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ORIGINAL ARTICLE

Dominance of *Oscillospira* and *Bacteroides* in the bacterial community associated with the degradation of high-concentration dimethyl sulfide under iron-reducing condition

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Abstract Microbial consumption of high-concentration dimethyl sulfide (DMS) under various redox conditions was investigated with freshwater sediments as inoculum. After about 1-year cyclic static enrichment at an initial DMS concentration of 10 mM, it was found that addition of ferric iron can lead to better DMS degradation efficiency compared to bicarbonate, nitrate, and oxygen as the electron acceptors especially, significantly higher than sulfate addition. The rate constant of DMS degradation was only 0.01106 ± 0.00139 day^{-1} under sulfate reduction, but increased to 0.02355 ± 0.00173 day^{-1} under iron reduction. Enriched bacterial communities under both aerobic and iron-reducing conditions were highly organized. Thus, the specialized bacterial communities were responsible for the different degradation conditions. The genera *Thiobacillus* and *Pseudomona*, which had been found previously to be capable of DMS degradation, belong to the most abundant bacteria in the aerobic microbial community. In the iron-reducing community, the four genera *Oscillospira*, *Bacteroides*, *Parabacteroides*, and *Petrimonas* are dominant, and in total account for 88 % of the total bacterial sequences. Species from the four anaerobic genera might be involved in ferric reduction and/or high-concentration DMS degradation. Thus, sediments in eutrophic lakes might harbor a diverse of functionally specific bacteria for DMS degradation.

Keywords Biodegradation · Dimethyl sulfide (DMS) · Iron reduction · *Oscillospira* · *Bacteroides*

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Introduction

The emission of volatile reduced sulfur compounds such as dimethyl sulfide (DMS) can be problematic due to their foul smell and low odor threshold. In addition, DMS has received special attention due to its impact on acid precipitation and climate control. Atmospheric oxidation products from DMS can form aerosol particles and cloud condensation nuclei, and thus DMS is suggested to play a major role in aerosol formation and cloud albedo (Lomans et al. 2002; Schafer et al. 2010).

In nature, DMS is mostly present in marine and freshwater sediments (Visscher et al. 1995; Lomans et al. 1997). In anoxic freshwater sediments, DMS is generally considered to be one of the dominant volatile organic sulfur compounds (VOSC) and originates mainly from the methylation of sulfide or from degradation of sulfur-containing amino acids such as methionine and cysteine. But the formation of VOSC in freshwater sediments is well balanced mainly by efficient anaerobic degradation, resulting in low steady state concentrations (Lomans et al. 1999a).

In addition, DMS is often emitted from a variety of industries such as wastewater treatment, kraft pulping, and animal rendering (Lecloirec et al. 1992; Glindemann et al. 2006). While DMS in natural environments was detected at low concentrations (μM range), DMS concentrations in some types of

wastewater from the refineries industry (van Leerdam et al. 2006) were high and even reached the mM range.

Several approaches have been tested to eliminate DMS (Cantau et al. 2007; Wu et al. 2014). Chemical and physical methods such as photooxidation and chemical scrubbing are often effective in DMS removal, but they are associated with high costs and often resulted in secondary pollutants. In comparison, a microbial method was preferred in DMS degradation (Hatton et al. 2004), as this method is performed at low-cost and has low environmental impact. Microbial processes include aerobic and anaerobic degradation of DMS. The aerobic microbial process has been extensively studied, and various groups of bacteria such as *Thiobacillus* and *Methylophaga* species were identified for aerobic catabolism of DMS (Visscher and Taylor 1993a; Endoh et al. 2003; Schafer 2007).

Alternatively, DMS can be eliminated through several anaerobic pathways, with a variety of methanogens, sulfate-reducing bacteria, phototrophic bacteria, and denitrifiers capable of growth on DMS (Tanimoto and Bak 1994; Visscher et al. 1995; Lyimo et al. 2009). Ferric iron is an important electron acceptor for microbial metabolism, and ferric reducing bacteria can outcompete sulfate-reducing bacteria as well as methanogens for organic matter degradation in anoxic environments (Lovley et al. 2004). So far, there are few studies about DMS degradation under iron-reducing conditions (Haaijer et al. 2008).

