

REPORT

# Population connectivity among shallow and mesophotic *Montastraea cavernosa* corals in the Gulf of Mexico identifies potential for refugia

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**Abstract** Successful management of spatially isolated coral reefs is contingent on an understanding of ecological connections across populations. To investigate genetic connectivity of the depth-generalist coral species *Montastraea cavernosa*, populations from both shallow (15–30 m) and mesophotic coral ecosystems (30–70 m) in the Gulf of Mexico (GOM) were analyzed with microsatellite genotyping. A series of upstream and downstream sites were chosen in marine protected areas including Carrie Bow Cay, Belize; Flower Garden Banks and nearby mesophotic bank habitats; Pulley Ridge; and Dry Tortugas. Patterns of genetic diversity within the northwest GOM supported relatively open coral populations with high levels of gene flow between shallow and mesophotic depth zones, consistent with strong oceanographic patterns and hypothesized availability of coral reef habitats in the GOM. Conversely, genetic differentiation within Belize and the southeast GOM indicate relative isolation of shallow and mesophotic *M. cavernosa* populations in these regions. Structure analysis showed dominant genetic clusters within each region that did not correlate strongly with depth zones, and identified a cluster of unknown origin contributing to high differentiation at Pulley Ridge. Migration modeling predicted historical region-wide panmixia for

most regions, with Pulley Ridge appearing to be a potential sink population. The GOM appears to demonstrate stronger evidence of vertical connectivity compared to elsewhere in the Tropical Western Atlantic, which may be the result of oceanographic variability and/or lack of local selection at depth. These findings are consistent with previous studies identifying genetic connectivity of broadcast-spawning corals across broad spatial scales and highlight the potential importance of mesophotic habitats in the GOM as larval sources to geographically distant populations.

**Keywords** Population genetics · Mesophotic coral ecosystems · Deep reef refugia hypothesis · Vertical connectivity · *Montastraea cavernosa* · Marine spatial planning

## Introduction

Identification of coral source populations and quantification of gene flow is important for effective resource management and conservation strategies (Palumbi 2003), especially in regions impacted by declining coral populations. Numerous studies have assessed coral population connectivity in the wider Tropical Western Atlantic (TWA) (Baums et al. 2005; Goodbody-Gringley et al. 2010, 2012; Nunes et al. 2011; Brazeau et al. 2013; Prada and Hellberg 2013; Serrano et al. 2014, 2016; Rippe et al. 2017), although the Gulf of Mexico (GOM) is relatively understudied in large-scale coral population genetics research. A few studies have included Flower Garden Banks National Marine Sanctuary, indicating that coral populations exhibit high gene flow within the sanctuary (Atchison et al. 2008; Goodbody-Gringley et al. 2012; Serrano et al. 2014; Rippe et al. 2017; Studivan and Voss 2018a). However,

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population connectivity for other coral habitats in the GOM, including those > 30 m deep, remains undocumented. Likewise, there is limited information regarding potential roles of GOM coral populations in larger models of population structure across the TWA.

Mesophotic coral ecosystems (MCEs) are found between 30 and 150 m, beyond no-decompression SCUBA depths but still suitable for photosynthetic corals (Lesser et al. 2009; Puglise et al. 2009; Sherman et al. 2010). A number of MCEs in the TWA have been described in terms of species presence and abundance, but relatively little is known regarding their ecology, ecosystem services, and genetic connectivity to nearby shallow populations (Puglise et al. 2009; Slattery et al. 2011; Kahng et al. 2014). A simple model based on bathymetry and bottom type estimated 178,867 km<sup>2</sup> of potential mesophotic habitat in the northern GOM, an order of magnitude greater area than the predicted 3892 km<sup>2</sup> in the U.S. Caribbean or 3299 km<sup>2</sup> in the Hawaiian Islands (Locker et al. 2010; Semmler et al. 2016; Reed et al. 2017). Little of this area has been explored and characterized, and combined with 247,453 km<sup>2</sup> of predicted shallow habitat in the GOM (Locker et al. 2010), there exists the potential for relatively high gene flow within the region.

It has been hypothesized that MCEs may be able to contribute larvae to degraded shallow populations, termed the deep reef refugia hypothesis (DRRH) (Glynn 1996; Bongaerts et al. 2010a). This theory has many underpinning assumptions regarding habitat availability, community overlap, and adequate larval dispersal between depth zones that must be met, but our knowledge of these fundamental processes is lacking for most regions. Therefore, understanding the connectivity of these potentially valuable ecosystems remains a priority. However, studies of vertical connectivity in the TWA have demonstrated significant genetic differentiation over depth zones in some regions (Brazeau et al. 2013; Prada and Hellberg 2013; Serrano et al. 2014, 2016; Hammerman et al. 2018), including specificity of algal symbionts at depth (Bongaerts et al. 2013, 2015; Pochon et al. 2015). Together, these results suggest that larval outflow from mesophotic to shallow depths may be constrained. It is important to note that patterns of vertical connectivity vary considerably by oceanographic conditions, coral species, and larval behavior (Holstein et al. 2015; Bongaerts et al. 2017).

Few coral species have been examined for connectivity across regional scales and depth zones. *Montastraea cavernosa*, a broadcast spawner and depth-generalist scleractinian coral, was selected for this study due to its abundance on shallow and mesophotic coral ecosystems throughout the TWA (Bak et al. 2005; Lesser et al. 2009; Nunes et al. 2009). Population connectivity of *M. cavernosa* using nuclear and mitochondrial markers has been

