

Annual Review of Marine Science

The Emerging Ecological and Biogeochemical Importance of Sponges on Coral Reefs

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Annu. Rev. Mar. Sci. 2020. 12:315–37

First published as a Review in Advance on
June 21, 2019

The *Annual Review of Marine Science* is online at
marine.annualreviews.org

<https://doi.org/10.1146/annurev-marine-010419-010807>

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Keywords

dissolved organic carbon, DOC, chemical defense, sponge loop, vicious circle, carbon cycle, food limitation

Abstract

With the decline of reef-building corals on tropical reefs, sponges have emerged as an important component of changing coral reef ecosystems. Seemingly simple, sponges are highly diverse taxonomically, morphologically, and in terms of their relationships with symbiotic microbes, and they are one of nature's richest sources of novel secondary metabolites. Unlike most other benthic organisms, sponges have the capacity to disrupt boundary flow as they pump large volumes of seawater into the water column. This seawater is chemically transformed as it passes through the sponge body as a consequence of sponge feeding, excretion, and the activities of microbial symbionts, with important effects on carbon and nutrient cycling and on the organisms in the water column and on the adjacent reef. In this review, we critically evaluate developments in the recently dynamic research area of sponge ecology on tropical reefs and provide a perspective for future studies.

INTRODUCTION

Over the past decade, interest in the ecology of sponges on coral reefs has grown rapidly, as evidenced by a 10-fold increase since 2001 in citations of papers containing the terms “coral reef” and “sponge ecology” (based on data from Clarivate Analytics’ Web of Science bibliographic indexing service in January 2019). The same query of the award search at the website of the US National Science Foundation returned eight active research grants totaling more than \$5 million in funding across 11 academic institutions and 17 principal or co-principal investigators. We credit this increase in scientific interest to two things: (a) the rapid and dramatic ecological changes affecting coral reefs in the Anthropocene and (b) a high level of critical evaluation of the science related to the topic of this review that stimulates attention, competition, and rigorous hypothesis testing. For this review, we were asked to “present a critical discussion of the current status of the field, rather than an encyclopedic coverage of papers” and to provide our “personal perspective, especially with respect to what [we] think is most important and where the field is going.” What follows is a straightforward and critical review, from the perspective of actively involved investigators, of a rapidly developing and frequently contentious research area within coral reef ecology.

Definitions

This review focuses on tropical coral reef ecosystems, particularly fore-reef habitats from the reef crest through the mesophotic zone (**Figure 1**). Fore-reef habitats are characterized as having relatively higher flow regimes and relatively constant temperatures, salinities, and oxygen levels

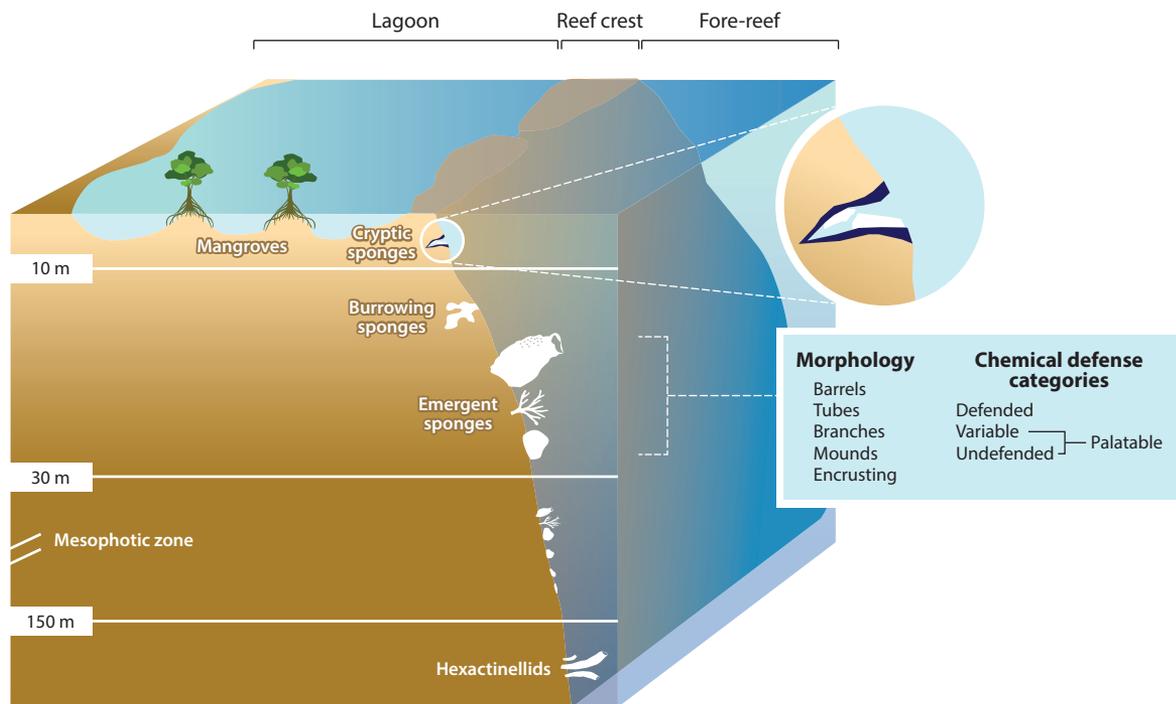


Figure 1

Sponges in coral reef ecosystems. With more than 500 sponge species estimated for the Caribbean, it is often easier to discuss sponges in terms of their location horizontally or with depth, their position relative to the substratum, their morphology, or their chemical defense category, rather than by species.

compared with the lagoonal habitats that are also part of the larger ecosystem. This distinction is important, because inferences about pattern and process in ecology are best learned from studies done in habitats with the fewest potentially confounding variables, and shallow lagoonal habitats, including seagrass meadows, mangroves, and adjacent hard bottoms, are much more strongly affected by abiotic and terrestrial influences (Nagelkerken et al. 2008; Pawlik et al. 2007a, 2018) than are fore-reefs that are adjacent to deep water. We should also mention that the definition of a coral reef is often debated, based on the degree to which limestone is actively accreted to the substratum by living, reef-building corals, but for the purpose of this review, any hard-bottom fore-reef that may sustain living coral will do.

