Biogeochemical and Microbial Variation across 5500 km of Antarctic Surface Sediment Implicates Organic Matter as a Driver of Benthic Community Structure

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Western Antarctica, one of the fastest warming locations on Earth, is a unique environment that is underexplored with regards to biodiversity. Although pelagic microbial communities in the Southern Ocean and coastal Antarctic waters have been well-studied, there are fewer investigations of benthic communities and most have a focused geographic range. We sampled surface sediment from 24 sites across a 5500 km region of Western Antarctica (covering the Ross Sea to the Weddell Sea) to examine relationships between microbial communities and sediment geochemistry. Sequencing of the 16S and 18S rRNA genes showed microbial communities in sediments from the Antarctic Peninsula (AP) and Western Antarctica (WA), including the Ross, Amundsen, and Bellingshausen Seas, could be distinguished by correlations with organic matter concentrations and stable isotope fractionation (total organic carbon; TOC, total nitrogen; TN, and $\delta^{13}C$). Overall, samples from the AP were higher in nutrient content (TOC, TN, and NH_4^+) and communities in these samples had higher relative abundances of operational taxonomic units (OTUs) classified as the diatom, *Chaetoceros,* a marine cercozoan, and four OTUs classified as *Flammeovirgaceae* or *Flavobacteria*. As these OTUs were strongly correlated with TOC, the data suggests the diatoms could be a source of organic matter and the *Bacteroidetes* and cercozoan are grazers that consume the organic matter. Additionally, samples from WA have lower nutrients and were dominated by *Thaumarchaeota*, which could be related to their known ability to thrive as lithotrophs. This study documents the largest analysis of benthic microbial communities to date in the Southern Ocean, representing almost half the continental shoreline of Antarctica, and documents trophic interactions and coupling of pelagic and benthic communities. Our results indicate potential modifications in carbon sequestration processes related to change in community composition, identifying a prospective mechanism that links climate change to carbon availability.

Keywords: benthic communities, Antarctica, aquatic microbiology, biogeochemistry, microbial ecology

INTRODUCTION

Changing climate in Antarctica has potential to initiate a domino effect that could impact ecosystems from continental ice sheets to the seafloor. Recent research has shown the West Antarctic Ice Sheet (WAIS) is one of the fastest warming locations on Earth (Bromwich et al., 2013; Hillenbrand et al., 2013). Consequently, the WAIS has been losing ice mass (Rignot et al., 2011; Pritchard et al., 2012; Shepherd et al., 2012; Depoorter et al., 2013), which not only has the potential to cause changes in sea-level (Bindschadler, 2006), but also to influence water temperature, salinity (Arneborg et al., 2012 and references therein) and nutrient cycling. The melt season is known to stimulate primary productivity (Smith and Gordon, 1997; Arrigo et al., 1998; Ducklow et al., 2006; Smith et al., 2007), which then increases the amount of organic matter sourced from the water column to sediments (Billett et al., 1983; Wefer et al., 1988; Honjo et al., 2000; Kennedy et al., 2002; Ducklow et al., 2006; Gillies et al., 2012). Further, increasing melt from the continental ice sheet would introduce more terrestrial carbon into marine and benthic environments, altering the quantity and type of carbon. Thus, a greater understanding of Antarctic ecosystems is essential to predict how changing climate will influence organic fluxes between benthic and pelagic communities.

Microbial marine communities play an important role in mediating nutrient cycling to both the water column (reviewed in Arrigo, 2005) and the deep biosphere (reviewed in Edwards et al., 2012) and diversity in these sediments is sensitive to environmental changes. Microbial sediment communities are important as they have been shown to play a major role in carbon cycling (Mayor et al., 2012), in addition to other biogeochemical cycles, such as sulfur, nitrogen, and phosphorus (Azam and Malfatti, 2007; Jorgensen and Boetius, 2007; Falkowski et al., 2008; Edwards et al., 2012). Further, marine sediment communities can be impacted by various chemical and physical parameters (Austen et al., 2002; Schauer et al., 2010; Zinger et al., 2011; Bienhold et al., 2012; Durbin and Teske, 2012; Liu et al., 2015; Nguyen and Landfald, 2015). In Antarctica, recent studies of planktonic marine microbial communities have shown beta diversity is correlated to both physical oceanographic (Wilkins et al., 2013) and chemical variation (Luria et al., 2014; Signori et al., 2014). Sediments from the Ross Sea (Carr et al., 2013) and the Drake Passage at the Antarctic Polar Front (Ruff et al., 2014) have shown organic matter can increase estimates of microbial abundance based on phospholipids and DNA sequencing, respectively. Another study examining sediments from the Southern Ocean (Jamieson et al., 2013) has shown organic matter did not impact species richness. Since climate change in Antarctica will alter the flow of organic matter and nutrients to benthic sediments, understanding how these changes will impact diversity is essential to predicting change in ecosystem functions.

In the present study, we examine the relationships between organic matter, nutrient content, and sediment microbial diversity. While several studies have examined microbial diversity in Antarctic sediments (e.g., Bowman and McCuaig, 2003; Bowman et al., 2003; Powell et al., 2003; Baldi et al., 2010; Carr et al., 2013, 2015; Jamieson et al., 2013; Ruff et al., 2014), each has used various sequencing methods, collected different types of geochemical parameters, and some have had a focused geographic scope. In contrast, we collected 24 sediment samples over a 5500 km transect of Western Antarctica that spans the Ross to the Weddell Seas. Small subunit (SSU) rRNA genes from all three domains of life were sequenced via Illumina MiSeq and correlated with geochemical and nutrient data. The total dataset greatly expands our existing understanding of benthic Antarctic sediments communities, and demonstrates important correlations between organic matter and sediment microbial diversity.

