Vol. 527: 275–279, 2015
doi: 10.3354/meps11307

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 7

FREE ACCESS

COMMENT

Trophic ecology of sponges from shallow to mesophotic depths (3 to 150 m): Comment on Pawlik et al. (2015)

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ABSTRACT: Pawlik et al. (2015; Mar Ecol Prog Ser 519:265–283) proposed 4 hypotheses regarding the influence of food limitation on growth and distribution of Caribbean sponges: (1) increasing sponge cover as particulate organic carbon increases with depth, (2) replacement of high microbial abundance sponges with low microbial abundance sponges at depth, (3) dominance of sponges with photosymbionts above the photosynthetic compensation point, and (4) sponge morphologies that reflect adaptations to feeding. Pawlik et al. (2015) concluded that there is no evidence of food limitation (i.e. bottom-up control), and that predation is the primary process that determines the growth, biomass and biodiversity of sponges on Caribbean coral reefs. Here, we address the conclusions of Pawlik et al. (2015) in the context of the observational, correlational, and manipulative studies they utilized in their analysis. We argue that both top-down (predation pressure) and bottom-up (food limitation) processes influence the distribution of sponges on coral reefs, that these factors vary in time and space, and that only when multifactorial manipulative experiments are undertaken will the magnitude of the roles of predation and food limitation be understood.

KEY WORDS: Bottom-up control · Top-down control · Dissolved organic carbon · DOC · Particulate organic carbon · POC · Experimental design

Introduction

Pawlik et al. (2015) reviewed the literature on trophic ecology of sponges, focusing on studies that incorporate observational data, correlational studies, and manipulative experiments with sponges on Caribbean reefs. They concluded that there is no evidence for food limitation, and that the observed patterns of distribution and abundance can be primarily explained by predation pressure (i.e. top-down control). This conclusion is extraordinary in ecological studies, as noted by Pawlik et al. (2015, p. 266): 'due to the complexity of most ecosystems … some combination of top-down and bottom-up processes [is] likely to be important'.

Sponge distributions and abundances

The observational data reported by Pawlik et al. (2015) represents a broad, but selective, survey of the literature related to the distribution and abundance of sponges throughout the Caribbean basin. The authors examine the percentage of sponges with particular characteristics, at depths above and below 15 m, to determine whether the data conform to any of their 4 hypotheses: (1) increasing sponge cover as particulate organic carbon (POC) increases with depth, (2) replacement of high microbial abundance sponges with low microbial abundance sponges at depth, (3) dominance of sponges with photosymbionts above the photosynthetic compensation point, and

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(4) sponge morphologies that reflect adaptations to feeding. However, the authors utilize percent cover as an indirect proxy for sponge biomass in their analysis. As discussed by Wulff (2012), and illustrated by our own data from the Bahamas and Chuuk (Slattery & Lesser 2012), sites can exhibit similar sponge percent cover yet have significant differences in sponge biomass due to dissimilarities in sponge growth forms and community composition. To be fair, most studies of sponge community dynamics use this metric, but percent cover cannot be used instead of sponge biomass to infer relationships between food availability and sponge growth.

Pawlik et al. (2015) also compiled data on sponge cover above and below a depth of 15 m; based on the work of Leichter et al. (1998) and Trussell et al. (2006) at Conch Reef, Florida, they assert that this 'critical depth' represents a breakpoint for the availability of POC resources. However, Trussell et al. (2006) did not cite 15 m as a critical depth for food differences. Moreover, the data from Leichter et al. (1998) and Lesser (2006) cited by Pawlik et al. (2015) actually report significant differences in food supply from 22 to 28 m (i.e. mostly zooplankton) and between 20 m and 30 m (i.e. mostly prochlorophytes and heterotrophic picoplankton), respectively. These differences, from the same reef, are a reflection of the influence of internal waves in the case of Leichter et al. (1998) and absence of internal wave activity during the study by Lesser (2006). Given that most of the 'deep reef' surveys reported in Pawlik et al. (2015, their Table 2) are between 15 and 20 m, their analysis is actually restricted to shallow water sponges. Moreover, even if one were to accept 15 m as a relevant break, many of the differences in mean values reported in Pawlik et al.'s Table 2 are so minimal that they are likely to be statistically insignificant. Thus, the rejection of their first 3 hypotheses, for which they rely on percent cover to explain distribution patterns, significantly undermines their conclusions. Pawlik et al. (2015) also reject their hypothesis that sponge morphology should reflect food limitation below the shallow depths of high water flow, since the morphotypes that are predicted to enhance POC capture are largely absent on shallow reefs, where particulate food concentrations are lower compared to deeper depths. Nonetheless, it is equally likely that the increase in POC with increasing depth acted as a selective factor for the sponge morphotypes that dominate the deep reef communities.