The biodiversity of sponges on coral reefs is remarkably high; in fact, there are probably more species of sponges present in coral reef ecosystems than any other taxon of benthic macroorganism (Diaz & Rützler 2001, Hooper & Levi 1994). Given this high diversity, combined with large numbers of rare species, morphological variation within species, similarities among species, and highly localized endemism, it is not surprising that many sponges are not yet described in the taxonomic literature. Even so, most of the sponges on Caribbean fore-reefs are readily identifiable (Zea et al. 2014), and the 10 most abundant species make up more than 50% of the benthic cover (Loh & Pawlik 2014). Taxonomically, most of the sponges on coral reefs belong to the class Demospongiae, with minor representation from the classes Homoscleromorpha (e.g., *Plakortis* and *Plakina* spp.) and Calcarea (e.g., *Clathrina* and *Leucetta* spp.). For this review, however, it is more useful to refer to sponges by one or more of the following functional categories (**Figure 1**):

- **Habitat:** Taxonomic keys to sponges often list species as specific to particular habitats, usually lagoons (mangroves and seagrass beds), shallow fore-reefs, or deep reefs, with some species present across several locations.
- **Position:** On fore-reefs, sponges can be excavating (boring or burrowing in stone or sediment), cryptic (in cracks or interstices in the reef structure), or emergent (exposed on the reef surface).
- **Growth form:** A wide variety of descriptors are used, including encrusting, branching, massive, and shape names such as barrel, tube, fan, and vase. Growth form has important implications for the ability of sponges to reproduce asexually (Leong & Pawlik 2010b), disrupt the boundary layer and extend into the water column, maximize surface area for photosymbionts, etc.
- **Chemical defense:** Many sponges contain unusual metabolites (natural products or secondary metabolites) in their tissues, some of which deter feeding by invertebrate or fish predators. For the Caribbean, more than 100 species have been placed into three categories: chemically defended, variably defended, and consistently undefended (Loh & Pawlik 2014). There are also putative sponge chemical defenses against competitors, pathogens, and even ultraviolet light, but those against predatory fishes have been the best examined (Pawlik 2011).
- **Microsymbionts:** Low microbial abundance (LMA) sponge species have few microbes in their tissues, while high microbial abundance (HMA) species have a high density of symbiotic microbes in their tissues (Gloeckner et al. 2014). This is not a binary category; instead, sponge species are distributed across a spectrum from LMA to HMA.
- **Photosymbionts:** HMA sponges are further categorized as being heterotrophic (having no nutritional benefit from photosymbionts), mixotrophic (deriving some nutritional benefit from photosymbionts), or phototrophic (relying on photosymbionts for most of their metabolic needs). Among the last category are foliose phototrophic sponge species, which show the greatest morphological adaptation to photosymbiosis and are found only in the Indo-Pacific (Wilkinson 1988).

Geography

Although coral reef ecosystems are globally distributed in the tropics, this review focuses on the Caribbean (i.e., the tropical western North Atlantic), because most of the research discussed in this review has been done there. There are several reasons for this. The sponge fauna of the Caribbean is much better taxonomically described than those elsewhere in the tropics (Zea et al. 2014). It is also more homogeneous in distribution, with most of the same species appearing as major components of the benthos throughout the biogeographic region (Loh & Pawlik 2014, Pawlik & Loh 2017) and with much less endemism than in most parts of the Indo-Pacific (Hooper & Levi 1994). Furthermore, on average, sponges are more abundant on Caribbean reefs than elsewhere in the tropics (Wilkinson & Cheshire 1990).

ECOLOGICAL IMPORTANCE

Climate Change: From Coral to Sponge Reefs?

As coral cover declines in response to more frequent warm-water anomalies and lower seawater pH, tropical reef systems that were previously dominated by reef-building corals may transition to those dominated by sponges (Bell et al. 2013, 2018a,b). Considering what we know about the ability of sponges to take and hold benthic habitat, this is not a surprising conclusion. To be clear, sponges on contemporary tropical reefs are not reef builders; indeed, excavating sponges actively erode limestone reefs and reduce reef complexity (Schönberg et al. 2017b). Biogenic reefs were built by sponges in association with microbes during the Paleozoic and Mesozoic (reviewed in Bell et al. 2013, Wulff 2016), and modern deposits have been formed of glass spicules of hexactinellid (Kahn et al. 2018) and lithistid sponges (Maldonado et al. 2015) in deep waters of the North Pacific and Mediterranean, respectively. Tropical sponge reefs of the future would rely for substratum on the stable remains of accreted limestone from past reef builders or on other forms of hard-bottom substratum that are common to rocky shorelines.

Considering that the great majority of sponge species on tropical reefs do not produce calcified skeletons, it would seem reasonable that they might be less affected than calcified organisms by low seawater pH from increasing atmospheric CO₂ levels. Add to this that some sponge species are sufficiently temperature tolerant that they are found in mangroves, seagrass beds, and fore-reef habitats, and the ascendancy of sponges on tropical reefs of the future would seem assured. Nevertheless, in a recent review of the impacts of ocean acidification and ocean warming on sponges, Bell et al. (2018a) reported that the data were decidedly mixed (the title of their review notwithstanding). Of the 25 species of sponges experimentally exposed to ocean acidification alone, 32% had negative responses, while the rest were neutral or positive; of 44 species exposed to ocean warming alone, 68% had negative responses; and of 15 species exposed to both ocean acidification and ocean warming, 20% had negative responses. Despite these data, Bell et al. (2018a) concluded that sponges, along with macroalgae and octocorals, would be winners in future benthic environments by comparing the data for these taxa with those for corals, brachiopods, bryozoans, and coralline algae, the presumed losers.

While reef-building corals and other biogenic calcifiers are important for limestone formation on reefs, excavating sponges recycle carbonate as dominant bioeroders, and ocean acidification is likely to affect both of these processes. In a recent review of the effects of ocean acidification on bioeroding sponges on coral reefs, Schönberg et al. (2017a) concluded that bioeroding sponges have increased in abundance, particularly in the Caribbean and Indonesia, although specific data are difficult to find. In concert with the loss of reef-building corals on these reefs, the balance of the carbonate cycle has tipped from depositional to erosional. Schönberg et al. (2017b) highlighted

our lack of understanding of important aspects of ocean acidification and the carbonate cycle as it applies to bioeroders relative to the number of studies on calcifying organisms, such as corals. Increasing cover of clionid sponges, the dominant excavating group in the Caribbean, was reported across the Florida Keys reef tract between 1996 and 2001, with mean cover nearly doubling from 2.3% to 4.3% of reef substratum (Ward-Paige et al. 2005). One species, *Cliona delitrix*, excavated 6–9% of coral colonies off San Andreas Island in the west-central Caribbean (Chaves-Fonnegra & Zea 2011).

Are emergent sponges taking over contemporary coral reefs? It is difficult to answer this question, because appropriate broad-scale or long-term survey data are scarce, but for the Caribbean, the answer appears to be a tentative yes. A cross-Caribbean survey of 69 fore-reef sites at 10–20-m depth reported that mean sponge cover was 15.9% of reef surface area, compared with 16.2% for corals and 28.6% for macroalgae (Loh et al. 2015). McMurray et al. (2015) followed the population dynamics of the giant barrel sponge, *Xestospongia muta*, over 12 years in the Florida Keys at three depths (15, 20, and 30 m) and documented a 122% increase in sponge density, accelerating population growth, and a 39% increase in volume, despite losses of some large sponges to a pathogenic condition called sponge orange band (Coward et al. 2006). De Bakker et al. (2017) analyzed an even longer time series for reefs off Curaçao and Bonaire using permanent quadrats at 10, 20, 30, and 40 m that were photographed at intervals from 1973 to 2013. Across sites and depths, there was a significant increase in overall sponge cover from 0.5% to 2.3%, tracking with increasing cover of cyanobacterial mats (22.2%), while other benthic groups declined. Note that there have also been reports of individual sponge species increasing their abundance on reefs (Aronson et al. 2002, Bell et al. 2013), but the longer-term status of these sites is not clear. Alternatively, sponge die-offs in locations such as Florida Bay or mid-lagoon between the mainland of Belize and the barrier reef crest have been cited as counterevidence to the above reports of increasing sponge abundance, but these studies are from shallow-water habitats, where the influence of phytoplankton blooms and temperature extremes are much more pronounced than they are on fore-reefs (Butler et al. 1995, Wulff 2013).

