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# Bacterial Communities on the Northern Gulf of Mexico Continental Shelf are Influenced by Sediment Characteristics Affected by the Mississippi River

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# Bacterial Communities on the Northern Gulf of Mexico Continental Shelf are Influenced by Sediment Characteristics Affected by the Mississippi River

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**Benthic bacteria in the Gulf of Mexico serve the base of the sediment food chain as a food source for various marine organisms. In this paper, we analyzed the bacterial community and sediment characteristics from 14 sediment samples collected along the continental shelf of the northern Gulf of Mexico. Using the bacterial community to assess relationships among our sites, the data revealed groupings of sites that correlated to the sediment characteristics, generally grouped as western sites in Louisiana near the outflow of the Mississippi River and eastern Florida sites more distant from the outflow. Cluster analysis and multidimensional scaling demonstrated significant groupings of Louisiana vs Florida bacterial communities, and distance-based redundancy analysis related these groupings to sediment characteristics. Given the directions of currents around the Mississippi River, our data suggested that the outflow of the river is a major factor affecting the benthic bacterial community in the northern Gulf of Mexico.**

## Introduction

The marine sediment bacterial community serves as a food source for other benthic organisms and recycles nutrients by decomposition, and is thus an important component of the marine sediment food web (Krumins et al., 2013). The stability of the microbial community is greatly affected by abiotic factors such as light, temperature, pollution, nutrient availability, physical mixing, etc. as well as by biotic factors such as predation, competition, and viral infection (Fuhrman et al., 2015).

The northern Gulf of Mexico (nGOM) is heavily influenced by the Mississippi River outflow. It brings in freshwater, sediment, and microorganisms, which affect the food chain in the region (Morey et al., 2003; Mason et al., 2016). The path of this outflow is determined by two currents: the westward-flowing current on the Louisiana/Texas (LATEX) shelf and the northeastward current on the Mississippi/Alabama/Florida (MAFLA) shelf (Kourafalou and Androulidakis, 2013). It was observed that the LATEX current moves southwest during the winter and appears to be stationary during the summer (Morey et al., 2003). In contrast, the MAFLA current moves onto the LATEX shelf during the winter and moves eastward during the summer along the Florida coast (Morey et al., 2003).

The sedimentation rate and distribution from the Mississippi River outflow varies along the shelf. The average sedimentation rate is approximately 1 mm/yr, but this rate can go up to 10 mm/yr in certain places like the Ursa Basin near the Mississippi River mouth (Behrmann et al., 2006). The organic matter brought by the Mississippi River affects the GOM ecosystem (Yáñez-Arancibia et al., 2013) and contributes to the distribution pattern of sediment along the outer nGOM continental shelf. Recent studies at Troy University have demonstrated that Louisiana shelf sediments can be distinguished from Florida shelf sediments using trace metals such as Al and Zn, which are deposited in the Gulf from the output of the Mississippi River (Martinec et al. 2014; Beaton et al., 2018; Landers et al. 2018). Louisiana sediment is rich in these two metals, whereas Florida sediments have elevated levels of Ca and Sr, which are biogenically deposited. Additionally, Louisiana shelf sediments have higher percentages of silt + clay than Florida shelf sediments.

In this research, we examined the bacterial communities in sediments collected from 14 sites (Fig. 1) that have been shown to differ in sediment characteristics (Beaton et al., 2018, Landers et al., 2018). Our hypothesis is that bacterial communities from similar sediment types will group with one another, reflecting the effect of the Mississippi River outflow on the sediment and the organisms living within that sediment. These correlations were demonstrated for the sites examined in this study when meiofaunal groups such as nematodes and kinorhynchs were analyzed (Beaton et al., 2018; Landers et al., 2018). This current study now examines whether a similar correlation exists between benthic bacteria and sediments, since

