# Sponge density increases with depth throughout the Caribbean

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**Abstract.** Mesophotic coral reefs (MCEs) are ecologically unique components of coral reef ecosystems that occur at depths from ~30 to 150 m where they support a high number of depth-endemic species. One ecologically important taxonomic group that can, especially in the Caribbean basin, dominate these habitats are sponges where they occur throughout the shallow (<30 m) to mesophotic depth range. There are an increasing number of studies on MCEs generally, and sponges have become a focal area for many of these studies as they exhibit a number of ecological and functional traits that vary with increasing depth. Here, we use an analysis of both historical and contemporary data to test the recently described "sponges increase with depth" hypothesis. While this hypothesis has recently been rejected without benefit of any quantitative analysis, we show that the density or percent cover of sponges increases over the shallow to mesophotic depth range for multiple reef sites in the Caribbean, and also in the Pacific at selected sites. The proximate cause for this pattern appears to be the increasing availability of trophic resources, and the ability to differentially use those resources, with increasing depth. The increase in sponge density or percent cover with depth is potentially global in nature and results in diverse, and unique, sponge-dominated communities at mesophotic depths.

**Key words:** coral reefs; mesophotic; sponge abundance; sponge diversity; sponge increase hypothesis.

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## INTRODUCTION

Mesophotic coral ecosystems (MCEs) are low-light-adapted deep reef communities that occur from ~30 to 150 m (Lesser et al. 2009); this depth range is based on the capabilities of diving technologies, with additional consideration for community composition (Lesser et al. 2009, 2018, Hinderstein et al. 2010). MCEs are further divided into the upper (30–60 m) and lower (60–150 m) mesophotic zones based on changes in the underwater light field and patterns of community structure (Reed and Pomponi 1997, Slattery et al. 2011, Laverick et al. 2017, Lesser et al. 2018). However, MCE depth definitions have recently been revised, including the establishment of a new faunal zone called the "rariphotic" (130–309 m: Baldwin et al. 2018, Rocha et al.

2018). These new depth definitions are based on the occurrence of different fish assemblages and have no supporting data such as co-occurring habitats composed of specific substrate types or benthic assemblages, or any description of co-occurring changes in abiotic factors such as light, that might provide an explanation for the occurrence of specific fish assemblages at different depths. As a result, they introduce unneeded confusion into the field and these depth definitions will not be considered further.

Changes in community composition of coral reefs from shallow (<30 m) to mesophotic depths have been historically described using both observational (Lang 1974, Reed and Pomponi 1997) and quantitative data (Liddell and Ohlhorst 1987, 1988). These changes in community composition with depth include variation in multiple taxa with

different functional attributes (Lesser et al. 2009, 2018) resulting in MCEs that repeatedly exhibit an apparent break in community composition and function at ~60 m (Lesser et al. 2018). While multiple taxonomic groups contribute to the community changes on MCEs, by either increasing or decreasing their abundance with increasing depth (Lesser et al. 2018), one taxon, sponges, has been reported to increase in diversity and abundance, measured as numerical density or percent cover, within the shallow reef zone (Rützler and Macintyre 1982, Schmahl 1990), from the shallow reef to upper MCE (Lesser and Slattery 2013), as well as from upper to lower mesophotic zones (Liddell and Ohlhorst 1988, Liddell et al. 1997, García-Sais 2010, Lesser and Slattery 2011, Slattery and Lesser 2012). Therefore, it is not surprising that sponges, especially on Caribbean MCEs, have become a focal taxon of ecological studies (Lesser et al. 2018) among the increasing number of studies on MCEs (Loya et al. 2016). Several of these studies on community structure of MCEs have further shown that a number of functional traits of sponges also change with increasing depths on coral reefs including size, growth rates, proximate biochemical composition, stable isotopic signatures, microbiome composition, and chemical deterrence (Lesser 2006, Lesser et al. 2009, 2018, Slattery and Lesser 2012, Lesser and Slattery 2013, Morrow et al. 2016, Slattery et al. 2016).