More difficult to find is evidence for sponges taking over Indo-Pacific coral reefs. This may be a matter of timing, in that Caribbean reefs had a head start, not only with greater abundances of sponges on reefs to begin with (Wilkinson 1987) but also with some of the earliest and most dramatic losses of coral cover providing substratum for other benthic organisms. Therefore, Caribbean reefs have had several decades for a shift to greater sponge cover to become apparent (Pawlik et al. 2016). Bell et al. (2013) reviewed the limited data for increasing sponge abundance in the Indo-Pacific, with reports of phototrophic sponges overgrowing fore-reefs after losses in coral cover in Wakatobi, Indonesia, and the Northern Mariana Islands. More recently, reefs around Zanzibar were described as transitioning to greater sponge cover, with 2 of 10 species having more than 2% cover on reefs at 10-m depth (Helber et al. 2018). In each of these reports, increasing sponge abundance was associated with changes in water quality due to sedimentation or pollution, a topic discussed below (see the section titled Nutrition, Nutrients, and Pollution).

On balance, evidence of an advantage for sponges under climate change scenarios and of a developing shift to sponge-dominated tropical reefs is weak but positive, particularly in the Caribbean. The worst of sponge die-offs that run contrary to the trend of increasing sponge abundances are from lagoonal habitats, not fore-reef environments, while coral loss on fore-reefs continues unabated, liberating ever more hard bottom for eventual sponge recruitment and growth. We predict that increases in sponge cover on fore-reefs will become more apparent within the next two decades. Sadly, the paucity of funded time-series programs for monitoring reefs at appropriate depths will likely result in poor documentation of this transition.

Abundance and Diversity into the Mesophotic Zone

Reefs within the tropical mesophotic zone are found at 30–150-m depth, and for obvious logistical reasons are far less studied than reefs above these depths (Kahng et al. 2014). Coral-dominated reefs within the mesophotic depth range have received considerable recent attention as potential refuges for benthic species that have incurred substantial losses of cover in shallower water due to climate change (Semmler et al. 2017). Despite limited information on mesophotic reef ecosystems, it has been frequently stated in the literature that there is a consistent, increasing pattern of abundance and diversity of sponges at 30–150-m depth throughout the Caribbean (Kahng et al. 2014, Lesser 2006, Lesser & Slattery 2013), an assertion that has been dubbed the sponge-increase hypothesis (Scott & Pawlik 2018). Scott & Pawlik (2018) reviewed the available literature and found only 17 studies that reported metrics of sponge abundance or diversity within the mesophotic zone of the Caribbean. Of these, none reported sponge biomass or diversity as a function of reef surface area, and for those that reported some metric of sponge abundance (cover or density), an increasing trend with depth was reported for 4 sites, a decrease at 5 sites, and a different pattern (variable, peak, dip, plateau, or no pattern) at 12 sites.

Despite the clear lack of published evidence for the sponge-increase hypothesis, Lesser & Slattery (2018) dismissed the review by Scott & Pawlik (2018). Modifying the hypothesis as the title of their contribution, “Sponge Density Increases with Depth Throughout the Caribbean,” Lesser & Slattery (2018) reanalyzed data from 3 of the 17 studies reviewed by Scott & Pawlik (2018), along with some of their own unpublished data from both the Caribbean and the Pacific, and reasserted their support for the hypothesis. Lesser & Slattery (2018) also used the additional limited data from the Pacific to extend the hypothesis to a global phenomenon. Pawlik & Scott (2019) responded by questioning the selective analysis of data by Lesser & Slattery (2018) and did the same analyses on a replicated study by Rivero Calle (2010), also reported in the review, which revealed a significant decline in sponge abundance with depth from 30 to 100 m at sites off Puerto Rico. Surprisingly, Lesser & Slattery (2019) dismissed the data provided by Rivero Calle (2010) as the product of flawed methodology, claiming that there are “well-known concerns” (p. 2) about using photographic images to estimate percentage cover because of parallax error between the plane of the camera image and the plane of the substratum. To support this contention, Lesser & Slattery (2019) cited a study by Parry et al. (2002) in which the abundance of crustaceans, worms, bivalves, and associated burrows in muddy sand was estimated by mapping and counting all of the features in the entire area of photographs taken from remotely operated vehicles (ROVs). Unlike Parry et al. (2002), Rivero Calle (2010) used randomized points on the photographic image to estimate percentage cover, which is not subject to parallax error because small differences in the area of the photograph caused by changes in the angle of the substratum have no effect on the randomness or number of points projected on the image. Not only were the methods used by Rivero Calle (2010) valid and quantitative, but the use of ROV photographs to estimate the percentage cover of sponges represents a better replicated and randomized methodology than the diver-acquired data advocated by Lesser & Slattery (2019), because divers have very limited time at mesophotic depths to perform transects and would be drawn to benthic features in performing surveys. Additionally, contrary to the sponge-increase hypothesis being a global phenomenon, both sponge diversity and density decreased below 70–90-m depth, based on analyses of 85 video transects from mesophotic reefs in the Mediterranean (Santin et al. 2018, 2019).

Why does this controversy matter? It matters because the mesophotic zone is an excellent location for testing hypotheses about the factors that limit sponge abundance. As discussed below (see the section titled Bottom Up or Top Down?), teasing apart the interactions between sponges and their environment is best done in habitats where there are the fewest potentially

confounding abiotic and biotic variables. Shallow, lagoonal habitats are the least appropriate for these studies, while fore-reef habitats at depths greater than 10 m offer the best compromise between environmental stability and research access. Mesophotic reefs are even more stable but are logistically difficult to survey, let alone conduct manipulative experiments in. Nevertheless, appropriately conducted studies of sponge feeding and growth along the depth cline of light and food availability through the mesophotic zone would provide important insights into the factors limiting sponge communities and the transition from demosponge to hexactinellid communities that occurs just below this zone.

Interaction with Corals

There is disagreement about the net impact of sponges on reef-building corals and, by extension, on the ability of corals to build and maintain reefs as “ecosystem engineers” (Wild et al. 2011). Recently, Wulff (2017) echoed past reviews (Wulff 2006, 2016) in concluding that sponges are helpful to reef-building corals, writing that “the great majority of sponges play positive roles, including increasing coral survival, filtering the water column, harboring hundreds of symbiont species, participating in nutrient flux and facilitating reef repair” (p. 1137). We disagree with this mutualistic generalization about coral–sponge interactions on coral reefs, particularly in the Caribbean. Beyond the negative effects of excavating sponges on reef-building corals (Schönberg et al. 2017b), sponges can negatively affect coral recruitment (Brandt et al. 2019), and many studies have demonstrated that sponges are aggressive competitors with corals for space, the single most important resource for these two benthic organisms (Diaz & Rützler 2001). One sponge species in particular, *Mycale laevis*, was credited with protecting coral skeletons by growing under them in a mutualistic manner (Goreau & Hartman 1966, Wulff 2006), but this growth form was subsequently demonstrated to be caused by the constant grazing activities of reef fishes (Loh & Pawlik 2009), and when released from predation pressure, *M. laevis* rapidly smothered corals (Loh et al. 2015). The preponderance of evidence suggests that any positive effects of sponges holding reef rubble together or improving water clarity are far outweighed by aggressive sponge overgrowth and the production of nutrients that enhance seaweed growth and negatively affect the coral directly, as well as its microbiome (Pawlik et al. 2016).

