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Joseph R. Pawlik
University of North Carolina, Wilmington

Roy A. Armstrong
University of Puerto Rico, Mayaguez

Stephanie Farrington
Harbor Branch Oceanographic Institution

John Reed
Harbor Branch Oceanographic Institution, Inc

Sara Rivero-Calle
University of Georgia Skidaway Institute of Oceanography

See next page for additional authors

Authors
Hanumant Singh
Northeastern University

Brian K. Walker
Nova Southeastern University, walkerb@nova.edu

Jason White
University of North Carolina, Wilmington

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OPINION PIECE

Comparison of recent survey techniques for estimating benthic cover on Caribbean mesophotic reefs

Joseph R. Pawlik[1,*], Roy A. Armstrong[2], Stephanie Farrington[3], John Reed[3], Sara Rivero-Calle[4], Hanumant Singh[5], Brian K. Walker[6], Jason White[7]

[1]Department of Biology and Marine Biology and Center for Marine Science, University of North Carolina, Wilmington, NC 28409, USA
[2]Department of Marine Sciences, University of Puerto Rico, Mayaguez, PR 00681, USA
[3]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL 34946, USA
[4]University of Georgia Skidaway Institute of Oceanography, Savannah, GA 31411, USA
[5]Electrical and Computer Engineering, College of Engineering, Northeastern University, Boston, MA 02115, USA
[6]Halmos College of Arts and Sciences, Nova Southeastern University, Dania Beach, FL 33004, USA
[7]Undersea Vehicles Program, Center for Marine Science, University of North Carolina, Wilmington, NC 28409, USA

ABSTRACT: Highly divergent estimates of benthic cover of sponges have been reported for Caribbean mesophotic reefs (90–100 m) based on quadrat point-intercept data collection using 2 methods: visual surveys conducted *in situ* by technical divers, and analyses of photographs taken by unmanned underwater vehicles (UUVs). The second method has been criticized for potential errors from image distortion caused by variable camera angle relative to the substratum, but without a broader comparison of both methods. We find that studies that have used the UUV-based method are advantageous for a number of reasons, most importantly: (1) access to the full mesophotic zone, (2) higher sample replication, and (3) reduced likelihood of sampling bias. For tech diving surveys conducted at 91 m, i.e. the deepest depth reported using this method but only midway through the mesophotic zone, studies have reported particularly high sponge cover (~80 vs. <10 % for UUV-based surveys), which may be a consequence of low replication and targeted sampling influenced by very short working times under hazardous conditions. When evaluating benthic abundance metrics from photographs, issues associated with variable substratum angle are common to any topographically complex surface, particularly within a quadrat. Nevertheless, point-intercept estimates are not dependent on quadrat area and are not subject to error due to image distortion or surface complexity. Unlike visual census data from tech dives, UUV photographs can be validated by taxonomic experts and archived for re-analysis. Past tech diving surveys should be repeated using the UUV-based method with greater replication over the full range of the mesophotic zone in order to reconcile divergent estimates of benthic cover.

KEY WORDS: Remotely operated vehicle · ROV · Autonomous underwater vehicle · AUV · Technical diving · Image distortion · Sponges · Coral reefs · Photogrammetry · Sampling

1. INTRODUCTION

Tropical mesophotic hard-bottom reef habitats, also called mesophotic coral ecosystems (MCEs) are found at a depth range of 30 to 150 m (Kahng et al. 2010). Within this transition zone, ecological conditions change considerably from shallow to deep, with a near complete attenuation in light levels, moderate

*Corresponding author: pawlikj@uncw.edu

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decrease in temperature, decrease in turbulent flow, as well as a variety of other abiotic and biotic changes (Lesser et al. 2009). Similarly, MCEs support a transitional community of shallow to deep-sea reef organisms, along with some endemic species (Reed & Pomponi 1997, Turner et al. 2017). Although the name 'mesophotic coral ecosystem' implies high coral cover, other benthic organisms, such as algae and sponges, are often the dominant living cover on the surface of these reefs (Scott et al. 2019). MCEs are considered by some to be among the most diverse and least protected ecosystems in the world's oceans (Soares et al. 2020).

