



Quantifying sponge communities from shallow to mesophotic depths using orthorectified imagery

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Abstract

Mesophotic coral reefs are estimated to represent up to 80% of the total areal coverage for coral reefs worldwide. Quantifying mesophotic coral reef community structure and function, at multiple spatial and temporal scales, and the ability to monitor these attributes repeatedly and accurately, is an ecological priority. Recent discussions on the relative merits of remotely operated vehicles and autonomous underwater vehicles (ROVs and AUVs, respectively) versus the use of technical divers using quadrats or photoquadrats to obtain quantitative imagery undervalues the distinct and important complimentary roles that both approaches bring to the study of mesophotic coral reefs. However, all platforms must adhere to fundamental photogrammetry principles to accomplish the goal of accurate and repeatable surveys of coral reefs. Here we show that quantifying the projected surface area of sponge populations for a tropical coral reef on Puerto Rico using ROV imagery, not originally collected for ecological characterizations, requires specific screening guidelines to ensure the images are orthogonal and processed to obtain orthorectified images for the quantification of benthic communities. This is required to minimize multiple sources of error that could confound quantitative estimates of percent cover, biomass, and/or abundance of benthic taxa on shallow and mesophotic coral reefs using plot, or plotless, designs.

Keywords Mesophotic · ROV · AUV · Geometric distortion · Photogrammetry · Imagery · Plotless design

Introduction

Interest in mesophotic coral reef ecosystems (MCEs) over the past twenty years or more has increased significantly (Loya et al. 2016), with one of the most profound findings being that MCEs are estimated to represent ~80% of the areal coverage of the world's coral reefs (Pyle and Copus 2019). At a time when shallow coral reefs are seeing significant declines globally (e.g., Hughes et al. 2017), the

structure and function of MCE communities may also have significant implications for coral reef resilience in the future (Slattery et al. 2011). Cataloging the extent and biodiversity of MCEs (30–150 m) requires quantitative community characterizations to understand their inherent ecological function, and their ecological function related to shallow (<30 m) coral reefs. The advantages and disadvantages of different methods used for quantifying biodiversity, changes in community structure (e.g., abundance and percent cover), species turnover, and therefore the functional differences between communities on coral reefs have long been a topic of discussion amongst coral reef ecologists (Loya 1978; Dodge et al. 1982; Jokiel et al. 2015) and continue to be evaluated and developed (Bryson et al. 2017; Barrera-Falcon et al. 2021; Kuo et al. 2022; Smith et al. 2022). The merits of these techniques have recently been argued relative to their application on MCEs (Lesser and Slattery 2021; Pawlik et al. 2022). However, if basic photogrammetric principles for collecting and processing underwater imagery (Lesser and Slattery 2021) are violated (e.g., Pawlik et al. 2022) then systemic errors in downstream analyses and community descriptions can occur (e.g., Scott et al. 2019).

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One of the increasingly dominant taxa on Caribbean coral reefs are sponges, which increase in abundance, biomass and biodiversity with increasing depth from shallow to mesophotic depths (Slattery and Lesser 2012; Lesser and Slattery 2018, 2019; Figs. 1, S1). These observations resulted in the establishment of the “sponge-increase hypothesis” (Scott and Pawlik 2019; Supplemental Material) the assessment of which has become a focus of MCE ecology (Lesser et al. 2018). Sponges have multiple functional roles on coral reefs such as providing food and habitat for many ecologically and economically important coral reef species (Diaz and Rützler 2001; Bell 2008), reef stabilization (Bell 2008) and benthic-pelagic coupling (Lesser 2006; Lesser and Slattery 2013;

