REVIEW

A review of evidence for food limitation of sponges on Caribbean reefs

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ABSTRACT: The diversity and biomass of sponges on Caribbean reefs exceeds that of all other benthic organisms. Wilkinson & Cheshire (1990; Mar Ecol Prog Ser 67:285–294) summarized evidence that sponge communities on Caribbean reefs were different from those on the Great Barrier Reef, Australia, reflecting food limitation of the latter, but not of the former. Since then, we have learned much about the ecology of sponges, and the concept of food limitation has recently re-emerged, seemingly without substantive reference to past inter-oceanic comparisons or pioneering studies of sponge physiology. Here, we review the literature in an attempt to correct this digression. Based on current knowledge of sponge nutrition and bottom-up resource gradients (particulate food, dissolved organic carbon [DOC], light, turbulence), we predict 4 patterns of sponge abundance that would suggest food limitation on Caribbean reefs. After a critical review of survey data, correlative studies and manipulative experiments, we can find no evidence for food limitation. Although there is good evidence for higher availability of picoplankton at greater depths, sponge abundance does not mirror this gradient, suggesting that other sources of nutrition are also important, and particulate food is not a limiting factor. Recent studies have renewed interest in the uptake of DOC by both high and low microbial abundance sponge species, suggesting that the absence of bottom-up effects for sponges on Caribbean reefs may be attributable to this mysterious, and likely ubiquitous, food source. The recent unambiguous demonstration of top-down effects of predation on sponge community composition across the Caribbean may owe its clarity to the relative lack of confounding influences of abiotic and bottom-up effects in this study system.

KEY WORDS: Bottom-up · Top-down · Food webs · Suspension feeding · Symbiosis · Photoautotrophy · DOC · Benthic–pelagic coupling · Coral reefs · Sponge loop

INTRODUCTION

Ecologists face the daunting task of attempting to explain the distributions and abundances of organisms that are influenced by a diversity of biotic and abiotic factors. A fundamental theory used to address this topic is food web dynamics, considered central to ecology (Fretwell 1987), which proposes that communities of organisms are structured by some combination of factors that are top-down (controlled by predation from the highest trophic levels) or bottom-up (controlled by the availability of resources such as nutrients or food to the lowest trophic levels). The relative importance of these 2 factors has been vigorously debated by ecologists for as long as the concept of food webs has existed (examples in Hunter & Price

1992, Power 1992, Heck & Valentine 2007, Turkington 2009). Marine ecologists have provided particularly good characterizations of food webs with studies of, for example, temperate rocky-shore intertidal communities (Paine 1969, Lubchenco 1978, Sousa 1979) and tropical benthic macroalgal communities (Hay 1981, Lewis 1985). Due to the complexity of most ecosystems, however, not only is some combination of top-down and bottom-up processes likely to be important (Hunter & Price 1992, Menge 2000, Ainley & Hyrenbach 2010, Denyer et al. 2010), but also the relative importance of these processes may change along with other factors, such as latitude (Marczak et al. 2011) or time (Whalen et al. 2013).

In this review, we specifically consider whether the community of sponges on Caribbean reefs is influenced by bottom-up factors. This assessment is warranted for several reasons. First, the importance of sponges on coral reefs worldwide is attracting more attention as the relative abundance of reef-building corals has declined (Bell et al. 2013). On Caribbean reefs in particular, sponge communities have greater diversity and biomass than any other benthic organisms (Diaz & Rützler 2001) and sponge abundance is increasing (McMurray et al. 2010, Colvard & Edmunds 2011, Ruzicka et al. 2013, Villamizar et al. 2014). Second, the topic of bottom-up control is made more complex because of the mechanisms by which Caribbean sponges gain nutrition: in addition to suspension feeding on particles that include picophytoplankton and bacteria (Reiswig 1974, Trussell et al. 2006), sponges may also absorb dissolved organic carbon (DOC) (Reiswig 1981, Maldonado et al. 2012), or may rely to some extent on photosymbionts (Erwin & Thacker 2008, Freeman et al. 2013). Most recently, it has been proposed that sponges not only rapidly absorb DOC from the water column, but also lose much of the acquired biomass through the production of cellular detritus that is returned to the reef ecosystem as part of a 'sponge loop' (de Goeij et al. 2013). Third, as has occurred with other study systems (Power 1992), a debate has emerged about the relative importance of bottom-up and top-down factors in structuring the ecology of sponges on Caribbean reefs (Lesser 2006, Trussell et al. 2006, Lesser & Slattery 2013, Pawlik et al. 2013). Here we will focus specifically on bottom-up control of sponges on Caribbean coral reefs, considering the evidence from observational, correlative and manipulative studies.

Before proceeding, it is important to briefly define terms that are commonly used in discussions of food webs and trophic interactions as we will apply them to sponges, keeping in mind that these animals are phylogenetically diverse, morphologically variable, and functionally clonal. The bottom-up resource of importance for Caribbean sponges and the focus of this review is food, which can take the form of particulate matter (including picoplankton), DOC, or photosynthate from endosymbiotic microorganisms. At issue is whether limitation of the quantity of food available to sponges on Caribbean reefs is sufficient to influence the overall biomass (a better term than 'population' for a functionally clonal animal) of individual species and the structure of sponge communities. Evidence for food limitation may be found in direct measurements of sponge growth, or indirectly as correlative measurements of biomass, usually as percentage cover of the reef substratum. Percentage cover is more useful than abundance (number of individuals), because of the wide range of sizes exhibited by many sponge species. These measurements may be specific for individual species, or they may include all species in the sponge community. Changes in the sponge community can include an overall increase in the biomass of sponges, or in the structure of the sponge community, as some species replace other species independent of changes in overall sponge biomass. Note that we will avoid the use of the term regulation in this review because it implies density-dependent control of a population, and it seems unlikely that sponges are near their carrying capacity on Caribbean reefs, either as individual species or as a community. It is also important to recognize that, other than the resource of food, Caribbean reef sponges may be limited by space, as most are required to be attached to the substratum. And while we will consider light and water movement as resource-related factors, we will not discuss other abiotic factors (salinity, temperature, sedimentation, oxygen content, etc.) because variation in these parameters is generally low at the depths (>5 m) of the area (slope of the fore-reef) where most reef sponges are found, but may strongly affect sponge populations in shallow water mangrove and grassbed environments (Pawlik et al. 2007a, Nagelkerken et al. 2008).

WHAT DO SPONGES ON CARIBBEAN REEFS EAT?

The species diversity of sponges on Caribbean reefs is very high, with more than 100 conspicuous species on most reefs within human access by scuba diving, and hundreds more species restricted to cryptic locations or at greater depths (Diaz & Rützler 2001). Among these species are representatives of 3

poriferan classes, the Calcarea, Homoscleromorpha and Demospongiae, with over 12 orders in the last of these classes. It is generally understood that sponges are suspension-feeding organisms that use a combination of their aquiferous system and the microvilli on their collar cells to remove particles >0.1 µm from seawater (Riisgård & Larsen 2010), but that is not the full extent of their ability to feed themselves (Maldonado et al. 2012). Our understanding of sponge nutrition is based on studies of a limited number of sponge species, but several of these are from Caribbean reefs.

The pioneering work of Henry Reiswig on the water transport and *in situ* energetics of 4 species of sponges from reefs in Jamaica and Barbados provided some of the most important concepts we have concerning sponge feeding (Reiswig 1974, 1981). By measuring rates of water pumping and respiration, 2 contrasting patterns were described among 4 species: 2 species had low bacterial biomass in their tissues and maintained high rates of water pumping (*Mycale laxissima*, *Tectitethya crypta*; formerly referred to as *Mycale* sp. and *Tethya crypta*; H. M. Reiswig pers. comm.), and the other 2 species had high bacterial biomass in their much denser tissues and lower rates of water transport (*Verongula reiswigi*, *Aplysina fistularis*; formerly *Verongia gigantea* and *Verongia fistularis*; H. M. Reiswig pers. comm.). These 2 categories were called non-bacteriosponges and bacteriosponges, respectively, but they have subsequently been renamed as low microbial abundance (LMA) and high microbial abundance (HMA) sponges to be more inclusive of archaea and eukaryotic microbes present in the sponge microbiome (Hentschel et al. 2003, Giles et al. 2013, Gloeckner et al. 2014, Poppell et al. 2014). A list of the Caribbean sponge genera and species that are known to belong to these 2 categories is presented in Table 1. Based on respiration measurements, Reiswig determined that the 2 LMA sponges could satisfy their dietary needs with particulate food, while the 2 HMA sponges could not, and that 70% or more of the energy budget of the 2 HMA sponges was dependent on the uptake of DOC, providing a mechanism for returning DOC to the reef as sponge biomass (Reiswig 1974, 1981).

