Reef Biology and Geology – Not Just a Matter of Scale

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Dennis K. Hubbard

Nature is what nature is. . ... science is what we think nature is on a given day.

(A. Conrad Neumann)

Abstract

The geological distribution and developmental history of coral reefs have been largely controlled by physical factors such as plate tectonics, sea-level changes, wave energy, salinity, light, temperature, nutrients, sediment, and antecedent topography. Although the geological and biological patterns have generally been consistent over the past 12,000 years, sub-millennial intervals of variation remind us that long-term patterns provide only part of the picture. Looking forward, changes in seawater temperature, storm intensity, aragonite saturation state and pH may bring a major shift in the balance between carbonate production, destruction and export. While rising sea level alone will probably not significantly change reef communities or over-top low reef islands, even small increases of water depth will have disproportionate effects on the wave energy passing over the reef crest. Moreover, the impacts of increasing storminess will rival declining coral cover as a major control over the carbonate budget of coral reefs in the coming century. Understanding what is to come will require a perspective that is impossible from any single discipline.

Keywords

Carbonate budget • Development • Holocene • Accretion • Zonation

3.1 Introduction

By the 1990s, the decline of “reef health” was already a focal point in both the popular and scientific literature. Outbreaks of the crown-of-thorns seastar *Acanthaster planci* had devastated large sections of the northern Great Barrier Reef (Endean 1973; Moran 1986). In the Caribbean, overfishing (McClanahan and Shafir 1990), followed by the sudden and still largely unexplained population crash of the long-spined sea urchin *Diadema antillarum* (Lessios et al. 1984) resulted in a shift from reefs dominated by corals to those on which macroalgae were the principal component (Hughes 1994; Jackson et al. 2014). In the years immediately following its original description (Gladfelter 1982), White Band Disease (WBD) had been largely ignored. However, the subsequent decimation of the *Acropora palmata* community throughout the Caribbean and western Atlantic by WBD (Aronson and Precht 2001b) put it at the center of the debate on community stability and its relationship to reef development. Harvell et al. (1999) described a host of new diseases and the list continues to grow. A scientific focus on increasing coral bleaching and disease triggered U.S. congressional hearings in 1992 and a greater popular awareness of the declining state of the world’s coral reefs.

None of these issues have gone away since “Life and Death in Coral Reefs” first appeared in 1997. Overall reef decline continues (Gardner et al. 2003; Hughes et al. 2003;

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Carpenter et al. 2008; Burke et al. 2011; De'ath et al. 2012). In the Caribbean, White Band Disease has been joined by others that have attacked the genus *Orbicella* in particular (Bruckner and Hill 2009). While the region is home to only 8 % of the world's coral reefs, it has been the focus of over half of the world's disease reports (Harvell et al. 2004). Looking ahead, we anticipate increased pressure by combined bleaching and disease (Miller et al. 2009), lower pH (Zeebe and Wolf-Gladrow 2001; Hoegh-Guldberg et al. 2007), accelerating sea-level rise (Church and White 2011) and increasing storm intensity (Webster et al. 2005).

Reef decline is nothing new, not historically and certainly not geologically. Caribbean coral diversity has been declining for at least the past 30 million years in response to a gradual restriction of what was once a great circum-equatorial Tethys Sea some 200 million years ago (Frost 1977). The final door was slammed shut on Atlantic-Pacific larval exchange with the formation of the Isthmus of Panama over the past few million years (Murdock et al. 1997; Vermeij 1978, 1993). More recently, *Homo sapiens* has exerted ever-greater control on reef development as population has increased and, with it, human exploitation of critical habitats and resources in tropical coastal areas. Changes in tropical wetness over the past 12,000 years (Hodell et al. 1991; Thompson et al. 1995; Gasse 2000) have facilitated an agrarian society and the more intense resource utilization that accompanies it. Jackson (1997) proposed that the reefs we all consider "pristine" in our recent discussions had already suffered significant decline long before ecologists started looking carefully at coral reefs, and certainly before serious monitoring efforts began.

In the 1980s the emphasis was more on site-specific and seemingly isolated decline related to nearby centers of human exploitation. Gradients of increased impact in the direction of cities, coastal development projects or other intensive anthropogenic activities drove research toward understanding the links between stress and coral decline on the scale of single reefs. Management strategies were largely focused on identifying problems that could be tied to a specific cause and then mediating that perceived source of stress by legal regulation. Inherent in this strategy was the pragmatic concept of establishing thresholds below which development could continue with "acceptable" levels of local decline.

More recent changes in how we think about reef decline have been driven by a growing awareness of the interconnectedness of global systems. It has become increasingly apparent that changes on "our" reef may be as much a result of distant forces as those we can measure locally. As our focus shifts more toward global controls, factors like intensification of atmospheric instability due to rising global temperatures, faster sea-level rise, and the potential for facilitating pathogenic stressors have expanded. As a result, our management perspective has broadened to include factors that are not specific to a single reef or even a single region. With this redirection has come a heightened awareness that we need to think about coral reefs at a variety of spatial and temporal scales: from genetic shifts at the cellular level to the response to pollution at the organism level and vertical accretion across entire reefs – all in light of recent climatic shifts occurring at local, regional and even global scales. Equally important is temporal scale – from the duration of individual studies where processes can be observed and measured up through time spans greater than the lives of individual researchers or even the disciplines of ecology or geology.

3.2 The Importance of Perspective

This chapter considers the processes that control the "look" of modern coral reefs and their fossil forebears. The scale on which these processes occur is discussed along with the varying perspectives of researchers from different disciplines. Biologists have the advantage of being able to directly observe and measure changes in both processes and the organisms that they control. The accuracy of their characterizations is limited only by their originality and the sensitivity of the methods and instruments that they use. However, this ability to directly observe comes at a price. The intensity and resulting costs associated with such detailed measurements make it difficult to conduct studies over larger areas. As a result, "typical" areas are often described as proxies for much larger pieces of real estate. Also, the lifetime of individual researchers and the short attention span of funding agencies severely limit the temporal perspective of even the best site-specific investigations. Mapping provides a detailed snapshot of what a reef looks like, the myriad interactions on that landscape and the processes that mediate either change or stability. Monitoring records provide a short "newsreel" of change over a funding cycle or, at best, the career of an individual researcher. Most recently the "headlines" have focused on decline. What is missing is the context of the longer-term record within which these brief events have occurred. To illustrate this one need only consider that the duration of a National Science Foundation Long-Term Ecological Monitoring program is typically a few decades at best.

In contrast, geologists must deal with a fickle record that has been ravaged by **taphonomy** (the selective and taxonomically biased preservation of different organisms in different physical settings), **diagenesis** (the chemical changes that obliterate or obscure details after burial) and **erosion** (the wholesale removal of entire, and often extensive intervals of time). What is left are the tattered remains of a full-length motion picture with pieces of film marred by countless splices, seemingly endless scratches that obscure fine detail, and even changes in the starring actors midway through the film. Evolutionary changes make comparison with modern scleractinians difficult at best, and the blurring of the record by unknown physical and chemical forces since original deposition only make things worse. The perspective of great space and time offers countless advantages over shorter-term studies. What is often missing, however, are the details that characterize modern biological investigation.

The challenge is to take the best of both and combine that into an integrated view that gives us our best chance of accurately separating natural from anthropogenic change. What can we take from modern biological studies to help us understand the distant past and the vagaries of reef evolution? What can we learn from the longer but poorer geologic record that might help us to put the recent decline revealed by monitoring studies into a longer-term natural context? While fraught with peril, this integrated approach should be the holy grail of management. However difficult the task, effectively integrating and comparing geological and biological data is what presently stands between effective management strategy and the misdirection of already limited environmental capital to things that are either beyond our control or “aren’t really broken”.

The initial version of this chapter that appeared in 1997 focused primarily on scale as a way to explain how biologists and geologists see reefs differently. While that is still a central theme, challenges related to climate change have added different dimensions that cannot be explained by simple scaling. Even biologists are thinking more about larger-scale carbonate cycling as carbonate producers are being lost, ocean chemistry has made it more difficult to maintain a skeleton and changing nutrient regimes are fundamentally changing the balance between carbonate producers and organisms that destroy substrate. However, this view still remains fundamentally biological in nature.

It is becoming increasingly obvious that physical factors are playing an expanding role that cannot be adequately addressed by even the best short-term study that focuses solely on biotic interactions. The contributions of diversity to the complex structure that we call a reef come full circle when we recognize that this heterogeneity, in turn, controls the organisms that it can support. Bioerosion is flattening reefs, changing both their physical and biological structures. The fate of bioeroded sediment within the system is changing drastically as larger storms appear to be more commonplace. Thus, the shift toward greater physical control may suggest that our different perspectives of “change” are more than just looking at the same suite of biologically dominated processes through different lenses. The fate of low-lying islands will be defined as much by physical factors like sediment transport, the increasing loss of protection by lagging reefs and the greater loss of detritus as storms become more violent as it will be by declining abundance and diversity.

This chapter is divided into three parts. The first outlines the dominant factors controlling the location and character of coral reefs today and, by extension, in the geologic record. Having established these basic controls, we will turn briefly to how corals have built the massive structures beneath them. Finally, we attempt to integrate all this information into a consideration of reefs under the influence of global change. For obvious reasons, the latter will carry an admittedly geologic bias, in large part due to the training of the author. However, it is also somewhat purposeful inasmuch as the biological perspective has historically dominated the discussion of reef decline. The greatest possibility for a new contribution to the dialog would, therefore, perhaps lie outside that area.

3.3 Processes That Control Reef Development

The following pages discuss the factors that are generally thought to be critical in determining where reefs occur today and what they look like. To facilitate the presentation, these have been broken down into three groups, based on the scale at which they are most important. However, some can operate at different scales and boundaries often overlap. Macro-scale processes are those that exert control either globally or over very large distances (i.e., thousands of kilometers) and over longer periods of time. Primary among these are worldwide changes in sea level and large-scale movements of the Earth’s crust. Meso-scale processes are generally physical-oceanographic in nature and operate within individual oceans or basins (e.g., latitudinal changes in mean water temperature, variations in wave energy across an ocean basin) and over historical time scales. Micro-scale processes are those that affect organisms at the spatial scale of individual reefs and over a time scale from individual studies to the career of a researcher. Purposefully absent from this discussion, although no less important, are even shorter-term (e.g., minutes to days), organism-level processes that are detailed in other chapters within this volume. The miniscule attention span of politicians is below the threshold of this discussion.

