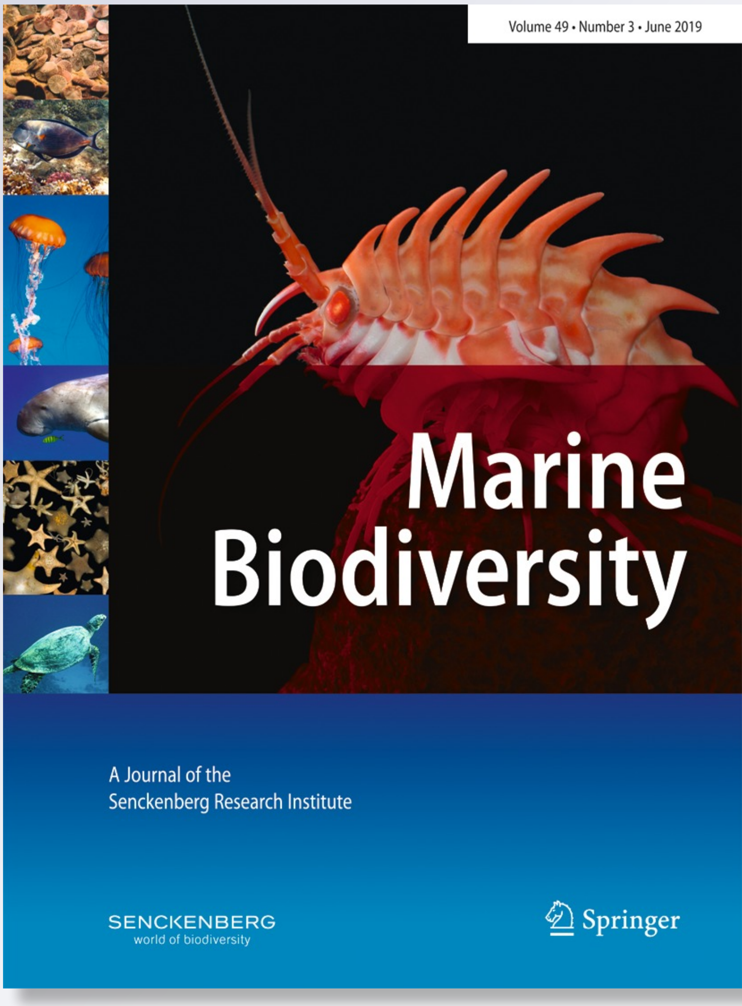
A review of the sponge increase hypothesis for Caribbean mesophotic reefs

Alexander R. Scott & Joseph R. Pawlik

Marine Biodiversity

ISSN 1867-1616
Volume 49
Number 3

Mar Biodiv (2019) 49:1073-1083
DOI 10.1007/s12526-018-0904-7



Marine Biodiversity (2019) 49:1073–1083
https://doi.org/10.1007/s12526-018-0904-7

SENCKENBERG

REVIEW

A review of the sponge increase hypothesis for Caribbean mesophotic reefs

Alexander R. Scott[1] · Joseph R. Pawlik[1]

Received: 21 February 2018 / Revised: 10 May 2018 / Accepted: 13 May 2018 / Published online: 30 May 2018

Abstract
Sponges are major components of benthic ecosystems, particularly on Caribbean reefs, where their importance in carbon cycling and ecosystem function is only beginning to be understood. There is a recurring statement in the literature, herein called the "sponge increase hypothesis," asserting that the biomass and diversity of sponges increase with depth on Caribbean reefs through the mesophotic zone (to 150 m). We reviewed evidence for the sponge increase hypothesis, beginning with electronically searchable contributions to the literature, then working backward in time through the bibliographies of more recent citations. We found 17 studies that report one or more metrics associated with sponge abundance or diversity as a function of depth through all or part of the mesophotic zone. None of these studies reported data on either overall sponge biomass or diversity as a function of reef surface area. Among abundance metrics, including cover and density, patterns as a function of depth were disparate across sites and locations. We conclude that there is no evidence to support the sponge increase hypothesis for Caribbean mesophotic reefs and suggest that patterns of sponge abundance as a function of depth are likely to vary for a number of reasons, including substratum type, slope, and orientation. General theories of sponge abundance and diversity as a function of depth await more sophisticated survey studies that employ standardized methods for relating sponge biomass and diversity to reef surface area.

Keywords Coral reefs · Deep sea · ROV · Sponge abundance · Sponge diversity · Porifera · Sponge ecology

Introduction

Mesophotic coral ecosystems (MCEs) are tropical benthic ecosystems that span the depth range between shallow coral reefs (< 30 m) and the bottom of the photic zone (~ 150 m) (Kahng et al. 2010). Ecological conditions change considerably with depth through the transition from shallow to deep benthic habitats; light attenuates almost completely, temperature decreases moderately, nutrients and particulate organic matter increase, and turbulent flow decreases, as well as a variety of other abiotic and biotic changes (Lesser et al. 2009). As zones of transition from shallow to deep, MCEs support a combination of shallow- and deep-water benthic species, as well as some unique taxa (Reed and Pomponi 1997; Bongaerts et al. 2013; Semmler et al. 2017). Although the name implies high coral cover, or that coral-derived limestone is the foundational substratum, other benthic organisms, such as algae and sponges, are usually dominant. MCEs are less subject to some of the stressors that have caused widespread degradation on shallow reefs, such as ocean warming and storm damage (Bak et al. 2005), hence MCEs may provide an important refuge habitat for threatened shallow-water species (Bongaerts et al. 2010; Semmler et al. 2017; but see Shlesinger et al. 2018).

Despite their potential importance to conservation and inherent importance as unique ecosystems, MCEs are much less studied than shallow coral reefs, primarily because of the technological limitations related to studying them (Menza et al. 2008; Lesser et al. 2009). Most of the depth range spanned by MCEs is beyond the depth limit of conventional SCUBA; therefore, MCEs must be explored by remote or automated underwater vehicles, submersibles, or by technical diving. These options are much more expensive and logistically complicated and are not well suited to sample collecting or conducting manipulative experiments. Because of these restrictions, much of the research conducted in MCEs to-date has

Communicated by B. W. Hoeksema

✉ Joseph R. Pawlik
pawlikj@uncw.edu

[1] Department of Biology and Marine Biology, Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC 28409, USA

focused on simply documenting the patterns of change in benthic assemblages with depth. The first studies to do this were primarily qualitative (e.g., Lewis 1965; Lang 1974) and established that hard corals, octocorals, macroalgae, and sponges were the dominant benthic organisms. Subsequent studies (e.g., Liddell and Ohlhorst 1988; Maldonado and Young 1996; Slattery and Lesser 2012) have used more quantitative approaches to analyze changes in community composition with depth, using a variety of survey methods and metrics.