It has been generally understood that sponges feed non-selectively on small particles using their aquiferous system and collar cells (Riisgård & Larsen 2010), but as the techniques for studying sponge feeding have become more sophisticated, much greater complexity has been discovered. Methods for directly sampling incurrent and excurrent flow from sponges

in situ have been developed, which, when coupled with flow cytometry, have revealed that sponges differentially retain some microbial cell types over others (Yahel et al. 2005). The use of stable isotopes and fatty acid signatures demonstrated that different sponges within a community in McMurdo Sound, Antarctica fed selectively on live cells of different classes and sizes (Thurber 2007). Application of flow cytometry to feeding by *Callyspongia* sp. off SW Australia revealed highly variable selectivity depending on the food type and time of the year, with general selectivity for bacteria with higher DNA concentrations (Hanson et al. 2009). Therefore, particulate feeding by sponges can be very complex, with both inter- and intraspecific variation in particle selectivity.

More recently, the nutritional role of DOC in Caribbean sponges was highlighted with the demonstration that 4 additional sponge species could not only absorb DOC, but also released a considerable fraction of their biomass into which this DOC was incorporated as cellular detritus (de Goeij et al. 2013). All 4 of these species were encrusting and usually found within reef interstices, unlike the large and conspicuous tube-shaped species studied by Reiswig (1974, 1981). While one of the species is categorized as an HMA sponge (*Chondrilla caribensis*), 3 are LMA sponges (*Haliclona implexiformis*, *Halisarca caerulea*, *Scopalina ruetzleri*) (Table 1), and the first of these LMA species had among the highest rates of DOC uptake and detritus production (de Goeij et al. 2013). Work by the same research group added 2 additional species to the list of those that primarily use DOC for food, the HMA burrowing sponge *Siphonodictyon* sp. and the LMA boring sponge *Cliona delitrix*, although production of detritus by these 2 species was 'unclear' (Mueller et al. 2014). Therefore, from these studies of a limited number of species we understand that (1) Caribbean reef sponges can feed on DOC in addition to particulate matter, and that (2) HMA sponges rely mostly on DOC, but that (3) some LMA sponges also consume DOC. We will add 2 additional points to this list in the paragraphs ahead.

Morphology is also likely to play a role in sponge nutrition. Vogel (1974, 1977) provided evidence that sponges that grew to have an osculum that was raised above the substratum could enhance pumping by taking advantage of ambient flow, and this concept has been validated and further developed more recently (Leys et al. 2011). Tissue density and thickness also affects pumping rates (Reiswig 1974), which for Caribbean sponges is congruent with the

Table 1. Alphabetical list of genera or species of Caribbean reef sponges, their relative morphologies, designation as high or low microbial abundance sponges (HMA/LMA), and presence or lack of photosymbionts in their tissues. ? = unknown

Species	Growth forms	HMA or LMA	Reference	Photo-symbionts?	Reference	Notes
Agelas spp.	Branch, fan, tube, encrusting	HMA	Richelle-Maurer et al. (2003), Gloeckner et al. (2014)	No	?	?
Aiolochroia crassa	Mound, tube	HMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	Erwin & Thacker (2007)	
Amphimedon spp.	Branch, encrusting, fan, tube	LMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	Erwin & Thacker (2007)	
Aplysina spp.	Branch, mound, tube	HMA	Reiswig (1981), Weisz et al. (2008), Gloeckner et al. (2014)	Yes (Synechococcus)	Erwin & Thacker (2007)	
Callyspongia spp.	Branch, fan, mound, tube	LMA	Hentschel et al. (2006), Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	
Calyx podatypa	Encrusting	HMA	Poppell, et al. (2014)	No?	?	
Cliona aprica, C. caribbaea, C. tenuis	Boring	?		Yes (zooxanthellae)	Rützler (1990), Granados et al. (2008)	
Cliona delitrix	Boring	LMA	A. Chaves-Fonnegra unpubl., Mueller et al. (2014)	No	A. Chaves-Fonnegra unpubl.	
Cliona varians	Boring	LMA	Gloeckner et al. (2014)	Yes (zooxanthellae)	?	
Chondrilla spp.	Encrusting	HMA	Poppell et al. (2014)	Yes	Arillo et al. (1993), Fromont & Garson (1999)	
Chondrosia reniformis	Encrusting	HMA	Gloeckner et al. (2014)	Yes	?	
Cribrochalina vasculum	Fan, vase	HMA	Gloeckner et al. (2014)	Yes	Steindler et al. (2005)	
Cinachyrella spp.	Mound	LMA	Gloeckner et al. (2014)	No	?	
Dysidea etheria	Encrusting, mound	LMA	Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	
Dictyonella funicularis	Branch, encrusting	LMA	Gloeckner et al. (2014)	Yes	Rützler (1981)	Same as *Ulosa funicularis*
Ectyoplasia ferox	Mound, tube	HMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	Erwin & Thacker (2007)	
Erylus formosus	Mound	LMA	Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	
Geodia neptuni	Barrel, mound	HMA	Hoffmann et al. (2005)	Yes?	Rützler (1990)	
Haliclona spp.	Encrusting, branch, tubes	LMA	Reiswig (1975)	No[a]	Erwin & Thacker (2007)	[a]Exception: *H. walentinae* (Díaz et al. 2007)
Halisarca caerulea	Encrusting	LMA	U. Hentschel pers. comm.	No	?	
Iotrochota birotulata	Branch	LMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	Erwin & Thacker (2007)	
Monanchora arbuscula	Branch, encrusting	LMA	Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	

Table 1. (continued)

Species	Growth forms	HMA or LMA	Reference	Photo-symbionts?	Reference	Notes
Ircinia spp.	Barrel, mound	HMA	Gloeckner et al. (2014)	Yes (Synechococcus)	Erwin & Thacker (2007)	
Mycale spp.	Encrusting, vase	LMA	Reiswig (1974), Rützler (1990), Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	
Myrmekioderma gyroderma	Mound	HMA	Gloeckner et al. (2014)	No	?	
Niphates spp.	Branch, encrusting, vase	LMA	Gloeckner et al. (2014)	No	Erwin & Thacker (2007)	
Plakortis spp.	Mound	HMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	Erwin & Thacker (2007)	
Ptilocaulis spp.	Branch	LMA	U. Hentschel unpubl., in Weisz et al. (2008)	No	?	
Scopalina ruetzleri	Encrusting	LMA	Poppell et al. (2014)	No	Erwin & Thacker (2007)	
Siphonodictyon coralliphagum	Burrowing	HMA	Gloeckner et al. (2014)	No	?	
Smenospongia spp.	Mound	HMA	Gloeckner et al. (2014), Poppell et al. (2014)	Yes (Synechococcus)	Erwin & Thacker (2007)	
Spheciospongia vesparium	Barrel, mound	HMA	Gloeckner et al. (2014), but see Poppell et al. (2014)	Yes	Rützler (1990), Steindler et al. (2005)	Synechococcus in *S. florida*
Svenzea zeai, *S. tubulosa*	Mound	HMA	Gloeckner et al. (2014)	Yes	Steindler et al. (2005)	
Tectitethya crypta	Mound	LMA	Reiswig (1974)	No	Erwin & Thacker (2007)	
Tedania ignis	Encrusting, mound	LMA	Poppell et al. (2014)	No	Erwin & Thacker (2007)	
Terpios fugax	Encrusting	?	Reiswig (1974)	Yes (Oscillatoria)	Rützler & Smith (1993)	
Verongula spp.	Mound, tube, vase	HMA	Hentschel et al. (2006), Gloeckner et al. (2014)	Yes (Synechococcus)	Erwin & Thacker (2007)	
Xestospongia spp.	Barrel, mound, encrusting	HMA	Steindler et al. (2005), Gloeckner et al. (2014)	Yes (Synechococcus)	Erwin & Thacker (2007)	Includes some *Neopetrosia* spp.

