



# A geological perspective on the degradation and conservation of western Atlantic coral reefs

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**Abstract:** *Continuing coral-reef degradation in the western Atlantic is resulting in loss of ecological and geologic functions of reefs. With the goal of assisting resource managers and stewards of reefs in setting and measuring progress toward realistic goals for coral-reef conservation and restoration, we examined reef degradation in this region from a geological perspective. The importance of ecosystem services provided by coral reefs—as breakwaters that dissipate wave energy and protect shorelines and as providers of habitat for innumerable species—cannot be overstated. However, the few coral species responsible for reef building in the western Atlantic during the last approximately 1.5 million years are not thriving in the 21st century. These species are highly sensitive to abrupt temperature extremes, prone to disease infection, and have low sexual reproductive potential. Their vulnerability and the low functional redundancy of branching corals have led to the low resilience of western Atlantic reef ecosystems. The decrease in live coral cover over the last 50 years highlights the need for study of relict (senescent) reefs, which, from the perspective of coastline protection and habitat structure, may be just as important to conserve as the living coral veneer. Research is needed to characterize the geological processes of bioerosion, reef cementation, and sediment transport as they relate to modern-day changes in reef elevation. For example, although parrotfish remove nuisance macroalgae, possibly promoting coral recruitment, they will not save Atlantic reefs from geological degradation. In fact, these fish are quickly nibbling away significant quantities of Holocene reef framework. The question of how different biota covering dead reefs affect framework resistance to biological and physical erosion needs to be addressed. Monitoring and managing reefs with respect to physical resilience, in addition to ecological resilience, could optimize the expenditure of resources in conserving Atlantic reefs and the services they provide.*

**Keywords:** *Acropora*, bioerosion, Caribbean, cementation, coral reef, Holocene geology, monitoring

Una Perspectiva Geológica de la Degradación y Conservación de los Arrecifes de Coral del Atlántico Oeste

**Resumen:** *La degradación continua de los arrecifes de coral en el Atlántico oeste está resultando en la pérdida de las funciones ecológicas y geológicas de los arrecifes. Con el objetivo de asistir a los administradores de los recursos y de los arrecifes en el establecimiento y medida del progreso hacia metas realistas para la conservación y restauración de los arrecifes de coral, examinamos la degradación de los arrecifes en esta región desde una perspectiva geológica. La importancia de los servicios ambientales proporcionados por los arrecifes de coral - como rompeolas que disipan la fuerza de las olas y protegen las líneas de costa y como proveedores de hábitat para innumerables especies - no puede ser exagerada. Sin embargo, las pocas especies de coral responsables de la construcción de arrecifes en el Atlántico oeste durante aproximadamente los últimos 1.5 millones de años no están prosperando en el siglo XXI. Estas especies son altamente sensibles a los extremos abruptos de temperatura, propensas a las enfermedades infecciosas y tienen un potencial bajo de reproducción sexual. Su vulnerabilidad y la baja redundancia funcional de los corales que forman ramas han llevado a la baja resiliencia de los ecosistemas arrecifales del Atlántico oeste. La disminución en la cobertura de coral vivo en los últimos 50 años resalta la necesidad de estudios sobre los arrecifes relictos*

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(senescentes), los cuales desde la perspectiva de la protección de la línea costera y la estructura del hábitat, pueden ser igual de importantes de conservar que la capa de corales vivientes. Se necesitan investigaciones para caracterizar los procesos geológicos de bioerosión, cementación de arrecifes y transporte de sedimentos conforme se relacionan a los cambios contemporáneos en la elevación de los arrecifes. Por ejemplo, aunque el pez loro (familia Scaridae) remueva macroalgas pesadas, lo que posiblemente promueva el reclutamiento de coral, no va a salvar a los arrecifes del Atlántico de la degradación geológica. De hecho, estos peces están mordisqueando rápidamente cantidades significativas de marco de trabajo sobre arrecifes del Holoceno. La pregunta de cómo la biota diferente que cubre los arrecifes muertos afecta al marco de trabajo sobre resistencia a la erosión física y biológica necesita ser atendida. El monitoreo y el manejo de los arrecifes con respecto a la resiliencia física, además de la resiliencia ecológica, podrían optimizar el gasto de los recursos para la conservación de los arrecifes del Atlántico y los servicios que proporcionan.

