Received: 15 November 2019 | Revised: 14 May 2020 | Accepted: 28 May 2020

DOI: 10.1111/mec.15495

ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Transcriptomic plasticity of mesophotic corals among natural populations and transplants of *Montastraea cavernosa* in the Gulf of Mexico and Belize

Michael S. Studivan[1,2] | Joshua D. Voss[1]

[1]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL, USA

[2]Cooperative Institute for Marine and Atmospheric Studies, University of Miami Rosenstiel School of Marine and Atmospheric Sciences, Miami, FL, USA

Correspondence
Michael S. Studivan, University of Miami Rosenstiel School of Marine and Atmospheric Sciences, Cooperative Institute for Marine and Atmospheric Studies, Miami, FL, USA.
Email: studivanms@gmail.com

Joshua D. Voss, Florida Atlantic University, Harbor Branch Oceanographic Institute, Fort Pierce, FL, USA.
Email: jvoss2@fau.edu

Funding information
National Oceanic and Atmospheric Administration, Grant/Award Number: NA09OAR4320073 , NA11NOS4780045 and NA14OAR4320260 ; Florida Atlantic University

Abstract

While physiological responses to low-light environments have been studied among corals on mesophotic coral ecosystems worldwide (MCEs; 30–150 m), the mechanisms behind acclimatization and adaptation to depth are not well understood for most coral species. Transcriptomic approaches based on RNA sequencing are useful tools for quantifying gene expression plasticity, particularly in slow-growing species such as scleractinian corals, and for identifying potential functional differences among conspecifics. A tag-based RNA-Seq (Tag-Seq) pipeline was applied to quantify transcriptional variation in natural populations of the scleractinian coral *Montastraea cavernosa* from mesophotic and shallower environments across five sites in Belize and the Gulf of Mexico: Carrie Bow Cay, West and East Flower Garden Banks, Pulley Ridge, and Dry Tortugas. Regional site location was a stronger driver of gene expression patterns than depth. However, mesophotic corals among all sites shared similar regulation of metabolic and cell growth functional pathways that may represent common physiological responses to environmental conditions at depth. Additionally, in a transplant experiment at West and East Flower Garden Banks, colonies transplanted from mesophotic to shallower habitats diverged from the control mesophotic group over time, indicating depth-regulated plasticity of gene expression. When the shallower depth zone experienced a bleaching event, bleaching severity did not differ significantly between transplants and shallow controls, but gene expression patterns indicated variable regulation of stress responses among depth treatments. Coupled observational and experimental studies of gene expression among mesophotic and shallower *M. cavernosa* provide insights into the ability of this depth-generalist coral species to persist under varying environmental conditions.

KEYWORDS
Gulf of Mexico, mesophotic coral ecosystems, RNA-Seq, Tag-Seq, transcriptomics, transplant experiment

1 | INTRODUCTION

The ecological roles of mesophotic coral ecosystems have been an area of increasing interest in the last decade (MCEs, ~30–150 m; Bongaerts & Smith, 2019; Lesser, Slattery, & Leichter, 2009), specifically the interactions of depth-generalist coral species found in both mesophotic and shallower habitats (Bongaerts & Smith, 2019; Kahng, Copus, & Wagner, 2014; Semmler, Hoot, & Reaka, 2016). In particular, the mechanisms that contribute to coral

species' success across broad depth ranges and, conversely, what limits depth-specialist species to certain depth zones are poorly understood. Knowledge of how these mechanisms may influence the connectivity of populations among depth zones is also lacking. The limits for depth-generalist coral species are often linked with the photosynthetic compensation point, where approximately 1% of surface light irradiance is available to maintain net photosynthetic output and metabolic needs (Lesser et al., 2009). Temperature variation across mesophotic and shallower habitats have been shown to influence coral depth distributions as well, especially in regions where cold water upwelling is known to occur at depth (Bongaerts et al., 2015; Leichter & Genovese, 2006; Lesser et al., 2010). Previous studies have quantified phenotypic and physiological changes that allow certain coral species to be successful across multiple habitats including mesophotic reefs, such as modification of photosynthetic physiology (Lesser, 2000; Lesser et al., 2010; Polinski & Voss, 2018), skeletal morphology (Graus & Macintyre, 1982; Studivan, Milstein, & Voss, 2019), and heterotrophic feeding (reviewed in Slattery, Lesser, Brazeau, Stokes, & Leichter, 2011), but there is a general lack of knowledge regarding the molecular mechanisms that allow such phenotypic variability for most taxa (Akman, Carlson, Holsinger, & Latimer, 2016; Alvarez, Schrey, & Richards, 2015; Evans, 2015). A notable study with the coral species *Porites astreoides* addressed such questions, where Kenkel and Matz (2017) identified that corals transplanted from reefs with naturally-variable environmental conditions were better adapted to surviving across multiple habitats, even following a thermal stress event leading to a breakdown of the coral-algal symbiosis (i.e., coral bleaching). Research is specifically needed to address the molecular contributions to acclimatization and adaptation (Matz, 2018; Voolstra et al., 2011) and to determine how corals can modify their existing structure and function to thrive in multiple environments such as those at mesophotic depths.

With decreasing costs of library preparation and sequencing, the number of genomic and transcriptomic reference libraries being generated and annotated for diverse taxa are increasing rapidly. As a result, using transcriptomic approaches to examine biological processes at the molecular level in non-model organisms is more feasible now than ever before (Matz, 2018; Oomen & Hutchings, 2017; Todd, Black, & Gemmell, 2016). One example of these cost-effective and practical transcriptomic tools is Tag-Seq, a variation of RNA-Seq that selectively amplifies sequences adjacent to the 3' poly-A tail, instead of amplifying multiple fragments along the length of each gene (Meyer, Aglyamova, & Matz, 2011). With RNA-Seq approaches including Tag-Seq, quantifying global gene expression allows the construction of related multi-gene pathways responding to a common stimulus based on functional annotation databases (Dixon et al., 2015; Strader, Aglyamova, & Matz, 2016). Of particular interest with relatively slow-growing coral species is the potential for gene expression profiling to identify differential regulation of functional pathways linked to phenotypic change, such as skeletal morphology (Gutner-Hoch, Waldman Ben-Asher, Yam, Shemesh, & Levy, 2017) or stress responses (Kenkel et al., 2011, 2014; Louis, Bhagooli, Kenkel, Baker, & Dyall, 2016; Meron et al., 2019; Wright et al., 2019), perhaps before any visible phenotypic change.

Most previous coral studies incorporating RNA-Seq approaches have quantified coral responses to a specific stimulus, most notably thermal stress (Anderson, Walz, Weil, Tonellato, & Smith, 2016; Davies, Marchetti, Ries, & Castillo, 2016; Kenkel, Meyer, & Matz, 2013; Kenkel et al., 2014; Meyer et al., 2011). However, it is perhaps equally important to understand genetic variation found among natural populations. Complementary analyses including observational and experimental designs allow for more comprehensive evaluations of plasticity, acclimatization, and adaptation (Alvarez et al., 2015; Kenkel & Matz, 2017). This study aims to increase understanding of the mechanisms behind coral functional modifications at depth through two approaches using *Montastraea cavernosa*, a ubiquitous coral species in the Tropical Western Atlantic and an extreme depth-generalist found between 3–113 m (Lesser et al., 2009; Nunes, Norris, & Knowlton, 2009; Reed, 1985). First, whole-transcriptome gene expression profiles were compared among *M. cavernosa* across mesophotic and shallower sites in Belize and the Gulf of Mexico (GOM) to quantify transcriptomic responses to sites and depth zones. Additionally, differentially-expressed genes within sites were examined to determine if a common transcriptional response to mesophotic conditions occurs in this species. Second, a one-year transplant experiment at West and East Flower Garden Banks in the northwest GOM was conducted to examine gene expression plasticity in *M. cavernosa*. Individual colonies were tracked to quantify: (a) global gene expression patterns within depth treatments over time; (b) overall transcriptional variation between depth treatments; and (c) potential gene expression plasticity in transplanted corals. The objectives of both complementary studies were to determine whether mesophotic and shallower conspecifics exhibit distinct gene expression patterns and if common functional pathways exist to facilitate plasticity in both depth zones.

2 | MATERIALS AND METHODS

2.1 | Study species and sample collection

To assess gene expression patterns in *Montastraea cavernosa* and their algal symbionts across mesophotic and shallower depth zones, coral samples were collected at five sites across the GOM and Belize: Belize (BLZ) near Carrie Bow Cay, West and East Flower Garden Banks (WFGB and EFGB, respectively), Pulley Ridge (PRG), and Dry Tortugas (DRT; Table 1; Figure 1). Depth zones sampled at each site were determined by the availability of reef habitats across depths and the relative abundance of the target coral species, where mesophotic corals were collected from upper mesophotic zones (35–65 m), while shallower coral samples were collected from mid-depth zones (15–30 m). Samples and transplant experiment groups from upper mesophotic and mid-depth zones are hereafter referred to as mesophotic and shallow, respectively. Despite lacking contiguous reef habitat, comparisons between Pulley Ridge and Dry

TABLE 1 Site and sample metadata for *M. cavernosa* natural gene expression analyses among mesophotic and shallower depth zones in the Gulf of Mexico and Belize

Site	Latitude	Longitude	Depth zone	Depth (m)	$n_{collected}$	$n_{natural}$
Carrie Bow Cay, Belize	16.77607	−88.07465	Mesophotic	35	45	24
	16.77607	−88.07465	Shallow	15	45	38
West Flower Garden Bank	27.87510	−93.82035	Mesophotic	45	42	33
	27.87495	−93.81637	Shallow	20	36	36
East Flower Garden Bank	27.91102	−93.59668	Mesophotic	45	35	21
	27.90987	−93.60021	Shallow	20	42	41
Pulley Ridge	24.79382	−83.67401	Mesophotic	65	54	41
Dry Tortugas	24.47279	−82.96807	Shallow	30	45	31
				Total	344	265

The number of samples collected shown as $n_{collected}$, and the number of samples that were successfully prepared and analysed with the Tag-Seq pipeline are $n_{natural}$. Geographic coordinates given as decimal degrees (WGS84)

