A Vicious Circle? Altered Carbon and Nutrient Cycling May Explain the Low Resilience of Caribbean Coral Reefs

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Coral reefs are economically important ecosystems that have suffered unprecedented losses of corals in the recent past. Why have Caribbean reefs in particular transitioned to coral-depleted systems and exhibited less coral resilience? A synthesis of recent research from diverse sources provides novel insights into the reciprocal interactions among sponges, seaweeds, and microbes. We propose that coral loss resulted in more abundant seaweeds that release dissolved organic carbon (DOC), which is consumed by sponges. Sponges return carbon to the reef but also release nutrients that further enhance seaweed growth. Both seaweeds and sponges compete for space with the remaining corals, and the cycling of carbon and nutrients alters microbial activity, with negative consequences for the coral microbiome. Adding to these interactions are geographic factors that enhance nutrients and DOC on Caribbean reefs, such as river discharge and windblown dust. Relatively higher abundances of sponges and the absence of phototrophic species suggest that sponge communities on Caribbean reefs have adapted to a different nutritional environment than is present elsewhere. This synthesis sheds new light on past hypotheses seeking to explain the disparity in the recovery of coral reefs across the tropics, provides new directions for research, and has implications for the conservation of Caribbean coral reefs that are related to fisheries and watershed management.

Keywords: DOC, nitrification, sponge loop, African dust, review

Coral reefs are among the most biodiverse and productive ecosystems on the planet and provide a host of economic services including shoreline protection, fisheries, and tourism (Moberg and Folke 1999). These habitats have experienced unprecedented losses of corals over the past four decades from a combination of anthropogenic and natural stressors, such as anomalous sea surface temperatures, diseases, storms, and shoreline development (Bellwood et al. 2004, Gardner et al. 2004). Perplexingly, not all reefs across the tropics have suffered equally (Roff and Mumby 2012). A key question among ecologists and for conservation and management is this: Why do some reefs recover whereas others have transitioned to seaweed-dominated, coral-depleted systems? Recent research suggests that resilience may differ strongly across ocean basins, with many Pacific and Indian Ocean reefs bouncing back whereas those in the Western Atlantic Ocean (henceforth “Caribbean”) fail to recover (Roff and Mumby 2012). New insights from diverse research programs are revealing factors that may maintain reef ecosystems in a coral-depleted state and explain why Caribbean reefs are different from those in many other parts of the tropics.

Corals, seaweeds, and fishes

Our traditional understanding of tropical reef ecosystems has focused on three groups of organisms: corals, seaweeds, and fishes. Despite many reefs being located in nutrient-poor waters, coral reefs have very high primary productivity (famously, “Darwin’s Paradox”), likely because of the efficient recycling of nutrients. Corals and seaweeds are the most important benthic primary producers, but they also compete with each other for space. When herbivorous fishes (such as parrotfishes and surgeonfishes) are abundant, they disproportionately feed on seaweeds, tipping the competitive balance in favor of corals. The conventional view among reef ecologists has been that the decline in coral cover is mostly because of coral death (from high temperature bleaching events, storms, and disease) combined with overfishing (Hughes 1994, Hughes et al. 2010, Adam et al. 2015). The resulting phase shift from coral- to seaweed-dominated reefs was viewed as a general phenomenon across the tropics.

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Figure 1. Giant barrel sponges (*Xestospongia muta*) on a reef in the Bahamas. Populations of this species increased by 122% between 2000 and 2012 in the Florida Keys (McMurray et al. 2015). Photograph: Joseph R. Pawlik.