The authors then provide an example (Villamizar et al. 2014) of shallow versus deep sponge populations in Belize (to depths of 30 m) to support their argument that there are no differences in diversity and abundance. However, the data in Lesser & Slattery (2013), from the same site, showed a significant break between shallow and deep reefs at 30 m, with respect to sponge diversity and abundance. Here we show, using the same data from Lesser & Slattery (2013), that sponge diversity and abundance increase significantly with depth in a linear fashion (Fig. 1A). This highlights the potential problem of setting any 'universal' depth breaks, since changes in sponge diversity and biomass reflect changes in food supply, irradiance, and/or predation pressure, and these factors will clearly vary over multiple temporal and spatial scales (Leichter et al. 1998, Lesser 2006, Slattery & Lesser 2012). Finally, Pawlik et al. (2015) suggest that their review of the literature shows no relationship between sponge abundance and food supply as it relates to depth, although 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).

Correlation of depth with size and growth

The correlational studies reported in Pawlik et al. (2015) relate to sponge growth data collected at sites with known concentrations of POC (e.g. Lesser 2006, Lesser & Slattery 2013). To illustrate their point, the authors provide data on *Callyspongia vaginalis* tube length as a function of site and depth. Pawlik et al. (2015) note that there is a positive relationship between tube length and increasing depth, but their statistical values suggest that depth explains very little of the variability. The results of their regression analysis are significantly constrained by the depth range of the samples targeted, as opposed to the factors (turbulence and predation) that they attribute to the patterns reported. Specifically, the Panama data all appear to be based on samples from a depth of about 2 to 5 m, and the Florida Keys data appear to represent samples from approximately 15 to 22 m. Thus, it is not particularly surprising to see a poor correlation between tube size and depth, since most of the samples come from a very narrow, and unrepresentative, depth gradient. In contrast, the data from Lesser & Slattery (2013), across a depth gradient from shallow to mesophotic (7.5 to 46 m) reefs, indicate a highly significant functional relationship between tube length and growth with depth in *C. vaginalis* (Fig. 1B) and 2 other tubular species (Fig. 1C,D; see also Lesser 2006).

