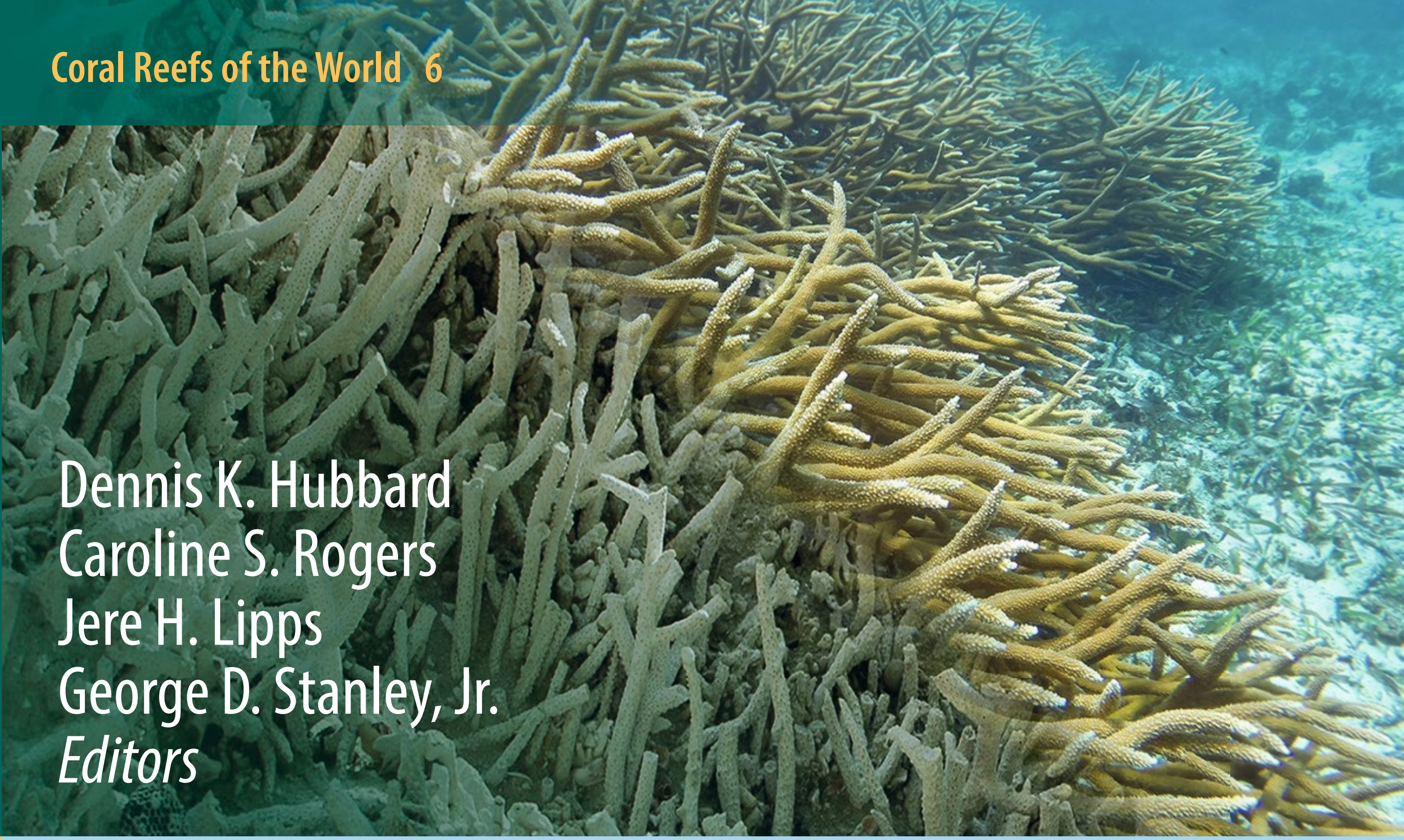
Coral Reefs of the World 6



Dennis K. Hubbard
Caroline S. Rogers
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George D. Stanley, Jr.
Editors

Coral Reefs at the Crossroads

Springer

Coral Reefs of the World

Volume 6

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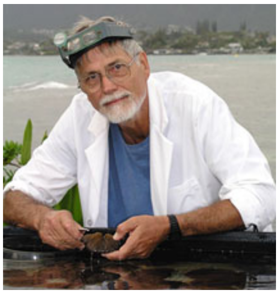

Paul L. Jokiel (1941–2016)

Paul Jokiel's career as a reef scientist spanned half a century. His interests were broad, and he always seemed to be ahead of the wave – whether it was his considerations of thermal stress in the 1970s, U/V light and photo-inhibition in the 1980s, the myriad roles of water motion in coral ecology, or the growing impact of humanity and climate change. His interests spanned the spatial spectrum from global (coral dispersal and connectivity) to microscopic (the topic of his chapter in this volume). More recently, his efforts broadened to include monitoring throughout the Hawaiian Islands, and he was an active participant in discussions of climate change, reef decline, and environmental management at scales ranging from local to global. We are grateful for his excitement about our project and regret that he did not get to see his significant contribution in print. However, we hope that his spirit of mentoring and his interest in science across broad disciplinary boundaries will be well served by this volume.

Preface

To every thing there is a season and a time to every purpose under heaven (Ecclesiastes 3:1).

I should have written this book in the early 1980s when I was at the West Indies Laboratory (WIL) on the Caribbean island of St. Croix. But, it was not the time; I was busy learning about coral reefs. Too late for the glory days of Discovery Bay in Jamaica, I had come to St. Croix for a year in 1977 right after graduate school and stayed for 22.

I should have written this book in the early 1990s. I had learned so much through the generosity of others and the benefits of living on the reef year-round for well over a decade. But, the West Indies Lab had just been destroyed by a hurricane.

For the next decade, I applied what I had learned at WIL to help frame a coastal-zone management process that was in its infancy in the US Virgin Islands. I learned tremendously as my interests broadened to include the management of already declining reef systems and how science fit into a larger social framework. I could have written this book then, but I was too busy making a living as a marine consultant outside the cloister of academia.

In the 12 years I spent at WIL, I worked with so many talented scientists and colleagues, but more important, I talked with them. . . after dives. . . over coffee. . . on vessels of all shapes and sizes. For me,WIL was a mecca of reef science for that brief time—and all the people who I would have traveled great distances to seek out were coming to me. Their generosity not only taught me about science, but also showed me how much more we can learn when we do it together. My students helped me to set out on what would be a life of not just teaching them but learning with and from them.

Marine labs are special places. Their ethos is difficult to understand until you have spent some time there. So much insight is derived not from carefully designed experiments but from just seeing the same places over and over again. . . over seasons and decades. . . and with different people who bring different perspectives and ask different questions. In the 1960s through the 1980s, marine labs were places where many of us came together not just to quantify a particular process or to answer a specific question, but to just try and understand how all the pieces fit together within an incredibly dynamic system—the coral reef. We were all "specialists" with our own sets of priorities. But we soon realized that as we talked to one another, we started asking new questions that were far grander than any of those we had framed on our own. We weren't just fisheries biologists, marine geologists, geochemists, seagrass or coral ecologists, and physical oceanographers. We were a group of researchers living in a special time and at a special place.