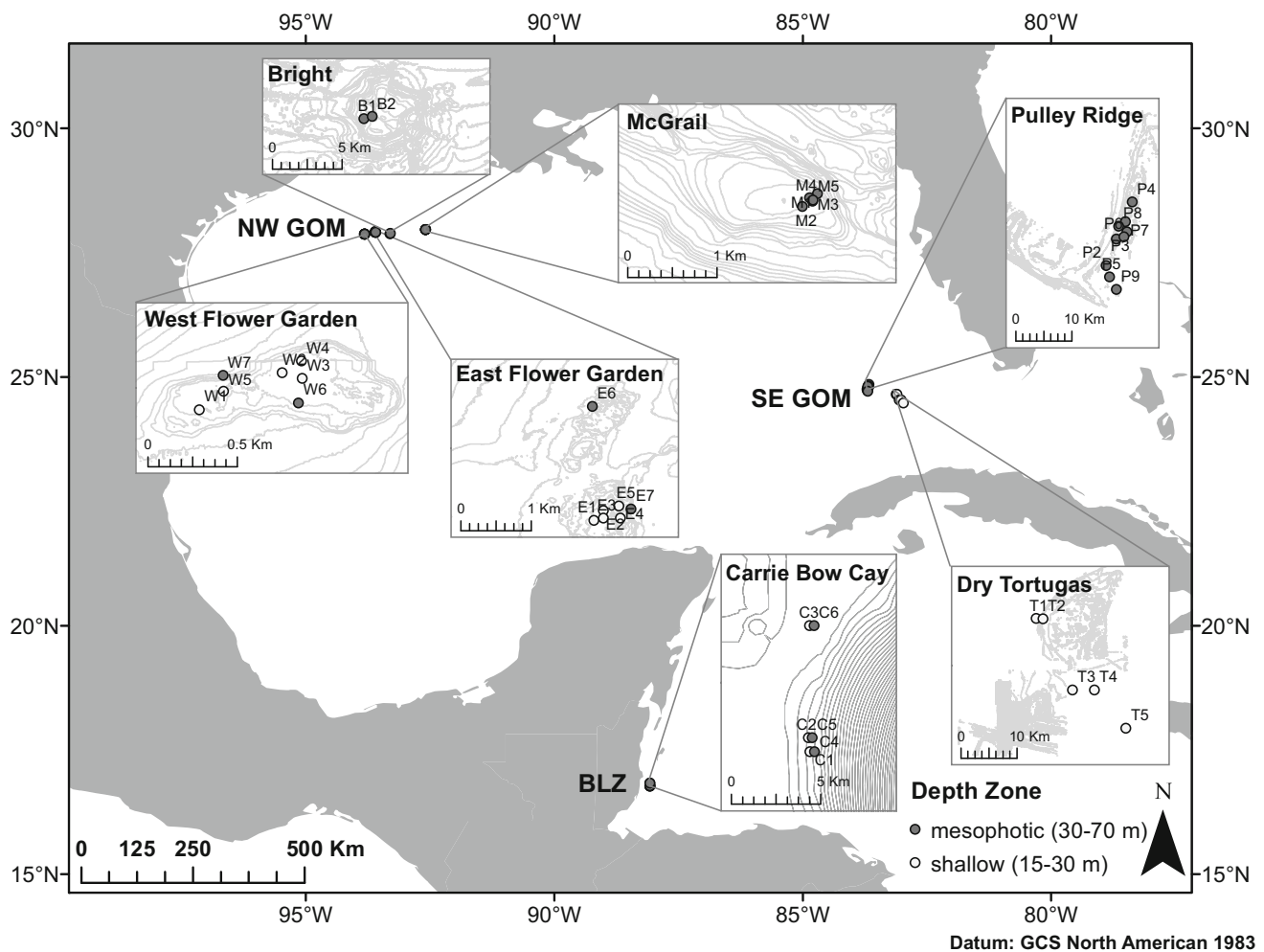
well-documented across relatively shallow sites (Atchison et al. 2008; Nunes et al. 2009, 2011; Goodbody-Gringley et al. 2012; Serrano et al. 2014), showing evidence of horizontal connectivity across populations in excess of 1000 km apart. Assessments of vertical connectivity, however, have demonstrated that *M. cavernosa* populations may either be well connected as in the NW GOM (Studivan and Voss 2018a) and Bermuda (Serrano et al. 2014), or highly differentiated as in the Bahamas, Cayman Islands (Brazeau et al. 2013), Florida Keys, and US Virgin Islands (Serrano et al. 2014). In the latter two studies, assignment methods suggested strong segregation of genetic clusters between relatively shallow or deep populations with limited evidence of admixture across depth in some regions of the TWA, but such a pattern has not been observed in the NW GOM (Studivan and Voss 2018a).

Coral populations in the GOM are seemingly able to persist in part due to warm water delivered by three main currents: the Yucatan Current, GOM Loop Current, and Mexican Current (Ezer et al. 2005; Jarrett et al. 2005; Oey et al. 2005; Precht et al. 2014). The main path of these currents tends to move in a clockwise direction from the Yucatan Peninsula into the Straits of Florida (Lugo-Fernández 1998). Additionally, eddy spinoff from the Loop Current occurs relatively frequently in the NW GOM and can persist for a year or more (Oey et al. 2005; Schmahl et al. 2008). Water movement within the major GOM currents can be > 3 knots (reviewed in Oey et al. 2005), potentially allowing rapid larval dispersal among depth zones across the GOM (Atchison et al. 2008; Davies et al. 2017; Garavelli et al. 2018). This study was designed with two objectives: (1) to evaluate larval-mediated connectivity among MCEs and shallow coral reefs in the GOM, and (2) to examine the potential contributions of MCEs under existing management protections to overall population connectivity in the region.

## Materials and methods

### Coral collection

Sites within marine protected areas were chosen based on dominant oceanographic patterns to model upstream and downstream populations (Fig. 1). In regions where contiguous shallow and mesophotic habitats were available, sampling was targeted at the top and bottom of reef slopes to maximize vertical range sampled in a single site. Belizean regions of the Mesoamerican Barrier Reef are possible upstream sources for coral populations in the GOM resulting from variations of the Loop Current (Ezer et al. 2005; Schmahl et al. 2008; Chollett et al. 2017). Belizean sites selected for this study are within the South Water Cay



**Fig. 1** Map of the Gulf of Mexico and sampling sites across three main regions: Belize (BLZ), northwest GOM (NW GOM), and southeast GOM (SE GOM). Gray markers correspond to mesophotic sites (30–70 m), while white markers correspond to shallow sites (15–30 m)

Marine Reserve near Carrie Bow Cay. Flower Garden Banks National Marine Sanctuary (FGBNMS) lies approximately 180 km off the coast of Galveston, Texas. Residing on salt domes on the continental shelf in the northwest GOM (NW GOM), both West and East Flower Garden Banks are comprised of relatively shallow ( $\sim 17$  m) coral caps and marginal mesophotic habitats to 55 m (Schmahl et al. 2008; Voss et al. 2014). East of FGBNMS, additional banks along the shelf margin provide habitat for mesophotic-only ecosystems including Habitat Areas of Particular Concern (HAPCs) Bright and McGrail Banks (Gulf of Mexico Fishery Management Council 2016). In the southeast GOM (SE GOM), Pulley Ridge Coral HAPC occupies  $\sim 160$  km<sup>2</sup> of the Florida continental shelf margin (Jarrett et al. 2005; Culter et al. 2006). Coral diversity on the ridge and surrounding habitats is low, but taxa including *M. cavernosa* and *Agaricia* spp. are present in the mesophotic coral communities found between 65 and 75 m (Reed et al. 2017; Slattery et al.

2018). The closest shallow coral habitat to Pulley Ridge is found approximately 66 km east at Dry Tortugas inside Florida Keys National Marine Sanctuary and Tortugas Ecological Reserve, with shallow coral populations between 1 and 35 m (Jaap 2015).