**Palabras Clave:** *Acropora*, bioerosión, Caribe, cementación de arrecifes, los arrecifes de coral, geología de Holoceno, monitoreo

## Introduction

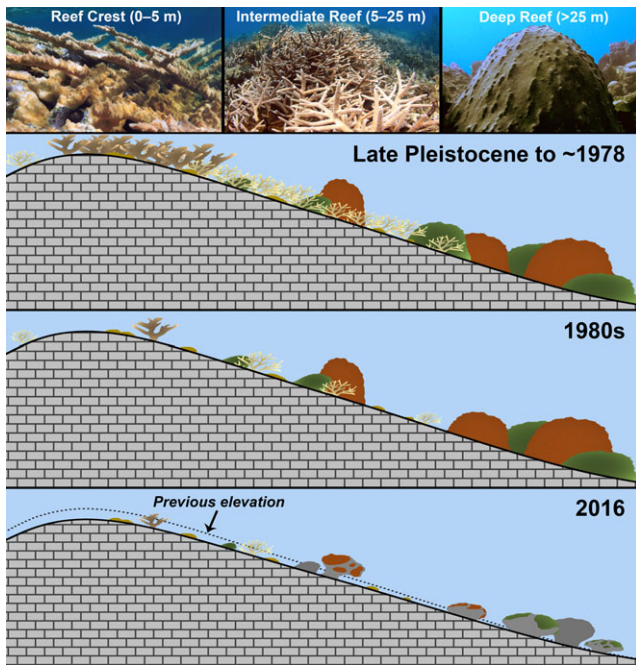
The ecosystem services provided by coral reefs are widely perceived as critical to human welfare (Costanza et al. 2014). Coral reefs are a first line of defense against coastal hazards such as hurricanes and tsunamis. Much like submerged sandbars and barrier islands, coral reefs dissipate wave energy, quieting the waters behind them and lessening shoreline erosion and retreat (Spalding et al. 2014). The complex architecture of coral reefs also provides valuable habitat for countless marine organisms and food security for coastal communities throughout the tropics (Sale et al. 2014). Unfortunately, over the last several decades, coral cover on reefs around the world has declined as a result of local- to global-scale perturbations (Bellwood et al. 2004; Hughes et al. 2010). Reefs in the western Atlantic region have been particularly affected (Wilkinson & Souter 2008; Roff & Mumby 2012; Jackson et al. 2014). If the trajectory of reef decline in this region continues, critical ecological and geologic functions of western Atlantic reefs may be lost (Wild et al. 2011).

We examined future prospects for the maintenance of key ecosystem services provided by the physical structure of reefs in the face of continuing coral-reef degradation in the western Atlantic. First, we summarize the species composition of coral reefs during the Quaternary Period (Pleistocene + Holocene, approximately 2.4 million years ago [Ma] to present) and consider the significance of recent changes in community structure, calcification, reef cementation, and bioerosion. We then present a geomorphological perspective on coral-reef degradation to remind readers of the seminal works on carbonate budgets from the previous century (Stearn et al. 1977; Land 1979; Scoffin et al. 1980; Hubbard et al. 1990) and to further the campaign to value a wider breadth of processes involved in carbonate production and destruction (e.g., Perry et al. 2008), rather than focusing on the thin veneer of living reef biota that is often the emphasis of ecological monitoring and restoration programs.

## Western Atlantic Coral Reefs of the Past

Throughout the Cenozoic Era (65 Ma to present), faunal turnover of Caribbean coral assemblages was largely driven by major tectonic and climatic changes (Budd 2000). The modern coral fauna are a mixture of species that mostly originated during a peak in speciation 5–3 Ma caused by the emergence of the Isthmus of Panama and subsequent changes in regional oceanic circulation (Budd 2000). The extant species then survived the Plio-Pleistocene extinction (2–1.5 Ma) brought about by the onset of glaciation in the Northern Hemisphere (Budd & Johnson 1999). Although age of origination, family affiliation, and geographic distribution did not determine which species ultimately survived, corals with more massive and thick-branching size and shape were favored over thin-branching and free-living species (Budd & Johnson 1999). The Plio-Pleistocene turnover marked the final divergence of the Atlantic and Pacific reef faunas. Aside from the introduced sun coral (*Tubastraea coccinea*), no coral species found in the Atlantic today occurs in any other ocean (Veron 2000).

