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Assessing the Diversity of Benthic Sulfate-Reducing Microorganisms in Northwestern Gulf of Mexico by Illumina Sequencing of *dsrB* Gene

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Abstract

This study investigates the community composition, structure, and abundance of sulfate-reducing microorganisms (SRM) in surficial sediments of the Northwestern Gulf of Mexico (NWGoM) along a bathymetric gradient. For these purposes, Illumina sequencing and quantitative PCR (qPCR) of the dissimilatory sulfite reductase gene beta subunit (*dsrB* gene) were performed. Bioinformatic analyses indicated that SRM community was predominantly composed by members of *Proteobacteria* and *Firmicutes* across all the samples. However, *Actinobacteria*, *Thermodesulfobacteria*, and *Chlorobi* were also detected. Phylogenetic analysis indicated that unassigned *dsrB* sequences were related to Deltaproteobacteria and Nitrospirota superclusters, *Euryarchaeota*, and to environmental clusters. PCoA ordination revealed that samples clustered in three different groups. PERMANOVA indicated that water depth, temperature, redox, and nickel and cadmium content were the main environmental drivers for the SRM communities in the studied sites. Alpha diversity and abundance of SRM were lower for deeper sites, suggesting decreasing sulfate reduction activity with respect to water depth. This study contributes with the understanding of distribution and composition of *dsrAB*-containing microorganisms involved in sulfur transformations that may contribute to the resilience and stability of the benthic microbial communities facing metal and hydrocarbon pollution in the NWGoM, a region of recent development for oil and gas drilling.

Keywords Gulf of Mexico · Sulfate-reducing microorganisms · *dsrB* gene · Illumina sequencing · qPCR

Introduction

Biological sulfate reduction to sulfide is a crucial step in the global sulfur, carbon, and metal cycles, particularly in marine sediments where sulfate is the main anaerobic oxidant [1–3]. This metabolism is mediated by the ubiquitous sulfate-reducing microorganisms (SRM) that dominate the anaerobic steps in the mineralization processes of sulfate-rich marine

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sediments, oxidizing as much organic matter to CO_2 as aerobic microorganisms [4, 5]. This specialized functional guild constitutes a phylogenetically and physiologically diverse group of anaerobes that mainly use sulfate as a terminal electron acceptor to oxidize several organic substrates or hydrogen, in a dissimilatory pathway resulting in sulfide as the end product [6].

Dissimilatory (bi)sulfite reductase enzyme (*DsrAB* enzyme) catalyzes the transformation of sulfite to sulfide, the last step in the dissimilatory sulfate reduction pathway (DSR). These enzymes, and the *dsrAB* genes that encode it, are conserved in all SRM and these are distributed in six bacterial (*Proteobacteria*, most within the class *Deltaproteobacteria*, *Nitrospirota*, *Firmicutes*, *Actinobacteria*, *Caldiserica*, *Thermodesulfobacteria*) and three archaeal phyla (*Euryarchaeota*, *Crenarchaeota*, *Aigarchaeota*) [2, 6, 7]. However, the genetic capacity for sulfate/sulfite reduction was recently discovered in other microbial genomes, expanding the number of microbial phyla associated with this process. For instance, *Chloroflexi* (e.g., *Dehalococcoidia*), *Verrucomicrobia*, Candidatus *Rokubacteria*, Candidatus *Hydrothermarchaeota*, and *Euryarchaeota* (e.g., *Diaforarchaea*) are some phyla that contain *dsrAB* genes [8–10]. The taxonomic distribution of *dsrAB* genes may reflect different microbial lifestyles and versatile metabolisms to survive under different environmental conditions [11].

The characterization of environmental SRM through 16S rRNA gene-based analyses has been difficult because SRM belong to different and distant lineages, and are often related to non-SRM [12, 13]. Instead, comparative analyses of the dissimilatory sulfite reductase (*dsrAB*) genes amplicon sequences are more accurate for this purpose [12]. The highly conserved *dsrAB* genes are in general organized in a single-copy operon [12, 14, 15]. These genes encode for the α and β subunits of the enzyme that catalyzes the transformation of sulfite to sulfide, the last step in the DSR pathway, and thus, they are present in all SRM. For these reasons, *dsrAB* genes have been frequently used to infer the evolutionary history, and to characterize and enumerate SRM in different environments [2, 16–22]. The combination of high-throughput sequencing and quantitative PCR (qPCR) of the *dsrAB* genes has provided comprehensive information about abundance and composition of SRM in marine environments [23]. Moreover, this approach has been identified to be a powerful approach for comparative analyses of SRM communities [23].

In the Gulf of Mexico (GoM), a large set of geochemical and isotopic data from the Deep-Sea Drilling Project gave the first indications of the importance of sulfate reduction (SR) in marine sediments [24] and the variables controlling this process, such as the organic sources, water depth, and sediment deposition rates [25]. Once SR was recognized as one of the dominant microbial processes in marine sediments mainly associated with seep environments [26, 27], several studies investigated the corresponding microbial taxonomy diversity [28–30]. The results indicated that SRM were involved in the degradation of simple hydrocarbons, suggesting that labile organic matter is an important factor shaping SRM diversity and activity in marine sediments [28–30]. After the significant amount of oil was released by the Deepwater Horizon (DWH) blowout in 2010, laboratory studies have demonstrated that SRM families within the *Deltaproteobacteria* are involved in the anaerobic hydrocarbon degradation in oil-polluted sediments [31–33]. PCR-dependent molecular analyses have recognized the importance in oil-polluted sedimentary environments, particularly in the Northern GoM [19, 33–37]. However, more information about SRM diversity, distribution, and the potential environmental factors related with them are needed for this region. Thus, the aim of the present study was the characterization of SRM communities in sediments spanning across the continental shelf and slope down to the abyssal zone in terms of geochemical variables influencing their abundance and composition.

