



REPORT

Mesophotic coral refuges following multiple disturbances

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Abstract As coral populations on shallow reefs decline globally, mesophotic coral ecosystems (MCE) have been proposed as potential coral refugia from thermal, storm, and anthropogenic disturbances in the face of climate change. The current study assesses the refuge potential of MCEs in the U.S. Virgin Islands (USVI) for *Montastraea cavernosa* by extrapolating reproductive potential through depth-stratified coral loss following regional storm, disease, and bleaching perturbations. Fecundity of this depth-generalist coral from 4 to 40 m was measured histologically, and polyp, population, and total habitat fecundities were then extrapolated across the species' depth range. The number of reproductively active female gonads per polyp and oocyte size experienced a significant, though small, decrease with depth, potentially due to energetic limitations. Notably, the population sex ratio was not different from 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 large spatial extent of mesophotic reefs relative to shallow reefs in the USVI makes MCEs the primary contributor of oocytes, despite the reduced proportion of females at depth. Following Hurricanes Irma and

Maria in 2017, the outbreak of Stony Coral Tissue Loss Disease in 2019, and a bleaching event in 2019, shallow and mid-depth *M. cavernosa* populations experienced severe coral cover declines. Shallow and mid-depth population fecundities were predicted to decline correspondingly. Coral cover in MCEs remained relatively stable following these largely shallow water perturbations, and predicted population and total habitat fecundities remained constant as well. Thus, MCEs in the USVI currently appear to be reproductive refuges for *M. cavernosa*, but the persistence of that refuge remains in question as disease perturbation begins to affect deeper reefs.

Keywords Mesophotic coral ecosystems · Deep reef refugia hypothesis · Coral reproduction · Fecundity · *Montastraea cavernosa*

Introduction

As shallow reefs continue to experience global declines due to climate change and local disturbances, interest has increased in identifying reef locations and coral traits that support resistance or resilience to environmental stress (Riegl and Piller 2003; Day et al. 2008; Bongaerts et al. 2010). 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) (Bongaerts et al. 2010). The DRRH posits that (1) corals found in mesophotic coral ecosystems (MCE), between 30 and 150 m, may experience less intense anthropogenic perturbation than shallow corals, and (2) mesophotic corals are reproductively viable and contribute demographically to coral persistence as a source of larvae for local and distal recruitment (Bongaerts et al. 2010;

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Holstein et al. 2015, 2016a; Davies et al. 2017; Shlesinger and Loya 2019). MCEs, therefore, could act as refugia, where coral populations persist despite climate change and other direct anthropogenic disturbances. Evidence to support this suite of hypotheses is scant and often contradictory, suggesting that MCEs will not be universal coral reef refuges and may only support the persistence of some species over unknown time scales (Bongaerts et al. 2010, 2017; Smith et al. 2016a, b, 2019b; Shlesinger et al. 2018; Bongaerts and Smith 2019).

Evaluating the DRRH requires a deep understanding of coral and larval physiology across depth. As MCEs are understudied due to their depth, the 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. The current study assesses the capacity of MCEs in the U.S. Virgin Islands (USVI) to support reproductive populations of a scleractinian coral in the face of multiple disturbances over the past five years, including two Category 5 hurricanes, a mass bleaching event, and the emergence of a novel disease. It aims to quantify the reproductive effort of the depth-generalist *Montastraea cavernosa* in the USVI across its depth range as a partial assessment of the viability of MCEs as coral refuges or refugia. We then project this viability through time, in response to empirically measured coral loss due to multiple coral reef disturbances.

Depth and isolation protect many MCEs from an array of anthropogenic and natural disturbances, such as coral bleaching (Glynn 1996; West and Salm 2003; Bongaerts et al. 2010); coastal pollution (Bak et al. 2005; Smith et al. 2008; Lesser et al. 2009; Bongaerts et al. 2010; Slattery et al. 2011); and hurricanes (Woodley et al. 1981; Kobluk and Lysenko 1992; Lesser et al. 2009; Robbart et al. 2009). Mesophotic corals, however, are not immune to disturbances. Because they are infrequently exposed to high temperatures, mesophotic corals may exhibit lower thermal tolerances than shallow corals (Smith et al. 2016b) and thus may be uniquely susceptible to thermal stress when it does occur (Bongaerts et al. 2010; Smith et al. 2016b). MCEs are also susceptible to sedimentation and debris following storm events (Bak et al. 2005; Bongaerts et al. 2010), which are most damaging to flat, plating coral morphologies, such as those most commonly found on MCEs (Kahng et al. 2019). MCEs may exhibit disturbance avoidance but may have varying or limited capacities of recovery afterwards.

It follows that MCEs are likely not universal refugia, in that they will not protect all 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. 2016b; Rocha et al. 2018), but refugia need not be pristine environments to protect biodiversity. Instead, networks of connected but imperfect, or even ephemeral, refuges could serve collectively as ecological refugia to support otherwise threatened species and communities (Keppel et al. 2012).

In the USVI, the upper mesophotic zone (30–45 m) is dominated by the genus *Orbicella*, with *M. cavernosa* among the most abundant species (Smith et al. 2019a). The known extent of mesophotic reefs in the USVI (204 km²) is almost three times larger than the extent of shallow reefs (71 km²), and coral cover on these reefs can far exceed that of disturbed shallow reefs (Smith et al. 2016a, 2019a). Thus, upper MCEs in the USVI support a high abundance of depth-generalist corals, which likely exceeds total coral abundance on struggling shallow reefs in the region.

In 2014, a highly deadly emergent coral disease appeared in Florida (Precht et al. 2016); affecting over 20 coral species (Lunz et al. 2017), it is commonly referred to as 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 had been isolated to the Florida Reef Tract for nearly 4 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 on shallow reefs, and the susceptibility of *M. cavernosa* appears to be somewhat lower than other coral species (FKNMS/DEP 2018; Aeby et al. 2019). If, in addition to decreased severity of bleaching and storm intensity at depth, SCTLD 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 cover 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 refugia for *M. cavernosa*.

Materials and methods

Study species

M. cavernosa is a gonochoric, broadcast spawning species and spawns a week after the full moons in August and September (Szmant 1986, 1991; Soong 1991; Wyers et al.