As more data from a variety of locations were published, some researchers proposed hypotheses about general patterns in benthic community composition with depth. One of the more specific hypotheses was articulated in Lesser (2006, p. 278), who proposed that "… sponges throughout the Caribbean show a pattern of increasing biomass and diversity with depth down to 150 m," hereafter referred to as the "sponge increase hypothesis." This hypothesis has been reiterated in subsequent publications (e.g., Lesser and Slattery 2013) and used in conjunction with an observed increase in picoplankton food resources with depth to support the proposition that sponges in the Caribbean are food limited. The sponge increase hypothesis has also been cited by several other studies (e.g., Bell 2008; Olson and Kellogg 2010), including a widely cited literature review on the community ecology of the mesophotic zone (Kahng et al. 2010).

The validity of the sponge increase hypothesis has not gone unchallenged, however. In a review of evidence for food limitation of sponges on Caribbean reefs, Pawlik et al. (2015) reviewed the literature for papers that reported sponge abundance values above and below 15 m in the Caribbean and found that values decreased with greater depth across this threshold in the majority of cases. Further, the point was made that low sponge abundance at depths < 10 m was generally due to turbulent flow in shallow water, an abiotic factor limiting sponge survival unrelated to food availability or other biotic effects. In a rebuttal, Slattery and Lesser (2015) argued that the points raised by Pawlik et al. (2015) against the sponge increase hypothesis were inadequate for three reasons. First, the analysis in Pawlik et al. (2015) was limited to relatively shallow reefs and only examined studies that reported sponge abundance above and below 15 m, whereas Lesser (2006) claimed that sponge biomass increased through a much greater depth of 150 m. Second, many of the studies included in Pawlik et al. (2015) surveyed a relatively small depth gradient above and below 15 m, which may not have been large enough to observe changes in sponge biomass against the backdrop of other ecological variation. Third, and most important, it was argued that Pawlik et al. (2015) were constrained in their analysis of sponge abundance as percentage cover of the benthos. Percentage cover is the most commonly reported metric of sponge abundance, but it is an inadequate proxy for biomass because sponge morphology is highly variable. Therefore, while Pawlik et al. (2015) cast doubt on the sponge increase hypothesis for shallow reefs and using percentage cover data, the hypothesis might be supported if deeper depths and estimates of sponge biomass were considered. Clearly, further critical evaluation of this often-cited hypothesis is necessary.

Before evaluating the evidence for the sponge increase hypothesis, it is important to parse its components. The hypothesis states that "…sponges throughout the Caribbean show a pattern of increasing biomass and diversity with depth down to 150 m" (Lesser 2006, p. 278). To support this claim, survey data would be required that: (a) provide estimates of biomass or diversity as a function of substratum area, (b) provide a representative sample of locations across the Caribbean, and (c) provide a representative sample of depths from 0 to 150 m, all of which demonstrate an increase in sponge biomass and diversity from shallow depths to 150 m.

Below, we review the scientific literature in order to examine the evidence for the sponge increase hypothesis. Because Pawlik et al. (2015) previously reviewed much of the relevant literature for shallow Caribbean reefs (< 30 m), this review will focus on the mesophotic zone, including only studies that provide data on sponge abundance at multiple depths between 30 and 150 m on reefs in the Caribbean. Because sponges are highly variable in morphology and size, even within species, the term "abundance" will be used for any metric related to the amount of sponge tissue present on a reef, including the more specific measurements of numerical density (number of individuals per unit area), percentage cover (percentage of the substratum covered), and biomass (sponge mass or volume).

Support for the sponge increase hypothesis

Lesser (2006), Lesser and Slattery (2013), and Slattery and Lesser (2015) cite several publications as evidence to support the sponge increase hypothesis. Lesser (2006) cites three publications: Rützler and Macintyre (1982), Schmahl (1990), and Reed and Pomponi (1997). Rützler and Macintyre (1982) found an increase in percentage cover of sponges with depth, and Schmahl (1990) found an increase in numerical density of sponges with depth, but neither surveyed deeper than 30 m, and neither study reported biomass. The third publication, Reed and Pomponi (1997), provided sponge collection data from 147 sites in the Bahamas from 30 to 922 m depth but only reported on sponge diversity as a general function of depth zone (not as a function of reef area) and included no data on sponge abundance.

Lesser and Slattery (2013, p. 1) reiterated the sponge increase hypothesis: "… sponges throughout the Caribbean show a repeatable pattern of increasing biomass and diversity with depth to 150 m," with the addition of the word "repeatable" in the statement. In addition to the publications cited in Lesser (2006) to support the claim, the authors add five others:

Suchanek et al. (1983), Liddell et al. (1997), Lehnert and Fischer (1999), Lesser and Slattery (2011), and Slattery and Lesser (2012). Suchanek et al. (1983) reported sponge cover from ~ 18 to ~ 37 m and found that the value for sponge cover was highest at intermediate depths, but that there were no statistically significant differences between any depths. Liddell et al. (1997) estimated percentage cover from 10 to 250 m but again found that the highest value for sponge cover was at an intermediate depth, in this case, 75 m, and that there were no statistical differences in cover between any mesophotic depths (30–150 m). Liddell et al. (1997) also reported changes in total benthic diversity with depth and found that both the Shannon index of diversity and number of species of all benthic organisms decreased with depth from 10 to 200 m. Lehnert and Fischer (1999) surveyed from 60 to 107 m and found that depth was an important determinant in community composition using a multivariate analysis, but did not report any values for sponge abundance. Lesser and Slattery (2011) surveyed from 30 to 91 m in the Bahamas and found that percentage cover of sponges increased from < 5% at 30 m to ~ 75% at 61 m, and plateaued at this level at 76 and 91 m. This pattern was repeated in surveys done in 2003 and 2005, but the sharp rise in abundance shifted to 76 m in surveys performed in 2009 after substantial losses in sponge abundance at 46 and 61 m, a change that was linked to dramatic increases in macroalgal cover following the loss of herbivorous fishes due to the invasion of lionfish at this site. Slattery and Lesser (2012) observed very similar trends in sponge cover for preinvasion reefs in the Bahamas and for those off Little Cayman Island. Slattery and Lesser (2012) also reported sponge biomass from the Bahamas, which was similar from 30 to 61 m, increased sharply to 76 m, and remained constant to 91 m, the deepest depth they surveyed. It is important to note, however, that these estimates of sponge biomass were not standardized to reef area.

Slattery and Lesser (2015, p. 276), in a rebuttal to Pawlik et al. (2015), rephrased the sponge increase hypothesis, writing: "… 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 (particulate organic carbon), throughout the Caribbean and Indo-Pacific (e.g., Slattery and Lesser 2012, and references therein)." Slattery and Lesser (2012), as indicated above, provided evidence of an increase in individual sponge biomass at one site in the Bahamas from 61 to 76 m, but there is only one reference in Slattery and Lesser (2012) that provides any data on sponge abundance in the mesophotic: Sherman et al. (2010) surveyed from 47 to 70 m, and while no statistics concerning sponge cover were reported, cover declined from 47 and 59 to 70 m.