But this view may be changing. Once coral cover is low, the effects of herbivory may become decoupled from fish abundance because of the large amount of space available for seaweeds to grow relative to the number of herbivores keeping seaweeds in check (Williams et al. 2001). A recent study comparing sites across the Caribbean reported that reefs in marine protected areas (MPAs) had similar, or even more, seaweed cover than reefs that are heavily fished (Loh et al. 2015), possibly because of the low coral cover on both types of reefs. Research from the Florida Keys, where coral cover is low and fishes are abundant, showed a positive relationship between overall fish biomass and the abundance of seaweeds (Burkepile et al. 2013). Enhanced seaweed growth was linked to nutrients excreted by abundant carnivorous fishes, with this fertilizer effect overwhelming the grazing effect of herbivorous fishes. The increase in seaweed cover may also inhibit coral recruitment, because the abundance of juvenile corals was also negatively correlated with both seaweed cover and fish biomass (Burkepile et al. 2013). Therefore, fish-derived nutrients may enhance seaweed growth and inhibit coral recovery once coral cover becomes too low, even on reefs where populations of herbivorous fishes are robust. This phenomenon might be expected to affect coral reefs similarly across the tropics, so why have Caribbean reefs generally experienced a greater loss of corals and less resilience in coral recovery?

Sponges, microbes, and DOC

Sponges have been historically ignored in reviews of coral reef ecosystem function, perhaps because they are relatively less common and more inconspicuous on reefs in the Pacific and Indian Oceans and, when common, are difficult to identify because of their high species diversity and morphological variability (Diaz and Rützler 2001). On Caribbean reefs, however, sponges are abundant and now cover about as much reef area as reef-building corals (Loh et al. 2015). Populations of the giant barrel sponge (*Xestospongia muta*), a common Caribbean species that can live for centuries (McMurray et al. 2008) and grow to more than a meter in height and diameter (figure 1), have increased by 122% over the period 2000–2012 on Conch Reef in the Florida Keys (McMurray et al. 2015). In addition, sponge communities have become dominated by fast-growing species that lack chemical defenses on reefs where sponge-eating angelfishes and parrotfishes have been removed by overfishing (Loh and Pawlik 2014), resulting in greater competition between sponges and reef-building corals (Loh et al. 2015).

Although sponges are important filter feeders on suspended particles, studies increasingly show that dissolved organic carbon (DOC) plays an equal or greater role than particles in sponge nutrition (Pawlik et al. 2015, McMurray et al. 2016). DOC in seawater is a poorly understood mixture of compounds that constitute one of the largest reservoirs of organic carbon on Earth (Hansell et al. 2009). An intriguing hypothesis called the “sponge loop” proposes that sponges remove DOC from the water column and return it to the reef as shed cellular detritus, thereby enhancing benthic productivity (figure 2; de Goeij et al. 2013). Although this hypothesis was developed using encrusting sponge species that live in reef interstices, larger sponge species that live on the reef surface return carbon to the benthos through growth as sponge biomass, perhaps in addition to the production of cellular detritus (Pawlik et al. 2015, McMurray

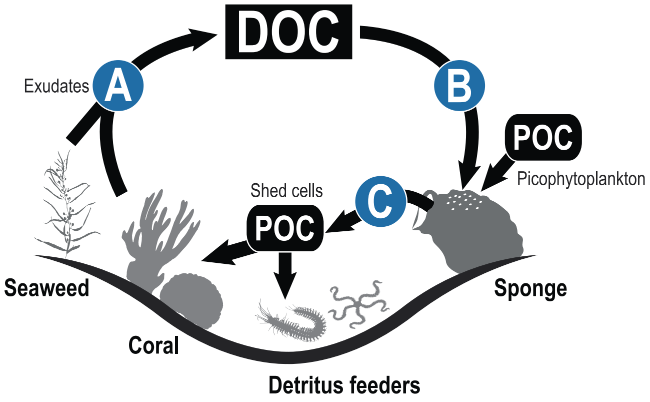

Figure 2. The sponge-loop hypothesis (de Goeij et al. 2013): Major components in blue. (a) Seaweeds and corals exude labile DOC as approximately 50% of productivity. (b) Cryptic sponges consume labile DOC. (c) Cryptic sponges produce particulate organic carbon (POC) as cellular detritus instead of growing. The consumption of sponge-produced POC by particle-feeding fauna and corals retains carbon in the coral reef ecosystem.

et al. 2016). The sponge loop has already been used in ecosystem models to help explain shifts in fish production on overfished reefs in the South Atlantic (Silveira et al. 2015). These trophic models suggest that an important relationship exists between the alteration of reef communities from overfishing and changes in the processing of DOC by sponges and water-column microbes.

