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REVIEW

Biogeochemical sulfur cycling coupling with dissimilatory nitrate reduction processes in freshwater sediments

Jin Zhu, Yan He, Yishuang Zhu, Minsheng Huang, and Yaping Zhang

Abstract: Dissimilatory nitrate reduction processes including denitrification, anaerobic ammonium oxidation (ANAMMOX), and dissimilatory nitrate reduction to ammonium (DNRA) are crucial nitrogen (N) cycling pathways in freshwater ecosystems. Denitrification has long been considered as the primary pathway of N loss from aquatic environments. Recently, ANAMMOX and DNRA have been gaining more attention in N dynamics at the sediment–water interface. The ubiquitous presence of various sulfur (S) species in sediments makes them an important role on N transport. Interactions between dissimilatory nitrate reduction and the S cycle are mainly embodied by the inhibitory or promoting effects of sulfide on nitrate-reducing pathways, as well as the competition of sulfate with nitrate reduction for substrates. This review summarizes the current progress in the coupling of S cycling with nitrate-reducing pathways in freshwater sediments, the distribution and diversity of related microorganisms, as well as the functional genes encoding related enzymes. Future perspectives of related research are discussed in terms of coupled N cycling with other element cycles and molecular detection of functional bacteria to better understand and manipulate N cycling in freshwater environments.

Key words: nitrogen removal, denitrification, ANAMMOX, DNRA, sulfur cycle, bacterial diversity, freshwater sediments.

Résumé : Les processus de réduction dissimilatoire des nitrates incluant la dénitrification, l'oxydation d'ammonium anaérobie (« ANAMMOX ») et la réduction dissimilatoire de nitrates à l'ammonium (« DNRA ») sont des cheminements essentiels du cycle de l'azote (N) dans les écosystèmes d'eau douce. On a longtemps considéré la dénitrification comme le cheminement principal de perte d'azote des environnements aquatiques. Récemment, l'ANAMMOX et la DNRA attirent plus d'attention au niveau de la dynamique de N à l'interface eau–sédiment. L'omniprésence de diverses espèces sulfureuses dans les sédiments fait en sorte qu'elles jouent un rôle important dans le transport de l'azote. Les interactions entre la réduction dissimilatoire de nitrates et le cycle du soufre (S) sont principalement manifestées par les effets inhibiteurs ou promoteurs de sulfure sur les cheminements réduisant les nitrates, aussi bien que par la compétition de sulfates avec la réduction de nitrates pour des substrats. Cette revue analyse le progrès actuel dans le domaine du jumelage du cycle du S avec les cheminements réduisant des nitrates dans les sédiments d'eau douce, de la répartition et de la diversité de micro-organismes apparentés aussi bien que du codage de gènes fonctionnels des enzymes connexes. On aborde les perspectives futures de recherche connexe en matière de cycle de N jumelé avec d'autres cycles d'éléments et la détection moléculaire de bactéries fonctionnelles afin de mieux comprendre et manipuler le cycle de N dans les environnements d'eau douce. [Traduit par la Rédaction]

Mots-clés : exportation d'azote, dénitrification, ANAMMOX, DNRA, cycle du soufre, diversité bactérienne, sédiments d'eau douce.

1. Introduction

Nitrogen (N) is a key nutrient that may biologically limit primary production in aquatic ecosystems (Burgin and Hamilton 2007; Santoro 2010). The increased input of N caused by anthropogenic activities has become a vital driver of environmental issues such as eutrophication and harmful algal blooms, and thus N removal from freshwater environments has long been a research hotspot (He et al. 2013; Zhu et al. 2017). Denitrification, anaerobic ammonium oxidation (ANAMMOX), and dissimilatory nitrate reduction to ammonium (DNRA) are important dissimilatory nitrate reduction processes regulating the N cycle in aquatic environments. Over the past few decades, denitrification has been viewed as the only important pathway of nitrate reduction responsible for N removal. (Tiedje et al. 1983; Seitzinger 1988; Cornwell et al. 1999; Dong et al. 2000; Kraft et al. 2014). However, more recently ANAMMOX has been found to be important contributors, accounting for 24%–70% of total N loss in marine systems. Particularly, in freshwater ecosystems, its contribution to N removal can account for up to 30% (Dalsgaard et al. 2003, 2005; Wenk et al. 2013). Both denitrification and ANAMMOX remove nitrate from aquatic environments in the form of N_2. In contrast to ANAMMOX and denitrification, DNRA reduces nitrate to ammonium and the bioavailable form of N is unfavorable to N loss from aquatic ecosystems (An and Gardner 2002; Penton et al. 2006; Jensen et al. 2008; Canfield et al. 2010; Rütting et al. 2011). The importance of DNRA in N cycling has been increasingly recognized.

Sulfur (S) is ubiquitously distributed in sediments; therefore, S cycling is another significant biogeochemical element cycle. The S cycle is mediated by a combination of both reductive and oxidative processes, including S oxidation and sulfate reduction (Wilkin and Barnes 1996; Valdemarsen et al. 2009; Wu et al. 2013; Purcell et al. 2014). The respiratory reduction of sulfate has been recognized as the initial segment of S cycling (Jørgensen and Fenchel 1974; Jørgensen 1990), accounting for a large percentage of total sediment respiration (Jørgensen 1977; Howarth 1984; Holmer and

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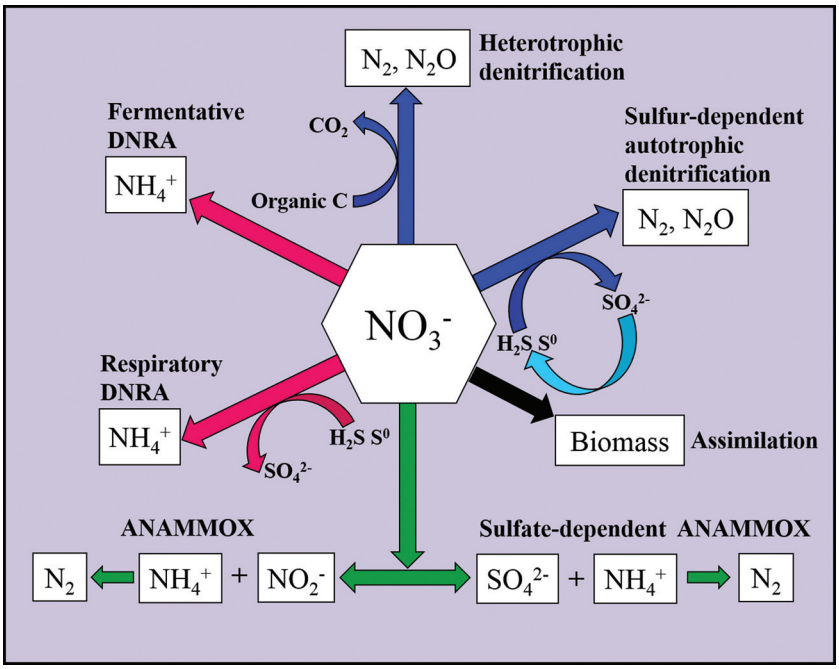
Fig. 1. Possible pathways and fates of nitrate reduction coupled with sulfur in the sediment. Modified and expanded from Burgin and Hamilton (2007).