1991; Van Veghel 1993; Acosta and Zea 1997). 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 begins in April to June, with Stage IV spermaries 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).

There are two 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). The morphs are not always easily visually distinguishable, and morphs are not predictably correlated with depth (Ruiz Torres 2004; Budd et al. 2012).

Field Collection

In May 2019, *M. cavernosa* tissue samples (from $N = 96$ colonies) were collected via open-circuit and technical decompression SCUBA from three reefs off the southern coast of St. Thomas, USVI, binned by habitat type (Fig. 1): Shallow fringing reef (Brewer's Bay, 4–13 m, $n = 40$); 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, $n = 28$). SCTLD outbreaks were ongoing during collection in May 2019 at Brewer's Bay; it was difficult to access shallow reefs that were not affected by SCTLD. Samples were taken from any colony observed within the time constraints associated with decompression diving, so long as they were: (1) larger than 225 cm² to ensure they were reproductively mature [Szmant (1991) suggests *M. cavernosa* colonies are reproductively mature after reaching 100–170 cm²]; (2) not showing signs of disease; (3) > 2 m from any diseased colony; and (4) a minimum of five fin-kicks (~ 8 m)

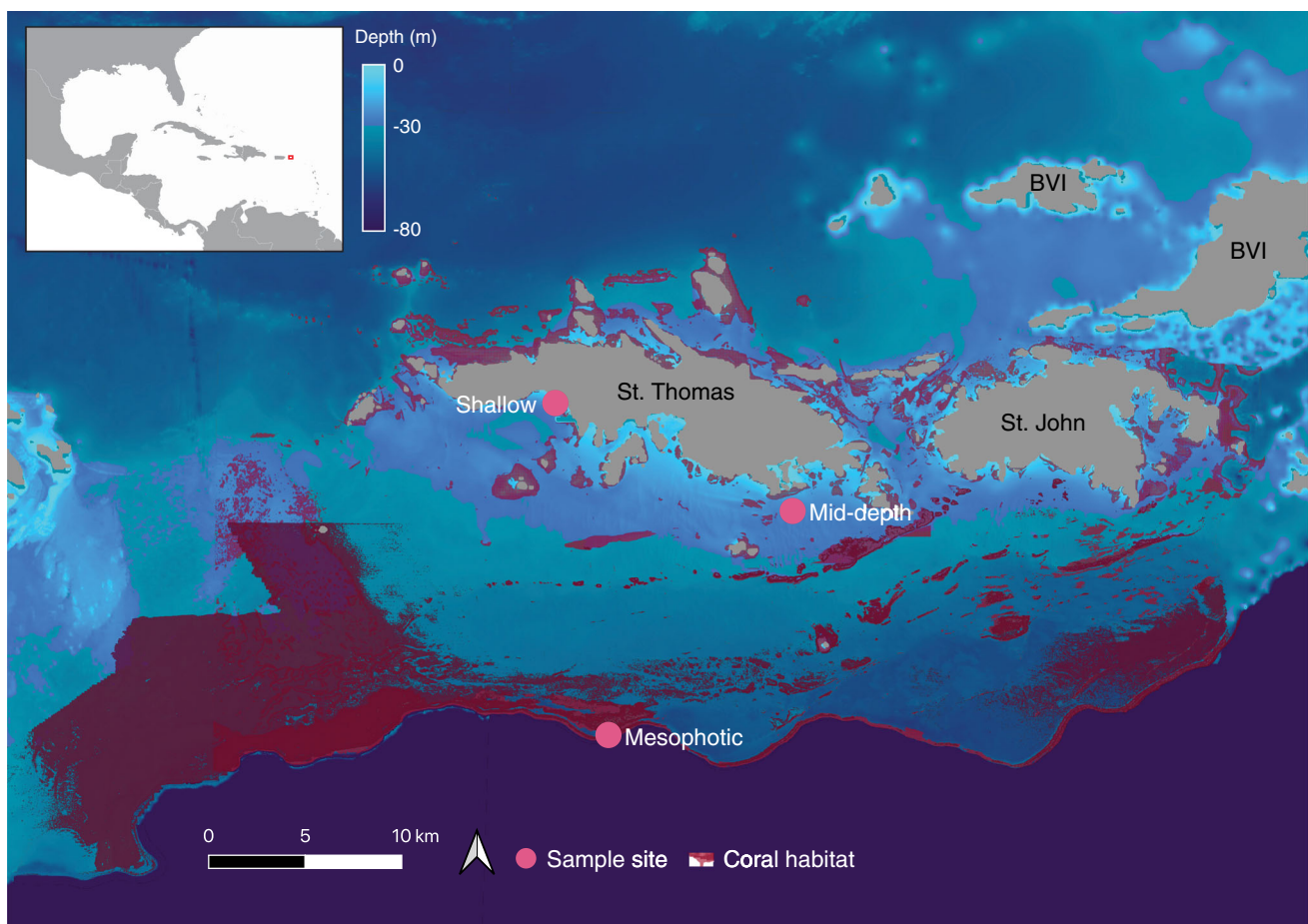


Fig. 1 The northern USVI islands of St. Thomas and St. John. Pink circles indicate collection reefs off the southern coast of St. Thomas, which correspond to shallow (Brewer's Bay), mid-depth (Seahorse

Reef), and mesophotic (Grammanik Bank) reefs. Red patches indicate coral habitat projections from shallow and deep datasets, including coral reef and coral colonized pavement (Costa et al. 2017)

from a sampled colony to minimize the probability of sampling clones. Neither morph was targeted for collection across depths, and no morphological distinctions were observed in sampled colonies.

Using a hammer and cold chisel, 15–25 cm² 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. Colony height, maximum diameter, and perpendicular diameter were recorded. Samples were immediately placed in zinc-buffered formalin (Z-Fix, Anatech Ltd., Battlecreek, MI) for ~ 24 h, rinsed in 20 µm filtered freshwater for 24 h, and stored in 70% ethanol.