HMA/LMA dichotomy, in that HMA sponges have denser tissues and pumping rates that are 52 to 94 % slower than LMA sponges (Weisz et al. 2008). Continuing the list in the above paragraph, then, (4) sponge morphology can influence pumping rates of Caribbean sponges.

Adding to the foregoing complexity, a subset of mostly HMA sponges contain a high proportion of photo-autotrophic microorganisms among their symbionts, which may result in the sponges being net primary producers (phototrophic species) or only having part of their nutritional needs provided by photosymbionts (mixotrophic sponge species) (Wilkinson 1983). Wilkinson determined that, while phototrophic and mixotrophic sponge species were both common on the oligotrophic reefs of the Great Barrier Reef (GBR), only mixotrophic species could be found on more eutrophic Caribbean coral reefs, also reflecting overall higher sponge community biomass on the latter (Wilkinson 1987, Wilkinson & Cheshire 1990). Some of the most common species of sponges on Caribbean reefs have photosymbionts in their tissues, and enhanced growth has been demonstrated under higher light levels in manipulative experiments with several sponge species (Erwin & Thacker 2008, Freeman & Thacker 2011, Freeman et al. 2013). However, none of the Caribbean sponge species with photosymbionts are known to derive >50 % of their nutritional needs from their photosymbionts, as has been described for the foliose phyllosponginiids from oligotrophic reefs of the GBR (Wilkinson 1988, Abdul Wahab et al. 2014). Moreover, it has been established that some Caribbean species, such as the giant barrel sponge *Xestospongia muta*, appear to derive no nutritional benefit from their photosymbionts (Gómez et al. 2002, López-Legentil et al. 2008). Also,

only 1 Caribbean sponge species that contains photo-symbionts grows in a plate-like manner similar to phyllosponginiids (*Cribrochalina vasculum*), but this species is not very common (let alone dominant, as phyllosponginiids are on oligotrophic reefs of the Indo-Pacific; Wilkinson 1988) nor is it known to derive substantial nutrition from photosymbionts. Therefore, despite the fact that Caribbean sponges with photosymbionts do not derive the level of nutrition of those from the Indo-Pacific, we can add to the list begun in the previous 2 paragraphs that (5) some sponges on Caribbean reefs possess photosymbionts in their tissues and have enhanced growth under higher light levels.

WHAT ARE THE BOTTOM-UP RESOURCE GRADIENTS ON CARIBBEAN REEFS?

Variation in 4 different factors could limit the nutrition of sponges on Caribbean reefs: particulate matter, DOC, light, and turbulence. Of these, we understand best the gradient of light with depth. From studies of sponge distributions on the GBR, the critical depth below which light levels are unable to support phototrophic sponges is 20 m (Wilkinson & Cheshire 1989, Wilkinson & Evans 1989). It has been proposed that light intensities may limit sponge growth in very shallow water, because of the harmful effects of UV radiation (Jokiel 1980, Wilkinson & Cheshire 1989), but experimental evidence of UV light damage to non-cryptic sponges is lacking, and the effects of turbulence due to storm damage are likely to be more important at shallow depths, confounding the effects of UV damage (see below in this section).

Particulate matter, or more specifically particulate organic carbon (POC), in the water column can exist in a wide variety of complex forms, ranging from metabolically unusable particles to living prokaryotic and eukaryotic cells (Heip et al. 1995). Our understanding of how POC varies across and between Caribbean reefs is limited, and is dependent on the analytical method used to measure some component of POC. Despite this, there is evidence that the concentration of POC increases with depth on some Caribbean reefs. Conch Reef in the northern Florida Keys, home to the Aquarius undersea research habitat, has among the best studied physical and biological oceanographic characteristics of any coral reef in the world (Leichter et al. 1998, Stokes et al. 2011), and a pattern of greater POC with depth has been consistently described there. Two-fold higher levels of

chlorophyll *a*, a pigment common to phytoplankton, were recorded at depths in excess of 25 m relative to shallower depths, reflecting the regular movement of internal waves over the reef (Leichter et al. 1998). More specific and sophisticated measurements of picophytoplankton in the water column over Conch Reef have been made using flow cytometry. These demonstrated significant increases in concentrations of cyanobacteria, prochlorophytes, phytoplankton and heterotrophic bacteria between 10 and 30 m depth in one study (Lesser 2006), more variable but largely similar results in another (Trussell et al. 2006), and similar results in a third study (Pawlik et al. 2013). The same relationship of increasing pico-plankton with depth has been reported for 2 other Caribbean reef sites: Lee Stocking Island, Bahamas and Carrie Bow Cay, Belize, although significant differences were not evident shallower than depths of 92 m off Lee Stocking (Lesser 2006) and 46 m off Carrie Bow (Lesser & Slattery 2013). However, it is important to note the magnitude of differences observed within and between sites. Specifically, the differences in total picoplankton cells between depths within these sites were fairly small (an increase across depths of approximately 1.5×10^5 cells ml^{-1} for Conch Reef, 1.0×10^5 cells ml^{-1} for Lee Stocking and 1.0×10^4 cells ml^{-1} for Carrie Bow; Lesser 2006) relative to the differences in the total concentration of picoplankton between reefs (total cell concentrations were approximately 4.0×10^5 cells ml^{-1} for Conch Reef, 2.5×10^5 cells ml^{-1} for Lee Stocking and 1.5×10^4 cells ml^{-1} for Carrie Bow, which is more than an order of magnitude difference across the 3 sites; Lesser 2006). Therefore, while there is evidence from 3 Caribbean reef locations that the picoplank-tonic component of total POC increases with depth, the variation in this component is much greater between reef locations than between depths at any one location. If the majority of the sponge community was food-limited and dependent primarily on particulate food, it would be expected that patterns of sponge abundance would mirror particulate food abundance across both depths and locations.

Despite constituting one of the largest reservoirs of organic carbon on the planet, the consensus viewpoint is that dissolved organic matter (DOM) in seawater is a 'black-box' of large and small molecules from both terrestrial and marine sources, most of which are not subject to cellular metabolism (Nebbioso & Piccolo 2013). Nevertheless, some components of DOM (DOC for the purpose of this review), including dissolved organic nitrogen (DON) compounds, are considered important in microbial

nutrition and trophic cycling (Berman & Bronk 2003). On Caribbean coral reefs, macroalgae are now the dominant benthic organisms (in terms of percentage cover) at sufficiently illuminated depths, and release large quantities of DOC that foster microbial communities, which in turn have cascading impacts on other benthic organisms (Barott & Rohwer 2012).

Information on the relative concentrations of DOC on coral reefs is difficult to find, which is probably not surprising, considering that only a small proportion of DOC has been identified at the molecular level (Tedetti et al. 2011). The importance of DOC to sponge nutrition discussed in the previous section has been inferred from energetic considerations (Reiswig 1974, 1981) or determined from tracer studies using prepared DOC from phytoplankton cell lysate that was added to flow chambers or reef cavities (de Goeij et al. 2008, 2013). While DOC may be important to sponge nutrition, particularly to HMA sponges, its concentration and nutritional quality remain a mystery.

While not a resource itself, water movement is important in the flux of particles or DOC to sponges, and may interact with sponge morphology to enhance feeding (Leys et al. 2011). Nearly continuous water movement is characteristic of coral reef environments at all depths, but destructive levels of turbulent flow due to storm surges and wave energy, depending on geography and bathymetry, are more common above 10 m although they can extend even deeper (Wilkinson & Cheshire 1988). The negative consequences of turbulent flow in shallow water are frequently cited in surveys of sponge abundances on coral reefs (Alcolado 1979, Wilkinson & Cheshire 1989, Wilkinson & Evans 1989, Diaz et al. 1990, Schmahl 1990, Zea 2001). Rather than predictable patterns or gradients of flow, coral reefs are recognized for unsteady flow regimes at scales ranging from millimeters to kilometers (Monismith 2007).