To date, information about biodegradation of DMS at high concentration is very limited. In this study, microbial communities from lake sediments were enriched to endure and degrade DMS at high concentrations and under the different redox conditions. And the primary objective of this investigation was to gain an insight into bacterial communities associated with the degradation of the high-concentration DMS under aerobic and iron-reduction conditions, using a 16S rRNA gene high-throughput 454 pyrosequencing approach.

Materials and methods

Sediment sampling

Sediment samples were taken by cylindrical collector from Taihu Lake (31°100′ N, 120°240′ E), the third largest shallow freshwater and subtropical lake in China. Sediment samples were transported to the laboratory within several hours under ambient temperature conditions.

Setup of microcosm experiments

The collected sediment samples were stirred, and 2 g of the homogeneous sedimentary sample and 50 mL mineral salts medium were dispensed in one 100-mL serum bottle. In addition to aerobic incubation, four different anaerobic redox conditions (nitrate-reducing, iron-reducing, sulfate-reducing, and methanogenic) were adopted by adding four different electron acceptors [100 mM sodium nitrate ($NaNO_3$), 120 mM ferric citrate ($FeC_6H_5O_7$), 40 mM sodium sulfate (Na_2SO_4), and 40 mM sodium hydrogen carbonate ($NaHCO_3$)] to serum bottles, respectively. After the pH of the liquid medium in bottles was adjusted to 7.0 with 0.5 M HCl or NaOH, the headspace of the bottles for anaerobic incubation was flushed with pure nitrogen for 5 min. Then, the bottles were sealed with grey butyl rubber stoppers (Xingya, Ningbo China) because they showed less absorption of DMS, followed by adding DMS as the carbon substrate to the bottles through syringe from stock solution DFs to a final concentration of 10 mM. The bottles were incubated in the dark without shaking at 25 °C. The bottles with sediment slurries autoclaved at 121 °C for 20 min served as abiotic control. Experiments were done in triplicate.

After the solution became turbid, the inocula (5 mL) were sub-cultured into the same fresh medium in serum bottles every 20–30 days. This procedure was lasted for nearly 1 year for cyclic enrichment of DMS-degrading microbial communities under various redox conditions. In the last enrichment cycle, the gas sample in the headspace of test bottles was sampled every 5 days with a syringe for measurement of residual DMS concentrations to determine DMS degradation kinetics. The DMS concentrations were computed by using experimentally calculated distribution coefficients (liquid concentration/vapor concentration) of 15.5 for DMS (Tanimoto and Bak 1994).

DMS analytical method

Gas samples (50 μL) were taken from each incubation bottle with a pressure-lock syringe and analyzed to determine DMS concentration with a Angilent 7890-A gas chromatograph equipped with a flame ionization detector and a GS-GasPro capillary PLOT column (60 m × 0.32 mm I.D.) as described previously (Lu et al. 2012).

Biodegradation kinetics

The biodegradation of DMS was described by the first order kinetics Eq. (1) (Li et al. 2010),

$$C = C_0 e^{-kt} \quad (1)$$

where C_0 is the concentration of DMS at time zero, C is the concentration of DMS in the medium at time t, and k is the first-order rate constant (biodegradation

rate) of the reaction. The half life for each DMS compound, $t_{1/2}$, was calculated by the following formula (2),

$$t_{1/2} = (ln\ 2)/k \quad (2)$$

Isolation and identification of bacterial strains

For isolation and purification of DMS-degrading microorganisms under various enrichment conditions, a slope agar medium was prepared in a serum bottle by mixing 1.5 % (w/v) agar and the mineral medium for each redox condition described above. Then, 100 μL of enriched liquid samples were streaked on the agar surface, followed by injection of DMS. Isolation from anaerobic enrichments was done in anaerobic chamber. Those serum bottles were incubated at room temperature. Single colonies were picked and then transferred to the fresh agar medium. This procedure was repeated several times to isolate pure culture.

For the genetic identification, bacterial genomic DNA was extracted according to the method described previously (Jiang et al. 2004). PCR reaction was carried out for bacterial 16S rRNA gene, using universal eubacterial forward primer 27F and reverse primer 1492R. PCR products were sequenced by BGI (Shanghai, China). Closest relatives were determined by comparison to I6S rDNA genes in the NCBI database (http://ncbi.nlm.nih.gov/BLAST) using BLAST.