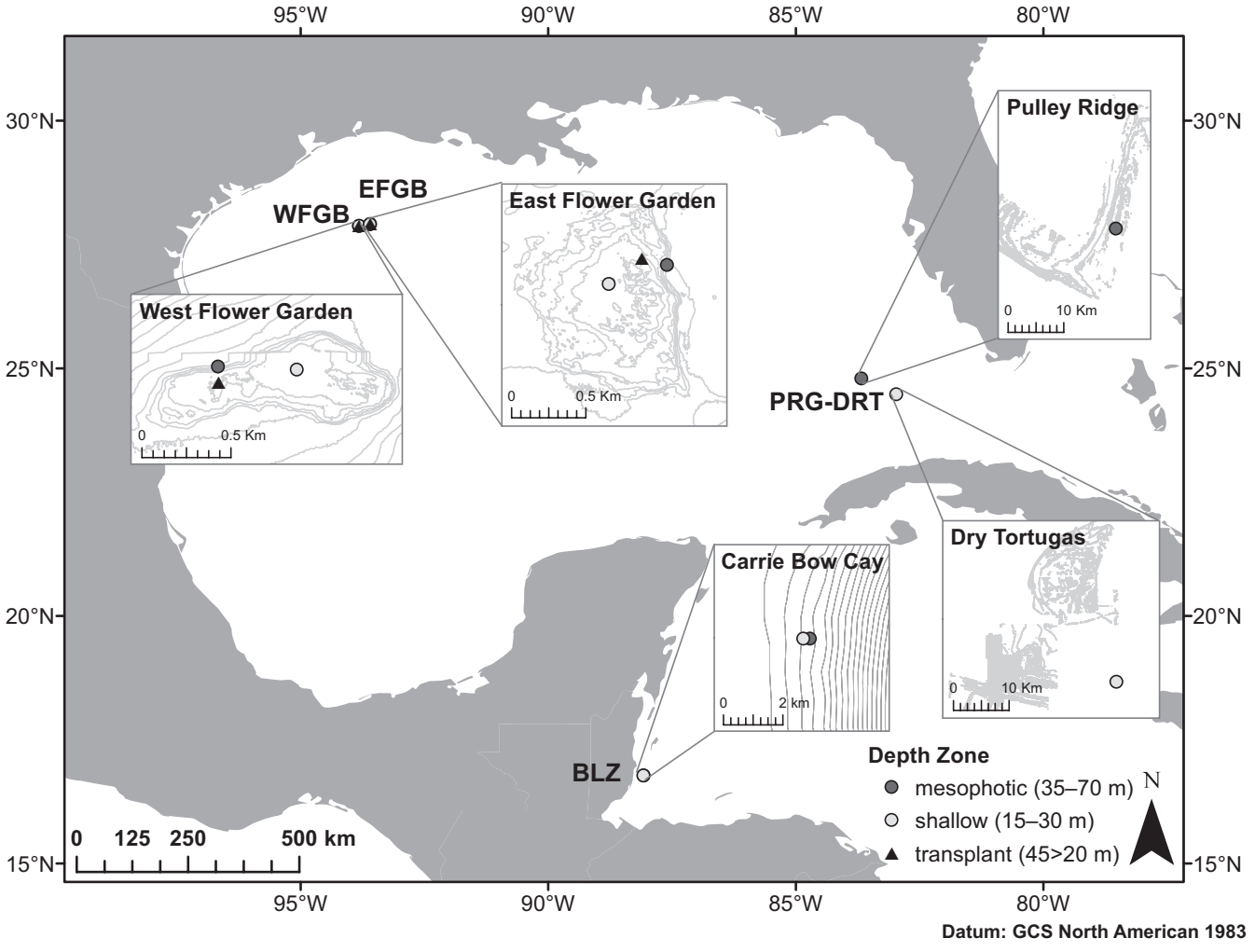

FIGURE 1 Map of the Gulf of Mexico, with inset boxes of the five sampling sites including available bathymetry data of sites, and locations of specimen collection colour-coded by depth zone (mesophotic 35–70 m, shallow 15–30 m, transplant 45 > 20 m). Geographic coordinates as in Tables 1 and 2

Tortugas as mesophotic and shallower sites have been identified as a research priority to assess ecological relationships between Pulley Ridge and the Florida Reef Tract (Reed et al., 2019). This combination introduces confounding effects of site into the comparison between depth zones, but allows inferences to be made regarding coral populations in the southeast GOM. Small tissue fragments (10–15 cm^2)

TABLE 2 Site and sample metadata for *M. cavernosa* plastic gene expression analyses from a one-year transplant experiment (Oct 2015–Sept 2016) at West and East Flower Garden Banks

Site	Latitude	Longitude	Depth zone	Depth (m)	$n_{collected}$			$n_{transplant}$		
					Oct 2015 (0 mo)	May 2016 (6 mo)	Sep 2016 (12 mo)	Oct 2015 (0 mo)	May 2016 (6 mo)	Sep 2016 (12 mo)
West Flower Garden Bank	27.8751	−93.82035	Mesophotic	45	5	5	5	5	5	5
	27.8743	−93.82033	Shallow	20	5	5	5	5	5	5
	27.8743	−93.82033	Transplant	45 → 20	5	5	5	5	5	3
East Flower Garden Bank	27.9110	−93.59668	Mesophotic	45	5	5	5	4	2	1
	27.9114	−93.59821	Shallow	20	5	5	5	5	5	4
	27.9114	−93.59821	Transplant	45 → 20	2	2	2	1	1	2
				Total	27	27	27	25	23	20

Abbreviation: mo, months.

The number of samples collected shown as $n_{collected}$, and the number of samples that were successfully prepared and analysed with the Tag-Seq pipeline are $n_{transplant}$. Geographic coordinates given as decimal degrees (WGS84)

were chiseled from the perimeter of visually healthy *M. cavernosa* colonies and preserved in TRIzol reagent within 30 min of collection. Coral samples for this study were collected across multiple expeditions from 2014 to 2016, including multiple expeditions within sites.

2.2 | Transplant experiment

Gene expression plasticity across mesophotic and shallower environmental gradients was assessed using a transplant experiment at WFGB and EFGB (Figure 1). A full reciprocal design with remove-and-replace controls was not logistically possible due to high skeletal density of shallower colonies, resulting in a single transplant treatment involving unidirectional relocation from mesophotic to shallower depths. At each bank, five apparently healthy *M. cavernosa* colonies approximately 15–50 cm in diameter were selected and tagged at both mesophotic and shallower depths. An additional seven mesophotic colonies (five at WFGB, two at EFGB) were removed from the reef at 45 m and transplanted near the shallow controls at 20 m. Colonies were sampled prior to any experimental manipulation in October 2015 and again at six and twelve month intervals in May and September 2016, respectively (Table 2).

Duplicate light and temperature loggers (Onset HOBO) sampling at 15 min intervals were deployed near the experimental corals at each site and depth zone for continuous monitoring of environmental data over the course of the study. Deployed loggers were replaced with fresh units at each of the sampling timepoints. Light intensity (lux) values were converted to PAR (μmol m^{-2} s^{-1}) according to the equation in Valiela (1995). Minimum, maximum, and mean daily temperature, as well as maximum and mean daily PAR (daily minimum PAR was always zero) were calculated for statistical analyses. The PAR data set was truncated to one month after each sampling event to minimize potential impacts of biofouling on accuracy of readings. Normality assumptions of daily temperature and PAR data sets could not be satisfied with transformation, therefore statistical analyses were conducted using separate single-factor Kruskal-Wallis tests across site and depth. Pairwise comparisons were made with Dunn's tests using the R package *FSA* across a single-factor combination of site and depth (Ogle, 2017; R Core Team, 2019).

Algal symbiont density (family Symbiodiniaceae; cells/cm^2), areal chlorophylls *a* and c_2 (chl/cm^2), cellular chlorophylls *a* and c_2 (chl/cell), and chlorophyll a:c_2 ratio data were quantified in response to an unexpected bleaching event that occurred during the 12 month timepoint. Available data for transplant experiment colonies (mesophotic: $n = 9$; shallow: $n = 10$; transplant: $n = 7$) were quantified as described in Polinski and Voss (2018). As the data could not be normalized with transformation, univariate repeated measures PERMANOVAs with pairwise tests were used to identify significant differences in symbiont and chlorophyll metrics among timepoints and depth treatments in the packages MANOVA.RM and NPARCOMP, respectively (Friedrich, Konietschke, & Pauly, 2019; Konietschke, Placzek, Schaarschmidt, & Hothorn, 2015). Multivariate differences were assessed with a three-factor PERMANOVA and pairwise comparisons in MANOVA.RM

and RVAIDEMEMOIRE, respectively (Hervé, 2019). Bleaching severity for each of the colonies was calculated as the percent change of symbiont density between May and September timepoints. Bleaching data were log transformed to meet normality assumptions and analysed for significant differences among depth treatments using a single-factor ANOVA with Tukey's pairwise comparisons.

2.3 | Library preparation and sequencing

For both experiments, total mRNA was extracted from preserved coral samples using a modified phenol chloroform extraction (Chomczynski & Sacchi, 1987, 2006), treated with DNase *I* (Ambion) to remove DNA contamination, and purified and concentrated using a 13.3 M LiCl precipitation. Samples that did not meet a total mRNA yield of 1 μg following purification were removed from the respective experiments (Tables 1 and 2). RNA libraries were prepared according to a Tag-Seq protocol originally designed by Meyer et al. (2011); modifications to the protocol used in this study are detailed in a GitHub repository (Studivan, 2020b). Due to variable initial RNA quality, cDNA amplification reactions were increased to 22 cycles to ensure consistent amplification across samples. Library preps that did not achieve sufficient cDNA amplification or final library concentration relative to other libraries were removed prior to final pooling. The number of samples in each pool was determined by a target raw read count of ~5.4–7.2 million reads per sample. Nine pooled sets encompassing libraries from both experiments were generated and sequenced by the University of Wisconsin Biotechnology Center using an Illumina HiSeq 2500 with V4 chemistry generating 1 × 50 bp single-end reads and 15% PhiX spike-in. For all samples across both studies, a total of 1.66 billion raw reads were produced, with a mean read count per sample of 5.32 ± 0.15 (mean ± SE) million. Following trimming and quality filtering, 514 million reads remained, with a mean of 1.65 ± 0.06 million trimmed reads per sample.

2.4 | Differential expression and gene enrichment analyses

Raw sequence data was processed according to a modified version of the Tag-Seq pipeline available on GitHub (https://github.com/z0on/tag-based_RNAseq; modifications described in Studivan, 2020b). Briefly, raw reads were combined across sequenced duplicates and filtered using a custom perl script to remove PCR duplicates and reads with missing base calls in the degenerate header. Following quality filtering using FASTX_TOOLKIT (http://hannonlab.cshl.edu/fastx_toolkit), cleaned reads were mapped to a reference transcriptome and counted using BOWTIE2 (Langmead & Salzberg, 2012). Algal symbionts have been identified to be primarily comprised of *Cladocopium* spp. (formerly *Symbiodinium* Clade C) for the majority of the samples used in this study (Eckert, Reaume, Sturm, Studivan, & Voss, 2020; Polinski & Voss, 2018), therefore an updated version of the *M. cavernosa* coral transcriptome (Kitchen, Crowder, Poole, Weis, & Meyer, 2015; https://matzlab.weebly.com/data--code.html) was concatenated with the *Cladocopium* spp. algal transcriptome (Davies, Ries, Marchetti, & Castillo, 2018) using unique host/symbiont isogroup identifiers. The creation of a combined transcriptome for the two dominant eukaryotes in the holobiont has been used in previous studies to identify potential interactions between host and symbiont transcriptomic trends (Davies et al., 2016, 2018; Gust et al., 2014; Kenkel & Matz, 2017; Wright et al., 2019). Transcriptome concatenation and annotation was completed according to protocols detailed on GitHub (Studivan, 2020a). The mapping efficiency to the concatenated holobiont transcriptome was 14% of trimmed sequences. Mapping was then repeated using a concatenated version of the original *M. cavernosa* transcriptome (Kitchen et al., 2015) and the same *Cladocopium* spp. transcriptome as before to assess whether mapping efficiency was improved. While mapping efficiency using the original host transcriptome was improved at 65%, and differential expression analyses were similar as with the updated transcriptome, a substantial number of both coral and symbiont functional pathways were not identified by the analyses. This may have been indicative of reduced gene annotation and/or symbiont transcript contamination in the original host transcriptome. Therefore, we proceeded with analyses using the most recent coral transcriptome. Alignment of sequences to the updated holobiont transcriptome resulted in 31,276 isogroups (17,901 host and 13,375 symbiont) mapped across all samples, compared to 60,146 isogroups (47,236 host and 12,910 symbiont) using the original *M. cavernosa* transcriptome. Count data were then separated into host and symbiont data sets for subsequent analyses.

Before analyses of differential expression, low-count genes (genes with a cumulative count <10 across all samples) were removed and outliers were detected with the package ARRAYQUALITYMETRICS according to the distances between sample arrays (S_a) criterion, where an outlier threshold was automatically established for each data set (Kauffmann, Gentleman, & Huber, 2009). For the natural populations study, one *M. cavernosa* and 10 *Cladocopium* spp. arrays violated the outlier thresholds and were removed prior to differential expression analyses (Figure S1). No arrays were removed for the transplant experiment from either host or symbiont data sets despite three minor violations in the symbiont data set, in order to maintain sample size (Figure S2). Differential expression analyses were conducted using the package DESEQ2, with contrasts using likelihood ratio tests (>2 factor groups) or Wald tests (2 factor groups) on DESEQ2 models (Love, Huber, & Anders, 2014). For assessment of gene expression across natural populations, a two-factor model tested for overall differences across site and depth. Pairwise comparisons between depth zones are presented as mesophotic expression over shallow, and pairwise site comparisons are presented in alphabetical order (e.g., EFGB over WFGB). Testing of differential gene expression for the transplant experiment was made using a two-factor model across time and depth, with contrast tests across depth treatments and timepoints. Initial comparisons between WFGB and EFGB assessed homogeneity of variance and effects of site on gene expression with a PERMANOVA using *betadisper* and *adonis* functions of the package VEGAN, respectively (Oksanen et al., 2015). Samples from both sites were then combined to preserve sufficient replication within timepoints for further analyses.