Although they have a depth span that is fourfold that of shallow-water tropical reefs and represent ~80% of potential coral reef habitat worldwide (Pyle & Copus 2019), MCEs are, by comparison, very poorly studied because of the technological difficulties associated with reaching them (Menza et al. 2008). Because MCEs are beyond the depth range of conventional (no decompression) SCUBA diving, they must be explored by technical diving, manned submersibles, or by unmanned underwater vehicles (UUVs). UUVs include remotely operated vehicles (ROVs), which are controlled from a support ship and are tethered, and autonomous underwater vehicles (AUVs), which are not tethered. All of these methods for studying MCEs are more logistically complicated and expensive than those commonly used for studying shallow-water reefs and are not well suited to the collection of samples or conducting manipulative experiments. As a consequence, the limited investigations performed on MCEs have mostly been descriptive studies of bottom topography and community composition. Nevertheless, these limited studies of MCEs have figured prominently in some compelling hypotheses about broader coral reef ecosystem function. These hypotheses include (1) that MCEs serve as a refuge habitat for reef-building corals subjected to bleaching or disease in shallower water (the 'deep reef refugia hypothesis,' Bongaerts et al. 2010), (2) that MCEs similarly serve as a haven for fishery-targeted species (Lindfield et al. 2016, Cobián-Rojas et al. 2021), (3) that there is a consistent and well-defined faunal break at 60 m (the 'faunal break hypothesis,' Slattery & Lesser 2012), and (4) that there is a pan-Caribbean phenomenon of increasing abundance of sponges with greater depth on MCEs that is associated with greater picoplankton food availability (the 'sponge increase hypothesis,' Lesser 2006, Scott & Pawlik 2019). Of these, the methods used for testing the sponge increase hypothesis (SIH) are the subject of the present contribution.

Why is the abundance of sponges on Caribbean mesophotic reefs important? Coral reef ecosystems have undergone dramatic changes in the past 3 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 in the Caribbean (e.g. McMurray et al. 2015, de Bakker et al. 2017). Not only are sponges often competitively dominant over reef-building corals (Loh et al. 2015), but they also 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 can have profound implications for carbon and nutrient 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 zone averages ~16% of reef substratum, or about the same as coral cover (Loh et al. 2015), some reports for the mesophotic zone are many times higher (Slattery & Lesser 2012); therefore, estimates of benthic–pelagic processing, and carbon and nutrient cycling (Pawlik & McMurray 2020), as well as sponge–coral competitive interactions, could be greatly affected by different estimates of sponge abundance in the mesophotic zone.

To summarize, the SIH was initially proposed by Lesser (2006, p. 278), who reported that '… sponges throughout the Caribbean show a pattern of increasing biomass and diversity with depth down to 150 m.' The SIH was reiterated in subsequent publications (e.g. Lesser & Slattery 2013), often with different abundance metrics 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 SIH was also referenced in several other studies (e.g. Bell 2008, Olson & Kellogg 2010), including a widely cited literature review on the community ecology of the mesophotic zone (Kahng et al. 2010). More recently, the status of the SIH was expanded upon by Lesser & Slattery (2019, p. 1): 'This [the SIH] was not stated as a hypothesis, but as a fully referenced statement of fact in the introduction of Lesser (2006).'

Scott & Pawlik (2019) reviewed the literature evidence for the SIH and found only 17 studies that reported one or more metrics associated with sponge abundance or diversity as a function of depth across all or part of the mesophotic zone in the Caribbean. Of these metrics, percentage cover of sponges on the reef substratum was the most common (see Table 1 in Scott & Pawlik 2019), and patterns were disparate

across sites and locations, prompting the conclusion that there was no evidence to support the SIH for Caribbean mesophotic reefs. Lesser & Slattery (2018, p. 2) dismissed this conclusion as lacking 'any quantitative analysis,' and selectively re-analyzed 3 of the 17 studies cited by Scott & Pawlik (2019), reasserting that 'sponge density increases with depth throughout the Caribbean' to quote the title of their contribution (Lesser & Slattery 2018). Pawlik & Scott (2019) responded by providing further analyses of 4 of the 14 studies that had been excluded by Lesser & Slattery (2018), all of which were AUV photo-transect surveys from off the coast of Puerto Rico (Rivero-Calle 2010), and contrary to the SIH, they showed decreasing sponge cover between 30 and 100 m (Pawlik & Scott 2019). This reproof was followed by the publication of an additional set of ROV photo-transect surveys from Puerto Rico (to 180 m), St. Thomas (US Virgin Islands, to 100 m) and Flower Garden Banks (Gulf of Mexico, to 100 m), none of which supported the SIH (Scott et al. 2019).