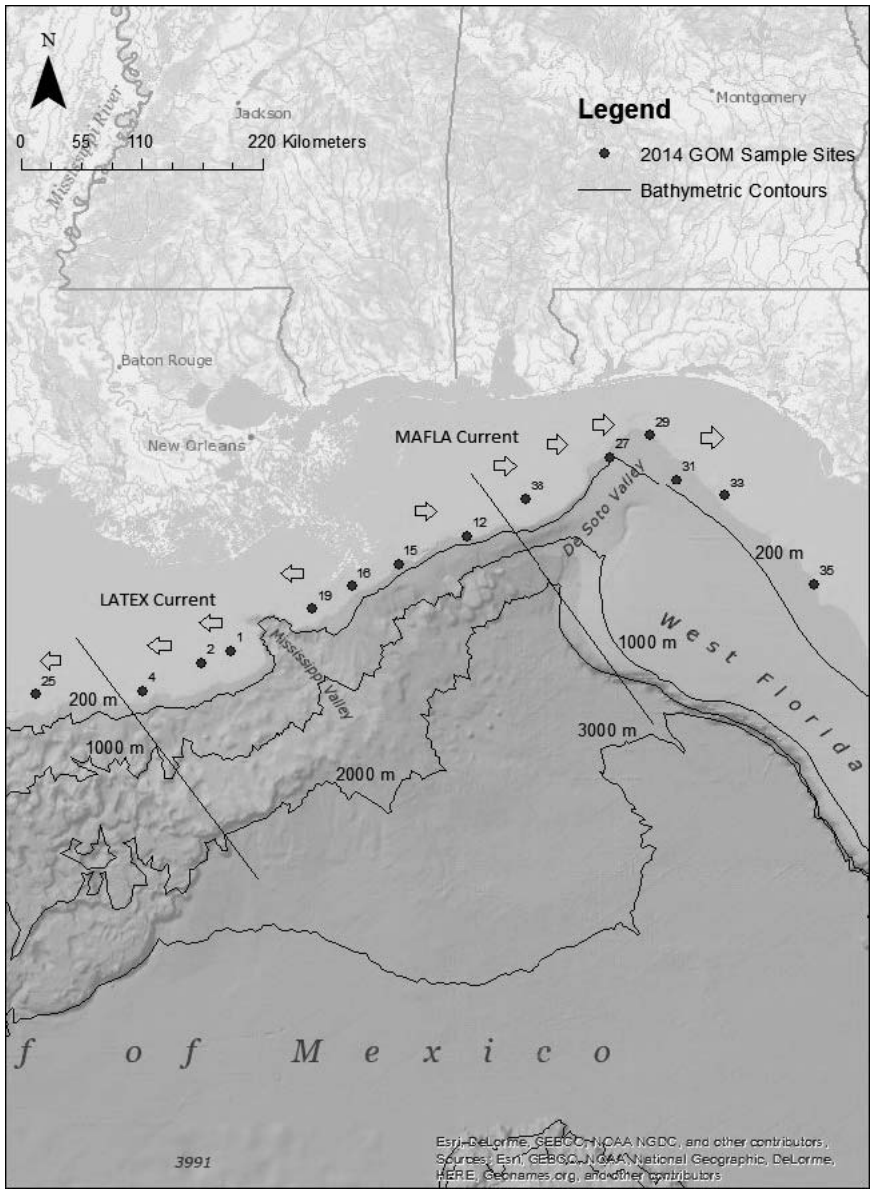


Fig. 1. Map of the Gulf of Mexico showing the sample sites from 2014 with lines dividing the eastern from the western sites on the basis of a statistical analysis of the bacterial communities at each site (Fig. 4). Numbers represent sampling stations. Arrows show the directions of westward LATEX and northeastward MAFLA currents (NOAA, 2017).

the benthic bacteria are major food sources for the meiofauna (Giere, 2009).

## Methods

*Sampling sites.*—Sediment samples were collected from 14 sites along the nGOM continental shelf, using a multicorer (Ocean Instruments®) aboard the National Oceanic and Atmospheric Administration (NOAA) ship *Gordon Gunter* in November 2014. Sites were chosen by NOAA as part of their annual "small pelagics" fish survey, with additional sites along the survey route allowed for sediment collection. Conductivity, temperature, and depth (CTD) data were collected by NOAA at each sediment site using a Seabird 9-11 CTD lowered at each multicorer location. Samples were collected from the top 5 cm of the


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TABLE 1. Gulf of Mexico sample site coordinates, depth, temperature, salinity, and dissolved oxygen data.