Count data were normalized using the variance stabilized transformation for data visualization and downstream analyses. PERMANOVAs identified significant effects of factors on global gene expression, and differences in normalized expression among factors were visualized with PCoAs using Manhattan distance to examine multivariate differences among samples. To determine whether individual gene expression patterns could be used to predict experimental factors in both data sets, discriminant analyses of principal components (DAPC) were conducted with the ADEGENET package (Jombart, 2008; Jombart, Devillard, & Balloux, 2010). For the natural populations data set, a discriminant function was created using the shallow samples across all sites, then the probability of site membership was estimated for each of the mesophotic samples. For the transplant experiment, a discriminant function was created from the mesophotic and shallow controls, where membership probabilities to depth treatments and timepoints were then estimated for the transplants (as in Kenkel & Matz, 2017). DAPC scores were modelled to generate MCMC-based *p*-values comparing the differences between transplants and both control groups using the package MCMCGLMM (Hadfield, 2010).

Differentially-expressed genes were compared to functional pathways with enrichment analyses using gene ontology (GO) and eukaryotic orthologous group (KOG) databases in the GOMWU (Voolstra et al., 2011; https://github.com/z0on/GO_MWU) and KOGMWU packages (Dixon et al., 2015; Matz, 2016; Strader et al., 2016).

3 | RESULTS

3.1 | Gene expression among natural populations

3.1.1 | Differential expression

Prefiltering resulted in 12,929 host and 5,014 symbiont genes across 264 and 255 samples, respectively. Analyses of mesophotic and shallow *M. cavernosa* transcriptomes in the GOM and Belize indicated that gene expression differed significantly for both host and symbionts over site and depth, with a significant interaction between the two factors (Table 3). Site was the strongest driver of differential expression with 3,530 host and 425 symbiont DEGs, while depth was an order of magnitude less influential with 162 host and 18 symbiont DEGs, and the site:depth interaction contributed to 999 host and 56 symbiont DEGs (Table S1). PCoAs also demonstrated that variation was higher among sites and that most of the differentiation between mesophotic and shallow corals was driven by interactive differences between depths across sites (Figure 2). Quantification of DEGs between mesophotic and shallower depth zones within sites indicated that some sites were more vertically differentiated (Table S1). For example, mesophotic and shallower depths at EFGB were most differentiated by 1,264 host and 141 symbiont DEGs, while WFGB was least differentiated across depth by 743 host and 32 symbiont DEGs. A total of 466 host and 27 symbiont genes were differentially expressed between mesophotic and shallow samples at all five sites (Figure 3). The number of DEGs unique to each site were also in proportion to the overall number of DEGs identified between depths within the sites. For example, 400 host and 39 symbiont DEGs were unique to EFGB, while 8 host and 0 symbiont unique DEGs were found at WFGB. DAPC site assignments were correct for the majority of mesophotic samples in both host and symbiont data sets at BLZ and PRG-DRT (host: 79% and 63%; symbiont: 70% and 85%, respectively); however, site assignments were often mixed between WFGB and EFGB samples (host: 27% and 43%; symbiont: 29% and 24%; Table S2, Figure S3).

3.1.2 | Gene enrichment analyses

Eukaryotic orthologous group enrichment patterns identified several differences between mesophotic and shallow corals within sites. Metabolic gene classes were generally underrepresented in mesophotic compared to shallow corals across all sites, with similar, but stronger, patterns in mesophotic compared to shallow symbionts (Figure 3). KOGs related to cell membrane components,

TABLE 3 PERMANOVA model results for tested factors in natural (site + depth) and transplant (time + depth treatment) experiments, split into host (*M. cavernosa*) and symbiont (*Cladocopium* spp.) analyses

Experiment	Transcriptome	Factor	*df*	*F*	*p*
Natural	*M. cavernosa*	Site	3	13.9127	0.001
		Depth	1	3.2819	0.007
		Interaction	3	2.8148	0.002
	Cladocopium spp.	Site	3	7.6313	0.001
		Depth	1	2.9114	0.001
		Interaction	3	1.8497	0.006
Transplant	*M. cavernosa*	Time	2	2.2172	0.012
		Depth	2	0.90866	ns
		Interaction	4	1.40767	ns
	Cladocopium spp.	Time	2	1.7563	ns
		Depth	2	0.9861	ns
		Interaction	4	1.5551	0.045

Insignificant *p*-values are shown as ns.

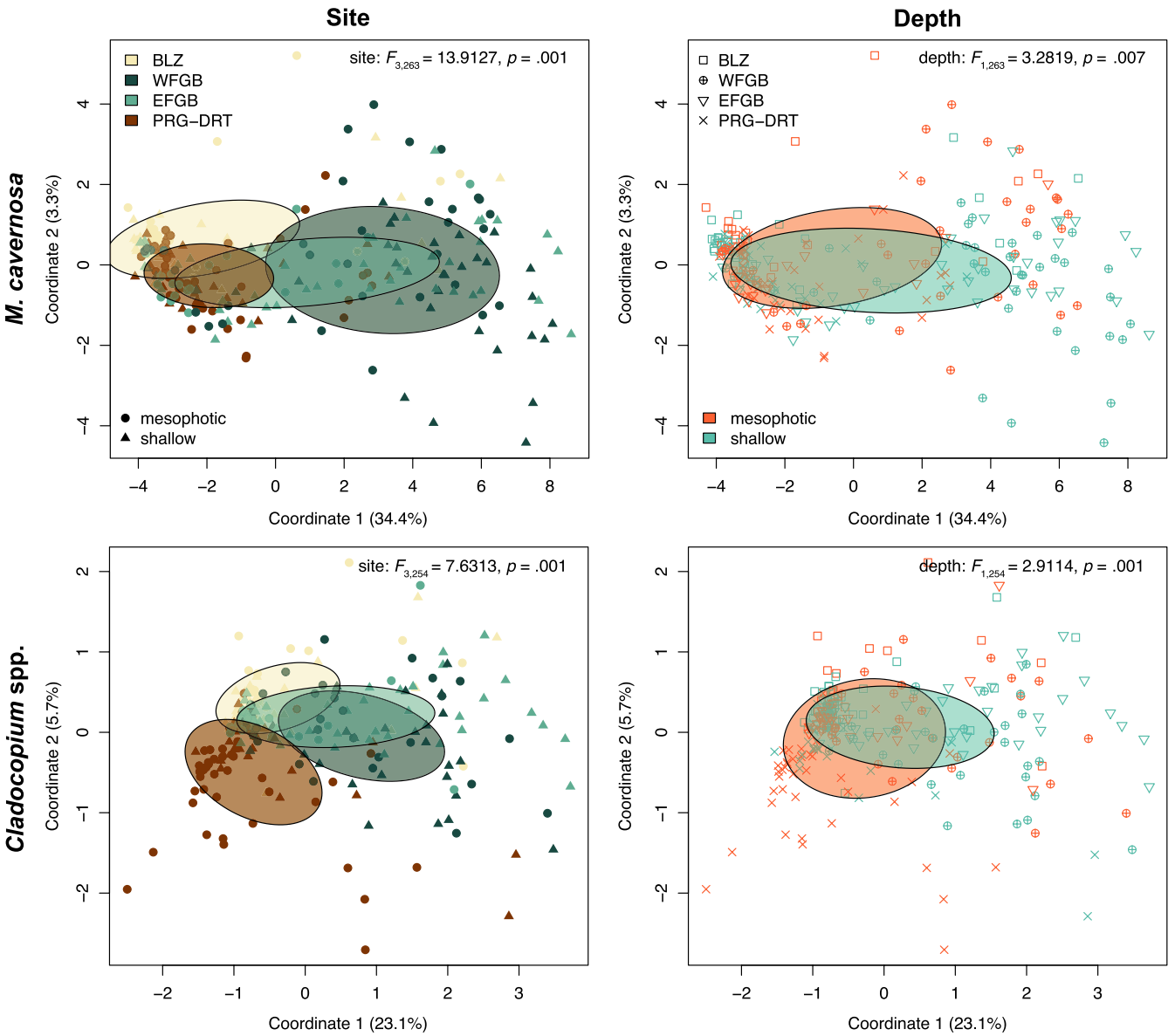

FIGURE 2 PCoAs showing variation in gene expression among five sites (BLZ, WFGB, EFGB, and PRG-DRT) and two depth zones (mesophotic, shallow), split into host (*M. cavernosa*) and symbiont (*Cladocopium* spp.) analyses. Raw count data were first normalized using a variance stabilized transformation in DESEQ2, then eigenvectors for each sample were calculated based on similarity to all other samples. Each coloured ellipse corresponds to a factor level, the boundaries of which are created by the dispersal of samples within the group. Test statistics and *p*-values generated from PERMANOVAs in VEGAN [Colour figure can be viewed at wileyonlinelibrary.com]

extracellular structures, and cell division were enriched with genes more highly expressed in mesophotic corals and their symbionts. Pairwise comparisons of KOG expression revealed significant correlations between sites for both host and symbiont data sets, while the mean correlation strength between pairwise site comparisons was higher for symbionts ($r = 0.85$) compared to the host ($r = 0.82$; Figure 3). KOG enrichment within the set of common DEGs (466 host, 27 symbiont) allowed the comparison of depth-specific pathways across sites (Figure S4). Metabolic KOGs in the common DEGs were once again less-expressed in mesophotic compared to shallow coral hosts and symbionts, and cell division and related pathways were similarly enriched as in the full set of genes. Correlation coefficients between pairwise sites were noticeably higher than in the analyses across all genes (Figure S4), suggesting similar expression of the common DEGs in mesophotic corals and their symbionts regardless of site.

Analyses of DEG pathways with GO annotations between depth zones identified significantly enriched GO categories in the host corals, and to a lesser extent, the symbiont data set (Figure S5). Translation-related GO categories were less-expressed in mesophotic compared to shallow corals for most sites. Metabolic GOs were weakly enriched for sites BLZ and EFGB. In the symbiont data set, carbohydrate catabolic process and nucleotide phosphorylation were the only significantly enriched GO terms identified.

