Coral Reefs of the World

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Coral Reefs of the Eastern Tropical Pacific

Persistence and Loss in a Dynamic Environment

Springer

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For Jerry (Gerard M.) Wellington,
a pioneer and devoted student of eastern
Pacific coral reefs

Tribute

Peter W. Glynn, Patriarch of Coral Reef Research in the Eastern Tropical Pacific

By his students and friends,

Peter Glynn grew up on Coronado Island, California, and began scuba diving in the late 1940s, making regular trips with his high school friends into México to explore marine life in the Gulf of California and other nearby sites. Heading inland for college, he earned his B.A. at the University of South Dakota in 1955 returning to the Pacific to earn a M.A. and Ph.D. from Stanford University in 1960 and 1963, respectively, working at the Hopkins Marine Station on the trophic relationships of an intertidal community, with Donald P. Abbott serving as his advisor. Peter started working on coral reefs in the Caribbean in 1959 when he offered his services to a Mexican fishing crew in exchange for passage to the Belizean barrier reef. In 1960, he became a professor at the University of Puerto Rico, and 7 years later moved to Panama to join researchers at the Smithsonian Tropical Research Institute (STRI), where he initiated a detailed and systematic study of eastern tropical Pacific (ETP) coral reefs that continues today. His unprecedented and seminal research legacy of contributions began with the basic description of the Pacific coral reefs of Panama (Glynn et al. 1972; Glynn and Stewart 1973; Glynn 1976), and continued with a prolific series of contributions, substantively changing our knowledge and perspectives of these systems.

These publications address a wide variety of topics, including Pacific coral reef Holocene growth history (Glynn and Macintyre 1977), interactions among reef organisms, such as the corallivorous seastar *Acanthaster planci* (Glynn 1973, 1974, 1977) and the symbiosis between pocilloporid corals and crustacean symbionts (Glynn 1976, 1980, 1987), the first papers on El Niño warming impact and subsequent biological responses (Glynn 1983, 1990; Glynn et al. 1988, 2001a), coral bioerosion (Glynn 1988, 1997), coral reproduction (Glynn et al. 1991, 1994, 1996a, 2000, 2008, 2011, 2012), description of new coral species (Glynn 1999, Glynn et al. 2001b) and a possible coral extinction (Weerdt and Glynn 1991; Glynn and Feingold 1992; Glynn et al. 2001a), plus other investigations too numerous to mention here (see references throughout this book). He also did pioneering coral reef research in the Galápagos Islands (Glynn et al. 1979; Glynn and Wellington 1983; Glynn 1994, 2003), Colombia (Glynn et al. 1982), Costa Rica (Glynn et al. 1983), Clipperton Atoll (Glynn et al. 1996b), southern Mexico (Glynn and Leyte-Morales 1997), and Easter Island (Rapa Nui) (Glynn et al. 2003, 2007).

Peter Glynn's careful documentation of the causes, short-term impacts, and long-term ecological consequences of one of the first mass coral bleaching events to severely impact reefs regionally (the 1982–1983 El Niño-Southern Oscillation in the ETP) has proven invaluable in helping reef scientists understand the growing global threat of climate change on reef ecosystems.

Peter Glynn has been the mentor of, and an inspiration for, many coral reef scientists who have worked in the ETP: Andrew Baker, Iliana B. Baums, Charles Birkeland, Mitch Colgan, Susan Colley, Jorge Cortés, C. Mark Eakin, Ian Enochs, Joshua Feingold, Peggy Fong, Gerardo Leyte-Morales, Derek Manzello, Priscilla Martínez, Juan Maté, Héctor

Reyes-Bonilla, Bob Richmond, Fernando Rivera, Tyler Smith, Bernardo Vargas-Ángel, and Jerry Wellington. In recognition of his unparalleled contributions to coral reef science, Peter Glynn was awarded the Darwin Medal in 1992, which is the most prestigious award granted by the International Society for Reef Studies (ISRS). He has also received two "Best Paper Awards" for articles published in the journal Coral Reefs (Glynn and D'Croz 1990 and Glynn 1993). As a distinguished professor at the University of Miami's Rosenstiel School of Marine and Atmospheric Science, he has shaped the scientific education of countless undergraduates who have taken his invertebrate zoology and coral reef classes. He launched and inspired decades of research on reefs of the ETP, revealing an entirely new coral reef environment and exposing many of the secrets they held.