EVIDENCE FOR FOOD LIMITATION FROM SPONGE DISTRIBUTIONS AND ABUNDANCES

Food limitation is a powerful selective force that affects the metabolism, growth and reproduction of organisms (Sokolova 2013). If sponges on Caribbean reefs are food-limited, the following 4 patterns of sponge distribution and abundance would be predicted based on the resource gradients described in the previous section:

(1) Increasing sponge cover with depth, starting below the level of damage due to turbulent flow and coincident with increasing concentrations of particulate food.

(2) Increasing relative cover of LMA sponge species in the sponge community with depth, reflecting dominance of HMA sponge species in shallow water where particulate food is scarce but DOC is still available.

(3) Dominance of cover by sponges with photosymbionts in the sponge community above the level of photosynthetically compensatory irradiance, both above and below the depth level of damage due to turbulent flow.

(4) Sponge morphology that reflects food limitation below the depth level of damage due to turbulent flow; particularly, elongated tubes, vases, or barrels that maximize induced flow through sponges that feed on particles or DOC, and horizontal fans and plates that maximize the surface area of photosymbiotic sponges.

To address these predictions, we compiled survey data from the literature that provided percentage benthic cover of sponges above and below 15 m depth (Table 2). Percentage cover is the most commonly measured estimate of sponge biomass in surveys of Caribbean reefs. The critical depth of 15 m was selected because concentrations of particulate food (mostly as picophytoplankton and heterotrophic bacteria) are generally greater below 15 m (Leichter et al. 1998, Lesser 2006). Further, a critical depth of 15 m has been cited in past manipulative experiments performed at Conch Reef, Florida Keys, as a depth separating the deeper benthos exposed, on average, to higher concentrations of particulate food than those that are shallower (Trussell et al. 2006, Pawlik et al. 2013). Additionally, we recognized the influence of turbulence and competition from corals and macroalgae as having an overriding effect on sponge abundance above 10 m depth for many reefs (Suchanek et al. 1983, Schmahl 1990). After examining sponge cover for surveys performed on reefs across the Caribbean (Table 2), we can find no evidence for any of the 4 predictions above.

For studies that included percentage cover survey data both above and below 15 m depth, 9 of 14 (64%) reported a decrease in sponge cover with depth, contrary to the prediction that percentage cover will increase with greater particulate food availability at greater depth. Also contrary to the pattern predicted if sponges are limited by the abundance of particulate food, the relative abundance of HMA sponges increased with depth (6 of 8 studies,

Table 2. Compilation of Caribbean reef sponge survey data in reverse chronological order (but keeping data from the same study together) indicating locations, depths surveyed, change in percentage cover with depth above and below 15 m, and percentage of 10 most abundant sponge species designated high microbial abundance (HMA), photosymbiotic, or tube/vase/barrel-shaped above and below 15 m. nd: no data. Arrows indicate increasing or decreasing trend in the data

Year	Location	Metrics recorded	Depths surveyed (m)	% cover above/below 15 m	% HMA above/below 15 m	% with photo-symbionts above/below 15 m	% tubular sponges above/below 15 m	Comments	Reference
2012	Dominican Republic	Cover	12–15	15.5 / nd	78 / nd	44 / nd	20 / nd		Loh & Pawlik (2014)
2012	Jamaica	Cover	13.5–15	11.5 / nd	22.2 / nd	10 / nd	36.4 / nd		Loh & Pawlik (2014)
2012	Cayman Islands	Cover	9–15, 16.8–18.3	11.5 / 4.8 ↓	70 / 70	60 / 70 ↑	20 / 30 ↑		Loh & Pawlik (2014)
2012	Mexico	Cover	9–15, 15–18	13.7 / 11.5 ↓	70 / 84.6 ↑	60 / 53.8 ↓	20 / 23.1 ↑		Loh & Pawlik (2014)
2011	Curaçao	Cover	12–15	4.5 / nd	69 / nd	38.5 / nd	38.5 / nd		Loh & Pawlik (2014)
2011	Martinique	Cover	9–13.5	19.8 / nd	50 / nd	30 / nd	50 / nd		Loh & Pawlik (2014)
2011	St. Eustatius	Cover	18	nd / 15.7	nd / 71.4	nd / 42.9	nd / 36		Loh & Pawlik (2014)
2011	St. Lucia	Cover	12–15, 15–16.5	19.0 / 18.4 ↓	50 / 50	30 / 30	33.3 / 33 ↓		Loh & Pawlik (2014)
2011	Puerto Rico	Cover	10.5–15, 15–16.5	15.7 / 14.6 ↓	45.4 / 63.6 ↑	36.4 / 54.5 ↑	18 / 9 ↓		Loh & Pawlik (2014)
2011	Bonaire	Cover	13–15	5.4 / nd	67 / nd	33 / nd	50 / nd		Loh & Pawlik (2014)
2010–2011	Bahamas	Cover	12–15, 15–18	15.0 / 6.7 ↓	60 / 64.3 ↑	30 / 35.7 ↑	10 / 36 ↑		Loh & Pawlik (2014)
2008–2009	Panama	Cover	1.5–6	47.5 / nd	50 / nd	50 / nd	0 / nd		Loh & Pawlik (2014)
2008	Florida Keys, USA	Cover	7–13	23.4 / nd	50 / nd	30 / nd	30 / nd		Loh & Pawlik (2014)
2011	Conch Reef, Florida, USA	Cover	15, 30	16 / 9.3 ↓	70 / 60 ↓	30 / 50 ↑	50 / 20 ↓		Pawlik et al. (2013)
2009	Carrie Bow, Belize	Abundance, cover	10–15, 15–30	2.6 / 4.6 ↑	54.5 / nd	45.5 / nd	45.5 / nd	No statistical differences in density across depth	Villamizar et al. (2014)
1998–2010	San Andrés, Colombia	Cover	9–13, 15–19	1.7 / 2.9 ↑	nd	nd	nd	SIMAC program	Ardila (2014)
1998–2010	Santa Marta, Colombia	Cover	9–13, 15–19	3.0 / 2.0 ↓	nd	nd	nd	SIMAC program	Ardila (2014)
1998–2010	Islas del Rosario, Colombia	Cover	9–13, 15–19	8.3 / 4.0 ↓	nd	nd	nd	SIMAC program	Ardila (2014)
2005	Punta Caracol, Panama	Density	5	nd	50 / nd	44 / nd	0 / nd		Gochfeld et al. (2007)
2004–2005	Isla Desecheo, Puerto Rico	Cover	15, 20, 25, 30, 40, 50	nd / ~15	nd	nd	nd	Cover increases from <5.0 at 15, 20, 25 m to >30.0 at 40, 50 m	Garcia-Sais (2010)
2003–2009	Lee Stocking Is., Bahamas	Cover	30, 46, 61, 76, 91	nd / ~50	nd	nd	nd	Cover increases from <5.0 at 30 m to >70 at 61, 76, 91 m	Lesser & Slattery (2011)
2003	NW Gulf of Urabá, Colombia	Cover, density	8–9, 16–22	4.7 / 3.7 ↓	75 / 45.5 ↓	25 / 54.6 ↑	0 / 18.2 ↑		Valderrama & Zea (2003)
2002	Bahía Cochinos, Cuba	Density	5–10, 15–20	nd	63 / 63	56 / 37 ↓	20 / 20		Caballero et al. (2009)
1994–1996	SW Caribbean atolls	Cover, density	6–9, 15.5–18	0.6 / 1.0 ↑	43 / 50 ↑	28 / 33 ↑	9.1 / 20 ↑		Zea (2001)

Table 2. (continued)