But how are sponges able to compete with water-column microbes for DOC? Seawater microbes, after all, are both abundant and well adapted to metabolize DOC and then pass the carbon up the food web to zooplankton through a process called the “microbial loop” (Azam et al. 1983). Sponges may be able to absorb transient patches of metabolites released by primary producers (seaweeds and corals) before microbes can absorb them (de Goeij et al. 2013, Rix et al. 2016). These metabolites are considered “labile” DOC because they are readily used in primary metabolism, but the vast majority of DOC in seawater is the more mysterious “refractory” DOC, which is poorly characterized and not thought to be easily used by living cells (Nebbioso and Piccolo 2013). Could it be that sponges are consuming refractory DOC that is unavailable to microbes? And is the greater abundance of sponges in the Caribbean linked to higher levels of DOC?

Equally intriguing is the concept that sponges are “eating” DOC released by seaweeds and corals (Rix et al. 2016) and then returning inorganic nutrients to these primary producers. Microbial symbionts in sponge tissue are important in nutrient cycling and may release more nitrogen to the benthos than other common nutrient sources do, such as sediment efflux and internal bores (Southwell et al. 2008). Sponges may act as localized nutrient hotspots through a reciprocal positive interaction, with seaweeds trading enhanced levels of labile DOC for sponge-derived inorganic nutrients (figure 3a). Although studies have yet to address this idea directly, a reciprocal trade-off could act as a positive feedback that facilitates the growth of both sponges and seaweeds.

Higher levels of DOC may also help to explain why coral diseases have been particularly aggressive on Caribbean reefs. Microbiologists have linked DOC to changes in the community of microbes associated with living corals that increase coral susceptibility to pathogenic microbes and viruses (Vega Thurber et al. 2009, Barott and Rohwer 2012). Seaweeds also alter the microbiome of corals when in direct competition, making corals vulnerable to infection by putative pathogens while simultaneously suppressing the abundance of bacteria that are likely to be beneficial (Vega Thurber et al. 2012). The recent increases in sponge abundance on Caribbean reefs, therefore, could be fundamentally altering nutrient dynamics, facilitating both sponge and seaweed competition with corals, negatively altering the coral microbiome, and reinforcing coral-depleted systems.

If sponges cycle DOC and nutrients on coral reefs, what distinguishes this process on Caribbean reefs from those in other parts of the tropics? Again, sponge abundance is much higher in the Caribbean, so the potential effects of reciprocal interactions with seaweeds and microbes are likely reduced on most other reefs. Recent surveys of sponge cover across 69 Caribbean reef sites ranged from 2.2% to 74.4% of the reef surface, with a mean of 15.9%, about the same cover as reef-building corals (Loh and Pawlik 2014). Similar benthic surveys on most other tropical reefs report lower values for sponge cover; they do not quantify sponge cover at all (e.g., Central Pacific, Vroom et al. 2010; Eastern Pacific, Stuhldreier et al. 2015) or report very low values (e.g., less than 1% for Red Sea, Benayahu and Loya 1981; Eastern Indian, McClanahan et al. 2009; and Central Pacific, Freeman and Easson 2016; less than 1.5% for Myrmidon, Great Barrier Reef, Reicheilt et al. 1986). Sponge cover is higher on some reefs of the Coral Triangle (29% for Wakatobi, Indonesia; Bell and Smith 2004), where large barrel sponges from the same genus as those in the Caribbean can be found. However, reefs with high sponge cover in the Indo-Pacific are dominated by foliose phototrophic sponge species that grow to maximize surface exposure to sunlight and gain much of their nutrition through a symbiotic relationship with photosynthetic microbes, much like reef-building corals (Wilkinson and Evans 1989, Powell et al. 2014). Phototrophic sponges are net primary producers (generate more fixed carbon than they consume) and likely cycle nutrients internally with their symbionts rather than releasing them. In contrast, sponge species in the Caribbean are primarily heterotrophic, although some do get a portion of their carbon from photosynthetic symbionts (Erwin and Thacker 2008). Indeed, one of the striking differences between the sponge assemblages of Caribbean reefs and reefs of the Western Pacific where sponge assemblages are present is that phototrophic species dominate the latter and