His seminal contributions continue to this day, as he just published a manuscript documenting the > 500 year growth history of a coral reef in the far Northern Galápagos Island of Darwin and its recovery from recurrent El Niño bleaching (Glynn et al. 2015). He aptly named this reef "Wellington Reef" in honor of his life-long friend and colleague, Jerry Wellington, with whom he discovered the coral reefs of the Galápagos Islands in the 1970s (Glynn and Wellington 1983).

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Preface

Just a few decades ago it was uncertain whether structural coral reefs were present in the eastern tropical Pacific (ETP) region. Several renowned scientists who characterized the global development of coral reefs, for example Charles Darwin, James Dana, A.E. Verrill, T. Wayland Vaughan, and David R. Stoddart embraced the erroneous idea that coral reefs were absent from western American shores. Ironically, these authorities spent little or no time researching corals or coral reefs on site in the ETP, but obtained their information from marine charts and secondhand often from the cursory observations of others.

Beginning in the 1960s and 1970s, studies were initiated (and continue) to document the widespread occurrence of structural coral reefs along western tropical American shores and offshore islands. Compared to coral reef provinces in the Indo-Pacific and broader Caribbean Sea, however, these ETP reefs are relatively small and discontinuous. Also, the numbers of reef-building species are few, exhibiting a limited variety of colony morphologies, and reef framework structures. Additionally, extant eastern Pacific reefs are generally restricted to shallow depths, sheltered shores, and exhibit little zonation. One of the reasons they have gone virtually unnoticed is their lack of emergent reef structures such as algal ridges, drying reef flats, rubble berms, and lagoons. Despite the absence of such geomorphologic features, these marginally developed reefs share essentially the same kinds of biotic interactions and ecological functions as coral reefs in the more diverse and celebrated Coral Seas' provinces. In this book we offer a comprehensive synthesis of recent progress in ETP coral reef research, providing a framework for understanding of the structure and dynamics of these ecosystems as they approach an uncertain future in the face of natural and human-related disturbances.

This volume is organized into three principal subject areas (physical environmental conditions, biology and ecology of coral reef biota, and impacts and management), and begins with a review by Peter W. Glynn on the history of coral and coral reef studies in the ETP region (Chap. 1). Surprisingly, despite an apparent depauperate reef-building biota and modest reef development, the eastern Pacific region boasts a relatively rich history of coral research. Following the historical framework, five chapters of the book's first section examine the physical setting of the eastern Pacific basin with particular attention to those areas supporting reef-building coral populations. The geology and paleoecology of early eastern Pacific coral reefs are traced by Andrés López-Pérez from the Eocene epoch and closure of the Isthmian Seaway to the development, distribution, biogeographic character, and evolution of Holocene reefs (Chap. 2). Basin-wide oceanographic conditions that control coral distributions and reef development, including ocean currents, upwelling centers, storm tracks, and location of the Intertropical Convergence Zone, are examined by Paul C. Fiedler and Miguel Lavín in Chap. 3. Chunzai Wang and co-authors trace the development, evolution, and spatial occurrence of El Niño warming events in Chap. 4. With the current recognition of two classes of El Niño, eastern and central Pacific events, our understanding of the spatial and temporal extent of disturbances to ETP coral reefs should now come into better focus. Peter Glynn and co-authors present an overview in Chap. 5 of the biogeographic occurrence of coral species, reef types, morphology, zonation, and their biotic composition in different eastern Pacific regions. This synoptic treatment is the product of several workers who have contributed their knowledge of particular reef areas. Information on the coral fauna and coral reefs of Mexico is provided by Héctor Reyes-Bonilla. Recently discovered coral assemblages in El Salvador and