Year	Location	Metrics recorded	Depths surveyed (m)	% cover above/ below 15 m	% HMA above/ below 15 m	% with photo- symbionts above/ below 15 m	% tube sponges above/ below 15 m	Comments	Reference
1993	Lee Stocking Is., Bahamas	Cover	10–200; compare 10 vs. 20, 30	1.2 / 2.1 ↑	nd	nd	nd	Below 30: range of 1.6 at 200 m to 11.1 at 75 m	Liddell et al. (1997)
1992	Imelda Bank, Colombia	Density, cover	14–20	nd / 3.6	nd / 44	nd / 25	nd / 60		González-Calderón (1992)
1990–1991	Santa Marta, Colombia	Cover	17–22	nd / 8.2	nd / 50	nd / 50	nd / 12.5		Zea (1994)
1990	Belize	Biomass, abundance	10, 20	nd	nd	nd	nd	Biomass and abundance increased with depth	Wilkinson & Cheshire (1990)
1986–1987	Santa Marta, Colombia	Cover	14–16, 24–36	14.5 / 38.0 ↑	60 / 75 ↑	20 / 25 ↑	10 / 20 ↑		Zea (1993)
1983–1984	Archipiélago de los Roques, Venezuela	Abundance, cover	0.1–35	No change below 18 m	nd	nd	nd	Abundance and cover listed for species across all depths	Alvarez et al. (1990), Díaz et al. (1990)
1983	St. Croix, US Virgin Is.	Abundance, cover	18, 24	nd / 25.7	nd / 70	nd / 40	nd / 40		Targett & Schmahl (1984)
1981, 1982	St. Croix, US Virgin Is.	Cover	18, 27, 37	nd / 13.1	nd	nd	nd	Sponge cover of 8.0, 19.1, 12.3, respectively	Suchanek et al. (1983)
1981	Biscayne Nat. Park, FL, USA	Abundance	6–12	nd	11.1 / nd	10 / nd	20 / nd	Turbulence cited for low abundance	Schmahl (1990)
1978–1980	Punta del Este, Cuba	Density	13.5–15, 30–40	nd	54 / 91 ↑	36 / 55 ↑	33 / 36 ↑		Alcolado (1985)

75%) and sponges with photosymbionts increased with depth (8 of 10 studies, 80%). There was increasing cover of sponges with tube, vase or barrel morphologies with greater depth (7 of 10 studies, 70%), also contrary to the prediction that sponges limited by particulate food in shallower water should adopt morphologies that enhance particle capture. In the paragraphs below, we discuss the data relative to each of these predictions.

Increasing sponge biomass and diversity with depth has been cited as a 'repeatable pattern' across Caribbean reefs, and offered as evidence of food limitation in shallower depths consistent with the gradient in particulate food (Lesser 2006, Trussell et al. 2006, Lesser & Slattery 2013). This pattern was not evident in our review of reef surveys, in part because we took into consideration the confounding effect of turbulent flow restricting sponge abundances at shallow depths (usually <10 m). Another important factor affecting sponge abundance with depth is the reduction in competitive interactions with macroalgae and zooxanthellate octocorals and stony corals, which will result in greater abundances of sponges at greater depths.

Unlike stony corals and octocorals, most non-encrusting sponge species are unable to survive high shear environments, such as those found at depths generally above 10 m, depending upon geography and bathymetry. This consideration has escaped others as well; for example, a recent report concluding that reefs of the Florida Keys have undergone a phase-shift to domination by octocorals employed long-term surveys of 'shallow forereefs' at 2 to 5 m, a small proportion of total reef habitat, and an area too turbulent for most sponges (Ruzicka et al. 2013, R. R. Ruzicka pers. comm.; survey depths were inadvertently not reported in the paper). The same study did find increasing sponge abundances on

'deep forereefs,' but those surveys were limited to depths of 10 to 18 m, which are likely to be the shallowest depths unaffected by storm-induced shear on Florida reefs (Schmahl 1990). Another long-term survey study published in the same year for Carrie Bow Cay, Belize, from data collected in 2009, provides an interesting comparison (Villamizar et al. 2014). The shallowest site in the Belize study, the 'low relief spur and groove' site, is at the same depth (10 to 15 m) as that considered 'deep forereef' in the Florida study (Ruzicka et al. 2013). However, the Belize study also surveyed 3 additional, deeper zones, extending to depths of 30 m. Like the Florida study, the Belize study reported large increases in octocoral cover in the shallowest surveys, but an expansion of the sponge community overall. Most relevant to this review, they found no statistical differences in sponge species richness, average density, diversity and evenness indices across all 4 depth zones (Villamizar et al. 2014).

Surveys conducted on deep mesophotic reefs and walls (>60 m) reported some of the highest sponge cover data (Garcia-Sais 2010, Lesser & Slattery 2011), but compare Liddell et al. (1997) for much lower cover data for Lee Stocking Island, Bahamas. Rather than representing a growth response to greater particulate food availability, however, these data are consistent with domination of space by sponges in an environment that experiences very little disturbance, no competition from light-requiring benthic organisms, and a competitive advantage for sponges employing allelopathic chemical defenses and physical smothering of competitors for space (Suchanek et al. 1983, Engel & Pawlik 2000, Pawlik et al. 2007b).

There was no pattern of decreasing abundance of HMA relative to LMA sponge species with increasing depth (Table 2). Despite the dramatic difference in tissue morphology (Gloeckner et al. 2014) and pumping rates (Weisz et al. 2008) exhibited by these 2 categories of sponges, the relative abundance of HMA sponges increased with depth for most of the locations for which we have comparative data. Given that the abundance of particulate food increases with depth, and assuming that DOC levels are about equal across depths, the expectation would be that LMA sponges would increase in abundance with depth if sponges are food-limited.

There was no pattern to suggest that sponges harboring photosymbionts are more abundant than other species on Caribbean reefs at depths where there is sufficient illumination for compensatory photosynthesis (Table 2). This conclusion is not a new one, and was made by Wilkinson in studies that com-

pared the reef sponge communities of Caribbean reefs with those of the GBR, where sponges do appear to be food-limited on outer shelf and oceanic reefs where phototrophic sponges dominate, while heterotrophic and mixotrophic sponge species predominate on inner-shelf reefs (Wilkinson 1987, Wilkinson & Cheshire 1990). Phototrophic sponges of Pacific oligotrophic reefs derive >50% of their nutritional needs from cyanobacterial symbionts, have characteristic cup and plate-shaped morphologies to maximize exposure to light, and many are in the keratose subfamily Phyllospongiinae (Abdul Wahab et al. 2014). In fact, the number of Caribbean sponges with photosymbionts increased with depth in most of the studies with comparative data (Table 2), perhaps reflecting the increase in HMA sponges, as most photosymbiont-containing sponges are also HMA sponges (Table 1).

There was no pattern in sponge morphology as a function of depth across Caribbean reefs that suggests food limitation (Table 2). Only 1 species of photosymbiont-containing sponge species common to the Caribbean has the horizontally flattened cup or plate morphology characteristic of phototrophic sponges that dominate food-limited oceanic reefs of the GBR (Wilkinson 1983, Abdul Wahab et al. 2014). That species is *Cribrochalina vasculum*, and it is not particularly abundant, nor is it distributed differentially at shallower depths (Loh & Pawlik 2014). Photosymbiont-containing sponges on Caribbean reefs take all possible forms: barrel-shaped, tubular, branching, mound forming and encrusting (Table 1). For some species, 2 or more of these morphologies can be found within a species, or even within an individual, as for *Aplysina fistularis* (Fig. 1). Similarly, the tubular morphology that would more likely result in enhanced induced flow (Leys et al. 2011), while common to several species, does not predominate among the sponge community at any depth or location (Table 2). Moreover, sponges of the genus *Callyspongia*, which often grow with a tubular morphology (*C. vaginalis*), may also form elongated fans, while closely related and co-occurring congeners form branches (*C. armigera*) or mounds (*C. eschrichti*; Zea et al. 2014).

EVIDENCE FOR FOOD LIMITATION FROM CORRELATION OF DEPTH WITH SIZE AND GROWTH

Bottom-up control of sponge distribution and abundance on Caribbean reefs has been investigated

using correlation analyses of measurements of overall sponge tube length (or tube elongation) compared to the particle concentration in seawater as a function of depth (Lesser 2006, Lesser & Slattery 2013). Spe-

Fig. 1. Morphological plasticity within a single individual of *Aplysina fistularis*, in which the tube, branched, and fistule forms are exhibited

cifically, the tube elongation of 2 HMA species, *Agelas conifera* and *Aplysina fistularis*, was monitored over 1 yr at depths spanning 3 to 30 m on reefs off Carrie Bow Cay, Belize, and Lee Stocking Island, Bahamas, respectively. The elongation of 1 LMA species, *Callyspongia vaginalis*, was monitored for 6 mo on Conch Reef, Florida, and for 1 yr off Carrie Bow Cay, Belize. Both studies reported depth-dependent increases in the length and elongation of all 3 species of tube sponges at 3 reef locations that reflected increasing picoplankton abundances with depth (Lesser 2006, Lesser & Slattery 2013). Given the correlative (not causative) nature of these comparisons and the confounding effects of variability in sponge morphology, predation pressure and DOC concentrations on sponge growth, it is important to consider alternative explanations of the observed trends.