Methods

Sample Collection

In May 2016, 23 soft-bottom sediment samples were collected using a 0.50 m^2 Hessler-Sandia box corer from four transects (A, B, C, and D) located perpendicular to the coastline in the NWGoM (Fig. 1). Sediment samples (one from each sampling site) were collected in a depth gradient from 44- to 3548-m water depth (Table 1). Immediately after collection, pH and redox potential were measured directly on the sediment samples using an Extech pH 100 probe and an Extech RE300 probe, respectively (MA, USA). A sediment subsample of the uppermost 10 cm of the sediment layer was collected with sterile syringes with cut-off tips and frozen at − 20 °C for later DNA extraction. Another subsample of 400 g of sediment for total organic carbon (TOC), organic matter (OM), and grain-size was collected and frozen at − 4 °C until lab analysis. An extra sample was collected for heavy metal determinations and stored in plastic bags after being washed with a 1N HNO_3 (Sigma-Aldrich pure grade) solution and deionized water. To determine the total hydrocarbon (THC) concentration, sediment subsample (100 g) was stored in glass containers previously washed with hexane and acetone (both Sigma-Aldrich chromatographic grade). Both samples were kept at 4 °C until analysis.

Physicochemical Properties Analyses from Marine Sediments

Sediment TOC% and OM% were determined following the Walkley-Black [38] titration method by using potassium

Table 1 Physicochemical variables of the bottom water and surface sediments, alpha diversity estimators, and *dsrB* gene abundance

Sample	Depth*	Temp.*[a]	DO[a]	pH[b]	Redox*[b]	TOC[b]	OM[b]	MS[b]	FS[b]	VFS[b]	V[b]	Ni*[b]	Cd*[b]	Pb[b]	THC[b]	ASVs[b]	*H'*[b]	*dsrB* gene[b]
A1	50.4	25.1	4.1	7.5	195.8	1.1	1.9	43.3	39.8	16.9	60.3	15.3	0.1	19.5	18.8	2253	7.6	5.5
A2	97.6	21.4	2.9	7.3	50.5	0.4	0.6	37.2	52.1	10.7	64.4	16.3	0.1	23.2	10	1289	7	6.1
A3	372.5	9.4	2.4	7.3	− 118.2	0.3	0.5	46.1	38.2	15.6	84.5	24.8	0.2	28.2	7.9	926	6.7	5.3
A4	1000	8.3	2.5	7.2	164.3	0.3	0.6	41.4	52.9	5.6	44.3	17.7	0.2	11.2	21.9	459	6	4.8
A5	1448	4.4	4.5	7.1	228.7	0.6	1.1	38.5	51.2	10.3	82.2	31	0.2	19.9	7.3	249	5.4	3.8
A6	1998	4.3	4.6	7.7	245.7	0.5	0.9	24.4	69.9	5.7	71.6	25.5	0.2	18.3	7.3	67	4	4.3
B1	47	26.8	4.6	7.2	− 125.4	0.9	1.6	89.6	8.5	1.9	70.7	18.1	0.2	24.5	11.7	873	6.6	5.6
B2	105.8	22.6	4.2	7.3	− 169.6	0.5	0.9	31.1	57.2	11.8	72.5	18.6	0.2	26.7	8.4	816	6.6	6.4
B3	503.8	5.4	3.6	7.3	− 132.2	0.2	0.4	33.6	55.3	11.2	50.7	14.7	0.1	17.7	7.6	692	6.4	5.4
B4	1065.7	5.1	3.8	7.3	264.7	0.1	0.2	46.4	32.2	21.4	87.8	30	0.3	27.1	6.5	530	6.2	5.3
B5	1971	4.3	4.7	7	241.7	0.3	0.4	25.9	62.7	11.4	86.7	30.7	0.3	24.2	14.7	696	6.5	4.2
B6	2676.8	4.3	4.6	7.3	237	0.1	0.2	29.3	54	16.6	90.4	28.4	0.2	20.8	15.3	955	6.7	5.7
C1	44	25	4.6	7.4	− 107.5	0.1	0.2	26.8	39.2	33.9	82.4	21.1	0.2	28.8	8.9	1035	6.8	6.3
C2	107	21.3	3.2	7.4	− 134.3	0.2	0.4	32.5	47.3	20.2	91.8	23	0.2	32.8	7.3	962	6.7	6.2
C3	473.4	9.5	2.4	7.5	− 112.1	0.1	0.2	32	48.9	19.1	84.4	23.5	0.2	31.6	9.7	682	6.4	5.2
C4	826	6.1	3.2	7.3	− 129	0.2	0.3	64.6	29.4	6	77.2	19.7	0.2	28.9	11.5	1513	7.2	5.7
D1	48.1	25	4.1	7.1	− 121.9	0.1	0.1	23.5	49.9	26.6	65.7	16.1	0.2	25.2	15	1976	7.4	6.1
D2	93	20.4	2.8	7.5	− 72.7	0.4	0.6	30.6	51.2	18.3	79.8	20.1	0.2	31.4	10.3	1109	6.9	4.7
D3	537	2.7	2.4	7.4	− 86.8	0.6	1.1	32.2	58.5	9.3	88.4	22.8	0.3	34.3	6.2	879	6.6	4.7
D4	1616	4.3	4.6	7	248.3	0.2	0.3	45.4	46.1	8.5	86.8	30.8	0.3	26.7	3.4	114	4.6	3.4
D5	1760	4.3	4.6	7.2	236.3	0.4	0.8	29.8	57.7	12.5	90.5	33.7	0.3	22.8	4.6	51	3.8	3.7
D6	3254.7	5.1	4.6	7	228.3	0.5	0.8	62.6	33.5	3.9	86.1	28.7	0.2	25.3	16.2	55	3.9	4.6
D7	3548	4.4	4.6	7.3	238.3	0.4	0.6	17.4	68.1	14.4	89.6	31.8	0.2	20.3	10.6	35	3.4	3.9

Depth, water depth (m); *Temp.*, temperature (°C); DO, dissolved oxygen (mg/L); Redox, redox potential (mV); TOC, total organic carbon (%); OM, organic matter (%); MS, medium sands (%); FS, fine sands (%); VFS, very fine sands (%). Heavy metals in mg/kg: V, vanadium; Ni, nickel; Cd, cadmium; Pb, lead. THC, total hydrocarbons (mg/kg). ASVs, alpha diversity estimators as the observed ASVs; *H'*, Shannon diversity value. *dsrB* (log10 of gene copies per gram of wet sediment weight), *dsrB* gene

*Environmental variables related to changes in the community structure of sulfate reducing microorganisms p value < 0.05

[a] Measured from bottom waters

[b] Environmental variables applied to surface sediments

dichromate and carbonates were acidified by using 0.1 N hydrochloric acid and back titration with 0.3 M sodium hydroxide. Sand grain structure was obtained by weighting the retained grains at different mesh sizes (2 mm, 500 μm, 250 μm, 125 μm, 63 μm) and compared according to the Wentworth [39] grain size classification. Temperature (°C), salinity (PSU), and dissolved oxygen concentration (DO mL L^{-1}) of the bottom water were recorded in situ using a CTD Seabird 9 plus®. Thermocline and oxycline were detected around 50-m depth in the water column.

