Reproductive effort of Montastraea cavernosa across depth in the context of both climate change refugia and emergent disease

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REPRODUCTIVE EFFORT OF *MONTASTRAEA CAVERNOSA*
ACROSS DEPTH IN THE CONTEXT OF BOTH CLIMATE
CHANGE REFUGIA AND EMERGENT DISEASE

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ABSTRACT

As coral populations on shallow reefs decline globally, mesophotic coral ecosystems (MCE) have been suggested as potential coral refugia in the face of climate changes, leading to the development of a comprehensive deep reef refugia hypothesis. The current study assesses the climate and disease refuge potential of MCEs in the U.S. Virgin Islands (USVI) for the gonochoric, broadcast-spawning species *Montastraea cavernosa*. Polyp, population, and total habitat fecundities were estimated across the species’ depth range, and changes to population oocyte production over time due to recent ecosystem disturbances were considered. The number of gonads producing oocytes in each polyp and oocyte size decreased significantly with depth, potentially due to energy limitations, although the effect sizes were small. Notably, the population sex ratio was 1:1 on shallow and mid-depth reefs, but it became significantly male-biased (3.6:1) at mesophotic depths. Population-level differences in oocyte production over depth were primarily driven by changes in coral cover and sex ratio. The high area of mesophotic reefs in the relative to shallow reefs USVI make MCEs the primary contributor of oocytes, despite the reduced proportion of females at depth. After Hurricanes Irma and Maria in 2017 and the outbreak of Stony Coral Tissue Loss Disease followed by bleaching in late 2019, shallow and mid-depth *M. cavernosa* populations experienced coral cover declines, resulting in corresponding declines to population fecundities. Coral cover in MCEs remained relatively undisturbed by these largely shallow water perturbations, and population and total habitat fecundities remained constant as well. Thus, MCEs in the USVI currently appear to be a reproductive refuge for *M. cavernosa*, but the persistence of that refuge remains in question as disease perturbation begins to affect deeper reefs.
INTRODUCTION

As shallow reefs continue to experience global declines due to a wide range of stressors, interest has increased in identifying reef locations and coral traits that support resistance or resilience to environmental stress. Glynn (1996) proposed that deep reefs may provide corals with a refuge from thermal and UV stress, leading to the development of the deep reef refugia hypothesis (DRRH). Gaining attention over the last 20 years, the DRRH posits that corals found in mesophotic coral ecosystems (MCE), between 30–150 m, may experience less intense anthropogenic perturbation than shallow corals. MCEs, therefore, would act as refugia, where coral populations persist despite climate change and other direct anthropogenic disturbances.

However, in addition to being protected or buffered from stressors, the DRRH also stipulates that coral refugia must be reproductively active to serve as a source of larvae for local recruitment and for other populations (Bongaerts et al. 2010; Holstein et al. 2015, 2016a; Davies et al. 2017; Shlesinger and Loya 2019). Thus, evaluating the DRRH requires deep understanding of coral and larval physiology across depth and of patterns of larval migration from, to, and between MCEs. As MCEs are understudied due to their depth, this second stipulation of the DRRH represents an important set of data gaps that limits our ability to predict coral reef trajectories and to manage coral reef resources in a changing climate. This study aims to quantify a coral’s reproductive effort in an MCE as a partial assessment of the ecosystem’s viability as a coral refugium.

The extent to which MCEs will act as coral refugia will vary in response to the type of disturbance, the location and physical environment of the reef, and the community assemblage considered. Depth and isolation protect many MCEs from an array of direct and indirect anthropogenic disturbances. For example, thermal and light stress can lead to coral bleaching,
which can result in eventual mortality, and is one of the greatest threats to shallow reefs (Glynn 1993; Spalding and Brown 2015). Due to their depth and location on continental shelf edges, MCEs often experience pulses of cooler water (Leichter et al. 1996) and reduced irradiance (Jones et al. 1998), which may reduce thermal bleaching disturbance. Because MCEs commonly occur offshore, their isolation often creates a buffer from coastal pollution, sedimentation, and eutrophication (Bak et al. 2005; Smith et al. 2008; Lesser et al. 2009; Bongaerts et al. 2010; Slattery et al. 2011). Also due to their depth, hurricanes generally cause less damage to MCEs than to shallow reefs (Woodley et al. 1981; Kobluk and Lysenko 1992; Lesser et al. 2009; Robbart et al. 2009).

Mesophotic corals are not immune to these disturbances, however. MCEs can experience periodic thermal stress events due to downwelling of surface waters, resulting in bleaching (Smith et al. 2016). Mesophotic coral species may exhibit a lower thermal tolerance than shallow corals, because they are infrequently exposed to high temperatures (Smith et al. 2016). Thus, MCEs may be uniquely susceptible to thermal stress despite infrequent thermal anomalies (Bongaerts et al. 2010; Smith et al. 2016). MCEs are also susceptible to sedimentation and debris following storm events, which can smother or damage corals (Bak et al. 2005; Bongaerts et al. 2010). Furthermore, sedimentation is most damaging to flat, plating coral morphologies, such as those most commonly found on MCEs (Kahng et al. 2019). Thus, despite being physically buffered from storm and land-based stressors, MCEs may be more vulnerable to perturbations when they occur. MCEs may exhibit disturbance avoidance but may have varying or limited capacities of recovery after a disturbance.

MCEs might not act as universal refugia in that they might not protect coral communities consistently through space and time. While a refuge is colloquially referred to as a short-term
shelter from a disturbance event, a refugium is a long-term shelter from multiple or extended disturbances (Bongaerts and Smith 2019). Recent literature erodes confidence in the DRRH through the lens of resistance or resilience to individual disturbances (Frade et al. 2010; Smith et al. 2016; Rocha et al. 2018), but refugia need not be pristine environments to protect biodiversity. Instead, networks of connected but imperfect or even ephemeral refugia could serve as an ecological crutch to support otherwise threatened species (Keppel et al. 2012). This, again, assumes the reproductive viability of corals in MCEs and the successful exchange of coral larvae between them.

Reproductive traits for over 450 scleractinian coral species have been described (Harrison 2011; Shlesinger and Loya 2019), the vast majority of which were studied on shallow reefs (< 30 m). Only 14 species from mesophotic reefs have had their reproductive traits described (Rinkevich and Loya 1987; Holstein et al. 2015, 2016b; Eyal-Shaham et al. 2016; Prasetia et al. 2016, 2017; Feldman et al. 2018; Shlesinger et al. 2018; Shlesinger and Loya 2019), three of them depth specialists found only on MCEs. Coral fecundity and oocyte size were compared between shallow and deep reefs in only 11 of those 14 species (Rinkevich and Loya 1987; Holstein et al. 2015, 2016b; Prasetia et al. 2017; Feldman et al. 2018; Shlesinger et al. 2018; Shlesinger and Loya 2019), despite ~25% of corals being depth generalists just in the Atlantic (Bongaerts et al. 2010). Only two Western Atlantic coral species have had their reproduction described throughout their depth ranges (Holstein et al. 2015, 2016b). As a result, we know little about how depth affects reproductive effort in phototrophic scleractinian corals.