Chemical Ecology

Sponges are a rich source of unusual secondary metabolites, and the subdiscipline of chemical ecology seeks to understand the function of these compounds, as well as their production, storage, costs, etc. Arguably, no system has been better characterized in this regard than the chemical ecology of sponges on Caribbean reefs (Pawlik 2011). Bioassay-guided laboratory and field experiments have identified sponge metabolites that serve several ecological roles, including protection from predators (Pawlik et al. 2013), competitors (Pawlik et al. 2007b), and pathogens (Kelly et al. 2005). For chemical defenses against predators, this research program moved beyond species-level studies to separate the dominant Caribbean sponge fauna (106 species to date) into three defense categories: chemically defended, variably defended, and consistently undefended (Loh & Pawlik 2014). Manipulative field experiments and studies of sponge recruitment onto artificial reefs demonstrated an interspecific resource trade-off between chemical defenses and growth or reproduction (Leong & Pawlik 2010a, Pawlik et al. 2008). The summation of these laboratory and local field experiments led to a testable conceptual model for the chemical ecology of sponges on Caribbean reefs, with trophic cascades from fish and sponge predators having indirect effects on the primary components of the reef benthos: corals, seaweeds, and sponges (Pawlik 2011). This conceptual model was put to the test in cross-Caribbean surveys of reef sites

that had been overfished for decades versus sites that had been relatively spared from overfishing (Loh & Pawlik 2014). The results of this long-term manipulative experiment demonstrated both the predicted trophic cascades and indirect effects of the fish-trapping removal of sponge predators: The sponge community was dominated by faster-growing or faster-reproducing undefended sponge species on overfished reefs, and those reefs had greater sponge overgrowth of reef-building corals (Loh et al. 2015).

Several more recent developments in Caribbean sponge chemical ecology are also worth noting. In addition to the effects of sponge predators across the biogeographic region, their impacts at the scale of the reef were demonstrated to drive undefended sponge species into close associations with defended refuge organisms, such as stinging fire coral or chemically defended sponges (Wooster et al. 2017). These results help to explain the persistence of undefended sponge species despite changing impacts of consumers. Unlike reef benthos that are phototrophic, such as corals and seaweeds, sponges can hide among refuge organisms or in cryptic locations. This may also explain why the diversity of sponges on coral reefs is so much higher than that of any other reef taxa: Species that can retreat to cryptic and refuge habitats are difficult to drive to extinction (Pawlik et al. 2018).

Recent contributions to historical ecology have reinforced the conceptual model of sponge ecology in the Caribbean (Pawlik 2011), as well as the importance of predators in driving differences in the sponge community. A synthesis of past data on the diet of hawksbill turtles, combined with estimates of the number of hawksbills from pre-Columbian times to the present, suggested a far greater effect of sponge predators in the historical past (Pawlik et al. 2018). Hawksbill numbers went from estimates of ~11 million to ~27,000 between the 1600s and the 1970s (McClenachan et al. 2006). Analyses of hawksbill gut contents revealed a preference for the same chemically undefended sponge species eaten by sponge-eating fishes (Meylan 1988, Randall & Hartman 1968). It is likely that hawksbill grazing eliminated undefended emergent sponge species and that turtles were forced to eat chemically defended sponge species when their numbers were ~400 times greater on Caribbean reefs, exercising intense top-down control on the sponge community (Pawlik et al. 2018). Supporting this theory, historical records of human use of hawksbill meat as food show a dramatic change in palatability from toxic to edible as the turtle populations declined (McClenachan et al. 2006), suggesting that the small number of remaining turtles on contemporary reefs have focused their grazing on the increasing abundance of chemically undefended sponge species, thereby rendering their own meat palatable to humans. This scenario was given additional support by recent analyses of sediment cores from Bocas del Toro, Panama (Lukowiak et al. 2018), which revealed an increase in spherical spicule types from the year 1600 onward that characterize the chemically undefended sponge species that are the preferred food of hawksbills.

Bottom Up or Top Down?

Among the controversies involved in recent studies of the ecology of Caribbean sponges, none has been more lively or polarized than that over the relative effects of bottom-up (food availability) and top-down (predation) control of sponge communities on fore-reefs. There is already a recent review on this topic (Pawlik et al. 2018), and many of the new developments have been repeated above, so here we provide only a brief synopsis. The controversy has its foundations in the 1960s, when Randall & Hartman (1968) stated that sponges on Caribbean reefs were unaffected by predation; then, the dichotomy was established in 2006 with publications asserting that sponge communities in the Caribbean were structured principally by food limitation, based on the relationship between the availability of living particulate food (picoplankton) and sponge

abundance, size, and tube elongation with depth (Lesser 2006, Trussell et al. 2006). This latter claim disregarded two important bodies of evidence that were already established in the literature at the time: (a) Sponges eat more than living particulate food [indeed, most of the diet of many sponges is made up of dissolved organic carbon (DOC) (Reiswig 1981)], and (b) sponge communities are demonstrably structured by predation (Pawlik 1998).

In the most recent review on this topic, Pawlik et al. (2018) concluded that sponges on Caribbean fore-reefs are not food limited for lack of living particulate organic carbon (POC), because DOC and detritus make up most of their diet. Furthermore, DOC and detritus are likely not limiting on Caribbean fore-reefs, and the capacity of sponges for optimal foraging allows them to maximize nutritional gains when higher-quality foods, such as picoplankton, become more available (Pawlik et al. 2018). Based on the historical information presented above, as well as data from manipulative and correlative studies summarized in the review, the importance of predation in structuring sponge communities on Caribbean reefs, both now and in the past, was undeniable (Pawlik et al. 2018).

What about tropical reefs beyond the Caribbean? Food limitation was proposed to reduce the abundance of sponges on offshore, oligotrophic reefs of the Great Barrier Reef compared with inshore reefs (Wilkinson & Cheshire 1989) and to drive the evolution and abundance of foliose phototrophic sponges common to Indo-Pacific reefs (Wilkinson 1988). Recent feeding studies of giant barrel sponges along an inshore–offshore gradient in the Red Sea confirmed that sponges on offshore reefs were food limited because levels of DOC and other potential sources of sponge nutrition were too low (Wooster et al. 2019). These findings, compared with identical feeding studies conducted on giant barrel sponges in the Caribbean (McMurray et al. 2016), corroborate the idea that sponges on Caribbean reefs are not food limited, which is reflected in their relatively high abundance and diverse morphology and in the absence of foliose phototrophic species (Pawlik et al. 2015, Wilkinson & Cheshire 1990).