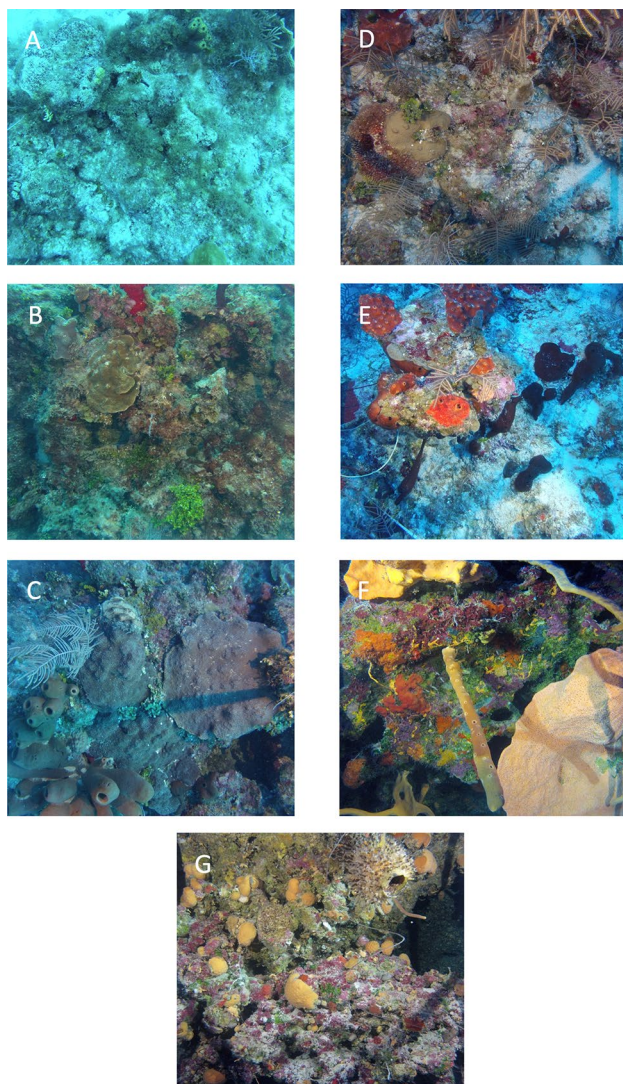


Fig. 1 Photographs of representative benthic communities from shallow to mesophotic depths on Grand Cayman Island; **A** 15 m, **B** 23 m, **C** 30 m, **D** 46 m, **E** 61 m, **F** 76 m, **G** 91 m. Images from each depth qualitatively represent sponge diversity and cover at that depth and are typical of multiple locations throughout the Caribbean Basin

Lesser et al. 2018). Sponges are conspicuous on MCEs (Lesser et al. 2009, 2018; Slattery and Lesser 2012, 2019) with communities structured primarily by depth-dependent changes in irradiance and trophic resources (Lesser et al. 2009, 2018; Lesser and Slattery 2019, 2020; Macartney et al. 2021a, b). Upper MCE (~30–60 m) communities represent a transition zone between shallow and lower mesophotic (~60–150 m) communities, while lower MCEs harbor many endemic species that contribute to the unique community structure of lower MCEs (Lesser et al. 2018, 2019). These depth-dependent definitions reflect consistent observations that changes in zonation patterns, and faunal breaks, generally occur at underwater irradiances between the 10% and 1% optical depths, or the mid-point and bottom of the euphotic zone (Lesser et al. 2018, 2019). Where a distinct faunal break at 60 m has been reported (Lesser et al. 2019) sponges increase in their percent cover, biomass, and biodiversity (Slattery et al. 2012; Lesser et al. 2018, 2019). Given the increasing ecological importance of sponges on shallow and mesophotic coral reefs, process related hypothesis testing must begin with an accurate description of sponge communities over the depth range of study. Here, we examine the utility of ROV/AUVs as platforms to provide high-quality, orthogonal, imagery from which orthorectified images can be used for the quantification of benthic communities along the shallow to mesophotic depth gradient. To do this we assessed the quality of imagery from ROV dives on MCEs in Puerto Rico and the United States Virgin Islands (Battista et al. 2017) previously used to describe mesophotic communities (Scott et al. 2019). Specifically, we quantified the sponge component of these communities using plot and plotless approaches and interpreted the data in the context of available transect and photoquadrat data from similar reef systems where the distribution and abundance of sponges as a function of depth were available. From this analysis we conclude that all community studies conducted using AUV/ROVs, or diver transects using quadrats, photoquadrats or video transects require orthogonal (=perpendicular), imagery to establish a sampling unit size suitable for the study, usable scale throughout the image and point density grids with an even distribution of points throughout the image for accurate and quantitative community descriptions of either cover or density (Butler et al. 1991; Durden et al. 2016; Vallès et al. 2019; Lesser and Slattery 2021). In the absence of specialized techniques (e.g., stereom imagery and photomosaics), imagery that is orthorectified is a basic requirement of photogrammetry irrespective of whether one is using a plot, or plotless, design and whether the data is normalized to area or not (Morgan et al. 2010; Durden et al. 2016; Zvuloni and Belmaker 2016).

Methods

Raw ROV imagery for Puerto Rico and St. Thomas in the United States Virgin Islands (USVI) were obtained from the National Oceanic and Atmospheric Administration, National Centers for Coastal Ocean Science (NOAA NCCOS) and were part of their seafloor characterization of the United States Caribbean program that included using bathymetric multibeam sonar surveys for seafloor mapping (Battista et al. 2017). As part of this program an ROV was used to visually identify, and qualitatively describe seafloor objects and habitats (i.e., “ground-truthing”) detected by the multibeam sonar (Battista et al. 2017). A detailed description of image acquisition, and global positioning system (GPS) coordinates for all ROV tracks can be found in Scott et al. (2019, their Table S1). Briefly, at each location, multiple ROV dives were conducted, but did not consist of parallel transects at pre-determined depths. Instead, the data consisted of multiple vertical dives from shallow to mesophotic depths, and beyond, taking random images at numerous depths without a predetermined, ecologically driven, plan of data acquisition (sensu Loya 1978). During each ROV dive digital photographs were taken of the substratum approximately every 30 s using a 10-megapixel camera with a maximum 80 W s^{-1} strobe mounted on a tilting platform. Parallel lasers spaced 10 cm apart were projected onto the field of view of the camera to provide scale. No correction for refraction error was required for this camera.