With UUV photo-transect survey data from multiple Caribbean locations and sites clearly failing to support the SIH (Rivero-Calle 2010, Pawlik & Scott 2019, Scott et al. 2019, Scott & Pawlik 2019), Lesser & Slattery (2021) have most recently questioned the validity of **any** studies that derive quantitative cover data from UUV photographs because of putative errors in photographic imagery due to parallax and geometric distortion. This blanket criticism extends to a substantial list of contributions from many different authors and research groups who have used UUVs to estimate benthic community structure on MCEs in the Caribbean (e.g. Singh et al. 2004, Armstrong et al. 2006, Locker et al. 2010, 2016, Armstrong & Singh 2012, Etnoyer et al. 2016, Reed et al. 2018, 2019), the wider tropics (e.g. Bare et al. 2010), and on deepwater reefs world-wide (e.g. Cánovas-Molina et al. 2016, Walker et al. 2021) with the summary statement: 'Thus, imagery collected by these vehicles, in the absence of post-processing, should only be used for qualitative descriptions, or presence/absence studies' (Lesser & Slattery 2021, p. 233). While their critique is specifically directed at perceived errors associated with UUV photographic imagery, it does not provide a broader comparison of the UUV-based method with the method that they have used to provide the percentage cover data that led to the SIH: specifically, *in situ* point-intercept visual surveys by divers using technical diving methods. The analysis that follows is a comparison of these 2 methods for generating the data that have informed our understanding of the SIH. It should be noted that this methodological comparison is limited to studies of Caribbean MCEs (although the SIH has since been expanded to a global phenomenon; Lesser & Slattery 2018) and to the most commonly cited benthic abundance metric for sponges, percentage cover of the reef substratum, which is derived from point-intercept estimates from replicate quadrats for both methods (Scott & Pawlik 2019). The relative merits of other metrics of abundance, such as density and biomass per unit area, have been reviewed in detail elsewhere (Pawlik et al. 2015). The topic of photographic image distortion, and its potential effect on point-intercept estimates, will be discussed last (see Section 7).

2. SURVEY DEPTH

Perhaps the most important thing to note in comparing the 2 methods that have been used to inform our understanding of mesophotic benthic community structure, specifically regarding the SIH, is that the UUV-based method permits surveying through the entire span of mesophotic depths (30–150 m) and beyond, while the tech diving method has only allowed replicated surveys through the top half of the mesophotic (to 91 m). Tech diving has been used to explore mesophotic reefs and collect benthic samples at greater depths (Rouzé et al. 2021), but replicated survey studies done using tech diving methods have been limited to the upper-half of the mesophotic (e.g. Pérez-Rosales et al. 2021). The UUV-based method is depth-limited only by the length of cables used to tether an ROV to the ship above it (or not at all for an AUV), and by whatever pressure limitations there are for the equipment on the vehicle, both of which are routinely operational to depths well below the bottom of the mesophotic zone (150 m). On the other hand, the use by divers of rebreathers and trimix gas that has been standard for technical diving in the past several decades has placed a diver-safety depth limit of 91 m on these methods (Lesser & Slattery 2011). While some tech diving studies claim to observe trends in benthic cover by observing the substratum below 91 m, data were not collected below these depths in any reported studies.

Equally important in assessing the relative merits of the 2 methods for surveying mesophotic reefs are the highly divergent results obtained for sponge cover at the maximum survey depth for tech diving (91 m) and the same depth using the UUV-based method. The 3 tech diving studies reported a mean of 79.3 % cover of sponges at 91 m depth for sites in the

Bahamas and Little Cayman Island (Lesser & Slattery 2011, Slattery & Lesser 2012), while 15 survey studies using the UUV-based method reported a mean of 9.3% cover for sites at the same depth interval (90–100 m) in the Bahamas, Jamaica, Puerto Rico, St. Thomas (USVI), and the Gulf of Mexico (Fig. 1; means are significantly different, *t*-test, $t_{16} = 16.2$, $p < 0.00001$; Scott & Pawlik 2019). The SIH predicts an increasing abundance of sponges throughout the entire mesophotic zone, so if sponge cover is already reported at the very high level of ~80% mid-way through this zone, sponge cover in the range of 90–100% would be expected below that point to 150 m. Considering the low variation in cover among the 15 survey studies done using the UUV-based method (Fig. 1), it would seem unlikely that only sites in the Bahamas and Little Cayman surveyed by tech diving would have consistently higher sponge cover than the sites in other parts of the Caribbean, although this is a possibility that should be explored (see Section 8). However, photo-transect surveys (10–250 m) performed off Lee Stocking Island by Liddell et al. (1997) reported maximum sponge cover of 11.1% at sites along the same reef drop-off and <10 km from Bock Wall where Slattery & Lesser (2012) used tech diving methods (30–91 m) and reported maximum mean sponge cover near 80%. Potential reasons for the contrary results shown in Fig. 1 will be considered in the following sections, and include some combination of low and unequal replication, sampling bias, and the effects or constraints of working under hazardous conditions.