In the mid-20th century, zonation of live coral species on reefs throughout the western Atlantic was very similar to that of Pleistocene and Holocene reefs (Fig. 1). Most shallow high-wave-energy reef crests were built by *Acropora palmata*. Adjacent to the reef crest was an *Acropora cervicornis* zone bordered by a head-coral community in deeper water that was usually dominated by the massive corals *Orbicella* (formerly *Montastraea*) and *Diploria* spp. (Goreau 1959; Macintyre & Glynn 1976; Geister 1977; Gischler & Hudson 2004). The back-reef or lagoonal community was composed of *A. cervicornis*, smaller colonies of *A. palmata*, and occasional head corals. Some western Caribbean lagoonal reefs, such as those in Belize (Aronson et al. 2004), Jamaica (Wapnick et al. 2004), and Mexico (Macintyre et al. 1977), were built almost entirely by *A. cervicornis*. Because populations today rarely exhibit more than small shrub-like



**Figure 1.** Changes in reef zonation of western Atlantic coral reefs from the Late Quaternary to the present. Photographs at the top show examples of the 3 reef zones present until the late 1970s and correspond to the reef schematic immediately below (brick pattern, reef carbonate underneath the living-reef veneer). The 1980s schematic shows the dramatic change in reef zonation as a result of widespread loss of acroporid corals. The 2016 (present) schematic is a generalized representation of modern western Atlantic coral reefs, characterized by fragmentation, undercutting, and loss of massive colonies and by loss of reef elevation from reef erosion.

colonies with spindly thin branches, the capacity of *A. cervicornis* to build a substantial framework has been forgotten. Branches that were 1 m long (Gladfelter 1984) and 10 cm in diameter were commonplace before the region-wide collapse of the species in the late 1970s. Samples of *A. cervicornis* recently collected from a back-reef rubble pile on the Florida (U.S.A.) reef tract, which dated to the early 17th century, reached cross-sectional diameters of 9 cm (27-cm circumference) and were almost unrecognizable to us (Fig. 2).

The framework-building assemblages of the western Atlantic generally demonstrated remarkable stability from the late Pleistocene (Budd & Johnson 1999; Multer et al. 2002; Pandolfi & Jackson 2006) through the Holocene (from 11,700 years ago to modern) until very recently (Lewis 1984; Aronson et al. 2004). Because these coral species originated before the Plio-Pleistocene extinction event, they presumably possessed ecological traits that allowed them to persist through the extreme climate



**Figure 2.** Photograph of the authors holding *Acropora cervicornis* dating to several centuries ago from Crocker Reef, Florida (left), and a typical specimen from today's reefs in the western Atlantic (right) (people in photograph for scale).

fluctuations that characterized the repetitive glaciation-deglaciation cycles of the late Pleistocene (Budd & Johnson 1999). Paradoxically, these same, putatively resilient species (i.e., *Acropora* and *Orbicella* spp.) have proven, over the past 50 years, to have low tolerance to both cold (Porter et al. 1982; Colella et al. 2012) and warm (Mendes & Woodley 2002) temperature extremes, to be susceptible to diseases (Aronson & Precht 2001; Miller et al. 2006), and to succumb readily to pests such as snails (Williams et al. 2014), fireworms, and damselfish.

The trajectory and main causes of decline for the important species in the genera *Acropora* and *Orbicella* differ. In contrast to the rapid decline of the acroporids in the late 1970s primarily from white-band disease (Aronson & Precht 2001), decline in *Orbicella* spp. has been more recent and more gradual. Wholesale mortality of *Orbicella* colonies does not generally occur from a single disease or bleaching event. Instead, partial mortality causes the colonies to fragment, which results in a slow dwindling of large colonies and a shift in size-frequency distributions toward right-skewed populations (Fig. 1) (Edmunds 2015). *Orbicella* populations throughout the western Atlantic region were significantly reduced by warm-water bleaching during the global event in 1998 (Wilkinson & Hodgson 1999) and again in the regional 2005 event (Miller et al. 2006; Wilkinson & Souter 2008). The impacts of the 2005 bleaching event were especially severe because bleaching was closely followed by white plague (Miller et al. 2006; Wilkinson & Souter 2008). Warm-water bleaching coupled with the continued reappearance of white-band disease has also limited recovery of western Atlantic *Acropora* spp. in recent decades (Aronson & Precht 2001).