For our study all images were subject to the following screening process before any analysis. Raw imagery from Puerto Rico and St. Thomas, USVI were screened for their suitability (i.e., orthogonal imagery) based on photogrammetric and ecological criteria consistent with discussions in Lesser and Slattery (2021), and include the following:

1. Max depth of 150 m.
2. Associated navigation data that includes ROV depth and altitude above substratum where the ideal ROV altitude is ~ 1.2 m, yielding an image of $\sim 1.25\text{--}1.5 \text{ m}^2$.
3. No obviously oblique imagery (e.g., no “horizon” in image, obviously sloped habitat, or looking at sides of macrofauna in image).
4. No 100% sandy bottoms, or 100% smooth consolidated coral pavement or isolated patch reefs.
5. Image completely in focus with adequate strobe coverage in image, and a usable laser scale in image.

Images that essentially complied with the screening criteria were then re-analyzed using two approaches: (1) a point-count overlay, using a random 50 point density grid over the entire image was established using Coral Point

Count with Extensions (CPCe) (Kohler and Gill 2006), in a plotless design (sensu Loya 1978) that analyzed the relationship between percent projected surface area of sponges versus depth using Model I linear regression, and (2) each image was also analyzed by placing a $1.0 \times 0.75 \text{ m}$ quadrat within the image using CPCe, based on the 10 cm scaling lasers in each image, and then the quadrat was overlaid with a 25 point density using a stratified random density pattern and described in Scott et al. (2019) as a plotless design (but see Supplemental Material). Differences in our protocol from Scott et al. (2019) include: (1) data were not binned (a.k.a., bucketing) which is a non-random data processing technique used to reduce the “noise” in data, or to smooth data, (2) since the orthogonal images were already screened (see above), the 0.75 m^2 quadrat that was automatically placed in the middle of the image by CPCe was not moved within the image as described by Scott et al. (2019), to avoid any potential user bias in the placement of the quadrat in the image, and (3) five images that otherwise passed screening were too close to the substratum to place an entire $1.0 \times 0.75 \text{ m}$ quadrat in the image. For these images we measured and analyzed the entire area available using a 25 point density grid. All statistical analyses were conducted using JMP Pro v. 16.1.

To illustrate the principles related to geometric distortion in images caused by changes in camera, and/or substrate angle a series of photographs were taken using the same photoquadrat described in Lesser and Slattery (2021, their Fig. 1) on a flat substrate at multiple camera angles from 0° to 50° in 10° increments. Area calculations were based on projecting, and marking, the four corners of the 2D image onto the substrate by looking through the camera lens, as camera angle changed. The four corners were then connected on the substrate using chalk (for presentation purposes the visualization of chalk lines was digitally improved in Microsoft PowerPoint®). The linear distances of the top, base, and sides of the 1 m^2 photoquadrat at 0° , and the top, base, sides and height of the trapezoid formed at each 10° change in camera angle of the photoquadrat up to 50° were measured. Formulae for calculating the area of a square and trapezoid were then applied as appropriate. Photographs of the quadrats at a camera angle of 0° and 50° are presented to illustrate the process and results.

Results

For the imagery from St. Thomas, USVI 253/1449 images passed screening, or $\sim 18\%$, with a depth range of 39–104 m. Most of the images failed screening because they were not orthogonal. No images were available for shallow depths < 30 m, and images for upper to lower mesophotic depths were represented but not evenly replicated (i.e., 20–30 m, $n = 0$;

30–40 m, $n=5$; 40–50 m, $n=31$; 50–60 m, $n=50$; 60–70 m, $n=71$; 70–80 m, $n=45$; 80–90 m, $n=25$; 90–100 m, $n=5$; 100–110 m, $n=1$, 110–120 m, $n=0$, 120–130, $n=0$; 130–140 m, $n=0$; 140–150 m, $n=0$). The benthic habitats of the seafloor northwest (~ 25 NM) of St. Thomas near the shelf break (i.e., 100 m bathymetry line) captured by the imagery primarily consisted of unconsolidated carbonate sediments interspersed with flat hard pavement, hard pavement with sediment channels, and hard pavement colonized by hard and soft corals with occasional high relief coral reef habitats and patch reefs (Bauer and Kendall 2010). While the imagery collected represents mesophotic habitat from a depth definition perspective, this mesophotic habitat within the insular shelf edge is spatially separated from nearshore coral reef systems and there is no comparative data available for this location. In the Caribbean Basin most MCEs are found directly adjacent to, and contiguous with, shallow coral reef systems which were not represented in this data set. Given these factors, and the fact that the depth range of the screened images does not adequately cover upper or lower mesophotic depths, these data were not considered further.