Nicaragua are characterized by H. Reyes-Bonilla and Juan J. Alvarado, respectively. Brief descriptions of equatorial eastern Pacific coral habitats are offered by Jorge Cortés and Carlos Jiménez (Costa Rica), Juan L. Maté (Panama), Fernando A. Zapata and Bernardo Vargas-Ángel (Colombia), and Stuart Banks, Joshua S. Feingold, Peter W. Glynn, Priscilla Martínez, and Fernando Rivera (Ecuador). Evie A. Wieters and Sergio A. Navarrete have provided information on the coral communities of remote Rapa Nui (Easter Island), now recognized as a distant outpost of the ETP region. This first section concludes with an overview of the distribution, development, and centennial- to millennial-scale history of structural reefs in the eastern Pacific by Lauren T. Toth and co-authors in Chap. 6.

The second thematic section of this volume, comprising 13 chapters, treats a variety of topics focused on the biology and ecology of eastern Pacific coral reef ecosystems. These chapters are framed in the context of functional ecology, i.e., processes and interactions that influence or control the structure and dynamics of coral communities and reef building. The species richness and diversity of reef-associated organisms, their habitats, niches, and varied ecological interactions in structuring reef communities are addressed by Jorge Cortés and co-authors in Chap. 7. In Chap. 8, P. Glynn and co-authors examine ENSO impacts on reefs with special attention to the severe 1982–1983 and 1997–1998 disturbances. In Chap. 9, I. Enochs and P. Glynn describe the major coral reef trophic guilds, their connectivity and contributions to reef function. Food webs demonstrating energy and nutrient inputs are examined and evaluated in terms of flow (gains and losses), regeneration and recycling processes. Coral community structure, dynamics and reef accretion are greatly influenced by corallivores in the eastern Pacific. The high diversity of invertebrate and fish corallivores, relative to their coral prey, is examined by I. Enochs and P. Glynn in Chap. 10. A process-focused account of algal dynamics and herbivory is presented in Chap. 11 by P. Fong and colleagues. This chapter considers algal diversity, patterns in distribution and abundance, the ecological controlling forces that may produce these patterns, and presents a simulation model based on empirical data that demonstrate that ETP reefs may currently exist as alternate stable states. In Chap. 12, Juan Alvarado and co-authors document the high rates of bioerosion that are exacerbated following ENSO-related coral mortality, and underscore the significance of this potentially important process that contributes to reef degradation in the ETP. The rates and effects of diverse excavating metazoan taxa are reviewed, from Mexico to several sites in the equatorial eastern Pacific of Central and South America.

The roles of symbiotic zooxanthellae in eastern Pacific reef-building corals are examined in two chapters. The first (Chap. 13) by Andrew C. Baker and colleagues focuses on the occurrence of endosymbionts in different coral host species and environments, e.g., upwelling and non-upwelling areas, and the temporal stability of these distributions. The presence of certain symbiont types impart a degree of thermal tolerance to host corals, which is considered in light of the adaptive bleaching hypothesis. In Chap. 14, Jorge H. Pinzón addresses the biogeographic patterns of corals and their symbiont types, coral host morphometrics, and species boundaries vis-à-vis symbiont associations. Molecular genetics and morphometric evidence are shown to be highly discordant in defining species boundaries in *Pocillopora*, with several fewer, but highly supported, species recognized by application of the former methodology.