Is the bottom-up-versus-top-down controversy settled? Working against a consensus on this topic are inappropriate studies that claim to address the debate. Recent reviews (Pawlik et al. 2015, 2018) have detailed the most common problems with studies that address either predation or nutrition of sponges, and we list them here:

- Studies are much more meaningful when performed on fore-reefs, preferably at 10–30-m depth. Studies of lagoonal and shallow-water patch reefs are confounded by many more biotic and abiotic variables than deeper fore-reefs.
- The growth of small replicate sponge pieces is best measured by changes in wet mass. Other methods, including estimating volumes of small sponge pieces by making linear measurements with a ruler or tape measure underwater and calculating geometric solids, are very imprecise, as is measuring the linear growth of sponge branches or tubes.
- Growth experiments require appropriate cage controls. Depending on the sponge species chosen, cages must be used when conducting sponge growth experiments to remove the negative effects of predators.
- Predation on sponges should be quantified as the volume or mass ingested by consumers, not simply the number of bites taken by predators. Sponge-eating fishes will bite off and consume substantial portions of sponges that they prefer (see movie in Loh & Pawlik 2014) but often bite on surfaces without removing or swallowing tissue. Therefore, volumetric gut content analyses are valid indicators of sponge predation, while counts of predator bites are not.

Regarding the first and last of these points, a recent study related sponge cover to the abundance of sponge-eating fishes on shallow patch reefs (~2–13 m) in Todos os Santos Bay, Brazil

(Lorders et al. 2018). The authors concluded that, unlike on Caribbean fore-reefs, there was no top-down control on sponge assemblages. In addition to this study being conducted on patch reefs near a seaport in an industrialized embayment, sponge consumption was measured by having divers follow fishes and count bites on sponges. As in the study by Wulff (2017), the methodological problems in the study by Lorders et al. (2018) preclude any meaningful comparisons with appropriately conducted studies done in fore-reef habitats.

BIOGEOCHEMICAL IMPORTANCE

There is an increasing awareness of the impact of animals on biogeochemical cycles in natural ecosystems. In a recent review, Schmitz et al. (2018) used the term zoogeochemistry to characterize the effects that terrestrial animals have on the carbon cycle by altering CO₂ uptake and loss, as well as carbon sequestration in plants and soils. As the authors explained, a more complete understanding of the process of storage and exchange of carbon in ecosystems is vital for carbon cycle models and to assess the potential for natural carbon storage as changes to Earth's climate continue. The oceans contain the largest pool of cycled organic carbon on earth as DOC (Hedges 1992), and among marine organisms, sponges are unsurpassed in their ability to pump large volumes of seawater and to simultaneously remove DOC. On Caribbean reefs, the population of one species alone—the giant barrel sponge, *X. muta*—was estimated to overturn a 30-m water column on the fore-reef every 2.3–18 days (McMurray et al. 2014), with carbon flux estimates of 1,575 mg C d⁻¹ m⁻² (McMurray et al. 2017) and DOC comprising ~70% of the sponge diet (McMurray et al. 2016). Needless to say, there is increasing interest in the ability of sponges to overturn the water column as they pump seawater through the extremely high surface area of their aquiferous system while transforming the chemistry of that seawater.

Carbon Cycling and the Sponge-Loop Hypothesis

The sponge loop is arguably the most important new hypothesis in marine ecology in the past decade, and seeks to explain Darwin's paradox: How are highly productive and diverse coral reef ecosystems maintained in a nutrient-poor, oligotrophic aquatic environment? The sponge loop (de Goeij et al. 2013) takes its name and components from the famous microbial loop, which transformed our understanding of plankton communities in the 1980s (Azam et al. 1983). The hypothesis provides a mechanism by which the large proportion of carbon fixed and released by seaweeds and corals as DOC is returned as POC to the benthic fauna, retaining biomass in the ecosystem (**Figure 2**). Sponges are responsible for completing the loop by feeding on DOC and producing POC in the form of shed cellular detritus (collar cells). This POC is then eaten by benthic detritivores and suspension feeders and eventually passed to higher trophic levels. While the sponge loop was based on studies of encrusting cryptic sponges, de Goeij et al. (2013) scaled up their results to suggest that the return of DOC to POC by sponges is on par with the daily gross primary production of the entire reef ecosystem. Therefore, the sponge loop could be a dominant component in the cycling of carbon for coral reef ecosystems. Indeed, it has already been invoked to explain phase shifts in fish biomass on impacted reefs (Silveira et al. 2015) and the lack of resilience of Caribbean coral reefs relative to those elsewhere in the tropics (Mumby & Steneck 2018, Pawlik et al. 2016).

The capacity of sponges to remove DOC from the water column was long suspected on the basis of early laboratory studies (Jørgensen 1976) and the identification of large discrepancies between POC uptake and respiratory carbon demand (Reiswig 1974, 1981). The first direct measurements confirmed that DOC constituted a large proportion of the sponge diet (Yahel et al. 2003), and this finding has been further corroborated (Archer et al. 2017; de Goeij et al. 2008b;

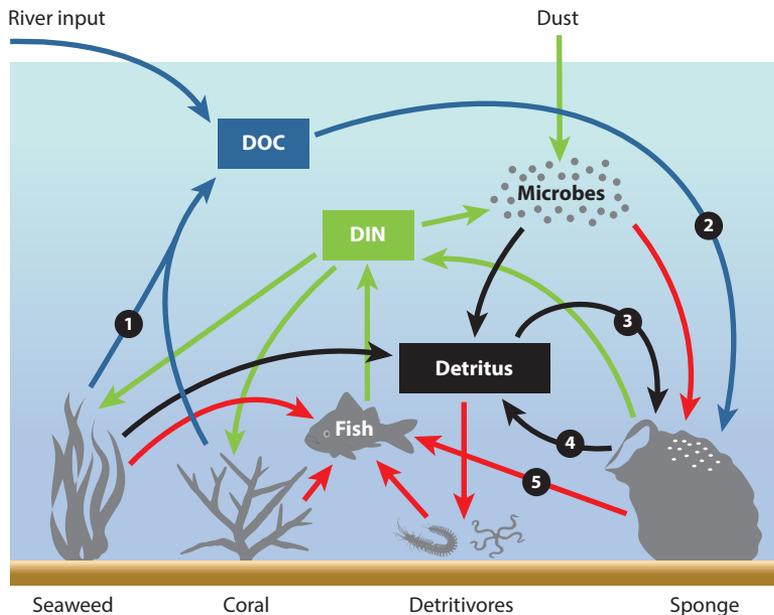


Figure 2

Cycling of dissolved organic carbon (DOC, *blue*), dissolved inorganic nitrogen and nutrients (DIN, *green*), and detritus (*black*) in Caribbean fore-reef environments. The consumption of component organisms is shown in red. This figure summarizes important components of the sponge loop (de Goeij et al. 2013) and the vicious circle (Pawlik et al. 2016, Mumby & Steneck 2018). As discussed in this review, there is growing evidence for the production of labile DOC from seaweeds (❶), which forms a major component of the diet of sponges (❷), along with detritus (❸). While the sponge-loop hypothesis proposed the transformation of DOC as detritus by cryptic sponges (❹), this does not occur for emergent sponges, which return DOC to the ecosystem as food for spongeivores (❺).

Hoer et al. 2018; McMurray et al. 2016, 2017, 2018; Morganti et al. 2017; Mueller et al. 2014; Ribes et al. 2012). The capacity to use DOC is important, as it frequently represents more than 90% of the total organic carbon available to sponges in the water column (Hansell & Carlson 2015). Moreover, reef corals and seaweeds release a large proportion of their photosynthetically fixed carbon as exudates that contribute to the bioavailable pool of DOC in these systems (Haas et al. 2011, Nelson et al. 2013).