All 3 of the aforementioned tube sponge species are highly variable in their morphologies (Zea et al. 2014), not only across locations and depth zones, but also on the same reef and at the same depth. For example, Fig. 2 shows the length of the longest tube for individuals of *C. vaginalis* for Conch Reef, Florida, USA, Bocas del Toro, Panama, Grand Anse, Martinique, and Carrie Bow Cay, Belize (the last taken as mean data from Lesser & Slattery 2013). Regressions of tube length of *C. vaginalis* with depth for the first 3 datasets each provide a positive slope, but depth does not explain much of the variability in
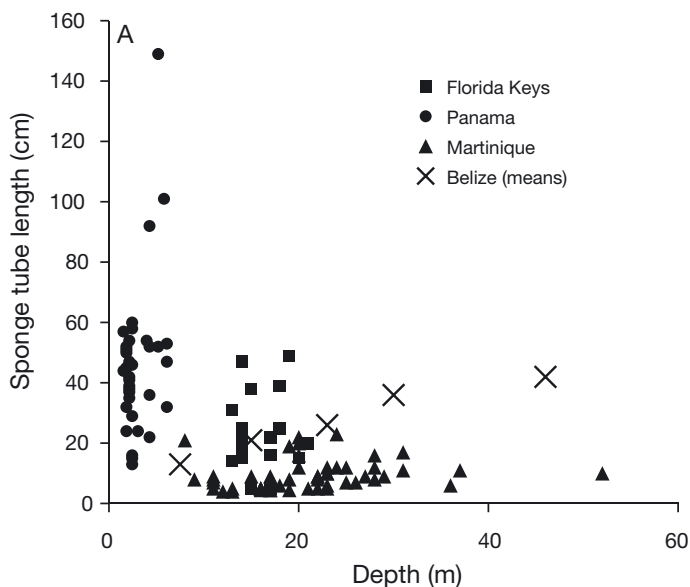

Fig. 2. (A) Variability in tube length in *Callyspongia vaginalis* as a function of depth and location. Data for Belize are mean values (Lesser & Slattery 2013); for all other sites, the longest tube per individual sponge was measured while diving along a linear depth profile. (B) *C. vaginalis* from Bocas del Toro, Panama (photo and data credit: M. J. Marty)

sponge tube length (R² values of 0.01, 0.14, and 0.03, respectively). Tube length depends more on exposure to turbulence from tidal flow and storm damage than on depth. Sponge tubes from the Panama location grew in a low shear environment that is seldom impacted by turbulence or storms. Moreover, the Panama location is heavily overfished so that this species is relatively free of predation (Loh & Pawlik 2014). These combined effects result in sponge tubes that are more than 3 times longer than the longest tubes at the same depth in Belize or Martinique (Fig. 2). The morphological plasticity of sponge growth is well known (Palumbi 1984) and may be influenced by multiple factors, the most important of which is water motion, which results in a more compact shape at higher velocities (Kaandorp 1999, Bell & Barnes 2000). Longer, or more rapidly elongating, sponge tubes as a function of depth may have multiple explanations, including different levels of predation (Pawlik et al. 2013), but the most likely explanation is that tube sponges grow differently in response to different flow regimes at different depths; at very shallow depths, differences in morphology can be in response to partial removal by turbulent flow followed by regrowth (Mercado-Molina & Yoshioka 2009).

Sponge morphology and growth also complicate the interpretation of feeding data presented in the studies that purport to demonstrate enhanced growth with depth of tube sponges (Lesser 2006, Lesser & Slattery 2013). All 3 species of tube sponge that were monitored in these studies most frequently form clusters of tubes with a common, shared spongocoel (the space within the tube of the sponge) within the base (Zea et al. 2014). All data on sponge feeding in the studies by Lesser (2006) and Lesser & Slattery (2013) were expressed for each individual tube, despite the fact that water flow was continuous among tubes, and that plasticity in growth can be affected by the biomass of the sponge base or by adjacent, connected tubes. Therefore, alternative explanations for the differences with depth seen in these studies could be differences in the biomass of the sponge base, or in the number of tubes that comprised the whole sponge individual.

As reviewed herein, an important nutritional role has been hypothesized for DOC in both HMA and LMA sponge species, and for the HMA tube sponges *Aplysina fistularis* and *Agelas conifera* in particular (Reiswig 1974, 1981, de Goeij et al. 2013, Mueller et al. 2014). Thus, *in situ*, correlative studies of bottom-up effects on sponge growth should consider all food resource gradients, including DOC. The absence of substantive consideration of DOC in the energetic budgets of Caribbean sponges restricts the interpretation of depth-dependent increases in sponge growth as evidence of food limitation.

Another recent set of studies was instigated, not to examine bottom-up influences, but to gather basic information about growth and demography of what is now the most important habitat-forming organism on most Caribbean reefs, the giant barrel sponge *Xestospongia muta* (McMurray et al. 2008, 2010, 2011). Fortuitously, these studies, which involved tagging individual sponges on 12 permanent circular plots (16 m diameter) and monitoring them for more than a decade, were done within 3 plots at each of 3 depths (15, 20, 30 m) on Conch Reef, Florida, where the gradient of increasing particulate food with depth is particularly well described (Leichter et al. 2005). Changes in sponge biomass were estimated over a 4.5 yr period using digital image analysis of the profile and oscular views of 104 tagged sponges to calculate specific growth rates (McMurray et al. 2008). No significant differences in growth were found across the 3 depths, despite the well-described gradient in particulate food at this site (Leichter et al. 2005). Subsequently, a demographic analysis of *X. muta* on Conch Reef also reported the opposite trend of sponge abundance to that expected if sponges were food-limited at this site, with lower abundance at 30 m relative to 15 and 20 m (McMurray et al. 2010). Further, sponge abundance was found to increase during the period 2000 to 2006 at all depths (McMurray et al. 2010) and has more than doubled during the period 2000 to 2012 (S. E. McMurray unpubl.).

EVIDENCE FOR FOOD LIMITATION FROM MANIPULATIVE EXPERIMENTS

Considering the complexity of the overlapping distributions of bottom-up resources (particles, DOC, light, water flow) available to sponges on Caribbean reefs, as well as the difficulty in measuring these resources, the most valid approach to testing food limitation of sponges lies with manipulative experimentation that attempts to control for as many confounding factors as possible. To date, only 2 studies have enlisted manipulative experiments to test for bottom-up effects on the growth of sponges on Caribbean reefs (Trussell et al. 2006, Pawlik et al. 2013).

In the first study, reciprocal transplant experiments were performed to assess growth of the LMA tube sponge *Callyspongia vaginalis* between 12 and 25 m depths at Conch Reef, Florida (Trussell et al. 2006). Analysis of the resulting data showed that tubes from

both the shallow and deep sites grew more at the deep site than the shallow site (Trussell et al. 2006, their Fig. 5). This difference, combined with data demonstrating higher levels of particulate food at the deep site, led the authors to conclude that growth of *C. vaginalis* was food-limited.