Histology

The samples' skeletons were dissolved in a decalcifying solution of 5% hydrochloric acid with 5.0 g EDTA L⁻¹. Upon complete decalcification, coral tissues were stored in 70% ethanol. Tissues were paraffinized in a Leica ASP6025 Tissue Processor and embedded for both cross- and longitudinal-sectioning using a Leica EG1150 H Embedding Station. Tissue blocks were sectioned 4 µm thick with a Leica RM2125 RTS Microtome. Serial sections were taken every 400 µm throughout the tissue.

Histological tissue sections were stained with hematoxylin and eosin or modified Heidenhain's aniline blue (Fig. 2). Histology slides were imaged using an Olympus BX41 Microscope with an Olympus SC180 digital camera or a Hamamatsu NanoZoomer slide scanner.

Fecundity analyses

Histological slides were assessed for the absence or presence of female or male gonads to estimate population sex ratio. Colonies containing no visible gametes were assumed to be male, as the sampling time may have been prior to spermatogenesis for most *M. cavernosa* colonies (Szmant 1986, 1991; Acosta and Zea 1997), and the colonies were of a size class to support female reproduction (Szmant 1991). Within female colonies, three metrics of reproductive effort 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, b). The number of oocytes per gonad was counted in longitudinal sections (Fig. 2c, d). Difficulty in capturing an entire gonad in a single longitudinal section is a common problem in coral histology. Mesenteries often appear folded in and out of the plane of section. Thus, estimations of oocytes per gonad are likely underestimates. To

accommodate this underestimation, oocytes were not counted from gonads with fewer than five visible oocytes.

Polyp fecundity (F_{polyp}) was defined as the total number of oocytes in a single polyp and estimated as:

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

Oocyte area and polyp area were measured using a rotated ellipse in CellSens Dimension software (Olympus). Oocyte area was 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-Froelich (1985) and Vargas-Angel et al. (2002).

Polyp fecundity (Eq. 1) was further extrapolated to estimate population-level fecundity (F_{pop}) as:

$$F_{\text{pop}} = \text{Coral cover} \div \text{Polyp area} \times \text{Female sex ratio} \times F_{\text{polyp}} \quad (2)$$

Colony-specific values (not means) were used for F_{polyp} and polyp area, and reef-specific values were used for coral cover and female sex ratio, resulting in depth-specific distributions of population-level fecundities. *M. cavernosa* coral cover was estimated using averages of each collection reef from the USVI Territorial Coral Reef Monitoring Program (TCRMP) data from 2016 to 2020. TCRMP datasets from 2017 to 2018 were used to estimate population fecundity following Hurricanes Maria and Irma, and 2019 and 2020 were used to estimate population fecundity following SCTLD and bleaching disturbances. On mesophotic reefs, population fecundity projections were calculated using both a 1:1 sex ratio and a sex ratio estimated from this study's results, in order to tease out the effects of changing coral cover and a male-biased sex ratio on population fecundity.

These reef-specific population fecundities (Eq. 2) were further extrapolated to estimate the total habitat fecundity (F_{hab}) over depth:

$$F_{\text{hab}} = F_{\text{pop}} \times \text{Coral habitat extent}_{\text{hab}} \quad (3)$$

Coral habitat area was estimated as per Smith et al. (2019a) with coral habitat area categorized into 10 m depth bins. Colony-specific population fecundity estimates and coral habitat from the corresponding depth bin were used to obtain a distribution of total habitat fecundity based on the results from each sampled colony.

Statistical analyses

To ensure that colony size did not affect the gender 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 per

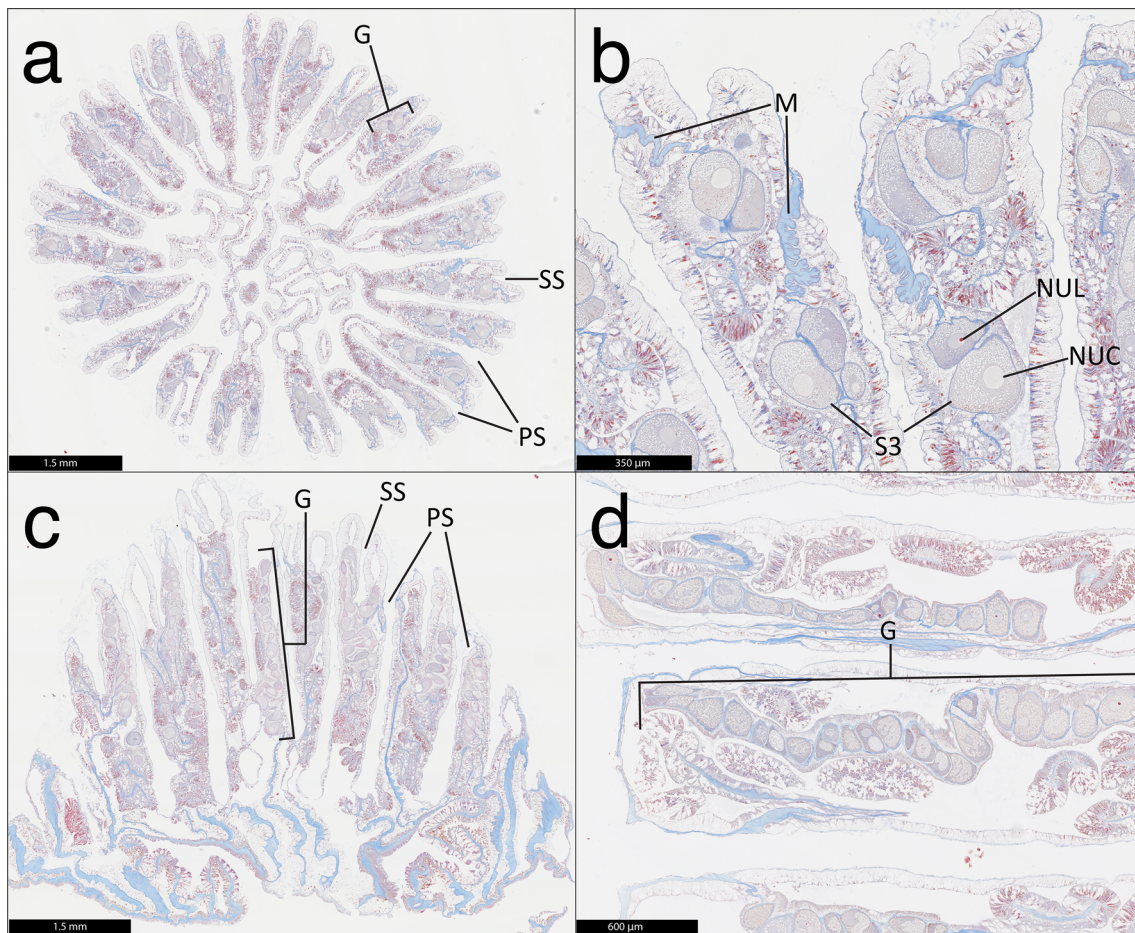


Fig. 2 Histological images of female *Montastraea cavernosa*. **a** Full polyp in horizontal cross section. **b** Septae with Stage III oocytes in horizontal cross section. **c** Full polyp in longitudinal cross

