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SEDIMENTS, SEC 2 • PHYSICAL AND BIOGEOCHEMICAL PROCESSES • RESEARCH ARTICLE

Bacterial community structure in the surface sediments of different habitats of Baiyangdian Lake, Northern China: effects of nutrient conditions

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Abstract

Purpose Baiyangdian Lake is located in the core of Xiongan New Area and is the largest freshwater lake in the North China Plain with a variety of habitats. Microorganisms are important drivers of material cycle and energy transport in freshwater ecosystems. To understand the biogeochemical circulations in Baiyangdian Lake, the bacterial community structures and influencing factors of surface sediments among the different habitats were investigated.

Materials and methods Samples were taken from five areas of Baiyangdian Lake. The concentration of nutrient elements and bacterial community structures was measured.

Results and discussion The bacterial community structures of different habitats were different and were influenced by the nutrients in surface sediment. Open water areas had the richest abundance of ecological functions, such as phototrophy, sulfur oxidation, sulfite respiration, nitrification, and nitrite respiration. The bacterial community structures among the different habitats were decided by different elements in sediment; sulfur was the key influencing factor of the bacterial community structure in open water; C/N ratio was the key influencing factor of reed marshes; nitrogen and organic carbon were the key influencing factors of river estuary habitat.

Conclusions The bacterial community structures and ecological functions of surface sediments among habitats were different, and the dominant bacteria played an important role in biogeochemical circulations, especially in the carbon and sulfur cycles of Baiyangdian Lake.

Keywords Baiyangdian Lake · Sediments · Bacterial community structure · Influencing factor

1 Introduction

Freshwater lake ecosystems account for about 90% of global liquid freshwater resources, playing an important role in biogeochemical circulation of natural ecosystems (Wang et al. 2016; Yang et al. 2018). Microorganisms are the main participants in the material cycle and energy transport of freshwater lake ecosystems and promote the cycles of carbon, nitrogen, phosphorus, and sulfur (Huang et al. 2016; Su et al. 2018; Wang et al. 2018). The material cycle and energy transport of the lake mainly occur at the sediment-water interface. Hence, surface sediment is an important part of the lake and always contains abundant nutrients and plentiful microorganisms (Pacesila 2015). By examining the microbial community structure of sediments, the key role of sediments in the material cycle and energy transport in freshwater lakes can be revealed, and it can also indicate the environmental conditions of freshwater lake ecosystems (Xiong et al. 2019; Kallistova et al. 2020; Pan et al. 2020).

The common microorganisms in the sediments of freshwater lakes are *Proteobacteria*, *Bacteroidetes*, *Verrucomicrobia*, *Firmicutes*, *Planctomycetes*, *Actinobacteria*, *Chloroflexi*, *Aminicenantes*, and *Acidobacteria*, etc. (Zhang et al. 2019a; Chen et al. 2020). Microorganisms in sediments participate in biogeochemical circulation through photosynthesis, nitrogen

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fixation, nitrification, sulfate reduction, and other biochemical reactions (Wan et al. 2019; Liu et al. 2020). For example, *Cyanobacteria* and photosynthetic bacteria can fix CO_2 by photosynthesis, and it was reported that *Cyanobacteria* could produce methane (Bižić et al. 2020); some *Nitrobacteria* and *Thiobacillus* can also fix CO_2 by chemoautotrophy reactions (Boschker et al. 2014). As for the nitrogen cycle in freshwater lakes, nitrogen fixation, ammonification, nitrification, and denitrification are the main processes of nitrogen conversion and migration (Klump et al. 2009; Zhao et al. 2019). For instance, denitrifying bacteria could use the nitrate/nitrite as the terminal electron acceptor to carry out biochemical reactions under anaerobic and aerobic conditions and convert nitrate/nitrite into N_2 (Wang et al. 2018). In recent years, the sulfur cycle in freshwater lake ecosystems has attracted much attention (Lomans et al. 2002; Watanabe et al. 2013). Microorganisms are important participants in the sulfur cycle in sediments, such as *Chromatium* and *Chlorobium*. Under aerobic conditions, sulfur-oxidizing bacteria can oxidize sulfur to sulfate; *Desulfovibrio*, *Desulfobacter*, and other sulfate-reducing bacteria can reduce sulfates into H_2S under hypoxia conditions (Lomans et al. 2002). Therefore, knowledge of microbial community structures is vital for understanding the biogeochemical circulation in freshwater lake ecosystems.