Determination of Heavy Metals and Total Hydrocarbon Concentration

Heavy metal concentration was obtained following Loring and Rantala [40] and Arcega-Cabrera et al. [41] techniques. Sediment samples were freeze-dried using a freeze dryer (LABCONCO FreeZone 2.5), for microwave-assisted acid digestion (CEM MARS 6) from 0.5 g of the sample that was placed in a Teflon vessel with 9 mL of HNO_3 (EMSURE ACS 60%), 3 mL of HF (EMSURE suprapur), and 1 mL of HCl (EMSURE suprapure). Quantification of metal concentration (Cd, Ni, V and Pb) was done using an ICP-MS (Mod. iCAP Q Thermo Scientific) with the ions V51, Ni60, Cd112, and Pb208. For quality analysis, SRM 2702 (NIST) was used, recovery percentage (%) and limit of detection (mg/g) were as follows: for V51, 88% and 0.0043 mg/g, for Ni60, 96% and 0.0001 mg/g, for Cd112 86% and 0.0039 mg/g, and for Pb208, 80% and 0.2066 mg/g.

For hydrocarbons analysis, freeze-dried sediment samples were sieved through a 0.5-mm mesh and placed in an ASE 350 Dionex Thermo pressurized solvent extractor at 1500 psi using DCM (dichloromethane GC grade). Hydrocarbon elution was done with TEDIA hexane GC grade (15 mL) and for

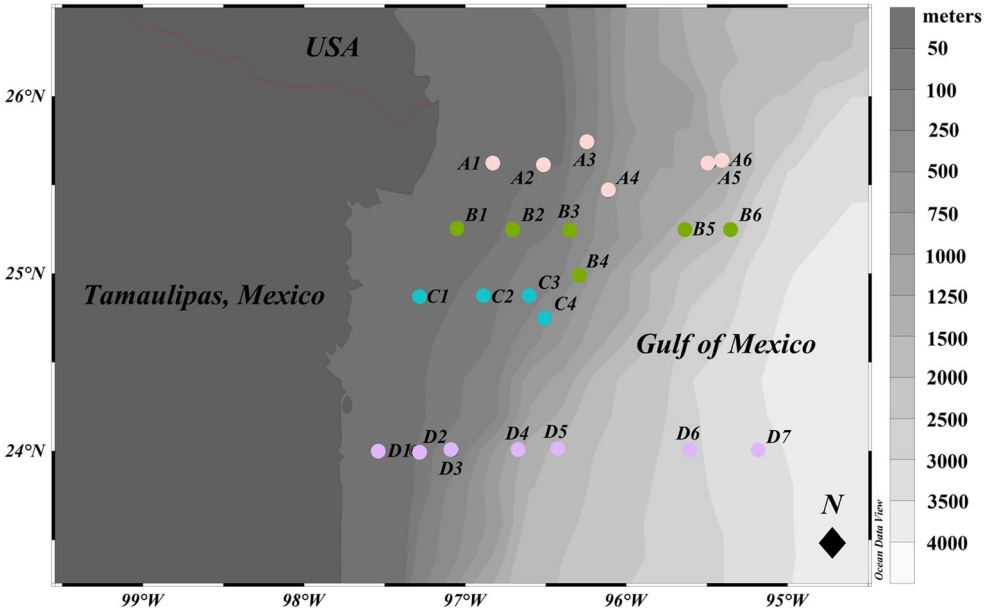


Fig. 1 Sampling stations in four transects (A–D) extended along the continental shelf toward the bathyal region in the Northwestern Gulf of Mexico

the second fraction, a 50:50 v/v TEDIA hexane GC grade and TEDIA DCM (15 mL) were used. Samples were added with a subrogated solution of deuterated PAHs (1-3 dimethyl-2 nitrobenzene, acenaphthene δ10, phenanthrene δ10, pyrene δ10, triphenyl phosphate, chrysene δ10, and perylene δ10 from UltraScientific). Also, the o-terphenyl (Supelco) was used as an internal standard. Compounds were analyzed using a gas chromatography with a flame ionization detector (GC-FID Agilent-7890A) and with a mass spectrometer (GC-MS Perkin Elmer-Clarus 500). Chromatographic conditions were as follows: GC-FID and GC-MS had an injector and oven temperature of 290 °C and 50 °C, respectively, a column type of 5% phenyl methyl siloxane (30 × 0.25 × 25) and a carrying gas of UHP Nitrogen. Detector temperature and ramp for GC-FID were 300 °C and 6 °C /min, respectively, and for GC-MS were 180 °C and 25 °C/min–160 °C and 8 °C/290 °C, respectively.

Environmental DNA Extractions

Sediment samples were thawed and centrifuged 1 min at 10,000×*g* to discard the remaining water and extract DNA from the settled microbial cells. Total DNA was extracted from 1 g of each sediment sample using the DNeasy PowerSoil Kit (QIAGEN, Gilden, Germany) following the manufacturer's protocol. All the extracted DNAs were stored at − 20 °C for subsequent Illumina sequencing and qPCR procedure.

dsrB Illumina Sequencing from Environmental Sediment Samples

Barcoded *dsrB* amplicons for Illumina sequencing were prepared from the extracted DNA by using the two-step PCR protocol (Illumina). In the first PCR, approximately 440 bp of the *dsrB* gene were amplified with the primer set DSR1762F1/DSR2107R1 including the Illumina sequencing adapters [42]. The first-step PCR program was performed in a "touch-down" mode with an initial denaturation at 95 °C for 3 min, followed by 35 cycles of 30-s denaturation at 95 °C, 30-s annealing at 60–50 °C (the temperature decreased by 1 °C per cycle during the first 10 cycles) and elongation for 1 min at 72 °C, and a final elongation step at 72 °C for 10 min. Each PCR reaction mixture (20 μL) included 1 μL of DMSO (5%), 1 μL of each primer (0.5 mM), 10 μL of 2x Phusion High-Fidelity MasterMix (Thermo Scientific, USA), and 2 μL of the DNA template (~ 10 ng/μL).