Approximately 10–15 cm<sup>2</sup> *M. cavernosa* fragments were collected at sites across the GOM and Belize (Fig. 1) using SCUBA divers with hammers and chisels or a Mohawk remotely operated vehicle (ROV) with high-definition cameras and sampling tools including a five-function manipulator and suction sampler with discrete sample bins. Corals were sampled over multiple cruises from 2010 to 2016, so distinct dive sites were selected to reduce the risk of repeatedly sampling the same colonies (Table 1). Additionally, in situ colony photos were taken to determine if any colonies were inadvertently resampled over cruises. Genetic subsamples were preserved in either TRIzol reagent or salt-saturated DMSO. In Belize, corals were sampled nearby Carrie Bow Cay (BLZ: mesophotic,

**Table 1** *Montastraea cavernosa* genotyped samples ( $n = 431$ ) collected across three regions in the Gulf of Mexico and Belize, compared with the number of unique multi-locus genotypes shown as  $n_g$  used for the analyses ( $n = 397$ ). Geographic coordinates given as decimal degrees (WGS84)

Region	Population	Acronym	Sampling site	Site in map	Depth (m)	$n$	$n_g$	Latitude	Longitude
Belize	Carrie Bow Cay	BLZ-meso	South Reef	C4	~ 35	45	45		
			Raph's Wall	C5	35	15	15	16.76895	– 88.07389
			Tobacco Cay	C6	35	15	15	16.77607	– 88.07465
		BLZ-shallow			~ 15	45	45		
			South Reef	C1	15	15	15	16.83244	– 88.07401
			Raph's Wall	C2	15	15	15	16.76895	– 88.07389
			Tobacco Cay	C3	15	15	15	16.77607	– 88.07465
Northwest GOM	West Flower Garden Bank	WFGB-meso			~ 45	42	40		
			West High Reef	W6	40	8	8	27.87371	– 93.81655
			West Transplant Mesophotic	W7	44	34	32	27.87510	– 93.82035
		WFGB-shallow			~ 20	38	38		
			West High Relief	W1	21	6	6	27.87337	– 93.82154
			West Cap 1	W2	21	7	7	27.87523	– 93.81737
			West Cap 2	W3	21	7	7	27.87495	– 93.81637
			West Cap 3	W4	21	4	4	27.87582	– 93.81640
			West Transplant Shallow	W5	22	14	14	27.87429	– 93.82033
	East Flower Garden Bank	EFGB-meso			~ 45	41	39		
			East High Reef	E6	40	10	10	27.92410	– 93.60160
			East Transplant Mesophotic	E7	46	31	29	27.91102	– 93.59668
		EFGB-shallow			~ 20	42	40		
			East High Relief	E1	22	7	7	27.90956	– 93.60139
			East Cap 1	E2	21	7	7	27.91085	– 93.60018
			East Cap 2	E3	21	6	6	27.90987	– 93.60021
			East Cap 3	E4	21	7	7	27.90987	– 93.59804
			East Transplant Shallow	E5	21	15	13	27.91140	– 93.59821
	Bright Bank	BRT-meso			~ 50	37	37		
			Bright Cap 1	B1	55	2	2	27.88467	– 93.30712
	McGrail Bank	MCG-meso	Bright Cap 2	B2	48	35	35	27.88620	– 93.30174
					~ 50	35	35		
			McGrail Cap 1	M1	54	1	1	27.96364	– 92.59216
			McGrail Cap 2	M2	50	5	5	27.96235	– 92.59369
			McGrail Cap 3	M3	49	6	6	27.96288	– 92.59266
			McGrail Cap 4	M4	49	4	4	27.96321	– 92.59295
			McGrail Cap 5	M5	49	19	19	27.96299	– 92.59262
Southeast GOM	Pulley Ridge	PRG-meso			~ 65	67	39		
			Pulley Ridge South	P1	62	1	1	24.78985	– 83.68648
			Pulley Ridge Middle	P2	65	2	2	24.80161	– 83.66920
			Pulley Ridge North	P3	66	2	2	24.84967	– 83.66083
			PR 16	P4	66	4	3	24.72903	– 83.69743
			PR 10	P5	67	36	15	24.79382	– 83.67401

**Table 1** continued

Region	Population	Acronym	Sampling site	Site in map	Depth (m)	<i>n</i>	<i>n<sub>g</sub></i>	Latitude	Longitude
	Dry Tortugas	DRT-shallow	PR 08	P6	66	16	11	24.81798	– 83.67190
			PR 09	P7	70	1	1	24.81100	– 83.68283
			PR 20	P8	66	3	2	24.70933	– 83.68635
			PR 14	P9	65	2	2	24.74767	– 83.70258
					~ 30	39	39		
			Tortugas North	T1	26	6	6	24.64907	– 83.11235
			Tortugas North 2	T2	23	1	1	24.64877	– 83.10162
			PR 51	T3	33	1	1	24.53420	– 83.05375
			PR 52	T4	29	12	12	24.53405	– 83.01850
			PR 58	T5	34	19	19	24.47279	– 82.96807

35 m; shallow, 15 m). In the NW GOM, corals were sampled at four sites: West Flower Garden Bank (WFGB: mesophotic, 45 m; shallow, 20 m), East Flower Garden Bank (EFGB: mesophotic, 45 m; shallow, 20 m), Bright Bank (BRT: mesophotic, 50 m), and McGrail Bank (MCG: mesophotic, 50 m). In the SE GOM, two sites were sampled: Pulley Ridge (PRG: mesophotic, 65 m) and Dry Tortugas (DRT: shallow, 30 m).

### Microsatellite amplification

Genomic DNA was extracted using the Qiagen DNeasy Blood & Tissue Kit for DMSO samples or modified phenol–chloroform extraction for TRIzol samples (Chomczynski and Sacchi 2006). Nine previously-developed microsatellite loci (Serrano et al. 2014) were amplified as in Studivan and Voss (2018a; Table S1). Amplified loci were visualized via gel electrophoresis and sized on an Applied Biosystems ABI 3130xl genetic analyzer with ROX500 size standard. Alleles were scored using GeneMapper 3.7. Samples with amplification failure in  $\geq 3$  loci were excluded from further analyses ( $n = 31$ ).