section. **d** Septae in longitudinal cross section. G: gonad; PS: primary septa; SS: secondary septa; S3: Stage III oocyte, M: mesoglea; NUC: nucleus; NUL: nucleolus

Holstein et al. (2015). To ensure that colony size did not affect polyp fecundity, the relationship between colony surface area and the number of female gonads per polyp was estimated using a linear regression (LR) 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 $\alpha = 0.05$.

X^2 -tests were used to determine if population sex ratio was (1) significantly different from 1:1 using data from all reefs, (2) significantly different from 1:1 within populations at each depth, and (3) significantly different between reefs. 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 cross-sectional area was estimated using natural log-transformed measurements and a linear mixed model (LMM) with colony, polyp, and histological slide as nested random

effects to avoid pseudoreplication. Analyses were completed separately for each oocyte stage.

The relationship between depth and the number of female gonads per polyp was estimated with a GLMM with a Poisson distribution, with colony and polyp 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 on a single histological slide and was analyzed using a GLMM with a Poisson distribution and colony as a random effect. Gonads were assessed as complete if (1) 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 end 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 depth and year (predictor) on population fecundity (response) were tested in a two-way ANOVA with Type III sum of squares. The variation in population fecundity (response) between depths (predictor) was examined for each year using an ANOVA, and multiple post hoc comparisons were made using Tukey's honest significant difference (HSD) post hoc test. Significance was evaluated at $\alpha = 0.05$. This analysis was repeated for total habitat fecundity.

Results

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. Colony size did not have a significant effect on the sex of the colony ($F_{1, 94} = 0.18$, $p = 0.67$) or on polyp fecundity (LR: $R^2 = 0.02$, $p = 0.41$).



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

Sex ratio

Across all depths, there were 56 presumed male and 40 female colonies, which was not significantly different from a 1:1 sex ratio. The sex ratio varied significantly according to reef 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 (shallow reef: 24 males, 16 females; mid-depth reef: 10 males, 18 females; Fig. 4). Grammanik Bank (mesophotic) had 22 males and 6 females, which was 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 shallow and mid-depth reefs and shallow and mesophotic reefs, but they were significantly different between mid-depth and mesophotic reefs ($p = 0.018$, Bonferroni adjusted p value).

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 reef depths. The mean oocyte area of Stage III oocytes was $0.026 \pm 0.010 \text{ mm}^2$ (mean $\pm$ SD, $n = 40$). When including only Stage III oocytes, the oocyte area decreased significantly with depth by 0.96% per meter (LMM: $t = -3.23$, $df = 37.55$, $p = 0.0027$, Satterthwaite's approximation of degrees of freedom; Fig. 5). The mean decrease in oocyte area was $-9.34 \times 10^{-9} \text{ mm}^2 \text{ m}^{-1}$ (Fig. 5). The mean oocyte area of Stage II eggs was $0.013 \pm 0.0047 \text{ mm}^2$ (mean $\pm$ SD, $n = 30$). When including only Stage II eggs, there was no significant relationship between oocyte area and depth.

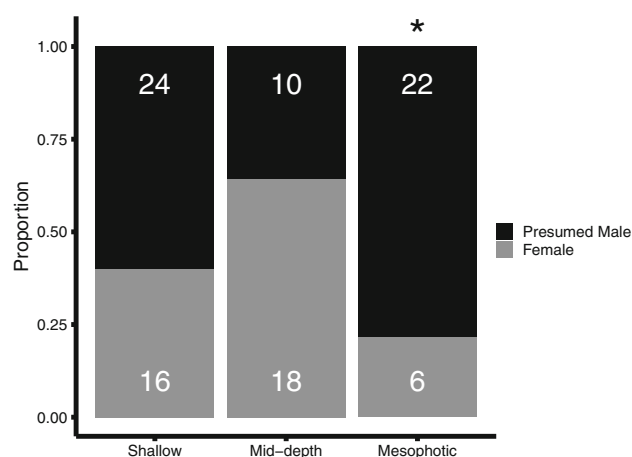


Fig. 4 Sex ratio of *Montastraea cavernosa* colonies at shallow, mid-depth, and mesophotic reefs. White numbers refer to the frequency of putative male or females at each reef. * indicates a sex ratio significantly different from 1:1

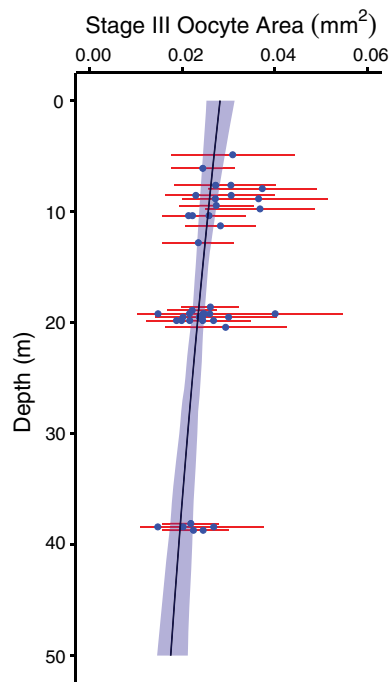


Fig. 5 Area of Stage III oocytes over depth. Black line indicates the back-transformed predicted values from a linear mixed model with colony, polyp, and histological slide as nested random effects. Blue ribbon is the 95% confidence interval of the model, calculated by parametric bootstrap. Blue dots refer to colony means, and red lines are standard deviations

Polyp fecundity

The number of female gonads per polyp decreased with depth (GLMM: $Z\text{-score} = -1.98$, $p = 0.048$, Normal Distribution $Z\text{-test}$, Fig. 6b), decreasing by 1.94% per meter. The mean decrease in gonads per polyp was -0.43 gonads m^{-1} (Fig. 6b). The mean number of female gonads per polyp was 28.91 ± 13.13 (mean $\pm$ SD, $n = 40$) for all depths combined. The mean number of oocytes per gonad (including only gonads with greater than 5 oocytes) was 7.77 ± 3.67 (mean $\pm$ SD, $n = 33$) and did not change significantly with depth. The mean number of oocytes per visually complete gonad was 19.09 ± 4.80 (mean $\pm$ SD, $n = 10$) and did not change significantly with depth (Fig. 6a).