Much of our understanding of how these systems worked was serendipity. But, the significance of even fortuitous observations would have been lost without the perspective of time. And, they would have soon faded without someone to tell about it. . . not in a journal article, but on the way back from a dive, or over breakfast, or at a local watering hole—many people simply observing the same places—again and again.

Great laboratories and large research institutions have existed over the centuries. And marine labs are certainly not limited to the Caribbean nor have they disappeared. But, there was something indefinable, at least to me, about the small marine labs of the 1960s, 1970s, and 1980s. They were perfectly positioned between the broad expeditions of the previous century and the exploding technology that followed. So much of what we take for granted today came out of these small oases. They were also positioned at a perfect time to document the decline that was already occurring.

In the Caribbean, the Bellairs Marine Lab flourished during the 1950s and beyond. Discovery Bay Marine Lab, on the north coast of Jamaica (Fig. 1), the creation of Tom Goreau (Fig. 2), opened in 1965. For decades, it provided a place for reef scientists to gather and ask questions about how the reef functioned as a physical, biological, and chemical system. Ecologists like Judy Lang and paleontologists like Jeremy Jackson started their careers there, and so many of the principles that have stood the test of time were developed at this facility. Lynton Land, a geologist, "excavated" into the reef (Fig. 3) to understand the nature of its interior and to quantify how calcification by organisms living on the surface built the edifice that supported them. He used the "carbonate budget" concept developed by Colin

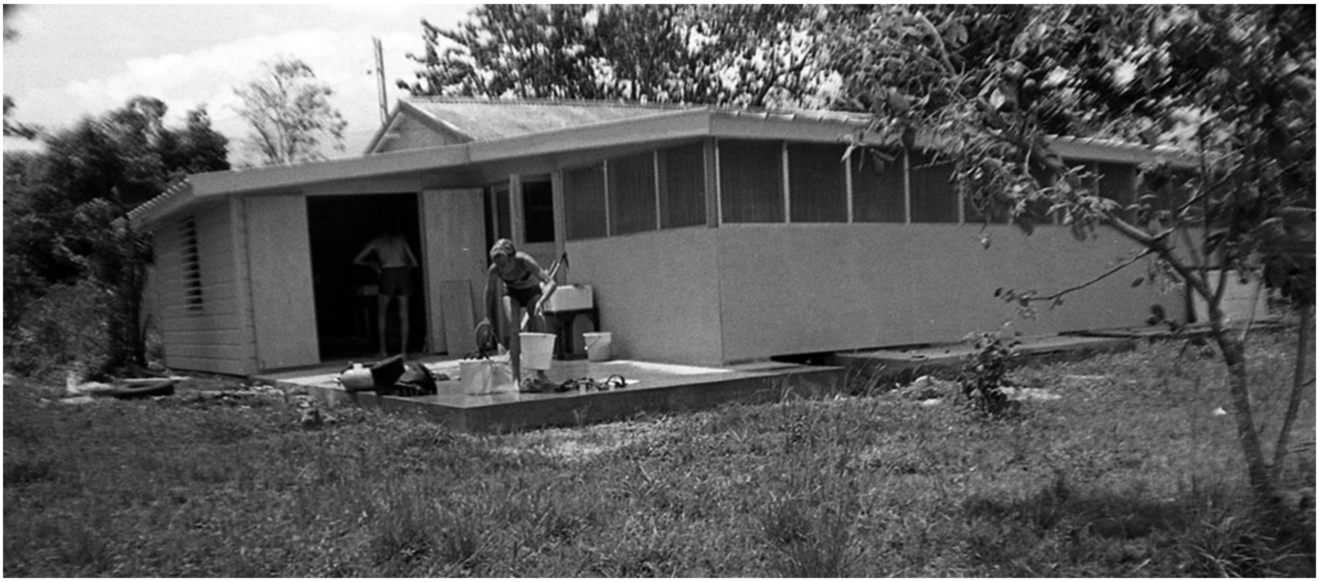

Fig. 1 The initial Discovery Bay Marine Lab on Jamaica (Photo by Eileen Graham, archived at the Natural History Museum in London. Courtesy of Ken Johnson and NHM)

Fig. 2 Tom Goreau observing the reef he knew best near the shelf edge off Discovery Bay, Jamaica (Photo by Eileen Graham. Courtesy of Ken Johnson and NHM)

Fig. 3 Lynton Land (*left*) and Reg Purdon excavating into the reef at “Lynton’s Mine” (Photo by Eileen Graham. Courtesy of Ken Johnson and NHM)

Fig. 4 View looking north over the West Indies Laboratory (*lower right*); Tague Bay and Buck Island National Underwater Monument are in the background (Photo by D Hubbard©)

Stern and Terry Scoffin on Barbados to think about the myriad processes that tie the community on its surface to the physical structure within.

For me, and so many others, it was the West Indies Laboratory on St. Croix (Fig. 4) that provided this opportunity. This brainchild of H. Gray Multer (Fig. 5a) was the unique blend of a strong undergraduate teaching program (Fig. 5b) and a well-respected research facility. While most others focused on the reef surface, some of us thought “deeper.” Using smaller drills, and eventually the SCARID drilling system, we cored through quaternary reefs in both deeper (Fig. 5c) and shallow water (Fig. 5d). In the latter 1970s and 1980s, WIL operated NOAA’s *Hydrolab* underwater research laboratory (Fig. 5e) that allowed research teams of four scientists to work at depths of over 45 m for a week at a time. Using it as a base, we cored