Assuming that western Atlantic reefs were subject to warm- and cold-temperature anomalies during repeated



glacial cycles throughout the late Pleistocene, deciphering what is different about the ecosystem controls on reef resilience today is at the crux of understanding the modern coral-reef crisis. The recent rates of increase in atmospheric greenhouse gases, temperature, and ocean pH are likely without precedent in the experience of contemporary western Atlantic fauna (Honisch et al. 2012). However, the causes of coral mortality do not have to be the same as those that prevent coral population recovery (Kuffner et al. 2015). The lack of recovery may be driven by recruitment failure (Hughes & Tanner 2000) and early life-history processes (Edmunds 2007) rather than high mortality rates per se. Population recovery of long-lived *Orbicella* species is slow because their reproductive capacity is low. Their recruits were reported as extremely rare in 22 studies since 1979 (Bak & Engel 1979; Williams et al. 2008; van Woesik et al. 2014 [see their table 1]). Similarly, for the acroporids, sexual reproductive success may be directly limited by population declines because the probability of successful fertilization decreases as population size decreases (Allee effect) (Knowlton 2001; Precht et al. 2004). Overall, it seems that the dominance of *Acropora* and *Orbicella* spp. that began in the Late Pleistocene may be coming to an end. Although these species thrived on western Atlantic reefs for the past 1.5 million years, they seem to lack resilience in the current regime of extreme, high-frequency environmental disturbance.

### Dominant Western Atlantic Corals of the 21st Century

Few species are available in the western Atlantic to take the place of the Quaternary framework-building taxa and to fill their role as ecosystem engineers (Roff & Mumby 2012). The low functional redundancy of Caribbean reef assemblages reflects the global disparity in coral diversity. For example, with 65 species of acroporids in the Indo-west Pacific (Veron 2000), reefs there would be more likely to absorb the local extinction of 2 species without losing functionality. In contrast, the near loss of 2 species in the Caribbean has resulted in the disappearance of at least 2 major reef zones (Fig. 1). No other branching species in the Caribbean can form the complex structures produced by *A. palmata* and *A. cervicornis* or approach their high rates of carbonate production.

Concurrent with the declines in the once-dominant *Orbicella* and *Acropora* spp., the relative abundance of coral species that do not build reefs has rapidly increased (Burman et al. 2012; Toth et al. 2014; Perry et al. 2015). These weedy hard corals (sensu Knowlton 2001), including *Agaricia*, *Porites*, and the hydrocorals, *Millepora* spp., have increased in relative percent cover throughout the western Atlantic (Aronson & Precht 2001; Burman et al. 2012; Toth et al. 2014). There is little evidence of these taxa being major players in Holocene reef building (Pandolfi & Jackson 2006); however, they have become

opportunistic dominants following coral-mortality events because they quickly move in after disturbances, in some cases increasing in both relative and absolute dominance (Aronson et al. 2014). Although *Porites* spp. and *Agaricia* spp. in the western Atlantic have consistently high larval-recruitment success (Rogers et al. 1984; Edmunds 2002), they are not very resistant to thermal stress, and, along with *Millepora* spp., they are highly susceptible to bleaching (Mayer 1914; Aronson et al. 2000; Kemp et al. 2011). Sensitivity analyses from a coral-assemblage modeling study reveal that under various global-warming scenarios, resistance to thermal stress, coral growth rate, and colony longevity were the most important predictors of the persistence of coral genera (Edmunds et al. 2014). Thus, whereas opportunistic species that do not build reefs have a high reproductive capacity and can quickly occupy open space, they do not fare well during episodic disturbances.

One possible exception to the observation that modern western Atlantic reef-building corals have low resilience to recent environmental change is the coral *Siderastrea siderea*, which can form colonies up to 1.5 m in diameter. This species is opportunistic in that it has the highest larval-recruitment success of all the species with massive morphology (van Woesik et al. 2014) and is resistant to warm- and cold-temperature stress (Mayer 1914; Kemp et al. 2011; Colella et al. 2012). *S. siderea* is now the most abundant coral species on the Florida reef tract (Burman et al. 2012; Toth et al. 2014), and it is locally abundant in other marginal reef areas including the southeastern Gulf of Mexico (Jaap 2015), Panama (Guzman et al. 1991), and Brazil (Neves et al. 2010). Its distribution in the Quaternary fossil record also supports the conclusion that this species can thrive in highly disturbed environments. Although *S. siderea* was rare in some areas, including the Pleistocene reefs of Barbados (Pandolfi & Jackson 2006) and in the Holocene reefs of Florida (<http://olga.er.usgs.gov/coreviewer/>), it was the dominant species in the sediment-stressed Holocene reefs of the Enriquillo Valley, Dominican Republic (Lescinsky et al. 2012). The species' resistance to stress and its resilience in the face of repeated disturbance events likely contribute to its persistence. Also, the reproductive cycle of this species is unique. Unlike most massive, hermaphroditic species that broadcast their gametes during mass-spawning events in late summer, *S. siderea* is gonochoric (i.e., has separate male and female colonies [Szmant 1986]) and does not participate in mass spawning. No field observations of spawning have been published to date. Histological analyses revealed, however, that gametes were ripe later in the autumn and longer than other broadcast-spawning species examined (Szmant 1986; Soong 1991).