What is known is that the effects of depth on coral reproduction vary by both species and location. On reefs of the Red Sea and Japan, nine species had their fecundities studied over increasing depth: six exhibited decreases, two exhibited no changes, and one exhibited a
decrease in fecundity in one reproductive season and no change in another (Rinkevich and Loya 1987; Prasetia et al. 2017; Feldman et al. 2018; Shlesinger et al. 2018; Shlesinger and Loya 2019). Furthermore, seven species had their oocyte sizes assessed over increasing depth: four exhibited decreases, one exhibited no change, and two exhibited a decrease in fecundity in one reproductive season and no changes in another (Rinkevich and Loya 1987; Prasetia et al. 2017; Feldman et al. 2018; Shlesinger et al. 2018; Shlesinger and Loya 2019). In the Western Atlantic, however, *Porites astreoides* experienced no change in fecundity over depth (Holstein et al. 2016b), while *Orbicella faveolata* displayed increased fecundity and smaller oocyte sizes at depth through most of its development, but no change at spawning (Holstein et al. 2015; Shlesinger and Loya 2019). Shlesinger and Loya (2019) suggest a potentially universal trend towards decreased coral fecundity on MCE. However, the polyp-fecundity estimates are not extrapolated to account for the reproductive effort of entire coral populations. Extrapolation is critical, as many mesophotic reefs have high coral cover and greater spatial extent than shallower reefs (Holstein et al. 2019; Smith et al. 2019). Furthermore, this trend may not hold true across geographic regions (Holstein et al. 2015, 2016b).

The primary trade-off associated with living at depth relates to coral energetic budgets. Photosynthetically active radiation (PAR) decays exponentially with depth (Kahng et al. 2019), and corals’ symbiotic relationship with algae of the Symbiodiniaceae relies on PAR for photosynthesis. As less light is available in MCEs for photosynthate production, coral holobiont energetic budgets may decrease with depth (Anthony and Hoegh-Guldberg 2003; Cooper et al. 2011). In response, some MCE corals become increasingly heterotrophic with increasing depth (Lesser et al. 2010; Crandall et al. 2016). Despite this shift, MCE corals may still be more energetically limited than shallower corals and need to shuttle energy usually reserved for
reproductive effort towards growth or tissue maintenance (Prasetia et al. 2016; Rinkevich 1989). Limitations on energy available for reproduction are potentially compounded by evidence that MCEs experience relatively lower temperatures, which may alter coral metabolism to limit coral reproduction, but apparently not adult physiology (van der Have 2002; Kahng et al. 2019). Alternatively, if disturbance in MCEs is low, mesophotic corals may utilize energy otherwise spent on maintaining tissue health for high reproductive effort (Holstein et al. 2015; Kahng et al. 2019).

For the purposes of community ecology, MCEs are often subdivided into upper, intermediate, and lower zones, which are distinguished by depth, light levels, and community assemblages (Pyle and Copus 2019). These zones, their depth-ranges, and associated community assemblages may vary by region. The current study took place in the U.S. Virgin Islands (USVI), where the upper mesophotic zone (30–45 m) is up to 60% *Orbicella spp.*, and, of that, ~90% *O. franksi* (Smith et al. 2019). *Montastraea cavernosa* is the next most abundant non-plating species. The lower mesophotic zone (60–100 m) is dominated by the genus *Agaricia*, which grows on steep slopes and walls of the continental shelf. Between these two zones, there is an intermediate zone with low scleractinian cover, and is colonized by macroalgae, sponges, octocorals, and antipatharians. The known extent of mesophotic reefs in the USVI (204 km²) is almost three times larger than the extent of shallow reefs (71 km²) (Smith et al. 2019). Thus, upper MCEs in the USVI support high abundance of depth-generalist corals, which potentially exceeds total coral abundance on struggling shallow reefs in the region. This extensive reservoir of corals in habitats even partially buffered from disturbance may function as important refugia for scleractinians.
M. cavernosa is a depth generalist, found ubiquitously across the USVI on shallow and mesophotic reefs. It is a gonochoric, broadcast spawning species (Szmant 1986, 1991; Soong 1991; Acosta and Zea 1997) and spawns a week after the full moons in late summer, potentially in a split spawn between August and September (Szmant 1986, 1991; Soong 1991; Wyers et al. 1991; Van Veghel 1993; Acosta and Zea 1997). There is no evidence that M. cavernosa is a simultaneous hermaphrodite, unlike the brooding and spawning species studied by Holstein et al. (2015, 2016b), or that it is capable of switching genders. Gender in M. cavernosa is not related to colony size, but there is evidence that female colonies have lower tissue thickness, skeletal density, and calcification rates (Mozqueda-Torres et al. 2018).

Oogenesis in M. cavernosa is an 11-month process, beginning 1–2 months after spawning occurs (Soong 1991; Szmant 1991; Acosta and Zea 1997). Spermatogenesis is a much shorter process, beginning in April to June, with stage 4 spermarys present within 2–4 months (Szmant 1986, 1991; Acosta and Zea 1997). The population-level sex ratio appears to be 1:1 (Soong 1991; Acosta and Zea 1997); however, this ratio may vary by population (Szmant 1991). Within female colonies, Soong (1991) used dissections and found 24 gonads per polyp and 10–20 eggs per gonad, while Acosta and Zea (1997) histologically found on average 34 gonads per polyp with about 3 eggs per polyp. There are, however, no previous studies examining M. cavernosa reproductive traits below 20 m.

Mesophotic M. cavernosa has been observed spawning at the same time as shallower conspecifics at the Flower Garden Banks in the Gulf of Mexico (Vize 2006). Serrano et al. (2014) found little genetic differentiation across depths in the USVI, indicating that there may be larval exchange between shallow and mesophotic reefs in the region. This pattern was also found in Bermuda, but not in Florida (Serrano et al. 2014) nor the Cayman Islands or Bahamas.
(Brazeau et al. 2013) where strong genetic differentiation was found between shallow and mesophotic reefs. This further suggests that mesophotic refugia will vary geographically, and that USVI MCEs might be a particularly effective *M. cavernosa* refugium. Recent disturbances, including two Category 5 hurricanes in 2017 and a mass bleaching event with emergent disease in 2019, created a unique opportunity to assess the refugia capacity of USVI MCEs in the face of multiple disturbances.