DNA extraction, PCR amplification, and pyrosequencing from enriched samples

Liquid microbial samples under aerobic conditions (AS1 and AS2) and anaerobic iron reduction conditions (ANFS1 and ANFS2) at the end of experiments were selected for bacterial community analysis. A 50-mL subsample was collected using a 60-mL syringe and then filtered by 0.2 μm pore-size polycarbonate filter (Millipore, GTTP, 47 mm diameter), and biomass on the filter was used for DNA extraction using the UltraClean Soil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's directions. The concentration and purity of extracted DNA was then determined using NanoDrop 2000/2000C spectrophotometer.

For the bacterial 16S rRNA amplification, forward primer 341F (5′- CCTACGGGAGGCAGCAG-3′) and reverse primer 907R (5′-CCGTCAATTCCTTTGAGTTT-3′) were used (Bernard et al. 2012). Twenty microliters of PCR mixture contained 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.5 μM of each primer, 0.4 μL of FastPfu Polymerase (TransGen, Beijing, China), and 10 ng of genomic DNA. The PCR amplification was performed in triplicate for each DNA extract, and a smaller number of PCR cycles were employed in this study. The amplification was conducted under the following conditions: initial denaturation at 95 °C for 2 min, and 25 cycles at 95 °C for 30s, 55 °C for 30s and 72 °C for 30s, and a final extension at 72 °C for 5 min. The amplicons were quantified by fluorimetry with PicoGreen dsDNA quantitation kit (Invitrogen, Life Technologies, Carlsbad, CA, USA) and pooled at equimolar concentrations. Roche GS-FLX 454 pyrosequencing was conducted by Meiji Biotechnology Company (Shanghai, China).

Sequence analysis

All 16S rRNA pyrosequencing reads were analyzed using QIIME (Quantitative Insights Into Microbial Ecology) (Caporaso et al. 2010) software package version 1.6.0 and MOTHUR version 1.30.0 (Schloss et al. 2011). Sequences were quality controlled using the Split_Libraries.py script. Quality criteria were a minimum sequence length of 200 bp, a maximum sequence length of 1000 bp, and a minimum average quality score of 25. Stringent quality control parameters were used to avoid ambiguous bases/mismatches in the primer sequence and barcode errors.

The trimmed sequences were then analyzed using Mothur. Sequences were aligned by align.seqs command against a Greengenes template alignment (http://greengenes.lbl.gov/Download/Sequence_Data/Fasta_data_files/core_set_aligned.fasta.imputed). Sequences were clustered into operational taxonomic units (OTUs) using dist.seqs and the average method in cluster with a 3 % distance cut-off criterion. OTUs were classified using classify.seqs at the 0.03 level using the Greengenes database (Quast et al. 2013).

To compare and perform statistics across samples, the numbers of sequences in each sample were first normalized down to the number in the sample with the fewest sequences. Library coverage, richness, and diversity estimates (ACE, Chao1, and Shannon) were calculated for the samples using MOTHUR's summary.single commands at a 0.03 distance cut-off sequences. Rarefaction curves were calculated using rarefaction.single. Pareto–Lorenz (PL) evenness curves were constructed to represent graphically the specific microbial community structure (Marzorati et al. 2008; Cai et al. 2014).

Statistical analysis

Statistical significance of differences was determined by one-way analysis of variance using the SPSS software (IBM SPSS Statistics 19). A $p < 0.05$ was considered significant.

16S rRNA gene sequencing data from this study were submitted to the NCBI Sequence Read Archive (SRA) under accession number SUB716763. The 16S rRNA gene nucleotide sequences reported in this paper were submitted to GenBank under accession number KP076657-KP076663.

Results and discussion

DMS degradation kinetics under aerobic and anaerobic conditions

The batch enrichments were carried out by adding high-concentration dimethylsulfide as the only catabolic substrate. After a long period of acclimation, the bacteria were adapted to the enrichment condition. The change of DMS concentrations with incubation time in the last enrichment cycle under different redox conditions is shown in Fig. 1. It is clear that DMS at this high concentration is partially used by the sediment microbial community with or without an external electron acceptor, and the addition of electron acceptors enhanced DMS biodegradation (ANOVA, $p < 0.05$). DMS concentration in the abiotic control treatment did not decrease significantly (ANOVA, $p > 0.05$), indicating that the decrease in DMS concentration in the other treatments was just due to microbial degradation.