Polyp area increased with depth by $0.38 \text{ mm}^2 \text{ m}^{-1}$ (LMM: $t\text{-score} = 2.46$, $\text{df} = 37.96$, $p = 0.019$, Satterthwaite's approximation of degrees of freedom) (Fig. 6c).

M. cavernosa percent cover

In 2016, percent cover of *M. cavernosa* was relatively even across depths (Fig. 7). It then decreased at shallow depths by 41.1% from 2016 (0.67% cover) to 2017 (0.39% cover) after Hurricanes Irma and Maria and by 62.9% from 2018

(0.41% cover) to 2019 (0.15% cover) after bleaching and the emergence of SCTLD (Fig. 7). On mid-depth reefs, *M. cavernosa* percent cover experienced a 14.5% decrease from 2016 (0.47% cover) to 2017 (0.40% cover) after Hurricanes Irma and Maria and a decrease to 0% cover in 2020 after SCTLD spread to mid-depths (Fig. 7). On mesophotic reefs, percent coral cover of *M. cavernosa* remained relatively stable through 2016–2019, but then experienced a 30.7% decrease in coral cover from 2019 (0.77% cover) to 2020 (0.53% cover) (Fig. 7).

Population fecundity

Corresponding with changes in coral cover (Fig. 7), population fecundity estimates for shallow and mid-depth reefs also fell from 2016 (shallow: 067% cover, 8.12×10^{10} oocytes km^{-2} ; mid-depth: 047% cover, 3.98×10^{10} oocytes km^{-2}) to 2020 (shallow: 0.12% cover, 1.40×10^{10} oocytes km^{-2} ; mid-depth: 0% cover, 0 oocytes km^{-2}) (ESM Table S1; Fig. 8a–e). In general, mesophotic reefs experienced smaller losses in living coral cover throughout multiple disturbances (0.67% cover in 2016; 0.53% cover in 2020) (Fig. 7), and thus, estimated mesophotic population fecundity also remained relatively stable (Fig. 8a–e). When calculated with a 3.6:1 male-biased sex ratio, population fecundity on mesophotic reefs only fell from 1.84×10^{10} oocytes km^{-2} in 2016 to 1.47×10^{10} oocytes km^{-2} in 2020 (ESM Table S1). Population fecundities were estimated at each depth and in each year using a 1:1 sex ratio. Estimates for mesophotic populations were also made using a 3.6:1 male-biased mesophotic sex ratio, which effectively reduced estimated mesophotic fecundity by 56.6% in all years. Unless otherwise noted, mesophotic results are given for both 1:1 and 3.6:1 male-biased sex ratio.

Estimated population fecundity varied significantly by depth ($F_{3, 210} = 19.48$, $p < 0.001$) and years ($F_{4, 210} = 29.37$, $p < 0.001$). There was also a significant interaction of population depth and year ($F_{12, 210} = 6.1262$, $p < 0.001$; Fig. 8a–e). In 2016 (preceding disturbances), the estimated population fecundity on shallow reefs was significantly higher than those on mid-depth ($p < 0.001$, Tukey's HSD) and mesophotic reefs with both a 1:1 ($p = 0.019$, Tukey's HSD) and 3.6:1 sex ratio ($p < 0.001$, Tukey's HSD; Fig. 8a). In 2017, after Hurricanes Irma and Maria, a loss of shallow coral cover caused a decrease in estimated population fecundity on shallow reefs, but mid-depth and mesophotic reefs remained relatively unchanged (Fig. 8b). In 2017, population fecundity estimates were significantly higher on shallow reefs than on mesophotic reefs only with a 3.6:1 male-biased sex ratio ($p = 0.0081$, Tukey's HSD; Fig. 8b). In 2018, there were no significant differences in population fecundities among depths (ESM