### Population differentiation and structure

Unique multi-locus genotypes were identified and clonal genotypes were removed from the dataset. GenAlEx 6.5 was used for tests of Hardy–Weinberg Equilibrium (HWE), allele frequencies, and genetic differentiation with fixation index ( $F_{ST}$ ) (Peakall and Smouse 2006, 2012). We tested for linkage disequilibrium (LD) using Arlequin 3.5 (Excoffier and Lischer 2010). False discovery rate (FDR) corrections were calculated for HWE and LD  $p$  values with the R package *FDRtool* (Strimmer 2008). Departures from HWE and LD were tested for the presence of null alleles

with MicroChecker 2.2.3 (van Oosterhout et al. 2006), and null-allele corrected  $F_{ST}$  values were compared to raw  $F_{ST}$  values with FreeNA (Chapuis and Estoup 2007). The probability of genetic bottlenecks was calculated for each population using the program Bottleneck 1.2.02 (Cornuet and Luikart 1996). Population differentiation was assessed in GenAlEx with an analysis of molecular variance (AMOVA; 9999 model permutations, 9999 pairwise permutations), calculation of FDR-corrected pairwise population  $F_{ST}$  values, and visualization with principal coordinates analysis using Nei genetic distance ( $D_A$ ). A pairwise geographic distance matrix was constructed across sites and tested for isolation by distance with a Mantel test (9999 permutations) (Peakall and Smouse 2006, 2012).

Bayesian assignment simulations were run to estimate the number of genetic clusters ( $K$ ) in Structure 2.3.4 (Pritchard et al. 2000), using ten replicate simulations for values of  $K$  between 1 and 13. The parameters for all tests included  $10^3$  burn-in iterations and  $10^6$  Markov Chain-Monte Carlo replicates, using the LOCPRIOR option to aid in simulation testing based on sampling location. Correlated allele frequencies and admixed populations were assumed in run parameters. The most likely value of  $K$  was predicted by comparing the change in model log likelihoods across simulations according to the Evanno method with the web-based Structure Harvester (Evanno et al. 2005; Earl and VonHoldt 2012). Replicate simulations from  $K = 2$ ,  $K = 3$ , or  $K = 4$  were then combined with CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and visualized with Distruct 1.1 (Rosenberg 2004).

### Estimation of migration rates

Migration rates were estimated across ancestral timescales ( $\sim 4N_e$  generations) using the software Migrate 3.6



(Beerli 2006; Beerli and Palczewski 2010). Migrate applies coalescence theory to estimate population sizes and migration rates among populations relative to DNA mutation rate according to user-specified a priori migration models. A priori models were developed with two objectives: (1) to identify vertical migration across shallow and mesophotic zones as a test of the DRRH within regions, and (2) to assess horizontal migration across the GOM and Belize. For the former, only samples from regions with both shallow and mesophotic habitats were used, thereby excluding Bright and McGrail Banks. While Pulley Ridge and Dry Tortugas are not contiguous coral habitats, information regarding coral connectivity among these sites was identified as a research priority (Reed et al. 2017) and were therefore examined in this analysis. Four separate models were tested using depth zone (shallow, meso) as populations within each site (Belize, West Flower Garden Bank, East Flower Garden Bank, Pulley Ridge/Dry Tortugas). For estimation of vertical migration, four different gene flow models within each of the four regions were tested: (1) *Symm*: full model with symmetric migration across shallow and mesophotic depth zones, (2) *Up*: asymmetric migration from mesophotic to shallow zones, (3) *Down*: asymmetric migration from shallow to mesophotic zones, and (4) *Pan*: panmixia.

For evaluating horizontal migration, sampled populations were grouped into three regions BLZ, NW GOM, and SE GOM. The four gene flow models were as follows: (1) *Symm*: full model with symmetric migration across regions, (2) *Downstream*: asymmetric migration from upstream to downstream regions, (3) *Upstream*: asymmetric migration in a countercurrent downstream to upstream pattern, and (4) *Pan*: region-wide panmixia. To achieve convergence across all models tested, the final parameters used were long-inc 100, long-sample 15,000, 20 replicates, burn-in 20,000, and four heated chains of 1, 1.5, 3,  $10^5$ . Additionally, the prior distributions for theta and migration rate were set at 0–100 and 0–1000, respectively. The most likely migration models were selected by calculating and ranking Bezier log marginal likelihoods (Kass and Raftery 1995).

All analysis protocols and data templates are available on GitHub (<https://github.com/mstudiva/Mcav-microsats.git>), and datasets generated are available in a Dryad repository (Studivan and Voss 2018b).

## Results

### Data validation and screening

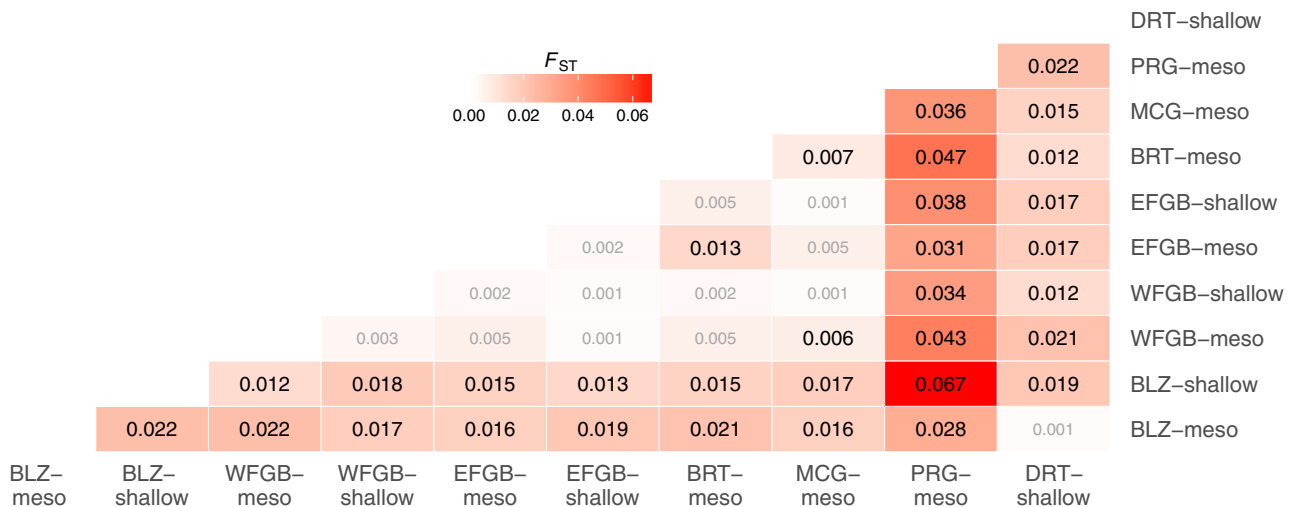
Of the 463 corals sampled, 431 amplified successfully across at least six of the nine microsatellite loci (Table 1).

Identification of multi locus genotypes revealed twelve clonal samples across six genets at either West or East Flower Garden Banks due to duplicate sampling across cruises, and 36 clonal individuals among eight genotypes at Pulley Ridge. True clones from Pulley Ridge were verified photographically and included thirteen separate colonies of a single genet. Further analyses were performed on a dataset excluding clonal genotypes ( $n = 397$ ; Table 1).