Baiyangdian Lake is the largest freshwater lake in North China Plain, with a total area of 366 km^2, which is an important water regulation hub of the Daqing River system (Yang et al. 2020a). Baiyangdian Lake has eight inflow rivers, including Zhulong River, Xiaoyi River, Fu River, Cao River, Pu River, Ping River, Tang River, and Baigouyin River. Additionally, the structure of Baiyangdian Lake is unique; the lake is crisscrossed by canals and ditches, and every separate lake is connected by ditches. Habitats of Baiyangdian Lake include estuary area, open water body area, fish farming area, and reed planting area. The habitat heterogeneity in Baiyangdian Lake makes it different from the southern inland lakes and the northern artificial reservoirs. Many studies have focused on the distribution of pollutants in Baiyangdian Lake, including the contents of heavy metals in lake aquatic plants (Yang et al. 2020a), and organic pollutants such as halogens and polycyclic aromatic hydrocarbons in sediments (Hu et al. 2010; Guo et al. 2011). Moreover, the composition and diversity of vegetation, zooplankter, phytoplankton, and benthic animals have been examined (Yang et al. 2020b; Zhu et al. 2020). However, few studies have investigated the bacterial community structure of surface sediments in different habitats of Baiyangdian Lake.

In this work, high-throughput sequencing method was used to investigate the bacterial community structure, and ecological functions of microorganisms in surface sediments of different habitats were analyzed in order to understand the biogeochemical circulation of Baiyangdian Lake. In addition, the biogenic elements of surface sediments in different habitats were measured. The effects of nutrient elements on bacterial community structures were analyzed, which can provide an insight into the pollution control of Baiyangdian Lake.

2 Material and methods

2.1 Sample collection

According to the different habitats of Baiyangdian Lake, five sampling points were determined: river estuary in Duancun area (RE), open water in Caiputai area (OW-C), reed marshes in Caiputai area (RM), fish farms in Quantou area (FF), and open water in Nanliuzhuang area (OW-N) (Fig. S1). Twenty-five-centimeter length of columnar sediment was sampled by a sediment corer and then equally divided into five sections in October 2019. Detailed information of each sampling point is shown in Table S1. The sediment samples were stored in sterile and sealable plastic bags and then transported to a freezer at −80 °C in the laboratory.

2.2 Sample analysis

2.2.1 Sediment analysis

The sediment samples were ground and passed through 100-mesh sieves for further use, after freeze-drying. The concentrations of total nitrogen (TN), total organic carbon (TOC), and total sulfur (TS) were determined by an elemental analyzer (VARIO EL cube, Elemantar, Germany). The concentration of total phosphorus (TP) was digested by potassium persulfate and measured by a UV-1900 spectrometer (Shimadzu, Duisburg, Japan) (Worsfold et al. 2005).

2.2.2 Deoxyribonucleic acid extraction and high-throughput sequencing

The sediment samples were sent to Sangon Biotechnology Company (Shanghai, China) for analysis. Deoxyribonucleic acid (DNA) was extracted from the sediment samples by using the E.Z.N.ATM Mag-Bind Soil DNA Kit (OMEGA, Norcross, USA) according to the provided instructions. The extracted DNA was sequenced using a MiSeq Illumina sequencing platform following the manufacturer's guidelines. High-throughput sequencing technology was used to evaluate the alpha diversity and bacterial community structure and composition.

2.2.3 Statistical analyses

Alpha diversity index values (Chao1 index and Shannon index) were compared and tested by using *T* test methods to assess the significant difference between different habitats

(p=0.05). Principal component analysis (PCA) and hierarchical clustering on operational taxonomic unit (OTU) level based on Bray-Curtis distance matrix were used to find out the similarity of bacterial community structure in different habitats by R with ape package (version 5.3). Kruskal-Wallis H test was used to find the significant different dominant phyla in different habitats by SPSS (version 9.0) (p=0.05), and LEfSe analysis was conducted to search for biomarkers that were significantly different in various habitats by LEfSe (version 1.1.0). To understand the biogeochemical circulation processes in Baiyangdian Lake, FAPROTAX was used for functional annotation prediction (Liang et al. 2020). Redundancy analysis (RDA) was used to investigate the relationships between OTUs and environmental factors, and Bioenv were used to seek out the best subset of environmental factors, by using R with vegan package (version 2.5–6).