3. SAFETY

Technical diving is a high-risk activity. At mesophotic depths, the nitrogen in compressed air causes narcosis, which may include euphoria, limits on the power of association, and a tendency to fixate on ideas (Bennett & Mitchell 2009). To mitigate these problems, technical divers use a mixture of gases designed to avoid narcosis, although individual diver responses to high pressure nervous syndrome may vary along with the relative effectiveness of gas mixtures (Bennett & Mitchell 2009). Despite the considerable training that is generally required before engaging in tech diving, fatalities regularly occur, with 83 deaths of divers using rebreathers in the period 1998–2006, or an average of >10 yr^{-1} (Denoble 2009). When actively tech diving, divers must be regularly monitoring their own equipment gauges, and the location and status of their dive buddy, which divides the time they would otherwise spend focused on their work or research tasks. In addition to the potential for cognitive impairment and the need for gauge- and buddy-monitoring, the working time at the deepest depth of 91 m is on the order of 20–30 min, with only 1 such dive per day (D. Kesling pers. comm.); hence, the time available to complete complex surveys of the benthos and fish communities is very short. It should also be noted that the adverse impact of diving stress on *in situ* benthic survey performance has been demonstrated, even for shallow-water diving (Benedetti-Cecchi et al. 1996). Nevertheless, to gather the data used to support the SIH, tech divers laid out 3 transect lines (30 m each) along the 91 m depth contour, then visually recorded the benthos to the taxonomic level of species under 100 points within each of 15 quadrats (see Section 6; Lesser & Slattery 2011).

Compared to tech diving, the operation of a UUV is relatively safe, although it does include the usual hazards associated with working on a research vessel and tending the tether to which the ROV is attached (if the unit is not fully autonomous). Unlike tech divers taking visual surveys, AUV cameras automatically record a permanent archive of digital images and video of the benthos over the entire mesophotic range and without variation in performance with depth.

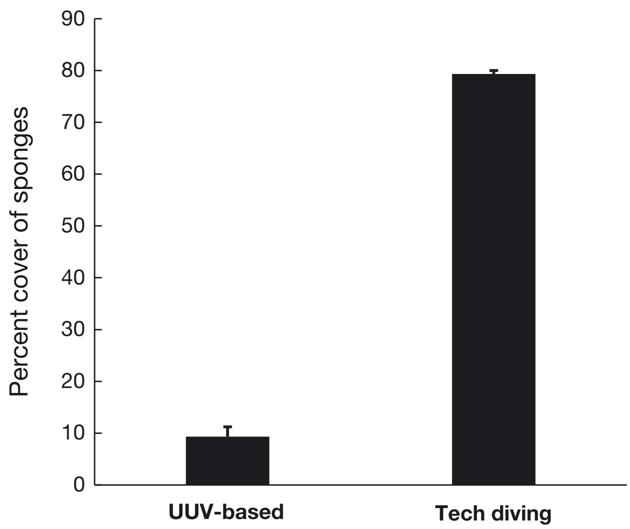

Fig. 1. Percentage cover of sponges from point-intercept estimates within quadrats at 90–100 m depth on mesophotic reefs using the unmanned underwater vehicle (UUV)-based method (photo-quadrats) and the tech diving method (*in situ* visual surveys of quadrats). Mean and SE are shown for n = 15 survey studies using the UUV-based method in the Bahamas, Jamaica, Puerto Rico, St. Thomas (USVI), and Gulf of Mexico, and n = 3 survey studies using the tech diving method for the Bahamas and Little Cayman Island. See Section 2 and Scott & Pawlik (2019)

4. REPLICATION

For both methods under discussion here, the quadrat is the unit of replication, with counts of point-intercepts within the quadrat providing estimates of percentage cover, whether recorded visually by a tech diver *in situ*, or from a photograph taken by a UUV. An important difference, however, is that quadrats recorded by tech diving were placed along transect lines at the same depth, because of the constraints of the diving method, so that transect lines were specifically laid out at depth contours of 30, 46, 61, 76, and 91 m (Lesser & Slattery 2011, Slattery & Lesser 2012, 2021). UUV dive tracks, however, were not similarly constrained, and moved at any angle relative to vertical and into the lower half of the mesophotic zone and deeper. Therefore, the data recorded by tech divers were discrete for specific depths, while the UUV data were recorded continuously across depths. This explains why UUV data were presented in datasets that are binned by depth (e.g. 10 m bins in Scott et al. 2019). While this issue of discrete vs. continuous data is not inherently problematical, when combined with the depth limitations of tech diving, it limits verification in data trends because the data set from tech diving has both lower resolution (15–16 m gaps between transect contours) and it is bounded at its lower depth (91 m). For example, it was repeatedly claimed, without survey data, that sponge abundance continued to increase with greater depth in the lower half of the mesophotic, based on the visual appearance of the benthic communities to tech divers looking down from 91 m, and this became a major component of the SIH (Lesser & Slattery 2019), yet when UUV-based surveys were performed below 100 m depth in Puerto Rico, sponge abundance decreased below 100 m and continued to decrease below 150 m (Scott et al. 2019).