| Station | Latitude | Longitude | Depth (m) | Temp. (°C) | Salinity (ppt) | $O_2$ (mg) |
|---|---|---|---|---|---|---|
| 01 | 28°25′48.7194″N | 90°14′10.3194″W | 57 | 23.28 | 36.470 | 5.4 |
| 02 | 28°20′30.8394″N | 90°28′20.6394″W | 53 | 23.46 | 36.272 | 4.5 |
| 04 | 28°8′30.8394″N | 90°57′5.3994″W | 97 | 21.98 | 36.530 | 5.3 |
| 12 | 29°15′10.08″N | 88°18′23.76″W | 90 | 18.58 | 36.391 | 4.0 |
| 15 | 29°3′1.4394″N | 88°52′5.1594″W | 112 | 18.09 | 36.302 | 3.8 |
| 16 | 28°53′37.3194″N | 89°14′53.88″W | 67 | 20.35 | 37.402 | 5.3 |
| 19 | 28°43′52.68″N | 89°34′16.32″W | 94 | 17.59 | 36.304 | 3.6 |
| 25 | 28°7′6.6″N | 91°49′34.32″W | 88 | 22.11 | 36.689 | 4.9 |
| 27 | 29°49′23.5194″N | 87°7′51.96″W | 149 | 16.98 | 36.232 | 3.9 |
| 29 | 29°58′28.9194″N | 86°48′12.16″W | 125 | 16.98 | 35.698 | 3.8 |
| 31 | 29°39′35.28″N | 86°34′58.08″W | 163 | 17.37 | 36.295 | 4.1 |
| 33 | 29°32′32.28″N | 86°11′33.3594″W | 98 | 18.86 | 36.352 | 4.2 |
| 35 | 28°54′29.88″N | 85°27′39.5994″W | 121 | 18.29 | 36.362 | 4.2 |
| 38 | 29°30′59.04″N | 87°49′35.7594″W | 50 | 21.79 | 35.972 | 6.9 |

sediment within the multicorer tubes and stored at −20°C before being analyzed. All sampling sites are located on the continental shelf (Fig. 1) and site coordinates are given (Table 1). The coordinates of all sites were mapped (Fig. 1) using ArcGIS with bathymetric data from http://pubs.usgs.gov/of/2005/1071/data/background/bathy_contours/bathyc.zip.

*Sediment analysis.*—Sediment from the top 5 cm of the multicorer samples was collected for abiotic analysis. Trace metals were determined at the Louisiana State University Agricultural Center using inductively coupled plasma–atomic emission spectrometry according to U.S. Environmental Protection Agency method 200.7 (USEPA, 2001) for trace metals. Granulometric characterization of the sediment was done at Troy University using sodium hexametaphosphate to separate the silt + clay fraction, and a mechanical shaker to separate the samples into five sand fractions (U.S. Soil Survey Staff, 1996).

*Deoxyribonucleic acid (DNA) extraction and nested polymerase chain reaction (PCR).*—DNA was extracted from 0.5 g of soil using the PowerSoil™ DNA isolation kit (MoBio Laboratories, Carlsbad, CA) as per the manufacturer's instruction. After extraction, the DNA samples were stored at −20°C before analysis. The first-round PCR was conducted using the 27F and 1522R primer set (Giovannoni, 1991) and the second-round PCR using the 341F with GC clamp and 534R primer set (Muyzer et al., 1993). These two sets of PCR primers target bacterial 16S ribosomal ribonucleic acid (rRNA) genes. The total PCR mix per samples was 50 µl, which contained 40 µl of distilled water, 2 µl of DNA, 5 µl of 10× green *Taq* PCR buffer, 0.25 mM deoxynucleotide triphosphates, 10 pmol of forward and reverse primers, and 1 U of green *Taq* DNA polymerase (GenScript, Piscataway, NJ). A DNA thermal cycler (GeneAmp PCR System 2700, Applied Biosystems, Foster City, CA) was used at an initial temperature of 94°C for 5 min. This was followed by either 30 cycles for the first-round PCR or 35 cycles for the second-round PCR of 94°C for 20 sec, 55°C for 45 sec, and 72°C for 45 sec. A final extension of 72°C was performed for 7 min. Subsequently, agarose gel electrophoresis was conducted and the gels were analyzed under an ultraviolet (UV) transilluminator (Fisher Scientific, Pittsburgh, PA) after staining with ethidium bromide for 10 min to confirm the validity of the PCR products.

*Denaturing gradient gel electrophoresis (DGGE).*—Eight percent polyacrylamide gel was used to separate the PCR products with a denaturing gradient of 40% and 60% by a BioRad DCode™ universal mutation detection system (Bio-Rad Laboratories, Hercules, CA) in 1× Tris–acetic acid–ethylenediaminetetra-acetic acid buffer. Electrophoresis was carried out at 60 V for 12 hr at 60°C. Thereafter the DGGE gels were stained with ethidium bromide for 15 min and photographed on an UV transilluminator (Fisher Scientific).