The second study was conducted a decade later in the same location (Conch Reef, Florida) as the previous study (Trussell et al. 2006) and included 2 iterations of the same experiment (Pawlik et al. 2013). In the first iteration, 4 species of branched sponges were used, 3 LMA species, *C. armigera*, *Iotrochota birotulata* and *Amphimedon compressa*, and 1 HMA species, *Aplysina cauliformis*. Of these, the last 2 are chemically defended from predatory fishes, while the first 2 are not. Analysis of the resulting data showed no difference in the growth of sponge pieces in pred-

ator-exclusion cages for 3 of the 4 species at 15 versus 30 m, but enhanced growth at the shallower site for *C. armigera* (Fig. 3). In the second iteration, the LMA tube sponge *C. vaginalis* was used, employing the same methods (Pawlik et al. 2013). Although winter storms removed 17 of 20 cages from replicates at the shallower site, data from the remaining sponge pieces showed the same pattern as the previous year for *C. armigera*. Citing the well-documented gradient in particulate food known for Conch Reef, the authors concluded that there was no evidence that differences in particulate food at the 2 depths had an effect on sponge growth. Moreover, there was significantly less growth for uncaged pieces of *C. armigera* and *I. birotulata* than for caged pieces at both depths, but this pattern was not seen for the chemically defended species, *Amphimedon compressa* and *Aply-*
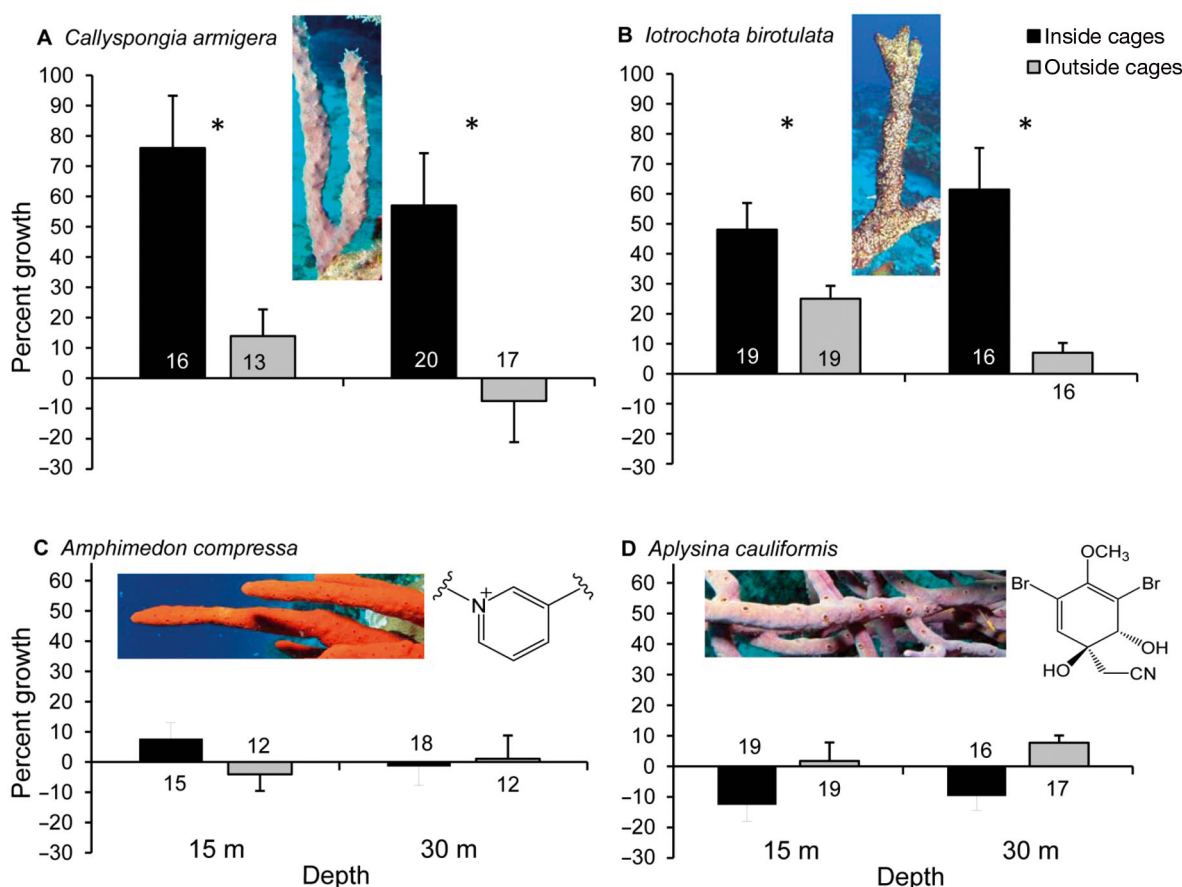

Fig. 3. Fig. 1 from Pawlik et al. (2013). Percentage growth of branched sponge pieces (change in wet mass) 287 d after attachment inside and outside of predator-excluding cages at 15 and 30 m depth on Conch Reef, Florida, USA. (A) *Callyspongia armigera* and (B) *Iotrochota birotulata* lack chemical defenses, while (C) *Amphimedon compressa* and (D) *Aplysina cauliformis* contain alkaloids that deter fish predators, represented by a portion of the chemical structure of amphitoxin for the former and aeroplysinin-1 for the latter. Surviving number of 20 replicates is shown for each bar; error bars are SE. Statistical analyses were performed on transformed data (growth index). *Significant difference in growth inside versus outside cages (p < 0.01)

sina cauliformis (Fig. 3). Based on the abundance of sponge-eating fishes on Conch Reef, the authors concluded that predation was an important determinant of net growth for chemically undefended species, but that growth of none of the 4 species was influenced by the difference in particulate food between depths (Pawlik et al. 2013).

The conflicting conclusions of these 2 studies may result from differences in experimental designs, in particular, the presence (or absence) of caged sponges to remove the confounding effects of predation on sponge growth. In the first study (Trussell et al. 2006), the sponge tubes were not protected from predation during the year-long time-course of the experiment, although this species is known to be a preferred prey item of sponge-eating fishes, particularly angelfishes, which are very common on Conch Reef (Randall & Hartman 1968, Pawlik 1997 and 'Angels on the pinnacle' video available at http://youtu.be/lgPuNMJdgrk). Thus, one alternative explanation for the difference in net growth between 12 and 25 m is that predatory fishes had a greater grazing impact on the sponges transplanted to the shallower site over the course of the year-long experiment. Considering that spongivore grazing reduced growth of the closely related sponge *C. armigera* by over 50% wet mass at Conch Reef after 10 mo in 2010 to 2011 (Fig. 3), the alternative explanation that predation, rather than food limitation, resulted in growth differences between depths is the more parsimonious.

Incorporating predator-exclusion cages into experimental designs allows researchers to control for tissue loss from predation events when assessing sponge growth, but may also introduce caging artifacts that have negative consequences for caged organisms (Hall et al. 1990). Within the context of the manipulative experiments discussed herein, such negative effects would reduce sponge growth inside the cages compared to individuals outside of the cages. For the 2 chemically undefended sponge species, growth of sponge pieces in cages was greater than that of sponge pieces outside of cages (Pawlik et al. 2013), which was the opposite outcome to that expected if there was a negative flow effect of caging on suspension-feeding sponge pieces. Therefore, enhanced growth of caged sponge pieces was a conservative result. Further, the absence of a difference in growth for the 2 chemically defended sponge species confirmed the lack of a caging artifact by comparison with the undefended species (Pawlik et al. 2013).

Additional differences in the experimental designs of these 2 studies include the number of sponge spe-

cies investigated, the morphology of examined species, and the transplantation method. The first study (Trussell et al. 2006) used a single, tubular sponge species and conducted reciprocal transplantations at shallow and deep sites. The second study (Pawlik et al. 2013) investigated the same tubular species and 4 additional species with branched morphologies, conducting transplantations from a general collection area to shallow and deep sites. Certainly, broader species coverage leads to more robust conclusions; however, more complex experimental designs (reciprocal transplantation) can determine the potential effects of genetic or environmental history differences among sponge individuals (Lesser & Slattery 2013). To date, experimental evidence has shown no transplantation effect for Caribbean sponges, in that growth was the same for tubes from different source sponges and populations (Trussell et al. 2006). The absence of a genotypic response, even for a sponge species that primarily reproduces sexually (Leong & Pawlik 2010b), the dominance of asexual reproduction (and clonal populations) in branched sponges (Wulff 1984, Leong & Pawlik 2010a), and results from 9 yr of manipulative sponge experiments (Leong & Pawlik 2010a) argue against this level of experimental complexity and in favor of broader species coverage. Similarly, branched sponge species are generally better suited for conducting manipulative growth experiments, being adapted to fragmentation and reattachment (Wulff 1984, Leong & Pawlik 2010a), exhibiting higher growth rates than tubular counterparts (Leong & Pawlik 2010b), and presenting a smaller cut surface area (thus less tissue damage) when generating sponge pieces. While trade-offs in experimental designs and species choices will continue to be debated, the important message in the context of the present review is that no unequivocal evidence for food limitation of sponges from Caribbean reefs has been reported from manipulative experiments.