Sponges also increase their feeding rates from shallow to upper mesophotic reefs, when the effects of body size are considered as a covariate, in proportion to increasing particulate organic matter (POM) resources (Lesser 2006, Trussell et al. 2006, de Goeij et al. 2008, Lesser and Slattery 2013). Specifically, sponges exhibit the highest filtration efficiency in the picoplankton size range for both autotrophs and heterotrophs due to the architecture of the aquiferous system (Weisz et al. 2008, Maldonado et al. 2012). Because of these results, it has been argued, using correlative and experimental data, that bottom-up effects (i.e., resource limitation) play an important role in the population ecology of sponges (Lesser and Slattery 2013) despite claims to the contrary (Pawlik et al. 2013). However, the abundance of these resources changes with depth such that POM increases (Lesser 2006) and dissolved organic matter (DOM) decreases (Slattery and Lesser 2015, Lesser and Slattery,

*unpublished data*) with increasing depth, and sponges appear to be able to utilize different proportions of these trophic resources with increasing depth (Slattery and Lesser 2015). Thus, data on changes in POM and DOM abundance with increasing depth and the utilization patterns of these resources along a shallow to mesophotic depth gradient by different sponges are important in order to assess the role of bottom-up effects on sponge ecology for both shallow and mesophotic sponge communities.

In a recent review, Scott and Pawlik (2018) present a new hypothesis called the "sponge increase hypothesis" and conclude, in the absence of any quantitative analysis, that sponges do not increase in abundance with increasing depth over the shallow to mesophotic depth range. Here, we present a quantitative analysis of both historical data from studies that occurred before the current increase in MCE research (Loya et al. 2016) and more contemporary data from the last fifteen years on the abundance of sponges over the shallow to mesophotic depth range for multiple reef sites in the Caribbean and elsewhere. We show that with remarkable consistency, and rare exceptions, (1) the numerical abundance or percent cover of sponges increases significantly from shallow to mesophotic depths in the Caribbean, (2) these patterns are potentially global in nature, and (3) this results in unique, sponge-dominated, communities at mesophotic depths that are the result of the depth-dependent availability and utilization of trophic resources (sensu Lesser and Slattery 2013) as the proximate cause for the observed patterns.

## MATERIALS AND METHODS

### Sponge abundance and percent cover data

The historical data for this analysis include the work of Liddell and Ohlhorst (1988: Table 1) from the W-Z line and M line transects at Discovery Bay, Jamaica (18°30′ N, 77°20′ W), and Liddell et al. (1997: Table 2) from the BA line transect in the Bahamas (23°46′ N, 76°06′ W). These studies used a combination of line transects, line point intercept techniques, as well as photo transects, using SCUBA and submersibles, to determine percent cover of sponges on hard substrate suitable for the settlement, recruitment, and growth of sponge communities. Mean values of percent cover ($m^2$) and 95% confidence intervals from

shallow to mesophotic depths in these studies are plotted as mean ± SE before regression analysis.

Data collected from the Bahamas in 2003 (Lee Stocking Island, Bock Wall: 23°46.5′ N, 76°05.5′ W) and Little Cayman Island in 2008 (Rock Bottom Wall: 19°42.03′ N, 80°03.25′ W) from Slattery and Lesser (2019), and Palau in 2011 (Turtle Cove: 7°05.06′ N, 134°15.32′ W) as described in Slattery and Lesser (2012), are re-analyzed here. Additionally, abundance data from Belize in 2000 (Carrie Bow Cay: 16°48.0′ N, 88°04.67′ W); Curacao in 2017 (Buoy 1: 12°7.33′ N, 69°03.8′ W); Honduras in 2012 (Bay Islands, Utila: 16°4.59′ N, 86°55.1′ W); and Grand Cayman in 2016 (Sand Chute: 19°21.43′ N, 81°24.44′ W) are included in the global analysis and presented here for the first time, while data from Palau in 2011 (Siaes Wall: 7°18.5′ N, 134°13.2′ W) and Chuuk in 2008 (Anaw Pass: 151°41.27′ N, 7°12.49′ W; South Pass: 151°47.83′ N, 7°34.55′ W), from Slattery and Lesser (2012), are re-analyzed for the global analysis. Data is available at https://www.bco-dmo.org/dataset/749941.