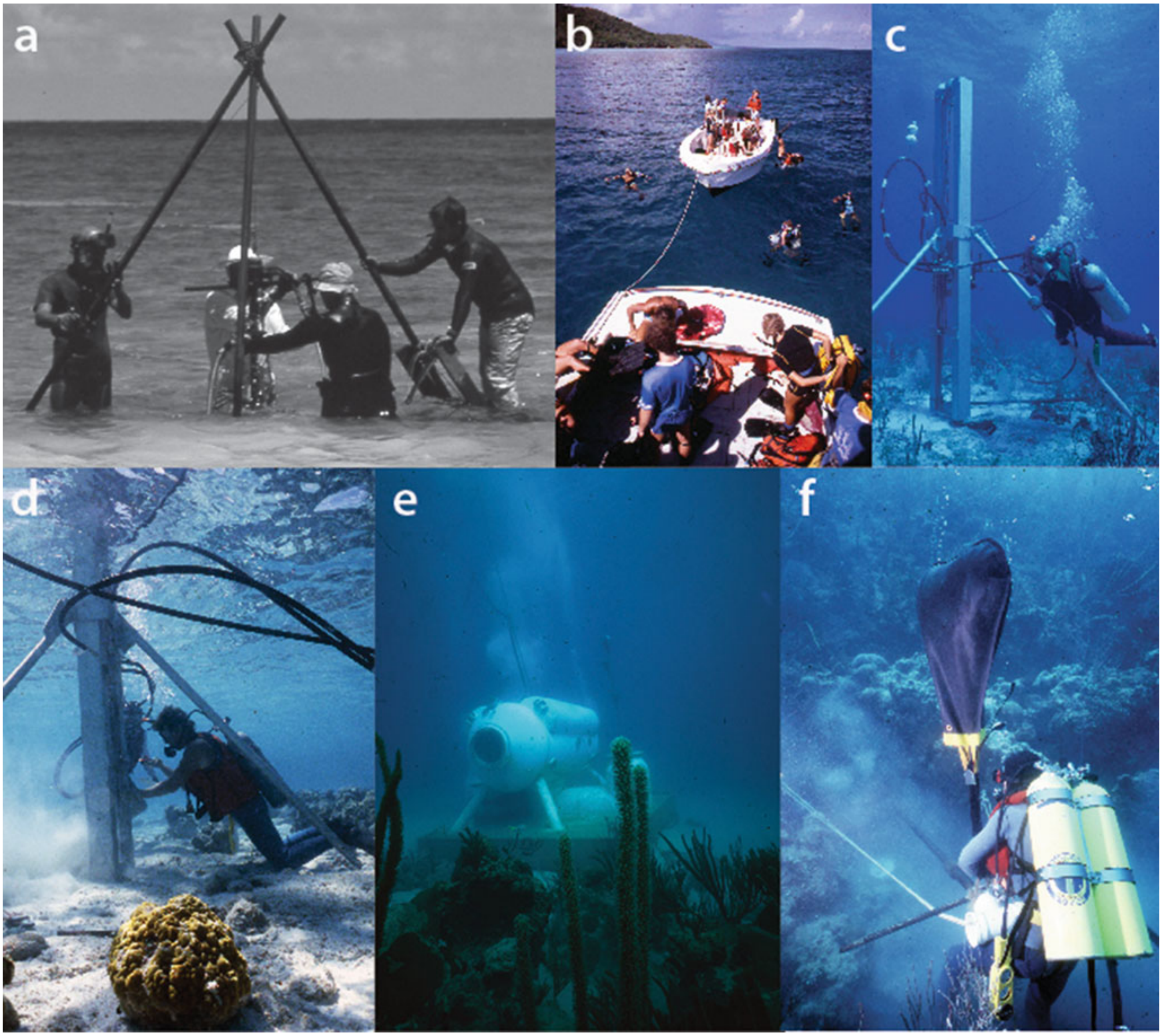

Fig. 5 (**a**) Founder and first director of WIL, H Gray Multer (*left*), coring the reef in Nonsuch Bay, Antigua, with Heinrich Zankl (University of Marburg), Ian Macintyre (Smithsonian Institution), and Kenny Burger (undergraduate, Fairleigh Dickinson University) (Photo by D. Hubbard). (**b**) Undergraduate students diving in WIL marine science classes. (**c**) SCARID drill in 15 m of water on Lang Bank, east of St. Croix. (**d**) SCARID drill near the reef crest of Buck Island National Monument, St. Croix. (**e**) Hydrolab underwater laboratory in Salt River Submarine Canyon on St. Croix. (**f**) Drilling horizontally into the west wall of the canyon (Photos by D Hubbard©)

into the walls of Salt River Submarine Canyon (Fig. 5f), spending over 12 h a day at depths up to 30 m. We also made many of our early observations of storm-related sediment transport from this facility, first in the Bahamas and later on St. Croix.

Marine labs have created myriad opportunities for reef scientists that would have otherwise been impossible. But more important, long-term measurements and observations provided a framework that benefitted every researcher who briefly passed through, each one adding texture to the picture that had developed over long years of repeated observation and sampling. It is always interesting to watch the discussions that follow some new paradigm as it catches on. The first contrarians are often those who have lived on a reef for an extended time. In most instances this is not due to superior intellect, but just having the benefit of going back to the same place with so many different people.

I never imagined it would take so long for the concept of this volume to emerge. However, it is fitting that it is not a collection of my own biases but rather a variety of views from valued friends and colleagues who have simply spent a lot of time looking at and thinking carefully about reefs. It is dedicated to those who created the marine labs and those who worked at them—as scientists, staff, and colleagues. I will never forget that, after Hurricane Hugo, the staff and scientists of West Indies Lab were back at work within 24 h, even though so many had lost heir homes in the storm. We were in the water within 2 days making observations and taking post-storm measurements as dedicated staff, graduate students, and visiting researchers started the long process of bringing WIL back to life while also tending to over 30 students trapped after the storm. Collectively, they and others like them have fostered the interdisciplinary spirit so deeply engrained in the early International Coral Reef Symposia. Hopefully, this volume will encourage the next generation of reef researchers to not view the details of reef function solely through their own disciplinary lens, but to think more about how we might ask questions together that we cannot even imagine alone.

Oberlin, OH, USA Dennis K. Hubbard

Acknowledgements

It is impossible to adequately acknowledge all the people that have brought this volume to this stage. At the great risk of forgetting so many, this includes colleagues at West Indies Lab—Bob Dill, Bill and Betsy Gladfelter, John and Nancy Ogden, Ivan Gill, Randy Burke, Percy and Wilmot, Hank Tonnemacher, Rich Berey. . . . and all those who brought me balance – my mom, Karla, Martha and Amy. And finally, I would be remiss if I did not thank the editors at Springer for all the help they have given us along the way. Martine van Bezooijen, in particular, encouraged us to undertake the effort in the first place. Unfortunately, her tragic passing will not let her see the end product. However, we have been fortunate to have had the continued support of Judith Terpos and Alexandrine Cheronet, without whom this would have been impossible.