For the second PCR, dual indices were attached during eight cycles by using the Nextera XT Index Kit. Individual barcoded amplicons were diluted and purified in 10 mM Tris (pH 8.5) and pooled at 9 pM equimolar concentration. Paired-end sequencing was performed in a MiSeq platform (Illumina, San Diego, CA, USA) with a MiSeq Reagent Kit V3 (2x250 cycles) at CINVESTAV-Merida, Mexico.

Quantification of *dsrB* Gene by qPCR

The quantification of the *dsrB* gene copies was carried out by qPCR with the primers DSRp2060F/DSR4R recommended by He and colleagues [43] using the SYBR Green method. These primers were selected due to their detection range of SRM [44], as shown in previous studies [23, 43]. The qPCR conditions included an initial denaturation at 94 °C for 15 min, 40 cycles of 30 s at 94 °C, 20 s at 60 °C, and 30 s at 72 °C. Each reaction of 12.5 μL contained 0.5 μL of each primer (0.4 mM), 6.5 μL Quantinova SYBR Green PCR Kit (Qiagen, Hilden, Germany), and 1 μL of the template (normalized to

1 ng μL^{-1} DNA). Data acquisition was performed in the PCR extension step, and the amplification specificity was verified by melting curve analysis (from temperature 72–98 °C with a 1 °C hold for 5 s) and on 1% agarose gels for visualization. Standard curves were obtained from 10-fold serial dilutions of a plasmid containing the *dsrB* gene and were linear within a range of 10 to 10^7 target gene copies per μL^{-1} template, with an efficiency of 101% and $R^2 = 0.99$.

Bioinformatics Processing and Data Analyses

The Illumina paired-end reads (2x250) were processed with QIIME2 (version 2019.10) [45]. After manual inspections, forward and reverse reads were trimmed in position 25 in the 5′ end and truncated in position 240 and 160 at the 3′ end, respectively. The amplicon sequences variants (ASVs) were resolved with the DADA2 plugin [46], removing chimeras with the "consensus" method.

The representative sequences of ASVs were analyzed with the DIAMOND software [47], using its blastx algorithm to compare the ASVs with the RefSeq protein database from NCBI, with the arguments: *e*-value < 0.0003 and "–sensitive". The DIAMOND output was imported to the MEGAN6 software [48]. With the aim to identify and annotate the ASVs that correctly codes to the dissimilatory sulfite reductase beta subunit (EC 1.8.99.3) protein, we mapped the MEGAN output file to the SEED metabolic annotation categories through the mapping file "acc2seed" with a min percent identity: 50 and the other LCA parameters as default. The ASVs that were not annotated as this protein were removed. The filtered ASVs were taxonomically assigned using the LCA classifier of MEGAN6, using the taxonomic classification from the NCBI (with the "prot_acc2tax" mapping file). With the following parameters to the LCA: min score 50; max expected 3.0E-4; min percent identity 50; top percent 60, and percent to cover 60 with the read assigned mode as "alignedBases." The classification was filtered, pruning out the taxonomic levels with a taxa path percent score < 50%, or marking it as an "ambiguous" level by an asterisk.

The classification and the ASV abundance table were exported to the R environment (version 3.6.0) to carry out the diversity and statistical analysis with the phyloseq [49] and vegan [50] packages. ggplot2 [51] was used for graphic visualizations.

The Shannon alpha diversity index was calculated. A principal coordinate analysis (PCoA) was calculated with the Bray-Curtis distance matrix. To identify the optimal number of sample clusters, a gap statistical analysis was carried out on the ordination with the cluster packages, using the clusGap function with "pam1" and 1000 bootstraps. The significant variables and clusters were tested with a PERMANOVA analysis at a p value < 0.05. A Linear discriminant analysis Effect Size (LEfSe) [52] was carried out to identify the ASVs with significant differential abundance between clusters. The Spearman correlation analysis between alpha diversity, *dsrB* gene abundance, and environmental variables was computed in R.

In order to gain insights into the phylogenetic relationship of the *dsrB* sequences with no taxonomic assignment at the family level, a phylogenetic analysis was carried out. Briefly, 3950 unassigned ASVs at the family level were clustered in operational taxonomic units at 90% similarity using the V-SEARCH algorithm [53], resulting in 1178 OTUs. An alignment with 1292 *dsrB* reference sequences [42] and all the query OTUs was performed with the Mafft algorithm [54]. The alignment was trimmed with the GBlocks algorithm [55]. ModelTest-NG software [59] was used to select the evolutionary model from the alignment. The phylogenetic tree was computed using RAxML software [56], using the model "GTRGAMMAIX" selected by ModelTest. The resulting phylogenetic tree contained 1292 tips from the reference database and 1178 tips from query OTUs. The phylogenetic tree (Fig. 4) was edited by the i-TOL online tool (http://itol.embl.de/) [57].

Raw input files used in this study are available in the Online Resources 7–14. Raw sequence data were deposited in NCBI under the Bioproject accession number PRJNA626626.

Results

Physicochemical Determinations for Site Description

Surficial sediments had pH values from 7.01 to 7.71 (7.29 ± 0.17). Redox potential was from − 169.6 to 264.67 mV (55.21 ± 176.32), from which most electronegative values were observed in sites < 1000-m water depth, with the exception of samples B1 and B2, which had electropositive redox values (Table 1). TOC and OM contents were 0.37 ± 0.26 and 0.65 ± 0.44, respectively; and the percentage of MS, FS, and VFS were 38.44 ± 16.03%, 48 ± 13.73%, and 13.56 ± 7.56%, respectively (Table 1). Heavy metals concentrations were as follows: Ni 23.6 ± 6.1 mg/kg, Cd 0.21 ± 0.1 mg/kg, V 77.8 ± 13.21 mg/kg, Pb 24.46 ± 5.1 mg/kg, and THC were 10.48 ± 4.63 mg/kg (Table 1). Finally, temperature in near-bottom waters varied from 26.8 to 2.7 °C (11.7 ± 9) and the DO concentration was between 2.4 and 4.66 mL L^{-1} (3.81 ± 0.88) (Table 1). Oxic conditions (> 2–~ 4 mL L^{-1}) were detected throughout the water column, with the oxycline occurring around 50-m depth. The detection of saturated oxygen ranged between 0 and 20 mL L^{-1}.