The recent decline of corals in the western Atlantic, largely associated with the loss of the *Acropora* and *Orbicella* spp., has resulted in significant reductions in

reef-building capacity throughout the region (Perry et al. 2013). Opportunistic coral taxa are now responsible for the majority of carbonate production on most western Atlantic reefs. However, the increase in relative and absolute abundance of these corals will likely do little to reverse the negative trajectories of carbonate production in the region (Perry et al. 2014). In fact, they may reinforce this pattern because foliaceous and thin-branching corals are more easily bioeroded and broken, leaving carbonate rubble and sediment vulnerable to removal from the reef by waves and storms. In sum, most corals that are abundant on today's reefs (e.g., *Porites* and *Agaricia* spp.) have short life spans, positively skewed size-frequency distributions, low thermal tolerance, and little resistance to breakage, and, as a result, their dominance in the western Atlantic may be fleeting and geologically insignificant.

### Vulnerability of Reef Framework

Although many reefs in the western Atlantic have continued to accrete into modern times, the fact that some surficial reef structure is actually quite old frequently goes unnoticed. Often assumed by ecologists to be thriving and contiguous throughout the Holocene, there are relict reefs that, while dotted with live corals, were built approximately 8000–6000 years ago, including Lang Bank, St. Croix (Hubbard et al. 2013), and much of the Florida Keys (Ginsburg & Shinn 1994). Reef accretion in these locations essentially ceased long ago for reasons that remain unclear. Until the late 1970s, however, even these relict reefs were covered with a layer of live coral that protected the framework from the onslaught of scraping, rasping, and bioeroding fauna (Glynn 1997). Today, most reefs in the western Atlantic have transitioned to net erosional systems as the balance between calcification by live corals and the amount of unprotected reef exposed to bioerosion has shifted (Perry et al. 2013). Investigating the variance in erodibility of surfaces devoid of live coral is a critical line of research that has not received much attention from coral-reef scientists and managers.

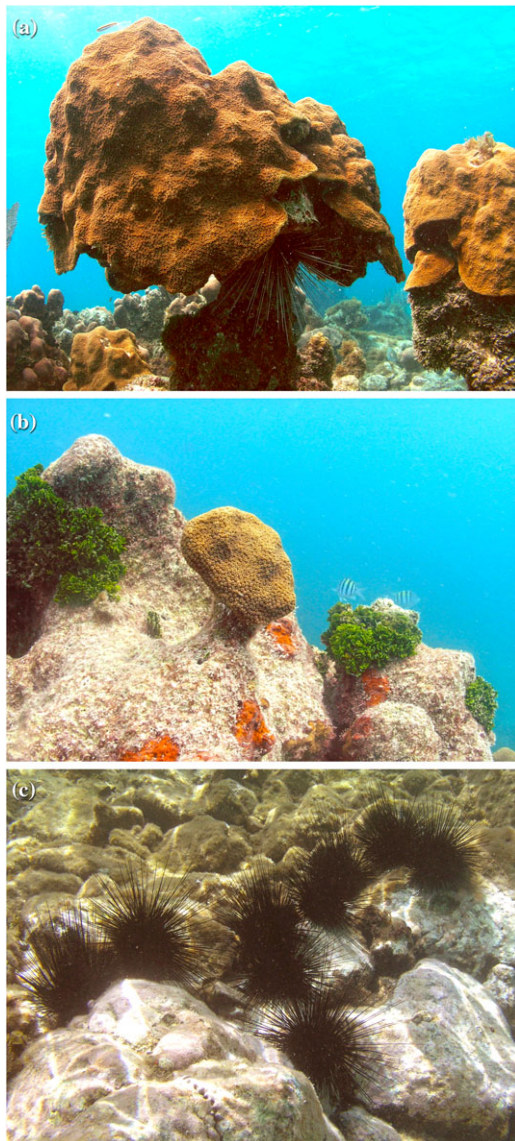
Individual reefs vary considerably in their porosity (Macintyre & Glynn 1976) and thus their resistance to erosion, but the character of a reef's framework is rarely quantified for modern reefs. After reef carbonates are initially deposited by corals and other marine calcifiers, the reef matrix itself is continually altered and infilled with sediments, rubble, and cements (Rasser & Reigl 2002). The postdepositional processes of cementation and submarine lithification decrease reef porosity, increase reef density, and should, therefore, decrease erodibility. The degree of cementation varies considerably among different parts of the reef. Cements are best developed on the fore reef and surrounding shallow pavements due to great amounts of water movement and lack of sediment accumulation in these areas (Marshall 1985; Macintyre