### Analyses

All data from Slattery and Lesser (2012), and the new data, were analyzed as follows. Benthic surveys at each depth consisted of random, replicate ($n$ = 3–9), 25-m transects with 10–20 one m$^2$ quadrats positioned at random points along each transect. Each quadrat was subdivided into 16 grids, and point intercepts (N = 100 per quadrat) were used to estimate the percent cover of macroalgae (upright foliose species), sponges, coral, and bare substrate. Additionally, in some locations (e.g., Bahamas and Little Cayman) 20 × 2 m band transects were conducted, and the total number of sponges was counted and divided by 40 to obtain the number of individual sponges m$^2$. The data for each site were graphed as scatter plots, and a Model I regression was performed with the $R^2$, the amount of variation explained by the regression, reported. In addition, an $F$ test statistic provided a metric of the overall significance of the relationship between abundance and percent cover of sponges with depth. A dataset of sponge abundance with depth was compiled from all sites described above, and regressed against depth, to examine the global question regarding the generality of sponge population increases with increasing depth. All

analyses were conducted using JMP Pro 13.0.0 (SAS Institute, Cary, North Carolina, USA).

## Results

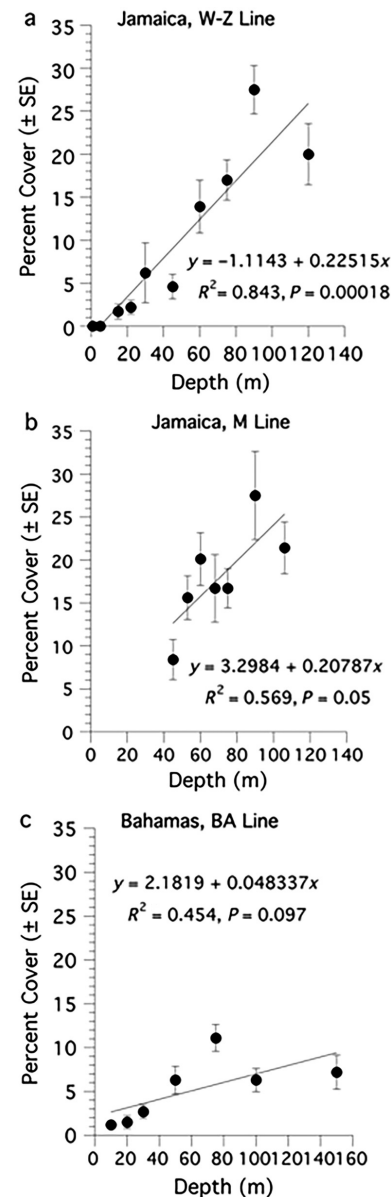For the historical data, depths ranged from 10 to 150 m and showed that the percent cover of