At the end of the last cycle, the DMS removal efficiencies under anaerobic iron-reducing, nitrate-reducing, and methanogenesis conditions did not have significant difference (ANOVA, $p > 0.05$), while the average DMS removal efficiency under anaerobic iron reducing reached 60.45 % and was the highest among all treatments (Table 1). On the contrary, it was reported previously that removal efficiency of low-concentration DMS under iron reduction was much lower than those under nitrate reduction and sulfate reduction (Haaijer et al. 2008). Thus, it seems that the microbial iron reduction process has specific advantages at high DMS concentrations. Additionally, DMS removal efficiency under aerobic conditions was about 50.80 %. The removal efficiency under sulfate-reducing conditions was only 30.40 % and the lowest among all treatments applied with electron acceptors.

DMS degradation kinetics were further assessed by a single first-order kinetic model fitted to the data in Fig. 1 and shown in Table 1. It was obvious that addition of electron acceptors led to higher first-order rate constants for DMS degradation. Aerobic degradation of DMS is previously known to be energetically more favorable than anaerobic conversion. As shown in Table 1, however, DMS degradation rate under aerobic conditions was not higher than those under anaerobic conditions, which might result from the oxygen limitation in the unshaken incubation (Lomans et al. 1999a).

The first-order rate constants reached 0.02355 ± 0.00173, 0.02267 ± 0.00256, and 0.02123 ± 0.00242 days^{-1} under ferric-reducing, methanogenic, and nitrate-reducing conditions, respectively (Table 1), and higher than that with sulfate as the electron acceptor. It was generally found that sulfate-reducing bacteria compete for DMS with methanogens at low concentrations. DMS-consuming sulfate-reducing bacteria might outnumber methanogenic archaea by virtue of their higher affinity for methylated sulfur compounds at low DMS concentrations (Lyimo et al. 2009). But they would lose their competitive advantage at high DMS concentrations because DMS is ecologically similar to methanol, which is a noncompetitive methane precursor (Oremland and Polcin 1982). Meanwhile, the ferric reduction in the sediment was the most important chemical change influencing the pathways of organic matter decomposition. A similar metabolism of organic matter with Fe(III) as the electron acceptor is theoretically possible and is more thermodynamically favorable than the

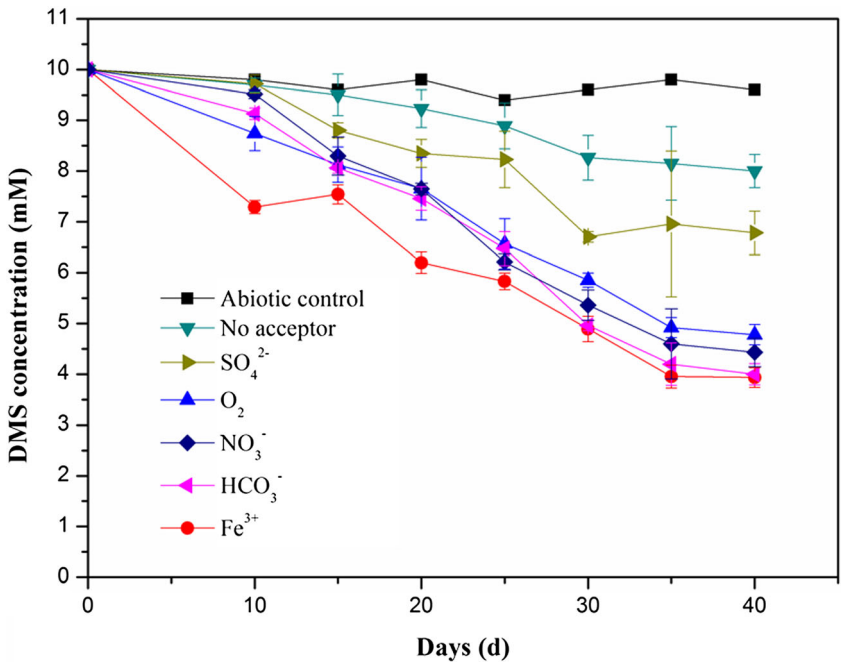

Fig. 1 The degradation of dimethyl sulfide with different electron acceptors

Table 1 The first-order rate constant (k) of DMS-degradation, half-lives ($t_{1/2}$), and correlation coefficient (r^2) in the last enrichment cycle of microcosm experiments, and the removal efficiency of DMS at the end of the last enrichment cycle