& Marshall 1988). Heavy, secondary cementation of reef framework at the edge of reef crests in the Lesser Antilles reportedly produces a “hammer-ringing,” porcelain-like limestone (Adey 1975). These cements are largely composed of high-magnesium calcite that form crusts around the outside of dead coral skeletons and infill the boreholes and skeletal cavities of encrusting organisms such as vermetids and serpulids (Macintyre & Marshall 1988). Thus, they provide a cap at the reef surface that potentially protects the carbonate underneath. The degree of submarine cementation is also a function of time available at the interface of the water column and the substratum (Macintyre & Marshall 1988). Thus, slower accreting reefs are more consolidated and cemented than those having higher accretion rates (e.g., Gischler & Hudson 2004; Stathakopoulos & Riegl 2015). In sum, high-wave-energy and slowly accreting reefs should be relatively resistant to erosion. Measures of reef hardness, density, and porosity and of how these parameters vary with time and environmental conditions will be highly relevant to understanding the resistance of reefs to erosion.

### Parrotfish and Western Atlantic Coral Reefs

It is well documented that phase shifts from coral to macroalgal dominance, hastened by the loss of herbivores and localized impacts of hurricanes, have occurred on some western Atlantic reefs (Hughes 1994; Jackson et al. 2014). However, in most locations, macroalgae have not actually become dominant (i.e., cover > 50% of the reef [Bruno et al. 2009]). The macroalgal-dominance problem may be more relevant in extremely overfished localities such as Jamaica, where herbivores are targeted as sources of food (Bruno et al. 2009; Côté et al. 2013). Suitable substratum for coral settlement persists at levels around 25% on many reefs throughout the Caribbean region (e.g., Edmunds 2002; Toth et al. 2014), leaving plenty of room for coral larvae. Degradation of western Atlantic reefs is first a coral-mortality problem (Aronson & Precht 2006) followed by lack of coral-recovery problem. Although evidence that no-take marine protected areas (MPAs) help reverse this trend does exist for one location (Mumby et al. 2006), most MPAs have not stimulated coral recovery (Selig et al. 2012; Toth et al. 2014).

Although parrotfish perform the ecosystem service of clearing dead-reef substratum of turf algae and preventing algal germlings from developing into shag carpets of fleshy algae, they are also quite destructive to reef framework (Figs. 3a & 3b). Their large, rasping, beak-like mouths remove carbonate material from the reef and deposit it as fine-grained sand (Bellwood & Choat 1990), and in the western Atlantic, the stoplight parrotfish (*Sparisoma viride*) is particularly destructive (Scoffin et al. 1980). Perry et al. (2014) estimate that parrotfish are responsible for >80% of the approximately 2 kg CaCO<sub>3</sub>·m<sup>-2</sup>·year<sup>-1</sup> removed from shallow (<10 m) reefs, and



**Figure 3.** Erosion of *Orbicella faveolata* colonies at (a) Harbor Point, St. John, U.S. Virgin Islands (sea urchin [*Diadema antillarum*] under colony) and (b) Hen and Chickens Reef, Florida Keys (U.S.A.). (c) *D. antillarum* clearing turf algae from the shallow-rubble zone in St. John, U.S. Virgin Islands.

their impact is even more severe within MPAs. The non-calcifying biota that now often drape reef framework in the absence of live corals, such as mat-forming zoanthids (e.g., *Palythoa caribaeorum*) and octocorals (*Briareum asbestinum* and *Erythropodium caribaeorum*), should be evaluated for their potential as reef protectors because they may deny scraping herbivores access to the reef.