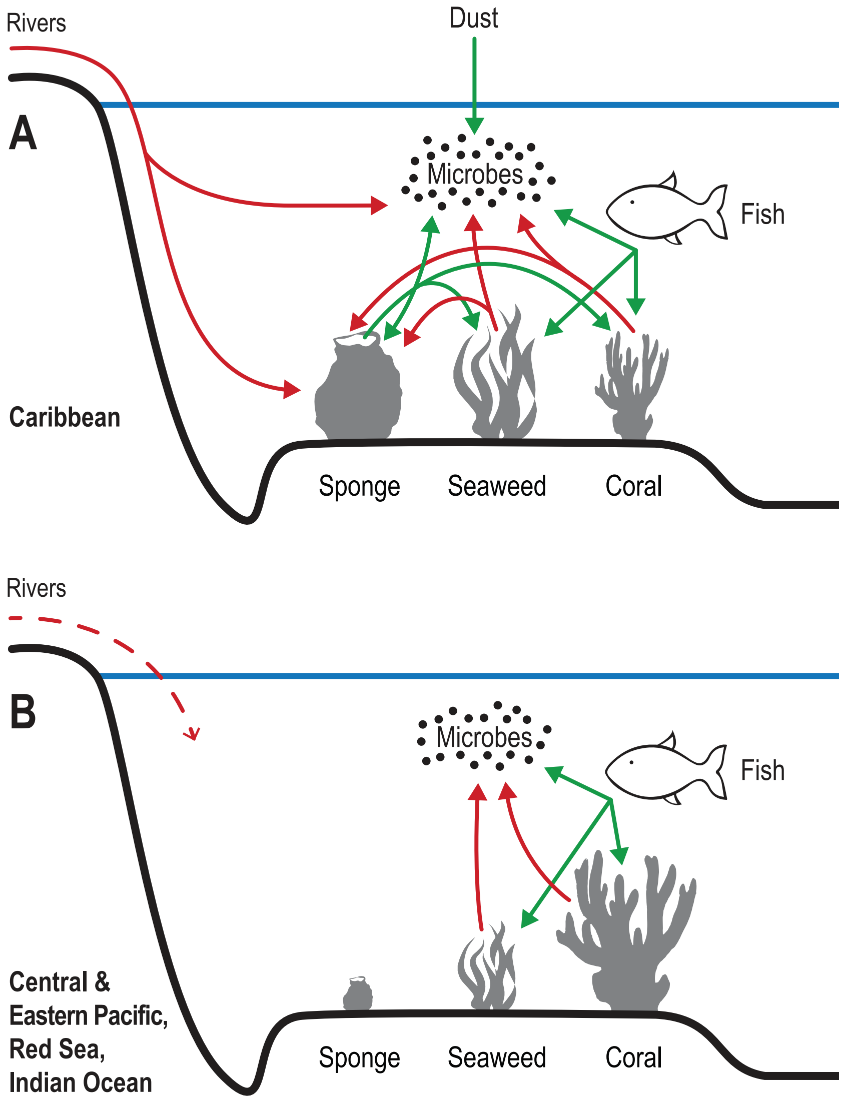

Figure 3. A hypothesis for the relative differences in the transfer of DOC (red) and nutrients (green) for reefs in the (a) Caribbean and (b) Central and Eastern Pacific, Red Sea, and Indian Ocean. The size of benthic components reflects relative abundance. See the text for further details. Some reefs, particularly those in the Coral Triangle (Indo-West Pacific) may be intermediate between these two extremes because of a greater abundance of some sponge species.

are absent from the former (Wilkinson 1987, Pawlik et al. 2015). Why this difference?