Electron acceptor	k (day^{-1})	r^2	$t_{1/2}$ (day)t	Removal efficiency (%)
Abiotic control	No fit [a]	No fit [a]	_ [b]	0.04 ± 0.001
No acceptor	0.00610 ± 0.00058	0.94	113.6	18.47 ± 0.036
O_2	0.01866 ± 0.00139	0.96	37.1	50.80 ± 0.118
Fe^{3+}	0.02355 ± 0.00173	0.96	29.4	60.45 ± 0.011
HCO_3^-	0.02267 ± 0.00256	0.92	30.6	58.01 ± 0.021
NO_3^-	0.02123 ± 0.00242	0.92	32.6	54.01 ± 0.035
SO_4^{2-}	0.01106 ± 0.00139	0.90	62.7	30.40 ± 0.072

[a] "No fit" means that no convergence is obtained in the model

[b] "–" indicates that no data are available

mineralization of organic matter with sulfate reduction or methane production as the terminal step (Achtnich et al. 1995; Roden and Wetzel 1996). Therefore, when Fe(III) was available, ferric reduction was more likely to happen in high substrate concentration conditions.

Bacterial community composition

The ferric iron treatment in this study showed a better DMS degradation ability, which compares with the nitrate reduction and methanogenic conditions. The denitrifying bacteria and methanogens were the special bacteria taking part in anaerobic DMS degradation in the previous study (Lomans et al. 1999b; Visscher and Taylor 1993b). Whether those bacteria and were involved in the ferric reduction process, also particular microorganisms, was unknown. In order to understand the composition of the bacteria involved in iron reduction and to compare the differences of aerobic and anaerobic microorganisms under the conditions of high-concentration DMS, the microbial communities were analyzed for 454 pyrosequencing.

The coverage of libraries at 0.03 cluster distances was high for both samples, indicating that the surveying effort covered almost the full extent of taxonomic diversity at this genetic distance. The rarefaction curves at a 3 % genetic level almost reached the saturation level (Fig. S1a) with coverages higher than 98 % (Table S1). Shannon or Simpson indexes of bacterial communities were almost the same for duplicate ferric-reducing samples, but showed much variation for duplicate aerobic samples.

For all the samples, the Pareto–Lorenz curves, which refer to the functional organization, were distributed in the same pattern as shown in Fig. S1b. It was observed that 20 % of the OTUs corresponded to 95–98 % of the cumulative abundance intensities for all the samples. The latter number is the *Fo* index, which when higher than 85 % represents a specialized community in which a small number of species is dominant and all the others are present in low number. Thus, we conclude that all these communities were highly functionally organized and might be affected by the DMS concentrations and the redox conditions.

As shown in Fig. 2a, the dominant phyla in bacterial communities under aerobic and anaerobic ferric-reducing conditions were markedly different. *Proteobacteria* was the most abundant phylum in the aerobic sample, accounting for 87–94 % of total bacteria sequence. The β-subdivision was the most dominant *Proteobacteria*, followed by α-, γ-, and δ-subdivisions (Fig. 2b). Additionally, *Bacteroidetes* was detected in aerobic samples as dominant with an abundance of about 2–6 %. *Flavobacteriia* and *Sphingobacteriia* were the major clades of *Bacteroidetes* in aerobic samples (Fig. 2b). This was similar to the analytical results of bacterial communities in the marine DMS-degrading enrichment culture (Schafer 2007; Vila-Costa et al. 2006). They found the dimethylsulfide consumption was stimulated by the addition of DMS, whereas there was no stimulation with other C1 compounds. And the DMS utilization as a growth substrate was carried out by specialized methylotrophs other than all bacteria. Thus, the dominant functionally organized species of aerobic and ferric-reducing samples (Fig. S1b) in this study might be associated with the DMS degradation. Under the anaerobic ferric-reduction condition, however, *Firmicutes* and *Bacteroidetes* were the most abundant phyla and accounted for 44 and 50 % of total bacterial sequences, respectively (Fig. 2a). *Bacteroidia* and *Clostridia* belonged to the most dominant classes in *Bacteroidetes* and *Firmicutes*, respectively (Fig. 2b).