In 2014, a highly deadly emergent coral disease appeared in Florida (Precht et al. 2016); affecting over 20 coral species (Lunz et al. 2017) and has been termed Stony Coral Tissue Loss Disease (SCTLD). At sites in Florida, disease prevalence reached 80%, with affected colonies often experiencing complete mortality within weeks to months (Lunz et al. 2017; Gintert et al. 2019). SCTLD has been isolated to the Florida Reef Tract for nearly four years, but a SCTLD-like disease was observed in the USVI in January 2019, and it has since spread rapidly. It is currently most severe in shallow reefs (June 2020, Dr. M. Brandt pers. comm.). In initial studies conducted in St. Thomas examining the susceptibility of different coral species, *M. cavernosa* appears to be more resistant to SCTLD than other coral species (Dr. M. Brandt pers. comm.). If the disease is less prevalent at depth and less deadly to *M. cavernosa*, then USVI MCEs may be both climate and disease refugia for *M. cavernosa* populations.

This study extrapolates coral polyp oocyte production by coral abundance and habitat extent to evaluate how multiple disturbances, including storms, bleaching and SCTLD, affect a coral’s population-level reproductive output across its depth range. By examining the reproductive effort of *M. cavernosa* over depth in the USVI, this study addresses the interplay of reproductive effort and disturbance to assess the viability of USVI MCEs as a refugium for *M. cavernosa*. 
METHODOLOGY

Field Collection

In May 2019, *M. cavernosa* samples (N=96) were haphazardly collected via SCUBA from four reefs off the southern coast of St. Thomas, USVI, binned by habitat type (Fig. 1): Shallow fringing reef (Brewer’s Bay, 4–13 m, \(n=29\); and Perseverance Bay, 6–11 m, \(n=11\)); mid-depth mid-shelf reef (Seahorse Reef, 18–21 m, \(n=28\)); and MCE bank reef near the insular shelf edge (Grammanik Bank, 37–40 m, \(n=28\)). To minimize the probability of sampling clonal colonies, a minimum distance of five fin-kicks (~8 m) separated sampled colonies. Samples were taken from colonies larger than 225 cm\(^2\) to ensure they were reproductively mature (Szmaň 1991). Colony height, maximum diameter, and perpendicular diameter were recorded. Using a hammer and cold chisel, 15–25 cm\(^2\) coral tissue and skeletal biopsies were removed from colonies at least 5 cm from the colony edge, aiming for 5–10 complete polyps per sample.
Figure 1. Map of collection sites. The northern USVI islands of St. Thomas and St. John. Red circles indicate collection sites off the southern coast of St. Thomas, which correspond to shallow, mid-depth, and mesophotic sites.

There are two known morphotypes of *M. cavernosa*: a diurnal morph with smaller polyps that feeds most commonly during the day, and a nocturnal morph that feeds only at night (Lasker 1979; Budd et al. 2012). Morphs are not predictably correlated with depth (Ruiz Torres 2004; Budd et al. 2012). The morphs are not always easily visually distinguishable, but neither morph was targeted for collection across depths.

SCTLD outbreaks were ongoing during collection in May 2019 at Brewer’s Bay and Perseverance Bay; it was difficult to access shallow reefs that were not affected by the disease. Samples were only taken from visually healthy colonies with no paling and were not taken from colonies that were within 2 m of a visually diseased coral of any species. Upon surfacing, a 1 cm$^2$ subsample was immediately placed in DNA/RNA Shield (Zymo Research, Irvine, CA) for
genetic analysis to be completed at a later date. The remaining tissue was immediately placed in zinc-buffered formalin (Z-Fix, Anatech Ltd., Battlecreek, MI) for ~24 hours, then rinsed in 20 µm filtered freshwater for 24 hours, and finally stored in 70% ethanol for further processing.

**Histology**

The samples’ skeletons were dissolved in a decalcifying solution of 5% hydrochloric acid with 5.0 g EDTA L⁻¹ for 2–9 days, with the solution changed 1–2 times per day. Upon complete decalcification of the skeletons, coral tissues were stored in 70% ethanol. Tissues were then paraffinized in a Leica ASP6025 Tissue Processor and embedded for both cross- and longitudinal-sections using a Leica EG1150 H Embedding Station. Tissue blocks were sectioned 4 µm thick with a Leica RM2125 RTS Microtome. Sections were taken every ~400 µm through the polyp.

Histological tissue sections were stained with hematoxylin and eosin for 23 initial samples, which stained the tissues dark pink or purple. Oocytes were easily identified and measured, but identification of early spermaries was difficult. To address this issue, the slides for the remaining 73 samples were stained in modified Heidenhain’s aniline blue, which stains the mesoglea blue, Symbiodiniaceae amber, oocytes gold, spermaries a deep red, and the remaining tissues light pink (Fig. 2). Histology slides were imaged using an Olympus BX41 Microscope or a Hamamatsu NanoZoomer slide scanner.

**Fecundity metrics: histology**

Histological images were assessed for the absence or presence of female or male gonads and for gametes to estimate the sex ratio. Within female colonies, three metrics of reproduction were estimated: number of gonads per polyp, number of oocytes per gonad, and oocyte cross-sectional area. Gonads were identified and counted in cross sections for up to seven polyps per
coral colony; in some cases, only 1–2 polyps were suitable for analysis (Fig. 2a, c). The number of oocytes per gonad was counted in the longitudinal sections (Fig. 2b, d). Capturing an entire gonad in a single longitudinal section was inconsistent, which is a common problem in coral histology. Mesenteries appeared folded within coral, so sections did not reflect true numbers of oocytes per gonad and are likely underestimates. To accommodate this underestimation, the number of oocytes per gonad was only recorded if at least 5 oocytes were visible in a gonad.

Polyp fecundity ($F_{\text{polyp}}$) was defined as the total number of oocytes in a single polyp, and estimated as per the equation:

$$F_{\text{polyp}} = \frac{\text{oocytes}}{\text{gonad}} \times \frac{\text{gonads}}{\text{polyp}}$$  \hspace{1cm} \text{(Equation 1)}

To find $F_{\text{polyp}}$, the number of gonads per polyp for each coral colony was multiplied by the mean number of oocytes per gonads.

Oocyte size was measured with CellSens Dimension software (Olympus). Using a rotated ellipse, oocyte area, perimeter, minimum diameter, and maximum diameter were estimated for oocytes with a visible nucleus, to ensure that the center and widest part of the oocyte was measured. For each measured oocyte, reproductive stage was assessed as per Szmant (1985) and Vargas-Angel et al. (2002).