Tests of HWE and LD revealed no significant patterns across sites or loci, with the exception of Pulley Ridge, which violated HWE assumptions with five of the nine loci and had significant deviations from linkage disequilibrium across nearly half of the pairwise locus comparisons (Table S2). Null alleles were detected in most sites across at least one locus, however, raw and corrected  $F_{ST}$  values by locus and population showed an almost perfect correlation in both cases ( $R^2 = 0.980$  and  $R^2 = 0.994$ , respectively). Therefore, uncorrected  $F_{ST}$  values were used for all subsequent analyses. Given the assumption violations and relative abundance of clones at Pulley Ridge, all populations were tested for the presence of genetic bottlenecks. Heterozygote excesses characteristic of bottleneck events were not evident across any population; however, heterozygote deficiencies were observed in mesophotic Belize, mesophotic East Flower Garden Bank, Bright Bank, and Pulley Ridge populations.

### Population differentiation and structure

The analysis of molecular variance indicated that the majority of observed genotypic variation occurred at the individual level within populations (AMOVA; 9%,  $df_{387,397}$ ,  $SS = 1337.507$ ), while differences across populations contributed to only 2% of the variation observed ( $df_{9,397}$ ,  $SS = 69.746$ ,  $p < 0.001$ ). Comparison of pairwise  $F_{ST}$  values indicated region-specific variability in *M. cavernosa* population differentiation (Fig. 2). Shallow and mesophotic zones in Belize were significantly different from one another and relatively isolated from most distant sites. Interestingly however, mesophotic *M. cavernosa* in Belize (35 m) were indistinct from those at relatively shallow Dry Tortugas (30 m) nearly 1000 km away. Shallow and mesophotic zones at West and East Flower Gardens, Bright, and McGrail Banks, were not significantly differentiated from one another, indicating a well-mixed NW GOM region. In the SE GOM, there was isolation of Pulley Ridge from all other sites, including nearby Dry Tortugas (Fig. 3). Pairwise  $F_{ST}$  comparisons suggested that sites geographically distant from one another appeared to be genetically distinct, which was supported by an isolation by distance test (Mantel;  $R^2 = 0.29$ ,  $p < 0.005$ ; Fig. S1). Pairwise geographic distances between sites for the isolation by distance analysis ranged from 0.01 to 1368.50 km.

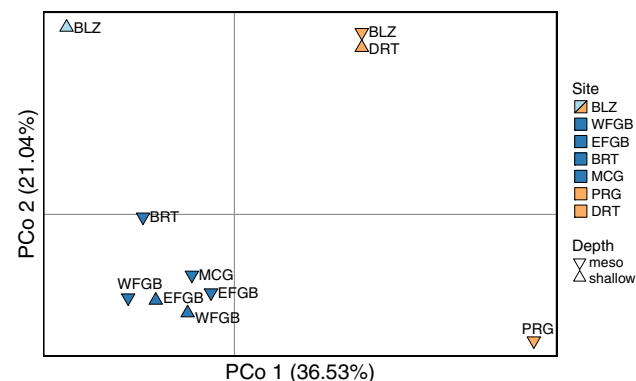


**Fig. 2** Comparison of pairwise population differentiation as measured by fixation index ( $F_{ST}$ ). The level of dissimilarity among populations is shown in increasing intensities of red. Significantly dissimilar  $F_{ST}$  estimates are shown in larger font ( $p < 0.05$  after FDR

correction). BLZ includes BLZ-meso and BLZ-shallow. NW GOM includes WFGB-shallow, WFGB-meso, EFGB-shallow, EFGB-meso, BRT-meso, and MCG-meso. SE GOM includes PRG-meso and DRT-shallow

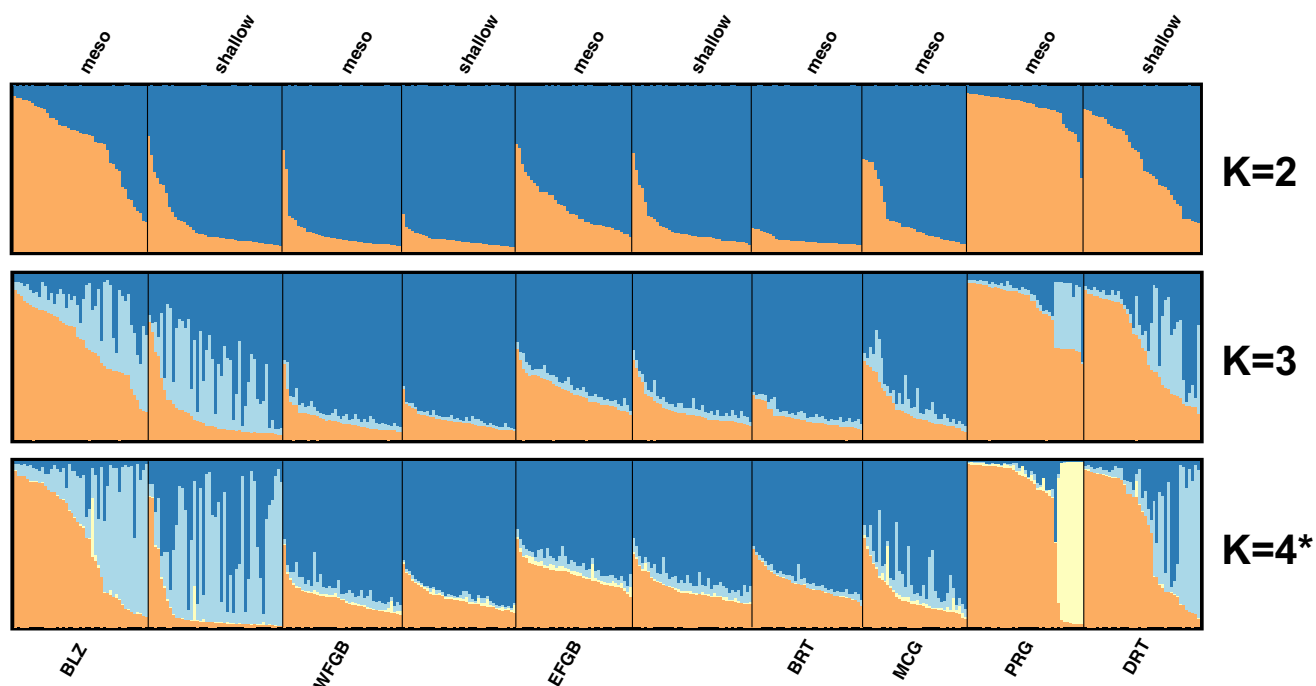
Structure analysis suggested four genetic clusters across the GOM and Belize ( $K = 4$ ; Table S3, Fig. S2). Membership of individuals to each of the clusters was region-specific (bottom panel of Fig. 4). A blue cluster was relatively ubiquitous across shallow and mesophotic sites in the NW GOM (ranging from 60 to 75% membership across all NW GOM sites), which is likely comprised of a panmictic population (Studivan and Voss 2018a). An orange cluster was identified at mesophotic sites in Belize (52%), Pulley Ridge (70%), and Dry Tortugas (56%). A light blue cluster was present at both Belize depth zones (mesophotic, 37%; shallow, 47%) and Dry Tortugas (25%). No clusters were found predominantly in one depth zone or the other as in the study by Serrano et al. (2014); rather, clusters

