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Sediment denitrification in Yangtze lakes is mainly influenced by environmental conditions but not biological communities

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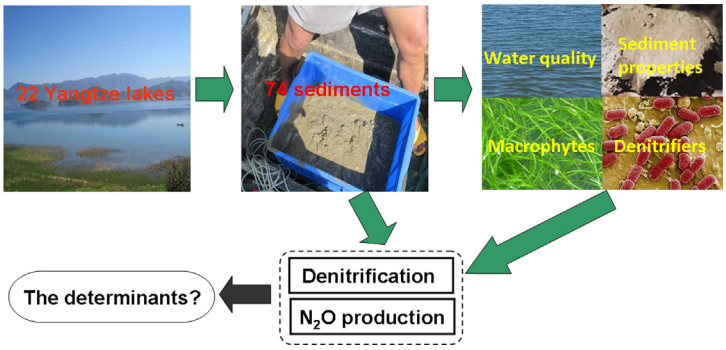
HIGHLIGHTS

- Plant functional groups had no effect on denitrification and N_2O production rates.
- Denitrification was mainly controlled by water quality but not sediment properties.
- Denitrifying communities did not significantly affect sediment denitrification rates.
- Water quality regulated denitrification and N_2O production directly and indirectly.

GRAPHICAL ABSTRACT



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ABSTRACT

Globally, shallow lakes have suffered from excessive nitrogen (N) loading due to increased human activities in catchments, resulting in water quality degradation and aquatic biodiversity loss. Sediment denitrification, which reduces nitrate (NO_3^-) to N gaseous products, is the most important mechanism for permanent N removal in freshwater lakes. However, the relative contribution of abiotic and biotic factors to the sediment denitrification is highly variable. Here, we determined the unamended denitrification rate and nitrous oxide (N_2O) production rate of 74 sediment samples from 22 eutrophic lakes in the Yangtze River basin. We also quantified the diversity and abundance of denitrifying communities using *nirK* and *nirS* genes. The results of variance partitioning analyses showed that water physicochemical properties (e.g., dissolved oxygen) and nutrients (e.g., NO_3^- concentration) but not denitrifier communities and submerged vegetation were the major factor groups predicting denitrification and N_2O production rates. Path analyses further revealed that water physicochemical properties and nutrients could affect denitrification and N_2O production rates both directly and indirectly, and the direct effects were considerably higher than the indirect effects mediated through changes in sediment characteristics, denitrifier communities and submerged vegetation. These findings suggest that the dominant N removal process in Yangtze lakes is largely regulated by abiotic factors rather than diversity and abundance of denitrifiers and submerged macrophytes. Additionally, the findings in this study are helpful in developing a targeted strategy to assess and enhance the N removal capability of eutrophic lakes in China.

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1. Introduction

Nitrogen (N) pollution has increased markedly over the past decades worldwide as a result of increased fertilizer use, sewage discharge, and atmospheric deposition (Galloway et al., 2003; Finlay et al., 2013). Although N is an essential nutrient for all life forms and can be the limiting or co-limiting nutrients for primary production in lakes and other aquatic systems (Carpenter et al., 1998), excess N has been linked to water eutrophication and many attendant ecological issues, including water quality deterioration, harmful algal blooms, and decline of aquatic biodiversity (Camargo and Alonso, 2006; Elser et al., 2009). For example, the percent of eutrophic lakes in China has increased from approximately 40% in 1980s to nearly 85% in 2005, partly due to increased N inputs (Liu et al., 2010).

The pathways of N removal from lake ecosystems have received considerable attention in recent decades (Jansson et al., 1994; Harrison et al., 2009; Small et al., 2016; Vila-Costa et al., 2016; Zhang et al., 2016). In general, mechanisms by which lakes remove N primarily include sedimentation, plant uptake, sediment anaerobic ammonium oxidation (anammox) and denitrification (Jansson et al., 1994; Hallin et al., 2015). Among these, sediment denitrification is widely recognized as the dominant N removal process in shallow lakes and involves the successive reduction of nitrate (NO_3^-) to nitrite (NO_2^-), nitric oxide (NO), nitrous oxide (N_2O) and dinitrogen gas (N_2) (Sirivedhin and Gray, 2006). NO_2^- reduction to NO is the rate-limiting step of denitrification process that is catalyzed by the Cu-containing enzyme encoded by *nirK* gene or cytochrome *cd* 1 enzyme encoded by *nirS* gene (Petersen et al., 2012). Both *nirK* and *nirS* genes have been widely used to investigate the community structure of denitrifiers in sediments (Vila-Costa et al., 2016).

Overlying water quality and sediment characteristics have been demonstrated to be associated with the sediment denitrification in lake ecosystems (Saunders and Kalff, 2001; Mccrackin and Elser, 2012; Wang et al., 2013). During the denitrification, NO_3^- can act as a terminal electron acceptor and organic carbon (C) as an electron supplier for denitrifying bacteria. Therefore, water or sediment NO_3^- and C concentrations are generally considered as the most important factors regulating the lake denitrification (Saunders and Kalff, 2001; Bruesewitz et al., 2011). Because denitrification is an anaerobic reaction, oxygen availability is also one of the key factors controlling the sediment denitrification process in lakes (Seitzinger et al., 2006). Several reports have shown that high sediment water content may inhibit oxygen diffusion into the sediments and thereby creating anaerobic conditions favorable for sediment denitrification (e.g., Liu et al., 2015).