SUMMARY AND QUESTIONS FOR FUTURE RESEARCH

At some level, it is likely that all organisms are resource-limited, in that additional provision of nutrients or food at the right time in their life cycle could result in incrementally greater growth or reproduction, but this individual-level response is not necessarily important at ecologically relevant scales of time or space. Nevertheless, for most populations or communities in which bottom-up and top-down factors have

been intensively examined, both factors are considered important, even if at different levels (Power 1992). This makes the absence of evidence for bottom-up effects among sponges on Caribbean reefs that much more intriguing, particularly because food limitation can be demonstrated for sponges on oligotrophic reefs of the GBR (Wilkinson & Cheshire 1990), where phototrophic phyllosponginiids of several genera have evolved similar morphologies to maximize autotrophic symbiosis (Abdul Wahab et al. 2014). It may be that Caribbean reef sponges are adapted to a certain range of food resources in combination, whether particulate food, DOC, or symbiont photosynthate, and because of the mechanisms by which they feed (which may include the sloughing of collar cells to form detritus), excess food may not be useful, or may clog the aquiferous system and be detrimental. The most successful (i.e. common) sponge species on Caribbean reefs may have adapted individually to their own combinations of resources, despite ranging between HMA and LMA, heterotrophic and photosymbiotic, and from branched to barrel-shaped, with each combination similarly successful across reef environments. Additionally, sponges may be able to switch between resources, depending on availability or nutritional quality; for example, primarily absorbing DOC when particulate food is scarce.

As often happens, the foregoing synthesis generates more questions than it answers. If, as recently demonstrated for small, encrusting and excavating sponges, DOC is a major nutritional component for both HMA and LMA sponges (de Goeij et al. 2013, Mueller et al. 2014), why do these 2 divergent morphological groups of sponges exist, given that one (HMA, with slow pumping rates) was thought to specialize in absorption of DOC, while the other (LMA, with fast pumping rates) was thought to specialize in particle capture (Reiswig 1974, Weisz et al. 2008)? If sponges convert most of the DOC they absorb into cellular debris that is then expelled (de Goeij et al. 2013), why do large tube sponges with their considerable tissue mass not have a visible stream of detritus emanating from the openings of their tubes? Or is this pool of DOC somehow only available to cryptic and excavating species, perhaps because of their proximity to 'leaky' benthic organisms, such as corals and macroalgae? And what would be the advantage to sponges of such an apparently wasteful process of cell shedding? Is this a necessary protective mechanism for suspension-feeding organisms that lack a more sophisticated immune system but are continuously exposed to pathogenic bacteria and viruses?

If DOC is such an important component of the diet of sponges, why are there no obvious or consistent increases in sponge abundances near areas of anthropogenic eutrophication? While it has often been predicted that sponge biomass would increase with increasing levels of pollution brought on by human activities (Wilkinson & Cheshire 1990), recent studies have suggested that sponges are unable to use the products of organic pollution as food, and are instead, negatively impacted by this form of eutrophication (Maldonado et al. 2010, Topcu et al. 2010). Several survey studies have inferred that anthropogenic eutrophication was responsible for enhanced sponge abundances (e.g. Zea 1994, Holmes 2000, Chaves-Fonnegra & Zea 2007, Ardila 2014), but this may instead be the result of greater substratum availability as corals have declined along the same gradient (Zea 1994) because of increased sedimentation, reduced light levels, etc. Comparisons of sponge cover across locations revealed much greater variation than across depth, with a range of 0.6 to 47.5 % of the substratum covered by sponges at depths above 15 m (Table 2). Rather than reflect food availability or eutrophication, abundance appears to track with a combination of other biotic and abiotic factors. The relationship between food availability and cover is best explored with the cross-Caribbean dataset of Loh & Pawlik (2014), which was compiled over a 3 yr period using consistent survey techniques (Table 2). Most sites between 9 and 15 m depths had mean sponge cover of 11 to 20 %, despite having likely anthropogenic nutrient impacts (based on human population density) that ranged from very high (e.g. Jamaica, Dominican Republic, Martinique) to very low (e.g. Cayman Islands, Bahamas, Mexican Yucatan). The lowest values for sponge cover (Curacao, Bonaire) occurred at sites with high abundances of predators and high coral cover (reflecting spatial competition), while the highest sponge cover values (Panama) were from sites that experience very little storm disturbance and lack predatory fishes due to overfishing (Loh & Pawlik 2014).

The absence of bottom-up effects on Caribbean reef sponges makes the evidence for top-down effects that much more striking (Pawlik 2011, Loh & Pawlik 2014). The same high level of sponge diversity in species across reefs (in terms of species, morphology, and presence of microbial and photosymbionts) that lacks a pattern in response to food limitation shows a strong pattern in response to predation, with species following 1 of 2 evolutionary trajectories: chemical defense or rapid growth and reproduction. For example, among the most abundant branched sponges on most

Caribbean reefs are 3 species, *Aplysina cauliformis*, *Amphimendon compressa,* and *Iotrochota birotulata* (Loh & Pawlik 2014), which fall into the following categories, respectively: HMA, photosymbiotic, chemically defended; LMA, heterotrophic, chemically defended; LMA, heterotrophic, undefended. Growth of the last of these species is strongly affected by predation, while the first 2 species grow much slower than the last (Pawlik et al. 2013).

After reviewing the literature, we can identify 3 depth-related factors that primarily influence sponge community structure on most Caribbean reefs: turbulence, spatial competition and predation (Fig. 4). The first two of these only influence sponge communities at shallow depths: turbulence from tidal currents and storm events mostly above 10 m, and competition with light-requiring gorgonians, stony corals and macroalgae mostly above 20 m. At depths below 15 m, sponge communities are mostly influenced by predation alone, the effects of which may vary as a function of predatory species, depth or location (e.g. some parrotfish species are found primarily at shallower depths and have less impact on sponges, while angelfishes are found at all depths and eat primarily sponges; Garcia-Sais 2010, Lesser & Slattery 2013, Loh & Pawlik 2014). On deep mesophotic reefs and

walls (below 60 m), the combination of low disturbance and competitive superiority through alleopathy and overgrowth (Suchanek et al. 1983, Engel & Pawlik 2000, Pawlik et al. 2007b) allows sponges to dominate the benthos (Garcia-Sais 2010, Lesser & Slattery 2011), although the effects of predation likely structure these communities in the same way as on shallower reefs. Among communities of organisms in biodiverse ecosystems, the relative lack of complexity of sponge communities on Caribbean reefs is remarkable, and may explain why the impact of predation on sponge community structure is observable across the entire biogeographic region (Loh & Pawlik 2014).
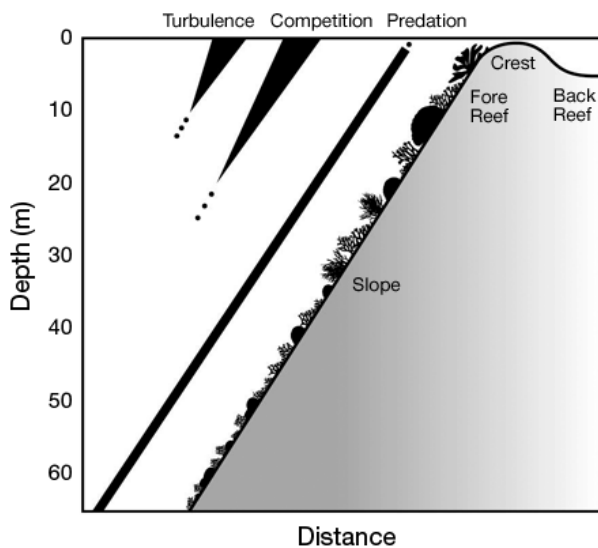
Fig. 4. Schematic representation of the 3 primary factors affecting sponge community structure on most Caribbean reefs as a function of depth. Sponges are removed from shallow water by turbulence from tidal currents and storm events. Sponges compete for space with light-requiring gorgonians, stony corals and macroalgae whose collective abundance decreases with depth. Predatory fishes (primarily angelfishes and parrotfishes) affect sponge community structure at all depths by removing species that lack chemical defenses

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