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Abbreviations and Acronyms

[X]	Concentration of X, e.g., $[H^+]$
^{14}C	Amount of radioactive carbon relative to stable carbon; used for age dating
AGRRA	Atlantic and Gulf Rapid Reef Assessment
AMS	Accelerator mass spectrometry; for age dating
A_T	Total alkalinity
ATP	Adenosine triphosphate
az-coral	Azooxanthellate corals
Ba	Billion years ago (age)
BBD	Black band disease
BBL	Benthic boundary layer
BL	Boundary layer
By	Billion years (time interval)
CA	Carbonic anhydrase
CalBP	Calendar years before present (1950)
CLIMAP	Climate: Long-range Investigation, Mapping, and Prediction
COTS	Crown-of-thorns starfish
DBL	Diffusion boundary layer
DIC	Dissolved inorganic carbon
DOM	Dissolved organic matter
ΔSL	Difference in sea level from today to some time in the past
ENSO	El Niño Southern Oscillation
FST	Falling systems tract
GBR	Great Barrier Reef
GCRMN	Global Coral Reef Monitoring Network
Gnet	Net calcification
GPS	Global positioning system
HST	Highstand systems tract
HTM	Holocene thermal maximum
ICRS	International Coral Reef Symposium
IPCC	Intergovernmental Panel on Climate Change
ISRS	International Society for Reef Studies
K-Pg	Cretaceous-Paleogene
K_{sp}	Solubility product
LEC	Light-enhanced calcification
LGM	Last Glacial Maximum
LIDAR	Light detection and ranging (a high-precision altimetry system)
LIT	Line intercept transect
LST	Lowstand systems tract
Ma	Million years ago (age)
MBL	Momentum boundary layer
MPA	Marine protected area
MWP	Meltwater pulse

My	Million years (time interval)
MYA	Millions of years ago
NASA	National Aeronautics and Space Administration
OA	Ocean acidification
OAE	Ocean anoxia event
P	Pressure
P-TR	Permo-Triassic
pCO_2	Partial pressure of CO_2 (in air or water)
PETM	Paleocene-Eocene Thermal Maximum
Pg	Gross (total) carbonate produced on a reef
pHT	pH at a stated temperature (in Chap. 2 = 25 °C)
PIT	Point Intercept Transect
P_n	Net amount of carbonate remaining on a reef after sediment is exported
P_{net}	Net photosynthesis
S	Salinity
S_R	Amount of sediment removed from a reef
SST	Sea surface temperature
SW	Seawater
T	Temperature
TAZ	Taphonomically active zone
TST	Transgressive systems tract
U/Th	Ratio of uranium to thorium; used for age dating
WBD	White band disease
ybp	Years before present
z-coral	Zooxanthellate coral
ZC	Zone of rapid calcification
ZP	Zone of rapid photosynthesis
μatm	Microatmospheres: gas pressure, equal to its mixing ratio in parts per million (ppm)
ΩX	Saturation state of X

Coral Reefs at the Crossroads – An Introduction

1

Dennis K. Hubbard

Abstract

Coral reefs are complex systems that are difficult to fully understand when viewed from a single perspective. As we have separated ourselves into increasingly smaller and more specific disciplines, we often lose sight of important connections between physical and biological factors and how they can change over different spatial and temporal scales. As stresses on these robust yet fragile systems broaden and deepen, it is becoming increasingly important that we break down artificial disciplinary barriers and ask questions that are difficult to frame from a single scientific perspective. This chapter provides a jumping-off point to examine coral reefs – sitting at both a disciplinary and a temporal crossroads.

Keywords

Interdisciplinary • Multidisciplinary • Scale • Perspective

Perhaps more than any other earth system, coral reefs sit at the crossroads of science. While organisms largely provide the raw materials, reef building responds to a wide range of non-biological processes. Water temperature confines today's scleractinean coral reefs to a narrow equatorial belt. Waves & currents control regional patterns of coral dispersal, dictate where larvae might or might not survive and create the critical linkages between reefs across individual ocean provinces. The underlying edifice provides a physical structure upon which wave energy, light intensity, sedimentation and chemical cues conspire to create zonation, the fundamental underpinning of reef characterization both today and in the geologic past.

The feedbacks among all these processes are myriad; spatial complexity is built by calcifying organisms that are in turn dependent on both surface topography and the vast network of environments on and in the reef for their success. More than 85 % of the reef's surface area exists within cryptic spaces that house roughly half of the fish species (Chap. 10) and similar proportions of other organisms living within the ecosystem boundaries. Understanding the nature and significance of these complex interactions is critical whether we are considering modern reefs (Chaps. 2, 4 and 5), their forebears throughout geologic time (Chaps. 3, 6, 7, 8, 9 and 10), or their descendants in an increasingly stressful world (Chaps. 9, 11 and 12).

Most recently, coral reefs have reached another crossroads. They evolved over the past 500 million years (Chap. 8) in response to large-scale changes in ocean processes (Chap. 9). While truly "pristine" reefs may not have existed for a very long time (Pauly 1995; Jackson 1997; Pandolfi et al. 2005), the past three decades have witnessed fundamental changes that have been far greater than anything documented over just the previous century (Wilkinson 2008; Jackson et al. 2014). Providing effective strategies for documenting and mitigating recent decline (Chap. 12) will require an approach that embraces a variety of disciplines that can transform scientific understanding into social will and political implementation. This volume will hopefully provide a starting point for reconnecting the different perspectives from which we view reef development.

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The persistence of this critical natural system may depend on our ability to tie together seemingly disparate views. In any event, this will certainly make our individual understanding richer.... and a lot more fun.

1.1 Coming Together

The proceedings of the first International Coral Reef Symposium in 1969 contained only 22 scientific papers. However, they covered 11 broad topics ranging from reef distribution and ecology to the geology of uplifted islands, research methods, and even the history of reef science – while spanning nine separate ocean regions. The number of papers from the second meeting increased fivefold and the topics were broadly distributed among biology, geology, chemistry, physical oceanography and management across an even wider geographic range. Presentations included some of our earliest discussions of coral biogeochemistry (Smith 1974), reef controls by sea-level rise (Hopeley 1974) and reef accretion in both the Atlantic (Land 1974) and the Pacific (Tracey and Ladd 1974).

Just as important was the consistent intersection of disciplines focusing on a single theme – coral reefs. The idea in the earlier meetings was to encourage the movement of participants freely and often from one topic or session to another. Their most unique element was that participants were drawn by a single interest in reefs and not the discipline that they occupied for the other 360 or so days of the year. More so than many that followed, the earlier ICRS meetings reminded us that we could learn more in a diverse group asking what we don't know than with close colleagues discussing what we think we do.

Our perceptions of coral reefs vary both spatially and temporally. Biologists can observe and manipulate complex processes in ways that are impossible for geologists to reproduce. However, these are generally limited to small areas and short intervals of time. Geologists have traditionally relied on biological models to understand the past, but are increasingly using their longer perspective to provide a view of reefs absent the stresses of climate change and other manifestations of human proliferation. Chemists can look at both minute and broad scales, providing what would be otherwise overlooked processes. Modelers can take seemingly disparate observations and combine them into simulations that can test existing ideas and generate new ones begging for field data. More recently, monitoring and management have increasingly relied on information generated from scientific studies to make wise decisions while, at the same time, asking questions that science has not yet realized are "important".