3 Results

3.1 Alpha diversity of bacterial community structures

The Illumina MiSeq offline data were rigorously filtered and assembled clean reads. As is shown in Table S1, a total of 1,946,643 clipped bacterial 16S rRNA sequences (ranging from 56,549 to 98,198) with an average length of 418 bp were detected. Good's coverage average values were over 97%, which indicated the depth of sequencing was enough and sufficient to represent the bacterial community structure of Baiyangdian Lake. When operational taxonomic units (OTUs) were grouped at a 97% similarity level, there were 117,818 OTUs, ranging in number from 3657 to 6353. The Chao1 index ranged from 5088.816 to 7701.175 which was known as microbial richness index. There were significant differences (p<0.05) of Chao1 index between open water with river estuary and fish farms by using T test methods. Reed marshes had the most abundant species, followed by fish farms, river estuary, and open water. In addition, the Shannon index, an important index for evaluating and comparing bacterial diversity (ranging from 5.64 to 7.20), indicating the abundance and diversity of bacteria in Baiyangdian Lake, was high enough. There were significant differences (p<0.05) of Shannon index between each habitat, but there was no significant difference between river estuary with reed marshes and open water habitats. Diversity of bacterial community was the highest in the river estuary, followed by reed marshes, fish farms, and open water. As for open water habitats which located in Caiputai and Nanliuzhuang areas, the richness and diversity of the bacterial community were similar, indicating that the spatial differences were not the dominant driving factors for these two areas.

3.2 Bacterial community structures and compositions

For bacterial community structures (Fig. 1), the sediment samples were clustered into two groups. The sediment samples from river estuary were clustered into one group. The samples from open water, fish farms, and reed marshes were clustered together. These results demonstrated that the bacterial community structures of river estuary were different from other habitats.

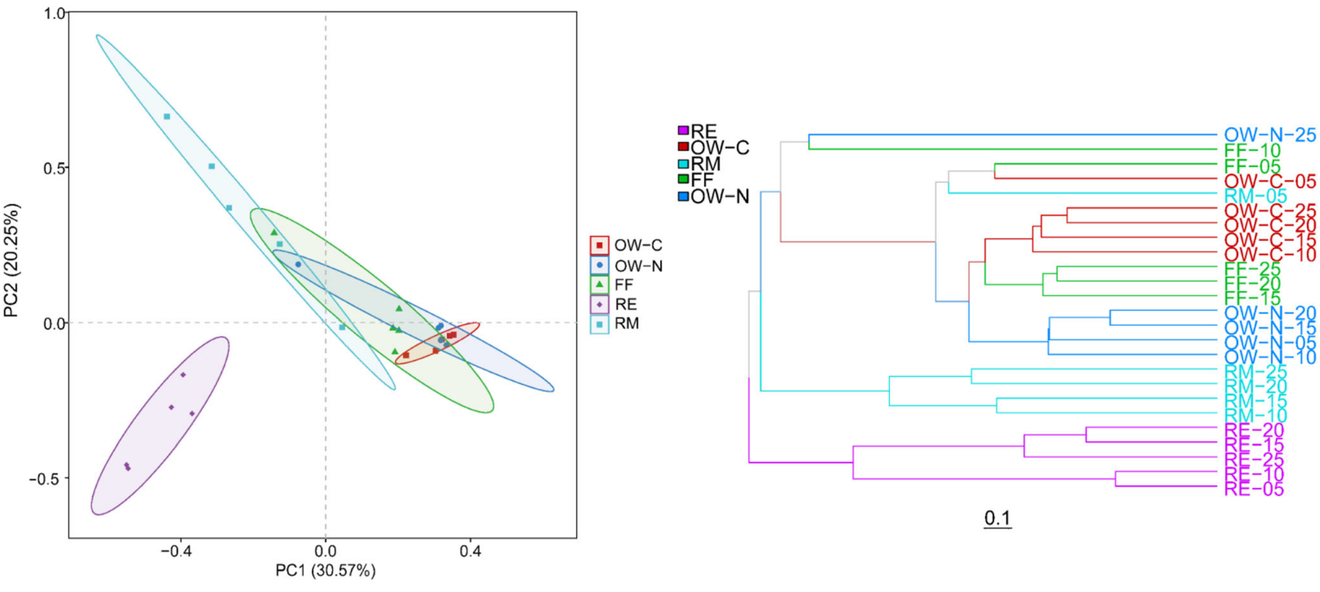
There were abundant bacteria in Baiyangdian Lake, which contained 43 phyla, 104 classes, 170 orders, 332 families, and 995 genera. The relative abundance of bacterial dominant phyla and genera within surface sediment samples in different habitats of Baiyangdian Lake is depicted in Fig. 2. On the phylum level, there were nine dominant phyla whose relative abundance was higher than 1%. *Proteobacteria*, *Chloroflexi*, *Firmicutes*, *Acidobacteria*, *Actinobacteria*, *Planctomycetes*, *Verrucomicrobia*, *Bacteroidetes*, and *Aminicenantes* were listed in descending order. On the genus level, the five dominant genera whose relative abundance was higher than 1% were *Clostridium sensu stricto*, *Thiobacillus*, *Gp6*, *Aminicenantes* genera *incertae sedis*, and *Desulfatiglans*.