The foundational publications cited by Lesser (2006), Lesser and Slattery (2013), and Slattery and Lesser (2015) to support the sponge increase hypothesis do not provide sufficient evidence to validate it. The only publication cited that reports estimates of sponge biomass (Slattery and Lesser 2012) did not report biomass as a function of reef surface area and surveyed to a maximum depth of 91 m at a single location, which cannot be extrapolated to 150 m or taken as generally representative of the Caribbean. The other publications that are cited only report percentage cover or numerical density, and report either peaks, plateaus or declines in these metrics well above 150 m. These studies are insufficient to support the claim that sponge biomass increases with depth to 150 m throughout the Caribbean. However, it might be argued that insufficient evidence exists to definitively reject the sponge increase hypothesis, because percentage cover and numerical density are poor proxies for biomass, and it is possible that sponge biomass could increase with depth while percentage cover or numerical density peak or plateau. It is also possible that there is sufficient evidence in the literature to support the sponge increase hypothesis, but that it was not included in these foundational citations. In order to assess these alternatives, we conducted an independent two-stage search of the literature: First, a keyword search was conducted, entering the search terms "mesophotic," "sponge," "depth," and "biomass" in all combinations into Google Scholar and compiled all publications that reported any metric of sponge abundance or diversity at multiple mesophotic depths (30–150 m). Second, bibliographies from the publications from the initial search were checked to find any other studies that met the same criteria. Combined with the foundational citations, this literature search resulted in 17 studies from five different locations in the Caribbean (Table 1; Fig. 1). We summarize these studies below. Note that the methods outlined in the some of these studies were very different from one another, and in some cases within a single study, and that important methods information was sometimes missing; nevertheless, we have done our best to interpret them.

Review of the literature

Biomass of sponges with depth

Only two studies could be found that determined sponge biomass (volume) as a function of depth on Caribbean MCEs. Slattery and Lesser (2012) estimated sponge volume at five mesophotic depth levels on Bock Wall, a nearly vertical NE-facing drop-off near Lee Stocking Island, Bahamas. Between 3 and 9 replicate 25 × 1 m^2 band transects were performed at 30, 46, 61, 76, and 91 m. Within each transect, 15 random points were selected, and the volume of the sponge nearest to that point was estimated using linear measurements and an approximation of volume from geometric solids, with the volume of a minimum of 15 sponges recorded. Note that this method did not provide a measure of sponge volume per surface area of substratum, but rather, a measure of the mean

Table 1 Studies that report metrics of sponge abundance or diversity at mesophotic depths (30–150 m) in the Caribbean

Location	Site	Metric	Min depth (m)	Max depth (m)	Survey method	Replication	Comments	Trend with depth	Reference
Jamaica	Discovery Bay	Volume	8	53	50 m wide band transect	1 transect, 98 individuals	Only 2 species	Peak, 40 m	Reiswig (1973)
Jamaica	Discovery Bay	Cover	15	56	10 m line transect, points every 20 cm	38 transects, 1811 points		Increase	Liddell et al. (1984)
Jamaica	Discovery Bay	Cover	15	30	10 m line transect, points every 20 cm	≤ 10 transects, 1303 points		Increase	Liddell and Ohlhorst (1988)
Jamaica	Discovery Bay	Cover	45	120	Photo transect, $0.14 m^2$ quadrats	12 transects, 6328 points		Peak, 90 m	Liddell and Ohlhorst (1988)
Bahamas	Golding Cay	density	91	531	Photo transect, $1225 cm^2$ quadrats every 6 m	12 quadrats, 91–175 m		Decrease	Maldonado and Young (1996)
Bahamas	Golding Cay	Diversity	91	531	Photo transect, $1225 cm^2$ quadrats every 6 m	12 quadrats, 91–175 m	Visual IDs	Decrease	Maldonado and Young (1996)
Bahamas	(147 sites)	Diversity	30	922	Collections across depth zones	3058 sponges	Voucher samples	Increase to 150 m	Reed and Pomponi (1997)
Bahamas	Lee Stocking Island	Cover	10	250	100 m photo transect at each depth, $0.2 m^2$ every 1 m	2 profiles, 13 transects, 117 quadrats		Peak, 75 m	Liddell et al. (1997)
Puerto Rico	La Parguera	Cover	20	125	Photo transect	1 transect, 200 photos		Dip, 60–80 m	Singh et al. (2004)
Puerto Rico	Bajo de Sico	Cover	26	53	10 m photo transect	30 transects, 300 photos, 7500 points		Peak, 32–40 m	García-Sais et al. (2007)
Puerto Rico	Abrir la Sierra	Cover	29	50	10 m photo transect	47 transects, 470 photos, 11,750 points		None	Garcia-Sais (2010)
Puerto Rico	Isla Desecheo	Cover	15	50	5–10 m photo transects	20 transects, 500 photos		Increase	Garcia-Sais (2010)
Puerto Rico	Bajo de Sico	Cover	50	100	Photo transect	2 transects, 198 photos		Variable	Rivero-Calle (2010)
Puerto Rico	Guanica	Cover	30	100	Photo transect	2 transects, 184 photos		Decrease	Rivero-Calle (2010)
Puerto Rico	Isla Desecheo	Cover	30	100	Photo transect	2 transects, 387 photos		Decrease	Rivero-Calle (2010)
Puerto Rico	La Parguera	Cover	30	100	Photo transect	4 transects, 225 photos		Variable	Rivero-Calle (2010)
Puerto Rico	Vieques	Cover	30	50	Photo transect	3 transects, 142 photos		Decrease	Rivero-Calle (2010)
Puerto Rico	SW coast	cover	47	70	10 m photo transects, 40 × 60 cm photos	17 transects		Decrease	Sherman et al. (2010)
Puerto Rico	El Seco	Cover	25	50	20 m photo transect	40 transects, 400 photos, 10,000 points		Dip, 40–45 m	García-Sais et al. (2011)
Bahamas	Bock Wall	Cover	30	91	30 m transects at 5 depth levels, $1 m^2$ quadrats, point intercept	3–6 transects, 10–20 quadrats		Plateau	Lesser and Slattery (2011)
Bahamas	Bock Wall	volume	30	91	25 × 1 m band transects at 5 depth levels	3–9 transects, ≥ 15 sponges per transect	Not standardized to reef surface area	Increase	Slattery and Lesser (2012)
Bahamas	Bock Wall	Cover	30	91	25 × 1 m band transects at 5 depth levels	3–9 transects		Plateau	Slattery and Lesser (2012)
Little Cayman	Rock Bottom Wall	Cover	30	91	25 × 1 m band transects at 5 depth levels	3–9 transects		Plateau	Slattery and Lesser (2012)

Table 1 (continued)

Location	Site	Metric	Min depth (m)	Max depth (m)	Survey method	Replication	Comments	Trend with depth	Reference
Belize	Carrie Bow Cay	Density	7.5	46	30 m transect at 5 depth levels	10 1 m^2 quadrats per transect		Increase	Lesser and Slattery (2013)
Belize	Carrie Bow Cay	Diversity	7.5	46	30 m transect at 5 depth levels	10 1 m^2 quadrats per transect	Visual IDs	Increase	Lesser and Slattery (2013)
Puerto Rico	Tourmaline Reef	Cover	30	50	10 m photo transect	28 transects, 280 photos, 7000 points		None	García-Sais et al. (2013)

volume of sponge individuals closest to random points, no matter the distance from these points. For the five depths studied, individual sponge biomass measurements from a minimum of 15 sponges per transect decreased from a mean of ~ 2.8 l per sponge at 30 m to ~ 1.8 and ~ 2.1 l at 46 and 61 m, respectively, then increased to 7.9 and 11.8 l at 76 and 91 m. Individual sponge biomass was reported as significantly higher at 76 and 91 m than at shallower depths, although the error bars in the graph of individual sponge volume (variance type not identified) were small enough to indicate a possible significant decrease in sponge volume from 30 to 46 m before increasing at greater depths (Fig. 2 in Slattery and Lesser 2012). Therefore, this study did not provide a conventional measurement of sponge biomass standardized to reef surface area, nor was it clear that a consistent increase in individual sponge biomass with depth was evident at the shallow end (30–91 m) of the mesophotic zone.