Community Structure and Abundance of SRM in Marine Sediments

Differences in the community structure of SRM were visualized with a PCoA ordination method on the Bray-Curtis

dissimilarity matrix (Fig. 2). PCoA ordination and PERMANOVA test revealed that SRM communities grouped into three significantly different clusters (R^2 = 0.28, $F_{2, 23}$ = 3.86, p value = 0.001) (Fig. 2). Samples in cluster I (A1, A2, B1, B2, C1, C2, D1, and D2) were collected at a water depth range from 44 to 107 m; samples in cluster II (A3, B3, B5, B6, C3, C4, and D3) were collected at a water depth range from 372.5 to 2676.8 m; and samples in cluster III (A4–A6, B4, and D4–D7) were collected at a water depth range from 1000 to 3548 m (Table 1; Fig. 2).

The differential abundance analysis of the community composition exhibited SRB whose relative abundances differed statistically (p value < 0.05) between clusters I, II, and III (Online Resource 1). Among the assigned ASVs with differential abundance, genus *Desulfovibrio* notably accounted for most of the ASVs, with a larger representation in samples in clusters I and II in comparison to samples in cluster III (Online Resource 1). ASVs with differential abundances and low similarity scores (< 50%) were indicated as ambiguous assignments (Online Resource 1).

PERMANOVA indicated that the differences in the community structure of SRM were significantly (p < 0.05) related to temperature ($F_{1, 23}$ = 4.15, R^2 = 0.2), water depth ($F_{1, 23}$ = 2.7, R^2 = 0.11), Ni ($F_{1, 23}$ = 2.3, R^2 = 0.1), redox ($F_{1, 23}$ = 2.2, R^2 = 0.1), and Cd ($F_{1, 23}$ = 2.1, R^2 = 0.1).

SRM communities in cluster III had lower diversity than samples in clusters I and II. Spearman correlation indicated positive correlations between the alpha diversity and temperature, while there was a significant negative relationship with depth, redox, and the content of Ni and Cd (Online Resource 6). The lowest abundance of SRM communities, determined by qPCR analyses of the *dsrB* gene, was also in the sediment samples from cluster III (Table 1).

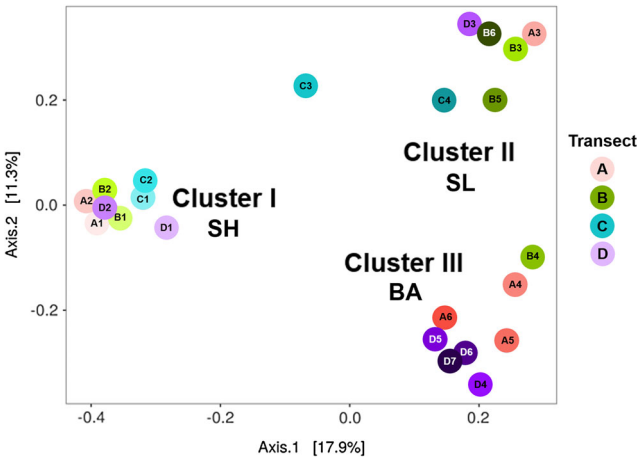


Fig. 2 Dissimilarity community structure of sulfate-reducing microorganisms visualized by a PCoA ordination method. Samples are displayed according to the Bray-Curtis dissimilarity matrix. Cluster I, sediment samples collected from 44 to 107 m water depth; cluster II, sediment samples collected from 372.5- to 2676.8-m water depth; cluster III, sediment samples collected between 1000- and 3548-m water depth. Color saturation is according to water depth of the samples in each transect. Lighter tones represent shallow sites while darker tones indicate deep sites

Composition of Sulfate-Reducing Microbial Communities

Sulfate-reducing microbial communities were dominated of the phyla *Proteobacteria* and *Firmicutes* across all the sediment samples. However, *Actinobacteria*, *Thermodesulfobacteria*, and *Chlorobi* were also detected for all depths (Online Resource 3). The communities were predominantly composed by members of the families *Peptococcaceae*, *Desulfovibrionaceae*, and *Desulfobacteraceae* (Fig. 3). At the family level, approximately 30% of the ASVs, coding for the *dsrB* gene, corresponded to unassigned sequences. Genera *Desulfotomaculum* and *Desulfosporosinus*, from *Peptococcaceae*, and *Desulfovibrio*, from *Desulfovibrionaceae*, were consistently detected for all depths (Fig. 3; Online Resource 5).

Phylogenetic analysis indicated that unassigned *dsrB* sequences were related to *Deltaproteobacteria* supercluster (253 OTUs), *Nitrospirota* supercluster (238 OTUs), and with the archaeal phyla *Euryarchaeota* (12 OTUs) (Fig. 4). However, most of these sequences (556 OTUs) were related to environmental clusters, including the Environmental supercluster 1 and several others indicated as reductive bacterial type *dsrAB* sensu lato. Interestingly, 13 environmental lineages (93 OTUs) were not affiliated with members of described taxonomic groups; these were found to contain *dsrB* sequences exclusively from this study (GoM groups 1 to 13). Moreover, some other sequences showed phylogenetic relation with the oxidative bacterial type (Fig. 4).