Storkholm 2001). In aquatic sediments, sulfate reduction may compete with nitrate for organic matter (Achtnich et al. 1995), although nitrate reduction has been reported by many studies to take precedence over sulfate reduction, both thermodynamically and kinetically (Scholten et al. 2002; Li et al. 2015). Additionally, the reduced sulfide can be used as an electron donor, promoting autotrophic denitrification. Hence, the rates and efficiency of denitrification, ANAMMOX, and DNRA are inextricably linked to the cycling of S (Whitmire and Hamilton 2005; Burgin and Hamilton 2008; Shen et al. 2014).

Information concerning interactions of N and S transformation will help us to understand N biogeochemical cycling more comprehensively (Payne et al. 2009). However, discrepancies exist in the inhibition or stimulation of S on dissimilatory nitrate reduction. Some investigations demonstrate that high concentrations of free sulfide may have an inhibitory effect on denitrification via decreasing the activity of nitric oxide and nitrous oxide reductase (Senga et al. 2006; Bowles et al. 2012), and have irreversible inhibition on the ANAMMOX process (Jensen et al. 2008), but favor the occurrence of the respiratory DNRA process in which sulfide is utilized as an electron donor (Schulz et al. 1999; Graco et al. 2001; An and Gardner 2002; Lu et al. 2013). In contrast, several studies maintain that sulfide can favor S-dependent autotrophic denitrification by acting as an electron donor (Hayakawa et al. 2013; Deng et al. 2015). Additionally, in the literature fairly disparate observations are also found concerning the effect of sulfate on dissimilatory nitrate reduction processes (Achtnich et al. 1995; Fdz-Polanco et al. 2001; Cai et al. 2010*a*). Taken together, the impacts of the S cycle on dissimilatory nitrate reduction processes in freshwater sediments are still not sufficiently understood.

Microbial N and S cycling are complicated processes mediated by a wide range of microorganisms (Nealson 1997; Wobus et al. 2003; Martins et al. 2011; Bai et al. 2012; Liu et al. 2012). Among them, denitrifying bacteria, ANAMMOX bacteria (AnAOB), and DNRA bacteria play significant roles in controlling N dynamics (Nelson et al. 2007; Feng et al. 2009; Zeng et al. 2009). Additionally, S-metabolizing bacteria including sulfate-reducing bacteria (SRB) and sulfur-oxidizing bacteria (SOB) have been considered as crucial microbe drivers of the cycling of S (Muyzer and Stams 2008). These microbial processes that are responsible for the fluxes of S and N are catalyzed by specific enzymes, and the functional genes encoded for relative enzymes are powerful molecular tools for studying dissimilatory nitrate reduction processes coupled with S (Zehr and Ward 2002).

Sulfur is widely recognized as a crucial element directly related to taste and odour issues of a waterbody. Studies concerning the coupled biogeochemical S cycle with dissimilatory nitrate reduction processes will help us to better comprehend N cycling and can provide a theoretical basis for manipulating the N cycle in aquatic environments. This review will (*i*) summarize the current progress in the interconnections between dissimilatory nitrate-reducing pathways and the S cycle in freshwater sediments; (*ii*) discuss distribution, diversity, and composition of microbes including denitrifiers, AnAOB, DNRA bacteria, SRB, and SOB as well as the functional genes encoded for relative enzymes; and (*iii*) point out future perspectives of related research including N coupled to other element cycles and microbial analysis of related microorganisms for a better understanding and manipulation of the N cycle.

2. The pathways and fate of nitrate coupled with the sulfur cycle in aquatic sediment

Dissimilatory nitrate reduction processes are inevitably linked to sulfide oxidation or sulfate reduction in aquatic sediment. Figure 1 summarizes possible pathways and fates of nitrate reduction coupled with S in sediment. Knowledge about the promoting or inhibitory effects of sulfide on dissimilatory nitrate reduction processes and their interactions with S is of necessity to obtain a more comprehensive understanding of the N cycle in aquatic environments.

2.1. Effects of sulfur on dissimilatory nitrate reduction processes

The predominance of denitrification, ANAMMOX, and DNRA in the ecosystem is greatly dependent on the level of sulfide and carbon (C) in aquatic sediment (Weber et al. 2001). In ecosystems that are rich in C and sulfide, sulfide oxidation will be coupled

with nitrate reduction and promote the occurrence of denitrification or DNRA. When the level of sulfide in a C-rich sediment environment is limited, the dominance of denitrification or DNRA will be primarily determined by the ratio of C to N (C/N). Moreover, there are inextricable and intricate links between nitrate-reducing pathways and S (Crowe et al. 2012; Zhou et al. 2014; Rios-Del Toro and Cervantes 2016). For instance, denitrification may be inhibited at high sulfide levels and DNRA coupled to sulfide oxidation is promoted. In addition, the presence of free sulfide can have inhibitory effects on ANAMMOX efficiency, while sulfate from S oxidation can act as an electron acceptor for the ANAMMOX process. Although much is known about these complex processes, there is still scope for researchers to expand their efforts in exploring the complicated coupling of the S cycle with nitrate reduction processes, thereby providing a more comprehensive understanding of N cycling.

2.2. Sedimentary denitrification coupled with sulfur

Heterotrophic (respiratory) denitrification refers to the dissimilatory reduction of nitrate or nitrite with the oxidation of organic matter under anaerobic conditions, producing byproducts NO, N_2O, and ultimately N_2. The availability of electrons in organic C substrates is one of the most important factors influencing denitrification activities (Johnson et al. 2012; Deng et al. 2015). Generally, respiratory denitrification takes precedence over other nitrate removal pathways when substrates of organic C are sufficient. Free sulfide may have inhibitory effects on respiratory denitrification. Additionally, S can be utilized as an electron donor thereby promoting denitrification which is known as S-dependent autotrophic denitrification (Cardoso et al. 2006; Burgin and Hamilton 2008; Campos et al. 2008; Moon et al. 2008; Cai et al. 2010*b*). Therefore, S is a crucial factor regulating the efficiency of denitrification in freshwater environments.