**Population and total habitat fecundities**

Polyp fecundity (Equation 1) was further extrapolated to estimate population-level fecundity ($F_{\text{pop}}$) as per the equation:

$$F_{\text{pop}} = \frac{\text{Coral cover}}{\text{Polyp area}} \times \frac{\text{Female sex ratio}}{\text{F}_{\text{polyp}}}$$  \hspace{1cm} \text{(Equation 2)}
Colony-specific values were used for $F_{\text{polyp}}$ and polyp area. Site-specific values were used for coral cover and female sex ratio. Total coral cover was estimated using averages of each collection site from the USVI Territorial Coral Reef Monitoring Program (TCRMP) data from 2016–2020. TCRMP datasets from 2017 and 2018 were used to estimate population fecundity following Hurricane Maria and Hurricane Irma, and 2019 and 2020 were used to estimate population fecundity following bleaching and SCTLD disturbances.

Population fecundity (Eqn. 2) was further scaled to estimate the total habitat fecundity ($F_{\text{hab}}$) over depth:

$$F_{\text{hab}} = F_{\text{pop}} \times \text{Total coral habitat area} \quad (\text{Equation 3})$$

Coral habitat area was estimated as per Smith et al. (2019) with habitat area categorized into 10 m depth bins. Each colony-specific population-fecundity estimate was multiplied by the average coral habitat from the corresponding depth bin to obtain total habitat fecundity estimates for each coral colony.

Data Analysis

To ensure that colony size did not affect the sex of the colony, an analysis of variance (ANOVA) was used to test the effect of colony sex (predictor) on the colony surface area (response). Colony surface area was calculated as half the surface area of scalene ellipsoid using the maximum diameter, perpendicular diameter, and the height of the colony. To ensure that colony size did not affect polyp fecundity, the relationship between colony surface area and the number of gonads per polyp was estimated using a linear model (LM). The model was conducted using with the ‘lm’ function from the stats R package (v4.0.0; R Core Team 2020). The $p$-values were calculated using Student's t-test, and significance was evaluated at $\alpha = 0.05$. 

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A series of $X^2$ tests were used to determine if the sex ratio was 1) significantly different from 1:1 using data from all sites, 2) significantly different from 1:1 within populations at each depth, and 3) significantly different between sites. Tests were done with the ‘chisq.test’ function from the stats R package. Bonferroni tests were used to calculate adjusted $p$-values for multiple comparisons. Significance was evaluated at $\alpha = 0.05$.

The relationship between depth and oocyte size was estimated using natural log-transformed oocyte measurements and a linear mixed model (LMM) with colony, polyp, and histological slide as nested random intercept effects to avoid pseudoreplication. Analyses were completed separately for each oocyte reproductive stage.

The relationship between depth and the number of septae per polyp was estimated with a generalized linear mixed model (GLMM) with a Poisson distribution with colony identity applied as a random effect. The relationship between depth and the number of gonads per polyp was estimated with a GLMM with a Poisson distribution. Colony and polyps were applied as nested random effects. The relationship between depth and the polyp size (as polyp area) was estimated with an LMM with colony identity as a random effect.

The relationship between depth and the number of oocytes per gonad was estimated with a GLMM with a Poisson distribution, with colony, polyp, and histological slide as nested random effects. This relationship was also estimated when including only gonads that appeared complete and was analyzed using a GLMM with a Poisson distribution and colony as a random effect. Gonads were assessed for completeness 1) ensuring oocytes were even in size, 2) there were no large gaps between oocytes that would indicate gonadal folding, and 3) intact mesoglea could be seen leading to and stemming from each side of the gonad to the polyp body wall. All LLMs were conducted using the ‘lmer’ function from the lme4 R package, and $p$-values were calculated
using Satterthwaite's approximation for degrees of freedom within the lmerTest package (Kuznetsova et al. 2017). All GLMMs were completed using the ‘glmer’ function from the lme4 R package, and $p$-values were calculated using the Normal Distribution Z-test. Significance was evaluated at $\alpha = 0.05$ for all regressions.

The effects of site and year (predictor variables) on population fecundity (response variable) were tested in a two-way ANOVA with a Type III sum of squares. The variation in population fecundity (response variable) between sites (predictor variable) was examined for each year using an ANOVA, and multiple post-hoc comparisons were made using Tukey’s HSD. Significance was evaluated at $\alpha = 0.05$.

The effects of site and year (predictor variables) on total habitat fecundity (response variable) were tested in a two-way ANOVA with a Type III sum of squares. The variation in total habitat fecundity (response variable) between sites (predictor variable) was examined for each year using an ANOVA and multiple comparisons using Tukey’s HSD. Significance was evaluated at $\alpha = 0.05$. 
RESULTS

From the 96 coral colonies sampled, a total of 1039 histological slides were prepared. Oocytes were identified in 40 colonies. Spermaries were identified in only one colony from 9.4 m depth (Fig. 3). Colonies with no visible gametes were assumed to be male with spermaries not yet developed enough to be identified visually.

Figure 3. Histological image of male *M. cavernosa*. Image comes from a horizontal cross section. G: gonad; S: spermary.

Colony size did not have a significant effect on the sex of the colony (*F*<sub>1, 94</sub> = 0.18, *p* = 0.67) or on polyp fecundity (LM: *t* = -0.84, *p* = 0.42, Student's t-test; *R*<sup>2</sup> = 0.018).
Sex ratio

Across all depths, there were 56 male and 40 female colonies, which was not significantly different from a 1:1 sex ratio ($X^2 = 2.67$, df = 1, $p = 0.10$). The sex ratio varied significantly according to reefs of different depths ($X^2 = 10.66$, df = 2, $p = 0.0049$). Neither Brewer’s Bay (shallow) nor Seahorse Reef (mid-depth) had sex ratios that were significantly different from 1:1 (Brewers Bay: 24 males, 16 females, $X^2 = 1.60$, df = 1, $p = 0.21$; Seahorse Reef: 10 males, 18 females, $X^2 = 2.29$, df = 1, $p = 0.13$; Fig. 4). Grammar Bank (mesophotic) had 22 males and 6 females, which is a significantly male-biased sex ratio of 3.6:1 ($X^2 = 9.14$, df = 1, $p = 0.0025$; Fig. 4). In post-hoc pairwise comparisons, the sex ratios were not significantly different between Brewer’s Bay and Seahorse Reef ($p = 0.51$, Bonferroni adjusted p-value), and Brewer’s Bay and Grammar Bank ($p = 1.0$, Bonferroni adjusted p-value), but they were significantly different between Seahorse Reef and Grammar Bank ($p = 0.018$, Bonferroni adjusted p-value).
Figure 4. Sex ratio of *M. cavernosa* colonies. Proportion of male and female colonies in shallow (Brewer’s Bay), mid-depth (Seahorse Reef), and mesophotic (Grammanik Bank) sites. White numbers refer to the frequency of putative male or females at each site. * indicates a sex ratio significantly different from 1:1 ($\chi^2 = 9.14$, df = 1, *p*-value = 0.0025).