MATERIALS AND EXPERIMENTAL METHODS

Sampling Details

Surface sediment samples were collected from the continental shelf of Antarctica during two research cruises. The first cruise (Dec. 2013–Feb. 2014, *RVIB Nathaniel B. Palmer*) sampled Western Antarctica (WA), which includes the Amundsen Sea, Bellingshausen Sea, and Ross Sea, using a multicorer (**Figure 1**). The second cruise (Nov.–Dec. 2014, *ASRV Laurence M. Gould*) sampled the Antarctic Peninsula (AP) using a box corer. Samples were collected on the Antarctic shelf at depths ranging from 223 to 820 m. The top 3 cm of sediments were transferred into sampling tubes and stored frozen ($-80°C$). Samples were shipped frozen to Central Michigan University (CMU) within 3 months of collection. More details about sampling locations are found in Table S1.

Sediment Chemical Analysis

Sediment samples were homogenized and shipped to EcoCore Analytical Services at Colorado State University for stable isotope (^{13}C and ^{15}N) and percent nitrogen and organic carbon analyses. Macronutrient (total organic carbon; TOC, total nitrogen; TN, NO_3^-, NH_4^+, S, P) analyses were conducted along with collection of available trace nutrient (e.g., metals) data at the Soil, Water, and Plant Testing Laboratory at Colorado State University (Table S1). The available fraction was defined as the metals that were extracted via Mehlich 3 acid digestions (Mehlich, 1984), and thus does not include an insoluble mineral component.

Correlations between chemical parameters were statistically examined via a Spearman's rank-order correlation in SPSS Statistics 22 (IBM, 2013). If a parameter had high correlation ($R > 0.9$ and significant at 0.01 level, two-tailed t-test) with another variable (%N and %TOC), then one parameter was removed from the dataset for downstream analysis (%N was removed). Also, data that were reported in percent or a ratio were transformed using an arcsine square root. Resulting nutrient data were then examined for broad trends via principal components analysis (PCA) in the statistical software PAST (Hammer et al., 2001).

Microbial Taxonomic Analysis

DNA was extracted using a PowerSoil DNA extraction kit (MoBio) following the manufacturer's protocol. Approximately
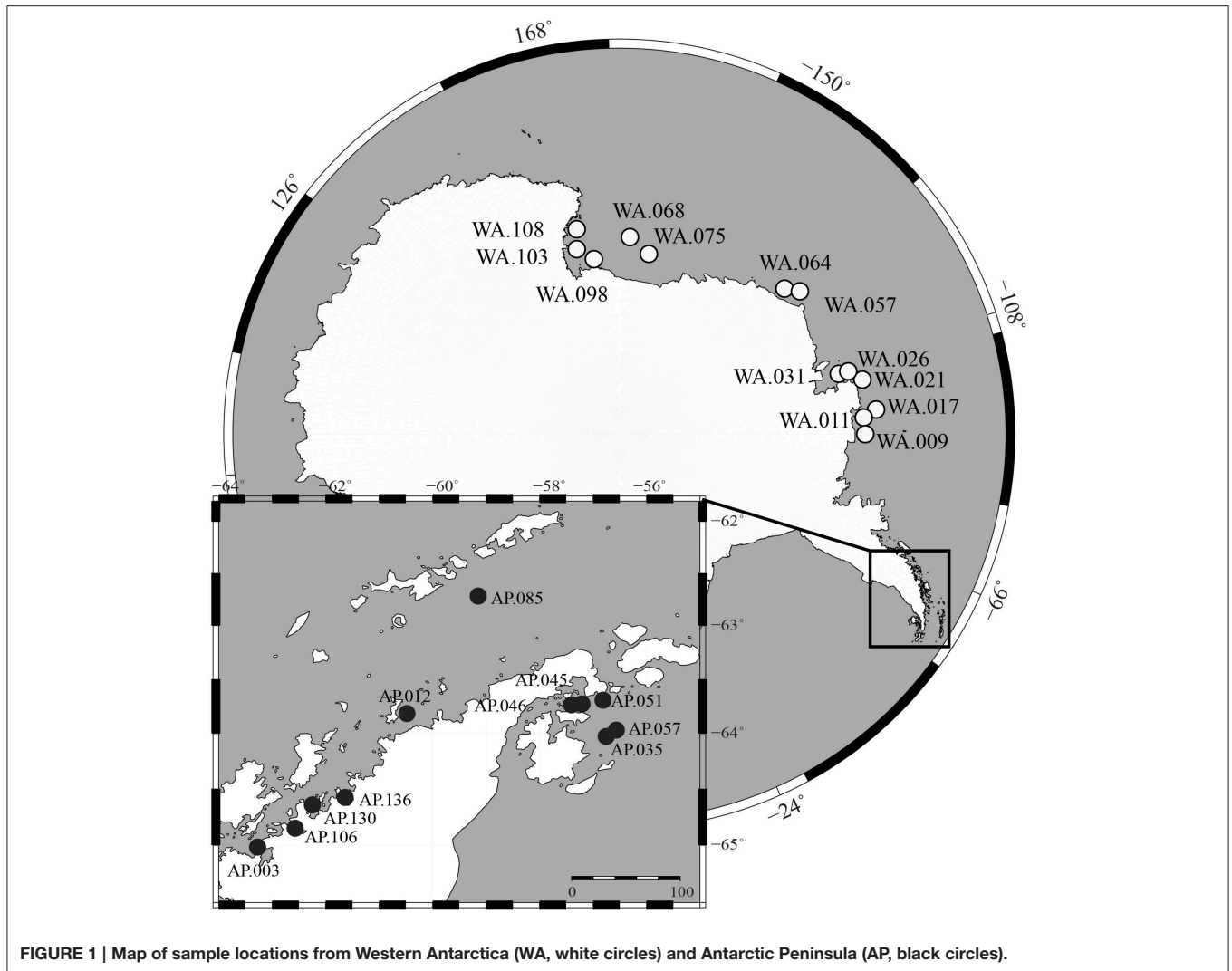
FIGURE 1 | Map of sample locations from Western Antarctica (WA, white circles) and Antarctic Peninsula (AP, black circles).