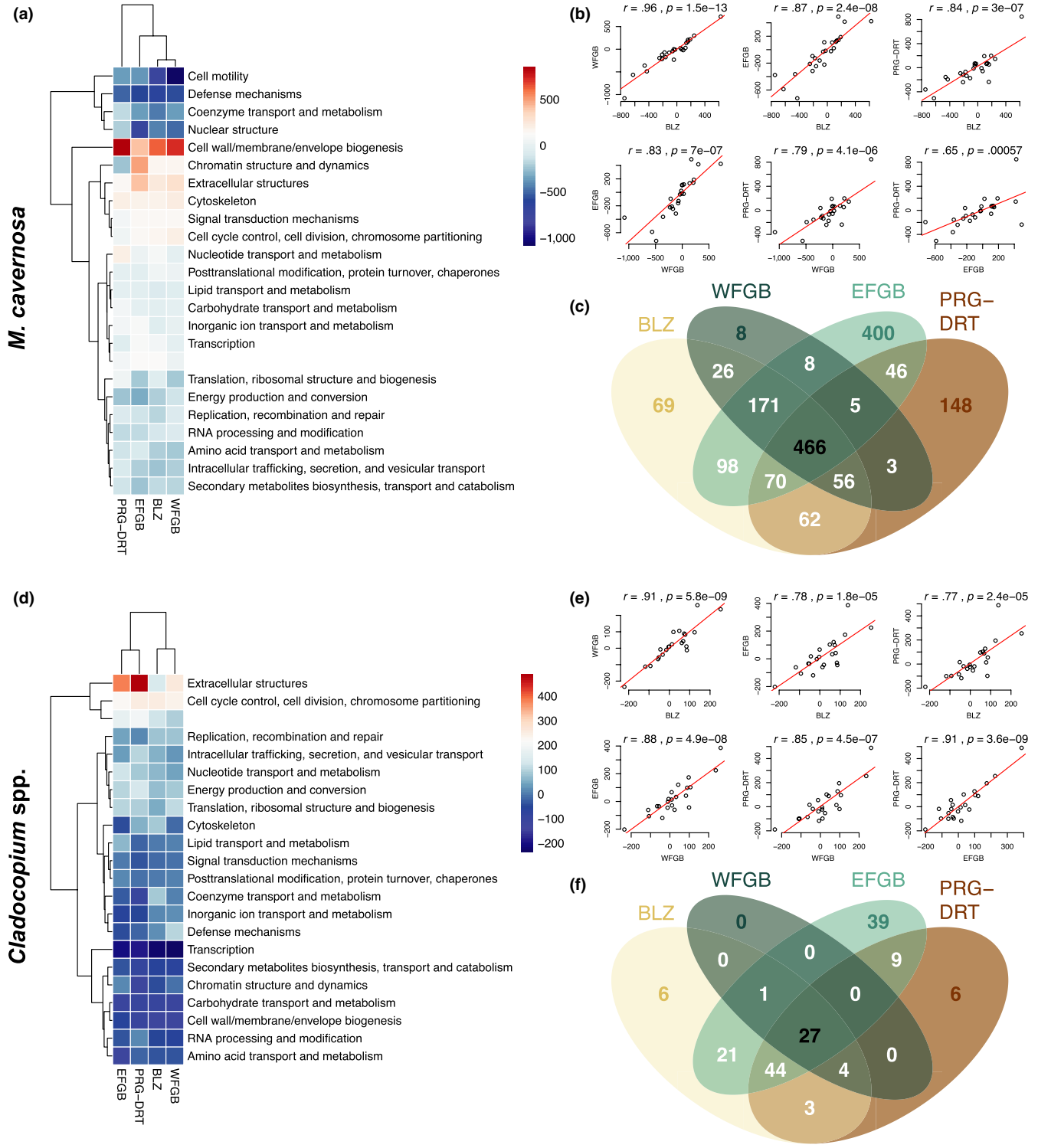

FIGURE 3 (a, d) Heatmaps of eukaryotic orthologous groups (KOGs) enriched with DEGs between mesophotic and shallow corals at five sites, split into host (*M. cavernosa*) and symbiont (*Cladocopium* spp.) analyses. Increasing intensities of red indicate enrichment of genes more-expressed in mesophotic versus shallow corals, while increasing intensities of blue indicate enrichment of genes less-expressed in mesophotic versus shallow corals. Color values represent ranks generated from Mann-Whitney U tests. Hierarchical networks on both axes display the similarities among sites (x-axis) and KOG classes (y-axis). (b, e) Panels of correlation analyses between pairwise site combinations. (c, f) Venn diagram displaying the number of DEGs across mesophotic and shallower depths zones within each of the five sites. Colour-coded numbers in each section correspond to genes unique to the sites, while overlapping numbers in white represent genes shared among factors. The DEGs in black indicate the number of genes conserved across all five sites [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Transplant experiment

3.2.1 | Environmental conditions and symbiont metrics

Mean daily temperature at WFGB and EFGB was significantly lower at 45 m compared to 20 m (1.58°C and 2.10°C lower, respectively). Daily minimum and maximum temperatures followed a similar pattern between depths (Figure S6). Mean daily PAR was significantly reduced at mesophotic compared to shallower depths (WFGB: 76.71%; EFGB: 79.72% reduction), with maximum daily PAR declining in a similar fashion. Mesophotic depth zones experienced lower daily and seasonal variance in both temperature and light compared to shallower depth zones (Figure S7). Depth was a significant factor for all environmental metrics, but site was only a significant factor affecting PAR metrics (Kruskal-Wallis: all significant $p < 0.002$; Table S3). During September 2016 (just prior to and during the 12 month timepoint), sea surface temperatures were >30°C, corresponding to a coral bleaching event observed at WFGB and EFGB (Johnston et al., 2019). All of the shallow controls and transplants at both sites exhibited some level of visible bleaching. All transplanted colonies were fully bleached and one colony appeared partially dead; in contrast, the shallow controls were typically only partially bleached (Figure 4). Follow-up observation at 36 months indicated apparent recovery of all shallow controls and transplants, with the exception of one transplant colony which exhibited partial mortality due to toppling unrelated to the bleaching event.

Areal symbiont and chlorophyll metrics showed significant variation across time but not depth treatment, while cellular chlorophyll metrics differed across depth treatment but not time (PERMANOVA: all significant $p < 0.047$; Table S4). These differences were attributable to the 12 month samples collected during the bleaching event which exhibited reduced symbiont density and reduced areal chlorophyll concentration for all depth treatments, including mesophotic controls (Figure S8). Pairwise comparisons of symbiont and chlorophyll metrics showed no significant differences between transplants and shallow controls. Multivariate analyses indicated that symbiont and chlorophyll metrics differed across depth and time, with a significant interaction (PERMANOVA: all $p < 0.001$; Table S4). Pairwise differences between transplants and mesophotic controls, and among all timepoints, were significant and contributed to overall differences between factors (pairwise PERMANOVA: all $p < 0.008$). Bleaching responses, as reflected in the percent change of symbiont density from 6 to 12 months, were significantly different across depth treatments but not between shallow controls and transplants, indicating a similar bleaching stress response (ANOVA: $F_{2,24} = 13.15$, $p < 0.0001$; Table S5; Figure S9).

3.2.2 | Differential expression

Initial comparisons between WFGB and EFGB identified heterogeneous variance between sites (*betadisper*; host: $F_{1,67} = 11.021$, $p = 0.002$; symbiont: $F_{1,67} = 13.724$, $p = 0.0004$) due to unequal sample sizes (Table 2), thus likely influencing observed differences in transcription between WFGB and EFGB samples (PERMANOVA; host: $F_{1,67} = 3.1242$, $p = 0.005$; symbiont: $F_{1,67} = 4.4081$, $p = 0.001$). Subsequent analyses are presented with samples combined across sites. Prefiltering resulted in 9,318 host and 1,628 symbiont genes across 68 samples. Two-way PERMANOVAs identified that time had a significant impact on gene expression patterns for the host only, while all other model factors were not significant, except for the time:depth interaction in the symbiont data set (Table 3). Time was the strongest driver of gene expression for both data sets with 118 coral host and 44 algal symbiont DEGs, while depth treatment had 0 host and 21 symbiont DEGs, and the interaction

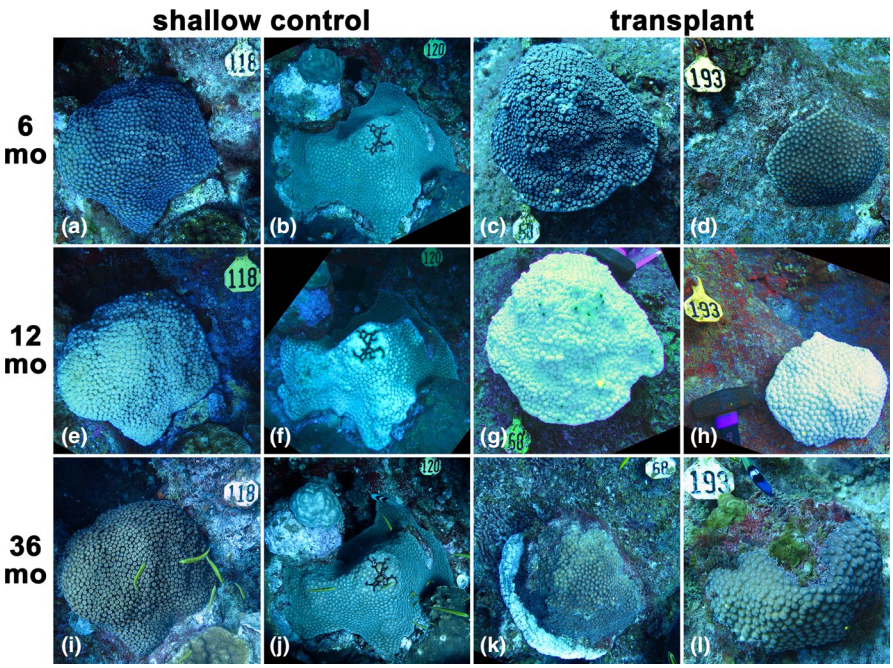

FIGURE 4 Panel showing variable bleaching of tracked colonies from the transplant experiment. The first two columns are shallow controls and the last two are transplanted colonies. The first row photos were taken at 6 months, the middle row photos were taken at 12 months during the bleaching event, and the bottom row after 36 months (panels a, e, i: shallow 118; panels b, f, j: shallow 120; panels c, g, k: transplant 68; panels d, h, l: transplant 193). Bleaching in panel k was the result of the transplant colony toppling in between 12 and 36 months [Colour figure can be viewed at wileyonlinelibrary.com]

had 16 and 1 DEGs, respectively (Table S1). Pairwise comparisons of depth treatments within each timepoint revealed a pattern in shifting expression through time (Figure S10). Differences between transplants and mesophotic controls increased over the three timepoints for the host only (84 to 107 to 317 DEGs), indicating initial variability among mesophotic corals and further differentiation following transplantation. Host differences between mesophotic and shallow controls varied over the three timepoints (50 to 73 to 57 DEGs), while transplants and shallow controls remained similar until 12 months (51 to 50 to 62 DEGs). The number of symbiont DEGs decreased slightly for mesophotic versus shallow controls (17 to 12 to 7 DEGs) and for transplants versus mesophotic controls (19 to 5 to 6 DEGs), while transplants versus shallow controls remained similarly low over the course of the experiment (1 to 2 to 1 DEGs).

PCoAs of timepoints indicated similar expression trends across depth treatments through time (Figure 5). Cluster overlap between 0 and 12 month samples suggests a seasonal component to gene expression patterns among the coral host, but this trend was less apparent for the algal symbionts. Assessment of the discriminant groups among depth treatments identified that transplants formed an intermediate group that was equally similar to mesophotic and shallow controls (MCMC: host p = .11; symbiont p = .13). DAPC depth treatment assignments for transplanted coral hosts identified 3 of the 7 host transplants to be initially assigned to the mesophotic group at 0 months, then to the shallow group for 6 and 12 months