Discussion

SRM Community Composition in NWGoM Sediments

SRM communities from all the samples analyzed in this study were predominantly composed of *Desulfovibrio* and *Desulfotomaculum* (*Proteobacteria* and *Firmicutes*, respectively) (Online resource 3 and 5). *Desulfovibrio* has been reported as the dominant taxa in coastal sediments [58] and also has been found in deep marine sediments [59, 60], while *Desulfotomaculum* species have been identified from estuarine [61, 62], marine [63, 64], and low-sulfate habitats [65, 66]. These organisms have also been reported as dominant bacteria in petroleum reservoirs [67]. The broad distribution of these genera in onshore-offshore GoM sediments could be explained for their physiological and metabolic versatility [68, 69] and by dispersal processes of water mass circulation, which is predominantly influenced by anticyclonic eddies of

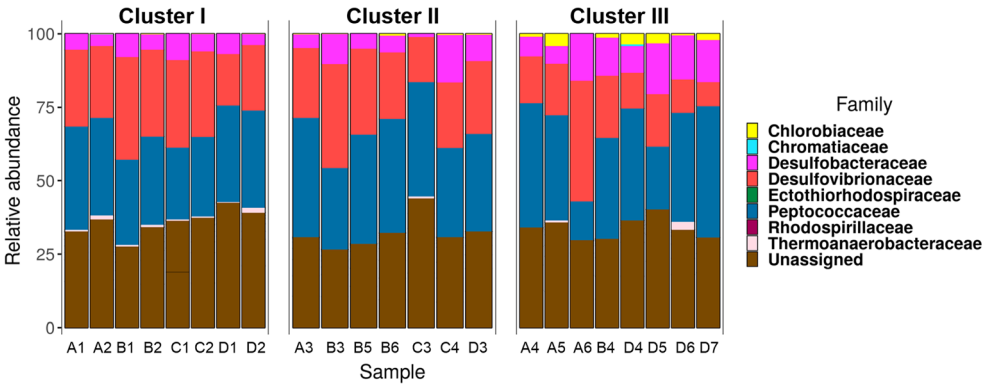


Fig. 3 Community composition of sulfate-reducing microorganisms at the family level in surficial sediments from the Northwestern Gulf of Mexico

warm water from the Loop Current that drift westward influencing the entire GoM [70, 71].

Differences in the community structure of SRM observed in the current study (Fig. 2) were related to unassigned *dsrB* sequences (Figs. 3 and 4; Online Resource 1). Phylogenetic analysis indicated that some OTUs were related to *Deltaproteobacteria* lineages, including complete (i.e., *Desulfoarculus baarsi*, *Desulfatiglans anilini*, and *Desulfomonile tiedejei*) and incomplete oxidizers (i.e., *Desulfobulbaceae*) [16, 72–74]. These taxa commonly use sulfate as an electron acceptor; however, some specific members have the ability to reduce other sulfur compounds and to gain energy from other mechanisms (i.e., thiosulfate dismutation) [73]. Nevertheless, these ecophysiological attributes, such as organic substrate oxidation, substrate utilization preferences, or mechanisms of energy conservation, were not assessed in the present work and it must be explored in further studies.

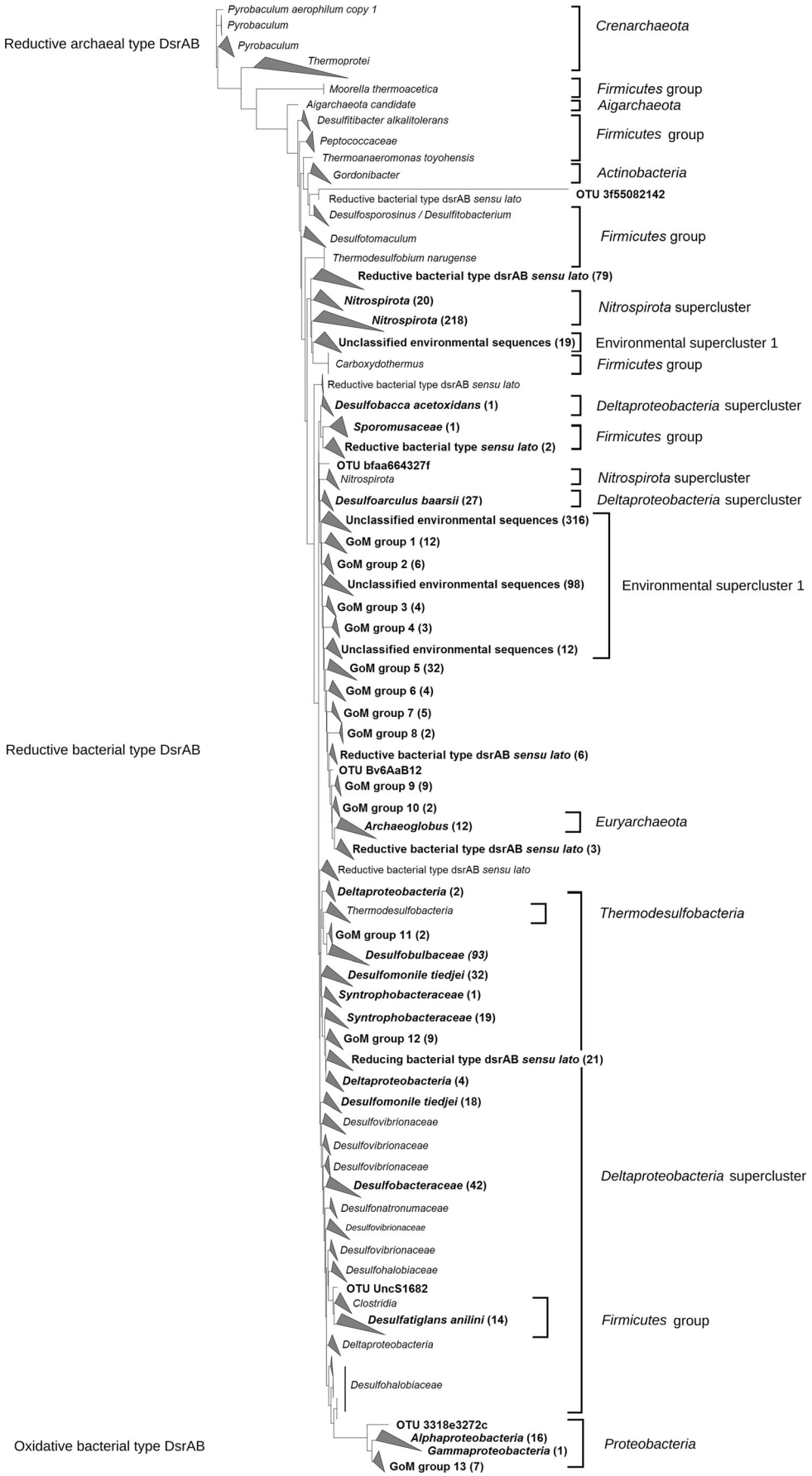
dsrB sequences related to *Nitrospirota* (formerly *Nitrospirae* or *Nitrospira*) and *Euryarchaeota* were also detected in this study (Fig. 4). These phyla include few cultured members and environmental sequences of *Thermodesulfovibrio* and *Archaeoglobus*, respectively. Some metagenome-assembled genomes (MAGs) have been done in *Thermodesulfovibrio*, and genes involved in dissimilatory sulfur metabolism have been identified in them. However, there is still no way to discriminate between sulfate-reducing and sulfur-disproportionating bacteria [75]. The analysis of *DsrAB* sequences in *Thermodesulfovibrio* and *Archaeoglobus* species has suggested that the presence of bacterial *dsrAB* genes in these organisms could be related to lateral gene transfer from a progenitor of the *Deltaproteobacteria* or from other SRM [7, 15]. Despite their thermophilic lifestyle [76–78], these microorganisms are commonly detected also in non-thermal marine environments [64, 79], as occurred in this work.