4–8 extractions were completed on each sediment sample and pooled and concentrated with a DNA Clean and Concentrator kit (Zymo) due to low yields from some of the samples. DNA was then quantified using the Qubit2.0 Fluorometer (Life Technologies) and stored at −20°C. Bacterial and archaeal sequences were generated from the V4 region of 16S rRNA gene using the primer set 515f and 806r (Caporaso et al., 2012) while eukaryotic sequences were obtained with the V4 region of the 18S rRNA gene using the primer set 1391r and EukBR (Amaral-Zettler et al., 2009). Resulting amplicons were sequenced on an Illumina MiSeq as paired-end (PE) reads of 250-bp at Michigan State University's (MSU) Research Technology Support Facility (RTSF) Genomics Core. 16S and 18S rRNA gene amplicons were analyzed with Mothur v.1.33.3 (Kozich et al., 2013) using the Silva v119 database (Quast et al., 2013). Briefly, SSU 16S rRNA gene sequences were assembled into contigs and discarded if the contig had any ambiguous base pairs, possessed repeats greater than 8 bp, or were greater than 253 bp in length. Contigs were aligned using the Silva rRNA

v119 database, checked for chimeras using UCHIME (Edgar et al., 2011), and classified using the Greengenes rRNA May 2013 database (DeSantis et al., 2003, 2006). Contigs classifying to chloroplast, eukaryotes, mitochondria, or "unknown" affinities were removed from the data and the remaining contigs were clustered into operational taxonomic units (OTUs) using a 0.03 dissimilarity threshold ($OTU_{0.03}$).

Due to sequencing error, 18S rRNA reverse sequences were shorter than expected, causing little to no overlap of the paired end contigs. Therefore, only forward read sequences were used in downstream analyses (mean sequence length = 250 bp). Those classified as "unknown," Archaea, or Bacteria were removed from the data and remaining contigs were clustered into OTUs using a 0.03 dissimilarity threshold ($OTU_{0.03}$).

Data analyses of OTUs was done using the R statistical environment v3.2.1 (R Development Core Team, 2008), within the package PhyloSeq (McMurdie and Holmes, 2013). For estimating alpha-diversity, the filtered OTUs were used to calculate species richness using the "estimate_richness"

command within PhyloSeq, which plots Simpson, Chao1, and Shannon diversity (McMurdie and Holmes, 2013, and references therein). After alpha diversity calculations were completed, potentially erroneous rare OTUs, those without at least a total of two sequences in two or more samples, were discarded. The amplicon reads were normalized using the package DESeq2 (Love et al., 2014) following the general procedure for normalization using a variance stabilizing transformation (see Supplemental Materials for all R code used). DESeq2 normalized reads were used for all downstream analyses. For 16S rRNA sequences, beta-diversity between samples was examined using Bray-Curtis distances and ordinated using non-metric multidimensional scaling (NMDS). For 18S rRNA sequences, the relative abundance counts were converted to a presence/absence matrix (due to the potential for eukaryotic organisms to be pluricellular) and beta diversity was calculated by generating Jaccard indices. Analysis of similarity (ANOSIM) was used to test the significance of differences between groups of samples (e.g., WP vs. AP) of the NMDS analyses. Correlation between measured geochemical and macronutrient (defined as TOC, TN, NO_3^-, NH_4^+, S, Fe, P) data and the beta-diversity data was investigated in R with the envfit function (Oksanen et al., 2013). In addition, environmental variables (pH, TOC, TN, NO_3^-, NH_4^+, S, P, Fe, Si, $\delta^{15}N$, and $\delta^{13}C_{org}$) were tested for significance when compared to the axes of NDMS plots compared to beta-diversity variables to examine patterns between geochemical data and beta-diversity plots. Further, correlations between geochemical parameters and relative abundance of OTUs were statistically evaluated with Spearman's rank-order correlation (SPSS).

Raw rRNA reads (16S and 18S) have been submitted to the European Nucleotide Archive (study accession number: PRJEB11496 and PRJEB11497, respectively). A table with OTU relative abundances can be found in the Supplementary Materials.

