reefs to observe its feeding behavior. In the first instance, all (hopefully all) of the introduced species were later found and removed by concerned reef workers. In the second example, my forceful objections prevailed and the crown-of-thorns sea star still remains an Indo-Pacific species, and a significant pest problem.

In recent years, examples of successful coral-reef management programs have been realized. Often a critical ingredient of this success is the involvement of local public support, which implies an understanding of conservation principles. An educational program designed to convey the benefits of coral reefs and how best to protect them is an important initial step in this effort. It is my hope that, by instructing and mentoring undergraduate and graduate students from various countries bordering the eastern tropical Pacific (Colombia, Costa Rica, Ecuador, México, Nicaragua, Panamá), I have made some contribution toward this end. In actuality, I am proud to announce that some of my former students are now engaged in coral-reef conservation and management in their home countries. In the pedagogical arena, there is no greater feeling of accomplishment than to know that one has influenced students to enter one's own discipline and, in my case, to see those students excel and become internationally recognized in coral-reef biological studies (Fig. 17).

How to end this essay? Let me propose one of my favorite quotations on the purpose of life, Preston Cloud's salubrious ethic, "to live it with as much grace and integrity as possible, to enjoy and improve it while you have it, and to leave the world no worse for your having been there." (Cloud, 1988). I believe that Preston Cloud left the world a little better off, and if each of us could make some contribution toward preserving coral reefs, then our brief stay on the Blue Planet would have been worthwhile.



Figure 17. Peter W. Glynn surrounded by a cadre of coral-reef colleagues, including former and present-day RSMAS, MBF (Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, University of Miami) students, who attended the Ninth International Coral Reef Symposium in Bali, Indonesia (23-27 October 2000). Top row (left to right): Iliana Baums (MBF Ph.D. student), Joshua Feingold (Ph.D., 1995, MBF, present address: Nova Southeastern University Oceanographic Center), Patrick Gibson (marine science undergraduate student, University of Miami), Nohra Galvis (M.A., 1992, MBF; Corporación Propuesta Ambiental, Bogotá, Colombia), P. W. G. (MBF faculty), Susan Colley (MBF Research Associate), Juan L. Maté (Ph.D., 2001, MBF, present address: Smithsonian Tropical Research Institute, Panamá), Jorge Cortés (Ph.D., 1990, MBF; Centro de Investigación en Ciencias del Mar y Limnología, University of Costa Rica), David O. Obura (Ph.D., 1995, MBF; Coral Reef Degradation in the Indian Ocean, Mombasa, Kenya), Héctor Reyes Bonilla (MBF Ph.D. student, Universidad Autónoma de Baja California Sur, La Paz, México). Bottom row: C. Mark Eakin (Ph.D., 1991, MBF; NOAA/National Geophysical Data Center, Boulder, Colorado), Christiane Hueerkamp (MBF intern, 1999-2000; Center for Tropical Marine Ecology, Bremen, Germany), Peggy Fong (RSMAS Fellow, 1992-94; University of California, Los Angeles), Andrew Baker (Ph.D., 1999, MBF; Wildlife Conservation Society, New York), Héctor Guzmán (MBF associate, 1984-present; Smithsonian Tropical Research Institute, Panamá), and Fernando Rivera (MBF associate, 1984-present, Ph.D. student, University of Melbourne, Australia).