For the binned data from Puerto Rico (Scott et al. 2019, their Table S2), we conducted a re-analysis of the projected percent cover of sponge data as depth increases. Using Model I linear regression (i.e., ordinary least squares), the percent cover of sponges decreased (Fig. S2) significantly with increasing depth ($y = 16.3 - 0.079x$, $F_{1,12} = 12.82$, $P = 0.004$ and very high effects size $R^2 = 0.538$) from 25 to 145 m. For non-normal distributions (i.e., bounded values of percent cover expressed as a decimal fraction) a regression using a non-normal probability distribution (e.g., β) is recommended. Like the results using a normal distribution, the fit using the β distribution showed a significant decrease in the percent cover of sponges with depth ($y = -1.57 - 0.006x$, (Generalized $R^2 = 0.019$, Wald $\chi^2 = 16.36$, $P < 0.0001$).

Mesophotic reefs around Puerto Rico have been studied for several years, providing data for comparison to the re-analysis of this imagery more ecologically relevant (Locker et al. 2010; Garcia-Sais et al. 2010, 2015; Sherman et al. 2010, 2019). The re-analyzed ROV imagery for Puerto Rico was collected on the Guayama Reefs and areas around the island of Caja de Muertos in southeast Puerto Rico which are part of the broader insular shelf habitats of Puerto Rico located closer to coastal coral reefs (~ 5 NM) (Battista et al. 2017) but contains the smallest amount of potential MCE habitat (Locker et al. 2010). The insular shelf of Puerto Rico gently slopes out to upper mesophotic depths (30–60 m) to the shelf break and lower mesophotic depths (60–150 m). Data for this area identified as dive track #7 from Scott et al. (2019, their Table S1) was unusable because no tracking information (e.g., height above bottom or depth of ROV) was collected due to technician error. For the remaining dive tracks only 37/953 images, $\sim 4\%$, passed the screening process described above with a depth range of

27–142 m. Again, most of the images failed screening because they were not orthogonal. Images for depths from shallow to lower mesophotic were better represented in this data set but still not evenly replicated (i.e., 20–30 m, $n=3$; 30–40 m, $n=2$; 40–50 m, $n=3$; 50–60 m, $n=4$; 60–70 m, $n=2$; 70–80 m, $n=1$; 80–90 m, $n=2$; 90–100 m, $n=4$; 100–110 m, $n=6$, 110–120 m, $n=4$, 120–130, $n=1$; 130–140 m, $n=3$; 140–150 m, $n=1$). These images show considerable variation in ROV altitude at 0.35–5.08 m above the substratum which resulted in the image area ranging from 0.26 to 5.16 m² (Mean \pm SD, 2.00 ± 1.12 m²). The relationship between ROV altitude and image area was significant ($y = 0.786 + 0.537x$, $F_{1,36} = 16.06$, $P = 0.0003$, and very high effects size $R^2 = 0.315$, Table S1). Despite this variation in image size, the screened imagery was considered appropriate to analyze here for sponges based on morphology, but not species.

Using Model I linear regression, the percent projected surface area of encrusting, emergent and sclerosponges for the plotless design, while trending positively, did not increase significantly ($y = 20.52 + 0.077x$, $F_{1,36} = 2.76$, $P = 0.106$ and low effects size $R^2 = 0.075$) from shallow to mesophotic depths (Fig. 2a). Similar to the results using a normal distribution, the fit using the β distribution showed a non-significant increase in the percent cover of sponges with depth ($y = -1.33 - 0.004x$, Generalized $R^2 = 0.082$, Wald $\chi^2 = 3.28$, $P = 0.69$). When the data are analyzed as described in Scott et al. (2019) the results show a non-significant positively trending relationship between projected surface area and depth ($y = 16.47 + 0.077x$, $F_{1,36} = 1.71$, $P = 0.199$ and low effects size $R^2 = 0.047$) from shallow to mesophotic depths (Fig. 2b). Unlike the results using a normal distribution the fit using the β distribution, however, showed a significant increase in the percent cover of sponges with depth ($y = -1.75 - 0.0058x$, Generalized $R^2 = 0.118$, Wald $\chi^2 = 4.86$, $P = 0.027$). In addition to conducting the regression analyses using a β distribution we also conducted linear regression analyses on ARCSIN transformed percentages of sponge projected surface area. Using this transformed data in the regression analyses did not change the results reported above when using a normal distribution. But as reported above for the non-transformed data from the Scott et al. (2019) analysis, the transformed data also showed a significant effect of depth on the percent cover of sponges using a β distribution ($y = -1.72 - 0.0058x$, Generalized $R^2 = 0.111$, Wald $\chi^2 = 4.51$, $P = 0.034$). All depth related sponge population data for the screened imagery are available as a supplemental spreadsheet (Table S1).