3.3.1 Macro-scale Controls

3.3.1.1 Tectonics

Our earliest reef studies focused on the role of major crustal shifts in preserving fossil reefs. Workers in the Italian Alps and elsewhere during the nineteenth and early twentieth centuries (e.g., Darwin 1842, 1913; Mojsisovics 1879) concluded that great upheavals of the Earth’s surface must have been responsible for fossil reefs that occurred so far

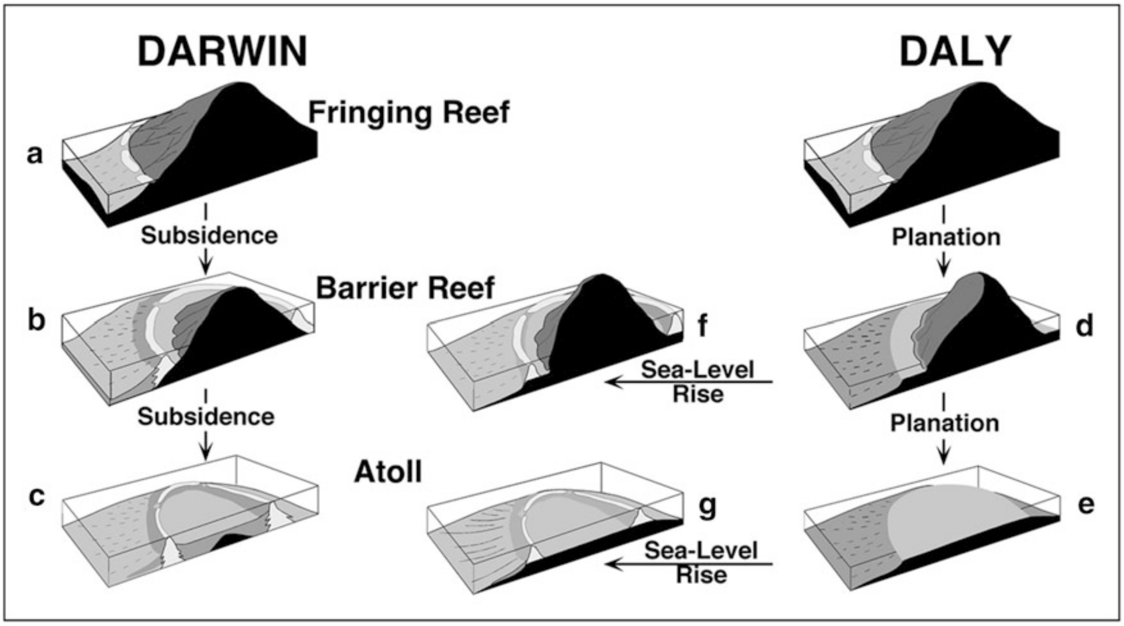


Fig. 3.1 Two theories on the origin of fringing reefs, barrier reefs and atolls. Darwin felt that the spatial patterns he observed from the H.M.S. Beagle reflected an evolutionary sequence. As a volcano subsides, the reef accretes vertically to stay near sea level and the fringing reef (**a**) evolves into a barrier reef (**b**) and, eventually, an atoll (**c**). In contrast, Daly (*right*) envisioned changing sea level as the sole determinant of reef character. During a lowstand, waves plane off a platform (**d**, **e**). During the ensuing sea-level rise, reefs form near the edge of the new shelf. Whether a barrier reef (**f**) or an atoll (**g**) will form depends on the extent of the island's removal. Deep cores through Eniwetak and Bikini Atolls eventually vindicated Darwin's hypothesis

above sea level. It was already known that, while modern shallow-water corals do not generally exist at depths greater than 100 m, many fossil reefs attained a thickness of hundreds or even thousands of meters. It was correctly posited that this reflected the upward building of the reef by organisms within the photic zone as the foundation beneath them sank gradually – the process of **subsidence** (Darwin 1842).

Throughout the 1800s, the geological community debated over how subsidence related to reef development. In 1832, Charles Lyell suggested that modern atolls might be thin calcareous crusts atop submerged crater rims with upward coral growth offsetting subsidence:

> . . . we might imagine, that if Java and Sumatra were submerged, they would give rise to a somewhat similar shape in the bottom of the sea; for the volcanos of those islands observe a linear direction, and are often separated from each other by intervals, corresponding to the atolls of the Maldivas; and, they might leave an unfathomable ocean in the intermediate spaces. p. 286

Lyell's early discussion of the continuum of process through geological time had a profound influence on a young Charles Darwin. Based on observations in Pacific and Indian Ocean atolls, Darwin (1842) similarly argued that the worldwide distribution of reefs could be explained by underlying geologic processes. He proposed that fringing reefs, barrier reefs, and atolls represented an evolutionary continuum from the former to the latter (Fig. 3.1). Like Lyell, he envisioned a volcanic island slowly sinking, but did not tie reef building to the crater rim; atolls formed only after full submergence of the volcanic cone, but fringing and barrier reefs formed as soon as volcanic processes abated to the point where reef building could begin.

In Darwin's model, **fringing reefs** initially built on the volcano slope – close to shore, owing to the steep flanks of the underlying cone (Fig. 3.1a). As the volcano sank, the reef close to shore built vertically into the growing **accommodation space**. As the island progressively disappeared and the reef built vertically, the expanse of water between the reef and shore grew wider and deeper; the reef would thus evolve into a **barrier reef** separated from the island by a broad lagoon (Fig. 3.1b) and eventually an **atoll** with no central island at all (Fig. 3.1c).

As evidence, Darwin cited a gradual shift in island/reef morphology from high volcanic peaks fringed by reefs at one end of an archipelago to barrier reefs and lower islands in the central reaches and finally to atolls at the other end. These ideas were published in "The Structure and Distribution of Coral Reefs" in 1842, 17 years before his better-known "The Origin of Species". Darwin's proposal that systematic spatial change was a proxy for temporal progression was a brilliant one but, without an underlying mechanism to drive the phenomenon, his ideas were not widely accepted until deep cores through Enewetak and Bikini atolls more than a century hence revealed the sunken volcanoes underpinning those reefs and Darwin's theory (Ladd and Schlanger 1960).

The relatively recent recognition of plate tectonics has provided a unifying theory to help explain the large-scale distribution of reefs on a global scale. The constant motion of giant fragments of oceanic and continental crust creates dynamic zones of seafloor spreading and crustal collision. Although the rates of movement that are involved will never affect transoceanic airfares, predictable patterns of uplift, subsidence, or stability have emerged as important, long-term controls of reef development. While his ideas about subsidence as a universal control of reef type were flawed, the works of Darwin and his contemporaries still provide many of the fundamental truths about reefs that are at the foundation of reef science today.

3.3.1.2 Sea Level

Periodic changes in the spatial relationship between Earth and the Sun have resulted in predictable and recurring changes in global climate (Milankovitch 1930) and, therefore, sea-level rise and fall. Changes in Earth's tilt and wobble, the shape of its orbit and the proximity of the planet to the sun during northern summer and winter all affect changes in the global heat budget. In warmer times, the ocean expands, freshwater is added from melting terrestrial glaciers, and sea level rises. During cooler periods, water contracts, continental glaciers grow larger and sea level falls. Climate-driven fluctuations in sea level have occurred throughout geological time, but appear to have become more pronounced after the breakup of the single supercontinent, Pangaea, 250–200 million years ago. The 40,000 and ca. 100,000-year glacial cycles predicted by Milankovitch have now been confirmed by isotopic data (e.g., Emiliani 1966) and have increased in their importance since the onset of icehouse conditions in the mid-Pleistocene.

With each waxing and waning of sea level, reefs that lived near the upper limit of each cycle have been alternately flooded and exposed. The result is a series of reefs, each built upon the remains of its predecessor, much like ancient cities stacked one upon another as favorable trade conditions remained constant each time territory was abandoned and then resettled. Present-day reefs, which have formed over the past 10,000–12,000 years, are simply the latest participants in this cycle of colonization and abandonment and sit atop their Pleistocene forebears.

In 1915, Reginald Daly proposed an alternative to Darwin's subsidence theory. It involved the formation of a wave-cut bench during each drop in sea level, followed by a subsequent sea-level rise and reef colonization on top of the resulting terrace (Fig. 3.1d–g). This idea was born from his observations that the depths of lagoons he examined tended to be similar. He argued that this reflected wave-cut platforms at similar depths from site to site, and proposed that the only plausible mechanism to explain this was a worldwide drop in sea level. The main blow to Daly's ideas came when Davis (1923) pointed out the lack of cliffed shorelines that should be commonplace behind the barrier reefs of Pacific islands were Daly's hypothesis correct. Without these logical remnants of the wave-planation process, the sea-level hypothesis of Daly became untenable.

As is often the case in great debates, the truth lay in the middle and involves both sea level and tectonics, although not in the precise ways envisioned by either Daly or Darwin. The rise and fall of sea level sets a global tempo for highstand reef exposure during lows and reoccupation during highs. Equally important, however, are the interactions with local tectonic motions that exert a complex control over the long-term development of reef communities as well as the character and history of the structures that they build. By identifying the patterns common to depositional sequences from many different ocean basins, seismic stratigraphy has been used to construct records of worldwide sea-level change through time (Vail et al. 1977; Haq et al. 1987). The commonality of these patterns from site to site argues for a global control (i.e., glacial eustasy). However, careful analyses of variations from this pattern at some sites have allowed us to understand the superimposed effects of local tectonics on global changes in sea level. The term **relative sea-level change** refers to variations in sea level at any one locality resulting from the combined effect of glacio-eustatic sea-level rise and fall (that related to changing climate) and local or regional tectonic motions.

3.3.1.3 Reef Accretion Under the Influence of Relative Sea-Level Change

Each time sea level rises over the edge of a tropical carbonate platform, reefs will usually form. The site of colonization will be dictated by factors discussed later in this chapter, but is often atop the previous generation of reefs. The fate of the reef will depend on the rate of relative sea-level rise compared to the rate of calcium carbonate production on the reef (Fig. 3.2). Under conditions of near balance, the carbonate produced in the reef just offsets sea-level rise, and reef accretion is vertical. In areas where sea level is rising slowly compared to the rate of carbonate production, the excess material will cause the reef to expand laterally. In the Caribbean, sea level has gradually slowed since ca. 7,000 calibrated years before present and the forereef is steep. This has resulted in seaward progradation (e.g., Buck Island in the U.S. Virgin Islands: Fig. 3.3). In many Indo-Pacific sites and along the Great Barrier Reef, sea level reached its maximum 6–8,000 years ago and little or no accommodation space was created after that. These reefs have been sites of ever-widening reef flats. When carbonate production cannot keep pace with rising sea level, the reef will either i) retreat

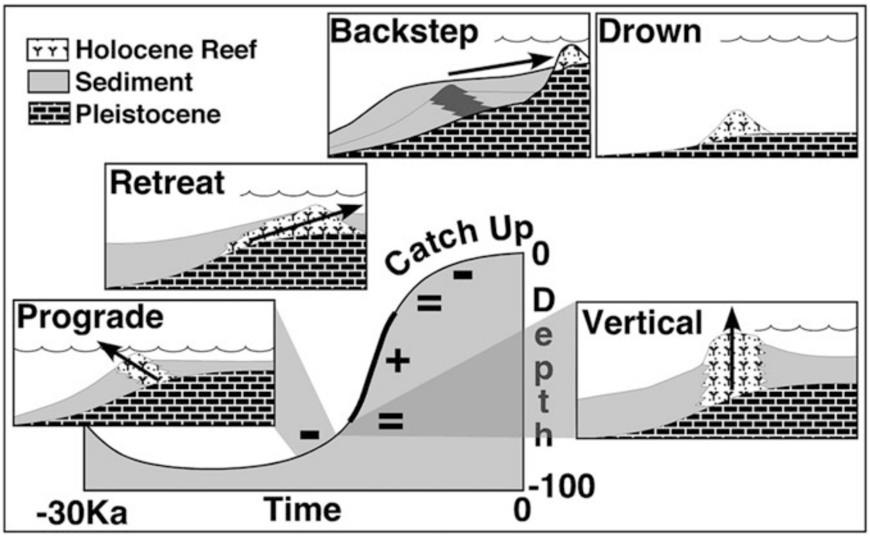


Fig. 3.2 Sea-level rise vs. reef accretion. The simplified sea-level curve represents a 100-m change in sea level over ca. 30,000 years. When sea level is rising slowly relative to the reef's ability to produce carbonate (−) the reef will prograde as it builds upward. A near balance between the accommodation space created by rising sea level and carbonate being produced by the reef (=) will result in vertical accretion. As rising sea level outpaces production (+, shown by *thicker line*), the reef will either retreat upslope (e.g., the Dominican Republic), backstep to higher ground (e.g., Puerto Rico) or "drown", depending on the severity and duration of the inequity. As sea level starts to slow down near the *top* of the curve, any reefs still within the photic zone will gradually "catch up". A drop in sea level will expose the reef until the ocean floods it again during the next glacio-eustatic cycle (After Hubbard 2011)

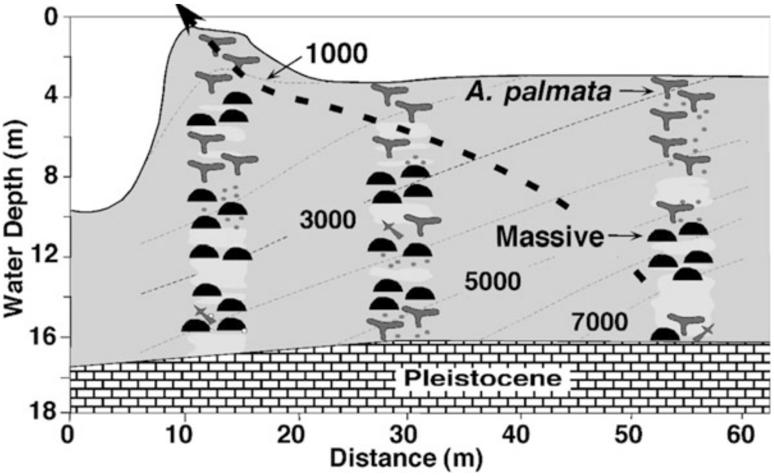


Fig. 3.3 Cross section through Buck Island reef. The upward transition from massive to branching corals and the sloping isochrons reflect both upward and seaward reef building (*arrow*) as carbonate production exceeded the space created by sea-level rise (After Hubbard et al. 2005)

upslope, ii) backstep to a landward and shallower site that is conducive to reef initiation (Blanchon 2011), or iii) drown. Hubbard et al. (1997) documented backstepping of Holocene reefs off Puerto Rico (Fig. 3.4) and showed a similarity of pattern and scale with Devonian examples from Australia (Playford 1980) and Canada (Viau 1988).