Additionally, for tech diving, the level of replication declines considerably with depth, again because the safety limitations of the diving technique restrict working time, dropping from 90 replicate quadrats at 30 m to 15 replicate quadrats each at 76 and 91 m. Not only does this introduce a potential sampling bias (discussed in Section 5), but it also results in levels of replication that are considerably lower than for similar depths reported by UUV studies. For example, for the depth range of 70 to 100 m, cover data for the tech diving method were based on 30 quadrats each for the Bahamas, Grand Cayman, Little Cayman, and Honduras (Slattery & Lesser 2021), while data from UUV photographs over the same depth range were based on 148 and 250 quadrats from Puerto Rico South and West, respectively (Rivero-Calle 2010, Pawlik & Scott 2019) and 87, 66, and 93 quadrats from Puerto Rico, St. Thomas, and Flower Garden Banks (Gulf of Mexico), respectively (Scott et al. 2019). The accuracy of any estimate is improved with greater replication (Greig-Smith 1983, Meese & Tomich 1992, Dethier et al. 1993), and for consideration of the SIH, replication is 2- to 9-fold higher for the UUV-based method than for the tech diving method.

Finally, it should be noted that for the tech diving surveys that have been used to inform the SIH, there has been no replication at a given location, with technical dives performed at a single site (e.g. Bock Wall, Lee Stocking Island, Bahamas), as indicated by Lesser & Slattery (2011, p. 1857): 'The logistical constraints of diving to mesophotic depths did not allow for quantitative spatial replication within the region, but within-site variation (i.e. depth) and temporal variation (i.e. year) were accounted for in our analyses.' Contrarily, most UUV-based studies include multiple dive tracks at a given location, which may cover a considerable survey distance. For example, the data presented by Scott et al. (2019) for Puerto Rico, St. Thomas, and Flower Garden Banks were from a total of 9, 24, and 11 ROV dive tracks, respectively. Sample replication over a greater spatial area will give a more accurate mean estimate of benthic cover for that location by better capturing the full range of relative abundances of organisms, and less potential influence by a single site with an unusually high or low cover of one or more benthic groups. Past studies of the relative merits of ecological survey methods have consistently agreed that techniques that result in both greater replication and more extensive sampling are always more desirable in providing estimates of percentage cover that approach the true value for percentage cover (Southwood 1978, Greig-Smith 1983, Meese & Tomich 1992, Dethier et al. 1993). Therefore, more accurate estimates of benthic cover in the mesophotic zone are likely to have come from UUV-based surveys, which have greater replication over a greater spatial area, than from tech diving surveys.

5. SAMPLING BIAS

Accurate estimates are dependent on a sampling procedure that is not biased for any particular benthic group. There is an extensive literature on the relative advantages of variations of methods to assess percentage cover in terrestrial, intertidal, and subtidal habitats (Southwood 1978, Greig-Smith 1983, Foster et al. 1991, Meese & Tomich 1992, Dethier et

al. 1993). Within the quadrat, the matrix of points used for counting is usually fixed, so if the process is to be influenced by bias, it is more likely to occur with the placement of the quadrat. Quadrat placement in a sampling scheme is often referred to as 'random' when it is not. Truly random assignment requires a specific randomization method (random number generation, dice throw, coin toss) to determine the quadrat position along a transect line, but this is seldom done because of the complexity it adds to the survey process. Instead, the quadrat corner may be consistently placed along the transect line (e.g. at every 3 m mark) prior to collecting data. Observer bias can arise if the surveyor is allowed to exercise control over placement of the quadrat anywhere along the transect line, as there is a natural, and perhaps subliminal, tendency to place the quadrat over areas of higher abundance of the organism of interest. Observer bias is not uncommon to *in situ* survey methods (e.g. Leujak & Ormond 2007), and is generally overcome with high levels of replication.

Among the UUV-based methods, the AUV has the least potential for sampling bias, because high-resolution photographs of the substratum are taken continuously and automatically (as a function of strobe recharge time or the camera timer) at intervals between 2.5 and 60 s as the vehicle traverses a haphazard track along the substratum (e.g. Rivero-Calle 2010). Greater control may be exercised by the operator of an ROV steering the vehicle to maintain a track that maximizes time over a substratum of interest (e.g. hardbottom versus sand plain) with the number of replicate photographs mostly dependent on the amount of time the ROV spends within a particular depth bin on a particular dive track (e.g. Scott et al. 2019). For this reason, replication can be uneven across bins, but this unevenness is haphazard in its distribution. While one bin may have a low level of replication, adjacent bins may have higher levels of replication, and relative trends in the data can be taken into account. It should also be noted that for UUV-based survey studies, a set of selection criteria is applied to the initial set of survey photographs to exclude those that are out of focus, too close to the substratum, at an oblique angle to the substratum, over inappropriate substratum (e.g. sand or mud), or clearly of non-random interest to the ROV operator (e.g. Scott et al. 2019).

For the tech diving survey method, there are potential issues of sampling bias at 2 levels: site placement and quadrat placement. As indicated above, for each location that tech divers sampled, there was only a single site. It is not clear how these dive sites were chosen, except that they were steep walls that were conducive to vertical tech diving profiles and that the surveys were conducted on hardbottom. Under these circumstances, it is reasonable to surmise that site selection would favor a reef with higher cover of a benthic organism of interest than another reef with lower cover.