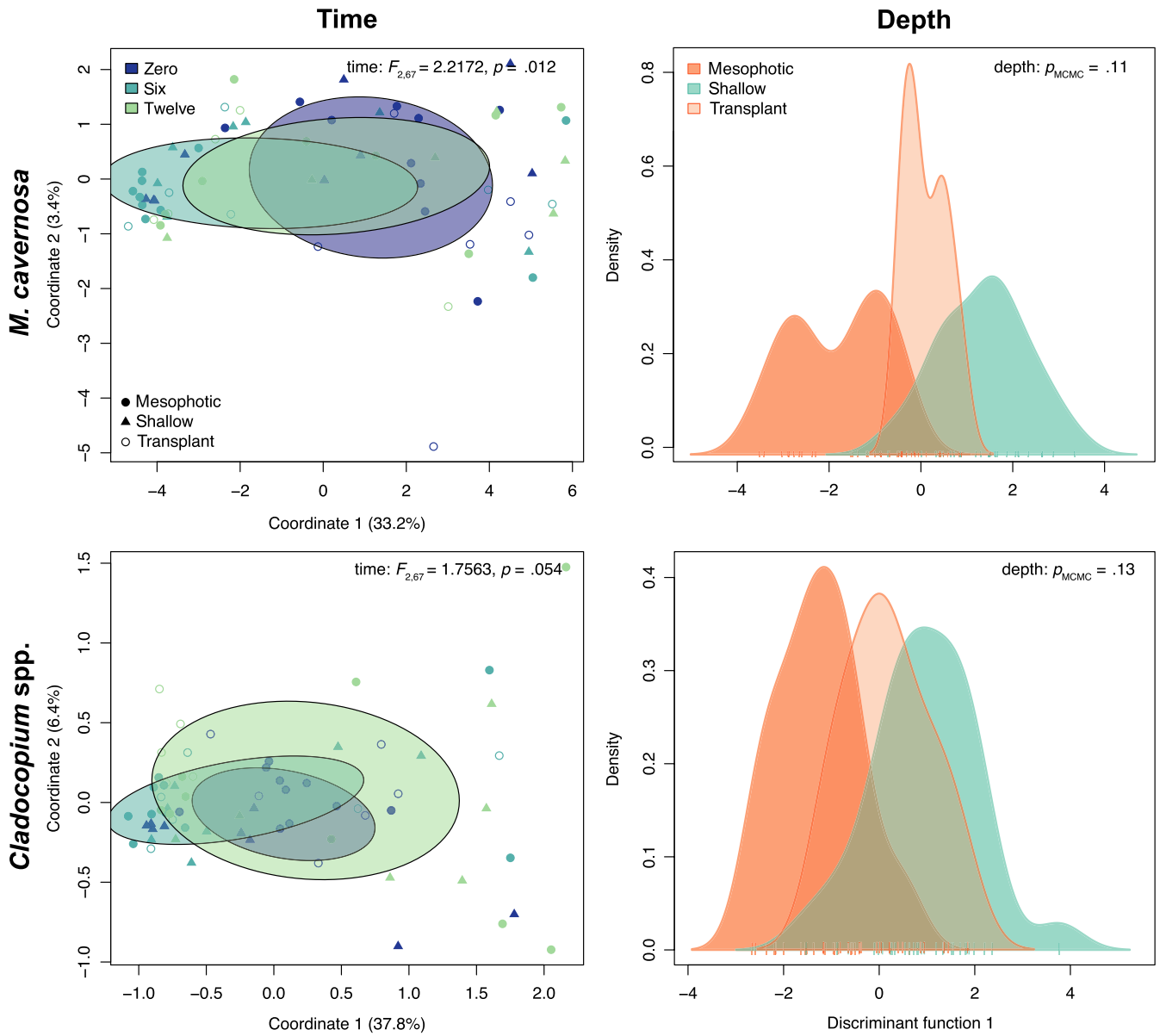

FIGURE 5 PCoAs showing variation in gene expression among timepoints (0, 6, and 12 months), split into host (*M. cavernosa*) and symbiont (*Cladocopium* spp.) analyses. Discriminant analyses of principal components (DAPC) assignments for the transplant experiment, for mesophotic and shallow controls (solid distributions) and mesophotic-to-shallow transplants (transparent distribution). Test statistics and *p*-values generated from PERMANOVAs in VEGAN for PCoAs, and from MCMC models in MCMCGLMM for DAPCs [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S6). For timepoints, most of the 6 and 12 month samples were assigned incorrectly to 0 months.

3.2.3 | Gene enrichment analyses

GOMWU analyses for pairwise combinations of depth treatments identified significant shifts in enriched GO categories between 0 and 12 months in the host data set only (Figure 6). At 12 months, mesophotic controls exhibited higher enrichment of genes related to catabolism and protein localization compared to shallow controls. Transplants also showed enrichment of catabolic, protein localization, and translational categories in relation to mesophotic controls. Compared to shallow controls, transplants demonstrated relatively less expression of genes associated with protein localization and translational GO categories. When examining additional GO divisions beyond biological process (BP), molecular function (MF) categories for ion transport were less-expressed in transplants versus mesophotic controls, while the GO category "structural constituent of ribosome" was enriched in transplants versus mesophotic controls, and in mesophotic versus shallow controls (Figure S11). Under the cellular component (CC) division, ribosomal and mitochondrial GO categories were enriched in transplants versus mesophotic controls, and in mesophotic versus shallow controls. The only GO categories that were significantly enriched in the symbiont data set for any timepoint or pairwise comparison of depth treatments were hexose catabolic process (6 months m.s; BP) and plastid stroma (6 months t.s; CC).

4 | DISCUSSION

4.1 | Gene expression among natural populations

The results of this study indicated that while site was an order of magnitude more influential on transcriptomic patterns among natural populations of *M. cavernosa* and their algal symbionts in the genus *Cladocopium*, conserved differences between mesophotic and shallower depth zones, in contrast, were remarkably consistent among sites. A subset of 466 host and 27 symbiont differentially expressed genes were commonly found across all sites and may represent a core group of genes related to *M. cavernosa*, and to a lesser extent, *Cladocopium* spp., physiology at mesophotic depths (Figure 3). Similar patterns have been observed across different environments with another coral species, *Orbicella faveolata* (Polato et al., 2010), and a marine fish species (Whitehead & Crawford, 2006a). Mesophotic corals and their symbionts demonstrated lower expression of genes associated with numerous metabolic, translational, and protein localization pathways (Figure 2 and Figure S5), which may be a response to low-light conditions (Bay, Guérécheau, Andreakis, Ulstrup, & Matz, 2013; Bay et al., 2009). It is also important to note that comparisons between mesophotic and shallow symbionts demonstrated significantly lower expression of metabolic KOG pathways than depth comparisons in the coral host (Figure 3), but this pattern was not well-represented with GO pathways, possibly due to poor representation of symbiont genes in GO annotations (Figure S5).

Previous studies quantifying photosynthetic and respiration responses at depth have observed that mesophotic corals have

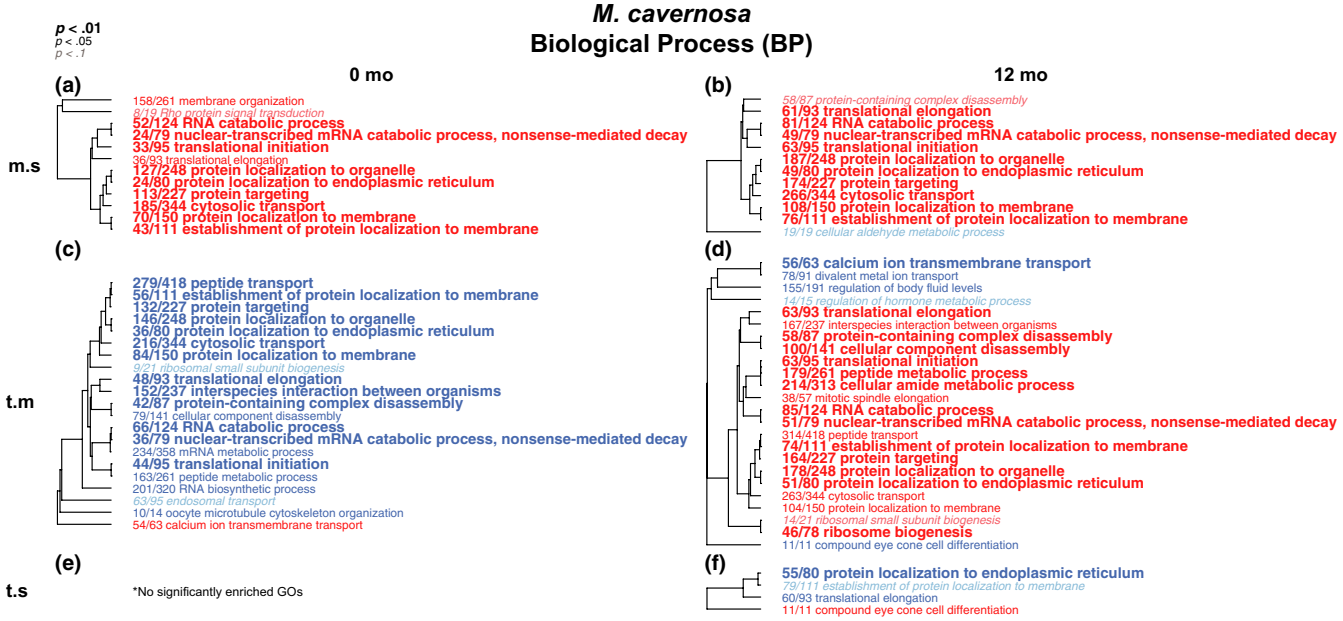

FIGURE 6 Hierarchical trees showing significantly enriched gene ontology (GO) categories across pairwise comparisons of depth treatments (m.s, mesophotic versus shallow; t.m, transplant versus mesophotic; t.s, transplant versus shallow) at 0 and 12 months following transplantation. Genes that passed an FDR-corrected *p*-value cutoff of .1 were clustered into GO terms based on functional annotations. Terms in red indicate enrichment of genes more-expressed in the first factor group versus the second, while terms in blue indicate less-expressed genes. The size of the font corresponds to the *p*-value threshold, where larger GO terms are more significantly enriched. Annotations presented for the host *M. cavernosa* transcriptome and the biological process (BP) GO division [Colour figure can be viewed at wileyonlinelibrary.com]

depressed metabolic rates compared to shallower conspecifics (Cooper et al., 2011; Lesser et al., 2010), which may correspond to reduced calcification and growth rates in some scleractinian species (Groves et al., 2018; Leichter & Genovese, 2006; Mass et al., 2007). Assessments of morphological variation over depth have suggested a similar trend, whereas flattened mesophotic colonies generally have lower tissue area (Klaus, Budd, Heikoop, & Fouke, 2007), which could contribute to the observed decline in metabolic activity (Cooper et al., 2011; Lesser et al., 2010). In this study, the few pathways highly expressed in mesophotic corals and symbionts were attributed to cell growth, including cell division, cytoskeleton, and extracellular structures (Figure 3). One hypothesis is that increased expression of genes associated with cell growth pathways in mesophotic corals and symbionts is reflective of host regulation of Symbiodiniaceae (Kuo, Chen, Lin, & Fang, 2004; Mayfield, Hsiao, Fan, Chen, & Gates, 2010; Toulza et al., 2010). Mesophotic *M. cavernosa* colonies in this region were observed to have increased symbiont densities compared to shallower conspecifics (Polinski & Voss, 2018), which may be a photoadaptive strategy in lower light environments (Lesser et al., 2010; Ziegler, Roder, Büchel, & Voolstra, 2015). Nutrient availability, which is hypothesized to be higher on MCEs compared to shallower reefs (Leichter & Genovese, 2006; Lesser et al., 2009), may also contribute to increased symbiont growth rates in mesophotic corals (Muller-Parker, D'Elia, & Cook, 2015; Wilkerson, Muller-Parker, & Muscatine, 1983). Taken together, reduction of coral metabolic pathways with simultaneous increases of symbiont-related growth pathways corroborate previously-described physiological trends for this species and may indicate a multifactor transcriptomic approach facilitating survival in low-light mesophotic environments.

The gene expression profiles presented here suggest that mesophotic and shallow *M. cavernosa* also demonstrated site-specific variation irrespective of genetic structure. Highly-connected *M. cavernosa* populations in the FGB (Studivan & Voss, 2018) exhibited distinct gene expression profiles between sites (Table S1; Site comparisons: 3,530 host and 425 symbiont DEGs), despite a similar response to depth between sites (Across site depth comparisons: 72 host and 24 symbiont DEGs). In this case, related genotypes may have been responding differently to microscale environmental variation at WFGB and EFGB, but the core set of "mesophotic genes" appeared to be responding similarly between sites. Additionally, genetically isolated populations such as those at mesophotic and shallower depths in BLZ and those at PRG and DRT (Studivan & Voss, 2018) responded to mesophotic conditions consistently between depth zones. Subtle differences in functional pathways of depth-generalist conspecifics may reflect tradeoffs in metabolic strategies to increase efficiency in each respective depth zone, or perhaps flexibility during seasonal and stochastic environmental changes. Site-specific effects in other taxa are commonly attributed to variable environmental conditions expected across broad spatial scales (Akman et al., 2016; Polato et al., 2010; Whitehead & Crawford, 2006b). In coral ecosystems, temperature, light irradiance, and oceanographic gradients are observed to be some of the dominant drivers of species distribution on subregional scales (Kahng et al., 2010; Lesser et al., 2009; Slattery & Lesser, 2012). These and other environmental conditions are expected to vary across thousands of kilometers in the GOM given the variability of the region and reef habitats (Locker et al., 2010; Oey, Ezer, & Lee, 2005; Reed et al., 2019; Schmahl, Hickerson, & Precht, 2008), likely playing a role in the site-specific patterns of gene expression observed in this study.

4.2 | Transplant experiment

The transplant experiment at WFGB and EFGB identified transcriptomic plasticity following relocation of entire *M. cavernosa* colonies from mesophotic to shallower depths. This experiment demonstrated that time had a stronger influence on gene expression compared to depth treatment, which was probably reflective of both seasonal variation for the first six months of the experiment (Edge, Morgan, & Snell, 2008; Warner, Chilcoat, McFarland, & Fitt, 2002), and the bleaching event at 12 months (see *Bleaching susceptibility of transplants*). Interestingly, pairwise comparisons of host DEGs between depth treatments found that only transplants versus mesophotic controls showed an appreciable increase in the number of DEGs, whereas transplants versus shallow controls, and mesophotic versus shallow controls demonstrated marginal changes over twelve months (Figure S10). DAPCs could not differentiate between timepoints for the transplants, but depth assignments were somewhat successful in recognizing differences between transplants in their original mesophotic environment versus final destination at shallower depths. Likewise, significance testing of discriminant groups determined that transplants formed a unique group, despite being equally similar to either control group (Figure 5).