Only one other study could be found that estimated sponge volume. Reiswig (1973) estimated the volume of two species at both shallow and mesophotic depths. A single band transect, 50-m wide, was oriented perpendicularly to depth contours from 8 to 53 m depth on the outer fore-reef at Discovery Bay, Jamaica. The volume of each individual of *Mycale laxissima* and *Verongula gigantea* was estimated using height, width, and length and a regression curve calculated from more detailed measurements of 10 individuals of each species (see Pawlik et al. (2015) for confirmation of species identities). Reiswig (1973, p. 217) also estimated overall sponge biomass based on "near-daily observation of this community over an 18-month period." Biomass as a function of area was adjusted to only include suitable substratum. The overall biomass of *V. gigantea* was 28.2 times higher than that of *M. laxissima*. Biomass of *M. laxissima* was relatively consistent across depths but peaked at ~ 30 m. *Verongula gigantea* was present at ~ 20–50 m depth, and biomass peaked strongly at ~ 40 m. Overall, sponge biomass followed a similar pattern, increasing sharply from 20 to 40 m, then declining sharply to 50 m. Therefore, for these two species combined, sponge biomass increased from 10 m to peak at ~ 40 m, and then declined to ~ 60 m. While this study did report sponge biomass as a function of suitable substratum, only two species were surveyed, and the maximum depth studied was 53 m.

Percentage cover of sponges with depth

The majority of studies from this review of the literature reported percentage cover or numerical density of sponges as a function of depth through the mesophotic zone. As previously stated, neither of these metrics is a proxy for biomass, because sponges are highly variable in tissue thickness and morphology. However, because past support for the sponge increase hypothesis has been predicated on studies that use these two

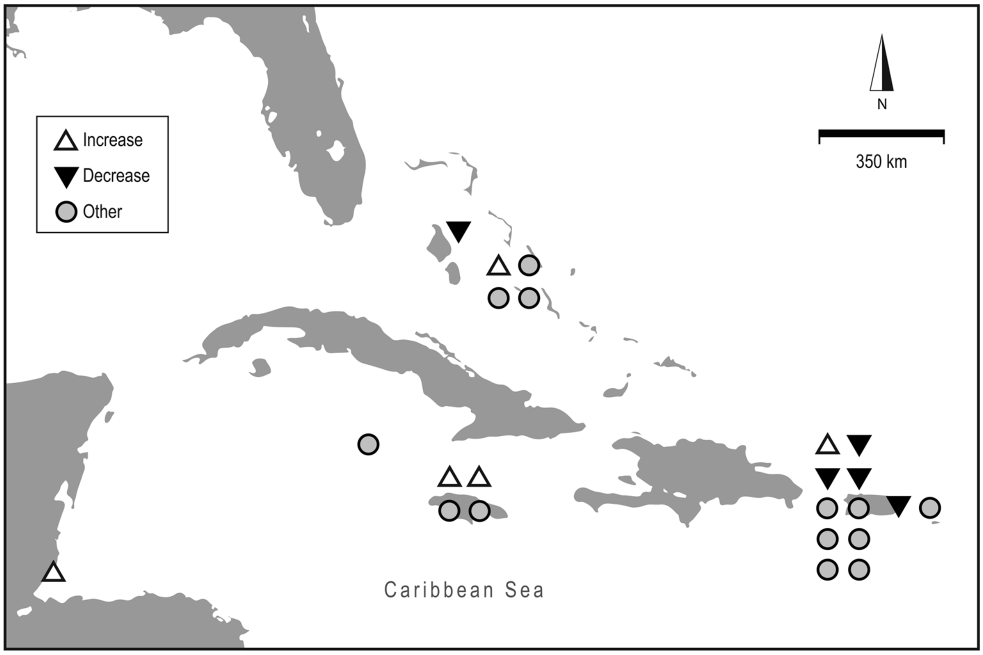


Fig. 1 Map of sites listed in Table 1 for which some measure of sponge abundance was reported at multiple mesophotic depths (30–150 m). When multiple sites are indicated at the same location, markers are offset in columns to make them visible. Legend for markers indicates change in abundance with increasing depth: an increase, a decrease, or some other pattern. Other patterns listed in Table 1 are a dip, peak, or plateau within the reported range, a variable pattern among transects at the site, or no consistent pattern

metrics, it is important to review this literature as well and to examine the patterns of abundance that have been described.

Liddell et al. (1984) used SCUBA to survey reef communities from 15 to 56 m depth in Discovery Bay, Jamaica. At each depth, along a transect from shallow to deep, 5–12 line-intercept transects were performed. For each transect, a 10-m-long line with markers at 20 cm intervals was draped over the reef, and the organism or substratum under each point was recorded. The transects at 15 m were on a fore-reef terrace, those at 22 m were on a reef escarpment, and those at 30, 45, and 56 m were on a fore-reef slope. The study makes the distinction between fleshy sponges (presumably meaning emergent), encrusting sponges, and boring sponges. Mean values for percentage cover of fleshy sponges increased consistently with depth from means of 1.5% at 15 m to 7.8% at 56 m, but variance was high, so there was no significant difference in cover between depths. Mean cover of encrusting sponges peaked at 6.7% at 56 m, significantly greater than at all depths other than 30 m. Mean cover of boring sponges decreased with depth from 20% at 15 m to 1.4% at 56 m.