Geography

The geological history of the Caribbean region has left it with far fewer species of reef-building corals and fishes than in most parts of the tropics, thereby reducing diversity that can play a role in enhancing ecological resilience (Roff and Mumby 2012). Caribbean reefs are also distinct in that they are contained within a fairly enclosed body of water bordered by continental landmasses. In addition, two other things distinguish the shallow-water habitats of the Caribbean: (1) substantial freshwater input from major river systems (e.g., the Mississippi, Magdelena, Orinoco), including the Amazon, which contains 20% of global river water and produces a surface plume that is driven by winds into the Caribbean during half the year (Salisbury et al. 2011), and (2) surface currents that circulate the region in a mostly clockwise fashion. The latter “mixing-bowl” effect likely contributed to the swift spread of coral disease affecting *Acropora* spp. in the early 1980s, the demise of the black-spined sea urchin (*Diadema antillarum*) in less than a year (1983–1984) from an unknown waterborne pathogen, and the rapid pace of invasion of the Indo-Pacific lionfish (*Pterois volitans*) across the entire region.

River water is a primary source of refractory DOC, which is used by oceanographers to trace the movements of river plumes as they diffuse across the ocean surface (Salisbury et al. 2011). The rivers that discharge into the Caribbean have among the highest DOC flux in the world, with estimates of 30.7, 4.3, and 2.3 teragrams carbon per year ($TgCyr^{-1}$) for the Amazon, Orinoco, and Mississippi, respectively (Dai et al. 2012). If sponges are able to consume some fraction of refractory DOC from river sources that is unavailable to microbes, it may explain the historically greater abundance of sponges and the presence of heterotrophic rather than phototrophic sponge species on Caribbean reefs (Pawlik et al. 2015). Furthermore, the enhanced productivity provided to the reef ecosystem, either as detritus (via the sponge loop) or as sponge biomass, may help explain why Caribbean reefs have suffered greater coral mortality, exhibited higher seaweed cover, and been less resilient than reefs in many other parts of the tropics.

In addition to run-off from rivers, the Caribbean may be unduly influenced by another terrestrial contribution: wind-blown dust. The African dust hypothesis proposes that coral decline across the Caribbean is at least partially due to some combination of enhanced primary production or pathogen-provision from the transatlantic delivery of Saharan dust (Shinn et al. 2000). In particular, the presence of iron in terrestrial dust is thought to promote nitrogen fixation by planktonic cyanobacteria (*Trichodesmium* spp.), thereby enhancing the microbial loop (Walsh et al. 2006). The interaction between dust and river input may also help explain why the Caribbean is recently experiencing unprecedented “blooms” of floating mats of seaweed (*Sargassum* spp.), with mounting cleanup costs and losses in tourism for Caribbean nations (Schell 2015). Seasonally enhanced eutrophication resulting from greater river input of nutrients or from greater wind delivery of atmospheric dust may be responsible for the proliferation of floating seaweed that is usually controlled by nutrient limitation.

A new hypothesis for interoceanic disparity in reef resilience

The abrupt decline of corals on reefs across the Caribbean, as well as the lack of resilience and recovery, has eluded easy explanation (Roff and Mumby 2012). Indeed, the factors that prevent reefs from recovering may be different from those that caused their original decline. For Caribbean reefs, it is likely that the rapid spread of coral diseases was primarily responsible for the original decline of the important reef-building *Acropora* species (Roff and Mumby 2012). We propose that the subsequent slow decline of other coral species, the increase in seaweeds and sponges, and the lack of system resilience have been influenced by nutrient and DOC cycling among sponges, seaweeds, and microbes, combined with higher levels of DOC and nutrients from terrestrial sources within a relatively contained and well-mixed oceanic region.