In 1985, Neumann and Macintyre proposed a tripartite classification for Holocene reefs viewed in cores or outcrop; reefs are inclined to either "keep up," "catch up," or "give up" (Fig. 3.5). "Keep-up" reefs were able to maintain their crests at or near sea level throughout their history. As such, the preserved corals (or other carbonate producers) exhibit growth forms typically found in shallow water (e.g., branching acroporids in the Caribbean). "Catch-up" reefs started in deeper water (ca. 10–20 m) but later caught up, usually after the rate of sea-level rise slowed. Such reefs are characterized by a lower (older) section dominated by deeper-water organisms that are overlain by younger biota formed in progressively shallower water as the reef "caught up." "Give-up" reefs are those that, for whatever reason, could not keep pace with sea level and simply stopped accreting.

A common misconception in the older literature is that reef building rates of 10–15 mm/year are commonplace. As

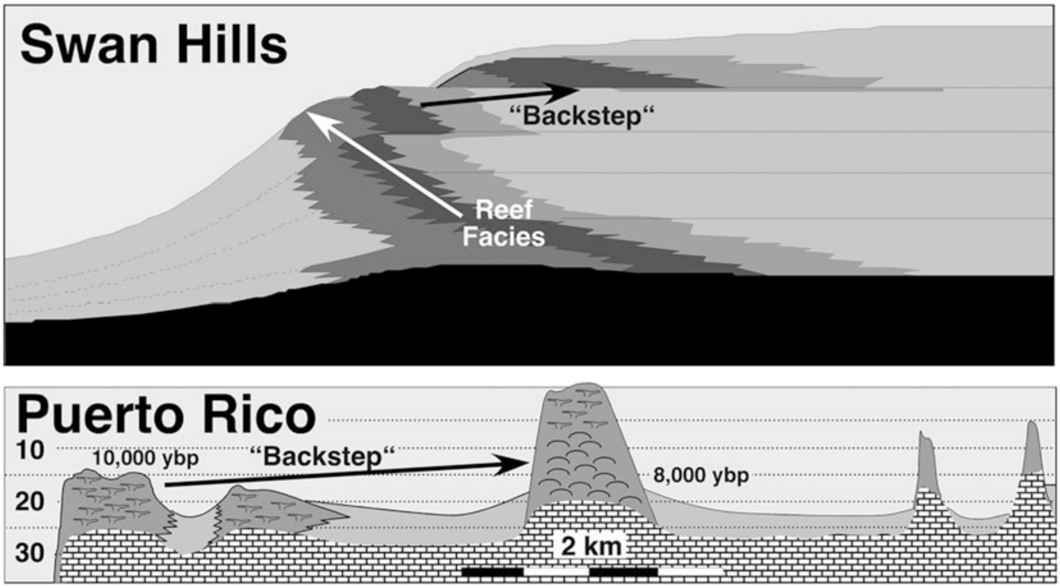
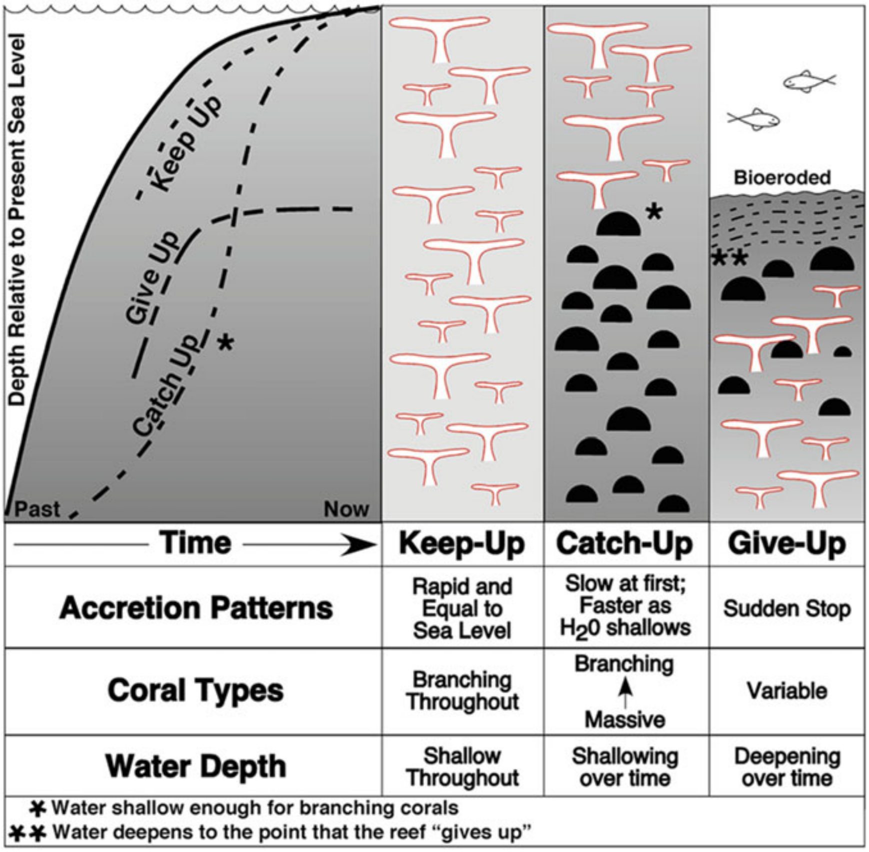


Fig. 3.4 Backstepping in Devonian reefs of Canada (*upper*) and Holocene reefs off Puerto Rico (*lower* – plotted at the same scale) (After Viau 1988). The Devonian reefs initially built up and out (like Buck Island: Fig. 3.3), but suddenly backstepped landward i.e., moved right) as sea level presumably sped up. Off Puerto Rico, shelf-edge reefs dominated by branching corals "gave up" as massive-coral reefs formed further landward. Note the similarity in reef thickness and the scale of backstepping in the two examples (After Hubbard et al. 1997)



Time →	Keep-Up	Catch-Up	Give-Up
Accretion Patterns	Rapid and Equal to Sea Level	Slow at first; Faster as $H_2$0 shallows	Sudden Stop
Coral Types	Branching Throughout	Branching ↑ Massive	Variable
Water Depth	Shallow Throughout	Shallowing over time	Deepening over time

* Water shallow enough for branching corals
** Water deepens to the point that the reef "gives up"

Fig. 3.5 Reef sequences as indicators of sea-level rise. A "keep-up" reef is capable of matching the rate of sea-level rise and will be comprised almost exclusively of shallow-water corals. "Catch-up" reefs generally started in deeper water e.g., massive corals) and gradually built closer to sea level (branching corals), usually after sea level slowed. "Give-up" reefs can be highly variable because their character will reflect the conditions before they gave up as well as those responsible for their demise. Reefs will generally give up if: (**a**) sea level is rising too fast, or (**b**) something compromises the ability of the reefs to keep up (After Neumann and Macintyre 1985) such, “give-up” reefs would predominantly reflect sudden jumps of sea level, e.g., the meltwater pulses of Fairbanks (1989) or dramatic declines in water quality (Adey et al. 1977; Schlager 1981; Blanchon 2011). However, more recent summaries of reef-accretion (Davies and Hopley 1983; Montaggioni 2005; Dullo 2005; Hubbard 2014) show that Holocene reefs built at rates closer to 3–4 mm/year and that rates above 10 mm/year are rare. Thus sea-level rise exceeded the accretionary capacity of most reefs throughout all but the latest Holocene, and drowning was as much “business as usual” as a reflection of extreme events as had been widely presumed.

This realization has important implications for our models of reef-building in response to sea-level rise in the twenty-first century. Coral reefs may soon be incapable of keeping pace with rising sea level, due to both accelerating sea-level rise (Grauss and Macintyre 1998; Church and White 2011) and perhaps slower rates of calcification in response to elevated CO_2 (Kleypass et al. 1999). This is not to say that they will soon be drowned or even that community structure will be significantly altered owing to greater water depth alone. However, even small increases in water depth over the reef crest can have disproportionate effects on wave energy passing over the reef and striking the shoreline behind it (Ogston and Field 2010). Combined with “flatter” reefs (Alvarez-Filip et al. 2009) that will provide less frictional attenuation of incoming waves and a higher frequency of intense tropical storms and hurricanes (Webster et al. 2005), this could increase beach erosion, accelerate ground-water salinization and generally render low-lying islands uninhabitable long before waves actually overtop their higher elevations (Hubbard et al. 2014).

3.3.2 Meso-scale Controls

3.3.2.1 Temperature

Coral reefs are generally restricted to water between 18° and 36 °C, with an optimal range of 26–28 °C. Today, this generally restricts coral reefs to latitudes between 20° and 25° north and south (Fig. 3.6). Exceptions do occur however. Abundant but low-diversity coral cover exists around Easter Island despite temperatures below 18 °C and a position at 27° S (Hubbard and Garcia 2003).

Within the normal range, certain corals will grow faster or slower, depending on temperature (Weber and White 1974; Glynn and Stewart 1973). Drastic thermal shifts can result in reduced coral vitality (e.g. bleaching, reproductive inhibition) or, in extreme instances, total destruction of entire reef systems. Glynn (1984) emphasized the importance of unusually high water temperatures in the widespread mortality of corals along the western coast of Panama. It is now generally accepted that recent episodes of coral bleaching, where corals expel their zooxanthellae (Chap. 5), are related to higher-than-normal maximum temperatures over the past several decades. At the other end of the scale, Walker et al. (1982) proposed that well-developed massive-coral communities in the northern Florida Keys were limited to areas shielded from the periodic influx of cold water pushed out from Florida Bay during the passage of major cold fronts.