Fig. 1. Linear Regression of percent sponge cover versus depth. Points are means (±SE) with regression equation, overall model fit $R$-squared value and $P$-value. Historical datasets from: (a) Jamaica W-Z line, (b) Jamaica M-line, (c) Bahamas BA line.
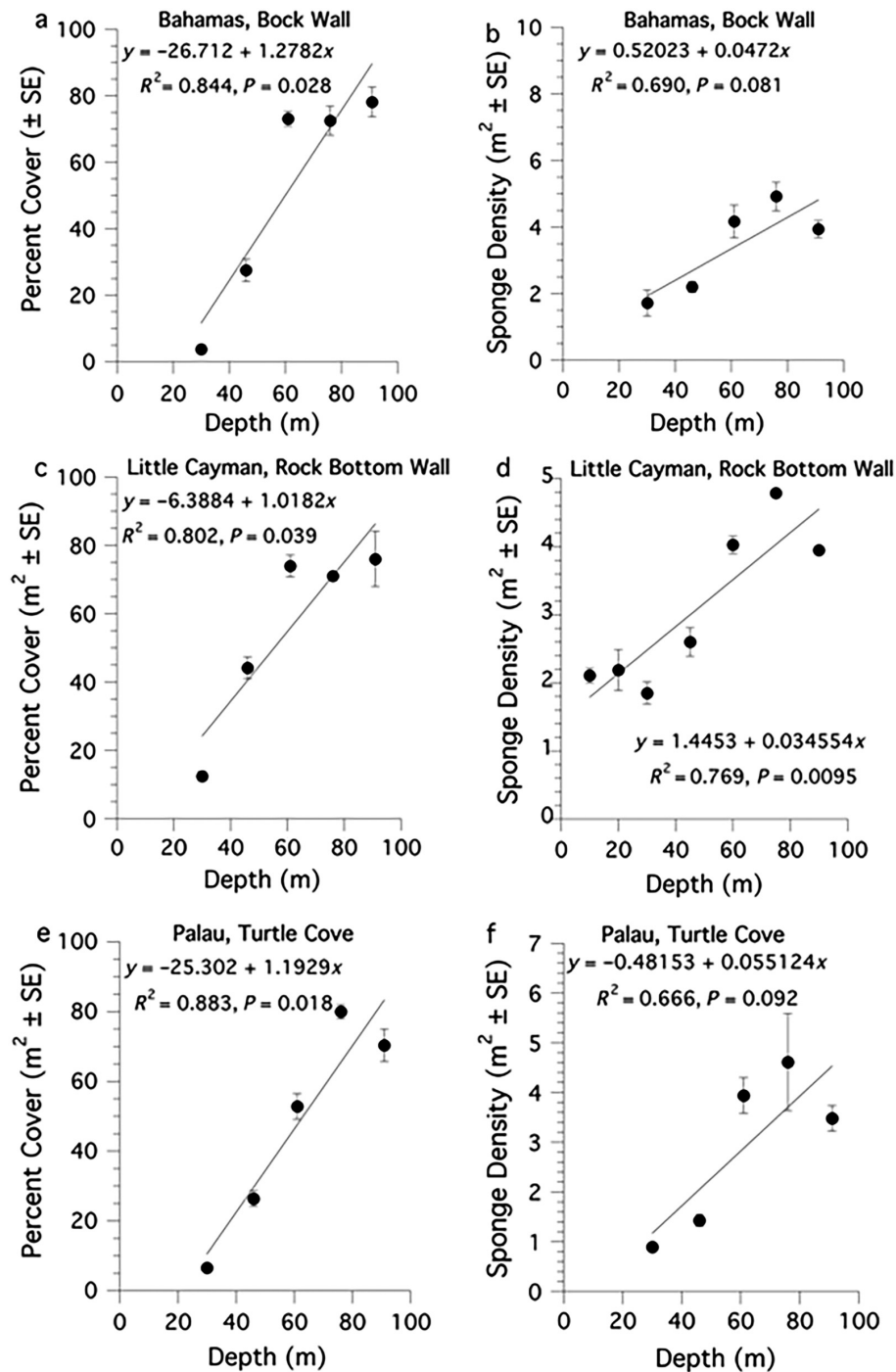
Fig. 2. Linear Regression of percent sponge cover or density versus depth. Points are means (±SE) with regression equation, overall model fit $R$-squared value and $P$-value. Contemporary datasets from: (a) Bahamas, Bock Wall percent cover, (b) Bahamas, Bock Wall density, (c) Little Cayman, Rock Bottom Wall percent cover, (d) Little Cayman, Rock Bottom Wall density, (e) Palau, Turtle Cove percent cover, (f) Palau, Turtle Cove density.

sponges increased significantly with increasing depth at both locations in Jamaica (i.e., W-Z line: $t(8) = 6.55$, $P = 0.00018$, and M line: $t(5) = 2.57$, $P = 0.05$; Fig. 1a, b), but not in the Bahamas where the data still trend positive with depth (i.e., BA line: $t(5) = 2.04$, $P = 0.097$; Fig. 1c). For the contemporary data, depths ranged from 30 to 91 m and showed that the percent cover of sponges increased significantly with increasing depth at Bock Wall, Bahamas (BA line: $t(3) = 4.03$, $P = 0.028$; Fig. 2a), but sponge density, although trending positive with increasing depth, was not significant ($t(3) = 2.59$, $P = 0.081$; Fig. 2b). On Little Cayman, the percent cover of sponges increased significantly with depth ($t(3) = 3.49$, $P = 0.039$; Fig. 2c), as did sponge density ($t(5) = 4.08$, $P = 0.0095$; Fig. 2d). In the Pacific basin, the percent cover of sponges also increased significantly with increasing depth in Palau (Turtle Cove; $t(3) = 4.76$, $P = 0.018$; Fig. 2e), while sponge density, although trending positive with increasing depth, was not significant ($t(3) = 2.45$, $P = 0.092$; Fig. 2f). A global analysis of sponge density demonstrates an increasing, and highly significant ($t(58) = 6.76$, $P \lll 0.001$), relationship with increasing depth (Fig. 3).
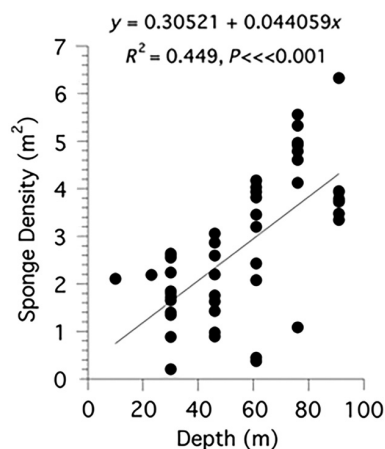