*Statistical analysis.*—Sediment sites were analyzed statistically with a principal components analysis (PCA) for abiotic characteristics of the sediment [granulometry (silt + clay, very fine sand), trace metals (Al, Zn, Ca, Sr), depth, salinity, oxygen,

and temperature]. Environmental variables for the PCA were normalized, checked for collinearity, and redundant variables (correlations > 0.9) were omitted. Bacterial community band data (presence–absence) from the DGGE gels were initially analyzed by the PyElph software (Pavel and Vasile, 2012) using the unweighted pair group method with arithmetic mean algorithm (Drummond and Rodrigo, 2000), and then further analyzed by cluster analysis with SIMPROF (similarity profile) and nonmetric multidimensional scaling (nMDS) ordination using the Bray–Curtis similarity and Primer® software. Briefly, the PyElph software was initially used to generate a binary matrix of DGGE band patterns with a 1 or a 0 for the presence or absence of each band, respectively. These data were used to construct a cluster analysis (PRIMER software) of the bacterial communities, with the additional use of the SIMPROF test for statistical significance ($P = 0.05$). Analysis of the relationship between the bacterial community by site and the abiotic data used BEST analysis (Primer) and distance-based linear models + distance-based redundancy analysis (DISTLM/dbRDA) using Permanova®+ for Primer software.

## Results

*Sediment characteristics.*—Louisiana shelf sediments were distinct from Florida shelf sediments, particularly with regard to granulometry and trace metals. Trace metals were analyzed, not because they were thought to influence the biotic community, but because they can be used as markers to distinguish river-influenced sediments from those sediments not affected by the Mississippi River (Wade et al. 2008). Trace metals known from our past surveys to be signature metals for Louisiana and Florida sediments (Martinec et al. 2014) were used in the current analysis. Specifically, Louisiana sediments had higher levels of Al and Al-associated trace metals such as Zn. Conversely, Florida sediment had higher levels of Ca and Sr. For our analysis, Al and Ca were used to represent Louisiana and Florida sediment (Zn and Sr were strongly collinear with Al and Ca, respectively, and added no value to the PCA). With regard to granulometry, Louisiana sediment had higher percentages of silt + clay sediment fractions than Florida sediments, whereas Florida shelf sediments had higher percentages of very fine sand fractions than Louisiana. Complete raw data for all sites (NOAA CTD data, trace metal concentrations, and granulometry percentages) are publicly available (Landers, 2016, Landers and Yu, 2016). The 14 sites separated into two broad groups using a PCA of abiotic characteristics (Fig. 2). Sites west of sample 12 clustered into a group of seven locations, all of which were along the Louisiana coast and shared sediment granulometric and trace metal characteristics. Sites east of sample 38 clustered into a group of five locations, all from Florida, which were similar in sediment characteristics. Sites 12 and 38 were transitional, with site 12 grouping with the eastern stations and with site 38 as an outlier.

*Bacterial community analysis.*—DGGE data of the 14 sediments samples from nGOM revealed 28 distinct bands among all sites that reflected the diversity of the bacterial community (Fig. 3). The PyElph and the SIMPROF analyses resulted in identical tree topologies, which revealed three major branches in the cluster, with western sites 12, 15, 19, 16, 4, 2, and 1 grouped together, whereas eastern sites 27, 29, 33, 35, 38, and 31 grouped in a different cluster (Fig. 4a). The bacterial community pattern of site 25, which is the westernmost sampling site, was significantly different from those in all other sites. The clustering of these three divisions (western, eastern, and site 25) was statistically significant (branches with solid lines in Fig. 4a). Additional significant branches also existed within the eastern and western groups. In particular, the significant branches within the western cluster are interesting in that they reflect their proximity on the continental shelf. Sites 1, 2, and 4 form a significant cluster with a similarity of approximately 90%. These three locations are close to one another, on the western side of the Mississippi Valley (Fig. 1). Sites 15, 16, and 19 are indistinguishable, with 100% similarity, and are located close to one another on the eastern side of the Mississippi Valley. The significant branches within the eastern cluster do not reflect their proximity on the Florida shelf, however. Sites 31 and 38 are grouped separately from the other four sites, though these sites are geographically separate, have very different depths, and are not similar when examined with the PCA. Overall, the three groups that are revealed with the cluster analysis (western, eastern, and site 25) can be visualized with nMDS [with a very low two-dimensional (2D) stress], which shows an internal similarity of 55% within the western and eastern clusters (Fig. 4b). Note that some sites (1 and 2; 15, 16, and 19; 33 and 35) are located at