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REFERENCES

- Allison, E. C.
1959. Distribution of *Conus* on Clipperton Island. *Veliger* 1:32-34.
- Baker, A. C.
1999. The symbiosis ecology of reef-building corals. Ph.D. dissertation, University of Miami, Coral Gables, 120 p.
- Baker, A. C.
2001. Reef corals bleach to survive change. *Nature* 411:765-766.
- Baker, A. C., and R. Rowan
1997. Diversity of symbiotic dinoflagellates (zooxanthellae) in scleractinian corals of the Caribbean and eastern Pacific. *Proceedings of the Eighth International Coral Reef Symposium*, Panamá 2:1301-1306.
- Bates, M., and D. P. Abbott
1958. Coral island: portrait of an atoll. Charles Scribner's Sons, New York, 254 pp.
- Birkeland, C.
1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the Third International Coral Reef Symposium*, Miami 1:15-21.
- Budd, A. F., and H. M. Guzmán
1994. *Siderastrea glynni*, a new species of scleractinian coral (Cnidaria: Anthozoa) from the eastern Pacific. *Proceedings of the Biological Society of Washington* 107:591-599.
- Buddemeier, R. W., and D. G. Fautin
1993. Coral bleaching as an adaptive mechanism. *BioScience* 43:320-326.
- Carriquiry, J. D., and H. Reyes Bonilla
1997. Community structure and geographic distribution of the coral reefs of Nayarit, Mexican Pacific. *Ciencias Marinas* 23:227-248.
- Carriquiry, J. D., M. J. Risk, and H. P. Schwarcz
1988. Timing and temperature record from stable isotopes of the 1982-1983 El Niño warming event in eastern Pacific corals. *Palaios* 3:359-364.
- Castro, P.
1982. Notes on symbiotic decapod crustaceans from Gorgona Island, Colombia, with a preliminary revision of the eastern Pacific species of *Trapezia* (Brachyura, Xanthidae) symbionts of scleractinian corals. *Anales del Instituto de Investigaciones Marinas de Punta de Betin* 12:9-17.

- Cloud, P. E.
1952. Preliminary report on geology and marine environments of Onotoa Atoll, Gilbert Islands. *Atoll Research Bulletin* 12:1-73.
- Cloud, P. E.
1988. Oasis in space: earth history from the beginning. W. W. Norton & Company, New York and London, 508 pp.
- Connell, J. H.
1997. Disturbance and recovery of coral assemblages. *Proceedings of the Eighth International Coral Reef Symposium*, Panamá 1:9-22.
- Cortés, J.
1997. Biology and geology of eastern Pacific coral reefs. *Proceedings of the Eighth International Coral Reef Symposium*, Panamá 1:57-63.
- Cortés, J., I. G. Macintyre, and P. W. Glynn
1994. Holocene growth history of an eastern Pacific fringing reef, Punta Islotes, Costa Rica. *Coral Reefs* 13:1-9.
- Crossland, C.
1927. Marine ecology and coral formations in the Panamá region, the Galápagos and Marquesas Islands, and the Atoll of Napuka. *Transactions of the Royal Society of Edinburgh* 55:531-554.
- Dana, J. D.
1843. On the temperature limiting the distribution of corals. *American Journal of Science & Arts* 45:130-131.
- Dana, J. D.
1890. Corals and coral islands. 3rd. ed., Dodd, Mead & Co., New York, 440 pp.
- Dana, T. F.
1975. Development of contemporary eastern Pacific coral reefs. *Marine Biology* (Berlin) 33:355-374.
- Darwin, C. R.
1842. The structure and distribution of coral reefs. London: Smith, Elder & Co., 214 pp.
- Druffel, E. R. M., R. B. Dunbar, G. M. Wellington, and S. A. Minnis
1990. Reef-building corals and identification of ENSO warming episodes. Pages 233-253 in P. W. Glynn (ed). Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier Oceanography Series 52, Amsterdam.
- Dunbar, R. B., G. M. Wellington, M. W. Colgan, and P. W. Glynn
1994. Eastern Pacific sea surface temperature since 1600 A.D.: the $\delta^{18}\text{O}$ record of climate variability in Galápagos corals. *Paleoceanography* 9:291-315.
- Durham, J. W.
1947. Corals from the Gulf of California and the North Pacific Coast of America. *Geological Society of America*, Mem. 20, p. 1-68.
- Durham, J. W.
1966. Coelenterates, especially stony corals, from the Galápagos and Cocos Islands. Pages 123-135 in R. I. Bowman (ed). The Galápagos: proceedings of the symposia of the Galápagos International Scientific Project. University of California Press, Berkeley and Los Angeles.