Liddell and Ohlhorst (1988) used SCUBA and a submersible to survey benthic cover at 0.5–120 m depth along the North coast of Jamaica. Transects were laid perpendicular to the depth contour along the Western fore-reef at Discovery Bay. From 35 to 55 m, there was a steep slope of 45–60°, followed by a wall from 55 to 105 m, and an escarpment of 60–90° to 130 m. The authors used different methods to estimate percentage cover at different depths. Between 15 and 30 m, a point intercept method was used, with up to 10 parallel 10-m lines spaced 1 m apart, each of which had a point every 20 cm. At 45 m, 0.14 m^2 photo-quadrats were taken at 1-m intervals along the depth contour via SCUBA. From 53 to 120 m, similar photo-quadrats were taken using a camera on a submersible. Percentage cover was calculated by overlaying an array of 27 points with 10 cm spacing on each photo. The reported values for percentage cover of emergent (non-boring) sponges generally increased from 30 to 120 m from a mean of ~6 to 20% cover with the peak value at 90 m on one of the transects, although there was no statistical difference in sponge cover from 53 to 120 m. In addition to percentage cover, the authors qualitatively describe changes in sponge morphology over depth; from the abstract: "At 60 m the community resembles that of shallower water, although scleractinians are less abundant and encrusting and erect demosponges are much more abundant … Encrusting sponges and coralline, filamentous, and macroalgae predominate in the middle region of the deep fore reef. A low-diversity assemblage occupying 40% of the substratum and dominated by diminutive encrusting and endolithic? [sic] demosponges and largely endolithic filamentous algae occurs from 100–130 m" (Liddell and Ohlhorst 1988, p. 413). While percentage cover of demosponges may be relatively consistent on the deep fore-reef, it appears that biomass is greatest at depths of 60–70, then decreases with depth through 130 m.

Liddell et al. (1997) surveyed benthic community composition off the NE coast of Lee Stocking Island in the Bahamas. Using both SCUBA and a submersible, they surveyed benthic cover over a range of depths from 10 to 250 m, along two landward/seaward transects spaced 2 km apart. From 35 to 50 m depth, there was a slope of 30–45°, from 50 to 100 or 125 m (depending on the transect), there was a vertical wall, below which the bottom became sloped again with greater sediment cover. At each depth surveyed, the authors quantified benthic cover of sessile organisms along 100-m-long transects parallel to depth contours. One photograph covering ~ 0.2 m^2 was taken approximately every meter, and benthic cover was determined using an array of 7 points overlaid on each photo. Every set of 11 photos was grouped together and treated as a subsample. Sponge cover increased from shallow depths (10–30 m) at ~2% cover, to mesophotic depths. Among the mesophotic depths surveyed (50–150 m), however, there were no significant differences in sponge cover. Sponge cover peaked at 75 m (11%) on the transect with the greatest range (10–250 m), and at 100 m (8.9%) on the transect with 50 m increments between 50 and 200 m.

Singh et al. (2004) used an autonomous underwater vehicle to quantify benthic cover off the coast of La Parguera (SW Puerto Rico). One transect was conducted from 20 to 125 m, and a total of 200 photographs were taken, but the dimensions of these photo quadrats were not indicated. The transect was on a steep slope (75°) and consisted primarily of hard-bottom substrate. Six distinct benthic depth zones were determined, < 24, 24–30, 30–60, 60–80, 80–90, and 90–100 m, although the specific characteristics of these bathymetric zones were not described. Statistics were not reported, but sponge cover was greatest for shallow and deep zones, decreasing steadily from ~ 6% cover at < 24 m to ~ 2% cover in the 60–80-m-depth range, then steadily increasing to ~ 5% cover in the 90–100-m range. This pattern, with a dip at 60–80 m, is unlike any of the others reported.

García-Sais et al. (2007) surveyed benthic mesophotic habitats in Bajo de Sico, a seamount off the western coast of Puerto Rico that rises from a deep platform at 177 m to a reef top at 25 m. Three habitat types at different depths were surveyed by divers using rebreathers: the tops of reef promontories, at 26–31 m, the vertical walls on the sides of reef promontories, at 32–40 m, and deep rhodolith reef, at 46–52 m. In each habitat zone, ten 10-m-long transects were laid. Along each transect, ten non-overlapping photos were taken, and percentage cover of organisms in each photo was determined for a randomized array of 25 points. Percentage cover values were averaged for each transect (total of 250 points). Mean sponge cover increased from 26.5% at the reef top (26–31 m) to 43.1% on the reef wall (32–40 m), then decreased to 20.2% on the rhodolith reef (46–52 m). Sponge cover peaked at an intermediate depth, although differences may have been the result of changing habitat rather than increasing depth, as authors noted that many sponges had settled on unattached rubble in rhodolith beds, which may not be a suitable long-term habitat.

García-Sais et al. (2010) was conducted similarly to García-Sais et al. (2007) but surveyed the mesophotic benthic communities of Abrir la Sierra, a shelf-edge reef off the west coast of Puerto Rico. Within the study area, there were two internal slope walls, a deep outer shelf terrace, and an insular slope wall. Diver surveys were divided into six zones: the inner wall of the deep terrace at 31–37 m, coral reef at 33 m, rhodolith reef at 36 m, and the outer insular slope at 29–33, 40, and 50 m. Benthic cover was determined using 25 randomized points overlaid on each of ten non-overlapping photos (each covering 0.85–1.1 m^2) taken along a 10-m transect, with a mean percentage cover derived from all of the photos in a transect. Sponge cover was 13.6% on the inner wall (31–37 m), 21.3% on coral reef (33 m), and 7.4% on the rhodolith reef (36 m), reflecting substratum differences at similar depths. On the insular slope at 29–33, 40, and 50 m, sponge cover was 16.3, 14.9, and 17.1%, respectively.

Garcia-Sais (2010) conducted benthic surveys on Isla Desecheo, a small island west of Puerto Rico. This citation included data from two reports (García-Sais et al. 2005a, b), so these three publications will be discussed as the same study but cited independently where appropriate. Five replicate transects per depth were performed at 15, 20, and 25 m off the Southern coast of Isla Desecheo, and percentage cover was calculated using the continuous intercept chain-link method (García-Sais et al. 2005a). All surveys were completed by divers using rebreathers. At 30 and 40 m, six 10-m-long transects were surveyed, and at 50 m, eight transects were surveyed (García-Sais et al. 2005b). For each of these transects, ten non-overlapping screenshots were extracted from videos taken at a constant distance from the substratum, and 25 randomly placed points were used to estimate benthic cover of organisms. Transects at 15, 20, and 25 m were performed over patch reefs on a gently sloping shelf. Transects at 30 and 40 m were performed at the top and bottom of a slope of between 30 and 45°, and transects at 50 m were performed on a gently sloping reef built over a well-consolidated rhodolith bed (García-Sais et al. 2005a, b). Sponge cover was ~ 2–4% and statistically similar at 15, 20, and 25 m, then increased to ~ 20% at 30 m and to ~ 30% at both 40 and 50 m, which were statistically similar (Garcia-Sais 2010).

Rivero-Calle (2010) studied benthic community composition at five sites around Puerto Rico (Bajo de Sico, Guanica, Isla Desecheo, La Parguera, and Vieques). At each site, two to four 1-km-long transects were conducted along a depth profile using an autonomous underwater vehicle. Photos were taken over a depth range of 30–100 m along each transect, although some transects only surveyed part of this depth range. Percentage cover of sessile organisms was analyzed using 60–80 randomly distributed points per photo, and cover values were averaged across 10-m bins. Across all sites and transects, the overall pattern was a decrease in sponge cover with depth, with peak values of 15–18% sponge cover. Three transects had the highest sponge cover at intermediate depths (peaking between 50 and 80 m), and sponge cover was highest at the deepest depth in two transects (although for one of these, LPtr7, there was a clear pattern of decrease except for at the deepest depth). For the remaining seven transects, sponge cover decreased with depth.