Discussion

As shown for Grand Cayman coral reefs, using diver deployed transects and photoquadrats, from shallow to mesophotic depths provided high quality orthorectified images

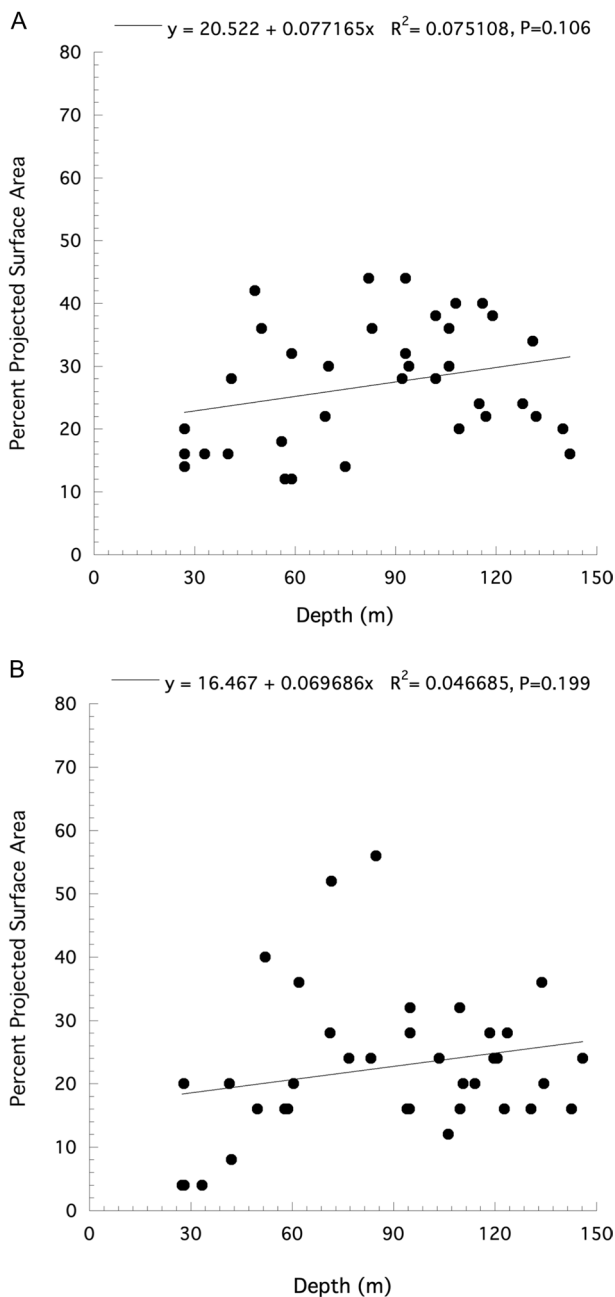


Fig. 2 Re-analysis of ROV images from Scott et al. (2019) based on two approaches: **A** Use of a point-count overlay of a random 50 point density grid in a plotless design, and **B** images analyzed as described by Scott et al. (2019)

with sufficient power to conduct a quantitative analysis, and detect changes with depth for sponge populations (Fig. S1). This is consistent with previous studies throughout the Caribbean Basin and elsewhere (Lesser and Slattery 2011, 2018; Macartney et al. 2020, 2021a, b; Slattery and Lesser 2012, 2019) where the percent cover of sponges was quantified using photoquadrats or in situ point-intercept quadrats from shallow to mesophotic depths. When you compare the

study by Scott et al. (2019) to previous work on shallow to upper mesophotic coral reefs in Puerto Rico, as opposed to a decrease in sponge cover with increasing depth, a significant increase in sponge cover (> 30% cover at 50 m) is observed (Garcia-Sais 2010). Like the work described above on Grand Cayman Island these data were collected using transects and divers with underwater digital video, as a function of increasing depth (Garcia-Sais 2010).