Once the site had been chosen by tech divers, quadrats were placed at 'random points' along 30 m transect lines, also placed at 'random,' along a particular depth gradient (e.g. Lesser & Slattery 2018). Because of the time constraints of tech diving discussed previously, it is unlikely that a strict *a priori* randomization method was used to place transect lines along a set depth, and then along the lines once they were in place.

We propose that some combination of the 2 levels of sampling bias described above, along with low site and quadrat replication, likely explain the much higher percentage cover of sponges estimated using the tech diving method than using UUV-based methods (~80 vs. ~10%, Fig. 1). Single sites chosen for tech diving estimates (Lesser & Slattery 2011, 2018, Slattery & Lesser 2012) may have had unusually high sponge cover, particularly in the mid-mesophotic, or low-replicate, non-random quadrat sampling in the mid-mesophotic may have generated unusually high sponge cover estimates. Indeed, evidence of the latter problem may be apparent in the 4- to 8-fold lower percentage cover of sponges at shallower depths recorded using tech diving methods as replication levels increased 6-fold (from n = 15 quadrats for 91 m to n = 90 quadrats for 30 m); as more quadrats were taken along the same transect lines, greater replication would result in more accurate estimates. This sampling bias was consistent in all studies, with much higher levels of replication at shallower depths (n = 90 quadrats at 30 m) and lower replication at the deepest depths sampled (n = 15 quadrats at 78 and 91 m), which again, was only midway through the mesophotic zone. UUV-based methods are unlikely to be influenced by similar sampling biases, and when combined with higher levels of replication and greater spatial sampling with access to the full mesophotic zone, are more likely to provide accurate estimates of benthic cover.

6. QUADRAT SCORING AND RE-ANALYSIS

Photographs that are taken using the UUV-based survey method and used as quadrats to assess the

benthic community of the mesophotic zone have several advantages over the visual census data obtained by divers using the tech diving method. First, photo-quadrats are generally available for taxonomic authorities to review at their leisure, while visual survey methods require that each of the survey divers is an expert in the identification of the organisms that are likely to be observed within the quadrats under hazardous tech diving conditions. For example, Slattery & Lesser (2021), reporting data that were taken over a decade earlier, identified from their quadrats and recorded in the field 72 species of sponges, 16 species of hard corals, and 14 species of gorgonian corals, among other benthic organisms, while working under the time constraints of 20–30 min tech dives along 30 m transects (n = 3) at 91 m depth in the Bahamas and Cayman Islands. On some of these same dives, they identified 24 species of reef fishes in 12 families along 30 × 2 m belt transects, with 10 min observation periods to check for site specificity among fishes (Lesser & Slattery 2011). In our experience, it would be difficult to train more than 1 diver to a similar level of taxonomic sophistication, let alone a pair, or a team of divers, and it would be asking a lot to expect divers to split their concentration between the taxonomy of benthic organisms and fishes and their depth and pressure gauges while tech diving at 91 m depth. Further, it is well known that the mesophotic zone is inhabited by many rare and endemic taxa that only a specialist would be able to identify (e.g. Turner et al. 2017). In comparison, photographs taken using the UUV-based method can be inspected at any time, by more than one taxonomic expert, even sent around the world electronically for the purpose of confirming identity. Scoring consistency can also be checked among experts recording the data by having the same quadrat scored by different experts, a form of validation that is not possible for *in situ* visual surveys. Of course, many invertebrate taxa (particularly sponges) cannot be identified visually by divers or using photographs but require a tissue sample for microscopic or molecular analyses (e.g. Díaz et al. 2019, 2021), and in this regard, the tech diving method has an advantage because benthic samples can be collected.

Second, unlike recorded notations from visual surveys, photo-quadrats are subject to long-term archiving and re-analysis. Not only does this allow for subsequent checks for errors, archived photographic data provide a particularly important time-series record to assess changes in the mesophotic community in response to climate change, the spread of pathogens, invasive species, etc. The photographs from which UUV photo-quadrats are derived are also accompanied by lower-resolution video, which can be helpful in getting a broader view of the habitat and may be used for outreach and education (e.g. via YouTube; see Section 7).

