



REPLY COMMENT

No evidence for food limitation of Caribbean reef sponges: Reply to Slattery & Lesser (2015)

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ABSTRACT: Slattery & Lesser (2015; Mar Ecol Prog Ser 527:275–279) offer a Comment on our review of the literature for evidence of bottom-up control of sponge communities on Caribbean reefs. We briefly address the criticisms presented in the Comment and reiterate the lack of evidence for food limitation, including inter-oceanic comparisons of Caribbean reefs with Indo-Pacific oligotrophic reefs, where sponge communities show strong evidence of food limitation, and past and recent evidence for the importance of dissolved organic carbon (DOC) in sponge nutrition. We did not claim that 'predation is the primary process that determines the growth, biomass and biodiversity of sponges on Caribbean coral reefs,' but we identified 3 depth-related factors that influence sponge community structure on Caribbean reefs: turbulence, spatial competition and predation. We agree that multifactorial manipulative experiments are the best way to address the interaction between top-down and bottom-up processes in this system; indeed, one such experiment has been performed, with an outcome that does not support bottom-up effects.

KEY WORDS: Bottom-up · Top-down · Trophic levels · Dissolved organic carbon · DOC · Particulate organic carbon · POC · Sponge loop

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Introduction

Sponges can be food-limited, as there is evidence for this from oceanic sites of the Great Barrier Reef, Australia, as opposed to landward sites of the same reef system and Caribbean reefs (Wilkinson & Cheshire 1990). Sponge communities on food-limited oceanic Pacific reefs are characterized by low percentage cover, low biomass, and the dominance of phototrophic sponge species that grow to maximize exposure to light. We find no similar evidence of food limitation in the percentage cover, microbiome characteristics, or morphology of sponges on Caribbean reefs (Pawlik et al. 2015, Table 2 therein). Slattery & Lesser (2012) provide further support for this

inter-oceanic comparison of sponge communities with data from mesophotic reefs from Chuuk, Micronesia, and Great Exuma, Bahamas, both of which are small islands far from terrestrial or anthropogenic impacts. For 5 depth profiles ranging from 30 to 91 m, sponge biomass values (as tissue volume) on reefs off Chuuk were exceedingly low (0 to 1000 cm³ per transect), while those off the Bahamas were much higher (~2000 to 12 000 cm³ per transect; Slattery & Lesser 2012, their Fig. 2). Thus, food limitation of sponges has been documented from several oceanic reefs of the Pacific, and it is of scientific interest to investigate why this is not evident on Caribbean reefs (Wilkinson & Cheshire 1990, Pawlik et al. 2015).

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Sponge distributions and abundances

Slattery & Lesser (2015, p. 276) assert that 'there is a well described gradient of increasing sponge diversity and biomass from shallow to mesophotic depths (3 to 150 m), corresponding with increased POC, throughout the Caribbean and Indo-Pacific (e.g. Slattery & Lesser 2012, and references therein)'. The data from their own reference (Slattery & Lesser 2012, their Fig. 2), however, provide strong evidence for the opposite relationship: sponge volume on reefs off the island of Chuuk drops from ~1000 cm³ per transect at 30 m to zero at 76 and 91 m, indicating a decrease in sponge biomass with increasing POC. These data are, however, consistent with the response of phototrophic sponges that are light-limited (and, therefore, food-limited) at greater depth (Wilkinson 1988), further strengthening the argument that there is food limitation for sponges on some Indo-Pacific reefs, but not in the Caribbean.

We acknowledged the importance of abiotic influences on sponge distributions, particularly turbulent flow on shallow reefs (generally <10 m depth), and that storm-induced turbulence is primarily responsible for increasing sponge biomass at the shallow end of the depth spectrum (Pawlik et al. 2015, Fig. 4 therein). Below this depth, where turbulence is a less confounding factor, we cannot find evidence of food limitation for sponges on Caribbean reefs. Slattery & Lesser (2015) criticize our test of 4 predictions consistent with food limitation because we used percentage cover data (Pawlik et al. 2015, Table 2 therein) rather than biomass, although they acknowledge that percentage cover data are the most readily available for a Caribbean-wide comparison. Indeed, if conclusions are to be drawn on the basis of surveys that document biomass alone, there are insufficient data on Caribbean sponges. Cover data are the next best option, because they relate to the limiting resource of space, and because methods of collecting these data are more consistently applied. Considering that 64% of 23 surveys reported decreasing sponge cover with depth (Pawlik et al. 2015, Table 2 therein), there simply is no 'well described gradient' in the opposite direction.