It is important to note that most corals exist near their upper thermal limits. Therefore, even a slight increase in tropical temperatures in the future could have significant impact on the distribution of corals in the tropics. It is also important to realize that bleaching need not be related to an

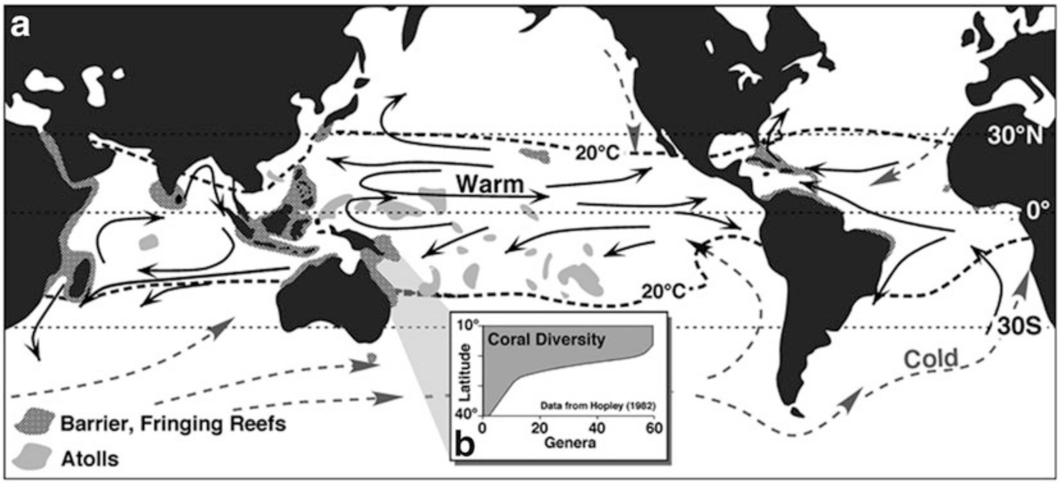


Fig. 3.6 **a** Worldwide distribution of reefs. Reefs are confined to areas bathed by warm currents (>20 °C). Reef locations are from Darwin (1842). (**b** – *inset*) Latitudinal variation in species diversity along the Great Barrier Reef. Note the increase in the number of genera toward the equator

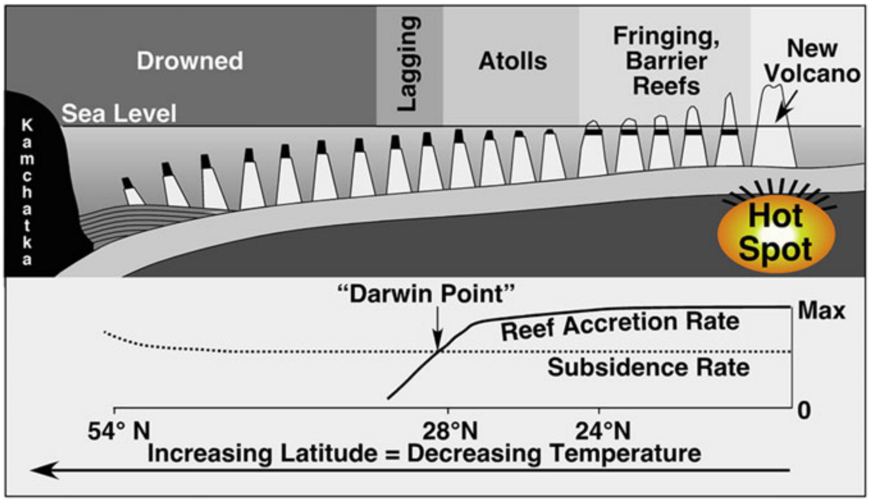


Fig. 3.7 The combined effects of subsidence and temperature on reef development in the Hawaiian Archipelago. As the Pacific crust beneath the Hawaiian islands moves to the northwest, it cools and subsides. South of roughly 29°N, the reefs can produce carbonate at a rate fast enough to offset subsidence. North of this, however, cooler water inhibits coral growth to the point that the reefs can no longer keep up. As a result, they are gradually drowned (After Grigg 1982)

absolute threshold above which corals will succumb. Many western Pacific corals (e.g., Indonesia) regularly experience temperatures that would induce bleaching in the Caribbean Sea. Conversely, scleractineans in the cold waters off Easter Island bleached at temperatures well below what is normal in the Caribbean (Wellington et al. 2000; Hubbard and Garcia 2003). If there is good news in any of this, recent studies have suggested that species within some back-reef areas where temperatures fluctuate significantly may offer a pool of more thermally resistant species (Oliver and Palumbi 2011).

On a geological scale, patterns of Pacific atoll development have been explained as a response to temperature changes in conjunction with tectonic effects. Grigg (1982) proposed that north of roughly 29°N in the Hawaiian Archipelago, lower temperatures have depressed carbonate production to the point where reefs cannot keep up with subsidence (Fig. 3.7). South of this "Darwin Point," barrier reefs and atolls are maintained. To the north, reefs are in various stages of "giving up." Similarly, cores through the Great Barrier Reef of Australia record a gradual shift from subtropical seas to a more tropical climate over the past 30 million years as the Australasian plate slowly moved toward the equator (Davies et al. 1987, 1991).

3.3.2.2 Salinity

Coral reefs are limited to areas of reasonably normal marine salinity (3.3–3.6 %). Below these levels, carbonate buildups are progressively dominated by vermetids, oysters, serpulids, and blue-green algae (Teichert 1958; Heckel 1974). Coral reefs do not generally occur above this range. Low salinity (along with high turbidity) is a primary reason why extensive coral reefs do not occur opposite the mouths of major rivers (e.g., the Amazon and Orinoco rivers of northern South America empty into seas that are otherwise suitable for reef development). On a smaller scale, the passes through many nearshore reefs can be controlled by present or past stream locations.

3.3.2.3 Wave Energy

The oceanographic regime in which a reef occurs is among the most important determinants of its character. Breaking waves generate currents that bring in large volumes of low-nutrient ocean water and remove waste products from the system. Benthic zonation within a single reef is to a large extent determined by the relative abilities of various organisms to either survive turbulent conditions or to take advantage of the vigorous water motion caused by passing waves. In shallow water, *Acropora palmata* grows quickly, and can grow rapidly above the traction carpet of sediment that is mobilized each time storm waves strike the reef crest. In deeper water, fragile platy corals are not negatively impacted because of the greatly attenuated surge at depth.

Regional variations in wave climate have been shown to exert a primary control on the character of the shallow-water reef crest and the zonation along the front of Caribbean reefs (Adey and Burke 1977; Geister 1977; Fig. 3.8). In addition, storms can play an important role in determining reef character. In the Caribbean, three primary hurricane tracks emerge from data compiled by Neumann et al. (1981) over the past century, and reef type is quite sensitive to this pattern (Hubbard 2011, 2014). Reefs along the most exposed Windward Islands are dominated by a high return frequency of storms that break up branching corals plus a high prevailing wave energy level that discourages grazing even in calmer times (Fig. 3.9). This encourages the formation of thick algal crusts and ridges in shallow water. In the Pacific, the location of Guam in the western monsoon trough correlates highly with the "topographically dull" reefs offshore and the architectural preponderance of "square cement bunkers with small windows and large shutters" on land (C. Birkeland, pers. commun.). Weaker but still frequent

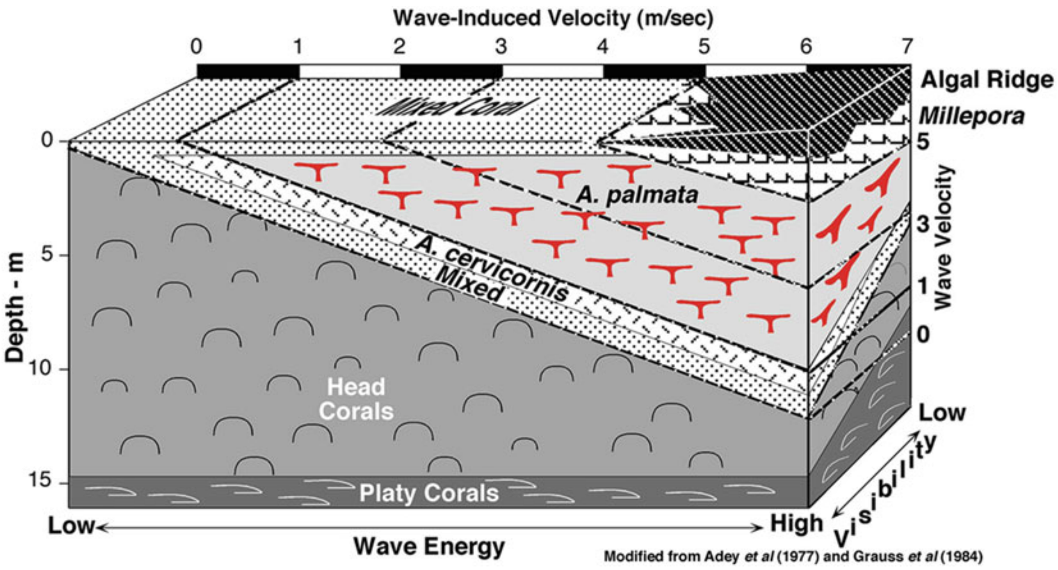


Fig. 3.8 Diagram summarizing the effects of wave energy and water clarity on the zonation of Caribbean reefs (After Adey and Burke 1977). With increasing wave energy, the boundaries between the *A. palmata*, the *A. cervicornis*, and the head-coral zones are progressively deepened. This is closely tied to magnitude of the wave-induced velocity that increases with larger waves (boundaries from Grauss et al. 1984). Turbidity and nutrient levels, which are often tied to one another (Hallock 1988), can also affect coral zonation. Increased sediment and nutrients in the water drive corals into ever-shallower water, seeking light. The shallowest zones (e.g., algal ridges, *Millepora*) are less affected by sediment as they occur in such shallow water that light attenuation is not a factor.

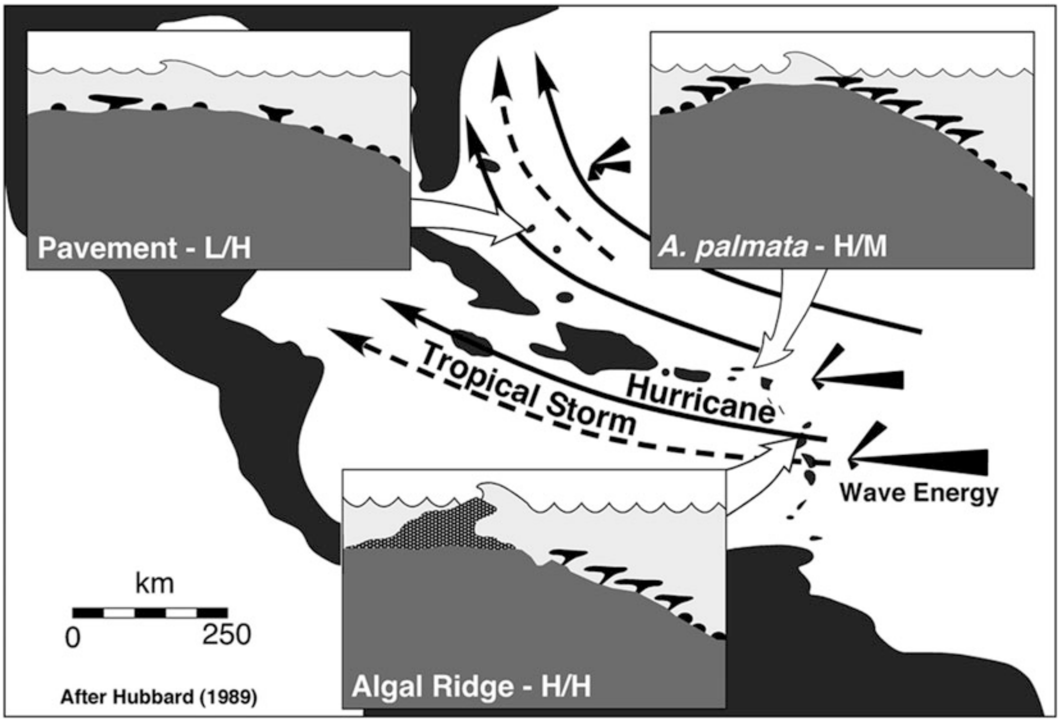


Fig. 3.9 Wave energy as a control of Caribbean reef type. Major storm tracks are shown by the *solid* and *dashed arrows*. Prevailing wave energy is shown graphically by the rose diagrams at individual sites and is based on synoptic wave observations for the region (U.S. Naval Weather Service Command 1979). The importance of ambient wave energy and major storm (e.g., L/H = **L**ow ambient wave conditions/ **H**igh hurricane frequency) and the resulting reef types are shown in the *insets*. Where both ambient wave energy and hurricane frequency are high, the reef crest is characterized by algal ridges (e.g., Windward Islands). Where day-to-day wave energy is still moderately high but hurricane frequency and intensity is somewhat less, well-zoned reefs occur (e.g., St. Croix). Areas that are generally less energetic except for the passage of major storms (e.g., the Bahamas) are typically broad, wave-swept pavements (Walter Adey's "false reefs"). (After Hubbard 2011, 2014)

storms in the western Atlantic, combined with much lower prevailing wave energy tend to encourage wave-swept pavements with poorer development of branching acroporids. Lower day-to-day wave energy makes it easier for grazers to operate anywhere on the reef. Intermediate wave energy and hurricane frequency in the northeastern Caribbean encourage varied coral-community relationships and some of the best-developed reef-front zonation seen in the region. In a sense, this regional pattern follows Connell's Intermediate Disturbance Hypothesis, although at a scale different from that of species diversity.