The phylogenetic analysis of the unassigned *dsrB* sequences also allowed the detection of environmental groups, composed solely by OTUs retrieved in this study (GoM groups 1 to 13; Fig. 4). These environmental groups may represent lineages from the GoM whose members are yet uncultured or not known to possess *dsrAB* genes, illustrating the still unexplored diversity of *dsrAB*-containing microorganisms in this region, as previously reported for other locations [7]. However, these did not meet a conservative criterion to consider them as uncultured family-level *dsrAB* lineages from the GoM and further studies need to be done.

Phylotypes related to sulfur-oxidizing bacteria (SOB) were also observed in this study forming a deep branching lineage clearly separated from the SRM (GoM group 13; Fig. 4). These phylotypes may represent sulfur oxidizers containing *dsrAB* genes in their genome. Previous studies have also detected *dsrAB* genes in SOB using primers for PCR amplification of reductive bacterial-type *dsrAB* sequences [7]. Other primers targeting *aprAB* and *soxAB* genes have been used as an alternative molecular marker to evaluate environmental SRM and SOB since these genes encode key enzymes for microbial sulfate reduction and sulfur oxidation processes [67, 80, 81]. Therefore, a better description of the diversity of SRM and SOB in the NWGoM could be addressed in further studies targeting other functional molecular marker genes (e.g., 16S rRNA, *dsr*, *sox*, *apr*).

SRM Communities and Environmental Variables

Although it has been reported that bottom-water oxygen levels may influence the sediment biochemistry [82] and the distribution and survival of SRM [83, 84], DO concentration in near-bottom waters was not related to SRM communities in the present study. According to the determined DO concentrations, oxic bottom-water conditions (> 2 mg L^{-1}) [85] were found in all the studied sites (Table 1), and it is congruent with previous reports for the region of the GoM [37, 86]. SRM are able to cope with the oxygen exposure from the overlying water by different strategies, such as oxygen tolerance, oxygen reduction, chemotactic behavior, or cell aggregates [83, 87–91]. Thus, the presence of oxygen in near-bottom waters does not appear to restrict the distribution of SRB in surficial sediments.


Reductive archaeal type DsrAB
Pyrobaculum aerophilum copy 1
Pyrobaculum
Pyrobaculum
Thermoprotei
Crenarchaeota
Moorella thermoacetica
Firmicutes group
Aigarchaeota candidate
Aigarchaeota
Desulfitibacter alkalitolerans
Peptococcaceae
Thermoanaeromonas toyohensis
Firmicutes group
Gordonibacter
Actinobacteria
OTU 3f55082142
Reductive bacterial type dsrAB sensu lato
Desulfosporosinus / Desulfitobacterium
Desulfotomaculum
Thermodesulfobium narugense
Firmicutes group
Reductive bacterial type dsrAB sensu lato (79)
Nitrospirota (20)
Nitrospirota (218)
Nitrospirota supercluster
Unclassified environmental sequences (19)
Environmental supercluster 1
Carboxydothermus
Firmicutes group
Reductive bacterial type dsrAB sensu lato
Desulfobacca acetoxidans (1)
Deltaproteobacteria supercluster
Sporomusaceae (1)
Reductive bacterial type sensu lato (2)
Firmicutes group
OTU bfaa664327f
Nitrospirota
Nitrospirota supercluster
Desulfoarculus baarsii (27)
Deltaproteobacteria supercluster
Unclassified environmental sequences (316)
GoM group 1 (12)
GoM group 2 (6)
Unclassified environmental sequences (98)
GoM group 3 (4)
GoM group 4 (3)
Unclassified environmental sequences (12)
GoM group 5 (32)
GoM group 6 (4)
GoM group 7 (5)
GoM group 8 (2)
Environmental supercluster 1
Reductive bacterial type DsrAB
Reductive bacterial type dsrAB sensu lato (6)
OTU Bv6AaB12
GoM group 9 (9)
GoM group 10 (2)
Archaeoglobus (12)
Euryarchaeota
Reductive bacterial type dsrAB sensu lato (3)
Reductive bacterial type dsrAB sensu lato
Deltaproteobacteria (2)
Thermodesulfobacteria
Thermodesulfobacteria
GoM group 11 (2)
Desulfobulbaceae (93)
Desulfomonile tiedjei (32)
Syntrophobacteraceae (1)
Syntrophobacteraceae (19)
GoM group 12 (9)
Reducing bacterial type dsrAB sensu lato (21)
Deltaproteobacteria (4)
Desulfomonile tiedjei (18)
Desulfovibrionaceae
Desulfovibrionaceae
Desulfovibrionaceae
Desulfobacteraceae (42)
Desulfonatronumaceae
Desulfovibrionaceae
Desulfovibrionaceae
Desulfohalobiaceae
Deltaproteobacteria supercluster
OTU UncS1682
Clostridia
Desulfatiglans anilini (14)
Firmicutes group
Deltaproteobacteria
Desulfohalobiaceae
OTU 3318e3272c
Alphaproteobacteria (16)
Gammaproteobacteria (1)
GoM group 13 (7)
Oxidative bacterial type DsrAB
Proteobacteria

◀ **Fig. 4** Phylogeny of *dsrB* amplicons. The phylogenetic tree was computed using RAxML software with the GTRGAMMAIX model. The phylogenetic tree contains 1292 tips from the reference database and 1178 tips from the query OTUs. Nodes were manually collapsed. Groups with *dsrB* sequences obtained from the current study are indicated in bold showing the number of OTUs in parenthesis. The image was generated using the Interactive Tree of Life (iTOL; http://itol.embl.de/)

Negative redox values found in shallow sediments (< 1000-m water depth) (Table 1) suggested reducing conditions for these sites. It is coherent with the oxygen depletion in the first few millimeters of the sediment layers in the continental margin sediments due to respiratory processes [92–94]. Nonetheless, positive redox values were also found in these sediments (Table 1) which could be attributed to sediment disturbance events that led to an influx of DO from the overlying water, resulting in a positive change in the redox condition, as it has been previously reported for shelf sediments [95, 96]. In these oxidized sediments, the diversity and abundance of SRM were relatively high (Table 1, Online Resource 2), supporting the idea that SRM could be adapted to oxygen exposure, or maybe a brief oxygen exposure by sediment disturbances could be beneficial to these anaerobes, as it has been suggested for other marine sediments [97].

