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REPLY

Sponge density increases with depth throughout the Caribbean: Reply

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Our recent paper in Ecosphere (Lesser and Slattery 2018) addressed an important question in coral reef ecology: Does sponge biomass and/or abundance increase with depth over the shallow (<30 m)-to-mesophotic (~30–150 m) gradient? Scott and Pawlik (2018), based on a review of 17 studies, concluded that the "sponge increase hypothesis" is not supported. It is important to note that any hypothesis is a "strawman" that may ultimately fall under additional scientific scrutiny, and that a more complete understanding of mesophotic coral ecosystems (MCEs) is currently hindered by the limited number of studies at these depths (Loya et al. 2016). Nonetheless, using both historical and contemporary data, we demonstrated a global phenomenon of increasing sponge density with depth on tropical shallow and mesophotic reefs (Lesser and Slattery 2018: Fig. 3; $R^2 = 0.449$, $P <<< 0.001$) that supports the sponge increase hypothesis.

In their response to our contribution, Pawlik and Scott (2019) take issue with our statement about their lack of any quantitative analysis. Scott and Pawlik (2018) did report many of the descriptive statistics, as well as quantitative statistics where available, by the authors of the studies they reviewed. Our comment reflected the lack of any new analysis, or re-analysis, by the authors, and thus, the lack of any new or novel findings. In contrast, our contribution was, in fact, a test of the sponge increase hypothesis as discussed in Scott and Pawlik (2018). Scott and Pawlik (2018) and Pawlik and Scott (2019) have also criticized our analyses because of the lack of a consistent standardized metric(s) to quantify sponge biomass, cover, and density, although many studies on shallow coral reefs, including studies on corals and sponges, have long suffered from this same problem (e.g., Wulff 2001, Edmunds et al. 2014). We have followed standard protocols in using, evaluating, and analyzing all of these metrics, including an understanding of the meaning and shortcomings of each. In addition, Scott and Pawlik (2018), and indirectly in Pawlik and Scott (2019), have misinterpreted the meaning of the text quoted in Lesser (2006)—"... sponges throughout the Caribbean show a pattern of increasing biomass and diversity with depth down to 150 m..."—as a stated hypothesis. This was not stated as a hypothesis but as a fully referenced statement of fact in the introduction of Lesser (2006). The original hypothesis was actually formulated by Scott and Pawlik (2018), which we sought to test in Lesser and Slattery (2018). And just as we did not formulate the original hypothesis, we never asserted that any metric of sponge cover, biomass, abundance, or diversity must span the entire mesophotic zone, as currently defined (i.e., 30–150 m), or a geographic area as large as the Caribbean basin, in order to be used in hypothesis testing for examining sponge distributions on MCEs as suggested in Pawlik and Scott (2019).

Pawlik and Scott (2019) note that many of the sponge studies they reviewed (Scott and Pawlik 2018) were limited in depth range, replication, and/or metric used to assess an increase in sponge cover or abundance, but they argue that while the trends are still important, they should not have been selectively discounted by Lesser and Slattery (2018). While we are in total agreement that many of the studies in Scott and Pawlik (2018) have flaws, we also feel it is important