Fig. 3. Global analysis of sponge density versus depth. Linear Regression points are means with regression equation, overall model fit $R$-squared value and $P$-value. Datasets included in analysis: Bahamas (BA line and Bock Wall), Belize (Carrie Bow Cay), Cayman Islands (Rock Bottom Wall and Sandchute), Chuuk (Anaw Pass and South Pass), Curacao (Buoy 1), Honduras (Utila), Jamaica (W-Z line and M line) and Palau (Siaes Wall and Turtle Cove).

## DISCUSSION

Ecological patterns on MCEs, such as community breaks at ~60 m (Lesser et al. 2018), and taxon-specific depth-related patterns on MCEs, such as increases in sponge abundance and diversity with increasing depth (Lesser and Slattery 2011, 2013), have recently been dismissed without the support of a quantitative analysis of the available, or new, data (Pyle et al. 2016, Scott and Pawlik 2018). Here, we have demonstrated that sponges from shallow to mesophotic depths on coral reefs exhibit a significant pattern of increasing percent cover and numerical abundance that occurs throughout the Caribbean basin, as well as at selected locations in the Pacific, representing a global pattern (i.e., the sponge increase hypothesis is supported).

We agree with Scott and Pawlik (2018) that multiple factors, both bottom-up and top-down, will contribute to ecological patterns on coral reefs from shallow to mesophotic depths (Lesser and Slattery 2011, 2013, Lesser et al. 2018), and recent studies on MCEs have shown that geological history and geomorphology will influence the population ecology of sponges (Lesser et al. 2018). However, while light is arguably the most important abiotic forcing factor on mesophotic populations of coral and algae, sponges are more influenced by the availability of trophic resources. Nonetheless, the important role of trophic resource availability, both POM and DOM, for sponges from shallow to mesophotic depths as a primary factor controlling the patterns of sponge abundance and distribution, is still contested (Pawlik et al. 2013, 2015a, b). This despite evidence supporting a strong role for bottom-up control of sponge populations through food limitation (Lesser 2006, Trussell et al. 2006, Lesser and Slattery 2013), lack of support for a strong role of top-down control on sponge populations (Wulff 2017, Lorders et al. 2018), and the use of poor experimental design and analysis (Pawlik et al. 2013) to support top-down processes as the primary control on sponge abundance and distribution (Slattery and Lesser 2015).

In addition to POM resources, the trophic biology of sponges includes the consumption of DOM, specifically DOC (de Goeij et al. 2008, 2013, 2017), and recent observations have suggested that

different species and/or communities of sponges consume different proportions of POM and DOM (Maldonado et al. 2012, Hoer et al. 2018, McMurray et al. 2018) depending on whether they are high microbial abundance sponges (HMA) or low microbial abundance sponges (LMA; sensu Weisz et al. 2008). Slattery and Lesser (2015) also showed that for *Agelas tubulata* the percentage contribution of POC to the sponge diet was significantly higher at 46 m versus 23 m, with a corresponding change in DOC consumption. In an environment where carbon does not appear to ever be limiting for sponges, it is nitrogen that may be a limiting resource and the reason why consuming increasing amounts of picoplankton with low C:N ratios is essential to support and maintain the large sponge biomass observed at mesophotic depths (Lesser et al. 2018).

That mixotrophy occurs in varying degrees in sponges is now well established (Yahel et al. 2003, de Goeij et al. 2008, Slattery and Lesser 2015, McMurray et al. 2018), as is the transition to increased dependency on heterotrophy with increasing depth (Lesser and Slattery 2013, Morrow et al. 2016). As a trophic strategy mixotrophy will also effect the relative roles of top-down and bottom-up control of sponge populations (Lesser and Slattery 2013, Wulff 2017), where the relative contributions of different carbon and nitrogen sources contributing to the growth and maintenance of sponge biomass, and the uptake of those resources by either sponge tissues or the sponge microbiome, vary spatially and temporally. Taken together, the sponge increase hypothesis is supported based on the analysis of the data presented here, and the most parsimonious explanation for that pattern is the increased availability, and differential utilization, of trophic resources such as POM and DOM over the shallow to mesophotic depth range.

## Acknowledgments

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