**Oocyte size**

Of the 3,888 oocytes measured, 95.5% were in Stage III and 4.5% were in Stage II. Stage II oocytes were distributed across all three sites. The mean oocyte area of Stage III oocytes was 0.026 ± 0.010 mm$^2$ (SD). When including only Stage III oocytes, the oocyte area decreased significantly with depth (LMM: $t = -3.23$, df = 37.55, $p = 0.0027$, Satterthwaite's approximation of degrees of freedom; Fig. 5) by 0.96% per meter. The mean decrease in oocyte area was $-9.34 \times 10^{-9} \text{mm}^2/\text{m}$ (Fig. 5). The mean oocyte area of Stage II eggs was 0.013 ± 0.0047 mm$^2$ (SD).

When including only Stage II eggs, there was not a significant relationship between oocyte area
and depth (LMM: $t = -0.97$, df = 25.61, $p = 0.34$, Satterthwaite's approximation of degrees of freedom).

Figure 5. Area of Stage III oocytes over depth. Black line is the back-transformed predicted values from the linear mixed model with colony, polyp, and histological slide as nested random effects ($t = 3.23$, df = 37.55, $p = 0.0027$, Satterthwaite's approximation of degrees of freedom). Blue ribbon is 95% confidence interval of the model, calculated by parametric bootstrap. Blue dots refer to sample colony means, and red lines are standard deviation of area per colony.

Polyp size

Polyp area increased with and depth (LMM: $t$-score = 2.46, df = 37.96, $p = 0.019$, Satterthwaite's approximation of degrees of freedom) of 0.38 mm$^2$/m (Fig. 6c). The number of
septa per polyp was not affected by depth (GLMM: Z-score = 0.92, \( p = 0.36 \), Normal Distribution Z-test). The mean number of septae per polyp was 21.78 ±2.64 (SD).

Figure 6. Polyp fecundity over depth. A. Relationship between the mean number of oocytes per gonad and depth. The dotted line represents the mean number of visually complete gonads (19.09 gonads). Model predictions were not used, as no effect of depth on the number of oocytes per gonad was detected. Blue dots refer to colony means, and red lines are the standard deviation per colony. Blue dots with no red lines had only one measurement per colony. B. Relationship between the number of gonads per polyp over depth (Z-score = -1.98, \( p = 0.048 \), Normal Distribution Z-test). Black line is predicted values from the generalized linear mixed model with a Poisson distribution; colony and polyps were applied as nested random effects. Blue ribbons are a 95% confidence interval of the model, calculated by parametric bootstrap. Blue dots refer to colony means, and red lines are the standard deviation per colony. C. Relationship between polyp area and depth. Black line is predicted values from a linear mixed model with colony identity as a random effect. Blue ribbons are a 95% confidence interval of the model, calculated by parametric bootstrap. Blue dots refer to colony means, and red lines are the standard deviation per colony.

**Polyp fecundity**

The number of gonads per polyp decreased with depth (GLMM: Z-score = -1.98, \( p = 0.048 \), Normal Distribution Z-test, Fig. 6b), decreasing by 1.98% per meter. The mean decrease in gonads per polyp was -0.43 gonads/m (Fig. 6b). The mean number of gonads per polyp was
28.91 ± 13.13 (SD) for all sites combined. The mean number of oocytes per gonad (including only gonads with greater than 5 oocytes) was 7.77 ± 3.67 (SD), and did not change significantly with depth (GLMM: Z-score = 1.59, p = 0.11, Normal Distribution Z-test). The mean number of oocytes per visually complete gonad was 19.09 ± 4.80 (SD). The number of oocytes per visually complete gonads did not change significantly with depth (GLMM: Z-score = 1.7, p = 0.087, Normal Distribution Z-test; Fig. 6a).

M. cavernosa percent cover

Percent coral cover of *M. cavernosa* at shallow depths decreased by 41.1% from 2016 to 2017 after Hurricanes Maria and Irma and 62.9% in 2019 after bleaching and the emergence of SCTLD (Fig. 7). In mid-depth habitats, *M. cavernosa* percent cover experienced a 14.5% decrease after Hurricanes Maria and Irma but decreased to 0% cover in 2020 after SCTLD spread to mid-depths (Fig. 7). In mesophotic habitats, percent coral cover of *M. cavernosa* remained relatively stable through 2016-2020 (Fig. 7).
Figure 7. Percent cover of *M. cavernosa*. Boxplots indicate percent cover in shallow (Brewer’s Bay), mid-depth (Seahorse Reef), and mesophotic (Grammanik Bank) habitats from 2016–2020. Black dots indicate outliers. Values are from USVI TCRMP data, which recorded *M. cavernosa* percent cover at each of the collection sites.

*Population fecundity*

Population fecundity varied significantly by site ($F_{3,210} = 19.48, p < 0.001$), year ($F_{4,210} = 29.37, p < 0.001$) and the interaction of site and year ($F_{12,210} = 6.1262, p < 0.001$; Fig. 8). The
high coral cover at shallow sites caused the extrapolated population fecundity estimates to decrease by 51.0% from shallow to mid-depth sites in 2016 ($p < 0.001$; Table 1; Fig. 8a). In 2017, extrapolated population fecundity decreased significantly by 63.3% from shallow to mesophotic sites (assuming a 3.6:1 male-biased sex ratio) ($p = 0.0081$; Table 1; Fig. 8b). Site did not have a significant effect on extrapolated population fecundity estimates in 2019 ($F_{3,42} = 6.1262$, $p = 0.087$; Fig. 8c). The decrease in coral cover at shallow sites in 2019 due to bleaching and SCTLD caused the extrapolated population fecundity estimates to have no significant difference between shallow and mesophotic sites (assuming a 3.6:1 male-biased sex ratio) ($p = 0.90$, Fig. 8d), but there was a 113% increase from shallow to mid-depth sites. Further coral cover loss at shallow depths in 2020 caused the extrapolated population fecundity estimates to increase by 4.37% from shallow to mesophotic habitats (assuming a 3.6:1 male-biased sex ratio) ($p = 0.0041$; Table 1; Fig. 8e). Coral cover loss at mid-depth due to the progression of SCTLD to deeper sites caused extrapolated population fecundity estimates to go to 0 oocytes/km$^2$ at mid-depth sites, which is lower than the population fecundity estimates at mesophotic habitats for both a 1:1 sex ratio and a 3.6:1 male-biased sex ratio ($p = 0.0012$; Table 1; Fig. 8e).
Figure 8. Population fecundity estimates from 2016–2020. A–E. Population fecundity estimates were calculated by Eqn. 2. Polyp fecundity (using mean number of oocytes in visually complete gonads) and polyp area were colony-specific values. Coral cover was calculated from site-specific mean coral cover from USVI TCRMP data. In grey boxes, a 1:1 sex ratio was used to calculate population fecundity. In blue boxes, a 3.6:1 male to female ratio was used to calculate population fecundity. Hurricanes Irma and Maria occurred between the 2016 and 2017 data collection. In 2019, SCTLD emerged in USVI at the shallow site followed by a mass bleaching event. SCTLD spread to the mid-depth habitat in 2020. Differing letters indicate significant differences in population fecundity estimates.