As we ponder the recent and dramatic changes on coral reefs, it is difficult to quantify factors beyond the scale of a single experiment or an individual researcher's career. Conversely, geologists consider broad expanses of time and space, but too often forget that this larger view is the cumulative result of small and short-lived events. The collective record was probably controlled more by these day-to-day factors than we acknowledge, and millennial scale processes alone cannot explain the time-averaged fossil record. Chemistry, physics, oceanography and a host of other related disciplines likewise contribute to the overall picture but, like biology and geology, each has its own unique perspectives, priorities and limitations. And, as short as the biological time-scale might seem to geologists, the election cycle of politicians and policy-makers can render coral reefs as little more than distractions. However, when all the perspectives of too-often disparate groups are combined effectively, they can provide insight that is impossible within any single discipline. This realization was at the core of the early reef symposia where much time was spent just talking about "how reefs work". This volume hopes to rekindle interests in viewing common problems from different perspectives.... together.

1.2 Our Changing View

On the morning of May 5th, 1961, Alan Shepard left Cape Canaveral on America's first manned flight into space, a journey that would last only 15 min and 22 s. Four minutes after launch, he deployed his periscope (windows were not added until two flights later) and reported, " What a beautiful view.... I can see Okeechobee.... identify Andros Island.... identify the reefs" (Hammack et al. 1961). Within a minute, he fired the first of three retro-rockets that would bring him back to the surface just 500 km from where he began.

Shepard's view from *Freedom 7* (Fig. 1.1) represents our earliest remote observation of Earth from space[1].... and what he saw were the reefs along Great Bahama Bank. Since then, we have seen photos of Earth from the moon . . . and even farther as Voyager 1 departed the solar system in August of 2012. As a result, we have become accustomed to the spectacular images generated by manned spacecraft and orbiting satellites (e.g., Fig. 1.2). Students who have easy access to images on "Google Earth" and "Google Maps" on their cell phones take these for granted, failing to appreciate the limited perspective from low-flying aircraft in the latter twentieth century, just as we failed to appreciate challenges on the deck of the Beagle and other nineteenth

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[1] Three weeks earlier (April 12, 1961), Yuri Gagarin had completed a single orbit around Earth. However, the small viewing port beneath his feet was configured to view Earth only for a final alignment during re-entry.

Fig. 1.1 Photograph taken by the automated camera system of *Freedom 7* on Alan Shepard's first US space flight in 1961 (Courtesy of NASA)

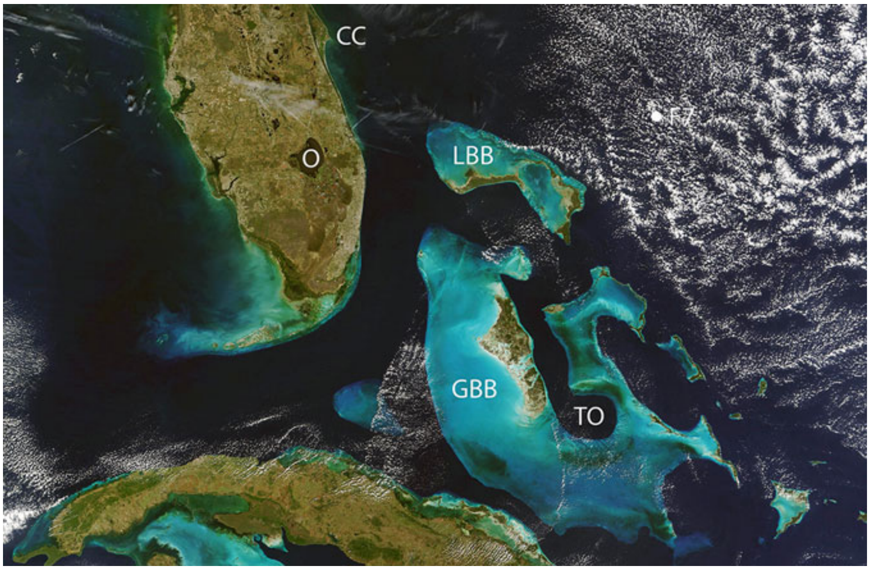

Fig. 1.2 NASA image of Florida and the northern Bahamas. The flight of *Freedom 7* lasted less than 16 min and covered only 500 km from Cape Canaveral (*CC*) to the "splashdown" site (F7) northeast of Little Bahama Bank (LBB). *O* Lake Okeechobee, *GBB* Great Bahama Bank, *TO* Tongue of the Ocean (Courtesy of NASA)

century sailing vessels. We have access to terabytes, petabytes, or even zettabytes of data and increasingly rely on satellite images, huge banks of remotely collected data and complex computer models of natural systems to conceptualize processes operating at scales ranging from microscopic to global.

However, this ever-broadening view has been accompanied by a narrowing of our individual focus. At the time of Darwin, natural philosophy blurred the boundaries between biology, geology, chemistry, physics and even the humanities. His seminal ideas on the role of subsidence in the evolution of Pacific reefs from narrow fringes along volcanic slopes to atolls were born not from the lofty perspective of orbiting satellites. Rather, they were the logical explanation for patterns revealed in early maps and the logs of observant seamen. According to Darwin, the solution was so obvious that "the whole theory was thought out on the west coast of S. America before I had seen a true coral reef".[2]

Today, the evolving scientific landscape has increasingly "organized" us into rigid disciplines or even sub-disciplines. Meaningful discussions still occur, but the goal is more often to seek validation or clarification of specific concepts than it is to question what we might be missing by staying in a familiar intellectual space. Even scientists working on large vessels that are funded by multi-disciplinary programs too often have separate research agendas and work on deck at

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[2] Barlow N (1958) The autobiography of Charles Darwin 1809-1882, with the original omissions restored: http://darwinonline.org.uk/content/frameset?itemID=F1497&viewtype=text&pageseq=1, page 98.

different hours to maximize costly ship time. It is more common for different research groups to focus on their own piece of the larger puzzle than it is to look for questions that can only grow out of interactions within a broader group. There are exceptions, but they are too few.

Past attempts to bring different perspectives together in a single volume have still tended to focus largely on one discipline, perhaps adding a thoughtful contribution from another for context. For example, treatments of reefs through time have tended to use a description of modern reefs as a backdrop against which a primarily historical discussion of deep time can be set. Conversely, a volume might start with a broad-brush treatment of reef controls or evolutionary changes in reefs over time to introduce the largely biological themes that follow. Even the seminal *Biology and Geology of Coral Reefs* was organized in four volumes that tended to treat the two disciplines separately.

The goal in the following pages is to focus on a few broader themes, using contributions by different authors to highlight alternative ways of thinking about each. Obviously, this cannot be exhaustive either within or between topics. The main strategy is to group contributions that address a few important areas from different perspectives. Our hope is that readers drawn to chapters written by experts in their discipline will also examine related chapters that consider the same topic from a different viewpoint.... and that this will inspire them to look elsewhere in the volume and in the annals of reef studies with a new eye.

1.3 A Brief Look Back

In the nineteenth century, naturalists struggled to understand both the structure of coral reefs and the distribution of organisms that inhabited them. Much of the early understanding of coral zonation came from sounding leads and dredging. However, even with the crude methods available at the time, the depth limits for most modern corals were surprisingly well constrained to between 20 and 30 m, seemingly at odds with suggestions that reefs appeared to have built from significant depths.