Slattery & Lesser (2015) also criticize our use of 15 m as a critical depth upon which to base the comparison of shallow and deep sponge communities (Pawlik et al. 2015, Table 2 therein). They seem to want to move this critical depth to 30 m or below, thereby shifting the argument to mesophotic depths. As we explained in our review, the 15 m critical depth was employed to separate sponge populations generally exposed to less and more POC on the basis

of a large body of work at Conch Reef, including the manipulative experiments of Trussell et al. (2006), who compared depths of 12 and 25 m. Even at mesophotic depths, a gradient of increasing sponge biomass with greater depth is not supported. Using video transects from submersibles, Maldonado & Young (1996) described a dramatic decrease in sponge abundance and species diversity on the Bahamian slope between 100 and 230 m, and a similar decrease in sponge abundance with depth was reported from dredge and trawl studies of the Barbados slope (Lewis 1965).

Correlation of depth with size and growth

Sponge tube length and tube elongation rate are inadequate as proxies for age and overall growth rate, respectively. We contend that sponge morphology is highly plastic due to site-specific differences in exposure to turbulence and predation. For many species, large variations in tube length can be observed as a function of depth and location (e.g. *Callyspongia vaginalis*; Pawlik et al. 2015, Fig. 2 therein).

The importance of dissolved organic carbon (DOC) as a source of nutrition for sponges has been known for decades (Reiswig 1981), and confirmed for sponge species with both high and low microbial biomass (e.g. Mueller et al. 2014). Indeed, Slattery & Lesser (2015, their Table 1) provide data indicating that DOC can contribute a large proportion of the carbon budget of the sponge *Agelas conifera*. Therefore, DOC must be considered in the energetic budget and scope for growth of sponges. Our long-term monitoring of *Xestospongia muta* across a gradient of increasing POC at 15, 20 and 30 m has provided no evidence of enhanced growth with greater depth (McMurray et al. 2008, 2010), which Slattery & Lesser suggest may be attributable to a trade-off between greater food availability and 'increased bleaching stress suffered by *X. muta*' (p. 278) at the deepest site, citing our data on sponge bleaching (McMurray et al. 2011). However, a key conclusion in our study was that bleaching is a 'cyclic response by the cyanobacteria symbionts of *X. muta* that has no negative effect on the host sponge' (McMurray et al. 2011, p. 2249).

Manipulative experiments

Slattery & Lesser (2015, p. 278) quote our review (Pawlik et al. 2015, p. 278), that 'no unequivocal evidence for food limitation of sponges from Caribbean

reefs has been reported from manipulative experiments'. The one manipulative experiment reporting food limitation (Trussell et al. 2006) lacked cages to prevent sponge-eating fishes from eating the palatable sponge *C. vaginalis* used in those experiments; indeed, angelfishes can be observed taking bites of *C. vaginalis* in video footage taken on the same reef (Loh & Pawlik 2014, Supporting information therein, Movie S1). Further, because this sponge species has a very rapid rate of healing (Walters & Pawlik 2005), it is not surprising that bite marks were not observed on the unprotected sponges.

While there is no unequivocal evidence for food limitation of sponges from Caribbean reefs, we maintain that there is good evidence against food limitation (Pawlik et al. 2013). The Comment suggests that a properly designed experiment was subject to 'statistical analysis issues,' when in fact this contention of Lesser & Slattery (2013) only applied to the second iteration of the experiment presented in Pawlik et al. (2013). In Pawlik et al. (2015), we explain in detail how the first iteration of this experiment was properly performed and analyzed (Pawlik et al. 2013, Fig. 1 therein), including measurement of the change in wet mass of 4 branched sponge species and use of caged treatments to assess predation. This experiment not only showed the importance of predation at this site for 2 palatable sponge species, it revealed no evidence of food limitation; indeed, the opposite for one species, with significantly less growth at greater depth for *Callyspongia armigera* that had been caged to prevent predation (Pawlik et al. 2013).