Table 1. Population fecundity post-hoc comparisons. Comparisons were made between depths for each year. P-values given for a post-hoc Tukey pairwise comparison test after separate a one-way ANOVAs for each year testing the effects of site on population fecundity estimates. Mesophotic (1:1 Sex ratio) indicates that a 1:1 sex ratio was used to calculate population fecundity. Mesophotic (3.6:1 Sex ratio) indicates that a 3.6:1 male to female ratio was used to calculate population fecundity. * indicates statistical significance of $\alpha = 0.05$. 
## Total habitat fecundity

Total habitat fecundity was significantly affected by site ($F_{3,210} = 19.48$, $p < 0.001$) and year ($F_{4,210} = 29.37$, $p = 0.011$), but not by the interaction of site and year ($F_{12,210} = 6.1262$, $p = 0.28$; Fig. 9). In 2016, there was no significant difference between the extrapolated total habitat fecundity estimates from shallow and mesophotic sites (assuming a 3.6:1 male-biased sex ratio) ($p = 0.12$; Table 2; Fig. 9a). In 2016, extrapolated total habitat fecundity estimates from mid-

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Total habitat fecundity was significantly affected by site ($F_{3,210} = 19.48$, $p < 0.001$) and year ($F_{4,210} = 29.37$, $p = 0.011$), but not by the interaction of site and year ($F_{12,210} = 6.1262$, $p = 0.28$; Fig. 9). In 2016, there was no significant difference between the extrapolated total habitat fecundity estimates from shallow and mesophotic sites (assuming a 3.6:1 male-biased sex ratio) ($p = 0.12$; Table 2; Fig. 9a). In 2016, extrapolated total habitat fecundity estimates from mid-

| 25 |
depth to mesophotic sites (assuming a 3.6:1 male-biased sex ratio) increased by 355% ($p = 0.019$; Fig. 9a). Due to coral declines in shallow and mid-depth sites, every year from 2017–2020 saw total habitat fecundity was significantly lower for shallow and mid-depth habitats than mesophotic habitats (for both a 1:1 sex ratio and a 3.6:1 male-biased sex ratio) (Table 2; Fig. 9b-e).

Figure 9. Total habitat fecundity estimates in the USVI from 2016–2020. A–E. Total habitat fecundity estimates were calculated by Eqn. 3. In orange boxes, a 1:1 sex ratio was used to calculate total habitat fecundity. In red boxes, a 3.6:1 male-biased ratio was used to calculate total habitat fecundity. Hurricanes Irma and Maria occurred between the 2016 and 2017 data collection. In 2019, SCTLD emerged in USVI at the shallow site followed by a mass bleaching event. SCTLD spread to the mid-depth habitat in 2020.
Table 2. Total habitat fecundity post-hoc comparisons. Comparisons were made between depths for each year. *P*-values given for a post-hoc Tukey pairwise comparison test after separate one-way ANOVAs for each year testing the effects of site on total habitat fecundity estimates. Mesophotic (1:1 Sex ratio) indicates that a 1:1 sex ratio was used to calculate total habitat fecundity Mesophotic (3.6:1 Sex ratio) indicates that a 3.6:1 male to female ratio was used to calculate total habitat fecundity. * indicates statistical significance of α = 0.05.

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DISCUSSION

This first assessment of *M. cavernosa* reproduction across its depth range suggests that this coral is sexually active on USVI MCEs. Although polyp fecundity and oocyte size of this coral vary subtly over depth, the principle difference in population fecundity between depths may be driven by changes in coral cover, habitat extent, and, interestingly, sex ratio. As shallow populations are increasingly perturbed by disturbance, the reproductive effort of mesophotic *M. cavernosa* will represent a rising proportion of the larval pool. The current study demonstrates that the interactions of anthropogenic, storm, and disease disturbances result in mesophotic refuges for this coral that are dynamic in time.

While this study provides evidence of a sexually reproductive mesophotic reef, albeit without addressing fertilization success, it does not test the capacity of MCEs to reseed associated metapopulations. Larval dispersal models do indicate vertical population connectivity between MCEs and shallow reefs in *P. astreoides* and *O. faveolata* (Holstein et al. 2016a), and genetic connectivity analyses indicate no genetic differentiation between MCE and shallow reefs (Serrano et al. 2014). These studies, in addition to the results presented here, strongly corroborate the DRRH for *M. cavernosa* in the USVI.

**Sex ratio**

The sex ratio of *M. cavernosa* varied significantly with depth, with shallow and intermediate depth populations exhibiting a ratio indistinguishable from 1:1, while the mesophotic population had a male-biased sex ratio. Skewed sex ratios in scleractinians and soft corals may be a result of asexual reproduction and fragmentation creating aggregations of one sex (Benayahu and Loya 1983; Soong 1991; Marchini et al. 2015). While *M. cavernosa* does,
like most corals, reproduce asexually via budding, it is not a brittle, branching species that is known for high levels of asexual fragmentation. While there are cases of the massive corals reproducing significantly by asexual fragmentation via breakage (Foster et al. 2007; Polato et al. 2010), it seems unlikely that this would be fully explanatory for differences in sex ratios at mesophotic depths, especially when considering that shallow corals generally experience higher levels of wave energy that cause breakage.

Male-biased sex ratios in benthic cnidarians is not uncommon. The gorgonian *Briareum asbestinum* has a male-biased sex ratio across its range, perhaps enhancing fertilization success in this broadcast spawner (Brazeau and Lasker 1990). This is an attractive hypothesis, especially considering the sperm-dilution effect of depth, which decreases the likelihood of successful fertilization (Babcock et al. 1994; Lasker et al. 1996). *M. cavernosa* produces buoyant eggs and neutrally buoyant sperm (Wyers et al. 1991). At deeper depths, there is a larger volume of water for these gametes to disperse through, which may decrease the chances of gametes meeting and fertilizing. A higher proportion of males to females at depth may mitigate the dilution effect and increase the probability of successful fertilization. However, as *M. cavernosa* in the USVI lacks genetic differentiation over depth (Serrano et al. 2014), there is no clear driver or selective pressure that would cause this skewed sex-ratio. It is not clear that this explanation alone could result in different sex ratios over depth.