The solution came from geologists in the form of subsidence. Charles Lyell (1832) suggested that atolls might have formed atop the rims of volcanic craters. As they sank, reef building offset subsidence, resulting in accumulations much thicker than the depth range across which corals were known to occur. Charles Darwin (1842) considered the specific tie to crater rims to be “a monstrous hypothesis”[3] and suggested instead that reefs evolved from fringes along the flanks of subsiding volcanic cones to barrier reefs and atolls as the central landmass sank beneath the waves. Darwin’s (1842) answer for “the coral reef problem” spurred a heated debate that would last for over half a century.

Mojsisovic (1879) similarly argued that the well-developed coral reefs preserved in the Dolomites were the result of major tectonic uplift rather than a biblical deluge or any other upward excursion of sea level. His argument benefitted from the general acceptance of uplift as an important geologic process. However, the evidence for Darwin’s subsidence hypothesis lay beneath the water, making his ideas just as problematic for empiricists like Alexander Aggasiz as they had been for biblical literalists like his father, Louis. The debate continued for over half a century until cores on Funifuti (Royal Society of London 1904) and Bikini Atolls (Emery et al. 1954; Tracey and Ladd 1974) revealed their volcanic ancestry.

The link between tectonic forces and carbonate island building remained the “important” question of the day... so much so that William Morris Davis (1928) characterized an overnight stay on the reef off Cairns as, “entirely fruitless as far as the origin of the reef is concerned”.[4] But, the “age of reef ecology” would soon come. A host of marine biological labs can trace their roots back to at least the nineteenth century, but anything akin to modern coral-reef ecology had to wait for the development of the demand regulator (aka scuba) in 1943. This opened an era of intense exploration that allowed us to closely observe, measure and photograph marine systems. In the early 1950s, Tom Goreau visited Discovery Bay where he would eventually create a small marine lab in 1965. For decades, it grew and attracted scientists from different disciplines who repeatedly demonstrated the value of interdisciplinary study focusing on a specific natural system – the coral reef. Another notable Caribbean example was the West Indies Laboratory in the U.S. Virgin Islands, the brainchild of H. G. Multer and Fairleigh Dickinson Jr. Many marine scientists, some of them contributors to this volume, benefitted from the thoughtful discussions among mentors and peers brought together at these two facilities. Marine labs and field stations have come and gone, but the latter part of the twentieth century marked what was arguably an unparalleled growth of interdisciplinary, field-based, coral-reef studies, much of this owing to such places.

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[3] Letter to Caroline S. Darwin dated 29 April, 1936: http://www.darwinproject.ac.uk/entry-301#mark-301.f2

[4] See the discussion of W.M. Davis’ support of Darwin’s subsidence theory by Hopley (1982).

1.4 Where Are We Now?

Until the 1980s, researchers spent most of their time documenting and explaining complex interactions among reef organisms and the edifice where they lived. The explosion of predators like *Acanthaster* on the Great Barrier Reef and the rapid decline of coral cover on Atlantic and Caribbean reefs suddenly expanded the "mundane" and underappreciated activity of coral-reef monitoring. The focus was more on decline than it was on function, and arguments over the relative importance of top-down (mostly overfishing) versus bottom-up stresses (e.g., nutrients) reflected a perception that impacts were to be found on this side of the horizon.

Arguments over methodology were often as heated as those over the dominant causes of decline and the solutions that might reverse it. What level of decline do we want to detect? Do we measure using fixed quadrats, rigid linear transects or irregular ones that take into account the spatial complexity of the reef surface? Direct measurement of coral abundance was the standard but required long and expensive hours spent underwater. Photographs and video were more efficient in the field but too often could not resolve small organisms, especially in hidden cryptic spaces. As field costs soared and image resolution improved, the scales gradually tipped toward photographic or video surveys. While we might think of this as a unique evolution of methods in response to new and specific needs, we should consider that the earliest practitioners had already had this discussion. While neither of the cameras in Fig. 1.3 enjoyed widespread use, the principles inherent to both underwater documentation and monitoring owe their origins to these and other early attempts.

Most recently, rising temperatures and changing ocean chemistry have broadened the discussion. The inadequacy of any single discipline to fully understand these and other problems we face should come as no surprise. Chemists and biologists have combined forces to address possible impacts of ocean acidification. Detailed genetic studies have revised our taxonomy and have provided unique ways to track evolutionary patterns of reef organisms and pathogens that threaten them. Remote sensing has evolved a complex alert system for bleaching and disease. Huge databases provide valuable repositories for information that can be combined to address critical problems, some never envisioned by their creators. And modeling can combine this information with new field and laboratory data to better constrain the controls of observed patterns and address future scenarios that we are yet to experience. Nevertheless, problems are growing faster than resources to study them and we need to figure out how to better triage the growing list of impacted species and systems. The answer is arguably the greater rigor and power of questions and protocols generated by groups of diverse investigators with related interests.

1.5 Where Are We Headed?

Wendell Berey (1987) reminded us that, "in order to understand what we are doing, we need to understand what nature would be doing if we were doing nothing." Observations and

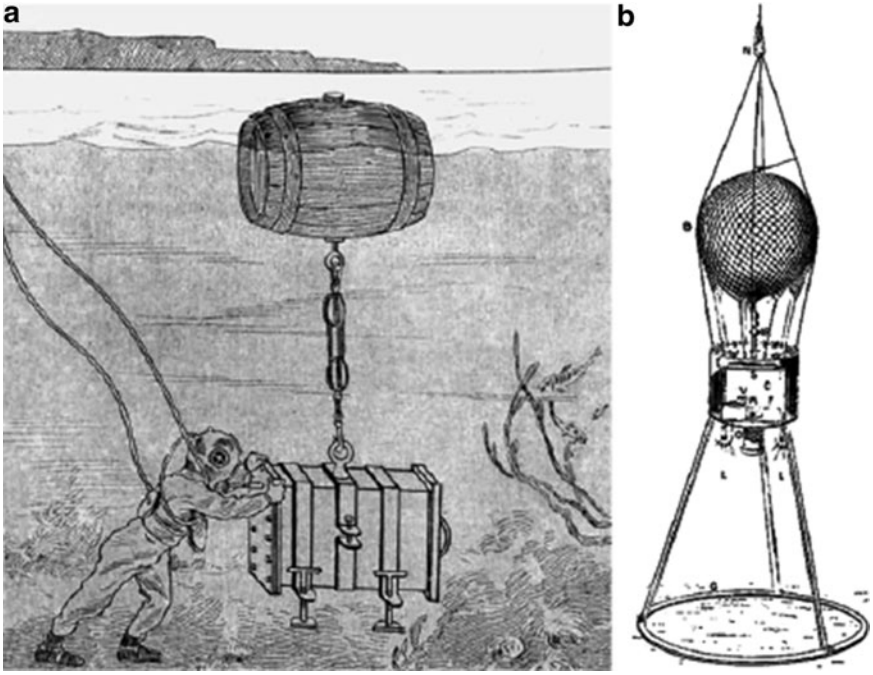

Fig. 1.3 Early underwater cameras. (**a**) Underwater camera system designed by Louis Boutan in the late nineteenth century for recording general underwater scenes. Low light levels and the insensitivity of early photographic plates required exposure times of up to 30 min (From Boutan 1900, p. 198). (**b**) Proposed camera for photographing the seabed. This apparatus, conceived by Regnard (1891, p. 72), was never put into practical use