appeared to denote region-specific origins (blue in NW GOM, orange in Belize and SE GOM). The presence of the light blue cluster in both depth zones in Belize indicates admixture between depth zones despite evidence for isolation with  $F_{ST}$  analyses (Figs. 2, 3). Furthermore, the similarities in orange and light blue cluster memberships between mesophotic Belize and shallow Dry Tortugas denote strong connectivity between geographically distant populations. Interestingly, 23% of individuals from Pulley Ridge were identified to be of a unique beige cluster. Probability of membership to the beige cluster was under 3% for all other sites, suggesting Pulley Ridge may have an alternate source population not shared by any of the other sites sampled in this study.



**Fig. 3** Principal coordinate analysis of Nei genetic distance ( $D_A$ ) matrix generated from pairwise population differentiation comparisons, explaining 57.57% of the total genetic variation (PCo 1: 36.53%, PCo 2: 21.04%). Shape of each point corresponds to depth zone and color represents the dominant genetic cluster from structure analysis in Fig. 4

In model scenarios with simpler genetic structure ( $K = 2$  and  $K = 3$ , top panels of Fig. 4), the membership to dominant clusters remain the same within each site, providing support for the previous conclusions. To explore the possibility that HWE and LD violations at Pulley Ridge may have masked patterns of genetic structure in other sites,  $F_{ST}$  and structure analyses were repeated using a dataset without Pulley Ridge samples. A PCoA reflected similar relationships among sites (Fig. S3), while structure analysis predicted  $K = 5$  (Table S4, Fig. S4). In the latter case, the overall patterns of cluster membership within sites remain the same as in Fig. 4, with the exception of increased membership to the light blue cluster (45%) at Bright Bank (Fig. S5).



**Fig. 4** Genetic structure of *Montastraea cavernosa* across shallow and mesophotic reefs in the Gulf of Mexico and Belize, given for models simulating 2–4 genetic clusters ( $K$ ). Individuals are represented as bars within each sampled population along the x-axis, and the relative height along the y-axis of the four colors (orange, beige,

light blue, blue) represents the probability of membership to the genetic clusters. Four genetic clusters were identified as the most likely model, shown with an asterisk (Structure;  $n = 10$  replications,  $K = 1-13$ ,  $10^3$  burn-in,  $10^6$  MCMC replicates, LOCPRIOR)

### Historical migration estimates

Despite strong signatures of genetic differentiation indicated by  $F_{ST}$  analysis, estimated migration across depth zones and sites was historically high. Vertical migration in Belize and both Flower Garden Banks supported population panmixia, while the SE GOM model suggested that net migration was from Dry Tortugas to Pulley Ridge (Table 2). Mutation-scaled population size was estimated to be an order of magnitude smaller at Pulley Ridge ( $\theta^1 = 0.77$ ) than all other populations including the nearby Dry Tortugas ( $\theta^2 = 6.57$ ), despite relatively high migration rates from Dry Tortugas to Pulley Ridge ( $M = 42.33$ ). When individual populations were combined into their respective regions, the horizontal (GOM-wide) migration model predicted that population panmixia was far more likely than symmetric or asymmetric migration (Table 2).

## Discussion

### Variable patterns of vertical connectivity

Previous studies assessing *M. cavernosa* population structure have shown relatively strong partitioning of genetic

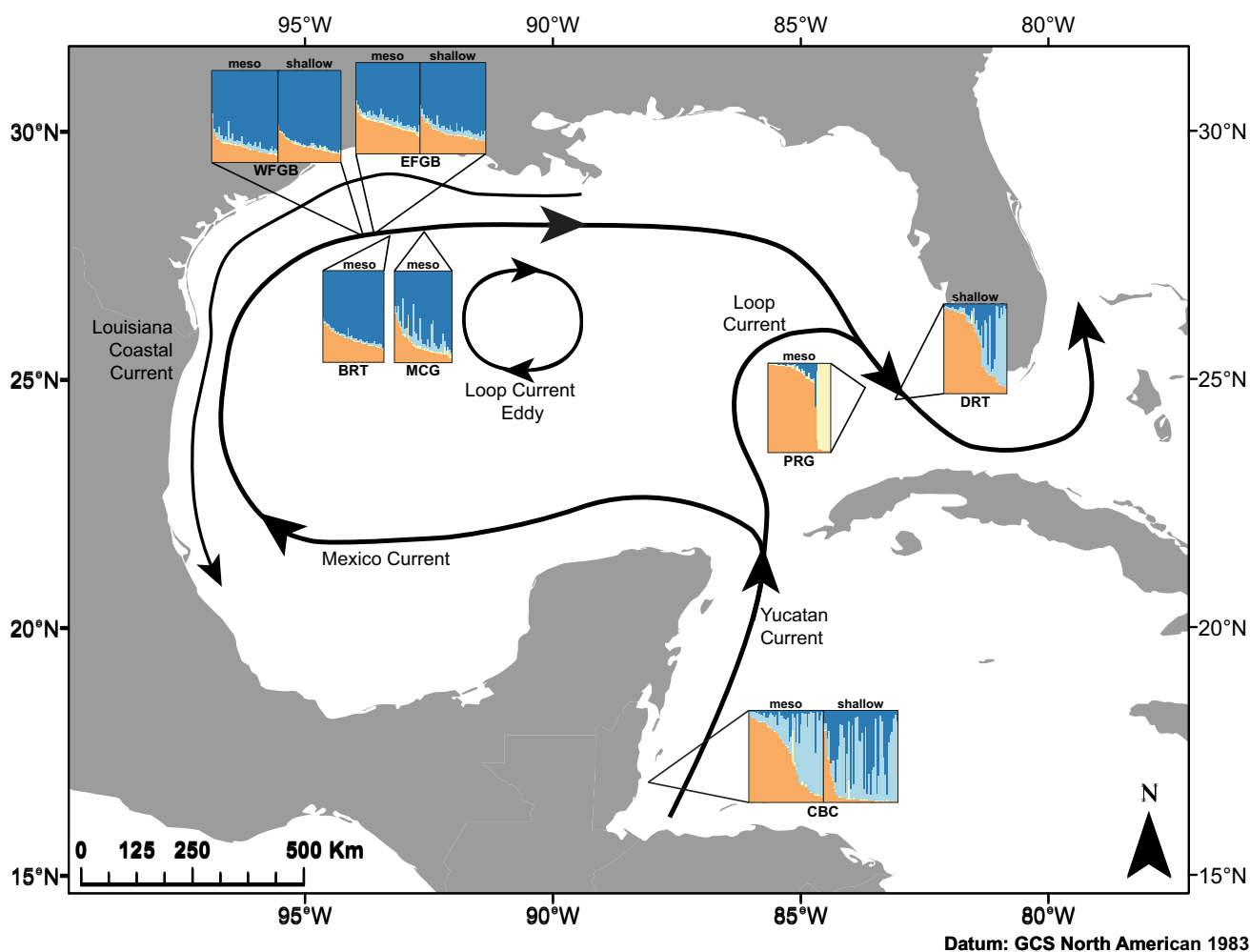
clusters across depth zones elsewhere in the TWA, including the Bahamas, Cayman Islands (Brazeau et al. 2013), Florida Keys, and US Virgin Islands (Serrano et al. 2014). In these cases, genetic clusters were strongly correlated with relatively shallow or deep sites, with little admixture between zones. As a result, the authors proposed that (1) deeper *M. cavernosa* are comprised of genetically separate populations in these regions, and (2) selection may have contributed to local adaptation. Selection is suspected to produce patterns of population specialization at depth in other coral species as well (Bongaerts et al. 2010b; van Oppen et al. 2011; Prada and Hellberg 2013). These conclusions do contrast, however, with sites demonstrating a lack of strong genetic differentiation, such as Lee Stocking Island in the Bahamas (Brazeau et al. 2013), Bermuda (Serrano et al. 2014), and the NW GOM (Studivan and Voss 2018a). This study observed that cluster membership appeared to be driven by region rather than depth, resulting in observed panmixia in the NW GOM, or isolation across depth zones in Belize and the SE GOM. We therefore suggest, that while selection over depth may still play a role in structuring shallow and mesophotic *M. cavernosa* populations across the TWA, local oceanographic