Figure 3a details five interactions that have likely led to the ratcheting down of corals on Caribbean reefs: (1) Sponges consume DOC from seaweed and coral exudates (labile DOC) and from river input (refractory DOC) and return carbon to the reef as sponge biomass or cellular detritus that increases the abundance of deposit-feeding animals. Sponges return nutrients (nitrogen) to the primary producers (seaweeds, corals, phytoplankton). Sponges also gain nutrients by feeding on nitrogen-rich microbes (POC in figure 2). (2) Seaweeds absorb nutrients from sponges and fishes and release labile DOC. (3) Corals absorb nutrients from sponges and fishes and release labile DOC. (4) Fishes feed on sponges or on invertebrates that consume sponge detritus and release nutrients. (5) Microbes in the water column absorb DOC from all sources. Photosynthetic microbes (phytoplankton) derive nutrients from sponges, and fishes and some microbes (cyanobacteria) use iron in terrestrial dust to fix nitrogen. The reciprocal interactions between these biotic components promote the growth of sponges and seaweeds, which compete with corals for space. In addition, the cycling of DOC and nutrients by sponges and seaweeds may alter microbial communities, with detrimental effects on the coral microbiome and greater incidence of coral disease.

In contrast, the oligotrophic reefs of the Pacific and Indian Oceans (figure 3b) generally lack the terrestrial sources of DOC (river input) and iron for nitrogen fixation (dust) and lack the high abundance of sponges that are important to the cycling of both DOC and nutrients. When present, sponges on Pacific and Indian Ocean coral reefs are mostly foliose and phototrophic (Wilkinson 1988, Powell et al. 2014, Freeman and Easson 2016) and cycle nutrients internally between sponge cells and photosynthetic microbial symbionts.

How did sponges affect Caribbean reefs before corals declined? The abundance of sponges was comparatively high on Caribbean reefs even before the dramatic loss of coral cover began in the early 1980s (Suchanek et al. 1983, Targett and Schmahl 1984). This, combined with the fact that foliose phototrophic sponge species are not present in the Caribbean but are dominant where sponges are common in the Pacific and Indian Oceans, suggests that Caribbean sponge communities have been, and continue to be, differentially adapted to the nutritional conditions present on Caribbean reefs. Before the coral die-off of the 1980s, there was likely more balance in the relative cycling of DOC and nutrients between sponges and the two primary producers, corals and seaweeds that may have helped to maintain coral dominance. As long as corals were healthy, their growth resulted in the formation of new, living reef substratum that was not subject to colonization by either sponges or seaweeds. Once coral diseases spread rapidly through the Caribbean “mixing bowl” in the early 1980s, this dynamic was overturned. Fast-growing seaweeds colonized dead coral skeletons, particularly on overfished reefs, followed by the slower colonization of sponges. In addition to these events, we speculate that urbanization and agricultural land-use changes within the drainage areas of the major rivers that empty into the Caribbean may have altered the concentration and composition of DOC entering the Caribbean “mixing bowl.” This increase in the influx of DOC, possibly combined with more frequent atmospheric dust events, may have further exacerbated the decline of Caribbean coral cover through altered nutrient and DOC cycling (figure 3a).