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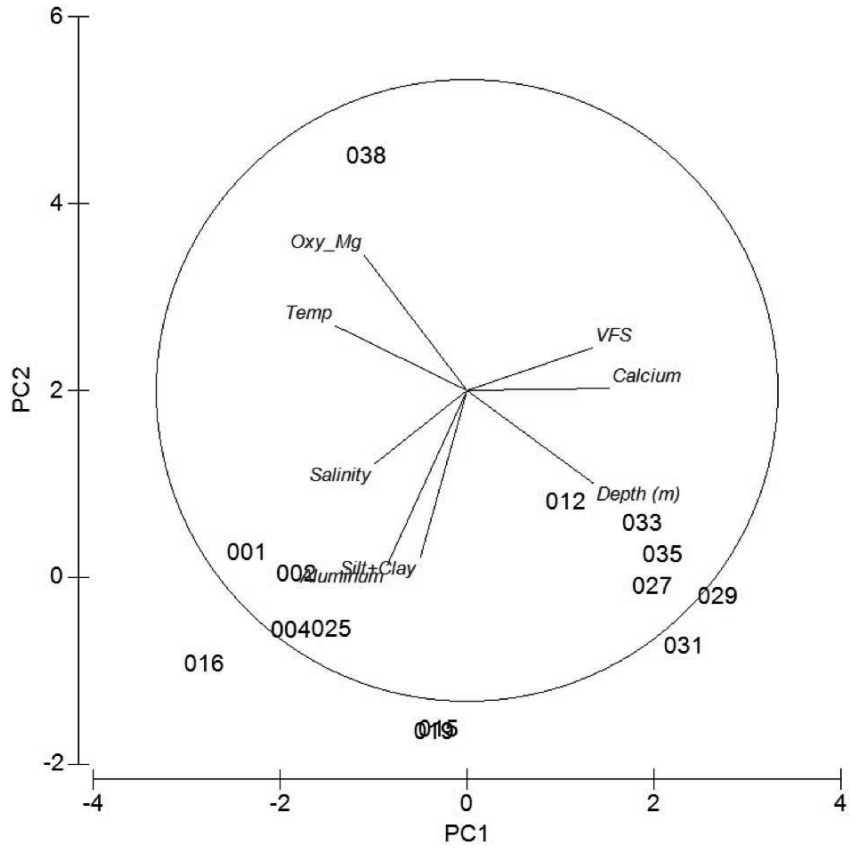


Fig. 2. Principal components analysis of 14 collection sites on the nGOM continental shelf (site locations indicated by numbers). PC1 accounted for 47.5% of the variation and was composed mainly of contributions from calcium, very fine sand (VFS), depth, and temperature. PC2 accounted for 27.8% of the variation and was composed of contributions from silt + clay, aluminum, and oxygen. The length of the vectors reflects each variable's contribution to the two PC axes. The circle is the maximum vector length (i.e., maximum correlation = 1).

the identical positions and thus they are overlapped.

When comparing bacterial communities with the PCA, the two data sets reflect similar trends, with sites having western sediment characteristics grouping together and with a similar grouping for eastern sites. Three locations are exceptional, though: sites 25, 12, and 38. Site 25 is located at the extreme western longitude of the study, and although that site fit well with the western sediment grouping (Fig. 2), it was an outlier when bacterial communities were analyzed. Sites 12 and 38 were located at a sediment transition, and thus their PCA grouping did not agree with the nMDS analysis on the basis of bacterial communities. This sediment transition has been previously reported (Beaton et al., 2018; Landers et al., 2018).

The statistical relationship of abiotic and biotic data sets was further analyzed using BEST and dbRDA. BEST analysis revealed a significant relationship between abiotic data and biotic band data ($r = 0.628$, $P = 0.002$) using Ca, Al, and very fine sand (though many solutions with three to five abiotic variables gave a $r = 0.628$ correlation, meaning all of the measured abiotics contributed to explaining the biotic data). The dbRDA revealed a 2D mapping of the sites on the basis of biotic data (DGGE band patterns), constrained by fitting environmental abiotic data into the model (Fig. 5). Thus, the dbRDA is similar to, though not exactly the same as, the PCA and nMDS combined. As expected, two groups of sites (western and eastern sites) based on biotic data were correlated with two abiotic sediment profiles based on trace metals and granulometry. The total variability accounted for