The kinds of dominant bacteria on phylum and genus were consistent among different habitats, whereas the relative abundance was different. By using Kruskal-Wallis H test technologies, we found that on phylum level, the relative abundance of *Proteobacteria*, *Chloroflexi*, *Firmicutes*, and *Planctomycetes* had significant differences (p <0.05) in different habitats (Fig. 3a). The relative abundance of *Proteobacteria*, *Chloroflexi*, and *Firmicutes* was the richest in open water habitats. Moreover, the relative abundance of *Planctomyces* was the richest in river estuary. On the genus level, *Clostridium sensu stricto* and *Desulfatiglans* had significant differences (p <0.05) in different habitats (Fig. 3b), and both with the most abundant in open water habitats.

3.3 Bacterial functional annotation and distribution among different habitats

The FAPROTAX was estimated to predict the ecological function genes of the bacterial community in different habitats of Baiyangdian Lake. According to the classification annotation results of 16S rRNA sequences, there were 49 ecological function genes were detected by FAPROTAX database (Fig. 4).

There were 17 dominant ecological function genes whose relative abundance was above 1%. The relative abundance of ecological function genes related to carbon and sulfur was the highest, indicating that the carbon cycle and sulfur cycle in the surface sediments of Baiyangdian Lake might be stronger than nitrogen cycle and phosphorus cycle. Among different habitats, the kinds of dominant ecological function genes were



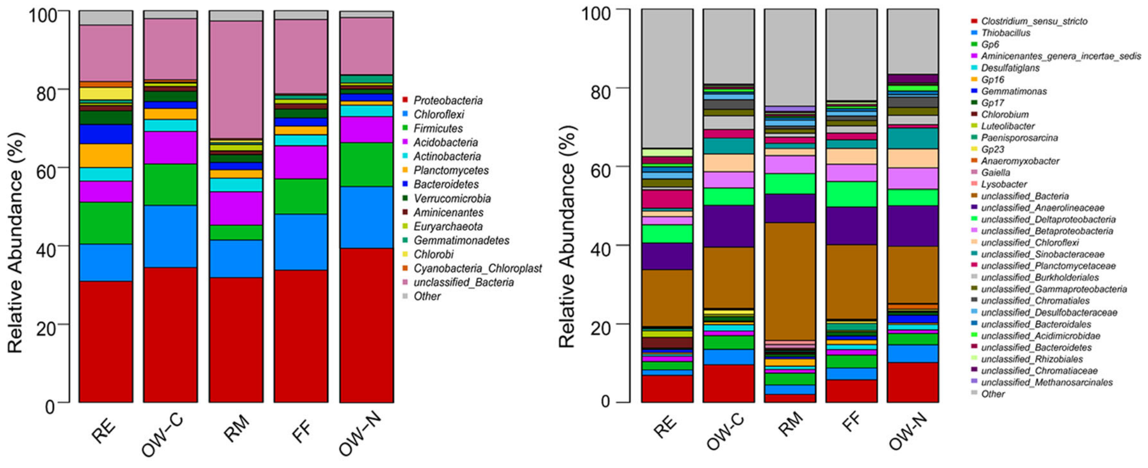
(a) (b)