Sherman et al. (2010) used remotely operated underwater vehicle (ROV) photo transects to study the mesophotic slope off the SW coast of Puerto Rico (closest to La Parguera relative to the studies above). Photos were taken in 17 transects, 10 m in length, over three depth levels between 47 and 70 m, and point counting software was used to determine relative abundance of benthic organisms and substratum types. Sponge cover was about the same at 47 and 59 m (16.2 and 16.9%, respectively), then declined to 13.4% at 70 m depth.

García-Sais et al. (2011) surveyed mesophotic habitats at El Seco, southeast of Vieques, Puerto Rico using techniques already described for this research group. Four different habitat types were surveyed in this location: colonized pavement at 25–30 m, bank coral reef at 33–38 m, patch coral reef at 40–45 m, and rhodolith reef at 43–50 m. As before, ten non-overlapping photos along 20 m transects were chosen and percentage cover of organisms calculated for 25 random points per photo with averages calculated for the transect. Sponge cover was 7.3% on colonized pavement (25–30 m), 3.9% on bank coral reef (33–38 m), 4.0% on patch coral reef (40–45 m), and 13.3% on rhodolith reef (43–50 m). While mean sponge cover was highest at the deepest depth, it was not statistically different from sponge cover at the shallowest depth, but there was a significant decrease at intermediate depths.

Lesser and Slattery (2011) conducted benthic surveys at mesophotic depths in the Bahamas. Using SCUBA, Trimix, and closed-circuit rebreather diving, the authors quantified percentage cover of sessile benthic organisms between 30 and 91 m on Bock Wall, a NE facing near-vertical wall near Lee Stocking Island. At each depth surveyed (30, 46, 61, 76, and 91 m), three to six replicate 30-m transects were performed, with ten to twenty 1-m^2 quadrats positioned randomly along each transect. Each quadrat was subdivided into 16 grids, and point intercepts ($N = 100$/quadrat) were used to estimate percentage cover. Sampling was conducted in three separate years; all depths were surveyed in 2003 and 2009, and all depths except 76 and 91 m were surveyed in 2005. A lionfish invasion occurred in 2006. In 2003 and 2005, sponge cover increased significantly with depth, from ~ 5% at 30 m to ~ 30% at 46 m to ~ 75% at 61 m, then plateaued between 61, 76, and 91 m. In 2009, after lionfish had invaded, sponge cover at 46 and 61 m was reduced to < 5%, which was attributed to higher macroalgal cover due to lionfish predation on herbivores, while sponge cover at 76 and 91 m remained at ~ 75%. The authors noted that "Many of the mesophotic corals and sponges had plate-like or encrusting morphologies that would easily allow overgrowth by algae and subsequent reduction in light by shading" (Lesser and Slattery 2011, p. 1865–1866), which could indicate that percentage cover was a possible proxy for biomass at this site.

Slattery and Lesser (2012) characterized percentage cover of benthic organisms at the same depth levels as above (30, 46, 61, 76, and 91 m) in both the Bahamas (also at Bock Wall but with a different survey methodology) and at Rock Bottom Wall, off the north coast of Little Cayman Island. Again, a combination of SCUBA, Trimix, and rebreathers was used. Although no specific description was given, Rock Bottom Wall is presumably a near-vertical wall similar to Bock Wall. At each site, three to nine replicate 25 × 1 m^2 band transects were used to quantify percentage cover of different benthic organisms. No specifics regarding the estimation of percentage cover over the transect area were provided. Slattery and Lesser (2012) found a similar pattern in the Bahamas and Little Cayman to Lesser and Slattery (2011), with an increase in sponge cover from 30 and 46 to 61 m where it remained at ~ 75% cover through 76 and 91 m.

Garcia-Sais et al. (2013) surveyed benthic habitats on Tourmaline Reef, a mesophotic reef off the west coast of Puerto Rico. Benthic cover was quantified by divers along ten transverse sections of the outer reef, with a 10-m transect along each section at 30, 40, and 50 m. Percentage cover was calculated using ten non-overlapping photos for each and 25 randomized points per photo, then averaging for the transect overall. Four different habitat types were found at various depths along transects: colonized pavement, scattered patch reef, wall, and rhodolith reef. Mean sponge cover was similar across depths, averaging 6.2, 6.8, and 7.8% at 30, 40, and 50 m, respectively. When analyzed within habitats, there were no significant differences in sponge cover with depth.

Numerical density of sponges with depth

Numerical density is likely a poor indicator of sponge biomass, because a single large barrel sponge could exceed the volume of many smaller sponge species by an order of magnitude or more. Lesser and Slattery (2013) reported the numerical density of all sponges, and *Callyspongia vaginalis* specifically, over a mesophotic depth profile off Carrie Bow Cay, Belize. A single 30-m line transect, parallel to each depth level was performed at 7.5, 15, 23, 30, and 46 m, and ten 1-m^2 quadrats were randomly placed along each transect. In each quadrat, all individual sponges were counted and identified to species where possible. Tube length was also measured for ten individuals of *C. vaginalis* at each depth. Numerical density of all sponges increased with depth; the densities at 30 and 46 m were similar to each other and higher than the densities at 7.5, 15, and 23 m. Additionally, both the density and tube length of *C. vaginalis* increased with depth. In the case of *C. vaginalis*, greater tube length has been used as a proxy for greater biomass, but differences in tube length and elongation may result from morphological plasticity rather than changes to the biomass of an individual (Pawlik et al. 2015).

Maldonado and Young (1996) used a submersible to study the distribution of sponges in the mesophotic zone south of Golding Cay, near New Providence Island, Bahamas. A single vertical transect was conducted from 91 to 531 m, with photo quadrats taken every 6 m of depth. While the methods are not entirely clear, it appears that four adjacent 306.25 cm^2 plots were sampled at each depth, for a total quadrat area of 1225 cm^2 at each depth. Frames that were out of focus were excluded, resulting in a total of 57 quadrats from 91 to 531 m. In a given quadrat, the number of sponge species and individuals were counted, as well as the morphology of each sponge. Substratum was categorized as vertical or horizontal based on whether or not there was a resting veneer of silt. There was an overall trend of declining sponge density with depth on vertical substrata from 91 to 175 m, a span that included 12 quadrats. Peak numbers of individuals (30–40 per quadrat) were recorded between 100 and 160 m depth, with lower numbers recorded (5–20 per quadrat), primarily on vertical substrata, through 531 m.

Diversity of sponges with depth

Diversity is the second of two metrics that were proposed to increase with depth through the mesophotic zone as part of the sponge increase hypothesis. We have even fewer data to establish a pattern of sponge diversity with depth than for sponge abundance with depth. Accurate identification of sponges to the species level is often difficult, even when tissue samples are available, and this is rarely the case for investigations of mesophotic reefs. One exception is Reed and Pomponi (1997), who sampled sponge tissue for subsequent taxonomic identification using SCUBA to depths of 45 m and using submersibles from 45 to 922 m on nine expeditions and 147 sites across the Bahamas Islands between 1987 and 1995. They collected a total of 3059 sponge samples, of which, 42% were identified to the species level. However, sampling effort was not standardized for substratum area, but categorized by one of five depth zones. Across all sites, species diversity rose from ~80 species per depth zone at 0–30 m to ~ 120 species at 61–150 m, then declined at greater depths.