**Table 2** Comparison of Bezier log marginal likelihood (lmL) differences for four vertical migration models (*Symm*: symmetric vertical migration; *Up*: migration from mesophotic to shallow; *Down*: migration from shallow to mesophotic; *Pan*: panmixia) at the sites indicated in Fig. 1

Vertical connectivity	lmL for model				Rank of model				$\theta^1$ ( $\pm$ 95% CI)	$\theta^2$ ( $\pm$ 95% CI)	$M$ ( $\pm$ 95% CI)
	<i>Symm</i>	<i>Up</i>	<i>Down</i>	<i>Pan</i>	<i>Symm</i>	<i>Up</i>	<i>Down</i>	<i>Pan</i>			
BLZ	– 180,221	– 48,217	– 233,668	0	3	2	4	1	18.90 (16.53–21.13)		
WFGB	– 253,208	– 193,934	– 156,217	0	4	3	2	1	18.83 (16.20–22.40)		
EFGB	– 505,800	– 431,632	– 931,394	0	3	2	4	1	7.77 (4.27–10.73)		
PRG-DRT	– 24,604	– 5741	0	– 443	4	3	1	2	0.77 (0–3.53)	6.57 (4.00–9.20)	42.33 (8.67–106.67)
Horizontal connectivity	lmL for model				Rank of model				$\theta^1$ ( $\pm$ 95% CI)	$\theta^2$ ( $\pm$ 95% CI)	$M$ ( $\pm$ 95% CI)
	<i>Symm</i>	<i>Down-stream</i>	<i>Up-stream</i>	<i>Pan</i>	<i>Symm</i>	<i>Down-stream</i>	<i>Up-stream</i>	<i>Pan</i>			
GOM	– 3,712,816	– 3,195,993	– 2,355,395	0	4	3	2	1	4.30 (1.53–11.07)		

For the horizontal connectivity model, populations were combined into the three regions (BLZ, NW GOM, and SE GOM) and horizontal migration was tested against predominant current patterns (*Symm*: symmetric horizontal migration; *Downstream*: upstream to downstream migration; *Upstream*: downstream to upstream migration; *Pan*: panmixia). Models were ranked according to increasing likelihoods (lmL), with the most likely model for each region (per row) indicated by a '1'. For the most likely migration model in each region, estimates of mutation-scaled population sizes ( $\theta^1$  and  $\theta^2$ ) and immigration rate ( $M$ ) with 95% confidence intervals in parentheses are provided



**Fig. 5** Map of the Gulf of Mexico with a diagrammatic representation of the dominant oceanographic currents. Sampling sites are overlaid with Structure cluster assignments using the most likely model with four genetic clusters ( $K = 4$ ; Fig. 4)

conditions may be more important factors affecting connectivity in this high dispersal, broadcast-spawning species.

Shallow and mesophotic *M. cavernosa* populations in Belize were genetically differentiated (Fig. 2). Recent studies of *Orbicella faveolata* connectivity across the Mesoamerican Barrier Reef found a similar isolation of coral populations in Belize, suggesting oceanographic conditions in the region may be limiting larval dispersal (Porto-Hannes et al. 2015; Rippe et al. 2017). Since a high degree of gene flow was observed between the mesophotic Belize and shallow Dry Tortugas populations (Fig. 3), we hypothesize that strong current dynamics may be creating a genetic block between shallow and mesophotic populations in Belize. Comparable patterns have been observed for other populations in the TWA through assessments of horizontal connectivity (Baums et al. 2005; Vollmer and Palumbi 2007; Foster et al. 2012). Shear currents typically travel northward along the outside of the barrier reef, while

inshore currents travel southward (Ezer et al. 2005), possibly carrying mesophotic larvae towards the GOM via the Loop Current (Fig. 5; Jarrett et al. 2005; Oey et al. 2005) rather than upward towards the shallow reef crest. Inshore eddy currents are also common during spawning season, increasing the likelihood of shallow local retention in Belize (Tang et al. 2006). Genetic isolation of depth zones across vertical reef structures has also been observed with several coral species throughout the TWA and likely reflects a common oceanographic pattern separating shallow and mesophotic populations with similar geomorphological characteristics (Bongaerts et al. 2013; Brazeau et al. 2013; Serrano et al. 2014; Costantini et al. 2016).