- Eakin, C. M.
1987. Damselfishes and their algal lawns: a case of plural mutualism. *Symbiosis* 4:275-288.
- Eakin, C. M.
1988. Avoidance of damselfish lawns by the sea urchin *Diadema mexicanum* at Uva Island, Panama. *Proceedings of the Sixth International Coral Reef Symposium*, Townsville 2:21-26.
- Eakin, C. M.
1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15:109-119.
- Eakin, C. M.
2001. A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science* 69:171-186.
- Eakin, C. M., D. B. Smith, P. W. Glynn, L. D'Croz, and J. Gil.
1989. Extreme tidal exposures, cool upwelling, and coral mortality in the eastern Pacific (Panamá). *Proceedings of the Association of Island Marine Laboratories of the Caribbean*, Puerto Rico 22:29 (abstract).
- Ebenhöh, W.
1994. Competition and coexistence: modeling approaches. *Ecological Modeling* 75/76:83-98.
- Fong, P., and P. W. Glynn
1998. A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the eastern Pacific? *Marine Biology* (Berlin) 130:663-674.
- Fong, P., and P. W. Glynn
2000. A regional model to predict coral population dynamics in response to El Niño-Southern Oscillation. *Ecological Applications* 10:842-854.
- Fong, P., and P. W. Glynn
2001. Population abundance and size-structure of an eastern tropical Pacific reef coral after the 1997-98 ENSO: a simulation model predicts field measures. *Bulletin of Marine Science* 69:187-202.
- Glynn, P. W.
1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panamá. *Journal of Marine Research* 35:567-585.
- Glynn, P. W.
1980. Defense by symbiotic Crustacea of host corals elicited by chemical cues from predator. *Oecologia* (Berlin) 47:287-290.
- Glynn, P. W.
1982a. Coral communities and their modifications relative to past and prospective Central American seaways. *Advances in Marine Biology* 19:91-132.
- Glynn, P. W.
1982b. *Acanthaster* population regulation by a shrimp and a worm. *Proceedings of the Fourth International Coral Reef Symposium*, Manila 2:607-612.

Glynn, P. W.

1983. Crustacean symbionts and the defense of corals: coevolution on the reef? Pages 111-178 in M. H. Nitecki (ed). *Coevolution*, University of Chicago Press.

Glynn, P. W.

1984a. An amphinomid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. *Bulletin of Marine Science* 35:54-71.

Glynn, P. W.

1984b. Corallivore population sizes and feeding effects following El Niño (1982-1983) associated coral mortality in Panamá. *Proceedings of the Fifth International Coral Reef Congress*, Tahiti 4:183-188.

Glynn, P. W.

1984c. Widespread coral mortality and the 1982/83 El Niño warming event. *Environmental Conservation* 11:133-146.

Glynn, P. W.

1985. El Niño-associated disturbance to coral reefs and post disturbance mortality by *Acanthaster planci*. *Marine Ecology Progress Series* 26:295-300.

Glynn, P. W.

1988. El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7:129-160.

Glynn, P. W.

1990. Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. Pages 365-400 in Z. Dubinsky (ed). *Coral reefs, Ecosystems of the world*, Elsevier, Amsterdam.

Glynn, P. W.

1994. State of coral reefs in the Galápagos Islands: natural vs anthropogenic impacts. *Marine Pollution Bulletin* 29:131-140.

Glynn, P. W.

1997. Eastern Pacific reef coral biogeography and faunal flux: Durham's dilemma revisited. *Proceedings of the Eighth International Coral Reef Symposium*, Panamá 1:371-378.

Glynn, P. W.

2001. Eastern Pacific coral reef ecosystems. Pages 281-305 in U. Seeliger and B. Kjerfve (eds). *Coastal marine ecosystems of Latin America. Ecological Studies* 144, Springer-Verlag, Berlin & Heidelberg.

Glynn, P. W.

In press. Coral communities and coral reefs of Ecuador. in J. Cortés (ed). *Corals and coral reefs of Latin America*. Elsevier Press, Amsterdam.

Glynn, P. W., and L. D'Croz

1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8:181-191.