3.3.3 Micro-scale Controls

3.3.3.1 Light

The influence of light intensity and spectral character has been generally understood since the pioneering work of Quoy and Gaimard (1825). Darwin (1842) clearly recognized light's importance in controlling the maximum depths to which he observed corals throughout the Pacific. More recent studies have further quantified this long-recognized pattern although the general relationships remain unchanged. In clear water, light intensity decreases exponentially with water depth and the light spectrum shifts rapidly toward the blue end. As a result, photosynthesis and $CaCO_3$ production drop off with depth.

In addition to changes in growth rate, reduced light at greater depths can cause polymorphic corals to change their shape from domes in shallow water to plate-like morphologies at greater depths. The latter is more efficient for light gathering as it places all the photoreceptors (in this case, symbiotic organisms within the coral tissue) along upward horizontal surfaces where light intensity is greatest – effectively a self-orienting "photocell"). Some of the best understood corals in this respect belong to the *Orbicella* complex from the Caribbean. (This was formerly called the *Montastraea* complex, but it is now known that *Orbicella* and *Montastraea* are in different families that diverged millions of years ago.) Coral-growth rate within most massive species drops from nearly a centimeter per year in shallow water (0–10 m) to a millimeter or less in deeper water (>12–15 m: Dustan 1975; Hubbard and Scaturo 1985). This is accompanied by a change in morphology from heads to plates. Similar patterns also occur for *Porites lutea* and *P. lobata* in the Pacific (Buddemeier et al. 1974; Isdale 1984).

Knowlton (1993) demonstrated genetic differences associated with the different morphotypes and, based on this information, *Orbicella annularis* was subsequently subdivided to include *O. franksii* and *O. faveolata*. It is worth remembering, however, that the experimentally induced changes in colony shape documented by Grauss and Macintyre (1982) occurred on individual colonies transplanted to different depths. Therefore, while genetic character may go hand-in-hand with species-related shape preferences at a given depth, individual colonies can still take on the shapes of their sibling species when light availability is varied.

3.3.3.2 Nutrients

Until the latter twentieth century, abundant nutrients were generally considered beneficial to reefs. Early references to reefs preferring areas of upwelling or other sources of nutrients underscore this misconception. More recently, it has been recognized that high nutrient levels are actually detrimental to "reef health" (Kinsey and Davies 1979). At the organism level, it has been proposed that high phosphate levels in the water may shut down the calcification mechanism (e.g., phosphate "poisoning" of Simkiss 1964). At the community scale, autotrophs within the reef (primarily zooxanthellae and algal turfs) are well suited to a steady stream of water with low nutrient levels. Higher nutrient levels tend to favor sponges (Wilkinson 1987) and macroalgae (Steneck 1988), which can outcompete corals and turf for space and prevent larval settling. Macroalgae may provide lower nutrient values than turfs, thus reducing the availability of useful biomass for grazers. Once the coral dies, higher levels of nutrient availability can support heavy infestation by infaunal borers (Hallock 1988), and in particular, sponges (e.g., *Cliona* spp.: Moore and Shedd 1977) that will progressively destroy the remaining skeleton and can remove any record of its existence (Chap. 4). Estep et al. (2008) documented a strong shift in dominant bioeroders from sponges in oligotrophic Caribbean fore-reef environments to molluscs (especially *Lithophaga* sp.) in the more restricted Holocene reefs of the Enriquillo Valley of the western Dominican Republic.

3.3.3.3 Sediment

Despite an impressive body of literature (for reviews, see Hubbard and Pocock 1974; Hubbard 1987), only limited quantitative information exists on the specific responses of reef organisms to sediment loading. Controlled experiments have documented surprising tolerance by corals to high doses of sediment over short periods of time (Taylor and Saloman 1978; Rogers 1983). Nevertheless, the literature is replete with postmortem autopsies of reefs killed by sediment. The obvious factor here is time. Although corals can survive acute loading at high levels, even lower-level stress can gradually wear down the reef's defenses and result in severe, and perhaps irreversible, degradation.

The most important effects of sediment stress include (1) smothering, (2) abrasion and (3) shading, all of which result in an inhibition of coral recruitment. Of the three, smothering is the easiest to visualize. Under natural conditions, reefs on the downwind flank of large carbonate platforms can be buried by sediment washed off the bank as it is flooded by rising sea level (Hine and Neumann 1977). During storms or, more recently, dredging of nearby areas, the levels of suspended sediment can increase markedly, resulting in extensive damage to reef corals and other sediment-sensitive biota. Such problems have been described in Australia (Fairbridge and Teichert 1948), Hawaii (Johannes 1975; Maragos 1972), Puerto Rico (Kaye 1959), and the U.S. Virgin Islands (van Eepol and Grigg 1970; Dubois and Towle 1985), among others.

During storms, physical abrasion by moving sediment can cause substantial damage to coral tissue (Hubbard 1992). Even under less energetic conditions sediment scour can play a role in limiting the types of corals that can thrive along the shallow reef crest. *A. palmata* grows quickly after settlement and is, therefore, less likely to be killed before it can build above the level of natural "sandblasting" associated with even small storms. Its success in times past was a balance between the destructive effects of high waves and wave-mediated removal of sediment from a coral that cannot perform that function itself.

While more subtle in its effects than abrasion or smothering, shading is probably the most important of all the sediment-related effects. Reduced levels of light due to suspended sediment in the water column can retard coral growth (Hubbard and Scaturo 1985; Hubbard et al. 1986), impact natural zonation patterns (Fig. 3.8; Morelock et al. 1979; Hubbard et al. 1986), and induce wholesale mortality if allowed to persist for an extended period of time.

All of these effects act together to exert a significant natural control on the distribution of coral reefs (Roy and Smith 1971; Morelock et al. 1979; Cortes and Risk 1985; Hubbard 1986). More recently, the dominant sources of increasing sediment loading have been related to land clearing for development and agriculture (McCulloch et al. 2003).

3.3.3.4 Antecedent Topography

Because of the fierce competition for space and the necessity for reefs to rid themselves of excess sediment produced by bioerosion, topographically elevated areas offer significant benefits to larval recruits and well-developed reefs alike. Roberts et al. (1977) showed that breaks in slope, especially at the platform margin, are focal points for wave and current energy and offer enhanced transfer of nutrients, sediment and metabolic waste. The constant input of carbonate ions also results in enhanced cementation and the generation of hard bottoms better suited for larval recruitment. Thus, bio-physically mediated topography is a primary influence on where corals can recruit and flourish.

Like ancient cities, reefs tend to be built upon the ruins of their predecessors (Fig. 3.10). As sea level falls and rises again, the remnants of the last generation of reefs serve as

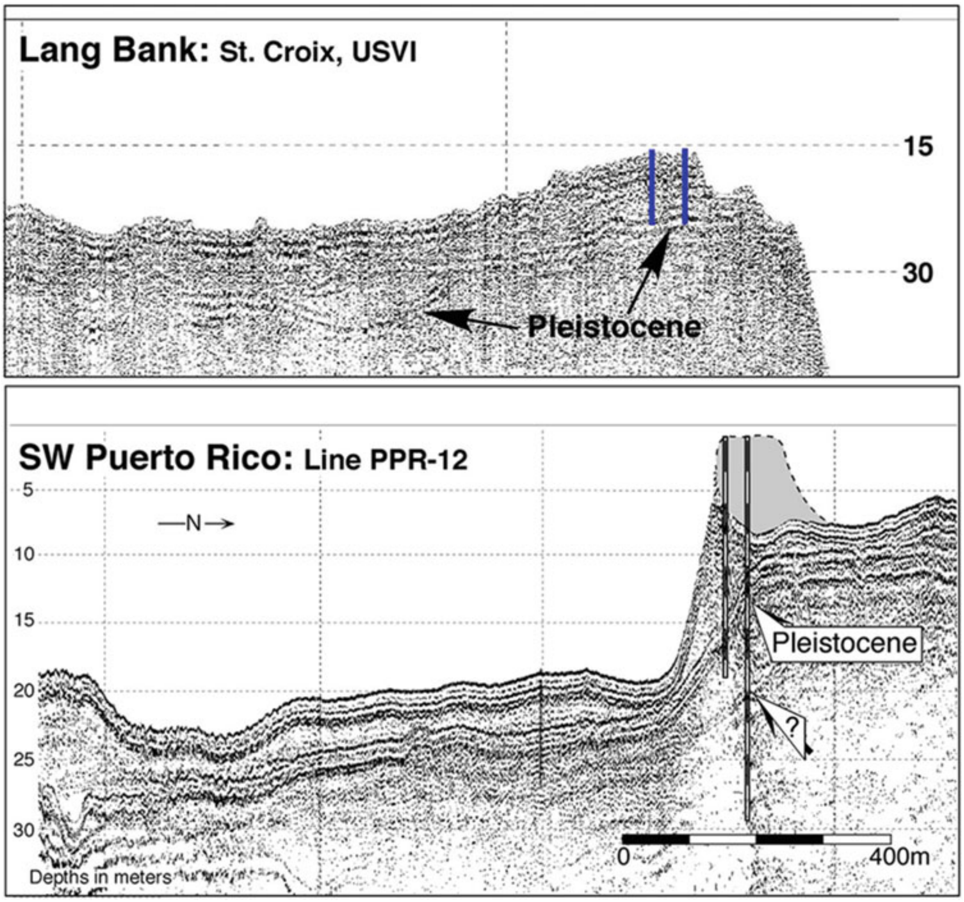


Fig. 3.10 Antecedent control of present-day reefs. The *upper panel* shows a seismic line across the southern margin of Lang Bank on eastern St. Croix (USVI) (After Hubbard et al. 2013). The seismic line in the *lower panel* is from the southwestern insular shelf of Puerto Rico. The underlying Pleistocene surface was verified by cores. Note how the Holocene build-ups sit atop highs on the underlying Pleistocene surface (Seismic data courtesy of U.S. Geological Survey)

areas of preferential coral recruitment. Reefs will tend to re-establish on previous reefs because they are hard and topographically elevated. Also, the conditions that favored the previous reefs likely return with re-flooding of the area by the next rise in sea level. In particular, elevation offers significant advantages during early shelf flooding when sediment that was created by weathering during previous exposure is stirred up by waves, increasing natural turbidity levels. Thus, reef sequences that are recognized in the fossil record are often not single depositional units, but rather a complex of several generations of reefs, each localized atop the remains of an earlier one. Many present-day reefs sit astride their Pleistocene ancestors that formed 120,000 years earlier.

One process that creates antecedent topography is **karst dissolution**. During episodes of lowered sea level, biologically produced and reactive limestone strata are dissolved by rainwater. Carbonate ions are transported down through the permeable strata until their concentration in the ground water is high enough to induce re-precipitation, usually as calcite. Thus, exposure to under-saturated rain and surface waters induces wholesale removal of carbonate at the surface. Citing both experimental studies and field examples, Purdy (1974) proposed limestone dissolution as a primary mechanism for creating antecedent topography. While reefs are forming, they are usually reinforced by aragonite and magnesium calcite cements that form within their interstices. The resulting mass is more resistant to dissolution than are the muddier and un-cemented sediments of the adjacent platform or lagoon. Thus the topography left by the reef system can be enhanced during exposure.