Oxidizing conditions in deep-sea surficial sediments (≥ 1000 m; Table 1) could be attributed to the oxygen from the deep-water masses which is not consumed in the first centimeters, and it may diffuse into the sediment at a greater depth [98]. Diversity and abundance of SRM decreased with depth (Table 1, Online Resource 2 and 6). However, phylotypes related to *Desulfovibrio* and *Desulfotomaculum* persisted in deep-sea sediments, and phylotypes related to *Desulfosporosinus*, *Desulfobacteraceae*, and *Chlorobi* even increased their abundance in samples from deep-sea sediments (Fig. 3; Online Resource 3 and 5). SRM related to *Desulfovibrio*, *Desulfotomaculum*, and *Desulfosporosinus* can grow autotrophically with hydrogen plus sulfate, to use other electron acceptors, including oxygen, and the latter two can form endospores to resist unfavorable conditions [8, 88, 89, 101, 102]. Microorganisms affiliated to *Desulfobacteraceae* exhibit high oxygen tolerance [84] and are commonly observed in high abundance in surface marine sediments [17, 99]. In the case of microorganisms related to the SOB *Chlorobi*, they have the potential of aerobic oxidation of sulfur compounds for autotrophic carbon fixation [100]. These metabolic features may explain the detection of these microorganisms in these deep-sea sites in which the presence of both SRM and SOB may indicate syntrophic cycling of sulfur in these oxic deep-sea environments.

dsrB gene sequences closely related to thermophilic spore-forming SRM of the class *Clostridia* (e.g., *Desulfotomaculum*) were detected in all the studied sites (Online Resource 4 and 5). However, the measured environmental temperature was not in the range previously reported to allow their vegetative growth (> 50 °C) [63, 64, 79, 101, 102]. Thus, we hypothesize that these microorganisms could be found as dormant endospores in the analyzed samples. Thermophilic endospores related to *Desulfotomaculum* have been previously detected in marine sediments in the Northern region of the GoM [70]. As endospores, often considered to be metabolically inert [103], they could not contribute to sulfate reduction in the studied sites.

Previous studies have concluded that SRM in sedimentary habitats appeared to be tightly coupled to both water depth and the organic carbon content [23, 30, 84, 104, 105]. In our study, differences between SRM communities were related to water depth too, but not to TOC and OM contents which varied in all the sites (Table 1). Moreover, Ni and Cd concentrations were related to differences in SRM community structure ($F_{1,\ 23}$ = 2.3, R^2 = 0.1 and $F_{1,\ 23}$ = 2.1, R^2 = 0.1, respectively). The enrichment of Ni and Cd toward deep-sea sediments (Online Resource 6) may derive from different sources that are likely not related to oil inputs, since they were not correlated to THC content (Online Resource 6). However, anthropogenic discharges may disperse heavy metals (HM) by marine currents prior to deposition [106]. HM, such as Ni and Cd, can influence SRM diversity and activity, having inhibitory effects [107, 108], specially Cd which may inhibit microbial growth inhibition or even cause cell death at a concentration of 0.1 mg/kg [109]. However, such metals can be precipitated with sulfide, the end-product of microbial sulfate reduction, and thus metal sulfide formation can mitigate metal toxicity. The participation of SRM in the precipitation of metal sulfides is well recognized [5, 110, 111]. Some SRM seem to display a degree of metal tolerance and resistance [66, 112, 113], such as the production of polypeptides that bind Ni in response to toxic levels of soluble Ni observed in *Desulfovibrio* and *Desulfotomaculum* species [114]. Given that some *Desulfovibrio* species possess periplasmic nickel containing hydrogenases, such as NiFeSe and NiFe hydrogenases for hydrogen oxidation [115], Ni could be a nutrient rather than a pollutant for them. In the present study, phylotypes related to *Desulfovibrio* were enriched in deep-sea sediments (Online Resource 1). Thus, although most of the *dsrB*-containing microorganisms observed in the present study (Figs. 3 and 4) have been previously reported in metal-contaminated environments [112], *Desulfovibrio* species could contribute to the resilience and stability of the sediment microbial communities experiencing metal pollution.

In conclusion, the results obtained from this study contribute with the understanding of the diversity of *dsrAB* containing microorganisms related to previously described taxonomic groups, as well as groups that may represent lineages from the GoM. Changes in community structure and abundance of SRM suggested that microbial sulfate reduction in continental sedimentary habitats gradually decreases toward deep-sea

sites in the NWGoM, due to environmental response variation in water depth, temperature, redox, and Ni and Cd content, as important environmental drivers throughout the transition between the continental margin and the deep seabed in the region of study.

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Author Contributions Ma. Fernanda Sánchez-Soto generated and designed the experiments, performed the experiments, analyzed the data, prepared the figures and/or tables, authored/reviewed drafts of the paper, and approved the final draft. Daniel Cerqueda-García analyzed the data, prepared the figures and/or tables, authored/reviewed drafts of the paper, and approved the final draft. Rocío J. Alcántara-Hernández and Luisa I. Falcón analyzed the data, contributed to the discussion of the obtained results, authored/reviewed drafts of the paper, and approved the final draft. Daniel Pech and Flor Árcega-Cabrera led the physicochemical analyses, authored/reviewed drafts of the paper, and approved the final draft. Ma. Leopoldina Aguirre-Macedo and José Q. García-Maldonado conceived the research, secured funding, contributed to the discussion of the results, authored contribute to the discussion of the results, reviewed drafts of the paper, and approved the final draft.

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