Glynn, P. W., and W. H. de Weerd

1991. Elimination of two reef-building hydrocorals following the 1982-83 El Niño warming event. *Science* 253:69-71.

- Glynn, P. W., and J. S. Feingold
1992. Hydrocoral species not extinct. *Science* 257:1845.
- Glynn, P. W., and I. G. Macintyre
1977. Growth rate and age of coral reefs on the Pacific coast of Panamá. *Proceedings of the Third International Coral Reef Symposium*, Miami 2:251-259.
- Glynn, P. W., and R. H. Stewart
1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panamá) in relation to thermal conditions. *Limnology and Oceanography* 18:367-379.
- Glynn, P. W., and G. M. Wellington
1983. Corals and coral reefs of the Galápagos Islands. With an annotated list of the scleractinian corals of the Galápagos (by J. W. Wells). University of California Press, Berkeley & Los Angeles, 330 pp.
- 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., and G. E. Leyte Morales
1997. Coral reefs of Huatulco, west México: reef development in upwelling Gulf of Tehuantepec. *Revista de Biología Tropical* 45:1033-1047.
- Glynn, P. W., and J. L. Maté
1997. Field guide to the Pacific coral reefs of Panamá. *Proceedings of the Eighth International Coral Reef Symposium* 1:145-166.
- Glynn, P. W., and J. S. Ault
2000. A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19:1-23.
- Glynn, P. W., H. von Prael, and F. Guhl
1982. Coral reefs of Gorgona Island, with special reference to corallivores and their influence on community structure and reef development. *Anales del Instituto de Investigaciones Marinas de Punta de Betin* 12:185-214.
- Glynn, P. W., M. Perez, and S. Gilchrist
1985. Lipid decline in stressed corals and their crustacean symbionts. *Biological Bulletin* 168:276-284.
- Glynn, P. W., J. E. N. Veron, and G. M. Wellington
1996. Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* 15:71-99.
- Glynn, P. W., J. L. Maté, and T. A. Stemann
2001. *Pavona chiriquiensis*, a new species of zooxanthellate scleractinian coral (Cnidaria: Anthozoa: Agariciidae) from the eastern tropical Pacific. *Bulletin of the Biological Society of Washington* 10:210-225.
- 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 the Sixth International Coral Reef Symposium*, Townsville 3:237-243.
- Glynn, P. W., G. M. Wellington, E. A. Wieters, and S. A. Navarrete
In press. Reef-building coral communities of Easter Island (Rapa Nui), Chile. In J. Cortés (ed). Corals and coral reefs of Latin America. Elsevier Press, Amsterdam.

- Glynn, P. W., J. L. Maté, A. C. Baker, and M. O. Calderón
2001. Coral bleaching and mortality in Panamá 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* 69:79-109.
- 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 (Berlin)* 109:355-368.
- Glynn, P. W., S. B. Colley, C. M. Eakin, D. B. Smith, J. Cortés, N. J. Gassman, H. M. Guzmán, 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 (Berlin)* 118:191-208.
- Glynn, P. W., S. B. Colley, N. J. Gassman, K. Black, J. Cortés, 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 (Berlin)* 125:579-601.
- Glynn, P. W., S. B. Colley, J. H. Ting, J. L. Maté, and H. M. Guzmán
2000. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp. a. *Marine Biology (Berlin)* 136:785-805.
- Guzmán, H. M.
1988. Distribución y abundancia de organismos coralívoros en los arrecifes coralinos de la Isla del Caño, Costa Rica. *Revista de Biología Tropical* 36:191-207.
- Guzmán, H. M., and J. Cortés
1989. Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). *Bulletin of Marine Science* 44:1186-1194.
- Guzmán, H. M., and J. Cortés
1992. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982-83 El Niño disturbance. *Revista de Biología Tropical* 40:309-324.
- Guzmán, H. M., and J. Cortés
1993. Los arrecifes coralinos del Pacífico Oriental Ecuatorial: revisión y perspectivas. *Revista de Biología Tropical* 41:535-557.
- Guzmán, H. M., J. Cortés, P. W. Glynn, and R. H. Richmond
1990. Coral mortality associated with dinoflagellate blooms in the eastern Pacific (Costa Rica and Panama). *Marine Ecology Progress Series* 60:299-303.
- Heck, K. L. and E. D. McCoy.
1978. Long-distance dispersal and the reef-building corals of the eastern Pacific. *Marine Biology (Berlin)* 48:348-356.
- Hertlein, L. G., and W. K. Emerson
1957. Additional notes on the invertebrate fauna of Clipperton Island. *American Museum Novitates* 1859:1-9.
- Highsmith, R. C.
1980. Geographic patterns of coral bioerosion: a productivity hypothesis. *Journal of Experimental Marine Biology and Ecology* 46:177-196.