RESULTS AND DISCUSSION

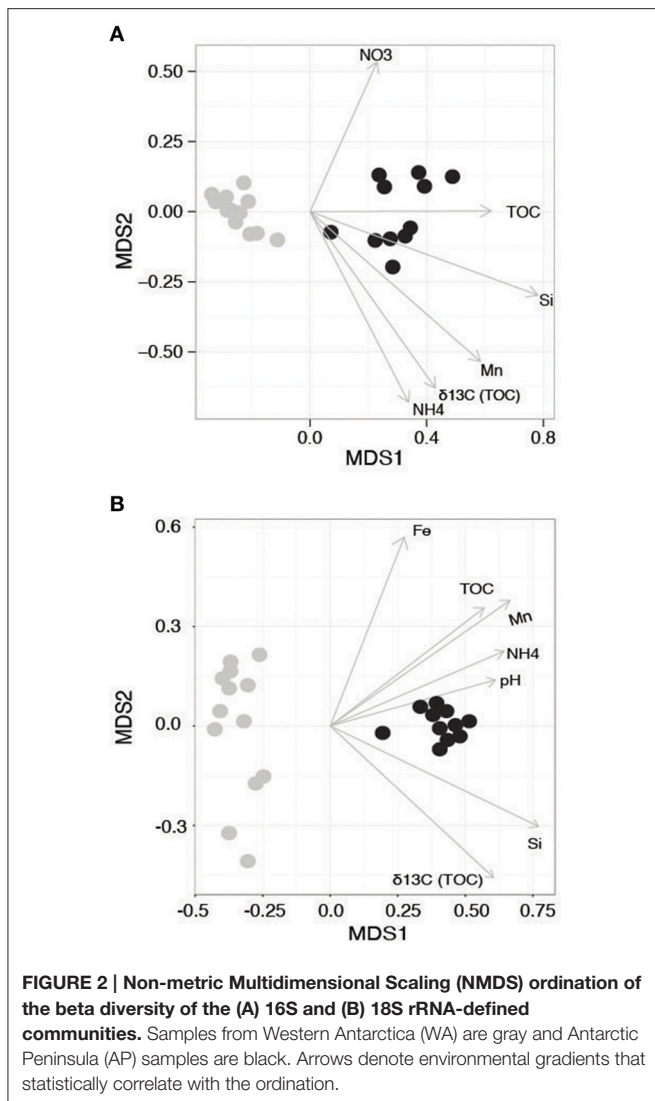### Relating Organic Matter (OM) and Nutrients to Benthic Diversity

This study shows community structure in benthic sediments is correlated to nutrient content and also suggests a possible coupling between pelagic and benthic communities. We collected 24 benthic samples spanning a 5500 km region of Antarctica that includes Western Antarctica (WA) and the Antarctic Peninsula (AP; **Figure 1**). Sediment macronutrients (TOC, TN, NO_3^-, NH_4^+, S, Fe, P) were differentiated based on geographic region, with the general trend that samples from AP had relatively higher TOC, TN, and NH_4^+ compared to WA (Figure S1). Stable carbon and nitrogen isotopes were collected from sediments to provide insight into the provenance of the organic matter. The $\delta^{13}C_{org}$-values found in the sediments ranged from −27.5 to −22.2‰ (average −24.6‰) and the $\delta^{15}N$-values range from 1.2 to 4.2‰ (combined average 3.0‰) (Figure S2). Other studies have shown phytoplankton and phytodetritus have $\delta^{15}N$-values from 3.2 to 7.9 and $\delta^{13}C_{org}$-values from −14.94 to −33.93

(Meyers, 1994; Cloern et al., 2002; Mincks et al., 2008). As the ranges of these data is large, it is difficult to determine exact sources, however, the data collected here does suggest phytoplankton as a possible source of organic material to sediments. Samples from WA had, on average, significantly lower $\delta^{13}C_{org}$-values than those from the AP (−25.5 and −23.4, respectively, t-test two-tailed $P < 0.0001$), suggesting WA samples had relatively more recalcitrant carbon. Overall, sediment geochemistry suggests organic matter predominantly sourced by phytoplankton deposition and degradation; however, samples from the AP had relatively higher quantities of macronutrients and more labile carbon. Since the AP is generally warmer than WA (Barnes et al., 2006), the possibility of a higher melting process could bring more nutrients into the water, which is one explanation for this variation. In addition, warmer temperatures could favor microbial activities and the remineralization of nutrients.

The 16S rRNA amplicon dataset included a total of 11,380 OTUs following filtering (initially 10,894,711 raw sequencing reads) and the 18S rRNA gene data generated a total of 4691 OTUs (initially 8,161,768 raw reads). Both 16S and 18S rRNA gene beta diversity ordinations showed communities strongly segregated according to the WA and AP collection regions and sampling time (**Figure 2A**, ANOSIM $R = 0.993$, $P = 0.001$ and **Figure 2B** ANOSIM $R = 0.989$, $P = 0.001$), driven by differences in macronutrients and organic matter (**Figures 2A,B**). The partitioning of diversity based on geographic region is also similar to the variation seen with the macronutrient data. Jamieson et al. (2013) examined the impact of chlorophyll content on Antarctica sediment communities and found few differences in bacterial diversity between sites with different chlorophyll content. However, the %N and TOC were similar between sampling sites, leading the authors to hypothesize that the minor variations found between them may be related to organic matter quality in addition to quantity. Quality of carbon might be a stronger driver in the present study as the samples from AP have relatively more liable carbon.