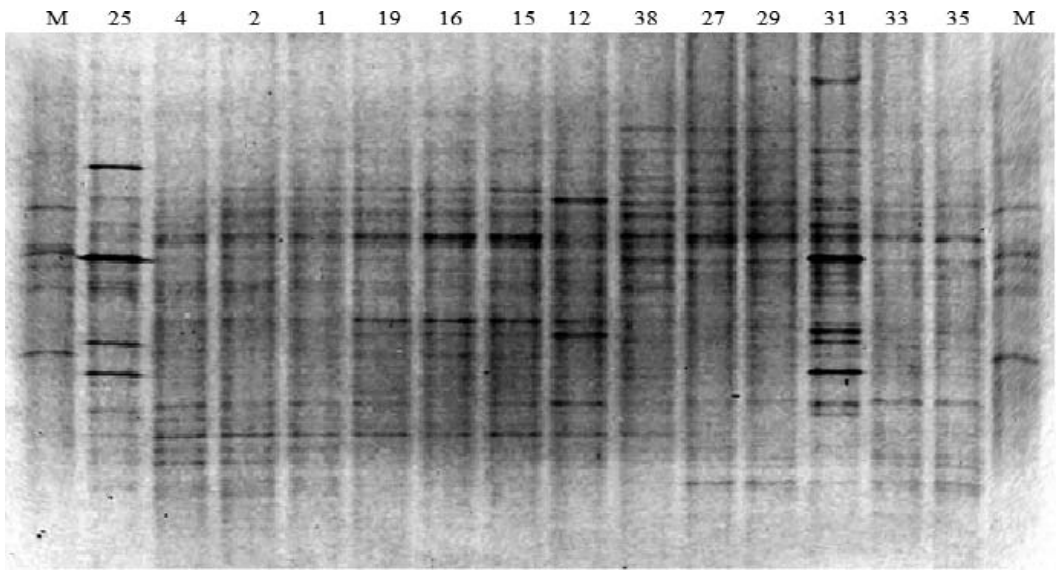


Fig. 3. DGGE profiles of PCR-amplified bacterial 16S rRNA genes in sediments collected from 14 stations in the Gulf of Mexico in 2014. The order of samples loaded onto the gel (from left to right) represents the sampling locations (from west to east). M = custom marker; numbers represent sampling stations.

by the two dbRDA axes was good (64.8%). All of the abiotics correlated with the biotic band data, with a significance of $R^2 = 0.72048$.

## Discussion

This research has shown that bacterial communities separate into two broad groups from either the Florida nGOM shelf or the Louisiana nGOM shelf. Sediment characteristics reveal a similar separation of Florida and Louisiana sites on the basis of abiotic data. The two data sets (bacterial communities and abiotic data) were significantly correlated with BEST analysis and dbRDA. The grouping of the bacterial assemblages parallels the results of earlier studies from these same sediment sites, in which kinorhynchs (mud dragons) and nematodes (roundworms) both revealed a clear eastern–western separation when analyzed using a community analysis based on animal identifications (Beaton et al., 2018; Landers et al., 2018). Those studies analyzed sediments collected from the same 14 sites reported in this research, and an additional 23 sites along the nGOM shelf. Thus the prokaryotes, as a major food source for meiofauna, demonstrated a similar eastern–western separation as the metazoan community. Since many bacteria use detritus as their energy sources and nematodes and kinorhynchs feed on the detritus and bacteria (Giere, 2009), it could be expected that differences in the bacterial communities would parallel differences in meiofauna communities (Urban-Malinga et al., 2006). Equally, however, it is recognized that abiotic characteristics of sediment may play a major role that would also influence the distribution of meiofauna species. This research supports the observations from our past and present studies that sediment abiotic differences affect the biotic community at multiple levels of the food web.

The influence of the Mississippi River outflow and offshore currents is involved in creating differences in sediment type in the Gulf, which is likely a principal factor affecting the bacterial communities. Our analyses demonstrated two distinct bacterial communities in the nGOM residing in Louisiana and Florida. These two sediment areas are influenced either by the westward LATEX current or by the northeastward MAFLA current (Fig. 1) (Kourafalou and Androulidakis, 2013). The LATEX current influences the outflow of the Mississippi River by distributing sediment with aluminosilicate compounds from the river on the Louisiana shelf (Martinec et al., 2014). The results of the metal analysis of the sediments revealed these stark differences in eastern and western sediments, which were reported not only from the 14 sediment locations in this study, but also an