DOC processing by sponges has been suspected to be microbially mediated (Hoer et al. 2018; Reiswig 1974, 1981). HMA and LMA sponge species differ morphologically, with HMA species having denser tissues and more complex aquiferous systems than LMA species, resulting in slower pumping rates (Weisz et al. 2008). With a greater internal surface area and an increased residence time of seawater within the sponge holobiont, HMA species are thought to be particularly well adapted to feed on DOC, whereas LMA species specialize in the filtering of particles (Hoer et al. 2018, Weisz et al. 2008). But there is increasing evidence that some LMA species may also consume DOC (McMurray et al. 2018; Morganti et al. 2017; Mueller et al. 2014; Rix et al. 2016, 2017). The greater surface-area-to-volume ratio of LMA sponges with encrusting morphologies may aid DOC uptake (de Goeij et al. 2017). Alternatively, processing of DOC by some LMA species may not be mediated by symbiotic microbes. In fact, for several sponges known to consume DOC, symbiotic microbes are intracellular and not in direct contact with seawater, suggesting the involvement of sponge cells in DOC processing (Yahel et al. 2003). Tracer experiments with

isotopically enriched DOC have provided evidence for direct uptake of DOC by both sponge cells and symbiotic microbes (de Goeij et al. 2008a; Rix et al. 2016, 2017).

Although there is broad support for sponge-mediated DOC uptake, naturally occurring DOC is a highly heterogeneous pool of compounds that exhibits a spectrum of bioavailability, ranging from labile to refractory forms (Hansell & Carlson 2015). Promising new technologies allow the identification of DOC constituents, but these have only recently been applied to characterize the effect of sponge feeding (Fiore et al. 2017). Nonetheless, it is generally thought that sponges feed primarily on the labile fraction of DOC for two reasons. First, after processing by the sponge, the concentration of DOC in seawater is typically reduced to a level ($\sim 70 \mu\text{mol C L}^{-1}$) that is consistent with concentrations in surface waters of the open ocean thought to contain primarily semilabile and refractory DOC (Yahel et al. 2003). Second, recent findings suggest that there is a threshold ambient concentration ($\sim 80 \mu\text{mol C L}^{-1}$) below which sponges cease to be net consumers of DOC (reviewed in Wooster et al. 2019). A similar relationship has been described for planktonic microbes (Middelburg 2015). Thus, the lower limit of DOC uptake may reflect the remaining concentration of semilabile and refractory DOC that sponges are unable to consume, plus any DOC emitted by the sponge. Rates of DOC uptake may vary depending on the pool of labile DOC (Rix et al. 2017). Large intraspecific variation in the rates of sponge DOC uptake is likely a consequence of the heterogeneous composition, concentration, and nutritional value of DOC available on coral reefs (Pawlik et al. 2018).

Since the sponge-loop hypothesis was proposed, there have been several developments in our understanding of sponge detritus production. The link between DOC consumption and detritus production has been described for an additional nine sponge species, and recent work has employed more ecologically relevant DOC types, including coral- and alga-derived exudates (Alexander et al. 2014; Rix et al. 2016, 2017, 2018). Two additional sponge species have been found to transfer coral-derived DOM up the food web to detritivores, thus corroborating all steps of the sponge loop (Rix et al. 2018).

Despite the above developments, the mechanism of detritus production as the penultimate part of the sponge loop has remained elusive. While detritus that included cellular debris has been observed in excurrent canals of encrusting sponges via microscopy, the quantity of shed cells observed is lower than expected based on proliferation rates, and a direct link has yet to be established (Alexander et al. 2014, de Goeij et al. 2017). Furthermore, Kahn & Leys (2016) found choanocyte proliferation rates for four cold-water sponge species to be much lower than those reported for tropical species, and no evidence of cell debris in excurrent canals, suggesting that detritus production may result from the excretion of waste rather than cell shedding. Although temperature may partially explain the discrepancy, it may also be an artifact of the use of 5-bromo-2'-deoxyuridine (BrdU) to label tropical species (Alexander et al. 2014, de Goeij et al. 2009), as BrdU can be mutagenic and trigger cell death (Kahn & Leys 2016, Maldonado 2016).

Not all sponge species produce detritus, despite consuming DOC. While both LMA and HMA species transfer DOC into detritus (Alexander et al. 2014, de Goeij et al. 2013, Rix et al. 2017), with the exception of the LMA rope sponge *Negombata magnifica* (Rix et al. 2018), the sponge-loop hypothesis has been supported solely by studies of encrusting sponge species. Interestingly, detritus production by *N. magnifica* (Rix et al. 2018) runs counter to work by Hadas et al. (2009), who found that detritus constituted approximately one-third of the diet of this species, a discrepancy that is likely due to differences in experimental design (see below). Tests of the sponge loop for emergent sponge species have confirmed DOC consumption but not detritus production. A study of carbon flux for nine Caribbean tube, vase, and barrel sponges reported mean uptake of DOC for HMA species, but none produced significant quantities of detritus (McMurray et al. 2018). Giant barrel sponges (*Xestospongia* spp.) from both the Caribbean and Red Seas consumed

significant quantities of both DOC and detritus (McMurray et al. 2016, Wooster et al. 2019). As an alternative to the penultimate step in the sponge loop, emergent sponge species produce biomass that feeds sponge predators (McMurray et al. 2018).

If detritus production by encrusting sponge species [averaging 9.3% sponge biomass⁻¹ d⁻¹ (Alexander et al. 2014)] were scaled up to the biomass of emergent species, one would expect to observe the discharge of detritus in their excurrent seawater; however, measured rates of POC production by sponges are three orders of magnitude lower. For example, assuming detritus production of 9.3% sponge biomass⁻¹ d⁻¹, the average-sized *X. muta* sampled by McMurray et al. (2018), having a volume of 31.5 L and a density of 0.62 g cm⁻³ (Fiore et al. 2013) and pumping seawater at a rate of 0.03 L s⁻¹ L_{sponge}⁻¹, would be expected to produce approximately 1,800 g of detritus each day, or 18.8 g of detritus over the approximately 15-min seawater sampling interval used by McMurray et al. (2018), with 37 mg of detritus expected to be produced per 1.5-L sample of excurrent seawater—a value that is three orders of magnitude larger than the mean excurrent POC (51.8 μg) measured in the 1.5-L samples of excurrent seawater for *X. muta* by McMurray et al. (2018).