Like the previous topics on coral/algal holobionts, several of the remaining chapters have relevance to coral resilience, i.e., the capacity of reef coral populations to recover from disturbances. This capacity for recovery is manifest in the reproductive potential of reef corals, their genetic connectivity within the eastern Pacific region, as well as the existence and possible effectiveness of deep reef refugia that could play a role in the repopulation of impacted shallow reef habitats. Both sexual and asexual modes of reproduction are critical life history processes in the maintenance and recovery of coral communities. Sexual reproductive patterns, spawning modes, seasonal timing of spawning, fecundity and recruitment are examined in the major reef-building coral species by P. Glynn and co-authors in Chap. 15. The prevalence of asexual propagation, commonly caused by foraging fishes, is also reviewed for branching and massive corals in Mexico, Panama, and the Galápagos Islands. Gene flow and population connectivity between major reef regions within the eastern tropical Pacific and

across the eastern Pacific Barrier are examined by H.A. Lessios and I.B. Baums in Chap. 16. They provide an analysis of all available DNA data, expressed as the genetic divergence between populations (F_{ST}), to better understand the connectivity of conspecific populations of reef-building corals, and reef-associated molluscs, echinoderms, and fishes. Tyler B. Smith and co-authors in Chap. 17 examine refuges and refugia for ETP corals and coral reefs in a highly dynamic ocean climate. The survival of deep coral communities and their ability to reproduce and promote recruitment to devastated shallow reef habitats, embraced in the "deep reef refugia hypothesis", is evaluated in this chapter in terms of eastern Pacific recovery processes.

In light of potentially stressful conditions affecting ETP coral reefs—high and low thermal swings, high CO_2 concentration, and demonstrated rapid bioerosion of carbonate structures—Derek P. Manzello and co-authors examine coral/algal calcification and the integrity of reef frameworks in Chap. 18. They conclude this treatment with consideration of present-day species-specific responses to such challenges, and the risks to eastern Pacific coral reefs in the coming decades. In Chap. 19, Julia E. Cole and Alexander W. Tudhope observe climate variability over multidecadal and century timescales from coral-based paleoclimate reconstructions during the Holocene. Coral-based reconstructions of ocean temperatures are examined in detail from geochemical records obtained in the Galápagos Islands, Panama, and Clipperton Atoll.

The third and last section of this book addresses issues stemming from the uses and abuses of coral reefs by humankind, from local and regional impacts to global-scale degradation. Direct and indirect sources of damage to coral reefs, e.g., fishing-related effects, coastal alteration, and deforestation, are examined by J. Cortés and H. Reyes-Bonilla in Chap. 20. Significant advances have been made during the past few decades in the establishment of marine protected areas (MPAs). Eastern Pacific MPAs harboring coral communities and coral reefs are characterized by J. Alvarado and co-authors in Chap. 21. Attention is directed to the location and size of MPAs, the types of coral communities and reefs present, and their degree of protection in relation to stressors and threats. A case is made in this final chapter for the role of MPA networks in the protection of coral refugia, source populations, and the potential for repopulation of degraded reef areas.

To assist in the recognition and systematic status of abundant and ecologically important species mentioned throughout the book, a pictorial field guide, assembled by Juan L. Maté and colleagues, is included in Chap. 22. This section is organized into brief species' accounts from each of the major metazoan phyla and algal divisions. Photographs and accompanying information sources, with the assistance of systematists familiar with the taxa considered, are offered.

Several research initiatives in the ETP have been shown to have universal relevance, thus serving to advance an understanding of coral reef ecology worldwide. For example, the cause and effect of elevated sea temperatures and widespread coral bleaching, first recognized in the ETP in the early 1980s, has subsequently been observed globally, signaling a clarion warning of reef degradation in step with climate change. Related coral bleaching research, initiated in the ETP, has demonstrated differential susceptibility of algal symbiont types to changes in sea temperature, rendering certain coral hosts relatively resistant to temperature extremes. Such environmentally induced responses have now been documented in other coral reef regions. The recognition that eastern Pacific reefs occur under naturally low pH conditions has provided important insights into how the structure and function of coral reefs might be affected by ocean acidification. These pioneering contributions to coral reef science, and others initiated in the eastern tropical Pacific, are considered in detail in the relevant chapters in this volume.