3.4 Reef Building

3.4.1 What Is a Reef?

To the earliest mariners, "reefs" were anything that might damage their keels (from the Nordic "rif"). These included biologically produced structures, the subject of this book, as well as piles of rocks left in shallow water by the last glaciation or the U.S. Army Corps of Engineers. Biologists are more concerned with the slate of organisms and the ecological interactions among them. In contrast, geologists focus more on the structures that they build – hence differences in definitions. The latter largely characterize reefs based on their shape in cross section and their relation to surrounding strata.

For purposes of our discussion, the following are considered to be critical factors or characteristics related to reefs. First, the features discussed here ultimately owe their origin to biological production. Even the cements that fill voids and were once thought to be the product of physiochemical precipitation are now understood to be universally mediated or created by micro-organisms. Second, reefs are rigid structures that stand topographically above their surroundings and, therefore, exert some degree of physical control over the oceanographic processes in their vicinity. For the geologist, topography is perhaps the most important trait that sets "true reefs" (**bioherms**) aside from flat hard-bottom communities (**biostromes** or "coral carpets": cf. Dunham 1970) that do not offer the spatial heterogeneity that is so important to the diversity on modern coral reefs.

Structural complexity is what the geologist is left with in the fossil record and this explains our fixation on this characteristic. However, large-scale topographic expression and more-local spatial heterogeneity are equally important to the modern ecologist; they help determine what organisms live on a particular piece of submarine real estate and how they interact with their peers. A suite of sessile organisms sitting atop a feature rising above its surroundings will function in fundamentally different ways than a similar community on a flat bottom. In fact, topography (or its absence) will in many cases preclude particular communities from occurring at all due to important differences in physical processes that are induced by abrupt topographic change (Roberts et al. 1977). Swimming over a modern reef, the associations with underlying structure are more obvious but still may be overlooked as researchers focus on smaller-scale species interactions. To the geologist, the presence or absence of this topographic relationship lay at the very heart of what is and is not a reef.

Traditionally, geological discussions have focused on what is responsible for creating topographic complexity and the rigidity that maintains it in the face of wave attack. Early workers stressed the obvious role of organisms in providing rigidity (Lowenstam 1950; Newell 1955; Heckel 1974). As a result, in-place and interlocking framework was traditionally seen as a prerequisite for the high-diversity geologic assemblage of calcifying organisms considered to be a "true reef" by most geologists. Conversely, anything not containing a preponderance of organisms in life position did not qualify (Fagerstrom 1987; Stanley and Fagerstrom 1988).

The popularity of this view is understandable. A paleontologist swimming across the surface of a modern reef 50 years ago saw a seemingly endless and topographically complex seascape of upright, living corals. The ecological literature of the day stressed the fierce competition for space and the superiority of certain species over others in light of their ability to occupy and defend this space. So, geologists visiting a modern reef usually came away with impressions that focused more on corals and calcification than biological erosion (Chap. 4) and the physical redistribution of detritus by waves and currents. The fish swimming across the reef taking the occasional, gentle nibble on the bottom was viewed as a process of perhaps academic interest but, at best, of secondary importance to the “real” reef story – calcification. Likewise, the myriad processes going on within the upper reaches of the reef substrate were out of sight. Thus “corals growing on the backs of other corals” was seen as the most logical way to build a rigid and topographically elevated structure.

However, applying this “framework model” to ancient reefs met with little success. In contrast to the dominance of in-place calcifying organisms envisioned in traditional models of modern reefs, researchers often found fossil reefs comprised of recognizable clasts “floating” in a matrix of sediment, skeletal debris and cement. Rather than questioning the prevailing model, researchers focused on why ancient reefs were so different from what modern reefs “must” look like inside… hence, Mike Lloyd’s quip “The present is the key to the late Pleistocene… perhaps” (email to Bill Precht shared with the author).

The introduction of the submersible rock drill by Ian Macintyre in 1975 gave geologists a cost-effective way to access to the interiors of modern reefs. Although some reefs contained measurable proportions of what was interpreted as in-place “framework” (e.g., Macintyre and Glynn 1976), most revealed what was arguably toppled coral skeletons mixed in with a high proportion of loose sediment and smaller coral debris (Hubbard et al. 1990). Based on an analysis of cores collected from a variety of reef environments all across the Caribbean (Fig. 3.11), Hubbard et al. (1998) proposed that the interiors of many, if not most, modern reefs were dominated by a mix of in-place and toppled corals set in a matrix of sediment, smaller skeletal fragments and open voids – a fabric similar to ancient reef-related deposits.

The importance of this is twofold. First, if so many modern coral reefs are not dominated by in-place and interlocking corals, then it should no longer be the primary criterion by which ancient reefs are judged. Second, while in-place and interlocking framework is a perfectly good way to create a rigid and topographically elevated structure, it is not the only pathway to that end. Further, given the dominance of sediment and rubble over corals in life position, it is difficult to build a wave-resistant structure by coral-growth alone given the importance of physical and biological erosion that we have taken for granted.

What emerges is a picture that acknowledges the importance of bioerosion that breaks down primary structure and marine cementation and encrustation that “glue” everything back into a more solid reef mass. Thus, bioerosion, cementation and encrustation are elevated from bit players to co-stars in Bob Ginsburg’s hypothetical long-running geologic play in which the plot stays the same even though the actors change over evolutionary time.

Most of the building blocks of a modern coral reef started as scleractinians, but they have been, to varying degrees, toppled and then modified by multiple generations of boring, sedimentary infill, encrustation and cementation (Schroeder and Zankl 1974; Schroeder and Purser 1986). The ultimate reef fabric is determined by the relative importance of (1) initial carbonate production, (2) physical and biological breakdown of this primary framework (3) the patterns of sediment storage within or removal from the reef, and (4) the levels of secondary cementation and encrustation.

This is not to say that reefs largely comprised of in-place organisms do not exist. To the contrary, the massive reef ridges of the Pacific and eastern Caribbean are dominated by layer upon layer of undisturbed massive coralline algae. These owe their existence to high waves that exclude grazers. Conversely, where wave energy is low enough to preclude extensive storm damage, in-place corals can dominate. A Holocene reef in the Enriquillo Valley of the Dominican Republic is largely comprised of in-place and well

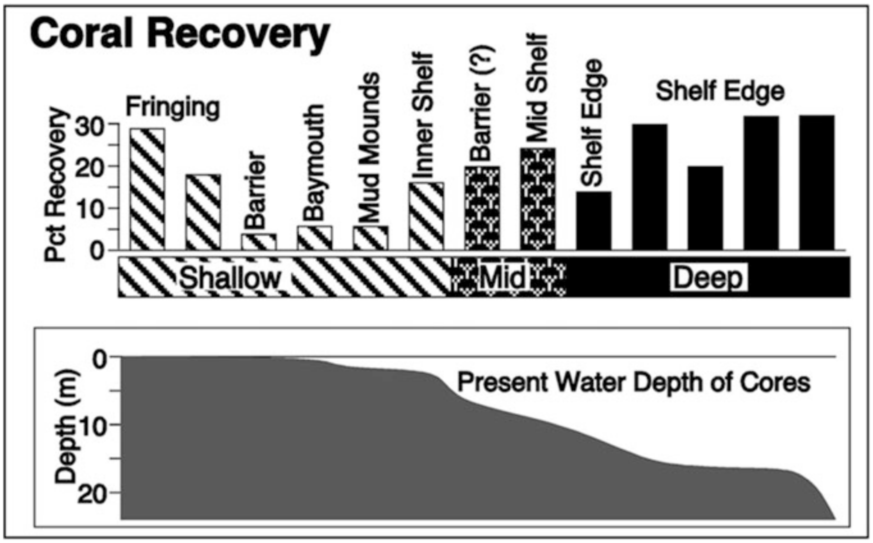


Fig 3.11 Core recovery (percent) from several Caribbean reefs. The composite profile shows the approximate depth from which each set of cores was recovered (i.e., cores are not from a single site). Note that recovery is less than 35 % overall and the highest is generally found in deeper reefs that are dominated by more resistant massive corals that grow more slowly but are harder to move. The majority of the reef fabric in all cores consists of open voids and sediment produced by bioerosion and not in-place and interlocking framework (After Hubbard et al. 1998)

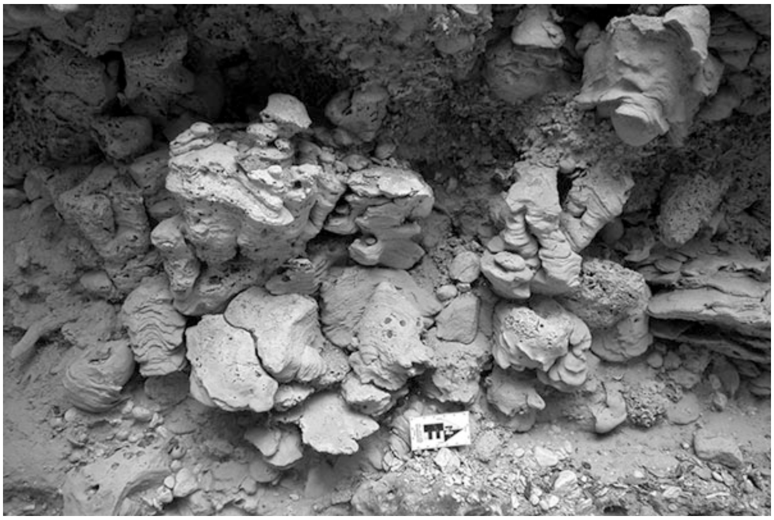


Fig. 3.12 Photograph of in-place, massive corals in Cañada Honda, Dominican Republic. The facies is interpreted as a moderate depth (ca. 20 m) fore reef in a regime of higher-than-normal sedimentation rates. Elevated sedimentation is responsible for both the limited species diversity (mostly *Siderastrea siderea*, *Orbicella faveolata* and *Agaricia* spp.) and the excellent preservation. The more bioeroded colonies (mostly *S. siderea*) probably grew at rates faster than local sedimentation. Less bioeroded colonies grew at rates approximately equal to the rate of sediment build-up. The scale *arrow* is 10 cm in length

zoned corals (Fig. 3.12) as are some of the protected *A. palmata* reefs on the leeward side of Curacao (Pandolfi and Jackson 2001). Nevertheless, there are countless other examples that we all agree are "reefs" as we swim over them but which are dominated inside by both in-place and toppled calcifying organisms in a sediment and rubble matrix that is volumetrically more important than corals, in place or otherwise. To use a dominance of in-place and interlocking primary organisms as the sole yardstick against which ancient reefs are measured is no longer appropriate.

Thus, our definition of a "true reef" must be expanded to include topographically elevated and rigid structures, built of organically derived materials that have to varying degrees been broken down and redistributed over both short distances (i.e., a toppled coral will usually remain in or near the community where it lived) and bound into the overall fabric by encrustation and cementation (Fig. 3.13).

3.4.2 Corals Grow: Reefs Build

We now understand that coral growth is only one part of reef building. Once a corals dies, it is subjected to both physical and biological breakdown. Algae that overgrow the dead substrate are a preferred diet of many fishes, echinoids, and other marine grazers. In the process of scraping or biting these algae, grazers remove bits of carbonate substrate. Alongside the grazers, countless other organisms bore into the reef, seeking shelter. The reader is referred to Chap. 4 which provides a more complete discussion of this important suite of processes.

Recent suggestions that coral reefs are "flattening" (Alvarex-Filip et al. (2009) have led us to revisit the important relationship between substrate production and destruction initially considered nearly 50 years ago by Scoffin et al. (1980) and Stearn et al. (1977). More recently, Perry et al. (2008, 2012) have developed protocols that resemble coral-monitoring but quantify both the organisms that create carbonate and those that break it down.