2.2.1. Inhibition of respiratory denitrification by free sulfide

Free sulfide has been confirmed by many studies to have obvious inhibitory effects on respiratory denitrification, which has been mainly attributed to its inhibition on NO and N_2O reductases (Sørensen et al. 1980; Sørensen 1987;Brunet and Garcia-Gil 1996; Senga et al. 2006; Bowles et al. 2012; Deng et al. 2015; Plummer et al. 2015). Although there is a general consensus that free sulfide may inhibit denitrification, the reported levels of sulfide required for this to occur differ among studies. For instance, Senga et al. (2006) indicated that denitrifying activity decreased markedly at a H_2S concentration of 3 mg S L^{-1} in sediment suspensions of lakes Shinji and Nakaumi, Japan. However, Bowles et al. (2012) have reported evidence of inhibited denitrification at relatively higher sulfide concentrations of 32–80 mg S L^{-1}. This difference is likely related to environmental conditions such as sulfide and pH level (Aelion and Warttinger 2009). Aelion and Warttinger (2010) found that denitrifying activity in freshwater sites was greatly affected by enzymatic toxicity of H_2S, which was mainly attributed to its sensitivity to high sulfide concentrations. Additionally, evidence also suggested that this toxicity can be mitigated at high pH levels (Rios-Del Toro and Cervantes 2016).

2.2.2. Denitrification coupled with sulfur oxidation

Reduced S compounds such as reduced sulfide, elemental S, and thiosulfate can act as electron donors coupled with nitrate oxidation producing sulfate. Among these reduced inorganic S compounds, sulfide is widely reported to be an electron donor for S-dependent denitrification ($NO_3^-/S^{2-} \rightarrow N_2/SO_4^{2-}(S^0)$) in freshwater sediments (Haaijer et al. 2007; Mahmood et al. 2007; Wenk et al. 2013; Vaclavkova et al. 2014). Conversion of sulfide to elemental S via S-dependent denitrification consumes four times less nitrate stoichiometrically compared to the complete oxidation to sulfate (Cardoso et al. 2006). For example, the incubation of Pearl River sediments indicates that simultaneous nitrate removal and sulfate production are observed at different nitrate levels, and sulfate production increases correspondingly with the higher nitrate input concentrations (Yang et al. 2012). Generally, the conversion of sulfide to sulfate coupled to complete denitrification ($NO_3^-/S^{2-} \rightarrow N_2/SO_4^{2-}$) is widespread in aquatic environments that have higher contents of nitrate and sulfide.

In freshwater ecosystems, iron sulfide (FeS) minerals have the potential to function as electron donors for S-dependent autotrophic denitrification (Haaijer et al. 2007; Schwientek et al. 2008; Jørgensen et al. 2009; Torrentó et al. 2011). Oxidation of metal sulfide minerals especially pyrite (FeS_2) and FeS has been studied because of its important role in the S cycle. Jørgensen et al. (2009) and Hayakawa et al. (2013) both observed the linear correlation between sulfate production and nitrate consumption coupled to FeS_2 oxidation, corroborating the capacity of sedimentary FeS_2 as an electron donor. However, there is evidence suggesting that FeS is able to enhance sulfide-dependent denitrification, whereas FeS_2 cannot function as an effective electron donor due to the crystalline form of this sulfide mineral (Haaijer et al. 2007). FeS_2 is resistant against proton attack and bacteria do not dissolve FeS_2, whereas FeS is more easily oxidized by nitrate reducers due to its acid solubility (Schippers and Jørgensen 2002). In all, the reactivity of FeS minerals and the acidity of the environment will determine the efficiency of nitrate reduction coupled to sulfide oxidation. Specifically, the high reactivity and the mineralogical composition of FeS minerals may stimulate the potential nitrate reduction capacity, and the acidity of the environment can increase the solubility and reactivity of these minerals.

2.2.3. Possible interactions between sulfur-dependent denitrification and ANAMMOX

In the anaerobic environment, sulfide-dependent autotrophic denitrification can utilize sulfide as an electron donor reducing nitrate to nitrite, and the nitrite that is generated may provide substrates for ANAMMOX. Thus, sulfide-dependent denitrification and the ANAMMOX process are coupled. Additionally, sulfide-dependent denitrification may outcompete ANAMMOX when the nitrite substrate is limiting. For instance, Rios-Del Toro and Cervantes (2016) assessed the coupling between ANAMMOX and sulfide-dependent autotrophic denitrification linked to nitrite reduction in enrichment cultures derived from Mexican littoral sediments. Ammonium and sulfide were added with the same reducing capacity according to the stoichiometry of ANAMMOX and sulfide-dependent denitrification, whereas nitrite was supplied to fully oxidize only one of the electron donors provided. Evidence revealed that ANAMMOX efficiency is more affected by nitrite limitation and is outcompeted by sulfide-dependent denitrification process, which is mainly due to more favorable thermodynamics of sulfide oxidation linked to nitrite reduction than that of the oxidation of ammonium. Furthermore, there is the added possibility that nitrate generated from ANMMOX will recycle back to nitrite via denitrifying activities, thereby fueling their coupling between ANAMMOX and sulfide-dependent denitrification.

Assessing the coupling/competition between these two N-removing processes is required not only to better comprehend the microbial processes responsible for the fluxes of S and N in aquatic ecosystems, but also to help project biotechnological processes that integrate ANAMMOX and sulfide-dependent autotrophic denitrification to achieve the synchronic removal of sulfurous and nitrogenous pollutants (Canfield et al. 2010; Wenk et al. 2013; Russ et al. 2014; Rios-Del Toro and Cervantes 2016).

2.3. Sedimentary ANAMMOX coupled with sulfur

Observations have reported ANAMMOX to be very important in the marine N cycle and an ideal alternative for the treatment of streams that are heavily polluted by nitrate (Dalsgaard et al. 2005; Kalyuzhnyi et al. 2006; Nicholls and Trimmer 2009). Two different pathways for ANAMMOX include the anoxic oxidation of ammo-

nium utilizing nitrate or nitrogen dioxide as electron acceptors, and sulfate reduction which is known as sulfate-dependent ANAMMOX that has been mostly applied in wastewater containing high sulfate content (Fdz-Polanco et al. 2001; Rikmann et al. 2012). ANAMMOX has been considered a "short circuit" in N-cycling, because N can disappear in the form of N_2 without complete oxidation of ammonium to nitrate.