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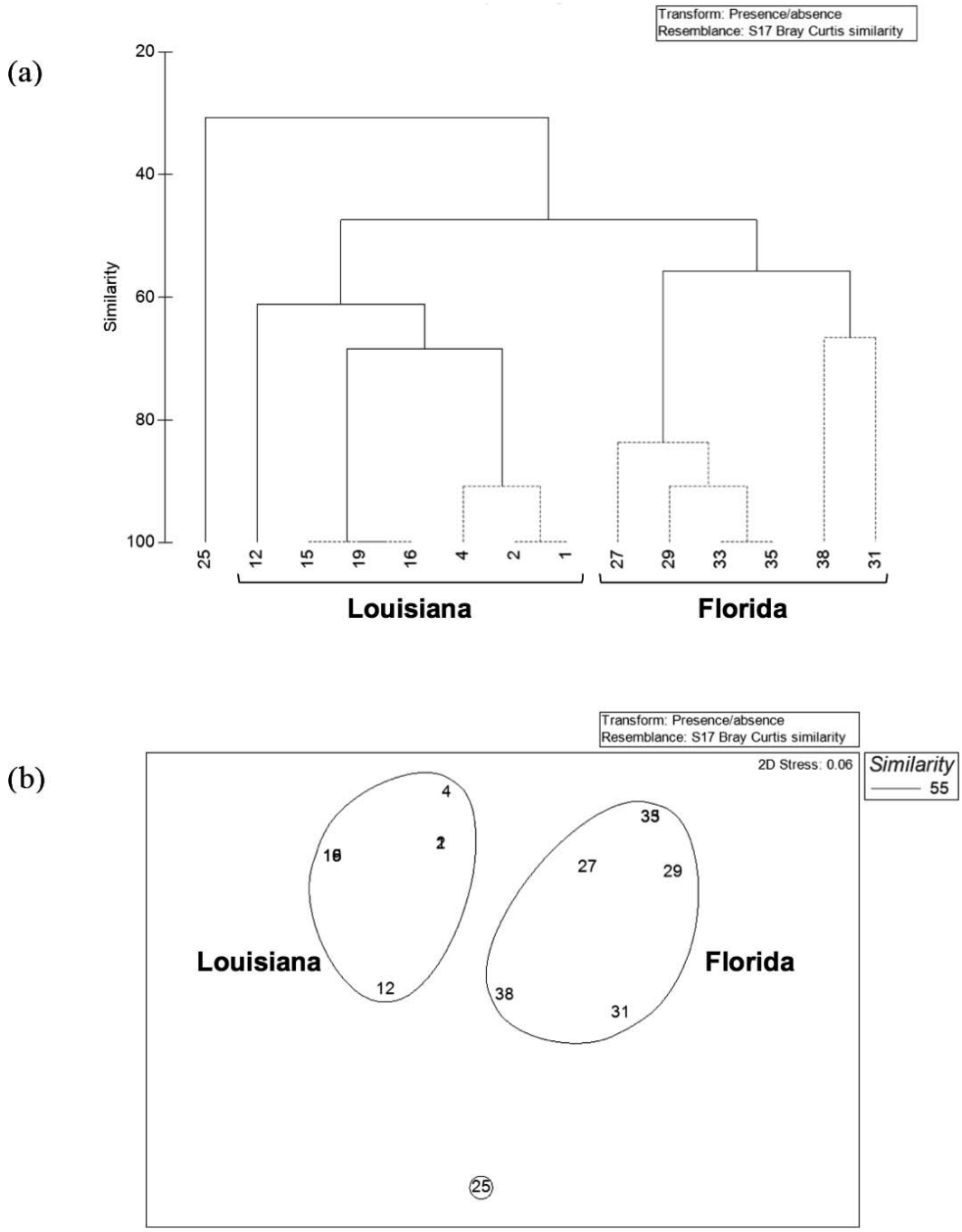


Fig. 4. Grouping of sampling sites based on the DGGE profiles. (a) Cluster analysis using the SIMPROF test indicates statistically significant branches with solid lines. (b) Nonmetric multidimensional scaling of the sediment sites. Western sites (Louisiana locations) group with one another with a 55% similarity, as do eastern sites (Florida locations). Site 25 is an outlier.