The novel framework described above and in figure 3 compliments and integrates across four of the six nonmutually exclusive hypotheses summarized by Roff and Mumby (2012) to explain the differences in decline and recovery of Caribbean versus Indo-Pacific coral reefs. Specifically, for Caribbean reefs, it clarifies potential mechanisms whereby (a) reef-building corals have exhibited greatly reduced growth rates since the disease-induced collapse of *Acropora* spp. in the Caribbean (hypothesis 1; Roff and Mumby 2012), (b) seaweeds have sustained higher recruitment and growth rates (hypothesis 3), (c) localized nutrient levels have been higher (hypothesis 4), and (d) nutrient limitation has been reduced (hypothesis 5). The components of this framework have few data supporting them to date but are subject to hypothesis testing at multiple levels. For example, the broader applicability of the components of the sponge-loop hypothesis, which were formulated from studies of cryptic sponge species (figure 2), can be tested for dominant Caribbean reef sponge species. Manipulative experiments can be used to identify and source the refractory and labile DOC that sponges consume. Similarly, relative production by sponges of cellular detritus (versus tissue growth) and inorganic nutrients have only begun to be explored. The interactions of sponges, seaweeds, corals, and fish can be tested through manipulative experiments (transplantation and caging) at the scale of individual reefs or by comparing sites where biotic components have been removed by anthropogenic intervention (e.g., Loh and Pawlik 2014). Finally, research into the distinct interoceanic differences in sponge community assemblages, with Indo-Pacific reefs dominated by foliose phototrophic species and Caribbean reefs dominated by heterotrophic species, could be a particularly enlightening endeavor.

Conclusions

Many factors have been cited to explain the initial rapid loss and the subsequent slow decline and lack of resilience of corals on Caribbean reefs, including disease, the overfishing of herbivorous fishes, and the demise of the herbivorous sea urchin *Diadema*, coral recruitment failure, among others. (Roff and Mumby 2012, Jackson et al. 2014). Here, we argue that the confluence of new studies described in this synthesis suggests that potential impediments to coral recovery could also come from alterations in the cycling of nutrients and DOC that result in positive feedback among sponges, seaweeds, and microbes and negative consequences for coral health (figure 3a).

Intriguingly, a similar reciprocal mechanism may explain the stability of another benthic group on Caribbean reefs: gorgonian octocorals (sea whips and sea fans). Whereas their reef-building cousins have declined, gorgonians have maintained or increased in abundance (Ruzicka et al. 2013, Lenz et al. 2015). Having both photosymbionts to provide them food and an upright growth form that allows particle feeding above the benthic boundary layer, gorgonians may owe their continued success to a mixed strategy of using sponge-derived inorganic nutrients to support photosymbionts and shed cellular detritus for particle feeding. In addition, with a greater relative surface area than most Caribbean reef-building corals, gorgonians may also take advantage of higher levels of DOC.

From the standpoint of reef conservation, the insights described above provide new justifications for fishing restrictions on Caribbean reefs that are distinct from those used for other tropical reef systems, which are often focused on protecting herbivorous fishes. The conservation of sponge-eating fishes and turtles may be crucial in the Caribbean so that these predators will control the fast-growing sponge species that not only smother reef-building corals (Loh and Pawlik 2014, Loh et al. 2015) but may also fundamentally change the patterns of nutrient cycling and primary production on reefs. Fortunately, parrotfishes are both important sponge-eating fishes (Dunlap and Pawlik 1996, Loh and Pawlik 2014) and dominant herbivores on Caribbean reefs (Adam et al. 2015), so efforts to reduce overfishing will help protect corals from both sponges and seaweeds. Furthermore, the emerging importance of DOC suggests that the management of coral reefs in the Caribbean likely has a strong link to the management of terrestrial ecosystems. For example, forest clearing or agricultural development in the watersheds of the Amazon or the central United States may influence the amount and type of DOC or nutrients reaching the Caribbean (Mora 2008). Similarly, land use and climate change in northern Africa may be influencing the seasonal deposition of dust, with additional effects on the sponge and microbial loops that enhance productivity on the opposite side of the Atlantic. Clearly, more research on the types, levels, cycling, and impacts of DOC is warranted. However, the patterns described above suggest that comprehensive programs for the protection and restoration of Caribbean coral reefs may require not only local mitigation efforts but also action on the part of nations far from the coastal areas where reefs are found.

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