As previously observed (e.g., Lesser and Slattery 2018) the pattern of increasing sponge cover with depth, while repeatable, can vary for different locations with geomorphology appearing to be a major factor (Locker et al. 2010; Sherman et al. 2019). This may be one of two reasons why the results of Scott et al. (2019) show the pattern of decreasing sponge cover with increasing depth. Changes in reef topography affect the attenuation of incident irradiance on MCE habitats (Lesser et al. 2021a, b), and sloping topography of both shallow and mesophotic habitats, like the shelf system of Puerto Rico, “see” higher irradiances compared to vertical walls on MCEs in the Bahamas and Cayman Islands, which experience significantly lower irradiances and productivity (Lesser et al. 2021a, b). On sloping habitats, such as the insular shelf of Puerto Rico, coral cover has been observed to increase with increasing depth while sponge cover does not change down to 70 m (Sherman et al. 2010). Increased light on sloping MCE habitats translates into deeper populations of corals and macroalgae, known competitors for sponges (Bell 2008). The decrease in these photoautotrophs with increasing depth on vertical walls, where lower irradiances occur at equivalent depths (Lesser and Slattery 2011; Slattery and Lesser 2011), results in the establishment of other ecologically important groups such as gorgonians, which in turn facilitates sponge recruitment onto mesophotic habitat (Slattery and Lesser 2021).

Secondly, most of the original imagery from Puerto Rico did not satisfy a set of reasonable criteria for quantitative photogrammetry (e.g., orthogonal images), resulting in a low number of acceptable images for analysis which affected depth coverage and analytical power. Despite this, the analysis of the screened imagery, based on both plotless and plot based designs, showed a positive effect of depth on sponge cover using regression analysis. Additionally, the plot design showed a significant, and positive, effect of depth on sponge cover using regression analysis and the β probability distribution. All of the new analyses described here still suffer from insufficient power (i.e., low sample size or Type II error) to detect significant temporal or spatial changes in MCE communities.

Based on our analysis as described above we would only say that data supporting the pattern of sponge cover as a function of depth for these specific habitats on the shallow and mesophotic coral reefs of Puerto Rico is preliminary in nature, and is contrary to the original analysis reported in

Scott et al. (2019). In this regard, a criticism of our analyses would be that in effect we subsampled the original data of Scott et al. (2019) resulting in a loss of statistical power, leading to Type II errors (false-negative). However, it also can be argued that the original analyses by Scott et al. (2019) suffered from Type I errors (false-positive) by rejecting null hypotheses that are true. These observations do not reveal the mechanism by which Scott et al. (2019) may have committed these Type I errors, but both Type I and II errors can occur because of bias. But errors due to bias are a priori not referred to as Type I or Type II errors, and in Scott et al. (2019) the most likely source of bias is the poor quality of the imagery used in their original analyses (Lesser and Slattery 2021).

The imagery from Scott et al. (2019) were initially compromised because the appropriately, and consistently, sized sampling unit (i.e., quadrat or line transect), based on an assessment of species-area curves, was never determined for those habitats (Loya 1978; Durden et al. 2016), but the primary issue with the imagery is geometric distortion. Changes in topographical relief (i.e., substrate slope) and/or camera angle relative to the substrate result in an oblique image, with subsequent changes in scaling and geometric distortion of that image (Lesser and Slattery 2021; Supplemental Material). This results in the placement of an inaccurate scale on each image because the isocenter of an oblique image is the only place in the image where the scale is correct. Because of the varying size of each image, due to the variation in the ROV altitude above the substratum, it would lead to the establishment of incorrectly sized 1.0×0.75 m quadrats throughout the dataset, and the placement of density grids with varying distributions of points in the near and far fields of the image, and therefore errors in the calculation of abundance or percent cover (Lesser and Slattery 2021, Supplemental Material).