The discrepancy in reported production of detritus by sponges may be linked to methodological differences used to test the sponge loop. One approach, the incubation method, has been used to study encrusting sponge species having multiple oscula (Alexander et al. 2014; de Goeij et al. 2013; Rix et al. 2016, 2017, 2018). Sponges were incubated in flow chambers or open pots with isotopically enriched DOC, and detritus was collected by filtration in chambers or via pipette. The second approach, the In/Ex method, has been used to study emergent species in situ by sampling seawater via syringe before (incurrent) and after (excurrent) processing by the sponge; living POC, total POC, and DOC in samples are then quantified, and detritus is estimated as the portion of total POC not accounted for by living POC (McMurray et al. 2016, 2018; Wooster et al. 2019). Elements of both experimental designs have been criticized (de Goeij et al. 2017). De Goeij et al. (2017) suggested that the short sampling interval of the In/Ex method (~15 min), relative to that for incubation (~3–12 h) may not capture detritus production if released sporadically. However, if encrusting and emergent species produce detritus at similar rates, one would expect to observe measurable detritus in excurrent seawater, especially if sampling is replicated, but this has not been the case (McMurray et al. 2016, 2018; Wooster et al. 2019). While ambient DOC is largely refractory, incubation experiments have used labile DOC, including diatom lysate (de Goeij et al. 2013), algal (Rix et al. 2017), and coral exudates (Rix et al. 2016, 2018), to track sponge DOC uptake and detritus production. Additionally, incubations have used either high concentrations of labile DOC (1.5 times ambient) (Rix et al. 2017) or coral species known for high rates of mucus production as a source of DOC (Rix et al. 2016, 2018). As discussed by Alexander et al. (2014), rates of cell proliferation are expected to be greatest when food is not limiting; thus, it remains unknown whether the detritus production observed in such food-rich incubations is ecologically relevant. By contrast, In/Ex tests of the sponge loop for emergent species using the natural pool of DOC available on coral reefs have not found significant detritus production by sponges (McMurray et al. 2018, Wooster et al. 2019). Future studies of detritus production by sponges should include similar in situ tests of the sponge loop for encrusting species, as well as analyses of samples of environmental detritus from open reef and cryptic locations, in an attempt to trace the origin of this potentially important link in the cycle to its source.

Nitrogen Cycling and the Vicious-Circle Hypothesis

Beyond their role in carbon cycling on coral reefs, sponges may have a significant influence on nitrogen biogeochemistry. Sponges are important sources of dissolved inorganic nitrogen (DIN)

through the metabolic breakdown of their food sources (Diaz & Ward 1997, Jiménez & Ribes 2007). On coral reefs, DIN flux estimates for emergent sponges surpass those of other benthic sources because of their high rates of organic matter remineralization and high biomass (Southwell et al. 2008), and cryptic sponges have similarly been linked to high levels of DIN production (Scheffers et al. 2004). Sponges are well known to obtain particulate organic nitrogen (PON) by consuming picoplankton (Hadas et al. 2009, Ribes et al. 2003). While detritus is a significant source of carbon for some sponges, the high C:N ratio of this food resource likely minimizes its contribution of nitrogen to the sponge diet (Hadas et al. 2009) but may balance the nitrogen budget for some species (Morganti et al. 2017). Similarly to their use of DOC, sponges may also use dissolved organic nitrogen (DON) (de Goeij et al. 2013; Rix et al. 2016, 2017). Few studies have quantified DON fluxes for sponges, likely because quantification is more challenging than it is for DOC (Hansell & Carlson 2015); nonetheless, recent work suggests that HMA species obtain the majority of their organic nitrogen as DON, while LMA species produce DON and rely on picoplankton as their source of nitrogen (Morganti et al. 2017; but see Ribes et al. 2012). Our understanding of DON processing within sponges is in its infancy, but available evidence suggests that both microbial symbionts and sponge cells may directly absorb DON (de Goeij et al. 2013; Rix et al. 2016, 2017).

While both HMA and LMA sponges release DIN as metabolic waste in the form of ammonium (NH_4^+), large quantities of nitrate and nitrite (NO_x) have also been observed (Diaz & Ward 1997, Southwell et al. 2008). Nitrification is particularly evident for HMA sponges, although some LMA species may also produce NO_x at relatively low rates (Morganti et al. 2017, Schläppy et al. 2010). HMA sponges hosting nitrifying microbes may additionally be net sinks of NH_4^+ , although NH_4^+ uptake may also be due to photosymbionts or anaerobic ammonium oxidation (anammox). Both aerobic and anaerobic ammonia-oxidizing microbes have been found in sponges (Bayer et al. 2008, Mohamed et al. 2010). Ambient NH_4^+ concentrations have been directly correlated with the release of NO_x for some sponges (Archer et al. 2017, Bayer et al. 2008), yet a relationship between NH_4^+ uptake and NO_x production is lacking for others, suggesting that other nitrogen metabolic pathways may co-occur (Morganti et al. 2017). Indeed, highly variable nutrient fluxes have been reported; for example, *X. muta* was found to be both a net source and a net sink of NO_x and NH_4^+ (Fiore et al. 2013, Southwell et al. 2008), likely reflecting the diverse nitrogen metabolic pathways within the sponge holobiont or differences in nutrient availability in ambient seawater (Archer et al. 2017).

Stable isotope signatures and biomarker genes have been used to infer N_2 fixation by sponge cyanobacteria and heterotrophic bacterial symbionts in both HMA and LMA sponges (Mohamed et al. 2008, Zhang et al. 2014), yet rates of N_2 fixation suggest that this process is not a major source of nitrogen to sponges (Ribes et al. 2015, Rix et al. 2015). Similarly, functional genes for denitrification and anammox have been detected within sponge microbial communities (Fan et al. 2012, Mohamed et al. 2010), and the anaerobic conditions required to support these processes may occur when sponges reduce or halt pumping (Hoffmann et al. 2005); however, the magnitudes of these nitrogen transformations within the sponge holobiont have remained largely unresolved, as denitrification has been quantified for three sponge species, while anammox has only been measured in one (Hoffmann et al. 2009, Schläppy et al. 2010).

The recycling of nitrogen by sponges may be especially important to the ecology of coral reefs, where nitrogen is often a limiting nutrient. Detrital PON produced by the sponge loop may provide a high-quality food source for benthic detritivores and suspension feeders (de Goeij et al. 2013), although it remains to be determined how sponge-derived detritus is enriched in nitrogen relative to the dissolved organic matter that fuels its production (de Goeij et al. 2017). Exchange of nitrogen compounds between HMA and LMA sponge species may account for the high diversity

and density of sponge communities, with the waste products of LMA sponges (i.e., NH_4^+ and DON) used by the microbiomes of their HMA counterparts (Morganti et al. 2017). Finally, reciprocal cycling of carbon and nutrients between sponges and macroalgae has been hypothesized to underpin the poor recovery and resilience of reef-building corals on Caribbean reefs relative to those in the Indo-Pacific (Pawlik et al. 2016).

The vicious-circle hypothesis speculates that the transition of reefs to a chronically coral-depleted state has occurred because the high abundance of sponges in the Caribbean has magnified a positive reciprocal interaction, with sponges exchanging DIN for macroalga-derived DOC, enhancing the growth of both sponges and macroalgae to the disadvantage of corals, through both direct spatial competition and negative effects on the coral microbiome (Pawlik et al. 2016). This feedback scenario is potentially enhanced by factors particular to the Caribbean, including the addition of huge amounts of DOC from major river systems and nutrient enhancement from wind-blown dust (Figure 2). The vicious circle has been further developed by Mumby & Steneck (2018), who proposed that the detritus produced by either sponges or decomposing seaweeds limits light penetration and increases coral stress on Caribbean reefs. These hypotheses are ripe for further research, including the use of developing technologies in metabolomics and isotopic signature and environmental DNA analyses to identify sources and sinks of DOC and detritus.