However, even this more holistic view still minimizes important physical processes that contribute to reef building. Land (1979) argued that carbonate found within the reef falls mainly into two categories: original coral skeletons and sediment derived from their physical and biological breakdown. The total volume of carbonate initially produced by a known distribution of organisms on the reef surface was termed **Gross Carbonate Production** (P_g). The net amount carbonate remaining within the reef (P_n) should consist of recognizable coral (both toppled and in life position) and sediment that has been incorporated into the reef edifice. The difference would be a measure of the amount of material that has been exported from the reef and permanently lost (SED_e). Stated mathematically:

$$P_g - P_n = SED_e : \qquad (3.1)$$

The most detailed carbonate budget to date is from a reef along the north coast of St. Croix (Hubbard et al. 1990). Using quantitative data on reef cover, coral growth rates, cores that document long-term reef accretion, and sediment export data, all from the same locale, they concluded that nearly 60 % of the carbonate that was produced within the reef was reduced to sediment by bioerosion. Nearly half of

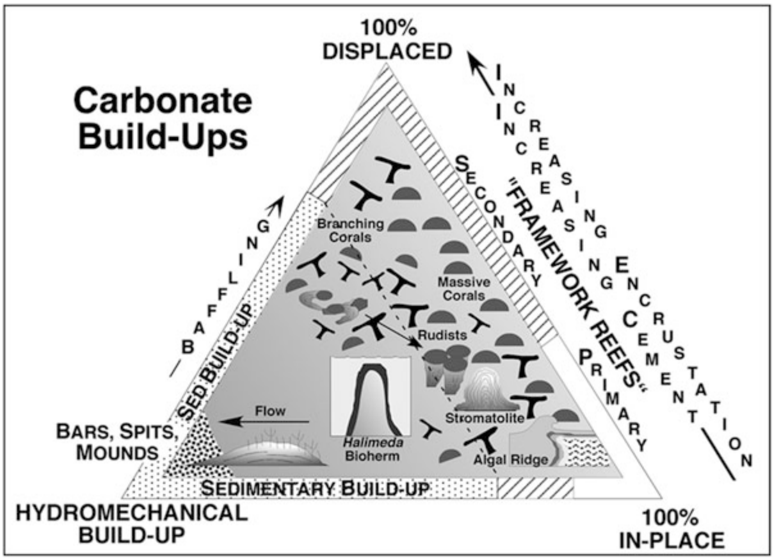


Fig. 3.13 Reef-classification based on the relative importance of skeletal elements that are (**a**) in growth position (in-place as primary framework), (**b**) displaced (i.e., toppled but close to where they lived – secondary framework) or (**c**) transported out of their original reef zone or the reef altogether – hydromechanical build-ups. The *dashed line* shows the approximate boundary between "reefs" and hydromechanical buildups (After Hubbard et al. 1998)

that was exported from the reef, primarily during storms (Hubbard 1992); the remainder was reincorporated within the reef interior. From this study, three important points emerged. First, recognizable coral (41 %) was less important in the reef than sediment (45 %) and open void space (14 %). Second, it was difficult to demonstrate that the majority of the remaining coral was in place while some pieces had been demonstrably moved or toppled. Finally, a reef that contains more loose detritus than in-place framework will probably not be a rigid structure. Thus, the stabilization of detritus by cementation and encrustation is an essential part of reef building that has been widely ignored. From these observations and measurements, they argued that in-place and interlocking framework is not necessarily an integral characteristic of all "true reefs" – and may exist in few. If we reconsider reef building to be the sum of all the processes discussed above, then the fate of all that bioeroded sediment is critical if we are to fully understand the vertical accretion of coral reefs in both the past and the future.

Total reef-carbonate production has been dropping dramatically due to the lower abundance of live corals. In addition, increasing calcification will reduce the capacity for each reef organism to create skeletal material (Hoegh-Guldberg et al. 2007; Doney et al. 2009). The growing interest in bioerosion provides important information on the destructive side of Land's simple equation. However, it does little to address the fate of the material produced by these destructive processes. If sediment is reincorporated back into the reef, then it adds to the edifice on which future coral recruitment and growth will occur. To the extent that it is stabilized by encrustation and cementation, it also contributes to the rigidity of the reef. However, this is only part of the story.

We know that carbonate production is significantly lower than it was five decades ago. . . and it is likely to continue to decline. The changing balance of bioerosion is more difficult to quantify. Fewer grazing organisms may equate to lower substrate loss and less sediment production. However, changing nutrient dynamics may shift that side of the equation more toward infaunal bioeroders. Whatever this balance looks like, we must also understand the fate of all that sediment if we are going to fully characterize the reef-building process.

3.4.3 A New Reef-Building Model

Numerous summaries have demonstrated the strong relationship between water depth and coral-growth rate. Boscher and Schlager (1992) developed a calcification model based on an exponential drop in light intensity and, therefore, photosynthesis. Using this model, they reproduced depth-related growth patterns for *M. annularis* (the taxonomy has since changed) derived from direct field measurements. They surmised that, while reef accretion would be slower than coral growth, it must follow a similar depth-related pattern, an assumption that prevails in recent models of coral reefs in the twenty-first century and beyond (DiCaprio et al. 2010; Toomey et al. 2013).

A recent summary of Caribbean reef accretion raises the likelihood that this fundamental assumption is flawed and that reef building is more than a collection of biological processes. Based on 151 reef-core intervals from 12 Caribbean sites, Hubbard (2009) found no correlation whatsoever between the rate of reef building and paleo-water depth. Moreover, the coral type (branching vs massive) preserved in the reefs had little effect on their rate of vertical accretion. Gischler (2008) came to the same conclusion based on reef cores from Belize and noted that reefs dominated by massive species built faster than those dominated by branching A. *palmata.*

Ultimately, this probably reflectes differences in the durability and transportability associated with different colony morphologies.

Clearly, these and similar summaries indicate that a reef-building model tied primarily to individual depth-related processes is critically flawed. The challenge is to figure out what might be missing. One possibility is that light may be affecting both photosynthetically driven calcification and the density of algae that are consumed by grazers in similar ways. In this scenario, carbonate production and bioerosion would co-vary with depth, resulting in a balance between the two over at least the depth range in which shallow reefs occur (Hubbard 2009). However, Weinstein et al. (2014) reported no differences in the loss from experimental substrates to a water depth of 30 m off the south side of St. Thomas in the US Virgin Islands. Similarly, a study from two reefs off nearby St. John showed no depth-related decline in bioerosion (Whitcher 2011; Whitcher et al. 2012). If these results are widely applicable, then the depth-related bioerosion patterns that have emerged when greater depths are considered may not apply to the upper photic zone inhabited by shallow-water reef corals.

Any attempt to explain the apparent lack of depth control in shallow-water reef building must take the following into account:

- Light, photosynthesis and coral-growth rates decrease with water depth
- Vertical reef accretion does not decrease with water depth (down to at least 23 m)
- Bioerosion apparently does not decrease with water depth (down to at least 30 m)
- Depth-related reef zonation generally persists in both outcrops and cores
- Sediment will preferentially move downslope, especially during storms

Resolving these observations requires a closer look at the behavior of the different types of carbonate material within the reef. Massive corals are less resistant to breakage than faster-growing shallow-water species and they will be less affected by wave action due to their position further down the forereef. If they do move, they are less likely to be transported as easily or as far as sediment. In contrast, sand and mud created by bioerosion will be easily transported unless it is sequestered well within the reef. It will move primarily during storms and the processes associated with such events tend to move sediment landward into the lagoon or downslope and out of the reef edifice altogether.

Given that there is more sediment than corals preserved in most reefs, its fate cannot be ignored in the accretionary balance. A model where detrital sediment is transported into deeper reef zones while the larger coral blocks stay closer to the sites from which they were toppled satisfies the constraints listed above and would blur depth-related accretionary patterns while still maintaining reef zonation. This infers that changes in carbonate budgeting in future reefs could be as much about changing patterns of sediment redistribution and export as it is about lowered carbonate production. Regardless of what the mix of processes looks like quantitatively, the fact that sediment transport is totally ignored in our present models argues that we need to rethink them – especially in the face of increased storminess in years to come.

3.5 Future Reefs and *Homo stupidus*

Having discussed the factors that control reef formation and the ways they accrete, the discussion returns to where it started – the changing reef seascape in recent years. Are reefs “declining”? If so, what is driving these changes? How do they fit into the known mechanisms of climate modulation? How might remaining reefs respond to the dramatic changes in sea level that have been proposed for the coming decades? And finally, what can.... and what should we be trying to “fix” – and how?

3.5.1 Reefs in Flux

It is inescapable that the world’s reefs are changing dramatically – and it seems to be for the worse. However, most of the study sites on which we base these ideas were chosen because they were, for example, the “best developed,” or the “most diverse” of the reefs that could be found at the time. Thus our starting points for earlier comparisons were to some extent skewed. Equally important, our anthropocentric perspective focuses on changes in our lifetime and the attendant assumption that the reef we saw on our first visit was “normal”. A survey of the coral communities around Easter Island found a luxuriant, albeit low-diversity, coral community all around the island – except for on the windward side (Hubbard and Garcia 2003), where conventional wisdom would tell us to look for the “best” reefs. The shallow community consisted of an assemblage of abundant corals (up to 100 % over large areas; avg. ca. 50 %). However, video from the 1970s show that the shallow insular shelf had been dominated by *Sargassum*. After the near extirpation of macroalgae following a severe El Niño, corals dominated by *Pocillopora* spp. gradually moved into the newly created space in shallow water. So, which was the “better” or “healthier” community, the algae that were compromised by climate change or the corals that replaced them? And, how does this tie into the complex story of colonization on Easter Island? It is perhaps ironic that the rapid takeover by coral was lamented by locals as a shift away from the “normal” and “healthy” community dominated by algae –

an argument that we are not used to hearing in the reef community.

To further complicate the picture, subsequent bleaching associated with La Niña warming devastated the shallow-water coral community that had dominated for over a decade (Wellington et al. 2000; Hubbard and Garcia 2003). Were algae or coral the "normal" shallow marine community around Easter Island? Which was "better"? What will replace the recently killed *Pocillopora*? Are the patterns of rapid change in this remote area new or just part of a longer "boom-and-bust cycle? What role, if any, did either the low diversity or the particular members of the community have to do with this unusual history? And finally, because Easter Island is farther from major land masses than just about anywhere on Earth, is there any area that is totally outside anthropogenic influence if we are at the heart of the problem?

The story from Easter Island might be cast off as interesting but not relevant to the larger global situation. Nevertheless, Jackson (1997) cautioned that historical evidence shows that many of the patterns we see as unusual today were already occurring at the time of Columbus. Thus, the reefs that we first studied in the 1950s were probably not "pristine" and some of the degradation that we have more recently documented had already begun. Rudimann (2005) argues that the shift in humans from hunter-gatherers to agrarians may have begun the present climate decline as early as 8,000 years ago.

None of this presumes that recent changes in coral reefs are not "real" or that increased human exploitation is not tied up in the story. However, if we are going to effectively use our limited environmental capital, then we need to take a hard look at our personal and often anthropocentric perspectives with respect to "good" and "healthy". The fundamental challenge is to separate natural from anthropogenic change and to come up with practical strategies based on that differentiation. To apply this to the fate of reef building in the near future, we need to make sure that we fully understand the processes that contribute to this venture in a wholly natural scenario.

3.5.1.1 Is the Past the Key to the Present?

Studies of Quaternary reefs provide an important longer-term look at patterns of reef development against which we might compare recent change. Paldolfi (2002) remarked that the Pleistocene reefs exposed in the cliffs around Curacao "show strikingly clear and repeatable differences in coral species abundance patterns among reef environments, similar to zonation patterns previously described for living reefs at Curacao and elsewhere in the Caribbean prior to the 1980s." Jackson (1992) similarly proposed that Pleistocene reefs were more stable in the long term and that the presence or absence of the classic reef-zonation pattern might be used to distinguish between "normal" versus "unhealthy" Caribbean reefs. However, they both cautioned that, while long-term stability may be the hallmark of large-scale Pleistocene reef development, variability and even anarchy may be the natural picture at smaller spatial and temporal scales (Jackson 1991; Pandolfi and Jackson 1997).