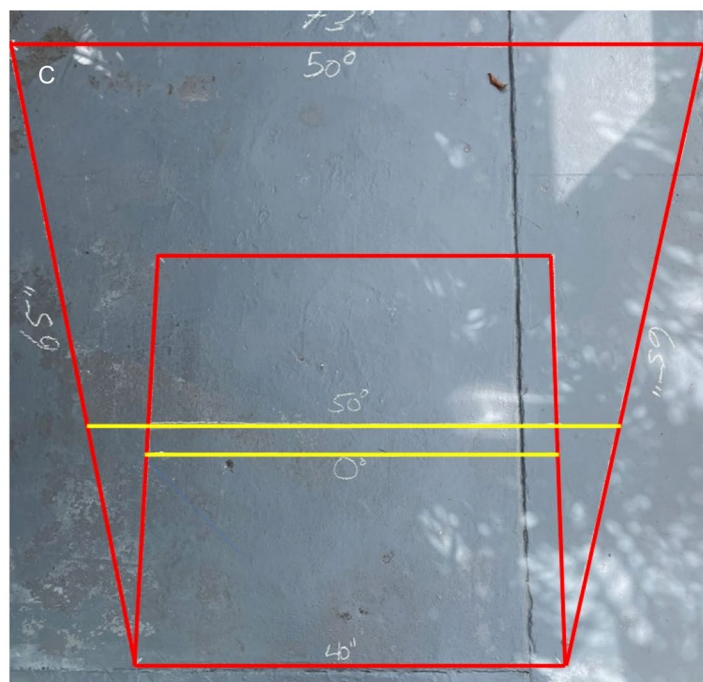
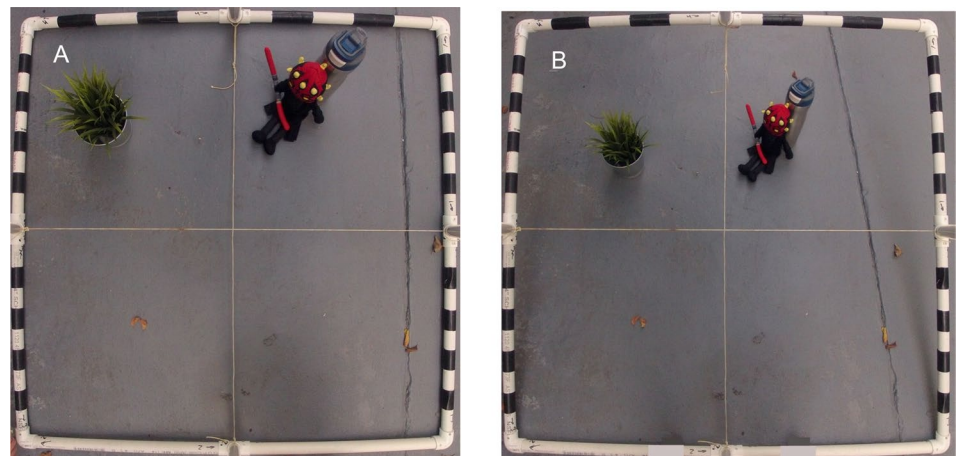
Many of the issues described here and in Lesser and Slattery (2021) have been largely overlooked but may be commonly occurring in studies using imagery from AUV/ROVs where clear geometric distortion of images is evident (Singh et al. 2004, see Figs. 4, 8, 13, 14; Rivero-Calle et al. 2008, see Fig. 10; Armstrong et al. 2006, see Fig. 3; Locker et al. 2010, see Fig. 4; Armstrong and Singh 2012, see Figs. 24.4, 24.5; Scott et al. 2019, see Fig. 3; Walker et al. 2021, see Fig. 8E). Even in studies where imagery obtained with AUVs shows the percent cover of sponges increasing with depth, the fact that the imagery is compromised by steeply sloping habitats resulting in geometric distortion without any post-processing to obtain orthorectified images, suggests that the data must be considered very carefully (e.g., Armstrong et al. 2008). For many ROV/AUVs this is the result of taking look-down photographs on mild to extremely sloped substrates, without considering the processing required to reduce the inherent errors associated

with geometric distortion, and scaling issues, for quantitative photogrammetry (Lesser and Slattery 2021).

Pawlik et al. (2022) provided multiple criticisms of diver-based acquisition of quantitative imagery for benthic communities concluding that using ROV/AUVs for imagery acquisition are superior for studies on mesophotic coral reefs (Supplemental Material). We believe that this could be correct, but only when proper procedural steps are taken to obtain orthogonal images on the varying topographies of MCEs. Here, to further clarify the geometric principles of, and the essential requirement for, collecting orthogonal imagery for quantitative community studies we demonstrate the consequences of changing camera angle on the quality of the imagery. When the camera angle increases, the image increasingly becomes trapezoidal in shape with a corresponding increase in area at camera angles from 0° to 50° (Fig. 3a–c). Also note the change in the size of the objects (i.e., they get smaller) in the far field when the angle is increased because the distance from the camera to the substrate increases in those areas of the image (Fig. 3a versus b). The geometric distortions of quadrat area, size of objects, and scale in the image are then embedded in the 2D format of the film, and in this case would be analyzed as if the image was a 1 m^2 image and that the scale throughout the image is the same (Fig. 3b). Both are false assumptions. The changes in size of an object with camera or substrate angle, not recognized on the 2D image, would affect calculations of both abundance and percent cover (Zveloni and Belmaker 2016; Lesser and Slattery 2021). Additionally, since the isocenter of the image shifts (Fig. 3c, yellow lines), it creates near field and far field portions of the image where there is only one line (i.e., the isocenter) in the image that the scale in the oblique image is now accurate because the camera to substrate distance varies throughout the remainder of the image (Lesser and Slattery 2021). This results in an uneven distribution of the points when a point-density grid is overlaid on the oblique image, creating additional systematic errors for quantitative photogrammetry (Lesser and Slattery 2021, see their Fig. 2).