7. IMAGE DISTORTION

Percentage cover estimates of the benthos derived from photographs using the UUV-based method have been criticized as generally erroneous because of parallax and geometric distortion caused by differences in the angle between the plane of the camera lens and the substratum (Lesser & Slattery 2019, 2021). These criticisms are incorrect, as previously explained (Scott et al. 2019). Point-intercept estimates are done using dimensionless points, not associated with measurements of area, and therefore not subject to error caused by optical distortion. As summarized by Zvuloni & Belmaker (2016), all visual sampling can be classified into 1 of 2 categories: plot-based techniques, in which sampling units are defined by specific areas, and plotless techniques, in which sampling units are lines or points, with the latter methods including linear transect, linear point-intercept and quadrat point-intercept. A quadrat point-intercept estimate of percentage cover for each benthic group from a replicate photo-quadrat is calculated by summing the number of occurrences of that benthic group under the points cast over the photograph and dividing that sum by the total number of points, then expressing that proportion as a percentage. As part of the usual protocol, and because the UUV may be at a variable distance from the substratum for each photograph, the photo-quadrat is standardized to size using the distance between 2 laser points cast by the UUV in the image, but this is done to allow for consistent identification of benthic organisms at the same relative scale. Further, as part of the standard selection criteria applied to the initial set of survey photographs, any unusable images, including those taken at oblique angles to the substratum, are excluded from analyses. Minor differences in the angle of the substratum relative to the plane of the camera lens, or tilt, will not alter the effectiveness of this method to provide an estimate of percentage cover (and camera tilt is likely to be less than the differences in the angle of the complex substratum within the quadrat, see below). Additionally, as the UUV moves along its track, the tilt of the camera relative to the substratum changes in a haphazard manner as photographs are taken, so the effect of

tilt is not consistent across the survey. For some AUVs, the platform is set at a constant distance from the seabed, and the pitch, yaw, and roll are recorded with every image, which can be used to assess the usefulness of the image for subsequent analyses (Rivero-Calle 2010).

The erroneous criticisms of percentage cover estimation from photographs by Lesser & Slattery (2021) are similar to those of Lesser & Slattery (2019), in that the analyses and citations used to support these criticisms are about metrics that require accurate measurement of **area** from photographs (i.e. plot-based techniques, Zvuloni & Belmaker 2016), for which optical distortion can be a problem. Lesser & Slattery (2019) cited the work of Parry et al. (2002), who estimated the abundance of crustaceans, worms, bivalves, and associated burrows in muddy sand by mapping and counting all of the features in the entire area of photographs taken with UUVs. Lesser & Slattery (2021) cited Wakefield & Genin (1987, p. 469), a methods paper for the implementation of a grid pattern over a photograph for '…accurate and precise calculations of sizes and densities of animals and other objects.' Like Parry et al. (2002), Wakefield & Genin (1987) provided methods for correcting for area when taking oblique photographs from a sled moving over the muddy plains of the deep sea. Similarly, a study by Morgan et al. (2010), which was referenced repeatedly by Lesser & Slattery (2021) for 'post-processing of imagery,' was about assessing landscapes using planar photographs taken obliquely from airplanes, including the size, shape, pattern, and texture of landscape features. Tusting & Davis (1993, p. 157) provided methods for 'estimating the scale of the study site and the size of individual specimens' from photographs from benthic surveys, again using planar figures. Unlike area-based metrics, percentage cover estimates derived from point-intercept methods do not rely on an accurate proportional representation of area within the photo-quadrat as discussed in these references. Indeed, we believe that Lesser & Slattery (2021) have confused percentage cover with density (number per unit area) in their discussion, as quoted here: 'All calculations of abundance based on this larger area would be incorrect because the assumed area of the image, or any overlaid quadrat in the image (*sensu* Scott et al. 2019), to normalize the imagery is smaller than the actual area, causing inflated estimates of abundance, percent cover, and/or biomass' (Lesser & Slattery 2021, p. 233).

Additionally, the techniques for 'post-processing of imagery' that are appropriate for area-based metrics and promoted by Lesser & Slattery (2021) would not apply to the complex 3D substrata common to most mesophotic reefs when photographed in 2 dimensions by a single camera. In addition to referencing area-based metrics such as density, size, and shape, the supporting citations in Lesser & Slattery (2021) all refer to photographs of planar substrata or landscapes; indeed, the first sentence of the 'Technique' section of Wakefield & Genin (1987, p. 470) reads: 'The basic assumptions of our approach are (1) a flat substratum with any measured dimension lying within its plane…' However, the substrata of mesophotic reefs are rarely flat. Consider Fig. 1 in Lesser & Slattery (2021), which shows a diver using a 'quadropod' stand to take a photograph with a camera held at fixed distance from the substratum (Fig. 1A) and a resulting 'typical' photo-quadrat image (Fig. 1B, not taken from the position in 1A). The topographical complexity of the substratum is clearly evident in both photographs: in Fig. 1A, the square base of the quadropod is contacting the boulder-strewn substratum along less than half of the base perimeter, with marked deviations from the plane of the base of greater than 15 cm down to low rubble heads and into sand holes; in Fig. 1B, a furrow runs through the horizontal center of the image and into a deep hole fading to darkness on the center-right. These are not images of planar surfaces for which 'post-processing' was designed or would be effective (Wakefield & Genin 1987, Morgan et al. 2010), and the actual substratum area under each of these 1 m^2 quadrats is substantially more than 1.0 m^2. While the legend to their Fig. 1 indicates that no additional correction was required for these images beyond refraction error, no amount of 'post-processing' of a single-shot image would have provided accurate area-based metrics from these photographs, because of the steep vertical surfaces among the topographically complex substrata within the quadrats. The foregoing constraints are equally true for *in situ* visual assessments of quadrats, as were used by tech divers to formulate the SIH (Lesser & Slattery 2011). It should be clear, then, that estimates of cover using point-intercept methods on topographically complex reef substrata have the distinct advantage over area-based metrics (such as density) because an accurate estimation of area is not required. Area-based metrics such as biomass per unit area are particularly important for understanding the impacts of taxa on ecosystem processes (particularly biomass per unit area, see Pawlik et al. 2015), but require photographs from multiple camera angles and subsequent photogrammetric analyses for proper measurements on topographically complex substrata (see methods of Olinger et al. 2019).