Phosphorus Cycling

In contrast to our understanding of sponge-mediated carbon and nitrogen cycling, very little is known about the influence of sponges on the cycling of phosphorus. Of the three forms of total phosphorus that occur in seawater, research has focused on sponge-mediated fluxes of dissolved inorganic phosphate (as PO_4^{3-}), and we are unaware of any studies that have considered phosphorus in dissolved or particulate organic forms. The majority of sponges investigated have been found to be a minor source of PO_4^{3-} (Hatcher 1994, Jiménez & Ribes 2007, Ribes et al. 2012), but more recent work suggests that some HMA species may also consume PO_4^{3-} (Morganti et al. 2017), and, as with findings for DOC and other nutrients, variation in PO_4^{3-} fluxes may be explained by differences in ambient PO_4^{3-} concentrations (Archer et al. 2017).

Microbial symbionts of sponges may also sequester significant amounts of phosphorus in the form of polyphosphate (Zhang et al. 2015), with up to 40% of total phosphorus in sponge tissue present as polyphosphate granules, potentially representing a large proportion of total phosphorus in coral reef ecosystems. Polyphosphate granules may serve to store phosphorus for the sponge holobiont but may also lead to the sequestration of phosphorus in sediments if polyphosphate is released by sponges (Zhang et al. 2015).

Nutrition, Nutrients, and Pollution

One particularly interesting area for new research is the relationship between sponge abundance on reefs and anthropogenic pollution. As discussed above, sponges eat primarily DOC and detritus, and both of these food sources should increase in proximity to sewage outfalls or more diffuse sources of organic pollution. Furthermore, enriched nutrients from anthropogenic sources should enhance picoplankton abundances, providing more of the highest-quality food source that sponges are known to eat (McMurray et al. 2016). Not surprisingly, many studies indirectly link enhanced abundance of sponges to eutrophication (e.g., Chaves-Fonnegrá et al. 2007, Helber et al. 2018, Ward-Paige et al. 2005, Wilkinson & Cheshire 1990), but more direct tests of the abilities of sponges to use the components of organic pollution for food have suggested otherwise (Maldonado et al. 2010b, Topcu et al. 2010).

The problem with correlative studies of sponge abundance relative to levels of pollution is that there are multiple variables associated with anthropogenic effects on reefs that may enhance sponge abundances—most importantly, loss of living coral cover that provides more substratum for sponge colonization. Sponges may be able to handle only a certain level of food availability before it becomes detrimental, whether by clogging the aquiferous system, overwhelming the selective feeding process, or altering the microbiome of the sponge. Different sponge species may have evolved for different spans of the spectrum of potential food availability, with foliose phototrophic species common to the most oligotrophic Indo-Pacific reefs on the lean end of the spectrum (Wilkinson 1988); the common sponges of Caribbean fore-reefs, with their many morphologies, somewhere in the middle (Pawlik et al. 2015); and sponges adapted to lagoonal habitats on the fat end of the spectrum (Engel & Pawlik 2005).

Other Biogeochemical Cycles: The Silicon Enigma

Silicon is an important component of the skeletons of many marine organisms, including some sponges, and it is tied to the global cycles of carbon, nitrogen, and phosphate in marine ecosystems because it is a limiting nutrient for diatoms. Silicon is biologically available to organisms as dissolved silicic acid (DSi), which is more abundant at greater depths and at higher latitudes. Maldonado et al. (2012) have reviewed the interaction between DSi and sponges. Notably, in shallow-water ecosystems, ambient concentrations of DSi are estimated at one to two orders of magnitude below the level at which sponges can process DSi at maximum efficiency; hence, sponges with glass skeletons are thought to endure chronic silicon limitation (Lopez-Acosta et al. 2018, Maldonado et al. 2012). Even so, many common Caribbean reef sponge species have glass skeletons that are 15–65% of tissue dry mass, and these sponges hold more than 88% of the total ecosystem silicon pool (Maldonado et al. 2010a).

On shallow coral reefs, the availability of silicon might be expected to limit the growth of sponges, and therefore of sponge communities, but this is not evident. On Caribbean reefs, 3 of the 10 most abundant sponges lack siliceous skeletons, including the single most abundant species, *Aplysina cauliformis* (Loh & Pawlik 2014). While the tissues of many of the dominant genera of emergent reef sponges are perfused with glass spicules (*Xestospongia*, *Agelas*, *Niphates*, and *Callyspongia*), other common genera lack spicules (*Aplysina*, *Verongula*, *Aiolochoira*, and *Ircinia*), and there are no apparent differences in sponge morphology between the two categories. If chronic limitation of DSi inhibited the growth of sponge species that make glass skeletons, resource allocation theory would predict that sponge species that lack glass skeletons would competitively dominate sponge communities, but this pattern does not exist. Interestingly, as described above, a resource trade-off can be observed in the sponge community for chemical defenses (Pawlik 2011). Glass spicules were once thought to protect sponges from vertebrate predators (Randall & Hartman 1968), but subsequent laboratory and field experiments did not support this function (Chanas & Pawlik 1995, 1996), suggesting that their role is mostly for structural support, which is accomplished by collagen fibers in species that lack glass spicules. The enigma of silicon for sponges on coral reefs is that sponge communities should be limited by DSi availability, but there is no evidence that this occurs.

Silicon limitation may help to explain the absence of hexactinellids on coral reefs. These sponges were important reef builders in shallow seas during the Mesozoic, when DSi concentrations were higher and before diatoms began to dominate the global silicon cycle (Maldonado et al. 1999). In modern tropical seas, hexactinellids are restricted to depths below the mesophotic zone, where DSi concentrations are much higher than they are in shallower water (Maldonado et al. 2012). Hexactinellids are found as shallow as 30-m depth at higher latitudes (Leys & Lauzon 1998), suggesting that both high DSi and low temperatures may be important for their survival.

While other factors, such as predation, might restrict them to the deep sea, it appears that hexactinellids, unlike demosponges, are limited in their distribution by some combination of silicon availability and temperature.

SUMMARY POINTS

1. Evidence of a transition from coral- to sponge-dominated reefs is localized and limited, likely due to a combination of insufficient time-series reporting and the slow speed at which sponge communities develop.
2. On fore-reefs, sponge abundance is highest in the Caribbean, where differences in the sponge community across the biogeographic region are largely attributable to the presence of sponge predators and their avoidance of chemically defended sponge species.
3. Sponge abundance may increase with depth into the mesophotic zone, but the opposite pattern has also been reported.
4. Perhaps the most exciting new developments in tropical sponge ecology have been in the area of biogeochemistry, with the advance of the sponge-loop and vicious-circle hypotheses, proposing, respectively, that sponges return dissolved organic carbon from the water column to the reef as detritus, and that sponges and seaweeds exchange nutrients and dissolved organic carbon in a feedback relationship that has negative consequences for reef-building corals.
5. While anthropogenic eutrophication is often linked to higher sponge abundance, the confounding effect of greater substratum availability from coral mortality provides an alternative explanation.
6. Enigmatically, silicon availability should limit the distribution of some sponges on coral reefs, but there is no evidence for this pattern.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank the National Science Foundation for supporting our research program and the preparation of this review (grant OCE 1558580) and Melissa Smith for graphics design.

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