The disparity between host and symbiont transcriptomic patterns provided evidence that corals and their symbiotic algae were responding differently to environmental stimuli. Symbionts exhibited less transcriptomic variability compared to their coral hosts, evidenced by low numbers of DEGs across timepoints and depth treatments (Figure S10), and high overlap between discriminant groups (Figure 5). Previous studies have also suggested that algal symbionts experience fewer transcriptional changes than the coral host following stress (Barshis, Ladner, Oliver, & Palumbi, 2014; Davies et al., 2018; Leggat et al., 2011). Corals in our transplant experiment had statistically similar symbiont and chlorophyll metrics through the first six months and among depth treatments during the bleaching event (Figure S8), suggesting that symbionts from the experimental colonies were probably similar in terms of photophysiology and metabolic responses, whereas there was clearer evidence for plasticity of the coral host following transplantation and in the face of bleaching stress.

Temperature and PAR variation monitored during the transplant experiment are likely to influence coral depth distribution in the region (Bongaerts et al., 2015; Lesser et al., 2009, 2010). Despite a 1.58–2.10°C lower mean temperature at the 45 m depth zone compared to the 20 m depth zone, this difference was primarily

driven by a more rapid increase in shallower temperatures from March–September 2016. Mesophotic temperatures increased more gradually until a rapid rise to similar temperatures as shallower depths in late summer (Figures S6 and S7). Over the duration of the experiment, both mean and maximum daily PAR were reduced by 76.7–80.4% in mesophotic compared to shallower depths, with the greatest differential in the summer months. Temperature and light combined may explain the slight increase in host DEGs between mesophotic and shallow controls at 6 months, indicating a seasonality component to transcriptomic patterns.

4.2.1 | Bleaching susceptibility of transplants

Perhaps the most interesting, yet unexpected, outcome of the transplant experiment was the opportunity to examine responses of transplanted corals following a thermal stress event. Previous monitoring efforts at WFGB and EFGB have demonstrated that temperatures of 29.5°C or greater for >50 days can cause bleaching events (Johnston et al., 2019). Mean daily temperatures at the shallower sites remained >30°C for at least 80 days through the 12 month timepoint (Figure S7), resulting in widespread coral bleaching observed at the shallower depth zones of both WFGB and EFGB. Neither of the mesophotic depth zones were exposed to temperatures above 29°C, and none of the mesophotic controls were observed to be visibly bleached due to thermal stress, although some colonies exhibited reduced symbiont densities. On the other hand, all of the shallow controls and transplants were bleached at 12 months (Figure 4). Transplants appeared fully bleached while shallow controls were only partially bleached, but statistical comparisons of symbiont and chlorophyll metrics indicated no significant differences (Figure S8). Rates of symbiont loss were also indistinguishable between shallow controls and transplants (Figure S9), and follow-up observation at 36 months indicated apparent recovery of all colonies. These results suggest that shallower colonies of *M. cavernosa* at FGB are not better adapted to handle thermal stress events than their mesophotic counterparts. Previous studies have demonstrated the opposite using transplant and thermal acclimatization experiments, where corals exposed to prior sublethal thermal stress (such as those in naturally-variable shallower environments) were more resistant to future stress events (Barfield, Aglyamova, Bay, & Matz, 2018; Barshis et al., 2013; Davies et al., 2018; Kenkel et al., 2013). Environmental data collected over the duration of the transplant experiment at both WFGB and EFGB support that shallower corals experienced more thermal and light variability than those at mesophotic depths. Symbiont and chlorophyll metrics, as well as gene expression patterns, identified mechanisms that may allow mesophotic corals to respond to bleaching stress differently than shallower corals.

Analyses of GO functional pathways at 12 months suggested that while all experimental corals exposed to the bleaching event were responding to thermal stress, responses were different depending on the original depth zone. GO categories for metabolic processes, protein localization and disassembly, translational elongation, and RNA catabolic processes were enriched in transplants versus mesophotic controls (Figure 6), which are indicative of metabolic modification, protein production, and photosystem damage in response to thermal stress (Davies et al., 2016; Murata, Takahashi, Nishiyama, & Allakhverdiev, 2007; Reyes-Bermudez et al., 2009; Seneca & Palumbi, 2015). Several of these categories, including protein localization to endoplasmic reticulum and translational initiation/elongation, were more highly expressed in shallow controls versus transplants, indicating variation in the strength of transcriptomic responses between depth treatments. Expression of ribosomal pathways was higher for mesophotic controls than shallow controls, and higher still between transplants and mesophotic controls (Figure S11). As ribosomal pathways are associated with protein synthesis and modification, this suggests that transplants may have been continuing to synthesize proteins during near-total bleaching of algal symbionts (DeSalvo et al., 2008), or possibly attempting to repair damage done to photosynthetic systems. There was little evidence to support that shallow controls were exhibiting the same transcriptomic responses, despite also being bleached.

Common transcriptomic responses to thermal stress in corals can include a reduction of ribosomal expression and increased expression of heat shock proteins and antioxidants (Császár, Seneca, & van Oppen, 2009; DeSalvo, Sunagawa, Voolstra, & Medina, 2010; DeSalvo et al., 2008; Kenkel et al., 2011; Seneca et al., 2010). Our study instead observed a distinct lack of typical bleaching response pathways, perhaps because sampling occurred after the likely onset of stress responses and production of proteins associated with thermal stress. Following initial damage control, a secondary response to establish homeostasis (DeSalvo et al., 2008; Kenkel et al., 2013; Kültz, 2003, 2005) may include an increase in ribosomal expression, as observed in this study's transplanted corals. Once activated, the homeostatic response can be permanent until environmental conditions change. Observations of the experimental corals at 36 months indicated that visible recovery had occurred, but it is unclear how long the recovery process had taken, and colonies were not sampled to quantify post-stress symbiont and chlorophyll metrics.

4.2.2 | CONCLUSIONS

The paired studies presented here reveal that mesophotic *M. cavernosa* colonies were generally similar to those found at shallower depths across reefs in the GOM and Belize. Through quantification of differential gene expression in natural populations, evidence for a potential shift in metabolic strategies was observed. Mesophotic corals demonstrated lower expression of metabolic and translational gene pathways, but higher expression of cell growth and division pathways relative to shallow corals, which may coincide with regulation of algal symbionts. Additionally, a common set of DEGs were identified between depth zones across all sites, suggesting a core set of genes related to depth. There was little evidence, however, to support that transcriptomic differences across depth zones are

contributing to genetic isolation among some *M. cavernosa* populations in the region (Studivan & Voss, 2018), nor that transcriptomic variation may limit coral connectivity in this case. In the transplant experiment, gene expression profiling through time revealed that colonies of *M. cavernosa* transplanted from mesophotic to shallower depth zones exhibited transcriptomic plasticity within six months. While entirely unexpected, a bleaching event near the end of the transplant experiment allowed the unique opportunity to examine how gene expression plasticity in transplanted mesophotic corals affected their responses to thermal stress compared to natural shallower populations. Despite appearing more visually bleached, transplants from the mesophotic depth zone were equally susceptible to bleaching as shallow controls. Given the results of both studies, it would appear that corals adapted to mesophotic conditions are able to acclimatize to shallower conditions even in the face of thermal stress, but this theory would require comparative genomic analyses (i.e., SNP genotyping) to elucidate patterns of adaptation versus acclimatization.

Additional studies combining multiple omics approaches are needed to understand the genetic variation present in natural populations (Alvarez et al., 2015) and to define the capability of individuals to acclimatize to new environments following experimental manipulation. While there are logistical challenges associated with conducting manipulative experiments on geographically-isolated mesophotic coral ecosystems (Bongaerts et al., 2015; Kahng et al., 2014), future research priorities should include full reciprocal transplantation to assess potential bidirectional plasticity in mesophotic and shallower environments. In particular, utilizing fragmented samples of the same parent colonies across treatment groups would allow the comparison of genotypic influence on transcriptomic and physiological patterns. With integrated omics and physiological data from natural and manipulated coral populations, studies can better understand the relative roles of genotype and plasticity on acclimatization/adaptation and survivability of individual corals across broad environmental ranges.

ACKNOWLEDGEMENTS

We are grateful to staff of Flower Garden Banks and Florida Keys National Marine Sanctuaries, crews of the R/V *Manta*, R/V *Walton Smith*, and M/V *Spree*, Lance Horn and Jason White from the University of North Carolina at Wilmington Undersea Vehicle Program, John Reed, Dennis Hanisak, and Kimberly Puglise from the Pulley Ridge Project, and Zach Foltz and Scott Jones from the Smithsonian Marine Station. Jeff Beal, Jake Emmert, Jennifer Polinski, Danielle Dodge, Amanda Alker, Patrick Gardner, Rachel Parmer, Rick Gomez, Casey Coy, Michael Terrell, Mike Echevarria, Milton Carlo, Evan Tuohy, Robbie Christian, Matt Ajemian, Mike McCallister, Chris Ledford, and Michael Dickson provided diving support. Jennifer Polinski, Diana Perez, Haley Clinton, Patrick Gardner, and Danielle Dodge aided in collection of the algal symbiont and chlorophyll data. Jeremy Niece and Joshua Hyman at the University of Wisconsin Madison Biotechnology Center, Mikhail Matz of the University of Texas at Austin, and Carly Kenkel of the University of Southern California Dornsife provided valuable sequencing support, advice, and pipeline optimization. High-performance computing was provided by Research Computing Services at Florida Atlantic University. Corals were collected from Flower Garden Banks National Marine Sanctuary under permits FGBNMS-2010-005 and FGBNMS-2014-014, and from Carrie Bow Cay under CITES permits 4224 and 7123. This research was funded by the NOAA Office of Ocean Exploration and Research under awards NA09OAR4320073 and NA14OAR4320260 to the Cooperative Institute for Ocean Exploration, Research and Technology (CIOERT) at Harbor Branch Oceanographic Institute and the NOAA National Centers for Coastal Ocean Science under award NA11NOS4780045 to the Cooperative Institute for Marine and Atmospheric Studies (CIMAS) at the University of Miami. This research was also supported by a donation from the Banbury fund in memory of John and Andreija Robertson to establish the Robertson Coral Reef Research and Conservation Program at Harbor Branch Oceanographic Institute, and by graduate student fellowships and grants from Florida Atlantic University. This is contribution 2273 from Harbor Branch Oceanographic Institute at Florida Atlantic University, and contribution 1038, Caribbean Coral Reef Ecosystems (CCRE) program, Smithsonian Institution.

AUTHOR CONTRIBUTIONS

M.S.S., and J.D.V. designed and performed the research and experiments. J.D.V. secured funding for this research. M.S.S. analysed the data and wrote the manuscript, with significant contributions and revisions by J.D.V.

DATA AVAILABILITY STATEMENT

Raw sequence data generated from this study can be found in the NCBI Gene Expression Omnibus repository under accession GSE107688. Transcriptome annotation pipelines are in a GitHub repository (Studivan, 2020a). Bioinformatics and statistical pipelines are in a GitHub repository (Studivan, 2020b). Data sets generated from this study, including analyses scripts, are available in a Dryad data repository (Studivan & Voss, 2020).