- Jackson, J. B. C.
1997. Reefs since Columbus. *Coral Reefs* 16 (n. suppl.):23-32.
- Jørgensen, S. E.
1994. Models as instruments for combination of ecological theory and environmental practice. *Ecological Modeling* 75/76:5-20.
- Joubin, L.
1912. Bancs et récifs de coraux (Madrépores). — Carte. *Annales de L'Institut Océanographique* 4(2): map no. 5, Amérique Équatoriale. Masson et Cie, Éditeurs, Paris.
- Ketchum, J. T., and H. Reyes Bonilla
1997. Biogeography of the hermatypic corals of the Revillagigedo Archipelago, México. *Proceedings of the Eighth International Coral Reef Symposium*, Panamá 1:471-476.
- Leyte Morales, G. E.
2001. Estructura de la comunidad de corales y características geomorfológicas de los arrecifes coralinos de Bahías de Huatulco, Oaxaca, México. M. S. thesis, Universidad del Mar, Oaxaca, 94 p.
- Linsley, B. K., R. B. Dunbar, G. M. Wellington, and D. A. Mucciarone
1994. A coral-based reconstruction of intertropical convergence zone variability over Central America since 1707. *Journal of Geophysical Research* 99:9977-9994.
- Lirman, D., P. W. Glynn, A. C. Baker, and G. E. Leyte Morales
2001. Combined effects of three sequential storms on the Huatulco coral reef tract, Mexico. *Bulletin of Marine Science* 69:267-278.
- Macintyre, I. G., P. W. Glynn, and J. Cortés
1992. Holocene reef history in the eastern Pacific: mainland Costa Rica, Caño Island, Cocos Island, and Galápagos Islands. *Proceedings of the Seventh International Coral Reef Symposium, Guam* 2:1174-1184.
- McCoy, E. D., and K. L. Heck
1976. Biogeography of corals, seagrasses and mangroves: an alternative to the center of origin concept. *Systematic Zoology* 25:201-210.
- Newman, W. A.
1972. The National Academy of Science Committee on the Ecology of the Interoceanic Canal. Pages 247-259 in M. L. Jones (ed). The Panamic biota: some observations prior to a sea-level canal. *Bulletin of the Biological Society of Washington*, No. 2, Washington, D. C.
- Palmer, R. H.
1928. Fossil and recent corals and coral reefs of western México. Three new species. *Proceedings of the American Philosophical Society* 67:21-31.
- Prahl, H. von, and A. Mejía
1985. Primer informe de un coral acropórido, *Acropora valida* (Dana 1846) (Scleractinia: Astrocoeniida: Acroporidae) para el Pacífico Americano. *Revista de Biología Tropical* 33:39-43.
- Reaka-Kudla, M. L., J. S. Feingold, and P. W. Glynn
1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. *Coral Reefs* 15:101-107.

Reyes Bonilla, H.

1993. Biogeografía y ecología de los corales hermatípicos (Anthozoa: Scleractinia) del Pacífico de México. Pages 207-222 in S. I. Salazar Vallejo and N. E. González (eds). *Comisión Nacional para el Conocimiento de la Biodiversidad y Centro de Investigaciones de Quintana Roo (CIQRO)*, México.

Reyes Bonilla, H.

- In press. Checklist of valid names and synonyms of stony corals (Anthozoa: Scleractinia) from the eastern Pacific. *Journal of Natural History* 2000.

Reyes Bonilla, H., and J. D. Carriquiry

1994. Range extension of *Psammocora superficialis* (Scleractinia: Thamnasteriidae) to Isla Socorro, Revillagigedo Archipelago, Colima, México. *Revista de Biología Tropical* 42:383-392.

Reyes Bonilla, H., and A. López Pérez

1998. Biogeografía de los corales pétreos (Scleractinia) del Pacífico de México. *Ciencias Marinas* 24:211-224.

Reyes Bonilla, H., and J. P. Carricart-Ganivet

2000. *Porites arnaudi*, a new species of stony coral (Anthozoa: Scleractinia: Poritidae) from oceanic islands of the eastern Pacific Ocean. *Proceedings of the Biological Society of Washington* 113:561-571.