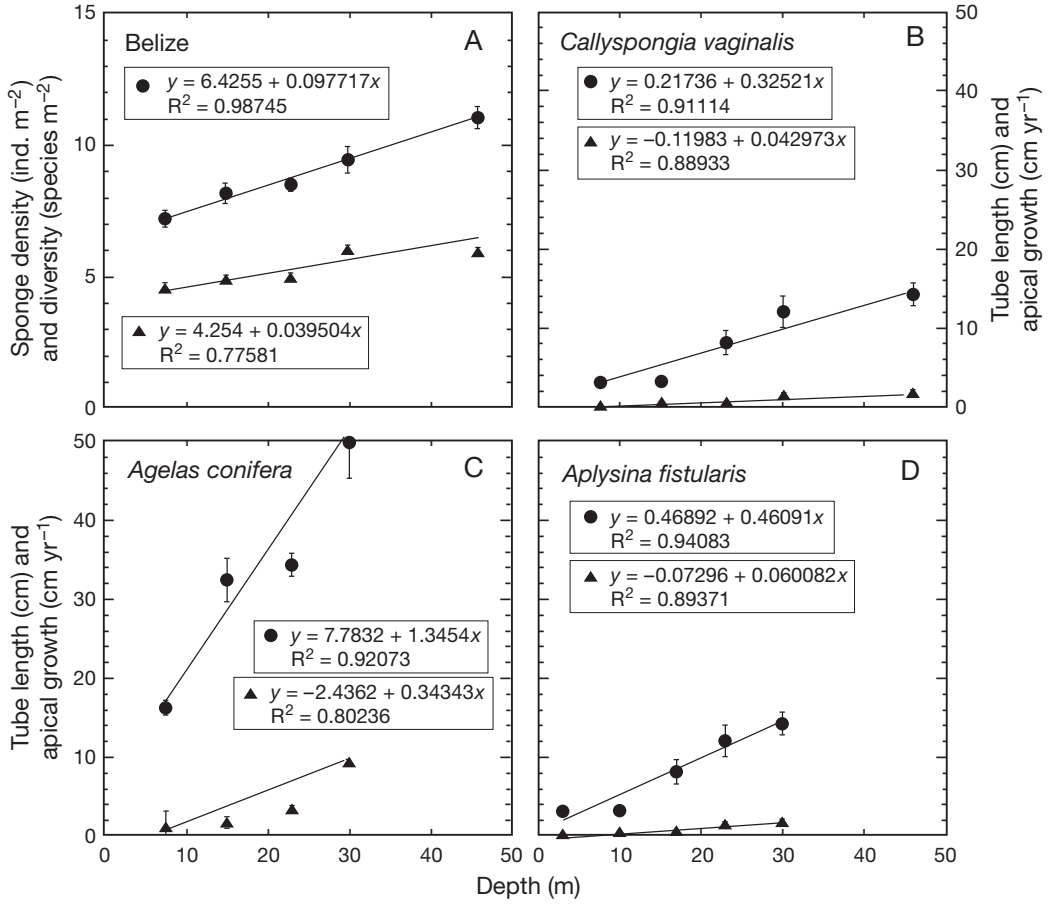

Fig. 1. (A) Sponge density (circles) and diversity (triangles) as a function of depth in Belize (N = 5 transects at each depth, n = 10 quadrats of 1 m^2 per transect). (B–D) Tube length (circles) and growth (triangles) as a function of depth in (B) *Callyspongia vaginalis* (N = 10 per depth) and (C) *Agelas conifera* from Belize (N = 3 per depth), and (D) *Aplysina fistularis* from the Bahamas (N = 5 per depth). All regressions were significant (ANOVA, $p \leq 0.05$). Data are mean ± SE, and are from Lesser (2006), Lesser & Slattery (2013)

Pawlik et al. (2015, p. 276) discuss a recently reported 'sponge loop' fueled by dissolved organic matter (DOM) uptake (de Goeij et al. 2013), and argue that: 'the absence of substantive consideration of DOC [dissolved organic carbon] in the energetic budgets of Caribbean sponges restricts the interpretation of depth-dependent increases in sponge growth as evidence of food limitation'. There is currently insufficient evidence for generalizing a sponge-loop detrital pathway on open reefs. The only way to balance the loss of carbon as sponge cellular detritus, assuming the intake of both POC and DOC, is to also assume—as do de Goeij et al. (2013)—that sponges exhibit little or no net growth. However, the assumption of no net growth is clearly wrong for many sponges (e.g. Lesser 2006, McMurray et al. 2008, Lesser & Slattery 2013), and sponges on open reefs have been found to depend upon POC for their carbon requirements (e.g. Hadas et al. 2009). We agree that sponges utilize DOC, as do most marine invertebrates, but the suggestion that the carbon budget from DOC exceeds that of POC is based on total POC and a single carbon conversion factor (de Goeij et al. 2013). In fact, the planktonic community is composed of multiple functional groups, each with its own carbon conversion factor (e.g. Lesser 2006). For example, if one converts the POC uptake consumed by the sponge *C. vaginalis* in Lesser & Slattery (2013) to units that are equivalent to those used in de Goeij et al. (2013), over 4 times more carbon in the form of POC is consumed when compared to the sponges studied in de Goeij et al. (2013). Moreover, the assumption that DOC levels are equivalent at all depths on coral reefs (Pawlik et al. 2015, p. 274) may not be correct. Our preliminary data show that DOC declines with depth in the Bahamas but not in St. Thomas, US Virgin Islands (Fig. 2), and we predict that as the benthic cover of DOC producers (corals and macrophytes) continues to decline

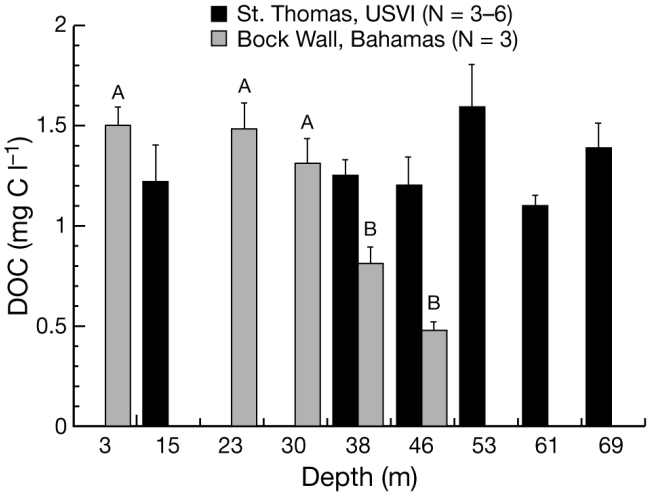

Fig. 2. Water column DOC concentrations (mean ± SE). Missing bars: no data. Significant differences (ANOVA: $F_{4,10}$ = 21.4, p < 0.0001; different uppercase letters above bars indicate significant differences [p < 0.05] among depths based on Tukey's test) with depth in the Bahamas likely due to vertical wall geomorphology, its effects on water flow, and changes in the benthic community, compared to insignificant changes with depth (ANOVA: $F_{5,21}$ = 0.14, p = 0.21) for DOC concentrations across a shallow sloping shelf reef community in St. Thomas, US Virgin Islands (all data from Lesser & Slattery unpubl.)

with depth, so will DOC. Thus, suggestions that DOC availability is responsible for the absence of bottom-up effects in sponges (Pawlik et al. 2015) is largely untested and at odds with both preliminary data of DOC on coral reefs and observations of sponge biomass at depth. Additionally, the percent consumption of DOC versus POC is significantly different for *Agelas conifera* as depth increases (Table 1). This is the result of an increasing reliance on POC with increasing depth, corresponding with declining DOC resources and DOC uptake with depth for this species. These data indicate not just a correlation between sponges and POC with increasing depth, but the selective use of this resource relative to DOC as depth increases.