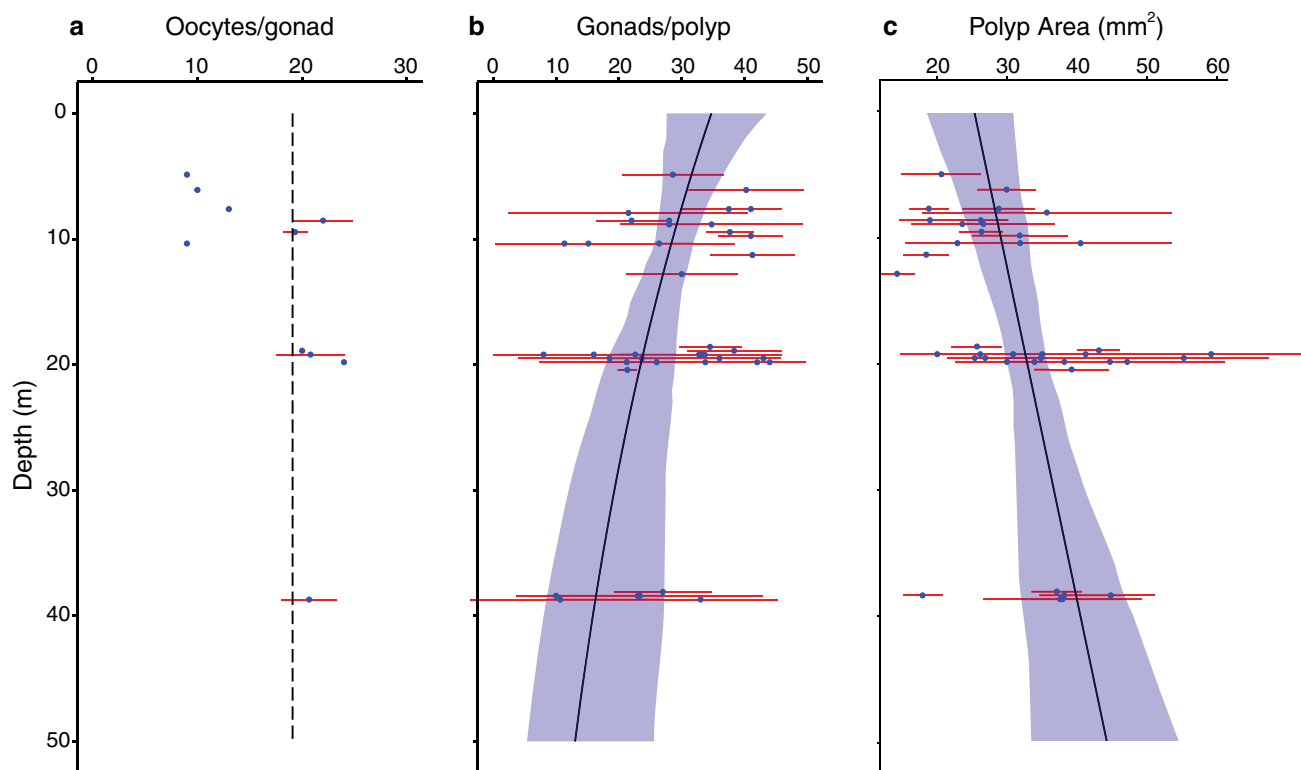


Fig. 6 Polyp fecundity over depth. a. Relationship between the mean number of oocytes per gonad and depth. The dotted line represents the mean number of visually complete gonads across all depths (19.09 gonads). Model predictions were not used, as no effect of depth on the number of oocytes per gonad was detected. b. Relationship between the number of gonads per polyp over depth. Black line represents predicted values from a generalized linear mixed model with a Poisson distribution; colony and polyps were applied as nested

random effects. Blue ribbon is the 95% confidence interval of the model, calculated by parametric bootstrap. c. Relationship between polyp area and depth. Black line represents predicted values from a linear mixed model with colony identity as a random effect. Blue ribbon is a 95% confidence interval of the model, calculated by parametric bootstrap. In all panels, blue dots refer to colony means, and red lines are the colony standard deviations. Blue dots with no red lines had only one measurement per colony

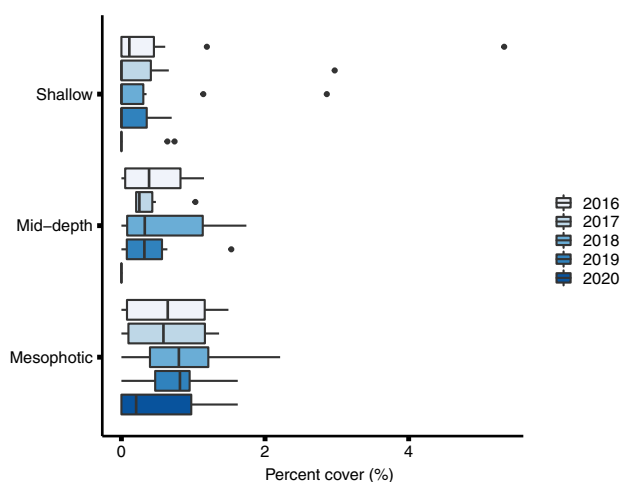


Fig. 7 Percent cover of *Montastraea cavernosa* on shallow, mid-depth, and mesophotic reefs from 2016 to 2020 USVI TCRMP. Boxes represent the interquartile range, and whiskers extend to minimum and maximum values. Black dots indicate potential outliers

Table S1; Fig. 8c). After the emergence of SCTL and a bleaching event in 2019, coral cover, and correspondingly,

population fecundity on shallow reefs further declined, and there was significantly lower population fecundity on shallow reefs than on mid-depth reefs ($p = 0.0056$, Tukey's HSD) and mesophotic reefs with a 1:1 sex ratio ($p = 0.0033$, Tukey's HSD; Fig. 8d). As SCTL extended deeper in 2020, population fecundity estimates at mid-depths dropped to zero oocytes km⁻² (Fig. 8e).

In 2019–2020, the estimated population fecundities on mesophotic reefs with a 1:1 sex ratio was higher than those on shallow and mid-depth reefs, but the population fecundities on mesophotic reefs with a 3.6:1 male-biased sex ratio did not exceed those on shallow and mid-depth reefs (ESM Table S1; Fig. 8d–e).

Total habitat fecundity

The extrapolated total habitat fecundity estimates assume that the reproductive effort found in each population holds true across all habitats at each depth. Total habitat fecundity was significantly affected by depth ($F_{3, 210} = 19.48$, $p < 0.001$) and year ($F_{4, 210} = 29.37$, $p = 0.011$). In every