ORCID

Michael S. Studivan https://orcid.org/0000-0002-3771-0415
Joshua D. Voss https://orcid.org/0000-0002-0653-2767

REFERENCES

Akman, M., Carlson, J. E., Holsinger, K. E., & Latimer, A. M. (2016). Transcriptome sequencing reveals population differentiation in gene expression linked to functional traits and environmental gradients in the South African shrub *Protea repens*. *New Phytologist*, *210*, 295–309. https://doi.org/10.1111/nph.13761

Alvarez, M., Schrey, A. W., & Richards, C. L. (2015). Ten years of transcriptomics in wild populations: What have we learned about their ecology and evolution? *Molecular Ecology*, *24*(4), 710–725. https://doi.org/10.1111/mec.13055

Anderson, D. A., Walz, M. E., Weil, E., Tonellato, P., & Smith, M. C. (2016). RNA-Seq of the Caribbean reef-building coral *Orbicella faveolata* (Scleractinia–Merulinidae) under bleaching and disease stress expands models of coral innate immunity. *PeerJ*, *4*, e1616. https://doi.org/10.7717/peerj.1616

Barfield, S. J., Aglyamova, G. V., Bay, L. K., & Matz, M. V. (2018). Contrasting effects of *Symbiodinium* identity on coral host transcriptional profiles across latitudes. *Molecular Ecology*, *27*(15), 3103–3115. https://doi.org/10.1111/mec.14774

Barshis, D. J., Ladner, J. T., Oliver, T. A., & Palumbi, S. R. (2014). Lineage-specific transcriptional profiles of *Symbiodinium* spp. unaltered by heat stress in a coral host. *Molecular Biology and Evolution*, *31*(6), 1343–1352. https://doi.org/10.1093/molbev/msu107

Barshis, D. J., Ladner, J. T., Oliver, T. A., Seneca, F. O., Traylor-Knowles, N., & Palumbi, S. R. (2013). Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences*, *110*(4), 1387–1392. https://doi.org/10.1073/pnas.1210224110

Bay, L. K., Guérécheau, A., Andreakis, N., Ulstrup, K. E., & Matz, M. V. (2013). Gene expression signatures of energetic acclimatisation in the reef building coral *Acropora millepora*. *PLoS One*, *8*(5), e61736. https://doi.org/10.1371/journal.pone.0061736

Bay, L. K., Ulstrup, K. E., Nielsen, H. B., Jarmer, H., Goffard, N., Willis, B. L., … van Oppen, M. J. H. (2009). Microarray analysis reveals transcriptional plasticity in the reef building coral *Acropora millepora*. *Molecular Ecology*, *18*(14), 3062–3075. https://doi.org/10.1111/j.1365-294X.2009.04257.x

Bongaerts, P., Frade, P. R., Hay, K. B., Englebert, N., Latijnhouwers, K. R. W., Bak, R. P. M., … Hoegh-Guldberg, O. (2015). Deep down on a Caribbean reef: Lower mesophotic depths harbor a specialized coral-endosymbiont community. *Scientific Reports*, *5*, 7652. https://doi.org/10.1038/srep07652

Bongaerts, P., & Smith, T. B. (2019). Beyond the 'deep reef refuge' hypothesis: A conceptual framework to characterize persistence at depth. In Y. Loya, K. A. Puglise, & T. C. Bridge (Eds.), *Coral Reefs of the World: Mesophotic Coral Ecosystems* (pp. 881–895). New York: Springer.

Chomczynski, P., & Sacchi, N. (1987). Single-step method of RNA isolation by acid guanidinium thiocyanate-phenol-chloroform extraction. *Analytical Biochemistry*, *162*, 156–159. https://doi.org/10.1016/0003-2697(87)90021-2

Chomczynski, P., & Sacchi, N. (2006). The single-step method of RNA isolation by acid guanidinium thiocyanate–phenol–chloroform extraction: Twenty-something years on. *Nature Protocols*, *1*(2), 581–585. https://doi.org/10.1038/nprot.2006.83

Cooper, T. F., Ulstrup, K. E., Dandan, S. S., Heyward, A. J., Kühl, M., Muirhead, A., … van Oppen, M. J. H. (2011). Niche specialization of reef-building corals in the mesophotic zone: Metabolic trade-offs between divergent *Symbiodinium* types. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1840–1850. https://doi.org/10.1098/rspb.2010.2321

Császár, N. B. M., Seneca, F. O., & van Oppen, M. J. H. (2009). Variation in antioxidant gene expression in the scleractinian coral *Acropora millepora* under laboratory thermal stress. *Marine Ecology Progress Series*, *392*, 93–102. https://doi.org/10.3354/meps08194

Davies, S. W., Marchetti, A., Ries, J. B., & Castillo, K. D. (2016). Thermal and pCO2 stress elicit divergent transcriptomic responses in a resilient coral. *Frontiers in Marine Science*, *3*, 112. https://doi.org/10.3389/fmars.2016.00112

Davies, S. W., Ries, J. B., Marchetti, A., & Castillo, K. D. (2018). *Symbiodinium* functional diversity in the coral *Siderastrea siderea* is influenced by thermal stress and reef environment, but not ocean acidification. *Frontiers in Marine Science*, *5*, 150. https://doi.org/10.3389/fmars.2018.00150

DeSalvo, M. K., Sunagawa, S., Voolstra, C. R., & Medina, M. (2010). Transcriptomic responses to heat stress and bleaching in the elkhorn coral *Acropora palmata*. *Marine Ecology Progress Series*, *402*, 97–113. https://doi.org/10.3354/meps08372

DeSalvo, M. K., Voolstra, C. R., Sunagawa, S., Schwarz, J. A., Stillman, J. H., Coffroth, M. A., … Medina, M. (2008). Differential gene expression during thermal stress and bleaching in the Caribbean coral *Montastraea faveolata*. *Molecular Ecology*, *17*(17), 3952–3971. https://doi.org/10.1111/j.1365-294X.2008.03879.x

Dixon, G. B., Davies, S. W., Aglyamova, G. A., Meyer, E., Bay, L. K., & Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science*, *348*(6242), 1460–1462. https://doi.org/10.1126/science.1261224

Eckert, R. J., Reaume, A. M., Sturm, A. B., Studivan, M. S., & Voss, J. D. (2020). Depth influences Symbiodiniaceae associations among *Montastraea cavernosa* corals on the Belize Barrier Reef. *Frontiers in Microbiology*, *11*, 518. https://doi.org/10.3389/fmicb.2020.00518

Edge, S. E., Morgan, M. B., & Snell, T. W. (2008). Temporal analysis of gene expression in a field population of the scleractinian coral *Montastraea faveolata*. *Journal of Experimental Marine Biology and Ecology*, *355*, 114–124. https://doi.org/10.1016/j.jembe.2007.12.004

Evans, T. G. (2015). Considerations for the use of transcriptomics in identifying the "genes that matter" for environmental adaptation. *Journal of Experimental Biology*, *218*(12), 1925–1935. https://doi.org/10.1242/jeb.114306

Friedrich, S., Konietschke, F., & Pauly, M. (2019). MANOVA.RM: *analysis of multivariate data and repeated measures designs*. R package version 0.3.2.

Graus, R. R., & Macintyre, I. G. (1982). Variation in growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): A quantitative evaluation of growth response to light distribution using computer simulation. *Smithsonian Contributions to the Marine Sciences*, *12*, 441–464.

Groves, S. H., Holstein, D. M., Enochs, I. C., Kolodzeij, G., Manzello, D. P., Brandt, M. E., & Smith, T. B. (2018). Growth rates of *Porites astreoides* and *Orbicella franksi* in mesophotic habitats surrounding St. Thomas, US Virgin Islands. *Coral Reefs*, *37*(2), 345–354. https://doi.org/10.1007/s00338-018-1660-7

Gust, K. A., Najar, F. Z., Habib, T., Lotufo, G. R., Piggot, A. M., Fouke, B. W., … Perkins, E. J. (2014). Coral-zooxanthellae meta-transcriptomics reveals integrated response to pollutant stress. *BMC Genomics*, *15*(1), 591. https://doi.org/10.1186/1471-2164-15-591

Gutner-Hoch, E., Waldman Ben-Asher, H., Yam, R., Shemesh, A., & Levy, O. (2017). Identifying genes and regulatory pathways associated with the scleractinian coral calcification process. *PeerJ*, *5*, e3590. https://doi.org/10.7717/peerj.3590

Hadfield, J. D. (2010). MCMCglmm: MCMC methods for multi-response GLMMs in R. *Journal of Statistical Software*, *33*(2), 1–22. https://doi.org/10.1002/ana.22635

Hervé, M. (2019). *RVAideMemoire: Testing and plotting procedures for biostatistics*. R package version 0.9-73.

Johnston, M. A., Hickerson, E. L., Nuttall, M. F., Blakeway, R. D., Sterne, T. K., Eckert, R. J., & Schmahl, G. P. (2019). Coral bleaching and recovery from 2016 to 2017 at East and West Flower Garden Banks, Gulf of Mexico. *Coral Reefs*, *38*(4), 787–799. https://doi.org/10.1007/s00338-019-01788-7

Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*(11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, *11*(1), 94. https://doi.org/10.1186/1471-2156-11-94

Kahng, S. E., Copus, J. M., & Wagner, D. (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, *7*, 72–81. https://doi.org/10.1016/j.cosust.2013.11.019

Kahng, S. E., Garcia-Sais, J. R., Spalding, H. L., Brokovich, E., Wagner, D., Weil, E., … Toonen, R. J. (2010). Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, *29*, 255–275. https://doi.org/10.1007/s00338-010-0593-6

Kauffmann, A., Gentleman, R., & Huber, W. (2009). arrayQualityMetrics - a bioconductor package for quality assessment of microarray data.

Bioinformatics, *25*(3), 415–416. https://doi.org/10.1093/bioinformatics/btn647

Kenkel, C. D., Aglyamova, G., Alamaru, A., Bhagooli, R., Capper, R., Cunning, R., … Matz, M. V. (2011). Development of gene expression markers of acute heat-light stress in reef-building corals of the genus *Porites*. *PLoS One*, *6*, e26914. https://doi.org/10.1371/journal.pone.0026914

Kenkel, C. D., & Matz, M. V. (2017). Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nature Ecology & Evolution*, *1*(1), 14. https://doi.org/10.1038/s41559-016-0014

Kenkel, C. D., Meyer, E., & Matz, M. V. (2013). Gene expression under chronic heat stress in populations of the mustard hill coral (*Porites astreoides*) from different thermal environments. *Molecular Ecology*, *22*(16), 4322–4334. https://doi.org/10.1111/mec.12390

Kenkel, C. D., Sheridan, C., Leal, M. C., Bhagooli, R., Castillo, K. D., Kurata, N., … Matz, M. V. (2014). Diagnostic gene expression biomarkers of coral thermal stress. *Molecular Ecology Resources*, *14*(4), 667–678. https://doi.org/10.1111/1755-0998.12218

Kitchen, S. A., Crowder, C. M., Poole, A. Z., Weis, V. M., & Meyer, E. (2015). *De novo* assembly and characterization of four anthozoan (Phylum Cnidaria) transcriptomes. *G3: Genes*, *Genomes*. *Genetics*, *5*(11), 2441–2452. https://doi.org/10.1534/g3.115.020164

Klaus, J. S., Budd, A. F., Heikoop, J. M., & Fouke, B. W. (2007). Environmental controls on corallite morphology in the reef coral *Montastraea annularis*. *Bulletin of Marine Science*, *80*(1), 233–260.