measurements on modern reefs provide important information that allows us to better understand the nature and the magnitude of recent change. However, they have often been short-lived and all of them record changes that occurred long after the first human stresses were applied. Historical records predate our most ambitious monitoring efforts, the lifetime of a scientist, and especially the attention span of the political body. However, they still fail to accurately record the accumulated stresses that were already contributing to environmental instability – even if their impacts remained hidden until recently. The geological past provides an opportunity to more-realistically consider reefs when "we were doing nothing", but the record is both intermittent and incomplete due to selective preservation and time averaging. However insightful any approach might be by itself, when combined with others, it can help us with the triage we are currently undertaking – whether we are looking to the past, trying to predict the future, or just want to understand how a reef works.

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2 Coral Calcification and Ocean Acidification

Paul L. Jokiel, Christopher P. Jury, and Ilsa B. Kuffner

Abstract

Over 60 years ago, the discovery that light increased calcification in the coral plant-animal symbiosis triggered interest in explaining the phenomenon and understanding the mechanisms involved. Major findings along the way include the observation that carbon fixed by photosynthesis in the zooxanthellae is translocated to animal cells throughout the colony and that corals can therefore live as autotrophs in many situations. Recent research has focused on explaining the observed reduction in calcification rate with increasing ocean acidification (OA). Experiments have shown a direct correlation between declining ocean pH, declining aragonite saturation state (Ω_{arag}), declining [CO_3^{2-}] and coral calcification. Nearly all previous reports on OA identify Ω_{arag} or its surrogate [CO_3^{2-}] as the factor driving coral calcification. However, the alternate "Proton Flux Hypothesis" stated that coral calcification is controlled by diffusion limitation of net H^+ transport through the boundary layer in relation to availability of dissolved inorganic carbon (DIC). The "Two Compartment Proton Flux Model" expanded this explanation and synthesized diverse observations into a universal model that explains many paradoxes of coral metabolism, morphology and plasticity of growth form in addition to observed coral skeletal growth response to OA. It is now clear that irradiance is the main driver of net photosynthesis (P_{net}), which in turn drives net calcification (G_{net}), and alters pH in the bulk water surrounding the coral. P_{net} controls [CO_3^{2-}] and thus Ω_{arag} of the bulk water over the diel cycle. Changes in Ω_{arag} and pH lag behind G_{net} throughout the daily cycle by two or more hours. The flux rate P_{net}, rather than concentration-based parameters (e.g., Ω_{arag}, [CO_3^{2-}], pH and [DIC]:[H^+] ratio) is the primary driver of G_{net}. Daytime coral metabolism rapidly removes DIC from the bulk seawater. Photosynthesis increases the bulk seawater pH while providing the energy that drives calcification and increases in G_{net}. These relationships result in a correlation between G_{net} and Ω_{arag}, with both parameters being variables dependent on P_{net}. Consequently the correlation between G_{net} and Ω_{arag} varies widely between different locations and times depending on the relative metabolic contributions of various calcifying and photosynthesizing organisms and local rates of carbonate dissolution. High rates of H^+ efflux continue for several hours following the mid-day G_{net} peak suggesting that corals have difficulty in shedding waste protons as described by the Proton Flux Model. DIC flux (uptake) tracks P_{net} and G_{net} and drops off rapidly after the photosynthesis-calcification maxima, indicating that corals can cope more effectively with the problem of limited DIC supply compared to the problem of eliminating

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H^+. Predictive models of future global changes in coral and coral reef growth based on oceanic Ω_{arag} must include the influence of future changes in localized P_{net} on G_{net} as well as changes in rates of reef carbonate dissolution. The correlation between Ω_{arag} and G_{net} over the diel cycle is simply the result of increasing pH due to photosynthesis that shifts the CO_2-carbonate system equilibria to increase $[CO_3^{2-}]$ relative to the other DIC components of $[HCO_3^-]$ and $[CO_2]$. Therefore Ω_{arag} closely tracks pH as an effect of P_{net}, which also drives changes in G_{net}. Measurements of DIC flux and H^+ flux are far more useful than concentrations in describing coral metabolism dynamics. Coral reefs are systems that exist in constant disequilibrium with the water column.

Keywords

Calcification • Corals • Ocean acidification • Seawater CO_2-carbonate system • Aragonite saturation state • Boundary layers • Phase lag

2.1 Introduction

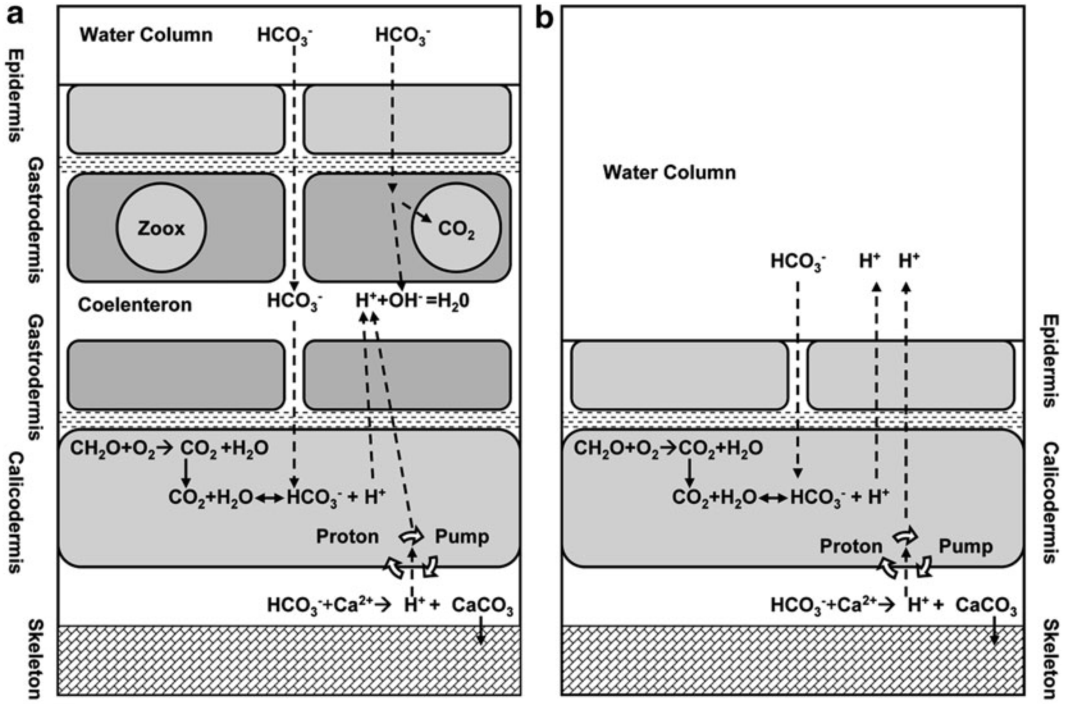
Reviews have recently been published on coral calcification (Allemand et al. 2011), on the effects of ocean acidification on coral calcification (Erez et al. 2011) and on the geological record of ocean acidification (Hönisch et al. 2012). These documents provide a wealth of background information. This chapter provides an updated synthesis including new insights on coral physiology and calcification relevant to the geology and paleo-ecology of coral reefs.