Population structure in the NW GOM demonstrated that oceanographic patterns likely maintain high genetic connectivity among these sites (Garavelli et al. 2018), including vertical connectivity between shallow and mesophotic populations in this region. *Montastraea cavernosa* populations were well connected across depth zones

and sites approximately 150 km apart, effectively acting as a single population (Studivan and Voss 2018a). These data provide evidence to support the role of MCEs in the NW GOM providing a potential refugia for *M. cavernosa*, both in demonstration of vertical connectivity within a single site, but also horizontal connectivity of MCEs to distant populations. Despite lower coral diversity resulting from a high-latitude location, abundant and resilient coral communities in the NW GOM are conducive to supporting healthy, reproductively-active populations (Schmahl et al. 2008; Johnston et al. 2016). Populations of *M. cavernosa* in the NW GOM likely do not rely heavily on larval immigrants from upstream sites, as indicated by high local retention within depth zones with some larval export outside the region (Atchison et al. 2008; Davies et al. 2017; Rippe et al. 2017; Garavelli et al. 2018). This larval supply combined with effective larval transport from the Loop Current and frequent eddies likely contribute to high gene flow among banks in the NW GOM.

Dry Tortugas was the most downstream site of the SE GOM in this study, and samples indicated evidence of connectivity with other sites (notably mesophotic Belize), but relative isolation from the nearest geographic neighbor Pulley Ridge. Shallower (10–25 m) *M. cavernosa* populations including those from additional sites in Dry Tortugas that were not examined in this study have also demonstrated strong connectivity to sites in the Florida Keys and U.S. Virgin Islands (Serrano et al. 2014), identifying Dry Tortugas as a potential intermediate population between the GOM and wider TWA. Additionally, the study by Serrano et al. identified relatively weak differentiation across depth in the Dry Tortugas compared to the other sites examined, which is likely facilitated by mesoscale eddies in the region (Kourafalou and Kang 2012) and potentially by strong horizontal migration from Belize (this study). While mesophotic-to-shallow genetic mixing is unlikely to supply shallow populations with larvae within Belize, these MCEs instead provide evidence that they may serve as an important population source to Dry Tortugas nearly 1000 km away.

### Historical panmixia in the GOM

While significant genetic differentiation was observed among some of the sites sampled, *M. cavernosa* populations maintain evidence of gene flow across depth zones and regions within the GOM. The disparity between  $F_{ST}$  and structure analyses demonstrate the contrasting patterns of historical panmixia with relative isolation at present. In particular, the similarities in membership to the light blue cluster in Belize provides evidence for a common population source between shallow and mesophotic depth zones (Fig. 4), while the dissimilarity in orange cluster

membership denote the present isolation seen in Fig. 3. Historical patterns of gene flow are likely the result of a combination of oceanographic dynamics and variable reef geomorphology due to changing sea level over time. Many of the existing carbonate structures in the GOM (Flower Garden Banks, Pulley Ridge, etc.) were fringing shallow reefs between ~ 18,000 and 11,000 yr ago when sea level was ~ 120 m below present depth, becoming submerged platforms due to post-glacial sea level rise during the Late Quaternary period (Fairbanks 1989; Jarrett et al. 2005; Hine et al. 2008; Gehrels 2010; Locker et al. 2010; Donoghue 2011). The availability of additional suitable coral habitat may have provided stepping stone populations with the potential for increased gene flow across large spatial scales. It is possible that the panmixia supported by our historical migration models is a remnant effect of a single, high gene flow population that may have existed up to 10,000–5000 yr ago (Precht et al. 2014). As sea level then began to rise to present levels, all but the shallowest reef habitats may have drowned and oceanic currents likely slowed (Benzie 1999), further limiting the dispersal of coral larvae among increasingly-isolated reef habitats.

### *M. cavernosa* at Pulley Ridge

Historical migration models also suggested that Pulley Ridge represents a sink population in the context of the study sites. High population differentiation was observed between Pulley Ridge and all other sites, and a unique genetic cluster appearing almost exclusively at Pulley Ridge was identified from the structure analysis (lower panel of Fig. 4). Perhaps combined with local selection, these signatures have resulted in more recent genetic isolation from other *M. cavernosa* populations in the GOM. The Pulley Ridge population also consistently violated assumptions of HWE and LD, which is often attributed to asexual reproduction and inbreeding (Stenberg et al. 2003), null alleles (van Oosterhout et al. 2006), or genetic bottlenecks (Cornuet and Luikart 1996). We discovered a relatively high proportion of clones within the Pulley Ridge samples (nearly 50% of all sampled colonies, including one ramet of thirteen individuals) compared to all other sites. However, there was no genetic evidence supporting a strong impact of null alleles or a recent genetic bottleneck.

A combination of oceanographic and population demographic factors may explain the present isolation of the Pulley Ridge *M. cavernosa* population. Strong eddy currents favoring local retention are common along Pulley Ridge which may prevent larval dispersal to nearby Dry Tortugas and Florida Keys (Pan et al. 2017). Connectivity assessments of damselfish across Pulley Ridge, Dry Tortugas, and Florida Keys have suggested that widespread

dispersal events are rare based on subregional eddies, but successful recruitment has been facilitated by spawning events of large populations (Vaz et al. 2016). Benthic community assessments indicate that coral populations of *M. cavernosa* are instead quite small, comprising < 1% of benthic cover (Jarrett et al. 2005). Repeated surveys at Pulley Ridge over the past 15 yr have also identified a loss of coral density and increased observations of recruit-sized colonies (< 5 cm diameter) west of the main reef structure (Reed et al. 2017; Slattery et al. 2018), yet evidence is lacking to connect the observed change in coral demographics to natural or anthropogenic causes. It may be that the Pulley Ridge *M. cavernosa* population persists at present, albeit in relatively low numbers, through asexual reproduction via fragmentation or budding. Based on the evidence presented in this study, Pulley Ridge appears to contribute little to the other sampled *M. cavernosa* populations across the GOM.

## Conclusions

In providing evidence of connectivity and gene flow from the NW GOM to distant *M. cavernosa* populations, this study highlights the importance of incorporating high-latitude coral populations in the GOM into regional management strategies regarding population dynamics across the wider TWA. Additionally, by assessing integrated gene flow over ecological timescales with molecular markers, this study builds on previous evidence that coral populations can be genetically connected across distances in excess of 1000 km (Nunes et al. 2009, 2011; Goodbody-Gringley et al. 2012). The variability observed in terms of MCE connectivity in this study corroborates trends from other studies in the TWA that the evidence for connectivity among MCE and shallow scleractinian populations can differ across sites (Bongaerts et al. 2013; Brazeau et al. 2013; Serrano et al. 2014) and species (Goodbody-Gringley et al. 2010; Serrano et al. 2016; Bongaerts et al. 2017). Assessment of MCE connectivity across regional scales requires additional examination of the underlying factors affecting connectivity including increased benthic habitat characterization, finer-scale oceanographic patterns, community composition, and life history characteristics. Furthermore, the relative isolation of Belize's mesophotic *M. cavernosa* from nearby shallow populations, coupled with evidence of gene flow from Belize's MCEs to the shallow Dry Tortugas population, reinforces the need for broad spatial scale investigations across multiple locations and depths to adequately assess the refugia and reseeding potential of MCEs.

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## Compliance with ethical standards

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

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