Richmond, R. H.

1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. *Proceedings of the Fifth International Coral Reef Congress*, Tahiti 6:101-106.

Richmond, R. H.

1990. The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. Pages 127-140 in P. W. Glynn (ed). Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. *Elsevier Oceanography Series* 52, Amsterdam.

Robinson, G.

1985. Influence of the 1982-83 El Niño on Galápagos marine life. Pages 153-190 in G. Robinson and E. M. del Pino (eds). El Niño in the Galápagos Islands: the 1982-1983 event. Publication of the Charles Darwin Foundation for the Galápagos Islands, Quito, Ecuador.

Rowan, R.

1998. Diversity and ecology of zooxanthellae on coral reefs. *Journal of Phycology* 34:407-417.

Rowan, R., and N. Knowlton

1995. Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceedings of the National Academy of Science* 92:2,850-2,853.

Rowan, R., and D. A. Powers

1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. *Science* 251:1348-1351.

Rowan, R., N. Knowlton, A. Baker, and J. Jara

1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265-269.

- Shen, G. T., and C. L. Sanford
 1990. Trace element indicators of climate variability in reef-building corals. Pages 255-283 in P. W. Glynn (ed). Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. *Elsevier Oceanography Series 52*, Amsterdam.
- Shen, G. T., T. M. Campbell, R. B. Dunbar, G. M. Wellington, M. W. Colgan, and P. W. Glynn
 1991. Paleochemistry of manganese in corals from the Galápagos Islands. *Coral Reefs* 10:91-101.
- Shen, G. T., J. E. Cole, S. W. Lea, L. J. Linn, T. A. McConnaughey, and R. G. Fairbanks
 1992. Surface ocean variability at Galápagos from 1936-1982: calibration of geochemical tracers in corals. *Paleoceanography* 5:563-588.
- Smith, F. G. Walton
 1948. Atlantic reef corals: a handbook of the common reef and shallow-water corals of Bermuda, Florida, the West Indies and Brazil. University of Miami Press, Coral Gables, 112 p., 41 pls.
- Squires D. F.
 1959. Results of the Puritan-American Museum of Natural History Expedition to western Mexico: 7. Corals and coral reefs in the Gulf of California. *Bulletin of American Museum of Natural History* 118:367-431.
- Stoddart, D. R.
 1962. Three Caribbean Atolls: Turneffe Islands, Lighthouse Reef, and Glover's Reef, British Honduras. *Atoll Research Bulletin* 87:1-151.
- Vaughan, T. W.
 1919. Coral and the formation of reefs. *Smithsonian Institution Annual Report for 1917*. pp. 189-238.
- Veron, J. E. N.
 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. Comstock/Cornell, Ithaca and London. 321 pp.
- von Prael, H., and A. Mejía
 1985. Primer informe de un coral acropórido, *Acropora valida* (Dana 1846) (Scleractinia: Astrocoeniida: Acroporidae) para el Pacífico americano. *Revista de Biología Tropical* 33: 39-43.
- Weerdt, W. H. de, and P. W. Glynn
 1991. A new and presumably now extinct species of *Millepora* (Hydrozoa) in the eastern Pacific. *Zoologische Mededelingen Leiden* 65:267-276.
- Wellington, G. M.
 1982. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs* 52:223-241.
- Wellington, G. M., and R. B. Dunbar
 1995. Stable isotopic signature of El Niño-Southern Oscillation events in eastern tropical Pacific reef corals. *Coral Reefs* 14:5-25.
- Wells, J. W.
 1951. The coral reefs of Arno Atoll, Marshall Islands. *Atoll Research Bulletin* 9:1-14 + 16 figs.

Wells, J. W.

1957. Coral reefs. *Treatise on Marine Ecology and Paleoecology*. *Ecology* 1:609-631.
Geological Society of America, Memoir 67.

Wells, J. W.

1963. Coral growth and geochronology. *Nature* 197:948-950.

Wells, J. W.

1982. Notes on Indo-Pacific scleractinian corals, part 9. New corals from the
Galápagos Islands. *Pacific Science* 36:211-219.

Wilson, E. O.

1992. *The diversity of life*. W. W. Norton & Company, New York. 424 pp.