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to test scientific hypotheses, including the sponge increase hypothesis, using the best data available for the question being asked. The data we used in Lesser and Slattery (2018) were not "selected" from those used by Scott and Pawlik (2018). Our approach was to analyze historical and contemporary data, including metrics of sponge percent cover and/or sponge abundance, that were available and covered multiple sites throughout the Caribbean Basin, as well as sites in the Pacific Basin, to assess how widespread this phenomenon is. As a result, we analyzed a broad range of published and unpublished datasets inclusive of shallow (<30 m) as well as upper (~30–60 m) and lower (>60 m) mesophotic coral reefs (Lesser et al. 2018), with broad geographic coverage and where we could be reasonably assured of the methods of data collection. This was how we chose the datasets analyzed for our test of the sponge increase hypothesis (Lesser and Slattery 2018), and not by selecting or eliminating a priori any of the data used in Scott and Pawlik (2018). With our dataset, we unequivocally demonstrated that the percent cover and abundance of sponges increases with depth, and significantly so in 7 out of 10 analyses, including our global analysis (Lesser and Slattery 2018). In fact, many of the studies reviewed by Scott and Pawlik (2018) found the same pattern, but they included additional qualitative categories such as "dip, peak, or plateau within the reported range" without any valid ecological reason, explanation, or analysis. The heterogenous features that exist on any coral reef, including MCEs, such as substrate angle, incident irradiance, sedimentation, nutrients, and even temperature (reviewed in Lesser et al. 2009, 2018), would, not surprisingly, result in variable patterns of sponge percent cover, biomass, abundance, and diversity at different depths. However, if the absolute change in sponge cover or abundance from the shallowest to the deepest depths of each study is considered, the sponge increase hypothesis is supported in most of the cases originally reviewed by Scott and Pawlik (2018).

Finally, Pawlik and Scott (2019) point out that one of the studies (Rivero Calle 2010) they felt was discounted in our contribution offered reasonable replication, a similar depth range, and metrics (i.e., percent cover), yet those results indicated a decrease in sponge cover with increasing depth. Unfortunately, that study contains a flaw that severely limits its value for any credible re-analysis. Briefly, Rivero Calle (2010) utilized AUV photo-transects at four sites on the insular shelf MCEs of the south and west coasts of Puerto Rico. While Rivero Calle (2010) cites Singh et al. (2004) as the authority relative to data collection and analysis, in neither paper is there any description of corrections for parallax error when using AUV video transect imagery collected with a vertically oriented camera, and substrates of varying distance and angle relative to the camera. This would create varying degrees of parallax error and would either under- or over-estimate percent cover of the benthic fauna. Despite these well-known concerns regarding AUV-assisted video transects, they calculated percent cover without any image correction for parallax (Singh et al. 2004, Rivero Calle 2010). In fact, Parry et al. (2002) state that ROV observations are typically qualitative due to parallax issues, and they further note that groundtruthing of the ROV/AUV data is required even with advanced laser diode projection technologies designed to maintain fixed areal perspective and remove parallax-related issues during analysis. Given the uncorrected parallax, the data from Rivero Calle (2010) should not have been used in the quantitative analyses performed by Pawlik and Scott (2019). To put a finer point on this, García-Sais (2010) quantified sponges across a shallow-to-upper mesophotic gradient (i.e., 15–50 m) at one of the same locations (i.e., Isla Desecheo) where the data used by Rivero Calle (2010) were collected. Those diver-acquired data, using continuous intercept chain-link transects and diver-conducted digital videos of permanent monitoring sites, revealed a significant increase in sponge percent cover from <10% cover in shallow depths to >30% cover in the upper mesophotic zone where Rivero Calle (2010) reported ~13.5% sponge cover from the AUV photo-transects.

It is worth reiterating that not all MCEs are created equal. We would not be surprised to learn of specific sites where sponge cover, abundance, or biomass does indeed decline with depth while other taxa increase (e.g., soft corals in Pohnpei: Rowley et al. 2019), but based on currently available, quality-controlled data, it appears that sponges increase with depth in many, if not most, MCEs. Finally, we thank Pawlik and Scott (2019) for addressing this important issue. MCE research advances, while increasing, are often overlooked by the broader coral reef community, and we need to ensure that those individuals, who do not conduct MCE research, thoroughly understand the difficulty of obtaining ecological data for MCEs, and the unique and critical role MCEs play in coral reef ecology. We agree that more data and further study on shallow and mesophotic reefs of different geomorphologies, oceanography, and community composition are needed to understand and conserve these critical ecosystems, as well as develop, test, and validate hypotheses regarding MCEs.

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