Another possible and non-exclusive explanation is gendered survivorship. The production of female gametes, which are rich in lipid, is far more energetically expensive than that of male gametes. Thus, metabolically stressed female colonies may have reduced survivorship at depth, where energy from PAR is limited, leading to a male-biased sex ratio. In the Mediterranean Sea, a positive thermal anomaly caused mass mortality in the gorgonian *Paramuricea clavata*.
Following the perturbation, the species’ sex ratio shifted from 1:1 to a male-biased ratio, possibly due to reduced female survivorship (Cerrano et al. 2005). Similarly, in the Red Sea, the hermaphroditic scleractinian *Stylophora pistillata* was found to produce five times as many female gametes in shallow habitats than at depth, and corals with high oocyte fecundity in one season produced only male gametes in the following season (Rinkevich and Loya 1987). This was attributed to the high energetic cost of female reproduction and energy limitations at depth (Rinkevich and Loya 1987). Thus, the observed male-biased sex ratio may be a consistent characteristic of depth-generalist gonochoric species in MCEs, which would have implications for local population dynamics as well as for mesophotic refugia. *M. cavernosa* is only the second gonochoric scleractinian to have its gametogenesis studied across depths (Shlesinger et al. 2018), and this study is the first known to assess the sex ratio of a gonochoric scleractinian across its depth range.

Some portion of the corals without visually identifiable gametes may have been non-reproductive colonies and potentially female. This would imply that the mesophotic male-biased sex ratio of *M. cavernosa* found in this study may be false or inflated, and that depth may have a more extreme effect on polyp, colony, and population fecundity. Only one coral sampled at any depth had clearly identifiable spermaries. The absence of obvious spermaries was likely due to sampling too early in spermatogenesis. Spermary development should begin in May (Szmant 1991; Acosta and Zea 1997), when we collected in an effort to ensure early spermaries were detectable. However, sampling later in the spermatogenic cycle may be necessary to confirm the sex ratios reported here. The costs of living at depth may be too great for some female colonies to produce gametes while maintaining tissue growth and metabolism, resulting in the misidentification of non-reproductive colonies as males. However, this appears unlikely based on
our results, as the magnitude of the effect of depth on polyp fecundity and oocyte size of clearly reproductively active females was small.

**Oocyte size**

The size of Stage III oocytes decreased significantly with depth, which is consistent with studies of other species in the Red Sea (Prasetia et al. 2017), Pacific (Feldman et al. 2018; Shlesinger et al. 2018), and other Western Atlantic (Holstein et al. 2015). Decreasing PAR with increasing depth may limit the coral’s energy budget allocation for gametogenesis. The majority of observed oocytes were in Stage III, as expected for *M. cavernosa* in May (Szmant 1991; Acosta and Zea 1997). However, oocyte size was more variable at shallow depths. Stage III tends to be the longest oocyte developmental stage. Oocyte size can vary considerably at this stage and may not converge until Stage IV (Szmant-Froelich et al. 1985). The variability of shallow oocyte size may indicate that corals have more free energy to devote to oocyte development.

If Stage IV oocytes are significantly smaller in mesophotic *M. cavernosa*, this would have implications for larval dispersal, because larvae with greater lipid stores can live longer as pelagic larvae and thus have greater dispersal potential (Richmond 1987; Harii et al. 2002). Lipid content also contributes to the buoyancy of eggs and larvae, with more buoyant larvae spending more time closer to the sea surface, allowing them to disperse via wind-driven currents (Harii et al. 2002, 2007). Furthermore, larvae with depleted energy reserves may not be able to metamorphose into recruits (Vermeij et al. 2006). Nonetheless, the magnitude of change in oocyte size with depth was small, so the biological implications may be limited.
**Fecundity**

Decreased *M. cavernosa* polyp fecundity with depth was driven by a change in the number of gonads found in each polyp, as opposed to the number of oocytes found in each ripe gonad. Despite reduced fecundity, mesophotic *M. cavernosa* polyps were found to produce 200–400 oocytes per polyp. This is similar to Soong (1991), who found via dissection that *M. cavernosa* polyps from Panama produced 240–480 oocytes per polyps (10–20 oocytes per gonad and 24 gonads per polyp). These estimates were much higher than those made by Acosta and Zea (1997), who found via histology that, on average, *M. cavernosa* polyps from Columbia produced 103 oocytes (3 oocytes per gonad and 34 gonads per polyp). Due to the nature of tissue histology, polyp fecundity estimates are almost certainly underestimated. Histological slides are two-dimensional slices of three-dimensional polyp structures, and gonadal tissues often appear folded or incomplete, which leads to undercounting of oocytes. Dissection is one method to account for this problem with histology, and because the polyp fecundities found via dissection (Soong 1991) were most similar to the results in this study, there is support of this study’s use of visually complete gonads to determine the number of oocytes per gonad. Dissections are also a possibility to limit this problem; however, dissections of *M. cavernosa* polyps attempted during the course of this study did not provide consistently reliable results.

Reduced polyp fecundity with depth in *M. cavernosa* contrasts with previous literature describing depth-independent fecundity in the Western Atlantic corals *O. faveolata* and *P. astreoides* (Holstein et al. 2015, 2016b). There is evidence that corals with large polyps devote proportionally less energy to their gonadal tissues and more to their somatic tissues (Leuzinger et al. 2003), which may partially explain this discrepancy as *M. cavernosa* has much larger polyps than *O. faveolata* and *P. astreoides*. Larger polyps might require thicker septae, which would
require more energy for maintenance and growth, leaving less available energy and space for reproductive development. This could perhaps explain this disparity, but the trend of reduced polyp fecundity over depth found in this study is consistent with those found in the Red Sea (Rinkevich and Loya 1987; Feldman et al. 2018; Shlesinger et al. 2018) and Japan (Prasetia et al. 2016), which studied species with a wide range of polyp sizes.

In an effort to relate histological findings to depth-specific contributions to regional *M. cavernosa* larval pools, polyp fecundity was extrapolated to the scale of populations using datasets describing depth-specific coral cover and habitat extent in the USVI. The extent of coral reefs is not evenly distributed across depth in the USVI; mesophotic reef area is almost three times larger than shallow reef area (Smith et al. 2019). So, although there appears to be a smaller proportion of females at depth, the total number of eggs that mesophotic habitats produce is greater than that produced by shallow and mid-depth habitats. However, the male-biased sex ratio of *M. cavernosa* at depth is skewed too strongly for mesophotic reef area to fully compensate for the reduction in the proportion of females in MCEs. Shallow and mid-depth reefs are not only experiencing disturbance and coral declines more strongly than mesophotic reefs, there is also less total reef area in these habitats. This further magnifies the effects of decreased population fecundity in shallow and mid-depth habitats due to disturbance.