Prokaryotic communities from WA had on average >1.4x higher richness (Chao1 standard error range 13,075.6–26, 868.7) than those from the AP (Chao1.se range 9051.0–25,498.8, Figure S3A), potentially due to a large number of low abundance (less than two reads) OTUs in the WA samples. Previous 16S rRNA gene studies have calculated Chao1-values between 360 and 899 in the Southern Ocean (Jamieson et al., 2013), 1166 in surface sediment from the Ross Sea (Carr et al., 2013), and 2217 (OTUs calculated at 98% identity) in the Polar Front region (Ruff et al., 2014). Though some variation in richness estimations is seen, this can be attributed to the advent of improved next generation sequencing technologies (i.e., Illumina MiSeq) that has greatly increased the number of sequences garnered from amplicon studies and therefore increased the number of observed OTUs.

The driving force behind diversity and nutrient differences found in WA and AP is likely to be related to multiple, intertwined parameters. Taken together, geochemical and microbial diversity data here suggests a combination of the state (e.g., liable vs. recalcitrant) of organic matter and relative nutrient

FIGURE 2 | Non-metric Multidimensional Scaling (NMDS) ordination of the beta diversity of the (A) 16S and (B) 18S rRNA-defined communities. Samples from Western Antarctica (WA) are gray and Antarctic Peninsula (AP) samples are black. Arrows denote environmental gradients that statistically correlate with the ordination.
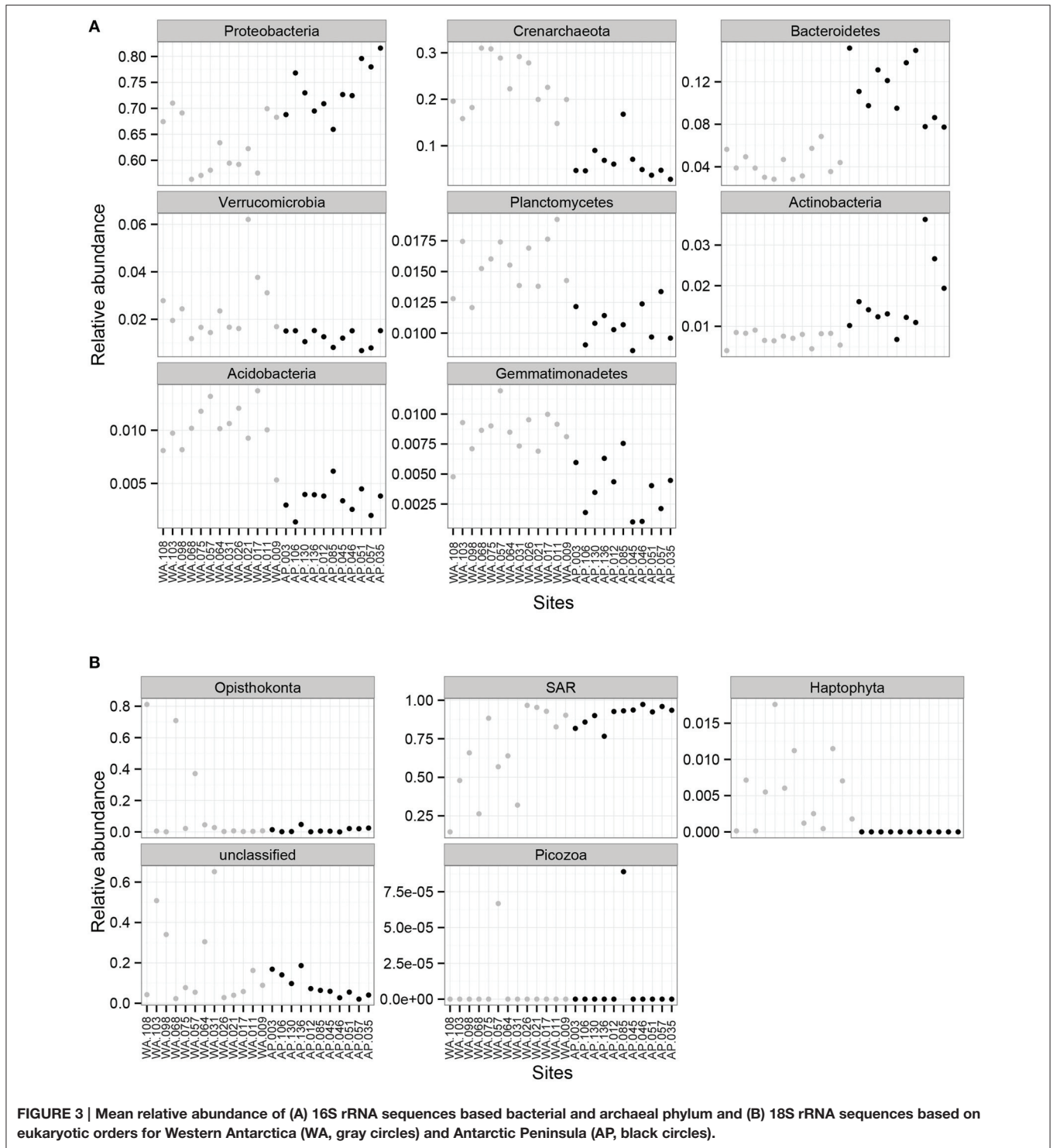
concentration influences Antarctic sediment communities. One possible explanation for the differences observed between WA and AP is that they were collected in two different austral summers. Both regions were sampled in the Astral Summer, during which particulate organic matter deposition begins and increases in the following months (Smith et al., 2008, 2012). However, organic matter deposition in Western Antarctica and the Antarctic Peninsula can be highly variable (Ducklow et al., 2006; Smith et al., 2006, 2008, 2012; Fragoso and Smith, 2012) and related to numerous factors such as temperature, sedimentation, ice cover, currents, and phytoplankton blooms (Arrigo et al., 1998; Ducklow et al., 2006; Smith et al., 2006).