2.3.1. Inhibition of ANAMMOX by free sulfide

ANAMMOX is sensitive to unfavorable environmental conditions and the presence of free sulfide may prevent the occurrence of ANAMMOX. Divergences exist on the inhibition of ANAMMOX by free sulfide. Several studies have demonstrated that sulfide has inhibitory effects on the ANAMMOX process and that these effects are irreversible, which is associated with the toxicity of sulfide to AnAOB (Sears et al. 2004; Jensen et al. 2008). The toxicity of sulfide to ANAMMOX microorganisms is embodied by its denaturation of proteins (Chen et al. 2008). Additionally, free sulfide such as H_2S is often recognized as a toxic and corrosive substance that can impair AnAOB metabolic function even at very low levels (Mahmood et al. 2007; Beristain-Cardoso et al. 2009).

In contrast to findings that the presence of free sulfide may inhibit the occurrence of ANAMMOX, other studies have reported evidence of effects to the contrary (Van de Graaf et al. 1996; Dapena-Mora et al. 2007; Rios-Del Toro and Cervantes 2016). For instance, Van de Graaf et al. (1996) found that there was an increase of ANAMMOX activity at sulfide concentrations of 5 mM, in contradiction to the research of Dapena-Mora et al. (2007) that reported the complete inhibition of ANAMMOX at the same sulfide level. Similarly, no sulfide inhibition was observed on ANMMOX by Rios-Del Toro and Cervantes (2016) in incubated sediment, and it was postulated that a pH value of 7.8 ± 0.2 might have mitigated the inhibitory effects of sulfide. In general, pH is a crucial factor determining toxicity of sulfide to AnAOB. Toxicity is enhanced at low pH levels because speciation will move towards the toxic S form H_2S, and high pH levels might contribute to mitigating sulfide toxicity (Jin et al. 2012, 2013). Considering the divergences of these studies on inhibition of ANAMMOX by sulfide, more effort should be devoted to understanding sulfide toxicity thresholds and to defining the possible mitigation of sulfide toxicity by other environmental controls.

2.3.2. ANAMMOX coupled with sulfate reduction

Sulfate-dependent ANAMMOX is a novel biological reaction, in which ammonium is utilized as the electron donor and sulfate as the electron acceptor producing N gas and elemental S (NH_4^+/$SO_4^{2-} \rightarrow N_2/S^0$). Compared to nitrite-dependent ANAMMOX, the new process is easy to manipulate and the energy for nitration can be saved since sulfate rather than nitrite serves as an electron acceptor (Zhang et al. 2009). The standard Gibbs free energy change of the sulfate-dependent ANAMMOX reaction is −47.8 kJ/mol, which confirms the feasibility of this novel anaerobic N and sulfate removal reaction (Fdz-Polanco et al. 2001; Liu et al. 2008). Sulfate-dependent ANAMMOX is a microbiological sulfate-reducing reaction and therefore optimal concentrations of substrates and environmental conditions play an important role in the process (Liu et al. 2008; Zhang et al. 2009). High substrate concentrations of ammonium and sulfate as well as low oxidation-reduction potential (ORP) are presumed to be favorable for biological reactions (Zhang et al. 2009). However, sulfide produced by excessive reduction of sulfate in anaerobic conditions may inhibit the activity of sulfate-dependent ANAMMOX.

To our knowledge, sulfate-dependent ANAMMOX has not been previously reported in natural aquatic environments, with the exception of Schrum et al. (2009) who evaluated the thermodynamics of sulfate-reducing ammonium oxidation in the Bay of Bengal (Indian Ocean). Significance of the ANAMMOX coupled to sulfate reduction have been gradually recognized in sediments of aquatic ecosystems (Habicht et al. 2002; Kuypers et al. 2003; Cai et al. 2010*a*). However, little information is available for the possible pathway of sulfate reduction coupled with ANAMMOX in freshwater ecosystems, especially in polluted urban rivers containing high ammonium and sulfate content, which might be favorable for the occurrence of sulfate-dependent ANAMMOX.

2.4. Sedimentary DNRA coupled with sulfur

It was not until the 1980s that the existence of the DNRA process was confirmed in natural ecosystems (Tao and Wen 2016). Different from other dissimilatory nitrate-reducing pathways, nitrate or nitrite is utilized as an electron acceptor and whereby ammonium is produced in DNRA (Tao and Wen 2016). There are two recognized DNRA pathways: one involving fermentation and the other linked to S oxidation, which is known as the respiratory DNRA (Burgin and Hamilton 2007; Burgin and Hamilton 2008). Fermentative DNRA couples the electron flow from an organic C source to the reduction of nitrate, while in respiratory DNRA nitrate is reduced to ammonium with the occurrence of sulfide oxidation.