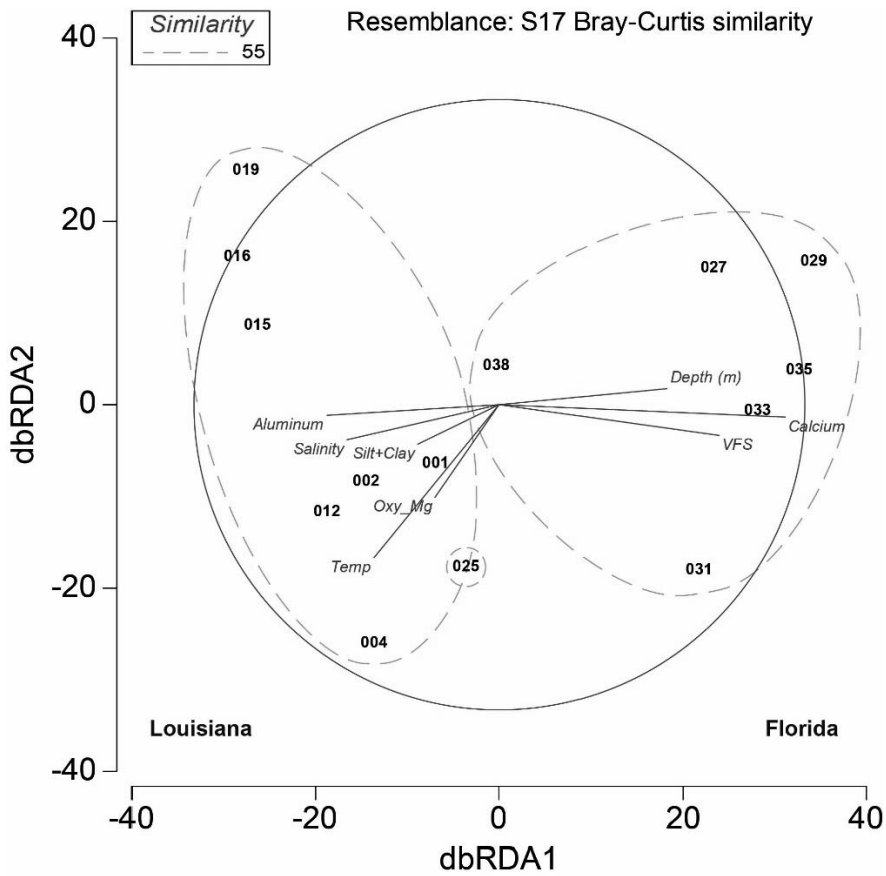


Fig. 5. Distance-based redundancy analysis (dbRDA) for modeling the relationship between biotic data (site locations indicated by numbers) and abiotic variables. This two-dimensional mapping of sites is constrained, as it maximizes the distance between stations but fits the abiotic model to the biotic data. The dashed line indicates 55% similarity among station groups, which group as Louisiana locations (01, 02, 04, 12, 15, 16, 19), Florida locations (27, 29, 31, 33, 35, 38), and extreme western location 25. Two sediment profiles are identified: high Al and silt + clay in Louisiana, and high Ca and very fine sand in Florida. The circle is the maximum vector length (i.e., maximum correlation = 1).

additional 23 locations from the same nGOM region (Beaton et al., 2018; Landers et al., 2018). Our data strongly suggest that the benthic bacterial communities of the western sites are influenced by the discharge from the Mississippi River. The microbial community introduced by the Mississippi River may also contribute to a difference in bacterial community structures between the western and eastern sites (King et al., 2013; Mason et al., 2016).

The salinity gradient along the water column (Morey et al., 2003) may influence bacterial community structure. Mason et al. (2016) demonstrated that the salinity of the Mississippi River plume increased with depth. However, the salinity levels at our benthic sampling sites were relatively constant between 35.7‰ and 37.4‰, suggesting that salinity is not a major factor affecting the bacterial community. Likewise, depth may not be an important factor affecting the bacterial community in this study. From the cluster analysis (Fig. 4), similar community structures were observed for sites of different depths. For example, sites 15, 16, and 19 have indistinguishable bacterial community structures even though their depth ranged from 67 m to 112 m. It is speculated that the depth of sampling sites may be a less important factor affecting the bacterial community, which may be a result of the narrow range of depths encountered in our sampling. Oxygen also does not seem to have a major effect on the bacterial community structure, since all sampling sites exceeded hypoxic levels (Table 1).


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## Conclusions

Our analysis of sediments sampled along the continental shelf of the nGOM demonstrated (1) differences in the bacterial communities between western and eastern sediment locations in the nGOM, and (2) the potential influence of the Mississippi River outflow and offshore currents in determining sediment characteristics and bacterial communities. The results parallel earlier studies that demonstrated a similar eastern–western division in meiofaunal communities, which rely on the bacterial communities as their food source.

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