*Disturbance: Storms, bleaching, and disease*

Disturbance since 2016 has reshaped coral communities in the USVI and drastically reduced the abundance of *M. cavernosa* in shallow and mid-depth habitats. In 2017, two major hurricanes impacted the shallow reefs of the USVI. In 2019, SCTLD appeared, followed by severe shallow bleaching. Mesophotic *M. cavernosa* populations appear to have been spared the
mortality experienced by shallow and mid-depth populations, which, of course, has implications for the number of reproductive units (i.e. eggs and larvae) these populations can produce.

Interannual variability in population and total habitat fecundity was driven by changes in coral cover. Coral cover is dynamic due to coral growth, disturbance, and recovery from disturbance. As the coral cover was measured from permanent transects, the variation between years is not due to random or haphazard selection of transect location. Changes are due to biotic and abiotic processes facilitating or inhibiting coral growth and survival.

Coral cover decreased dramatically with depth in 2016, so potential population fecundity was highest at shallow reefs. However, in 2017, a large decrease in shallow reef *M. cavernosa* cover drove a decrease in population fecundity, which was sustained in 2018. In the months preceding the 2017 TCRMP data collection, the USVI experienced two Category 5 hurricanes: Irma and Maria. The hurricanes devastated reef communities, and coral cover experienced a 1–4% decrease (Edmunds 2019). However, when extrapolated to the high magnitude of polyp fecundity per square kilometer, small changes in coral cover can have extremely large impacts on population fecundity. This was demonstrated in the order of magnitude difference in shallow population fecundity between 2016 and 2017.

However, at mesophotic depths, the changes in population fecundity from 2016 through 2018 were relatively small, indicating that mesophotic coral cover was minimally impacted by Hurricanes Maria and Irma. This has strong implications for refugia if corals in MCEs are able to continue to reproduce following devastating storms. Furthermore, comparing population fecundities at mesophotic reefs with the application of both depth-independent and depth-dependent sex ratios allows for the effects of coral cover and sex ratio to be teased out. When applying a 1:1 sex ratio across depth, the population fecundity of MCEs is relatively constant
over time, and, in 2017 and 2018, constant over depth. However, when applying a male-biased sex ratio at depth, the population fecundity on MCEs decreases dramatically, indicating that sex ratio is inhibiting MCE’s ability to fully offset shallow coral declines. In this system, sex ratio is the major driver of differences in fecundity despite relatively even coral cover over *M. cavernosa*’s depth range in 2017 through 2018. In almost all cases, if it were not for the reduced proportion of females at depth, MCEs would be more fecund than shallow ecosystems, even in the face of multiple perturbations.

In 2019, SCTLD was first observed in St. Thomas, and, months later, the most severe bleaching event since 2005 occurred (Dr. T. Smith pers. comm.). While SCTLD only affected shallow sites at this time, there was a dramatic decrease in percent coral cover. This is unsurprising given the compounding effects of bleaching and white plague disease caused a 60% decline in coral cover in 2005 (Miller et al. 2009), and SCTLD is expected to be just as devastating to coral communities, if not more, than white plague disease. In response to these two disturbances, shallow corals contributed very little to the larval pool in 2019. In 2020, SCTLD spread deeper and affected reefs at intermediate depths, further skewing the *M. cavernosa* larval pool towards mesophotic larvae. However, there is no reason to expect that mesophotic reefs are immune from SCTLD; this relationship will likely continue to be dynamic as the disease spreads. SCTLD has begun to be reported in MCEs around St. Thomas (The Virgin Islands Coral Disease Advisory Committee), and continued monitoring of the spread of the disease will be important to understanding the potential for SCTLD refuge.

As SCTLD begins to reach mesophotic depths, the literature remains ambiguous as to how SCTLD will affect *M. cavernosa*. Initial studies in the USVI suggest *M. cavernosa* may be more resistant to SCTLD than other coral species (Dr. M. Brandt pers. comm.), and SCTLD
appears to progress across the coral colony tissue more slowly in *M. cavernosa* than it does in other species (Meyer et al. 2019). However, along the Florida reef tract, *M. cavernosa* had the highest frequency and prevalence of SCTLD (Muller et al. 2020). These early studies show a lack of consensus regarding species-specific susceptibility, and they indicate that there is much that is still unknown about how SCTLD will spread and affect *M. cavernosa*. Therefore, it is uncertain if the trend of increasing importance of mesophotic reproduction will continue with time, and if USVI MCEs are a short-term refuge or a long-term refugium for *M. cavernosa*. 
CONCLUSION

The loss of shallow coral cover due multiple disturbances, causing decreases in inferred population fecundity, suggest that USVI MCEs may be a reproductive refuge for *M. cavernosa*. Resistance to degradation from hurricanes, thermal stress, and disease indicate that mesophotic habitats are important for maintaining *M. cavernosa* populations in the face of disturbances. As severe storms (Knutson et al. 2010; Holland and Bruyère 2014) and bleaching events (Hoegh-Guldberg et al. 2007; Hughes et al. 2018) become more frequent with climate change, this pattern may become more extreme. Although there is less *M. cavernosa* reproductive effort per square kilometer in MCEs, mesophotic *M. cavernosa* populations are still the largest contributors of overall reproductive effort due to higher mesophotic habitat extent. While the stability of USVI MCEs as consistent refugia through time is still under question, MCEs are likely to play an important and dynamic role in maintaining *M. cavernosa* populations in the face of future disturbances.
WORKS CITED


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VITA

Jeanne Bloomberg, born in Mendota Heights, Minnesota, gained her Bachelor of Science in marine biology at Northeastern University in Boston, Massachusetts. As an undergraduate student, she participated in the Three Seas Program, where she gained experience as a marine biologist in Nahant, Massachusetts; Bocas del Toro, Panama; and Friday Harbor, Washington. Upon graduation, she worked in Carlsbad, California monitoring kelp forests and in St. Croix, U.S. Virgin Islands working with the Nature Conservancy’s coral restoration project. She then decided to attend graduate school and pursue a Master of Science from Louisiana State University in the Department of Oceanography and Coastal Sciences. She anticipates graduation in August 2020, after which she will work for the NOAA RESTORE Science Program as a National Academy of Sciences Gulf Research Program Science Policy Fellow.