A recent paper by Bell et al. (2023), using simulated communities in a virtual space and a plot design, suggested that increasing the ROV to substrate angle significantly overestimated the percent cover of large gorgonians by 0.31% per degree camera angle, or a total of 15.5% error at a camera angle of 50° . But for tubular sponge morphologies a significant error of only 0.02% per degree of camera angle was detected resulting in a 1.0% total error at a camera angle of 50° . Unresolved are the issues, if any, associated with using 0.25 m^2 quadrats without an analysis of the appropriateness of this sized quadrat in their medium and highly complex habitats (i.e., species-area curves). Also, each change in the angle of the image changes the areal coverage of those quadrats; a 0.25 m^2 image at a camera angle of 10° is no

Fig. 3 **A** Photoquadrat image (1 m^{-2}) at an orthogonal (0°) camera angle relative to the substrate and, **B** Photoquadrat image at an oblique 50° camera angle relative to the substrate and, **C** Actual areas of 3A and 3B with the isocenter marked in yellow. Note the change to a trapezoidal shape as the camera angle increases as well as the displacement of the isocenter creating a near and far field. The actual area captured in 2D images as camera angle changes was as follows, $0^\circ = 1.00 \text{ m}^2$, $10^\circ = 1.15 \text{ m}^2$, $20^\circ = 1.41 \text{ m}^2$, $30^\circ = 1.63 \text{ m}^2$, $40^\circ = 1.94 \text{ m}^2$, $50^\circ = 2.33 \text{ m}^2$



longer 0.25 m^2 and so on, and the size of the organisms and scale in the image change as camera angle increases (see above). Bell et al. (2023) placed a reference scale on each image to calculate percent cover using planar area and point intercept calculations, but there is no indication that Bell et al. (2023) accommodated the change in scale across the image for every change in camera angle caused by geometric distortion, as described above and in Lesser and Slattery (2021), in their model. These issues require a re-assessment of the inputs of these modeling efforts to include all possible sources of error in oblique imagery at varying angles.

Using technical diving or ROVs to provide data to qualitatively survey shallow and mesophotic coral reefs (Lehnert and van Soest 1996; Reed et al. 2018) can be an essential component of planning for more quantitative

sampling, again, by either ROV/AUV or by diver deployed transects and videography/photoquadrats. But all quantitative community studies conducted using AUVs, ROVs, or divers using transects and employing photoquadrats requires orthogonal imagery, of the appropriate sampling unit size, to be used for post-processing and quantitative descriptions. It does not matter whether one is using a plot, or plotless, design and whether the data is normalized to area or not. In all cases the imagery obtained must adhere to a set of acceptable geometric standards relative to ecological sampling and quantitative photogrammetry which includes considerations for camera and substrate angle and their effect on geometric distortion of the imagery (Lesser and Slattery 2021).

Conclusions

Quantifying changes in marine communities and in particular the sponge fauna, both spatially and temporally, on shallow and mesophotic reefs is essential to identify and understand their roles in benthic–pelagic coupling, the biogeochemistry of nutrients on coral reefs, and their response(s) to climate change (e.g., Lesser and Slattery 2020). Quantitative community descriptions and manipulative experiments on shallow and mesophotic coral reefs are essential to understand the ecological processes (i.e., top-down versus bottom-up effects) that regulate sponge populations (e.g., Macartney et al. 2021a, b), and their interactions with other members of the coral reef community (Lesser and Slattery 2013; Wulff 2017; Slattery and Lesser 2021). As a complimentary approach, we embrace the utility of ROV/AUVs surveys for obtaining qualitative descriptions of MCE habitats, particularly as a prelude to technical divers collecting quantitative data from these habitats (e.g., Slattery et al. 2018). This does not preclude using ROV/AUVs to obtain orthorectified imagery for quantitative studies. It does require planning to realize the benefits of using ROV/AUVs for these purposes. The results of recent studies (e.g., Scott et al. 2019), however, as described above and where quantitative metrics on the community structure of MCEs using ROV/AUVs have been derived, must be considered with caution. The imagery, and the approach described in Pawlik et al. (2022), does not account for the errors associated with geometric distortion and scaling effects and should not be used for quantitative community level ecological descriptions which requires fully orthorectified imagery, or alternative analytical techniques (i.e., perspective grids), as appropriate.

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Author contributions All authors contributed to the study conception and design. The screening and analysis of the ROV imagery was conducted by MPL. The rarefaction analysis was conducted by KJM. The initial draft of the manuscript was written by MPL, and all authors commented on previous versions of the manuscript. All authors read and approved the final, submitted, version of the manuscript.

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Data availability The raw ROV imagery is available online from the NCCOSS web site or by contacting Dr. Tim Battista (tim.battista@noaa.gov). The data analyzed from the screened imagery is available in Table S1.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. The authors have complied with all known ethical standards at the University of New Hampshire, the University of Mississippi, and the National Science Foundation. The authors declare no competing financial interests.

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