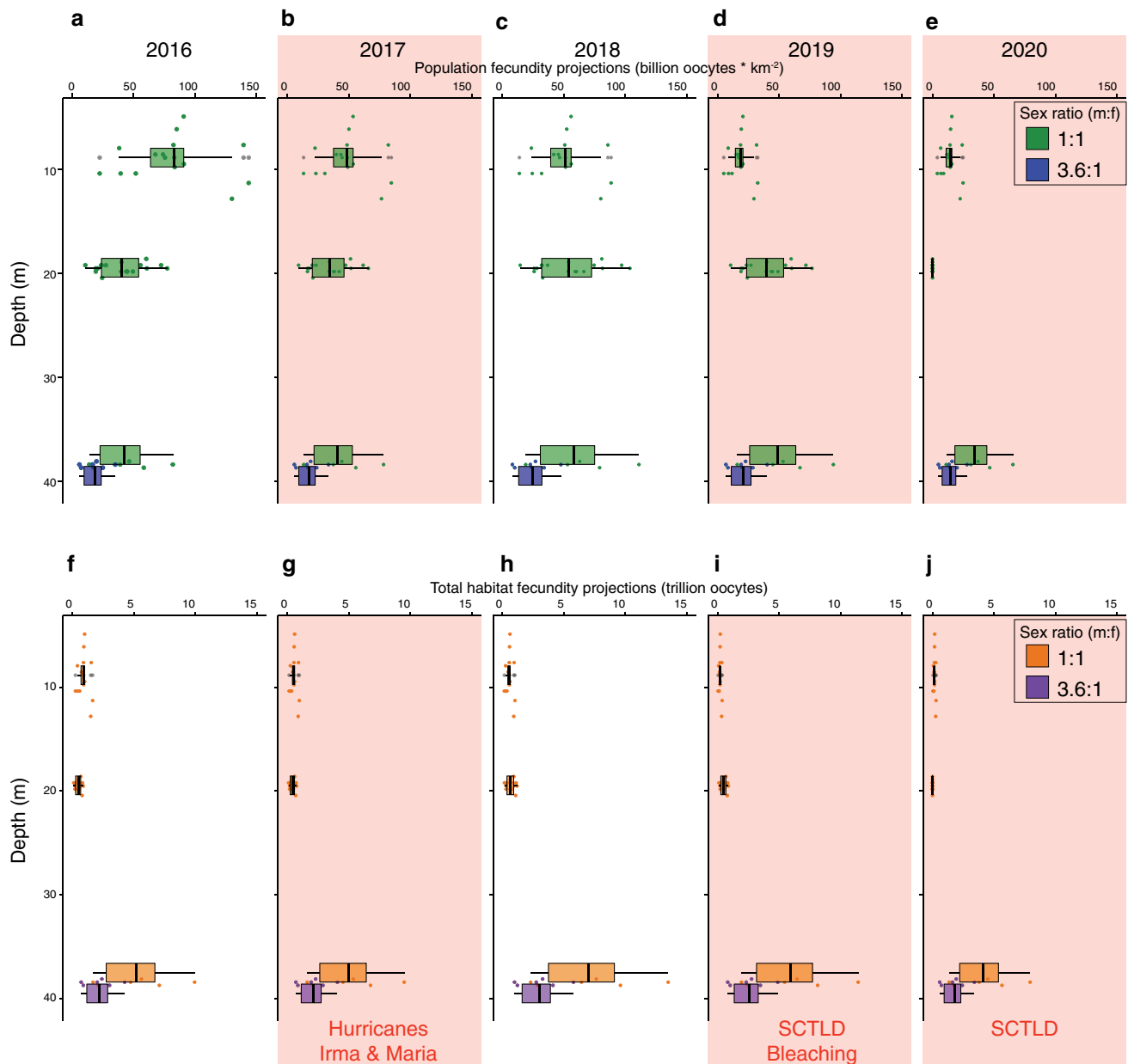


Fig. 8 a–e Population fecundity estimates from 2016 to 2020 calculated by Eq. 2. In green boxes, a 1:1 sex ratio was used to calculate population fecundity. In blue boxes, a 3.6:1 male to female ratio was used to calculate population fecundity, f–j total habitat fecundity estimates in the USVI from 2016 to 2020 calculated by Eq. 3. In orange boxes, a 1:1 sex ratio was used to calculate total

habitat fecundity. In purple 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 reef followed by a mass bleaching event. SCTLD spread to the mid-depth reef in 2020

year from 2016 to 2020, habitat fecundity estimates were lower by an order of magnitude at shallow (2016: 9.14×10^{11} oocytes; 2020: 1.58×10^{11} oocytes) and mid-depth (2016: 4.90×10^{11} oocytes; 2020: 0 oocytes) reefs than at mesophotic reefs with both a 3.6:1 male-biased sex ratio (2016: 2.23×10^{12} oocytes; 2020: 1.78×10^{12} oocytes) and a 1:1 sex ratio (2016: 5.20×10^{12} oocytes; 2020: 4.15×10^{12} oocytes) (ESM Table S2; Fig. 8f–j), due to the large spatial extent of mesophotic habitat (Fig. 8f–j).

Discussion

This first assessment of *M. cavernosa* fecundity across its depth range suggests that female colonies, and perhaps male colonies, of this species are contributing to reproductive effort 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, which was found to be male-biased at mesophotic depths. However, because colonies without gonads were assumed to be male, it is possible that the skewed sex ratio is inflated. Nonetheless, the results still indicate that there is a proportionally less female reproductive effort on mesophotic reefs. Regional disturbances led to loss of *M. cavernosa* cover over time, but much less dramatically so at mesophotic depths, and, therefore, reproductive output appears to be dynamic in both space and time. As shallow populations have been increasingly perturbed, the reproductive effort of mesophotic *M. cavernosa* represents a rising proportion of total reproductive effort in the region. The current study demonstrates that mesophotic refuges for this coral are dynamic in time, due to interactions of anthropogenic, storm, and disease disturbances.

The male-biased sex ratio found in *M. cavernosa* on MCEs is in direct contrast with previous studies that found a 1:1 sex ratio (Soong 1991; Acosta and Zea 1997). To acknowledge that this result could be an aberration, analyses were done with both 1:1 and male-biased sex ratios. A skewed sex ratio may be the 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, but see Foster et al. (2007) and Polato et al. (2010). Because shallow corals generally experience higher levels of wave energy associated with fragmentation, it seems unlikely that this would fully explain for differences in sex ratios at mesophotic depths.

Male-biased sex ratios may enhance fertilization success in broadcast spawning species (Brazeau and Lasker 1990). This is an attractive hypothesis to apply to mesophotic *M. cavernosa*, especially considering the sperm-dilution effect of depth (Babcock et al. 1994; Lasker et al. 1996). At deeper depths, there is a larger volume of water for these gametes to disperse through, and as *M. cavernosa* eggs are positively buoyant (Wyers et al. 1991), the large volume of water may decrease the chances of gametes meeting and fertilizing. A higher proportion of males at depth may mitigate the dilution effect and increase the probability of successful fertilization before the eggs rise to the surface. 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 result in this skewed sex-ratio, and it is not clear that this explanation alone could be explanatory.