As denitrification is a microbial process, the characteristics of denitrifier community may directly affect the process rate (Wallenstein et al., 2006). Rocca et al. (2015) conducted a meta-analysis and found that the association between microbial community structure and corresponding biogeochemical processes varied considerably among habitat types. To date, only a few studies have related abundance and diversity of denitrifiers to sediment denitrification rates in lakes, and these studies have primarily focused on oligo-mesotrophic lakes (Rissanen et al., 2013; Vila-Costa et al., 2016). For instance, Vila-Costa et al. (2016) reported that sediment denitrification potential in small ultraoligotrophic lakes was positively related to *nirS* gene abundance, but not significantly associated with diversity of *nirS*-type denitrifiers. However, to date, the effects of denitrifier community on sediment denitrification process in eutrophic lakes remain unknown. In addition to denitrifying microbes, aquatic plants may regulate sediment denitrification by competing for NO_3^-, introducing oxygen via diffusion from plant roots, altering sediment C quantity and quality and trapping particulate organic matter from waters (Alldred and Baines, 2016).

In this study, a total of 74 surface sediment samples were collected from 22 eutrophic lakes in the Yangtze River basin, where nitrogen loadings were relatively high. We measured the sediment unamended denitrification and N_2O production rates and quantified denitrifier abundance and diversity using *nirK* and *nirS* genes. The objectives of our study were (1) to determine the total and relative contributions of abiotic factors (water physicochemical properties, water nutrients and sediment characteristics) and biotic factors (denitrifier communities and submerged vegetation) to sediment denitrification and N_2O production rates and (2) to examine the direct and indirect effects of abiotic and biotic factors on sediment denitrification and N_2O production rates.

2. Materials and methods

2.1. Study sites

The Yangtze River (Changjiang River) has a total length of 6300 km and a watershed area of approximately 1.8 million km^2 (Fig. 1). In the Yangtze River basin there are >600 natural lakes with an area larger than 1 km^2. Most of these lakes are shallow (mean depths <5 m) and mostly located in the middle and lower Yangtze River basin, where alluvium predominates. Over the past decades, Yangtze lakes have faced several environmental problems including nutrient enrichment, water quality degradation, toxic algal blooms, and declines in submerged vegetation due to increased human impacts (Liu et al., 2012). Approximately 86% of the lakes in the Yangtze River basin are eutrophic or hypereutrophic (Yang et al., 2010). In addition, the diversity of submerged vascular plants has declined in many Yangtze lakes due to the loss of certain species which are sensitive to eutrophication and water pollution (Fang et al., 2006). Moreover, the biomass of submerged plants has decreased sharply in most of the Yangtze lakes (Yang et al., 2010).

2.2. Field sampling and vegetation investigation

In July 2013, twenty-two eutrophic lakes in the middle and lower Yangtze River basin of China were selected for the study, mainly based on the ease of access to the lakes (Fig. 1). These lakes are listed in Table S1 and cover a wide range of hydrological and physicochemical conditions (Yang et al., 2010). In each lake, three to four sites were sampled at the lake's mean water depth (1.2–5.5 m), and each site was separated by a minimum distance of 5 km (Bruesewitz et al., 2011). At each sampling site, three replicate surface sediments (approximately the top 7 cm) were randomly collected within an area about 20 m^2 using a home-made grab sampler, and then mixed and homogenized to form a composite sample. If aquatic macrophyte was present in a sampling site, rhizosphere sediments were obtained from the whole root zone by shaking off sediments that were loosely adhering to the plant roots. For each site, approximately 500 g of sediments was collected in a plastic bag and stored at 5 °C in a refrigerator. Moreover, about 10 g of sediment was collected at each site in a centrifuge tube and immediately frozen in liquid N_2.

Before sediment collection, 500 mL of bottom water was collected at approximately 0.5 m above the sediments at each sampling site. We used a pronged grab (25 cm × 35 cm) to collect submerged plants three times in the same area of sediment sampling. Here, the species richness of submerged plant communities (reflecting α-diversity) was defined as the mean species number recorded in a sampling site. The fresh plant biomass was also calculated and used as a proxy for the abundance of submerged plants. A total of 14 submerged plant species were recorded, including 12 native and 2 exotic species (Table S2). We classified these plant species into different functional groups such as Myriophylloides and Parvopotamids (Vila-Costa et al., 2016; Table S2). Submerged plants were thoroughly rinsed to remove sediments, alga, and invertebrates and then put into cloth bags. In the laboratory, submerged plants were dried in oven at 80 °C for 48 h to determine the plant total nitrogen (PTN) using the Kjeldahl method.

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