Shared Community Members across a 5500 km Portion of Western Antarctica

Proteobacteria dominated the 16S rRNA sequenced communities of all sites, with major contributions (~15.5% of the sequenced community) from *Crenarchaeota*, primarily *Nitrosopumulis*-type Thaumarchaeota (these are classified

as Phylum *Crenarchaeota* by the Greengenes database). Other OTUs were represented by organisms from the phyla *Bacteroidetes*, *Verrucomicrobia*, *Planctomycetes*, *Actinobacteria*, *Acidobacteria*, and *Gemmatimonadetes* (**Figures 3A**, **4**), and minor contributions (phyla with <0.52% relative abundance) from dozens of others (Figure S4). Relative abundances of *Thaumarchaeota*, *Planctomycetes*, *Acidobacteria*, and *Gemmatimonadetes* decreases along the WA to AP transit, whereas *Bacteriodetes* and *Actinobacteria* showed the opposite trend (**Figure 3A**, statistical differences calculated with a *t*-test, two-tailed $P < 0.0001$ for all mentioned other than *Actinobacteria*, $P = 0.0010$). Notable class level distinctions showed a relative abundance of *Gamma-* and *Delta-proteobacteria* across all samples, and an increase in *Cytophagia* of *Bacteriodetes* in the AP (**Figure 4**). Overall, the relative abundant phyla identified in these sediments have been seen in other studies on Antarctic sediments. Specifically, Ruff et al. (2014) documented sediment that were relatively abundant with *Proteobacteria* and various other studies (Bowman and McCuaig, 2003; Powell et al., 2003; Baldi et al., 2010) all found *Gamma-* and *Delta-proteobacteria* to be relatively dominant community members. In addition, the taxa documented in this study have also been identified as relatively abundant in marine sediments in general (Zinger et al., 2011). Notably, the 16S primer set used here has recently been shown to overestimate *Gammaproteobacteria* and under represent *Alphaproteobacteria* (see Parada et al., 2015), which could impact these data.
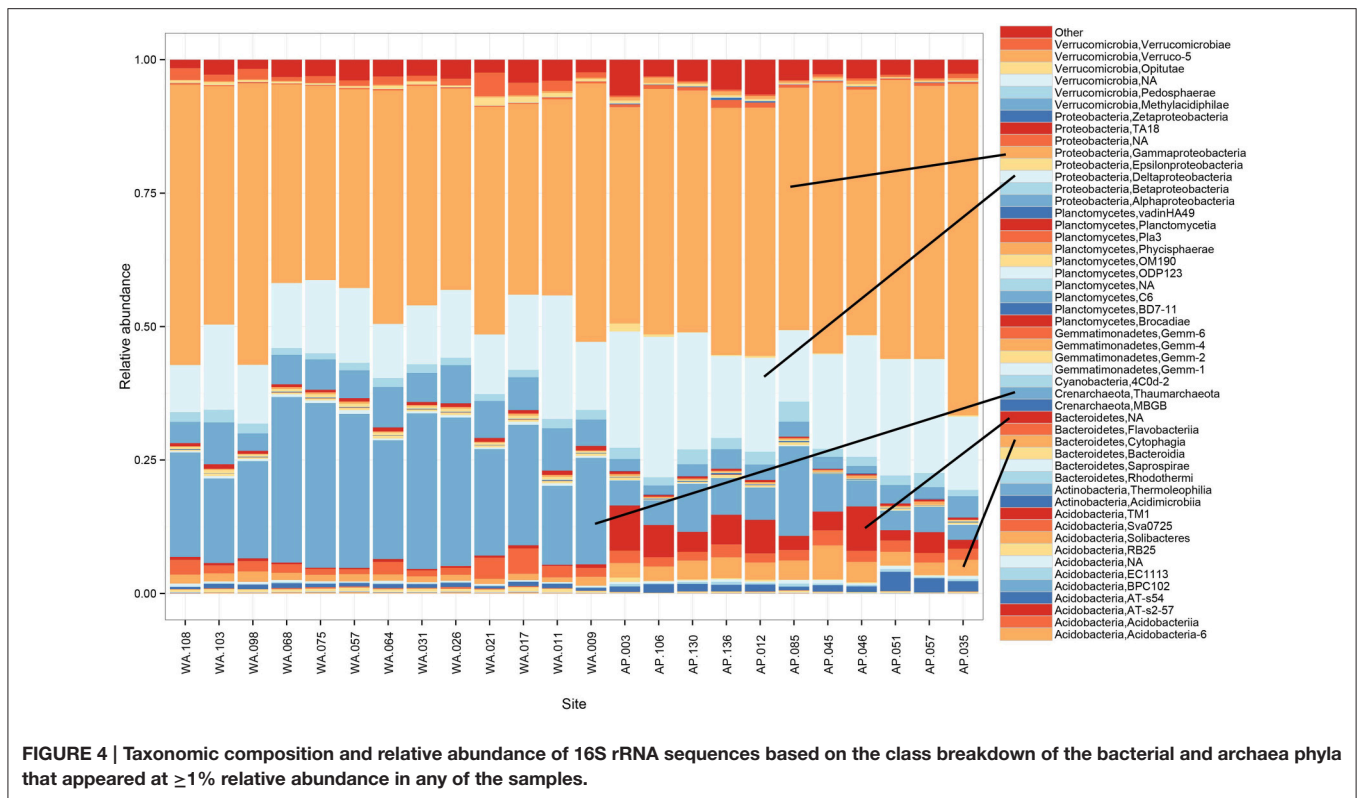
In general, the sequenced 16S rRNA communities of all benthic sediments had similar dominant OTUs. Both WA and AP shared three of the top five most abundant OTUs. OTU0000001, classified to the family of *Piscirickettsiaceae,* was the most dominate OTU in samples from AP (Figure S5A) and its relative abundance negatively correlated with $\delta^{13}C_{org}$, NH_4^+, and Si (Table S2). Bacteria within the family *Piscirickettsiaceae* have been identified in planktonic communities (Giovannelli et al., 2012; Wang et al., 2015) and *Cycloclasticus pugetii* (found within the family *Piscirickettsiaceae*) has been shown to degrade complex carbon (Geiselbrecht et al., 1998; Kasai et al., 2002; Wang et al., 2008). OTU0000002, classified to the genus *Nitrosopumilus,* was extremely abundant (Figure S5A) and its relative abundance was statistically correlated with $\delta^{13}C_{org}$ and Si (Table S2). All known isolates of *Nitrosopumilus* are lithotrophic archaea (Konneke et al., 2005, 2014; Walker et al., 2010; Qin et al., 2014), and these have been documented as dominant community members in Antarctic sediments in the Weddell Sea (Gillan and Danis, 2007), as well as in a variety of pelagic environments (Konneke et al., 2005; Labrenz et al., 2010; Baker et al., 2012). OTU0000004 (Figure S5A) is a member of the OM60/NOR5 clade and its relative abundance correlated with pH, $\delta^{13}C_{org}$, NH_4^+, and Si (Table S2). OM60/NOR5 clade members are known inhabitants of surface water and coastal sediments (Connon and Giovannoni, 2002; Yan et al., 2009; Spring et al., 2013; Sharma et al., 2014). A recent study has also implicated members of this clade as key in degrading phytoplankton-derived organic matter in sediments of the Drake Passage at the Antarctic Polar Front (Ruff et al., 2014). The correlation of the *Piscirickettsiaceae* and OM60/NOR5 clade OTU to carbon isotope values and carbon