Konietschke, F., Placzek, M., Schaarschmidt, F., & Hothorn, L. A. (2015). nparcomp: An R software package for nonparametric multiple comparisons and simultaneous confidence intervals. *Journal of Statistical Software*, *64*(9), 1–17. https://doi.org/10.18637/jss.v064.i09

Kültz, D. (2003). Evolution of the cellular stress proteome: From monophyletic origin to ubiquitous function. *Journal of Experimental Biology*, *206*(18), 3119–3124. https://doi.org/10.1242/jeb.00549

Kültz, D. (2005). Molecular and evolutionary basis of the cellular stress response. *Annual Review of Physiology*, *67*(1), 225–257. https://doi.org/10.1146/annurev.physiol.67.040403.103635

Kuo, J., Chen, M.-C., Lin, C.-H., & Fang, L.-S. (2004). Comparative gene expression in the symbiotic and aposymbiotic *Aiptasia pulchella* by expressed sequence tag analysis. *Biochemical and Biophysical Research Communications*, *318*(1), 176–186. https://doi.org/10.1016/j.bbrc.2004.03.191

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, *9*(4), 357–359. https://doi.org/10.1038/nmeth.1923

Leggat, W., Seneca, F., Wasmund, K., Ukani, L., Yellowlees, D., & Ainsworth, T. D. (2011). Differential responses of the coral host and their algal symbiont to thermal stress. *PLoS One*, *6*(10), e26687. https://doi.org/10.1371/journal.pone.0026687

Leichter, J. J., & Genovese, S. J. (2006). Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Marine Ecology Progress Series*, *316*, 95–103. https://doi.org/10.3354/meps316095

Lesser, M. P. (2000). Depth-dependent photoacclimatization to solar ultraviolet radiation in the Caribbean coral Montastraea faveolata. *Marine Ecology Progress Series*, *192*, 137–151. https://doi.org/10.3354/meps192137

Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, *375*, 1–8. https://doi.org/10.1016/j.jembe.2009.05.009

Lesser, M. P., Slattery, M., Stat, M., Ojimi, M., Gates, R. D., & Grottoli, A. (2010). Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. *Ecology*, *91*(4), 990–1003. https://doi.org/10.1890/09-0313.1

Locker, S. D., Armstrong, R. A., Battista, T. A., Rooney, J. J., Sherman, C., & Zawada, D. G. (2010). Geomorphology of mesophotic coral ecosystems: Current perspectives on morphology, distribution, and mapping strategies. *Coral Reefs*, *29*, 329–345. https://doi.org/10.1007/s00338-010-0613-6

Louis, Y. D., Bhagooli, R., Kenkel, C. D., Baker, A. C., & Dyall, S. D. (2016). Gene expression biomarkers of heat stress in scleractinian corals: Promises and limitations. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *191*, 63–77. https://doi.org/10.1016/j.cbpc.2016.08.007

Love, M. I., Huber, W., & Anders, S. (2014). Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biology*, *15*(12), 550–571. https://doi.org/10.1186/s13059-014-0550-8

Mass, T., Einbinder, S., Brokovich, E., Shashar, N., Vago, R., Erez, J., & Dubinsky, Z. (2007). Photoacclimation of *Stylophora pistillata* to light extremes: Metabolism and calcification. *Marine Ecology Progress Series*, *334*, 93–102. https://doi.org/10.3354/meps334093

Matz, M. V. (2016). *KOGMWU: Functional summary and meta-analysis of gene expression data*. R Package Version 1.1.

Matz, M. V. (2018). Fantastic beasts and how to sequence them: Ecological genomics for obscure model organisms. *Trends in Genetics*, *34*, 121–132. https://doi.org/10.1016/j.tig.2017.11.002

Mayfield, A. B., Hsiao, Y. Y., Fan, T.-Y., Chen, C.-S., & Gates, R. D. (2010). Evaluating the temporal stability of stress-activated protein kinase and cytoskeleton gene expression in the Pacific reef corals *Pocillopora damicornis* and *Seriatopora hystrix*. *Journal of Experimental Marine Biology and Ecology*, *395*(1–2), 215–222. https://doi.org/10.1016/j.jembe.2010.09.007

Meron, D., Maor-Landaw, K., Weizman, E., Waldman Ben-Asher, H., Eyal, G., Banin, E., … Levy, O. (2019). The algal symbiont modifies the transcriptome of the scleractinian coral *Euphyllia paradivisa* during heat stress. *Microorganisms*, *7*(8), 256. https://doi.org/10.3390/microorganisms7080256

Meyer, E., Aglyamova, G. V., & Matz, M. V. (2011). Profiling gene expression responses of coral larvae (*Acropora millepora*) to elevated temperature and settlement inducers using a novel RNA-Seq procedure. *Molecular Ecology*, *20*(17), 3599–3616. https://doi.org/10.1111/j.1365-294X.2011.05205.x

Muller-Parker, G., D'Elia, C. F., & Cook, C. B. (2015). Interactions between corals and their symbiotic algae. In C. Birkeland (Ed.), *Coral reefs in the anthropocene* (pp. 99–116). Dordrecht: Springer. https://doi.org/10.1007/978-94-017-7249-5

Murata, N., Takahashi, S., Nishiyama, Y., & Allakhverdiev, S. I. (2007). Photoinhibition of photosystem II under environmental stress. *Biochimica Et Biophysica Acta - Bioenergetics*, *1767*(6), 414–421. https://doi.org/10.1016/j.bbabio.2006.11.019

Nunes, F. L. D., Norris, R. D., & Knowlton, N. (2009). Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. *Molecular Ecology*, *18*(20), 4283–4297. https://doi.org/10.1111/j.1365-294X.2009.04347.x

Oey, L., Ezer, T., & Lee, H. (2005). In W. Sturges, & A. Lugo-Fernandez (Eds.), *Circulation in the Gulf of Mexico: Observations and models* (Vol. *161*, pp. 31–56). Washington, D.C.: American Geophysical Union. https://doi.org/10.1029/161GM04

Ogle, D. (2017). *FSA: Fisheries stock analysis*. R Package Version 0.8.17.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R., Wagner, H. (2015). *vegan: community ecology package*. R package version 2.0-10.

Oomen, R. A., & Hutchings, J. A. (2017). Transcriptomic responses to environmental change in fishes: Insights from RNA sequencing. *Facets*, *2*, 610–641. https://doi.org/10.1139/facets-2017-0015

Polato, N. R., Voolstra, C. R., Schnetzer, J., DeSalvo, M. K., Randall, C. J., Szmant, A. M., … Baums, I. B. (2010). Location-specific responses to thermal stress in larvae of the reef-building coral *Montastraea faveolata*. *PLoS One*, *5*(6), e11221. https://doi.org/10.1371/journal.pone.0011221

Polinski, J. M., & Voss, J. D. (2018). Evidence of adaptation to mesophotic depths in the coral-*Symbiodinium* symbiosis at Flower Garden Banks National Marine Sanctuary and McGrail Bank. *Coral Reefs*, *37*(3), 779–789. https://doi.org/10.1007/s00338-018-1701-2

R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Reed, J. K. (1985). Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. Proceedings of the 5th International Coral Reef Congress, Tahiti, Vol. *6*, 249–254.

Reed, J. K., Farrington, S., David, A., Harter, S., Pomponi, S. A., Diaz, M. C., Hanisak, M. D. (2019). Pulley Ridge, Gulf of Mexico, USA. In Y. Loya (Ed.), *Coral Reefs of the World* (Vol. *12*, pp. 57–69). New York: Springer. https://doi.org/10.1007/978-3-319-92735-0

Reyes-Bermudez, A., DeSalvo, M. K., Voolstra, C. R., Sunagawa, S., Szmant, A. M., Iglesias-Prieto, R., & Medina, M. (2009). Gene expression microarray analysis encompassing metamorphosis and the onset of calcification in the scleractinian coral *Montastraea faveolata*. *Marine Genomics*, *2*(3–4), 149–159. https://doi.org/10.1016/j.margen.2009.07.002

Schmahl, G. P., Hickerson, E. L., & Precht, W. F. (2008). In B. M. Riegl, & R. E. Dodge (Eds.), *Coral Reefs of the USA* (Vol. *1*, pp. 221–261). Dordrecht: Springer. https://doi.org/10.1007/978-1-4020-6847-8_6

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2016). Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? *Coral Reefs*, *36*(2), 433–444. https://doi.org/10.1007/s00338-016-1530-0

Seneca, F. O., Forêt, S., Ball, E. E., Smith-Keune, C., Miller, D. J., & van Oppen, M. J. H. (2010). Patterns of gene expression in a scleractinian coral undergoing natural bleaching. *Marine Biotechnology*, *12*(5), 594–604. https://doi.org/10.1007/s10126-009-9247-5

Seneca, F. O., & Palumbi, S. R. (2015). The role of transcriptome resilience in resistance of corals to bleaching. *Molecular Ecology*, *24*(7), 1467–1484. https://doi.org/10.1111/mec.13125

Slattery, M., & Lesser, M. P. (2012). *Mesophotic coral reefs: A global model of community structure and function*. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, Vol. *1*, 9–13.

Slattery, M., Lesser, M. P., Brazeau, D. A., Stokes, M. D., & Leichter, J. J. (2011). Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, *408*, 32–41. https://doi.org/10.1016/j.jembe.2011.07.024

Strader, M. E., Aglyamova, G. V., & Matz, M. V. (2016). Red fluorescence in coral larvae is associated with a diapause-like state. *Molecular Ecology*, *25*(2), 559–569. https://doi.org/10.1111/mec.13488

Studivan, M. S. (2020a). mstudiva/Mcav-Cladocopium-Annotated-Transcriptome: Final *Montastraea cavernosa/Cladocopium* spp. transcriptome assembly (Version 2.0.0). Zenodo. https://doi.org/10.5281/zenodo.3728261

Studivan, M. S. (2020b). *mstudiva/Transcriptional-plasticity-mesophotic-Mcav: Final Tag-Seq scripts for analysis of mesophotic Montastraea cavernosa (Version 2.0.0)*. Zenodo. https://doi.org/10.5281/zenodo.3728281

Studivan, M. S., Milstein, G., & Voss, J. D. (2019). *Montastraea cavernosa* corallite structure demonstrates distinct morphotypes across shallow and mesophotic depth zones in the Gulf of Mexico. *PLoS One*, *14*(3), e0203732. https://doi.org/10.1371/journal.pone.0203732

Studivan, M. S., & Voss, J. D. (2018). Population connectivity among shallow and mesophotic *Montastraea cavernosa* corals in the Gulf of Mexico identifies potential for refugia. *Coral Reefs*, *37*(4), 1183–1196. https://doi.org/10.1007/s00338-018-1733-7

Studivan, M. S., & Voss, J. D. (2020). Data from: Transcriptional plasticity of mesophotic corals among natural populations and transplants of *Montastraea cavernosa* in the Gulf of Mexico and Belize. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.73n5tb2t8

Todd, E. V., Black, M. A., & Gemmell, N. J. (2016). The power and promise of RNA-seq in ecology and evolution. *Molecular Ecology*, *25*, 1224–1241. https://doi.org/10.1111/mec.13526

Toulza, E., Shin, M.-S., Blanc, G., Audic, S., Laabir, M., Collos, Y., … Grzebyk, D. (2010). Gene expression in proliferating cells of the dinoflagellate *Alexandrium catenella* (Dinophyceae). *Applied and Environmental Microbiology*, *76*(13), 4521–4529. https://doi.org/10.1128/AEM.02345-09

Valiela, I. (1995). *Marine ecological processes*. New York, NY: Springer.

Voolstra, C. R., Sunagawa, S., Matz, M. V., Bayer, T., Aranda, M., Buschiazzo, E., … Medina, M. (2011). Rapid evolution of coral proteins responsible for interaction with the environment. *PLoS One*, *6*(5), e20392. https://doi.org/10.1371/journal.pone.0020392

Warner, M. E., Chilcoat, G. C., McFarland, F. K., & Fitt, W. K. (2002). Seasonal fluctuations in the photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral *Montastraea*. *Marine Biology*, *141*, 31–38. https://doi.org/10.1007/s00227-002-0807-8

Whitehead, A., & Crawford, D. L. (2006a). Neutral and adaptive variation in gene expression. *Proceedings of the National Academy of Sciences*, *103*(14), 5425–5430. https://doi.org/10.1073/pnas.0507648103

Whitehead, A., & Crawford, D. L. (2006b). Variation within and among species in gene expression: Raw material for evolution. *Molecular Ecology*, *15*, 1197–1211. https://doi.org/10.1111/j.1365-294X.2006.02868.x

Wilkerson, F. P., Muller-Parker, G., & Muscatine, L. (1983). Temporal patterns of cell division in natural populations of endosymbiotic algae. *Limnology and Oceanography*, *28*(5), 1009–1014. https://doi.org/10.4319/lo.1983.28.5.1009

Wright, R. M., Correa, A. M. S., Quigley, L. A., Santiago-Vázquez, L. Z., Shamberger, K. E. F., & Davies, S. W. (2019). Gene expression of endangered coral (*Orbicella* spp.) in the flower garden banks national marine sanctuary after hurricane Harvey. *Frontiers in Marine Science*, *6*, 672. https://doi.org/10.3389/fmars.2019.00672

Ziegler, M., Roder, C. M., Büchel, C., & Voolstra, C. R. (2015). Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. *Frontiers in Marine Science*, *2*, 4. https://doi.org/10.3389/fmars.2015.00004

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Studivan MS, Voss JD. Transcriptomic plasticity of mesophotic corals among natural populations and transplants of *Montastraea cavernosa* in the Gulf of Mexico and Belize. *Mol Ecol*. 2020;29:2399–2415. https://doi.org/10.1111/mec.15495