In the early 1980s, *Diadema antillarum*, the long-spined sea urchin that historically shared the algae-removal job with the parrotfish, was nearly extirpated from western Atlantic reefs by an unidentified pathogen

(Lessios 2016). *Diadema* has recovered in some areas, particularly in shallow, nonreef habitats (Fig. 3c), but has yet to return to historical levels (Lessios 2016). High densities of *Diadema* just prior to the die-off were perhaps anomalous, however, because their predators were heavily overfished in some areas (Leviton 1992). Regardless of natural population size, the feeding behavior of *D. antillarum* (especially large individuals) resulted in substantial carbonate removal on reefs prior to their die-off (Scoffin et al. 1980; Bak 1994). Rates of bioerosion on today's coral reefs would be even higher if these urchins were still abundant (Perry et al. 2014). As bioerosion becomes an increasingly dominant process, the importance of restoring herbivores for removing macroalgae must be balanced against their capacity for reef-framework destruction.

### Erosion and Flattening of Reef Framework

Much of the sedimentary material (rubble, sands, and silts) created by erosion is transported away from reefs during storms, leaving only about 60% available for sedimentary accumulation within the reef framework (Hubbard et al. 1990). Sediment accumulations that remain on reefs can be stabilized and cemented (Rasser & Reigl 2002). However, the rising severity of hurricanes caused by ocean warming (Webster et al. 2005) could increase storm-generated swell and the removal of carbonates from reef environments because even small changes in wave energy can trigger huge increases in sediment loss from the reef (Hubbard et al. 1990). With fewer corals available to replace the reef framework that is lost, the destructive processes of erosion and sediment transport are increasingly driving carbonate budgets as the supply side of the equation shrinks. This shift in the equation is causing the loss of the physical structure that is so critical to preserving the ecological and geological function of western Atlantic reefs.

Maintenance of reef framework is critical to the preservation of reef topographical complexity. The three-dimensional structure of coral reefs provides countless holes and crevices for fish and other organisms to find shelter in (Friedlander & Parrish 1998), and structural complexity is strongly and positively correlated with fish biomass and density (Graham & Nash 2013). Despite an increase in research on structural complexity relationships with fish assemblages in recent decades (Graham & Nash 2013), reef complexity is still rarely considered explicitly in reef-monitoring programs, but it should become an increasingly important conservation goal as reef degradation continues (Bozec et al. 2015). The complexity of a reef also directly affects its ability to reduce wave energy and thus the risk of shoreline change resulting from storms (Ferrario et al. 2014). Topographical complexity has declined in concert with the degradation of western Atlantic coral reefs since the 1970s, largely



resulting from the loss of *Acropora* spp., and has led to the flattening of reef crests throughout the region (Alvarez-Filip et al. 2009). Although reef complexity is traditionally measured by scuba divers with a transect tape and a chain, technological advancements such as light detection and ranging (lidar) offer new opportunities to augment the quantification of reef complexity on various scales (Brock et al. 2004). In remote areas, where acquisition of lidar bathymetry is not cost-effective, multi-beam sonar can be applied from small vessels (even jet-skis) to yield fine-scale bathymetry in very shallow water, which allows repeated and regular sampling to quantify changes in reef topography (Dugan et al. 2001). Considering the overwhelming importance of the ecosystem services related to reef topographical complexity and elevation, we suggest these variables be brought to the forefront of research and management priorities for coral-reef ecosystems.

### The Role of Ocean Acidification in Western Atlantic Reef Decline

Whereas a declining trend in pH is clear in the Atlantic open-ocean time series from Bermuda (Bates 2007), data are equivocal in nearshore waters (Duarte et al. 2013). The carbonate chemistry surrounding reef habitats is extremely dynamic on diel and seasonal timescales because of biological processes including photosynthesis, respiration, and calcification (Ohde & Van Woessik 1999). To date, there is no documentation that ocean acidification (OA) has been a source of mortality for live adult corals. Although OA-related reductions in coral calcification rates may occur (Gattuso et al. 1998), the relatively minor impacts of OA on the supply side of the carbonate budget will likely be swamped by the loss of live corals (Kleypas et al. 2011) driven mainly by increases in the frequency of high-temperature anomalies (Toth et al. 2015). Reefs may well be geologically dead (net erosion) by the time OA measurably affects carbonate budgets on reefs, and many western Atlantic reefs are already experiencing this fate (Perry et al. 2013).