Another possible and non-exclusive explanation is gendered survivorship. The production of female gametes, which are rich in lipids, is far more energetically expensive than producing male gametes (Arai et al. 1993; Leuzinger

et al. 2003). Thus, metabolically stressed female colonies may have reduced survivorship at depth, where energy from photosynthetically active radiation is limited, leading to a male-biased sex ratio (Rinkevich and Loya 1987; Cerrano et al. 2005). *M. cavernosa* is only the second gonochoric scleractinian to have its gametogenesis studied across depths (Shlesinger et al. 2018), and this study presents the first evidence for the potential of a depth-dependent sex ratio in a scleractinian.

Some portion of the corals without visually identifiable gametes may have been non-reproductive colonies and potentially female. The costs of living at depth may be too great for some female colonies to produce gametes while maintaining tissue growth and metabolism (Rinkevich and Loya 1987), resulting in the misidentification of non-reproductive females as males. The mesophotic male-biased sex ratio of *M. cavernosa* found in this study could then be false or inflated. However, the absence of obvious spermaries was likely due to sampling too early in spermatogenesis. The small magnitude of the effect of depth on polyp fecundity and oocyte size found in this study implies that the deleterious effects of energy limitations are correspondingly small, and that polyps lacking spermaries were, in fact, male.

Male-biased sex ratios in benthic cnidarians are not uncommon. 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, male-biased sex ratios or proportionally enhanced male gamete production may be a consistent characteristic of depth-generalist species in MCEs.

In 2016, before the regional disturbances addressed in this study, relatively low population fecundity on mesophotic reefs was driven by lower polyp fecundity and fewer females at depth, because coral cover was relatively equal across depths in this year. Yet this pattern does not hold true for habitat fecundity, because high coral abundance and habitat extent in MCEs offset the deleterious effects of depth on fecundity (Holstein et al. 2015, 2016b; Smith et al. 2019a). Yet, the Stage III oocytes found at depth were smaller than those in shallow and mid-depth reefs, which is consistent with studies of other species in the Pacific (Prasetia et al. 2017), Red Sea (Feldman et al. 2018;

Shlesinger et al. 2018), and Western Atlantic (Holstein et al. 2015). Smaller oocytes may indicate lower lipid stores, which could limit pelagic larval duration and dispersal potential (Richmond 1987; Harii et al. 2002). Decreased egg and larval buoyancy could affect dispersal via wind-driven currents (Harii et al. 2002, 2007). Lower energy could also prevent larval metamorphosis into recruits (Vermeij et al. 2006). Nonetheless, the magnitude of change in oocyte size with depth was small, and, therefore, the biological implications may be limited.

Disturbances have drastically reshaped shallow coral reef communities in the USVI (Miller et al. 2009; Edmunds 2019; Smith et al. 2019a). Since as recently as 2016, the abundance of *M. cavernosa* on shallow and mid-depth reefs has been drastically reduced through a series of unfortunate events, including two category 5 hurricanes in 2017, the appearance and proliferation of SCTLD in 2019, and, shortly thereafter, a severe shallow bleaching event. Mesophotic *M. cavernosa* populations appear to have been spared the mortality experienced by shallow and mid-depth populations, which, compounded with the dramatically higher habitat extent of mesophotic reefs, strongly skews the *M. cavernosa* larval pool toward mesophotic origin. The effects of decreased polyp fecundity and a male-biased ratio do not seem to limit USVI MCEs from supporting reproductive populations despite multiple disturbances, at least in part because USVI MCEs are so extensive.

While this study provides evidence of a reproductive mesophotic coral population—albeit without addressing fertilization success—it does not test the capacity of MCEs to reseed adjacent populations of different depths. Larval dispersal models of the region indicate vertical population connectivity is possible between MCEs and shallow reefs (Holstein et al. 2016a), and there is no genetic differentiation between mesophotic and shallow populations of *M. cavernosa* in the region (Serrano et al. 2014, 2016). These studies, in addition to the results presented here, suggest that mesophotic populations of *M. cavernosa* contribute demographically to regional recruitment in the USVI.

It is important to note that, while estimating population and total habitat fecundities, this study assumes that the polyp fecundity estimates found from the 2019 sampling year were true for every year from 2016 to 2020. There is no temporal variability in the estimates of polyp fecundity, and, therefore, in population and total habitat fecundity estimates as well. However, there is evidence that some coral exhibit lowered fecundity levels after experiencing stress, for example from storms, bleaching, or disease (Lirman 2000; Ward et al. 2000; Weil et al. 2009; Harrison 2011). These disturbances occurred in the USVI during 2016–2020 and may have affected *M. cavernosa* polyp fecundities. We expect that thermal, disease, and storm disturbance is lower on mesophotic reefs in the USVI

(Smith et al. 2019a). Thus, if disturbance has sub-lethal effects on polyp fecundities, this would exacerbate the pattern of decreased population and total habitat fecundities at shallow and mid-depth reefs as compared to those on mesophotic reefs.

However, there is no reason to expect that mesophotic reefs are immune from future SCTLD disturbance; although USVI MCEs appear to be a disease refuge in the first 2 years of the outbreak, this will likely continue to be dynamic as the disease spreads. SCTLD has begun to be reported in MCEs around St. Thomas, with moderate to severe levels of SCTLD as of 31 January 2021 (Kramer et al. 2019). 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 (FKNMS/DEP 2018), 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 USVI MCEs will maintain sufficient *M. cavernosa* coral cover to continue to support regional populations as the disease spreads.

The severe loss of coral cover in shallower USVI reefs—and throughout the Western Atlantic—due to multiple disturbances is a cause for great concern for the persistence of functioning coral reef populations. The fact that deeper reef populations may continue to reproduce despite these disturbances lends credence to the potential for mesophotic reef refuges. Abundant and reproductive populations currently remain on USVI MCEs despite extreme thermal, storm, and disease disturbance, further highlighting these habitats as important for regional coral persistence. As severe storms (Knutson et al. 2010; Holland and Bruyère 2014) and bleaching events (Hoegh-Guldberg et al. 2007; Maynard et al. 2015; Hughes et al. 2018) become more frequent with climate change, this pattern may become more extreme. While the stability of USVI MCEs as refugia through time is still questionable, MCEs no doubt play an important and dynamic role in maintaining *M. cavernosa* populations in the face of recent, current, and proximate disturbances.

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Declaration

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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