2.4.1. DNRA coupled with sulfide oxidation

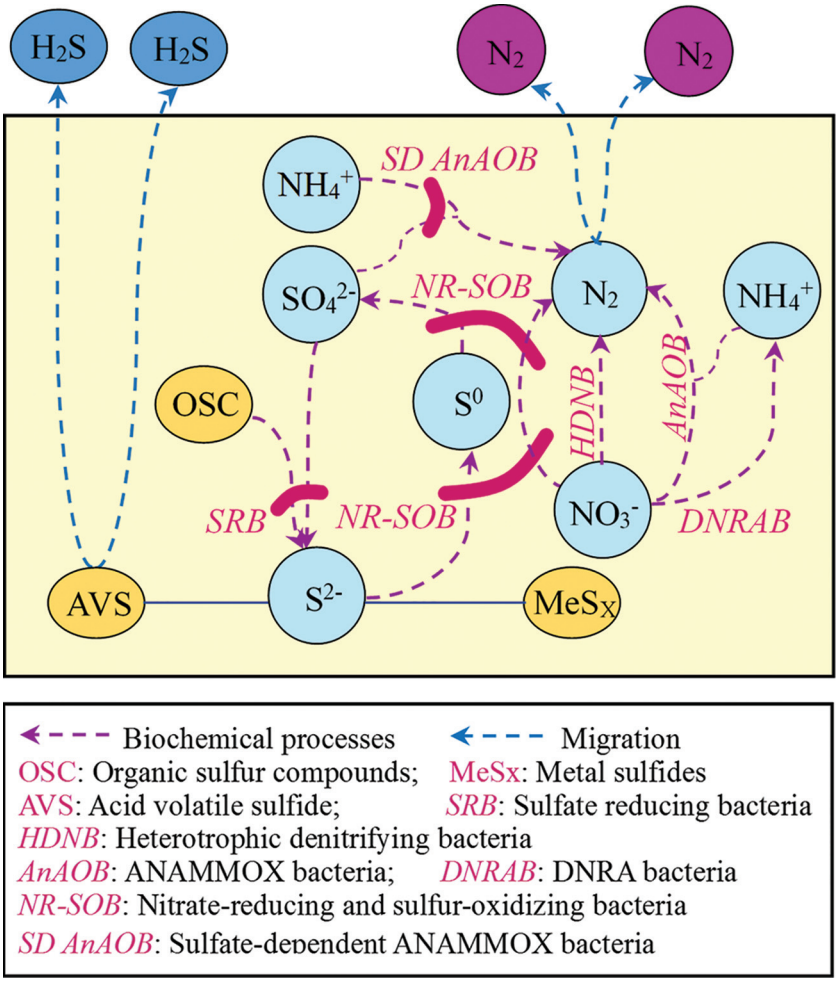
In freshwater environments, C and N sources and the C/N ratio have been considered as the most crucial factors regulating DNRA efficiency (Yin et al. 2002; Tao and Wen 2016). Environments with high labile C and limited nitrate concentrations have been confirmed to favor fermentative DNRA processes (Nizzoli et al. 2010). Different from fermentative DNRA that is dependent upon organic C sources, respiratory DNRA is a chemolithoautotrophic process that links nitrate reduction to the oxidation of reduced S compounds (Brunet and Garcia-Gil 1996; Otte et al. 1999; Burgin and Hamilton 2007). High concentrations of free sulfide can have inhibitory effects on denitrification and favor the occurrence of respiratory DNRA, because accumulated nitrate/nitrite after the inhibition of denitrification and sulfide can be used by DNRA bacteria as an effective electron acceptor and donor, respectively (Schulz et al. 1999; Graco et al. 2001; An and Gardner 2002). For instance, in a study undertaken at Laguna Madre/Baffin Bay, Texas, by An and Gardner (2002), it was found that high sulfide concentrations inhibited nitrification and denitrification but may enhance DNRA by providing an electron donor. Similarly, Lu et al. (2013) indicated that sulfide inhibited denitrification and fermentative DNRA, whereas high addition (100 mg S kg^{-1} dried weight) of free sulfide significantly increased respiratory DNRA rates.

2.4.2. Possible interactions between respiratory DNRA and denitrification

Fermentative DNRA and respiratory denitrification are analogous in their favorable conditions such as providing available nitrate, organic C, and an anaerobic environment (Herbert 1999; Abril et al. 2000). DNRA transfers eight electrons per mole of nitrate reduced, whereas denitrification only transfers five electrons, suggesting that the availability of high labile C would favor DNRA bacteria to utilize electron acceptors efficiently (Kelso et al. 1997).

There is a general consensus in the peer-reviewed literature that the initial concentration of free sulfide is likely a determining factor for nitrate-reducing pathways (Brunet and Garcia-Gil 1996; Senga et al. 2006; Yang et al. 2012; Hayakawa et al. 2013; Lu et al. 2013). Conditions with high levels of free sulfide and low nitrate concentrations favor the respiratory DNRA process. At extremely low levels of free sulfide, nitrate is reduced by denitrification, whereas at higher sulfide concentrations with a lower nitrate level, respiratory DNRA and incomplete denitrification take place (Brunet and Garcia-Gil 1996; Yang et al. 2012; Hayakawa et al. 2013). Specifically, high levels of free sulfide inhibit nitric oxide and nitrous oxide reductases of denitrification, and thus nitrite is accumulated, providing electron donors for DNRA coupled to oxidation of sulfide (Graco et al. 2001; An and Gardner 2002).

Fig. 2. Microorganisms mediating the coupling of sulfur with dissimilatory nitrate reduction processes.



3. Microbial mechanisms for the coupling of the sulfur cycle with dissimilatory nitrate reduction in freshwater sediments

Sediments shelter a complex ecosystem for microbes and they are mainly affiliated with the phyla Proteobacteria, Chloroflexi, Actinobacteria, Bacteroidetes, and Planctomycetes (Ye et al. 2009; Y. Wang et al. 2012; Zhang et al. 2015). Microorganisms mediating the coupling of S with dissimilatory nitrate reduction include S-dependent autotrophic denitrifirs (NR-SOB), sulfate-dependent ANMAMMOX bacteria, and S oxidizers functioning as DNRA bacteria (Fig. 2). Knowledge about their bacterial communities and functional genes encoding specific catalyzing enzymes is essential to better comprehend the interconnection between nitrate reduction and S cycling.

3.1. Sulfur oxidizers functioning as denitrifying bacteria

Sulfur-metabolizing microorganisms include sulfate reducers and S oxidizers that utilize S compounds as electron acceptors and donors, respectively. Most of them are within the bacterial domain (Giovannoni and Stingl 2005; Sievert et al. 2007). All forms of S metabolism can be found within the Proteobacteria (a-, ß-, ɣ-, δ-, and ε-Proteobacteria), whereas as other lineages include Chlorobiaceae, Firmicutes, Chloroflexaceae, Thermodesulfobacteriaceae, Aquificae, and Nitrospiraceae. Denitrifying bacteria are widespread among the bacterial domain and are phylogenetically diverse (Braker et al. 1998). Most denitrifiers are heterotrophs, while some S oxidizers (SOB) are reported to function as chemolithotrophic denitrifying bacteria, which are capable of utilizing nitrate as the terminal electron acceptors, and are known as sulfide-dependent autotrophic denitrifiers (Campos et al. 2008; Moon et al. 2008; Burgin et al. 2012).

The sulfide-dependent denitrifiers have been identified from various habitats such as hydrothermal vents, marine sediments, soda lakes, and wastewater treatment plants (Shao et al. 2010). To date, all microorganisms mediating S-driven autotrophic denitrification have been affiliated with a-, ß-, ɣ-, and ε-Proteobacteria (Shao et al. 2010). Among them, *Thiobacillus dentrificans* and *Sulfurimonas denitrificans* are the most commonly studied and applied sulfide-dependent denitrifiers (Trouve et al. 1998; Beller et al. 2006*a*, 2006*b*; Sievert et al. 2008; Chen et al. 2016).