FIGURE 3 | Mean relative abundance of (A) 16S rRNA sequences based bacterial and archaeal phylum and (B) 18S rRNA sequences based on eukaryotic orders for Western Antarctica (WA, gray circles) and Antarctic Peninsula (AP, black circles).

quality might be related to the ability of each organism to metabolize carbon.

Overwhelmingly, the dominant organisms were members of the SAR (Stramenopiles, Alveolates, Rhizaria) supergroup (Burki et al., 2007), with some exceptions in WA (**Figure 3B**). Members of SAR have been found in marine environments, including

the Antarctic water column (Luria et al., 2014) and sediments (Habura et al., 2004; Pawlowski et al., 2011). Other notable groups documented in the sediments were Opisthokonts and Haptophytes. Alpha diversity calculations show richness (Chao1) and evenness (Shannon and Simpson) values as being higher in WA then AP (Figure S3B).

FIGURE 4 | Taxonomic composition and relative abundance of 16S rRNA sequences based on the class breakdown of the bacterial and archaea phyla that appeared at ≥1% relative abundance in any of the samples.

Nutrient Quantity and Quality Drive Relative Abundance of Dominant Taxa

In general, the relative abundance of *Thaumarchaeota* was higher in samples from WA (**Figure 4**), which contained fewer organics and nutrients when compared to samples from AP (Figure S1). In addition, relative abundance of the class *Thaumarchaeota* and an abundant *Thaumarchaeota* OTU (OTU000003, most abundant OTU in WA) were both inversely correlated (0.01 level, two tailed *t*-test) with pH, $\delta^{13}C_{org}$, NH_4^+, and Si (Table S2). Representatives from *Thaumarchaeota* have been previously reported in Antarctic marine environments (Delong et al., 1994; Murray et al., 1998; Alonso-Saez et al., 2012; Signori et al., 2014; Hernandez et al., 2015), sediments (Gillan and Danis, 2007), and soils (Ayton et al., 2010; Richter et al., 2014). Known *Thaumarchaeota* are lithotrophs capable of ammonium oxidation and some are known to degrade proteins (Leininger et al., 2006; Wuchter et al., 2006; Alonso-Saez et al., 2012; Luo et al., 2014). The overall low nutrient content in the sediments from WA and the statistical relationship between *Thaumarchaeota*, low TOC, and slightly more refractory carbon (e.g., lower $\delta^{13}C_{org}$) suggests these are conditions that allow these organisms to flourish.