2.1.1 Basic Coral Anatomy and Physiology

Reef corals are coelenterates formed by an outer body wall and a basal body wall that enclose a space called the coelenteron. Terminology used here follows that of Galloway et al. (2007). The outer body wall in contact with sea water consists of two tissue layers – an outer epidermis and an inner gastrodermis separated by a jelly-like substance called mesoglea (Fig. 2.1a). Likewise, the basal body wall is a mirror image that consists of the calicodermis and a gastrodermis separated by mesoglea. The space between the two body walls is a cavity called the coelenteron, which interconnects the polyps of the colony and opens to the external seawater through the polyp mouths. The intracellular symbiotic zooxanthellae reside mainly within the cells of the gastrodermis of the surface body wall. The zooxanthellae are photosynthetic and are capable of providing all of the energy needed for basic metabolism of the coral (Muscatine et al. 1984). However, heterotrophic food inputs are still important. Well-fed corals exhibit higher growth rates and greater stress tolerance compared to less-fed colonies (Ferrier-Pagès et al. 2003; Grottoli et al. 2006; Edmunds 2011; Connolly et al. 2012). Calcification occurs in the calcifying fluid located between the calicodermis and the skeleton. A presumed proton transfer process increases the pH and saturation state of the fluid to a point where $CaCO_3$ crystallizes onto the skeleton as aragonite (Furla et al. 2000a, 2000b; Cohen and McConnaughey 2003; Allemand et al. 2004; Cohen and Holcomb 2009; Venn et al. 2011). Energy is needed to drive this process with up to 30 % of the coral's energy budget devoted to calcification (Allemand et al. 2011).

The contemporary four cell-layer structure with metabolic pathways as proposed by Furla et al. (2000a, 2000b) and Allemand et al. (2004) is shown in Fig. 2.1a. This model requires neutralization of the H^+ produced by calcification using OH^- produced by photosynthesis. However, there is a contradiction. The distal areas of the corallum that are growing most rapidly lack gastrodermal cells and their contained zooxanthellae (Gladfelter 1982; Brown et al. 1983; Gladfelter 1983; Tambutté et al. 2007). Jokiel (2011a) hypothesized that H^+ is released directly into the water column in rapidly calcifying areas of the coral (Fig. 2.1b). An alternative explanation is that OH^- is transported from areas of the coral undergoing rapid photosynthesis to areas of the coral undergoing rapid calcification. McConnaughey and Whelan (1997) proposed that calcification at branch tips could discharge protons into seawater within the coelenteron. This water could be transported by ciliary currents to the abundant photosynthetic zooxanthellae in the lateral polyps.

Most studies involve incubation of corals in static containers under controlled conditions with extrapolation of the changes measured in the carbonate-CO_2 chemistry of bulk seawater to precipitation of $CaCO_3$ in the calcifying fluid adjacent to the coral skeleton. These results must be viewed with caution because there is an organism located between the calcifying space and the bulk water being measured as well as a boundary layer (BL) between the organism and the water column. Calcification is under biological control and mediated by organic tissue that separates the calcifying surface from overlying seawater. Therefore calcification occurs in a medium (i.e. the



Four cell layer model
(Furla et al. 2000; Allemand et al. 2004).

Two cell layer modification of model
for areas of rapid calcification.

Fig. 2.1 Classic four cell-layer model of calcification (**a**) compared to two cell layer structure of rapidly calcifying areas of the corallum (**b**) as described by Tambutté et al. (2007). Note that protons generated by calcification in (**b**) are shown being released directly into the water column rather than being neutralized by photosynthesis as proposed by Furla et al. 2000a, 2000b; and Allemand et al. 2004 (Figure from Jokiel (2011b) used with permission from the Journal of Experimental Marine Biology and Ecology)

calcifying fluid) that has different carbonate-CO_2 chemistry than the bulk seawater as materials are exchanged through the BL. Additional information on processes occurring within the coral tissues and the BL has been provided through use of microprobes (Kühl et al. 1995; Al-Horani et al. 2003a, 2005a), isotope chemistry (Goreau 1977; Allison et al. 1996; Al-Horani et al. 2005a) and direct measurement of pH within coral tissues (Venn et al. 2009, 2011, 2013). Most of the models have focused on rates of biological processes that occur at the interface between the calicodermis and the coral skeleton (Fig. 2.1a). More recently, Jokiel (2011a, 2011b) has developed a model based on physical control of material flux through the BL and into the water column (Fig. 2.1b).

2.1.2 Coral Morphology

The growth forms of reef corals (Fig. 2.2) are extremely varied (Veron 2000), which has confounded understanding of basic metabolic processes and patterns of calcification. How can a simple organism consisting of only two tissue layers with a total of four cell layers produce so many intricate growth forms? The key to understanding lies in the observation (Fig. 2.3) that all coral growth forms can be reduced to the topological equivalent of a hemisphere containing the photosynthetic polyps and/or tissues containing dense concentrations of zooxanthellae (zone of rapid photosynthesis or ZP) surrounded by a hemisphere dominated by calcification polyps and/or tissues devoid of zooxanthellae (zone of rapid calcification or ZC). Cells and polyps located in the distal portions of a colony (ZC) have few or no zooxanthellae, giving these areas a white appearance (Figs. 2.2 and 2.3).

2.1.3 Models of Light Enhanced Calcification (LEC)

The discovery that calcification in reef corals is accelerated in the light (Kawaguti and Sakumoto 1948) led to the conclusion that photosynthesis by zooxanthellae must somehow be involved in the biochemical pathways of calcification. Experimental evidence was eventually developed by Vandermeulen et al. (1972) who showed that blocking photosynthesis results in a marked reduction in calcification. A number of LEC models have been presented (reviewed by Gattuso et al. 1999; Cohen and Holcomb 2009; Allemand et al. 2011). Goreau (1959) proposed that calcification is