Although OA may not directly cause the loss of corals, it may impact some important reef processes indirectly affecting coral cover. Recovery rates of reefs could be slowed by OA via effects on coral recruitment (Albright et al. 2008; Cohen et al. 2009) and crustose coralline algae (Kuffner et al. 2008) that corals use as settlement cues (Ritson-Williams et al. 2014). Ocean acidification may also accelerate rates of carbonate-framework destruction by facilitating the work of bioeroding sponges (Enochs et al. 2015). In reef areas naturally exposed to upwelling low-pH waters, reduced levels of reef cementation and increased bioerosion are already observed (Manzello et al. 2008). Any organism that manipulates pH to achieve carbonate dissolution (e.g., etching by boring sponges) will expend less energy in a high-CO<sub>2</sub> environment and there-

fore could accelerate their destructive activities (Wisshak et al. 2012).

The scientific community's intense focus on OA may have misled many resource managers into thinking OA has been a major cause of reef decline in recent decades. The mechanisms of OA impacts on the calcification process (Jokiel 2015), the nature of OA effects on a range of spatial and temporal scales (Andersson et al. 2015), and the species-specific nature of OA effects on corals (Marubini et al. 2003) deserve further attention. Viewing the nearshore environment more holistically, taking into consideration all human disturbances of the global carbon cycle (Mackenzie & Lerman 2006), namely, distributions of organic matter, hydrology, and nutrient dynamics (Andersson et al. 2005), will be necessary to understand the observed changes in nearshore ocean chemistry and concomitant effects on reef processes. With the existing uncertainty about how much of an OA signal will be noticeable in the heterogeneous nearshore environment, ocean warming, coral disease, and land-based sources of pollution pose more immediate threats to coral reefs.

### Conclusions

As humans come to grips with the realities of Earth's changing oceans, new assessment techniques and metrics are required to quantify the decline of coral-reef ecosystems and the critical services they provide. It is an injustice that small island states that contributed so little to the perturbation of the global carbon cycle now bear the brunt of impacts from climate change and sea-level rise (Donner & Potere 2007). With adaptation-and-mitigation discussions now giving way to loss-and-damage negotiations during international climate-agreement talks, we suggest the scientific community be at the ready to assist in this process with a mechanistic understanding of reef-ecosystem degradation that incorporates both the biotic and geologic components of a reef.

Although reef-monitoring programs have carefully quantified the decline of the biological film that lives on the surface of reefs, it is time to move beyond percent live coral cover as the metric du jour. Directly measuring rates of carbonate production, erosion, and transport can more effectively quantify the future potential for reef development. The return to the use of carbonate budgets pioneered during the last century (Stearn et al. 1977; Land 1979; Scoffin et al. 1980; Hubbard et al. 1990) is a step in the right direction. Currently, our most comprehensive tools for calculating carbonate budgets (Perry et al. 2015) are largely based on benthic ecological data and chain-transect estimates of reef rugosity, together with limited data on calcification that were primarily collected during the environmental regime of the past century. Because efforts to date have focused on characterizing the biotic

components of coral reefs, understanding of erosional processes is rudimentary. We suggest that improvements can be made to ecologically focused work by quantifying changes in reef geomorphology, for example, by using remote- and near-remote-sensing methods to produce fine-scale maps of bathymetry and structural complexity (Brock et al. 2004). Increases in reef topographical complexity and elevation should be central metrics in determining the efficacy of reef preservation and restoration efforts.

Although putting our efforts into mapping the loss of reef elevation and quantifying erosion rates could be construed as pessimistic endeavors, we contend that continuing to monitor the last 3% of living coral cover in the western Atlantic is not productive. Furthermore, with the primary causes of coral decline operating on scales well beyond the confines of individual MPAs, we suggest it is time to recognize that coral reefs cannot be saved simply by protecting parrotfish. Reef-monitoring programs should consider shifting emphasis from inventorying organisms to directly measuring reef processes such as rates of coral and algal calcification (Mallela 2007; Kuffner et al. 2013), coral recruitment (Edmunds 2002), bioerosion, sediment transport, and cementation. A better understanding of the processes that control the long-term resilience of reefs as geomorphic structures, not just as ecological communities, may help optimize management activities aimed at increasing both reef longevity and the delivery of critical ecosystem services.

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