In general, *Thiobacillus*-like bacteria are reported to be the dominant sulfide-dependent denitrifiers in freshwater sediment (Haaijer et al. 2007; Burgin et al. 2012; Yang et al. 2012). For example, in a study of the freshwater wetlands (Het Zwart Water) in the Netherlands by Haaijer et al. (2007), the most abundant group of sulfide-dependent *Thiobacillus*-like denitrifiers were affiliated with the ß-proteobacterial genus, containing 62% of total clones as revealed by 16S rRNA gene analysis. Similarly, Yang et al. (2012) similarly found that bacteria affiliated to *Thiobacillus* were the dominant sulfide-dependent denitrifiers in sediment from the Pearl River in Guangdong, China, and they appear to exist in deep sediment layers. In addition, microbial studies also suggest that the importance of denitrifiers such as *Beggiatoa*, *Sulfurimonas* bacteria, and *Thiohalomonas denitrificans* in freshwater sediment cannot be overlooked (Sweerts et al. 1990; Burgin and Hamilton 2008; Burgin et al. 2012). Taken together, more systematic studies on the

existence and distribution of S-dependent denitrifiers should be carried out.

3.2. ANAMMOX bacteria functioning as sulfate reducers

Sulfate reducers are ubiquitous in anoxic habitats where they utilize sulfate as terminal electron acceptors for the degradation of organic matter to produce sulfide. Sulfate reduction have been reported to be responsible for more than 20% of total anaerobic mineralization in freshwater sediments (Sass et al. 1998). Sulfate reducers belonging to genus *Deltaproteobacteria* are the dominant SRB in freshwater sediments followed by genera *Desulfovibrio* and *Desulfobacterium* (Muyzer and Stams 2008; Sass et al. 2009; Haller et al. 2011; Yu et al. 2012). Contaminated freshwater environments might shelter a better ecosystem for sulfate reducers than less anthropogenic-disturbed systems because high concentrations of pollutants such as organic matter and nutrients can lead to intense sulfate reduction-dominated mineralization (Haller et al. 2011).

ANAMMOX bacteria branches deeply in the phylum Planctomycetes (Schmid et al. 2003; Shimamura et al. 2007; Yoshinaga et al. 2011; Bale et al. 2014). Five taxa, including the members of the genera *Candidatus* Brocadia, *Candidatus* Kuenenia, *Candidatus* Scalindua, *Candidatus* Jettenia, and *Candidatus* Anammoxoglobus have been discovered to date (Yoshinaga et al. 2011; Hu et al. 2012; Van Niftrik and Jetten 2012). Some microorganisms are sulfate-dependent AnAOB that are capable of ammonium oxidization and sulfate reduction simultaneously. These bacteria are mostly reported in wastewater where they play dual roles of sulfate reducers and ANMMOX bacteria. For instance, Liu et al. (2008) evaluated the efficiency of a new species "*Anammoxoglobus sulfate*" belonging to Planctomycetales for simultaneous ammonium and sulfate removal in a rotating biological contactor reactor. In addition, Cai et al. (2010*a*) have reported the isolation, identification and characterization of an autotrophic bacterial strain related to *Bacillus benzoevorans* that can reduce anaerobic ammonium and sulfate simultaneously.

To our knowledge, there is currently little evidence to show the occurrence of sulfate-dependent AnAOB in natural freshwater systems, whereas nitrate-dependent AnAOB are widely reported (Jetten et al. 2003; Kartal et al. 2006; Dale et al. 2009). The first direct evidence of ANMMOX bacteria in natural freshwater systems was reported in Lake Tanganyika by Schubert et al. (2006) who found that *Candidatus* Scalindua brodae were the dominant AnAOB in the sediments. Subsequently, accumulating evidence showed that *Brocadia* and (or) *Kuenenia*-like organisms were the dominant freshwater sedimentary AnAOB (Zhang et al. 2007; Yoshinaga et al. 2011; S. Wang et al. 2012; Wenk et al. 2013). Additionally, observations by Hu et al. (2012) indicated that bacteria from the genera *Brocadia*, *Kuenenia*, and *Scalindua* can be detected in sediments from both West Lake and the Qiantang River in Zhejiang, China.

3.3. Sulfur bacteria functioning as DNRA bacteria

To date, 11 genera of DNRA bacteria, including *Escherichia*, *Klebsiella*, *Citrobacter*, *Proteus*, *Desulfovibrio*, *Wolinella*, *Haemophilus*, *Achromobacter*, *Clostridium*, *Streptococcus*, and *Neisseriasubflava*, have been discovered (Tao and Wen 2016). Some respiratory DNRA bacteria are autotrophic S bacteria that are capable of oxidizing sulfide coupled to the reduction of nitrate or nitrite to ammonium (Tiedje et al. 1983; Sayama et al. 2005). For example, Eisenmann et al. (1995) demonstrated that *Sulfurospirillum deleyianum* can grow by the anaerobic oxidation of sulfide to elemental S coupled with the reduction of nitrate to ammonium. In addition, Zopfi et al. (2001) indicated that S bacteria affiliated to *Thioploca*, can produce ammonium via DNRA when sulfide is available, because *Thioploca*-like S bacteria possess large nitrate-filled vacuoles that can store and utilize nitrate substrates effectively. In addition, there is also evidence showing that sulfate reducers such as *Desulfovibrio desulfuricans* CSN and *Desulfobulbus propionicus* can function as DNRA bacteria (Dannenberg et al. 1992; Schumacher and Kroneck 1992). To date, existing studies have mainly focused on DNRA microbes and their activity in submerged rice paddy soil, and estuary and marine sediments (Koike and Hattori 1978; Yin et al. 2002; Lu et al. 2013; Song et al. 2014). However, there is a lack of systematic research with regard to DNRA processes that are mediated by S-metabolizing bacteria in freshwater environments.

3.4. Molecular detection of sulfate reducers, sulfur oxidizers, denitrifiers, ANMMOX, and DNRA bacteria with functional genes encoding related enzymes

The processes of denitrification, ANAMMOX, DNRA, sulfate reduction, and S oxidation are catalyzed by specific enzymes. These enzymes and genes are powerful means for studying the microbial dissimilatory nitrate reduction processes that are coupled with S. Knowledge of these gene-encoding enzymes provides useful tools that not only detect gene expression but also determine the abundance and diversity of bacteria that are involved in specific nitrate reduction pathways (Zehr and Ward 2002).