At the level of family or genus, *Thiobacillus* was the most abundant genus in the aerobic sample and accounted for 34–58 % of the total bacterial sequences in the duplicate aerobic samples (Fig. 2c). The genus *Pseudomona* was the second dominant with an abundance of 13–19 %. Correspondingly, one *Pseudomona* strain was isolated with DMS as the sole carbon substrate (Table S2). The genera *Brevundimonas*, *Gelidibacter*, and *Lysobacter* were also detected with abundances of around 8–10 % in the aerobic samples. Some species of the two dominant genera *Thiobacillus* and *Pseudomona* were found to be capable of aerobic DMS degradation and could grow on DMS as a sole carbon or sulfur source (Visscher and Taylor 1993a; Endoh et al. 2003). While there were many bacterial strains for aerobically degrade

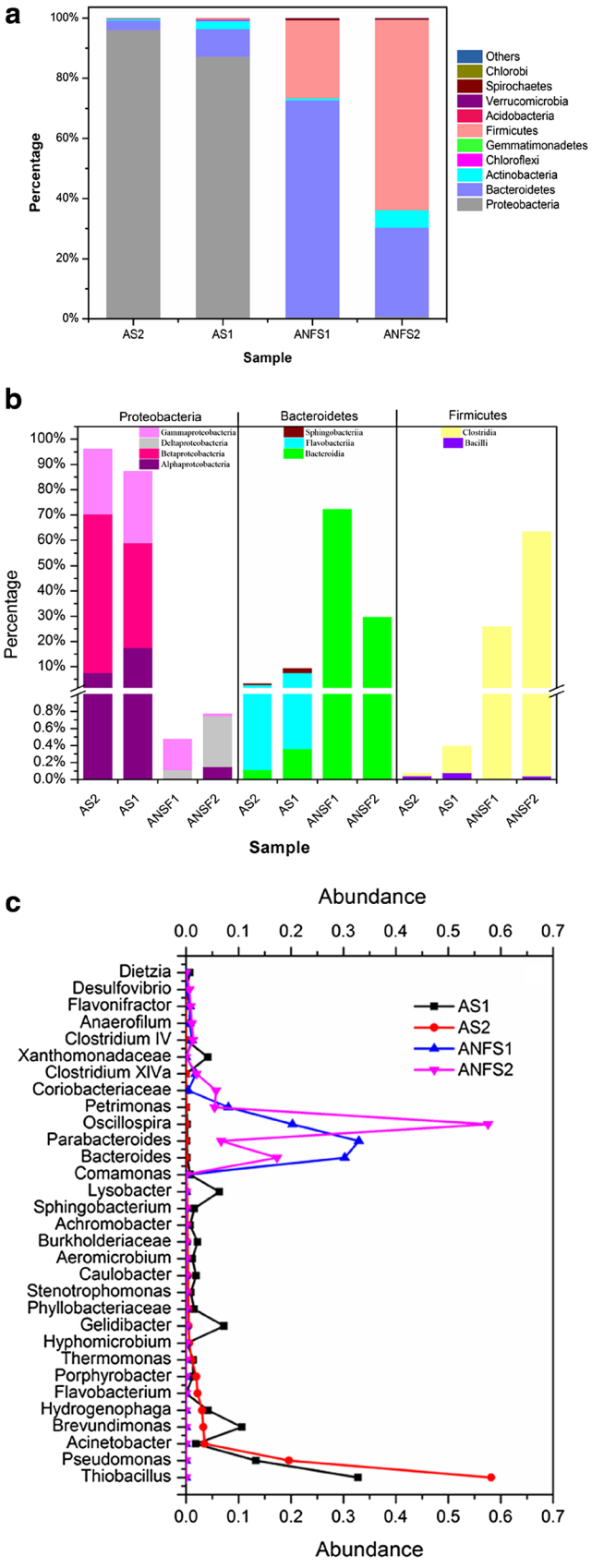

Fig. 2 Abundances of different phyla (**a**), classes of the most abundant phylum (**b**), and genera with an abundance higher than 0.5 % (**c**) in the aerobic sample (AS) and anaerobic ferric-reduction samples (ANFS). Phylogenetic groups accounting for 0.25 % of the classified sequences are summarized in the artificial group "others"

DMS, the dominant existence of bacteria from *Thiobacillus* and *Pseudomona* indicated that strains from the two genera could adapt to high concentrations of DMS (Schafer et al. 2010).