Two other studies reported sponge species diversity from visual identification of sponges. Maldonado and Young (1996) reported the species diversity of sponges in 12 video quadrats of 1225 cm^2 area between 91 and 175 m of the southern side of Golding Cay, near New Providence Island, Bahamas. Species diversity was highest at the shallowest depth studied (91 m), with ten species recorded, and dropped to three species on non-horizontal surfaces by 175 m. At greater depths (to 531 m), sponge species diversity on non-horizontal surfaces fluctuated between zero and six species. Lesser and Slattery (2013) recorded sponge species diversity on the basis of visual inspection within 1-m^2 quadrats at five depth levels between 7.5 and 46 m. Diversity was ~ 4.8 species/m^2 at 7.5, 15, and 23 m depth, and ~ 5.8 species/m^2 at 30 and 46 m depth, and this mean difference of one species per m^2 was reported as significantly different.

Summary and conclusions

A thorough review of the literature reveals that there is insufficient evidence to support the hypothesis that sponges throughout the Caribbean show a pattern of increasing biomass and diversity with depth through 150 m. Only two studies (Reiswig 1973; Slattery and Lesser 2012) specifically report sponge biomass, and both of these have methodological problems (not standardized to reef area, only two species, respectively); in any case, neither offers sufficient replication nor range of depth to make generalizations about patterns of biomass through the mesophotic zone across the Caribbean. Regarding diversity, Reed and Pomponi (1997) provided some support for the hypothesis for the Bahamas, but diversity was not standardized for reef area, and Maldonado and Young (1996) reported a decrease in diversity with depth, standardized for reef area, also for the Bahamas. Again, the lack of geographic range makes any generalizations about diversity with depth unsupportable.

As for the larger number of studies that report other metrics of sponge abundance, an increase with depth is reported at four sites, a decrease with depth at five sites, and a different pattern (variable, peak, dip, plateau, or no pattern) with depth at 12 sites. Surveys were conducted through the mesophotic zone (to 150 m or greater) at only two of these sites (one reporting a peak in sponge abundance at 75 m and the other a decrease throughout). Rather than a single trend that occurs across the Caribbean, variation in sponge abundance appears to be the norm. The same conclusion was reached by Pawlik et al. (2015) after compiling survey data of sponge abundance above and below 15 m from studies across the Caribbean (Table 2 in Pawlik et al. 2015).

Interestingly, the analysis provided in this review touches on the proposition that there may be a consistent and well-defined faunal break at 60 m in the mesophotic zone (Slattery and Lesser 2012), an hypothesis that was not supported by a two-decade study that encompassed fishes, benthic invertebrates and macroalgae within the extensive MCEs of the Hawaiian Archipelago (Pyle et al. 2016) or a more recent study of fishes in Curaçao (Baldwin et al. 2018). While the present review focused only on sponges, and the data are admittedly limited, the highly variable pattern in diversity and abundance seen in Table 1 does little to support a distinct faunal break at 60 m.

Clearly, we have much left to learn about the patterns of sponge abundance and diversity with depth into the mesophotic and beyond. It is surprising that we know so little. While the exploration of mesophotic reefs is logistically difficult, ROV and submersible transects across mesophotic profiles have been ongoing for decades in many parts of the Caribbean, and the methods employed generally include video or still-photographic records of the benthos with detailed metadata. Standardized methods should be brought to bear on these existing transect data to establish depth-related patterns of sponge abundance, minimally as percentage cover, as a function of slope (grade and orientation) and other abiotic factors, and across the biogeographic region. Going forward, developing photogrammetric technologies (e.g., Ferrari et al. 2017) should be employed that allow the estimation of sponge volume (biomass) across depth profiles of the mesophotic zone.

Why are standardized studies of sponge abundance and diversity as a function of depth important? Coral reef ecosystems in the Caribbean have undergone dramatic changes in the past three decades, and we are now becoming aware of the role of sponges in those changes (Pawlik et al. 2016), as well as their increasing abundance on shallow water reefs (e.g., McMurray et al. 2015; de Bakker et al. 2017). Not only are sponges usually competitively dominant over reef-building corals (Loh et al. 2015), with possible exceptions (García-Hernández et al. 2017), they pump huge volumes of seawater through their bodies in the process of feeding predominantly on dissolved organic carbon while releasing nutrients that act as localized sources of fertilizer for macroalgae, all of which has profound implications for carbon cycling and ecosystem function on Caribbean reefs (Pawlik et al. 2016, 2018; McMurray et al. 2017). While sponge cover on Caribbean reefs above the mesophotic averages ~16% of reef area, or about the same as coral cover (Loh et al. 2015), some records for the mesophotic zone are two to five times higher (e.g., Garcia-Sais 2010; Slattery and Lesser 2012). What sustains this high biomass of sponges at mesophotic depths? What effect does their carbon and nutrient cycling have on mesophotic ecosystems, and on potential refuge habitats for reef-building corals? And why is there an apparent change from a community dominated by demosponges to hexactinellids below the mesophotic zone? These are all important questions that await future study.

Acknowledgements We are grateful for the funding that supported the analyses, compilation and writing of this review, including a grant from the US National Science Foundation (OCE 1558580) and a pilot project award from UNCW's Center for Marine Science. Additional thanks to two reviewers for helpful comments.

Funding This study was funded by US NSF grant OCE-1558580.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

Sampling and field studies No sampling or field studies were done for this review.

References

Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. Coral Reefs 24:475–479

Baldwin CC, Tornabene L, Robertson DR (2018) Below the mesophotic. Sci Rep 8:4920

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353

Bongaerts P, Ridgway T, Sampayo EM (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327

Bongaerts P, Frade PR, Ogier JJ, Hay KB, Bleijswijk JV, Englebert N (2013) Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2-60 m) on a Caribbean reef. BMC Evol Biol 13:205–205

de Bakker DM, van Duyl FC, Bak RPM, Nugues MM, Nieuwland G, Meesters EH (2017) 40 years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. Coral Reefs 36:355–367

Ferrari R, Figueira WF, Pratchett MS, Boube T, Adam A, Kobelkowsky-Vidrio T, Doo SS, Atwood TB, Byrne M (2017) 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. Sci Rep 7: 16737

García-Hernández J, van Moorsel GWNM, Hoeksema BW (2017) Lettuce corals overgrowing tube sponges at St. Eustatius, Dutch Caribbean. Mar Biodivers 47:55–56

Garcia-Sais JR (2010) Reef habitats and associated sessile-benthic and fish assemblages across a euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico. Coral Reefs 29:277–288

García-Sais JR, Castro-Gomez R, Sabater-Clavell J, Carlo M (2005a) Inventory and atlas of corals and coral reefs, with emphasis on deep-water coral reefs from the US Caribbean EEZ (Puerto Rico and the United States Virgin Islands). Final report submitted to the Caribbean Fishery Management Council (CFMC/NOAA). 215 pp.