3.4.1. *Detection of sulfide-dependent autotrophic denitrifiers*

Similar to heterotrophic denitrification processes, sulfide-dependent autotrophic denitrification consists of four reaction steps ($NO_3^- \xrightarrow{Nar} NO_2^- \xrightarrow{Nir} NO \xrightarrow{Nor} N_2O \xrightarrow{Nos} N_2$) that reduces nitrate into N_2 through metalloenzymes. These enzymes include nitrate reductase (Nar), nitrite reductase (Nir), nitric oxide reductase (Nor), and nitrous oxide reductase (Nos). These enzymes are usually induced sequentially under anaerobic conditions (Philippot 2002; Yang et al. 2013). Specifically, functional gene-encoding S oxidation has not been used to determine sulfide-dependent autotrophic denitrifiers.

The widespread occurrence of denitrifiers including heterotrophs and sulfide-dependent autotrophs have been detected in freshwater ecosystems with the help of functional gene-encoding catalytic subunits of the denitrifying reductases, such as *narG*, *napA*, *nirS*, *nirK*, *norB*, and *nosZ* (Table 1). Among these denitrifying genes, *nirS* and *nirK* are the most widely used biomarkers for molecular detection of denitrifiers in sediment followed by *nosZ* (Braker et al. 1998; Angeloni et al. 2006; Graham et al. 2010; Mao et al. 2017). Particularly, *nosZ* is important for the investigations of nitrous oxide emitted by denitrification (Philippot et al. 2011; C. Wang et al. 2012). Detection of a single functional gene may not be sufficient to elucidate the abundance of denitrifiers. For example, Yang et al. (2012) revealed that the abundance of *nirK*-haboring and *nosZ*-harboring denitrifiers decreased dramatically with sediment depth, while that of *nirS*-harboring denitrifiers increased. In fact, variations of denitrifying genes respond differently to environmental conditions (Dandie et al. 2011). Therefore, the selection of proper functional genes is critical for determining the abundance of denitrifying bacterial communities in sediments.

3.4.2. *Detection of ANMMOX bacteria*

Molecular detection of AnAOB has been successfully conducted using PCR amplification of ANMMOX bacterial 16S rRNA genes (Schmid et al. 2003; Hu et al. 2012; S. Wang et al. 2012). The highly conserved nature of 16S rRNA may limit its efficacy as a tool to examine the full diversity of AnAOB and their distribution (Hirsch et al. 2011). Furthermore, the 16S rRNA genes of some non-AnAOB belonging to Planctomycetes can also be amplified during the PCR amplification for ANXMMOX detection. Compared to the 16S rRNA genes, functional genes encoding for hydrazine oxidation (*hzoA* and *hzoB*, Table 1) were proposed to be more useful genetic markers for AnAOB (Francis et al. 2007). Functional genes such as *hzoA*, *hzoB*, and *hzsA* (Table 1) have been used to detect the presence

Table 1. Functional gene targets used for studying the diversity and abundance of nitrate reducers and sulfur-metabolizing bacteria in freshwater ecosystems.

Process	Gene	Function	Ecosystem	Reference
Denitrification	*napA* *narG*	Nitrate reductase	An artificial lake in East Anglia campus; Pearl River	Flanagan et al. (1999); Yang et al. (2012)
	nirS *nirK*	Nitrite reductase	Cheboygan Marsh wetland; Pearl River	Angeloni et al. (2006); Yang et al. (2012)
	norB	Nitric oxide reductase	Red Cedar River	Braker and Tiedje (2003)
	nosZ	Nitrous oxide reductase	Pearl River; Dianchi Lake	Yang et al. (2012); Mao et al. (2017)
ANAMMOX	*hzoAB*	Hydrazine oxidase	Cape Fear River; Lake Taihu	Hirsch et al. (2011); Wu et al. (2012)
	hzsA	Hydrazine synthase	Ditch in the Ooijpolder	Harhangi et al. (2012)
	nirS	Nitrite reductase	Peruvian oxygen minimum zone; Lake Grevelingen	Lam et al. (2009); Li et al. (2011); Li and Gu (2011)
DNRA	*nrfA*	A pentaheme cytochrome *c* nitrite reductase	Pearl River; Lake Taihu	Yang et al. (2012); Krausfeldt et al. (2017)
Sulfate reduction	*aprA*	Dissimilatory adenosine-5′-phosphosulphate reductase	Lake Pavin; Lake Biwa; subglacial Lake Whillans	Biderre-Petit et al. (2011); Watanabe et al. (2013, 2016); Purcell et al. (2014)
	dsrAB	Dissimilatory sulfite reductase	Freshwater fish pond in Mai Po	Shao et al. (2012)
Sulfide oxidization	*aprA*	Dissimilatory adenosine-5′-phosphosulphate reductase	Lake Pavin; Lake Biwa; subglacial Lake Whillans	Biderre-Petit et al. (2011); Watanabe et al. (2013, 2016); Purcell et al. (2014)
	soxB	Sulfate thioesterase/thiohydrolase	Lake Mizugaki	Kojima and Fukui (2010)
	sqr	Sulfide quinone reductase	Lake Mizugaki	Kojima et al. (2014)

Note: Denitrification: $NO_3^-/S^{2-}(OC) \xrightarrow{Nar} NO_2^- \xrightarrow{Nir} NO \xrightarrow{Nor} N_2O \xrightarrow{Nos} N_2/SO_4^{2-}$; ANAMMOX: $NH_4^+/SO_4^{2-}(NO_3^-) \xrightarrow{Hzo\ Hzs\ Nir} N_2/S^0$; DNRA: $NO_3^-/S^{2-}(OC) \xrightarrow{Nrfa} NH_4^+$; Sulfate reduction: $SO_4^{2-} \xrightarrow{Apr\ Dsr} S^{2-}$; Sulfide oxidation: $S^{2-} \xrightarrow{Apr\ Sox\ Sqr} SO_4^{2-}$.

of AnAOB in freshwater ecosystems (Hirsch et al. 2011; Harhangi et al. 2012; Wu et al. 2012).