A number of recent studies have built on this theme of long-term stability and have proposed that the events associated with recent coral-reef decline are not the norm. Comparing Pleistocene and modern reefs on San Salvador, Greenstein (1999) proposed that, "the current and rapid decline of *A. cervicornis* observed on Bahamian patch reefs may be a unique perturbation that contrasts with the long-term persistence of this coral species during Pleistocene and Holocene time." Aronson and Precht (2001b) similarly noted a recent community change from *A. cervicornis* to *Agaricia tenufolia* on Belize patch reefs. Cores through the upper part of the reefs revealed no such widespread community change between the two species over the past few thousand years. Based in large part on these findings, they wrote, "paleontological data suggest that the regional *Acropora* kill is without precedent in the late Holocene" (Aronson and Precht 2001a). These statements infer that the recent geologic record is unambiguous and that short-term changes documented by reef monitoring over the past two to four decades are in fundamental contrast to stability before humans came to be an important factor in the coral reef equation.

3.5.1.2 Buck Island: A Tale of Two Analyses

One of the longer coral-reef monitoring records comes from Buck Island Underwater National Monument in the eastern Caribbean. Surveys were initiated in the late 1970s, before the onset of coral diseases and other changes we have documented in reefs. The successive surveys chronicle decline related to disease, hurricanes and a variety of other factors in an area administratively protected from direct human impact – especially nutrients and over-fishing. This was the site of the first described incidence of White Band Disease (WBD) by Gladfelter (1982). As part of the effort to understand reef development within the park, seven reef cores were drilled along two of the long-term monitoring transects. The goal was to interpret the geological history of the reefs and to relate that to community structure within the present-day reef system.

Figure 3.14 compares the relative abundance of corals in the seven cores to the changing composition of the recent reef community since 1970. The importance of *Acropora palmata* in the cores over the past 6,000 years closely matches the pre-WBD community (i.e., 1976), suggesting that a community absent *A. palmata* has not been the geologic norm in this area. It was initially suggested that, "this may indicate that 'White Band Disease' and similar

Fig. 3.14 Graph of coral abundance along the northern Buck Island monitoring transect versus what was found in cores from the same reef. Note the close agreement between the abundance of *A. palmata* in the cores (i.e., the longer-term "geological trend") and the monitoring transect in 1976, prior to the onset of White Band Disease. It might be concluded from this figure that the dramatic loss of *A. palmata* after 1976 was an event that was "unprecedented" over the 7,000 years represented by the Buck Island cores

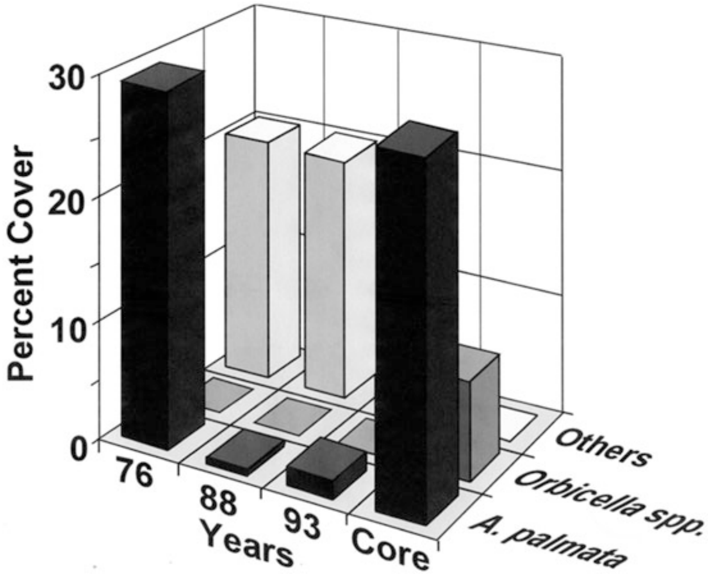
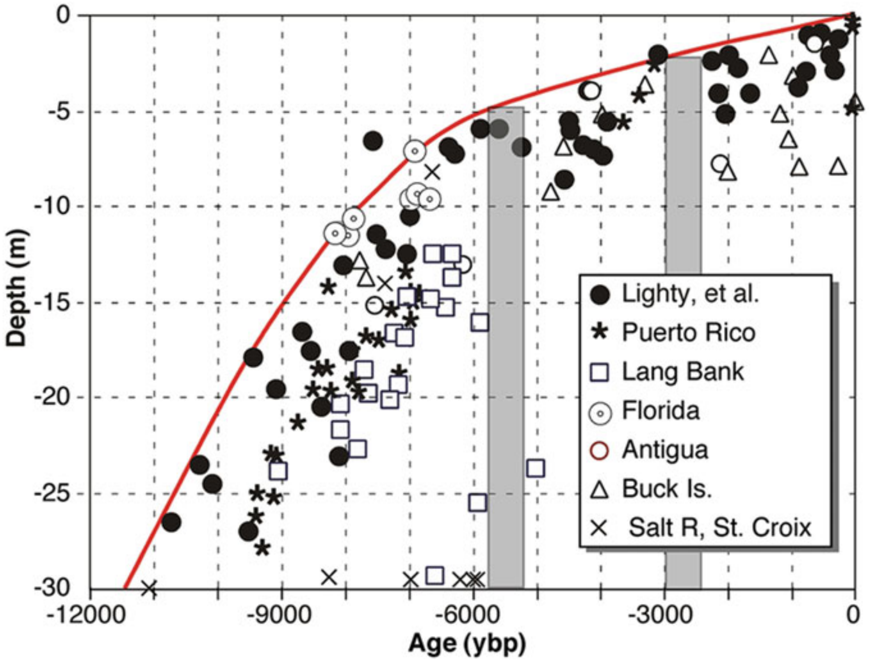


Fig. 3.15 Summary of the Caribbean record of *A. palmata* over the past 12,000 years. Two 500-year intervals of either greatly reduced abundance or absence of *A. palmata* (*gray shaded*) are in apparent contradiction to recent statements about the "unprecedented" nature of such events (After Hubbard et al. 2005)



afflictions have been less important in the geologic past" (Hubbard et al. 1994), a conclusion similar to those just described for other sites.

However, more detailed analyses of the cores identified two gaps in the record of *A. palmata* at Buck Island (Hubbard et al. 1998, 2000, 2005). A compilation of all radiometrically dated *A. palmata* samples found in the literature suggests that these gaps persist throughout the Caribbean and western Atlantic region (Hubbard 2014). The first gap, about 5,700 years ago (Fig. 3.15), was associated with regional abandonment of Caribbean shelf-edge reefs and an abrupt landward shift in reef position (i.e., backstepping). The second, about 3,000 years ago, is related to no such event and remains largely unexplained.

Each gap spans nearly a millennium and is followed by what appears to be full recovery of the *A. palmata* community.

Whatever happened at Buck Island, it appears to have been coincident with what was happening regionally. While a reef crest dominated by *A. palmata* was spatially dominant in the overall history of the reef, it was absent for nearly a third of the time. Thus, we need to be very careful to not equate spatial dominance to temporal persistence.

Earlier scientific wisdom held that reefs were inherently stable systems in which little changed from year to year.

With further study, we have come to realize that present-day reef equilibrium can be very dynamic, and that reefs are potentially capable of significant change over relatively short spans of time – even when “nothing is wrong”. The question now before us is how the changes that we are seeing fit into the grand scheme of things over the longer haul.

The all-too-common decrease in coral cover and the attendant rise in macroalgae on so many of the world’s coral reefs are the cumulative result of bleaching, disease, increased nutrients, sedimentation, and myriad other factors related to growing human population growth and ever-expanding exploitation. If we ignore these basic truths while we try to sort out other pressing but more complex and indirect global issues, we run the risk of exceeding an environmental “angle of repose” before our data are good enough to assess blame with certainty. On the other hand, we can little afford to “fix” everything that seems broken. It is difficult to decide which reflects greater hubris, our earlier sense that we could manipulate our environment without impact or our sense that we can now repair the damage caused by this misconception.

3.5.2 So, What Do We Do?

Bruce Hatcher posited that “paleontological and sclerochronological studies of corals and reef provinces provide the best available tools to expand the temporal horizons of observation” (from Pandolfi 2002). However, the shift from coral to macroalgal dominance is virtually impossible to detect in the fossil record because such algae do not preserve well, if at all. Also, important gaps in the fossil record can be missed if we use a visually discernable change in species composition as the sole way to detect them. How many of the gaps identified for *A. palmata* for the last 10,000 years exist in the spatially persistent Pleistocene records of Barbados, Curacao and other places cited as examples of pre-anthropogenic stability in Caribbean reefs? It may be premature to dismiss Grigg’s (2000) concerns over the effects of temporal scale and measurement artifacts on comparisons of long-term geological and short-term biological data. Careful radiometric dating is the only obvious solution, but the cost of such an effort at a scale that will allow us to address regional or global phenomena is daunting. Nevertheless, it may remain as the only plausible approach to a real understanding of short-term change in reef-community structure over longer periods of time – short of centuries of monitoring.

Having said all this, whether or not past gaps in the *Acropora* record exist or not, and who has the better understanding of community stasis is no longer the main issue. Even if such gaps are commonplace, the stress levels that accompanied subsequent recovery in the past were less intense and undoubtedly different than what is occurring today. While the resolution of such issues is of great importance to science and, once resolved, will have overwhelming bearing on conservation policy, the answers are not available now and will probably not be for some time to come.

In the meantime, we may be left with something no more complex than “Pascal’s Wager” in the seventeenth century relating to the existence of God. What we are in effect doing today, as was Pascal centuries ago, is weighing the relative consequences of acting on a premise that might eventually be proven wrong. Pascal argued that if we presumed God’s existence and were wrong, the world would simply be left with “an excess of virtue”, certainly preferable to the “eternal damnation” that would follow incorrectly denying God’s existence. Applying this to the present environmental situation (Hajek 2001), a policy that moves toward sustainability even if no crisis actually exists, still results in “infinite utility” – we will have coral reefs to pass on to future generations.

So, is science irrelevant to the growing environmental debate? Absolutely not! Science has given us our present understanding of the issues; we have done our jobs well. There is still an important role for science as we continue to unravel the intricacies of community structure on a variety of scales and use that information to propose sound environmental and conservation policy, hopefully well into the future. Our continued participation is demanded. However, the time it will take to arrive at the level of scientific certainty that skeptics demand is a luxury that we no longer have. The pressing goal for now is to change public attitudes and create a consensus toward sustainability – and fast!

Consider for a moment the body of information that was provided to support the existence of Weapons of Mass Destruction in Iraq. We willingly embarked on a track that was infinitely costly in dollars, international good will and quality of life for countless groups; this was ultimately shown to have been based on seriously flawed information. By comparison, consider the quality of the information that points to elevated levels of carbon dioxide in our atmosphere, the adverse environmental and economic impacts of an economy totally dependent on fossil fuels, the increased degradation of coral reefs in proximity to centers of human population, and the spent biotic systems that we will be handing down to future generations. Yet, we refuse to act upon this infinitely better body of information because it is “too costly” to respond until we “know for sure”.

This paradox will be solved only by a fundamental change in public perception and political will. While scientists must play a role in this process, the change will not be driven by good science alone – recent history has painfully demonstrated this. Perhaps it really is as simple as Pascal posited centuries ago. If we act on a presumed environmental crisis – one that is ultimately shown to be less severe than we presently think, we will have perhaps overspent dollars that some presume we can ill afford.

However, we will have a planet that is fundamentally better off and will have acted on behalf of those least represented in the recent debate – future generations, lost species and increasingly degraded habitats. If, on the other hand, we choose to deny what is ultimately proven to be a real crisis, we will be faced with a failed life-support system and a path that no amount of capital wealth can reverse. We need to replace the present economic mindset that our dollars need to be preserved until we can absolutely quantify the problem with one that places a much higher value on environmental capital that cannot be regained in the next rebound of the stock market.

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