García-Sais JR, Castro R, Esteves R, Sabater J, Carlo M (2005b) Monitoring of coral reef communities at Isla Desecheo, Rincon, Mayaguez Bay, Guanica, Ponce and Isla Caja de Muertos, Puerto Rico, 2005 Department of Environmental and Natural Resources (DENR), US Coral Reef National Monitoring Program, NOAA. 126 pp.

García-Sais JR, Castro R, Sabater-Clavell J, Carlo M, Esteves R (2007) Characterization of benthic habitats and associated reef communities at Bajo de Sico seamount, Mona Passage, Puerto Rico. Final report submitted to the Caribbean Fishery Management Council (NA04NMS4410345) p 91

García-Sais JR, Castro-Gomez R, Sabater-Clavell J, Esteves R, Williams S, Carlo M (2010) Mesophotic habitats and associated marine communities at Abrir La Sierra, Puerto Rico. Final report submitted to NOAA (FNA07NMF4410117) p 115

García-Sais JR, Sabater-Clavell J, Esteves R, Capella J, Carlo M (2011) Characterization of benthic habitats and associated mesophotic coral reef communities at El Seco, Southeast Vieques, Puerto Rico. Final report submitted to the Caribbean Fishery Management Council p 91

García-Sais JR, Williams SM, Esteves R, Sabater-Clavell J, Carlo MA (2013) Characterization of mesophotic benthic habitats and associated reef communities at Tourmaline Reef, Puerto Rico. Final report submitted to the Caribbean Fishery Management Council. https://doi.org/10.13140/RG.2.1.2752.1361

Kahng SE, García-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275

Lang JC (1974) Biological zonation at the base of a reef: observations from the submersible Nekton Gamma have led to surprising revelations about the deep fore-reef and island slope at Discovery Bay, Jamaica. Amer Sci 62:272–281

Lehnert H, Fischer H (1999) Distribution patterns of sponges and corals down to 107 m off North Jamaica. Mem Qld Mus 44:307–316

Lesser MP (2006) Benthic-pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. J Exp Mar Biol Ecol 328:277–288

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biol Invasions 13:1855–1868

Lesser MP, Slattery M (2013) Ecology of Caribbean sponges: are top-down or bottom-up processes more important? PLoS One 8:e79799

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. J Exp Mar Biol Ecol 375:1–8

Lewis JB (1965) A preliminary description of some marine benthic communities from Barbados, West Indies. Can J Zool 43:1049–1074

Liddell WD, Ohlhorst SL (1988) Hard substrata community patterns, 1-120 m, North Jamaica. Palaeos 3:413–423

Liddell WD, Ohlhorst SL, Boss SK (1984) Community patterns on the Jamaican fore reef (15-56 m). Palaentogr Am 54:385–389

Liddell WD, Avery WE, Ohlhorst SL (1997) Patterns of benthic community structure, 10-250 m, the Bahamas. Proc 8th Int Coral Reef Symp 1:437–442

Loh T-L, McMurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. PeerJ 3:e901

Maldonado M, Young C (1996) Bathymetric patterns of sponge distribution on the Bahamian slope. Deep-Sea Res I 43:897–915

McMurray SE, Finelli CM, Pawlik JR (2015) Population dynamics of giant barrel sponges on Florida coral reefs. J Exp Mar Biol Ecol 473:73–80

McMurray SE, Pawlik JR, Finelli CM (2017) Demography alters carbon flux for a dominant benthic suspension feeder, the giant barrel sponge, on Conch Reef, Florida Keys. Funct Ecol 31:2188–2198

Menza C, Kendall M, Hile S (2008) The deeper we go the less we know. Int J Trop Biol 56:11–24

Olson JB, Kellogg CA (2010) Microbial ecology of corals, sponges, and algae in mesophotic coral environments. FEMS Microbiol Ecol 73:17–30

Pawlik JR, McMurray SE, Erwin P, Zea S (2015) A review of evidence for food limitation of sponges on Caribbean reefs. Mar Ecol Prog Ser 519:265–283

Pawlik JR, Burkepile DE, Thurber RV (2016) A vicious circle? Altered carbon and nutrient cycling may explain the low resilience of Caribbean coral reefs. Bioscience 66:470–476

Pawlik JR, Loh T-L, McMurray SE (2018) A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. PeerJ 6:e4343

Pyle RL, Boland R, Bolick H, Bowen BW, Bradley CJ, Kane C, Kosaki RK, Langston R, Longenecker K, Montgomery A, Parrish FA, Popp BN, Rooney J, Smith CM, Wagner D, Spalding HL (2016) A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian Archipelago. PeerJ 4:e2475

Reed JK, Pomponi SA (1997) Biodiversity and distribution of deep and shallow water sponges in the Bahamas. Proc 8th Int Coral Reef Symp 1:1387–1392

Reiswig HM (1973) Population dynamics of three Jamaican Demospongiae, vol 23. University of Miami–Rosenstiel School of Marine and Atmospheric Science, pp 191–226

Rivero-Calle S (2010) Ecological aspects of sponges in mesophotic coral ecosystems. University of Puerto Rico. 85 pp.

Rützler K, Macintyre IG (1982) The habitat distribution and community structure of the Barrier Reef Complex at Carrie Bow Cay, Belize, vol 12. Smithsonian Institution Press, Washington, DC, pp 564–564

Schmahl GP (1990) Community structure and ecology of sponges associated with four Southern Florida coral reefs. In: Rützler K (ed) New perspectives in sponge biology. Smithsonian Institution Press, Washington, DC, pp 376–383

Semmler RF, Hoot WC, Reaka ML (2017) Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? Coral Reefs 36:433–444

Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, Pagán F, Schärer M, Weil E (2010) Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of Southwest Puerto Rico. Coral Reefs 29:347–360

Shlesinger T, Grinblat M, Rapuano H, Amit T, Loya Y (2018) Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. Ecology 99:421–437

Singh H, Armstrong R, Gilbes F, Eustice R, Roman C, Pizarro O, Torres J (2004) Imaging coral I: imaging coral habitats with the SeaBED AUV. Subsurf Sens Technol Appl 5:25–42

Slattery M, Lesser MP (2012) Mesophotic coral reefs: a global model of community structure and function. Proc 12th Int Coral Reef Symp 9C-2, p 5

Slattery M, Lesser MP (2015) Trophic ecology of sponges from shallow to mesophotic depths (3 to 150 m): comment on Pawlik et al. (2015). Mar Ecol Prog Ser 527:275–279

Suchanek TH, Carpenter RC, Witman JD, Harvell CD (1983) Sponges as important competitors in deep Caribbean coral reef communities. In: The ecology of deep and shallow coral reefs Symposia Series for Undersea Research. Office of Undersea Res., NOAA, Rockville, MD, 1:55–60