Particularly, cytochrome cd_1 containing the nitrite reductase encoding gene *nirS* (Table 1) has been confirmed as a new functional biomarker for the detection of AnAOB. This *nirS* targeting AnAOB is clearly distinct from denitrifier *nirS*, and to our knowledge, studies have only reported ANAMMOX bacterial *nirS* in saline aquatic environments (Lam et al. 2009; Li et al. 2011, Li and Gu 2011; Lipsewers et al. 2016). For instance, in a study from Peru, Lam et al. (2009) designed primers specifically targeting the putative cytochrome cd_1-containing nitrite reductase gene (*nirS*) that is unique to *Candidatus* Scalindua. Results show that *Scalindua-nirS* is strongly expressed and has a much higher abundance than denitrifier *nirS* in the Peruvian oxygen minimum zone (OMZ). Similarly, Li et al. (2011) uses a newly designed primer set AnnirS to target ANAMMOX bacterial *nirS* from three different marine environments. Sequences targeted by AnnirS are more closely affiliated with the *nirS* of *Candidatus* Kuenenia stuttgartiensis and even form a new phylogenetic *nirS* clade, which might be related to other genera of the AnAOB. It is demonstrated that ANAMMOX bacterial *nirS* appear to be a better functional biomarker for AnAOB than 16S rRNA and *hzo* genes, since the ANMMOX bacterial *nirS* gene sequence is specifically targeted by the PCR primer sets, and only one copy of the *nirS* gene has been confirmed in different genera of AnAOB (Li et al. 2011).

3.4.3. *Detection of DNRA bacteria*

The pentaheme cytochrome *c* nitrite reductase (*NrfA*) plays an important role in DNRA process and catalyzes the reduction of nitrite to ammonium without producing any intermediate N compound (Einsle et al. 1999). The *nrfA* gene is frequently used as a molecular tool for DNRA identification (Giblin et al. 2013; Song et al. 2014), and has also been reported for the molecular detection of DNRA bacteria in freshwater environments (Table 1) (Krausfeldt et al. 2017). The functional gene *nrfA* is present in a diverse number of bacteria, including Proteobacteria, Planctomycetes, Bacteroides, and Firmicutes (Mohan et al. 2004; Giblin et al. 2013). Simon et al. (2011) concluded that *NrfA* may also use other compounds as an alternative substrate such as hydroxylamine, S compounds, and hydrogen peroxide. Additionally, while the *nrfA* gene is frequently targeted as a marker for DNRA, DNRA may not be restricted to the bacteria carrying the *nrfA* genes (Giblin et al. 2013). Thus, future studies are required to identify the diversity of the enzymes and genes involved in DNRA pathways and DNRA coupled to S oxidation.

3.4.4. *Detection of sulfate reducers and sulfur oxidizers*

The phylogenetic complexity of S-metabolizing bacteria hampers the concomitant detection of sulfate reducers and S oxidizers in natural habitats using only a single 16S rRNA gene-targeted primer (Watanabe et al. 2013). The use of functional gene-encoding related enzymes as an alternative molecular approach can overcome the limitations of the 16S rRNA gene based methods. The dissimilatory adenosine-5′-phosphosulfate (*APS*) reductase is a key enzyme for mediating the microbial processes of sulfate reduction and S oxidation. Furthermore, the functional marker gene *aprA* (Table 1), which is encoded for the *APS* alpha subunit, is highly conserved among SRB and some SOB. Therefore, *aprA* is quite suitable for molecular profiling of the S-metabolizing bacterial community in freshwater environments (Meyer and Kuever 2007*b*, 2007*c*; Watanabe et al. 2016). It is noteworthy that the *aprA* primer set was originally employed to assess SRB diversity; thereafter, *aprA*-harboring SOB were established from the phylogenetic studies of nearly the entire *aprBA* gene (Meyer and Kuever 2007*a*, 2007*c*).

Functional gene *dsrAB* (Table 1) encoding dissimilatory sulfite reductase (*DSR*) can also be used as an effective molecular tool for the detection of SRB in freshwater ecosystems. In addition, despite the fact that the *aprA* gene has been commonly used as a biomarker for analyzing community structure of SOB, it is important to note that S oxidation processes may be independent of *APS* and that some SOB lack the *aprA* genes. SOB are phylogenetically and physiologically diverse, differing in their utilization of the various reduced S compounds. Consequently, the enzymatic pathways used for dissimilatory S oxidation are found to be widely variable and may involve different intermediates (Friedrich et al.

2001, 2005; Meyer and Kuever 2007*a*). Several marker genes have been applied to analyze SOB with different pathways in freshwater environmental samples (Kojima and Fukui 2010; Kojima et al. 2014). For example, *soxB* (Table 1) gene encoding sulfate thioesterase/thiohydrolase and *sqr* (Table 1) gene encoding sulfide: quinone oxidoreductase. More studies are still required to explore the S-oxidizing enzyme system and related biomarkers considering the variety of S oxidization metabolic pathways.

4. Future perspectives

Biogeochemical N cycling is one of the most complicated processes in freshwater ecosystems. Microbial processes such as denitrification, ANAMMOX, and DNRA have a direct impact on the pathways and fate of N. The cryptic S cycle (i.e., sulfide oxidation, sulfate reduction) is closely related to dissimilatory nitrate reduction as demonstrated above. In addition, the N cycle is inextricably coupled to other crucial biogeochemical processes such as the carbon, phosphorus, and iron cycles (Weber et al. 2001; Shen et al. 2014). A comprehensive description of their interactions is essential to maintain a healthy aquatic environment.

Over the past decades, molecular techniques have been rapidly developed using culture-independent methods to identify and analyze the activities of microorganisms. Among these, high-throughput sequencing technology and quantitative real-time polymerase chain reaction (q-PCR) techniques are showing powerful advantages in deciphering the abundance, diversity, and composition of microbes in the sediments (Shen et al. 2014). Nevertheless, the presences of certain functional genes alone do not provide enough information about microorganisms mediating nitrate reduction, since the genes might not have been expressed or its transcript/enzyme might have been inactivated. DNA stable isotope probing (DNA-SIP) has been considered as a more useful method to study microbial ecology because it can link microbial identity (e.g., 16S rRNA sequences) to the incorporation of a growth substrate (Dumont and Murrell 2005).

Because of extensive anthropogenic activities, urban rivers are often heavily polluted and the resulting smells are directly related to elemental S (He et al. 2013; Martins et al. 2014; Wang et al. 2017; Zhu et al. 2017). Solutions to problems of N overloading and taste and odour issues arising from S are crucial for a healthy aquatic environment. In particular, there is scope for simultaneous removal of S and N by S-dependent autotrophic denitrification or sulfate-dependent ANAMMOX. Previous studies concerning the coupling of S with dissimilatory nitrate reduction are mainly concentrated on ecological habitats, such as lakes, estuaries, and reservoirs, and little information is available for affected rivers. To obtain a more comprehensive knowledge of nitrate removal pathways coupled with S, and to guarantee a healthy aquatic environment for citizens and urban sustainable development, continued research focusing on taste and odour issues in rivers are necessary.

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