Returning to the conclusion of Lesser & Slattery (2021) that the use of the UUV-based point-intercept method will result in overly high estimates of percentage cover (quotation above, p. 233), it is interesting that Scott et al. (2019) and other UUV-based methods (e.g. Rivero-Calle 2010) have provided estimates of sponge cover that are 8-fold lower than visual surveys done using the tech diving method for the middle of the mesophotic zone (90–100 m; Fig. 1). To further illustrate these differences in sponge abundance, video clips at 20 m intervals, moving upward from 160 to 40 m for 3 ROV tracks off Puerto Rico and 1 manned submersible track off Roatan, Honduras, are shown in a YouTube video, along with comparative graphs derived from the tech diving and ROV-based methods (https://youtu.be/NSkN0NkJwc0). While the resolution of the video images is of lower quality than the photographs from which photo-quadrat data were derived, the video provides greater visual breadth to confirm the veracity of the photo-quadrat results (Scott et al. 2019).

8. CONCLUSIONS

We reject as erroneous the notion that quantitative point-intercept estimates are invalid when derived directly from photographs taken by UUVs on transects through the mesophotic zone (Lesser & Slattery 2021). Instead, the UUV-based method for assessing mesophotic reef community structure is more likely to provide accurate estimates of benthic cover than the tech diving method for the reasons described above (summarized in Table 1). Eight-fold higher estimates of sponge cover in the 90–100 m depth range of the mesophotic zone from tech diving surveys relative to UUV-based surveys are likely due to some combination of low and unequal replication, sampling bias, and the effects or constraints of working under hazardous conditions. To help understand the reasons for these disparate results, and to further test the SIH for the full mesophotic zone, UUV-based surveys should be conducted at the same sites in which tech diving surveys were performed, and the results compared.

The tech diving method has advantages that make it an important tool in mesophotic exploration, particularly related to direct inspection and collection of samples for taxonomic identification (e.g. Hoarau et al. 2021, Rouzé et al. 2021). Further, some of the aforementioned problems associated with the formulation of the SIH may be remedied by tech divers using photo-quadrats (e.g. Pérez-Rosales et al. 2021) instead of visual survey techniques. Photographs taken by divers with a photo-quadrat stand have a set distance and orientation from the camera, and if properly lighted, can be of very high quality. The relative speed of photographing quadrat frames along a transect line as opposed to visually recording point-intercept data from quadrats would allow for greater replication over the same period of time during short tech dives.

Overall, it is puzzling that so many specific hypotheses about the ecology of the mesophotic zone have been advanced with so few data and without sampling the full range of the mesophotic zone. Paraphrasing a summary statement from a recent review of the very limited data available to date, there is insufficient evidence to support generalized hypotheses about community structure across the full range of the mesophotic zone (30–150 m) and across the Caribbean (Scott & Pawlik 2019).

Table 1. Comparison of 2 methods used to study benthic cover on Caribbean mesophotic reefs within the context of the sponge increase hypothesis (unmanned underwater vehicle [UUV]-based method using point-intercept estimation from photo-quadrats; tech diving method using point-intercept estimation from visual scoring of quadrats)

	UUV-based method	Tech diving method
Maximum survey depth	>150 m, beyond mesophotic	91 m, mid-way through mesophotic
Safety hazard while collecting data	Minimal	Considerable
Distraction while collecting data	None	Considerable
Number of replicate quadrats	High	Low
Vertical spacing of quadrats	Continuous	Discrete
Spatial replication within a location	Yes, multiple tracks	No
Change in replication across depth gradient	Haphazard	Decreases, constant
Placement of replicate quadrats	Haphazard	Biased with depth?
Requires taxonomic expert *in situ*	No	Yes
Quadrat data can be independently validated	Yes	No
Quadrat image can be archived	Yes	No

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