The four genera *Oscillospira*, *Parabacteroides*, *Bacteroides,* and *Petrimonas* were detected in the two ferric-reducing samples with an abundance higher than 5 %, and the genus *Clostridium* X1Va accounted for 1–1.5 % in the two anaerobic samples. The sequences assigned to *Oscillospira*, belonging to the class *Clostridia*, had abundances of 21 and 57 % in the two iron-reducing samples, respectively. In fact, the genus *Oscillospira* was also wildly presented in the rumen (Mackie et al. 2003) and was similar to the closest neighbour of strain *Clostridium* (Iino et al. 2007). Some strains of the *Clostridium* were anaerobic sulfate-reducing bacteria that are able to metabolize the sulfate final product of DMS in environments containing organic matter for survival (Chung et al. 2010). Both *Bacteroides* and related *Parabacteroides* were found to predominate in human gastrointestinal (Qin et al. 2010) and other mammalian organs (Paster et al. 1994). *Parabacteroides* species show a high similarity with *Bacteroides* in terms of sharing a high number of protein families and functional characteristics, likely because they share habitat (Karlsson et al. 2011).

There are many bacterial strains that are known to use Fe(III) as the sole terminal electron acceptor and conserve energy to support growth from Fe(III) reduction (Lovley et al. 2004). Some strains from *Bacteroides* and *Clostridium* could anaerobically reduce iron primarily through fermentative processes (Park et al. 2001; Lovley et al. 2004; Wang et al. 2010). The isolate DMS-F1 from the ferric-reducing enrichment (Table S2) was affiliated with *Anaerofilum agile*, which belongs to fermentative species (Zellner et al. 1996). Although *Anaerofilum sp.* DMS-F1 might not be a dominant strain in the iron-reducing community, the growth of this isolate on ferric enrichment further suggested that the iron-reducing fermentation process may occur in the DMS utilization.

In addition, 16S rRNA gene sequences affiliated to *Bacteroides* were also detected in other iron-reducing enrichments (Lin et al. 2007; Wang et al. 2009). *Bacteroides* are known to be proficient in degrading large molecular compounds. Recently, genomics analysis suggested that *Bacteroides* has the potential to degrade a wide number of xenobiotic compounds (Karlsson et al. 2011). *Bacteroides* were belonged to the class *Bacteroidia* of the phylum *Bacteroidete*. The class *Flavobacteriia* and *Sphingobacteriia* also belong to the phylum *Bacteroidete*. The genuses *Gelidibacter*, *Flavobacterium*, and *Sphingobacterium* belong

to classes *Flavobacteriia* and *Sphingobacteriia* dominant in this study as shown in Fig. 2c were capable of DMS turnover (Green et al. 2011; Schafer 2007; Vila-Costa et al. 2006). *Flavobacteriia* and *Bacteroidia* have phylogenetic proximity, and some functional operons transferred between them (Thomas et al. 2012). The predominant existence in the anaerobic samples suggested that *Bacteroides* takes part in the iron reduction and DMS degradation, but the real metabolic pathway behind needs to be further studied.

Conclusion

The addition of an electron acceptor can enhance DMS removal at an initial high concentration of 10 mM. Addition of ferric iron led to comparable or even a little better DMS degradation compared to bicarbonate and nitrate as the electron acceptors and significantly higher removal efficiency than sulfate addition. Enriched bacterial communities under both aerobic and ferric-reducing conditions were highly organized. While bacteria closely related to the genera *Thiobacillus* and *Pseudomona* belonged to the most abundant in the aerobic microbial community, the four genera *Oscillospira*, *Bacteroides*, *Parabacteroides*, and *Petrimonas* were found as dominant in the iron-reducing community. Bacteria from these dominant genera might be able to handle high-concentration DMS.

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Compliance with ethical standards

Conflict of interest No conflict of interest declared.

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