Regarding the second iteration of the experiment presented in Pawlik et al. (2013), Slattery & Lesser (2015) repeat assertions from Lesser & Slattery (2013) regarding flaws in design and statistical analysis. This iteration was designed in the same way as the first, but used the same palatable tube sponge (*C. vaginalis*) previously employed without cage controls by Trussell et al. (2006). The initial design was robust, but winter storms hit Conch Reef during the 358 d experiment, removing 3 to 7 of each of 20 treatment sponges at each depth, and all but 3 of the cages from caged treatments at 15 m (Pawlik et al. 2013, Fig. 2 therein). Acknowledging the limitations of statistical analyses on the data from the sponge treatments that survived, we reported 'Despite the loss of cages, growth of the remaining sponge tubes was greater at the shallow than at the deep site for uncaged sponge tubes (...1-tailed Student's *t*-test, $t = -2.20$, $df = 29$, $p = 0.0180$), and the effect of caging at the deep site was significant, with virtually no sponge growth outside of cages (... $t = -1.72$, $df = 28$,

$p = 0.0486$)' (Pawlik et al. 2013, p. 3). Lesser & Slattery (2013) contested the use of *t*-tests to analyze this incomplete data set, suggesting that a more appropriate test would have yielded a p -value >0.05 . While arguable, these criticisms overlook the clear signal in the data from the remaining replicates that supported the first iteration of the experiment: (1) the absence of enhanced sponge growth at the deeper site, indicating a lack of food limitation, and (2) a strong effect of predation at the deeper site where cages were left intact. We maintain that the first iteration of the experiment reported in Pawlik et al. (2013) is an unequivocal test of the bottom-up control hypothesis of Lesser (2006), and that the second iteration, while incomplete, supports the first and reveals that the lack of cage controls was a design flaw in Trussell et al. (2006).

Summary

On the subject of publishing in the scientific literature, the astrophysicist and educator Carl Sagan wrote 'Every scientist feels a proprietary affection for his or her ideas and findings. Even so, you don't reply to critics, "Wait a minute; this is a really good idea; I'm very fond of it; it's done you no harm; please leave it alone." Instead, the hard but just rule is that if the ideas don't work, you must throw them away' (Sagan 1996, p. 33). The hypothesis that bottom-up processes primarily, or even substantially, influence the ecology of sponges on Caribbean reefs is not supported by evidence. As previously acknowledged, this is an unusual conclusion, because most communities are characterized by some mixture of top-down and bottom-up control, including sponge communities on Indo-Pacific reefs (Wilkinson & Cheshire 1990). We know of no other community about which scientific opinion has shifted so dramatically, from the absence of top-down effects (Randall & Hartman 1968), to the primacy of bottom-up effects (Lesser 2006), to the absence of bottom-up and the dominance of top-down effects (Pawlik 2011, Pawlik et al. 2015). The apparent lack of food limitation for Caribbean sponges may be due to high DOC levels (Wilkinson & Cheshire 1990), combined with multiple other nutrition sources (particles, photoautotrophy) used by the taxonomically diverse sponge species that dominate Caribbean reefs (Loh & Pawlik 2014). Food limitation should not be inferred from sponge distribution and abundance alone, because these data are confounded by other factors, such as predation, competition and turbulence.

The ecology of sponge communities on Caribbean reefs can be further understood by addressing the research topics suggested at the conclusion of Pawlik et al. (2015). These include studies of selective feeding by sponges, their use of available DOC, and the role of their diverse microbiome in trophic processes, which may provide mechanistic insight into surprising discoveries, such as the 'sponge loop' (de Goeij et al. 2013).

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