The principal ETP coral reef study sites examined in this book extend from the Gulf of California in northern Mexico through Central America to coastal Ecuador in South America (Fig. 1). Oceanic island sites are also identified, from the Revillagigedo Islands off Mexico to remote Rapa Nui, $\sim$4,000 km west of Chile. Throughout this book, Latin American countries and major cities are anglicized following National Geographic's Collegiate Atlas of the World (2006). Most other geographic names retain their Spanish spelling, which should be helpful in

Fig. 1 Eastern Pacific ocean basin from the Gulf of California, Mexico to Rapa Nui (Easter Island), Chile showing major oceanic islands and continental sites with coral reef development. Modified from the World Physical Map. *Source* US National Park Service (http://www.arcgis.com/home/item.html?id=c4ec722a1cd34cf0a23904aadf8923a0)

the location of in-country coral reef study sites. Recently some Latin American authors have dropped accents from their names. Current literature citations often list both, accented and unaccented names. Since it is difficult to determine the year the omissions occurred, we have attempted to retain accented names throughout for the sake of consistency and as a guide for correct pronunciation. Acronyms representing institutions and agencies are used according to their country of origin. With respect to cultural preferences, paternal and maternal surnames (in that order) identify most Latin American workers. In a few instances, accents have been omitted from proper names according to individual preference.

Nearly all of the information contained in this book has originated from research conducted in Latin America and Clipperton Atoll, an overseas territory of France. Without the insights, dedication, and camaraderie of local researchers, students, and technicians, the body of research making up this volume would not have been possible. The editors wish to thank many individuals who have made significant contributions to eastern Pacific coral reef studies, and who have benefitted this volume at several levels, including those who offered help beyond the chapters they co-authored: **Mexico**—Luis E. Calderon-Aguilera, David A. Paz-García, and H. Reyes-Bonilla; **Clipperton Atoll**—Lt. Col. Graeff (Chief, Bureau d'Etudes, Haut-Commissariat de la République en Polynésie Française), and J.D. Jackson; **Costa Rica**—J.J. Alvarado, J. Cortés, Ana C. Fonseca-Escalante, Héctor M. Guzmán, Carlos E. Jiménez, Ian G. Macintyre, and Manuel M. Murillo, Michael J. Risk, and Paula J.B. Scott; **Panama**—Lawrence G. Abele, Irwin Bethancourt Acosta, Rebecca Albright, Charles Birkeland, Peter Castro, Thomas F. Dana, Luis D'Croz, Juan B. Del Rosario, Ellen R.M. Druffel, Robert B. Dunbar, J. Wyatt Durham, Caitlin R. Fong, Sandra L. Gilchrist, Héctor M. Guzmán, Leslie Harris, Gordon Hendler, Raymond C. Highsmith, Gena Hockensmith, Jeremy B.C. Jackson, Nancy Knowlton, Martin Moynihan, William A. Newman, James W. Porter, Robert H. Richmond, D. Ross Robertson, Adrienne Romanski (Adrienne M.S. Correa), Ira Rubinoff, Aníbal Velarde, Matthew J. Wartian, and Ingo S. Wehrtmann; **Colombia**—Henry von Prahl, Bernardo Vargas-Ángel, and Fernando A. Zapata; **Ecuador**—Stuart A. Banks, Margarita Brandt, Victor W. Brandtneris, Andrew Bruckner, Rodrigo H. Bustamante, Ángel I. Chiriboga, Lenín Cruz, Graham J. Edgar, René Espinosa, Priscilla C. Martínez, Thomas Okey, Marjorie L. Reaka, Günter Reck, Philip Renaud, Fernando Rivera, Gerard M. Wellington, John W. Wells, and Jon Witman; **Easter Island**—Eric H. Borneman, Henri and Michel Garcia, Dennis K. Hubbard, and G.M. Wellington.

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In Memoriam

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Contents

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