Finally, Pawlik et al. (2015) discuss data from their laboratory on demographics of *Xestospongia muta* at 3 depths on Conch Reef, Florida (McMurray et al. 2008, 2010). They indicate that there were no significant differences in growth rates across depths and a lower abundance of sponges at 30 m, in contrast to predictions that these metrics should be greater with the increased POC at this depth. Their results may have less to do with an increase in food with increasing depth (Leichter et al. 1998, Lesser 2006), and may instead be due to increased bleaching stress suffered by *X. muta* at depths of 30 m on Conch Reef (McMurray et al. 2011), and reduced growth due to energetic trade-offs between growth and the repair of damage associated with environmental stress.

Table 1. Percent consumption of carbon sources for *Agelas conifera* in the Bahamas (mean ± SE; N = 3). Depth-dependent differences were significant for both DOC and POC (*t*-test, p < 0.001). Data from Lesser & Slattery (unpubl.)

Depth (m)	POC cons. (%)	DOC cons. (%)
23	2.6 ± 0.6	97.4 ± 0.4
46	43.9 ± 8.0	56.1 ± 4.6

Manipulative experiments

Pawlik et al. (2015, p. 276) note that manipulative experiments represent 'the most valid approach to testing food limitation of sponges', and they present an assessment of the only 2 studies to examine this issue to date (Trussell et al. 2006, Pawlik et al. 2013). Both studies occurred at Conch Reef over a shallow (10 to 30 m) gradient of increasing particulate food (Leichter et al. 1998, Lesser 2006), and both studies used a common sponge species, *C. vaginalis* (Pawlik et al. 2013 included 4 additional sponge species). The 2 studies came to vastly different conclusions: Trussell et al. (2006) provide evidence for the role of food in enhanced sponge growth and biomass with increasing depth, whereas Pawlik et al. (2013) reach the conclusion that predation is the only process of consequence. Pawlik et al. (2015, p. 278) note that disparities in experimental design might account for some of the variability in results (the major difference being a caged design by the Pawlik group and an uncaged design by the Trussell group), but they go on to state that: 'no unequivocal evidence for food limitation of sponges from Caribbean reefs has been reported from manipulative experiments'. Instead, they suggest that spongivores had a greater impact on uncaged sponges transplanted to the shallow reef in the experiments of Trussell et al. (2006), despite observations of very little predation (i.e. number of bite scars) on transplanted sponges. However, the data of Pawlik et al. (2013) on undefended sponges (reproduced in Pawlik et al. 2015, their Fig. 3A,B, outside cages) demonstrate that grazing pressure at 30 m is the same as at 15 m. Since all spongivores had equal access to *C. vaginalis* in the experimental design of Trussell et al. (2006), the differences in growth rate are principally due to bottom-up processes. Lesser & Slattery (2013) also point out con-

cerns with experimental design and statistical analysis in recent publications by the Pawlik group that cast doubt on the conclusions in Pawlik et al. (2015, p. 265); specifically, that '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'.

Summary and suggestions for future research

In conclusion, Pawlik et al. (2015, p. 278 & 279) note that 'at some level, it is likely that all organisms are resource-limited' and 'the most successful (i.e. common) sponge species on Caribbean reefs may have adapted individually to their own combinations of resources'. Despite this understanding, Pawlik et al. (2015) favor a hypothesis that is at odds with existing observational, correlational, and manipulative data. The role of bottom-up processes in the ecology of sponges is not universally accepted (Pawlik et al. 2013, 2015), and top-down processes may yet prove to be more important, as they are in herbivore–algae–nutrient dynamics on coral reefs (e.g. Burke pile & Hay 2006), but scientific debate on the importance of top-down and bottom-up processes hardly represents a 'digression' (Pawlik et al. 2015, p. 265). Both top-down and bottom-up processes affect the distribution and abundance of sponges in the Caribbean and elsewhere, and multifactorial experiments to determine the relative importance of each of these processes have yet to be conducted.

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Editorial responsibility: James McClintock, Birmingham, Alabama, USA; Matthias Seaman, Oldendorf/Luhe, Germany

Submitted: March 3, 2015; Accepted: April 14, 2015
Proofs received from author(s): April 24, 2015