The relative abundance of the phylum *Bacteroidetes* correlated with TOC, Si, NH_4^+, and $\delta13C_{org}$ (Table S2). Of the five most abundant OTUs classified as *Bacteroidetes, four* were positively correlated with TOC, Si, and $\delta13C_{org}$ (Table S2) and the other was negatively correlated with pH, TOC, Si, and $\delta13C_{org}$ (Table S2). Bacteria from the *Bacteroidetes* phylum are very diverse and have

been found in numerous environments from freshwater, soils, and oceans, and are expected to play a role in degrading complex carbon (reviewed in Kirchman, 2002; Gupta, 2004; Thomas et al., 2011).

Strikingly, the bulk of the measured SAR abundance across the AP could be accounted for by a single OTU (OTU0000013), designated SAR "unclassified" by GreenGenes taxonomy (Figure S5B). NCBI BLAST of the representative sequence for OTU0000013 returned hits with a 98% identity to the phylum *Cercozoan*. A marine cercozoan, *Cryothecomonas*, has been identified as a heterotroph that can feed on diatoms (Thomsen et al., 1991; Thaler and Lovejoy, 2012). Similarly, OTU0000010, designated as a *Stramenopile*, was only found in the AP. Examination of the representative OTU sequence for OTU000010 returned a 100% identity score to organisms classifying as *Chaetoceros*, the largest genus of diatoms. Conversely, an OTU (OTU0000030), classified as *Stramenopiles, Ochrophyta*, had the highest mean relative abundance in WA samples (Figure S5B), although its distribution was highly variable. In contrast to bacterial and archaeal data, relative abundance of broad phylogenetic eukaryotic categories was not significantly correlated with the nutrient data, however OTU0000013 (*Cercozoan*) and OTU0000010 (*Chaetoceros*), were correlated (0.01 level two tailed *t*-test) with pH, TOC, Si, and $\delta13C_{org}$ (Table S2).

Although, it is only speculation, the relationship between *Bacteroidetes* and SAR OTUs with TOC and Si could suggest a trophic relationship. Our data demonstrated an increased

proportion of TOC, TN, NH_4^+, Si, and labile carbon in the AP relative to the WA samples, suggesting a recent diatom bloom and increased deposition of these components to the sea floor. Relative abundance of the phylum *Bacteroidetes* and four OTUs that fall under this phylum were also strongly correlated to TOC (Table S2). One of the OTUs that positively correlated with TOC was classified to the family *Flavobacteriaceae*. Members of this family have been linked to organic matter degradation in Antarctic sediments (Bowman and McCuaig, 2003; Baldi et al., 2010) and the Southern Ocean, with their relative abundance positively correlated with chlorophyll (Abell and Bowman, 2005) and algal biomass (Ruff et al., 2014), and genomic and metagenomic evidence for a role in processing organic matter from algae (Bauer et al., 2006; Fernandez-Gomez et al., 2013; Williams et al., 2013). Thus, our isotopic and SSU sequence results are consistent with the hypothesis that AP sediment organics were sourced by diatom sedimentation with subsequent degradation by *Bacteroidetes* and *Cercozoan* taxa. While this is only one possible explanation, sampling may have captured the remnants of a phytoplankton bloom and the subsequent trophic interaction.

CONCLUSIONS

This study offers a unique look at a spatially diverse sample set covering 5500 km of Antarctic surface sediment. Analyses revealed a diverse benthic microbial community that was highly variable throughout the two cruises and geographic regions. Though the cruises were conducted during two different field seasons, one of the possible drivers of the highly variable communities could be quality and quantity of organic matter (TOC and $\delta^{13}C$). WA was characterized by relatively more recalcitrant carbon and had a larger influence of archaea, specifically *Thaumarchaeota*. Additionally, AP was characterized by relatively higher organics and had a large presence of sequences corresponding to diatoms (e.g., *Chaetoceros)* and taxa from the phyla *Bacteroidetes* and *Cercozoan*, which have been known to be associated with degradation of the corresponding organics from sinking particles and fecal pellets from blooms and their associated grazers. In addition, similarities were found throughout the entire sample set as three of the top five OTUs documented in the 16S rRNA sequenced communities were shared: OTU0000001 (*Piscirickettsiaceae),* OTU0000002 (*Nitrosopumilus),* and OTU0000004 (OM60/NOR5 clade).

Future variability in ice coverage, light, temperature, and food web structure could have a profound influence on the amount of organic carbon reaching the bottom, thus influencing the benthic community structure and their associated functions. With the continued warming of the WAIS, the amount of melt water entering coastal water around the ice shelf is predicted to increase, which impacts both coastal and open ocean water composition (Dierssen et al., 2002; Rignot et al., 2011; Pritchard et al., 2012; Shepherd et al., 2012; Depoorter et al., 2013). This increase in melt water could lead to the increase in phytoplankton blooms in these areas (Smith and Gordon, 1997; Arrigo et al., 1998; Ducklow et al., 2006; Smith et al., 2007) and, therefore, could increase organic matter transport to the sea floor. These increases of organic matter may ultimately influence communities that were once composed predominately of lithotrophic organisms, as observed in WA samples, to ones often associated with degradation of increasing organic matter, as observed in AP samples. Thus, changes to these communities in the form of their taxonomic members and resulting impacts on global nutrient cycling must continue to be studied.

AUTHOR CONTRIBUTIONS

DL, MH, JT, BT, and PB analyzed data and prepared figures and tables. AM, PB, and KH collected samples. All authors contributed to writing the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmicb.2016.00284

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