Fig. 1 PCA analysis (**a**) and hierarchical clustering tree (**b**) on OTU level

consistent, but the relative abundance was different. In detail, the relative abundance of sulfur oxidation genes and sulfite respiration genes showed the highest abundance in the river estuary and the least abundance in the open water habitats. Combined with the physicochemical properties of surface sediments (Table S2), it corresponded to the concentration of TS in the surface sediments of river estuary. Furthermore, the relative abundance of nitrate reduction genes, nitrification genes, and nitrite oxidation genes in river estuary habitat was also higher than other habitats. As for open water habitats located in the Nanliuzhuang area and Caiputai area, there was no significant difference in the relative abundance of ecological function genes. This indicated that different geographical locations had no obvious effect on the ecological function of bacteria.

3.4 Correlation analysis between sediment properties and bacterial community structures

In order to explore the environmental influencing factors of bacterial community structures in Baiyangdian Lake, the physical and chemical properties of surface sediments were taken to research the influence of these properties on bacterial community structures, by using redundancy analysis (RDA) (Fig. 5). For bacteria, TN ($r^2 = 0.62$, $p = 0.001$), TS ($r^2 = 0.58$, $p = 0.001$), and C/N ratio ($r^2 = 0.52$, $p = 0.001$) were the most significant influencing factors in explaining the total variation. Among different habitats, the environmental influencing factors of bacterial community structures were significantly different. TS was the dominant influencing factor for the river estuary habitat, C/N ratio was the dominant influencing factor



(a) (b)

Fig. 2 Relative abundance of dominant bacteria at taxonomic levels of **a** phylum and **b** genus

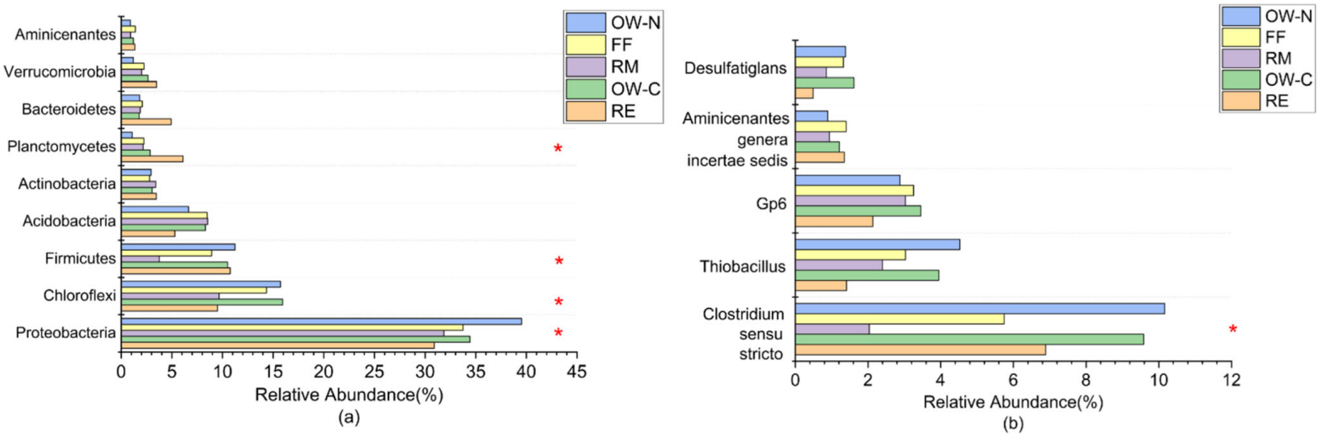
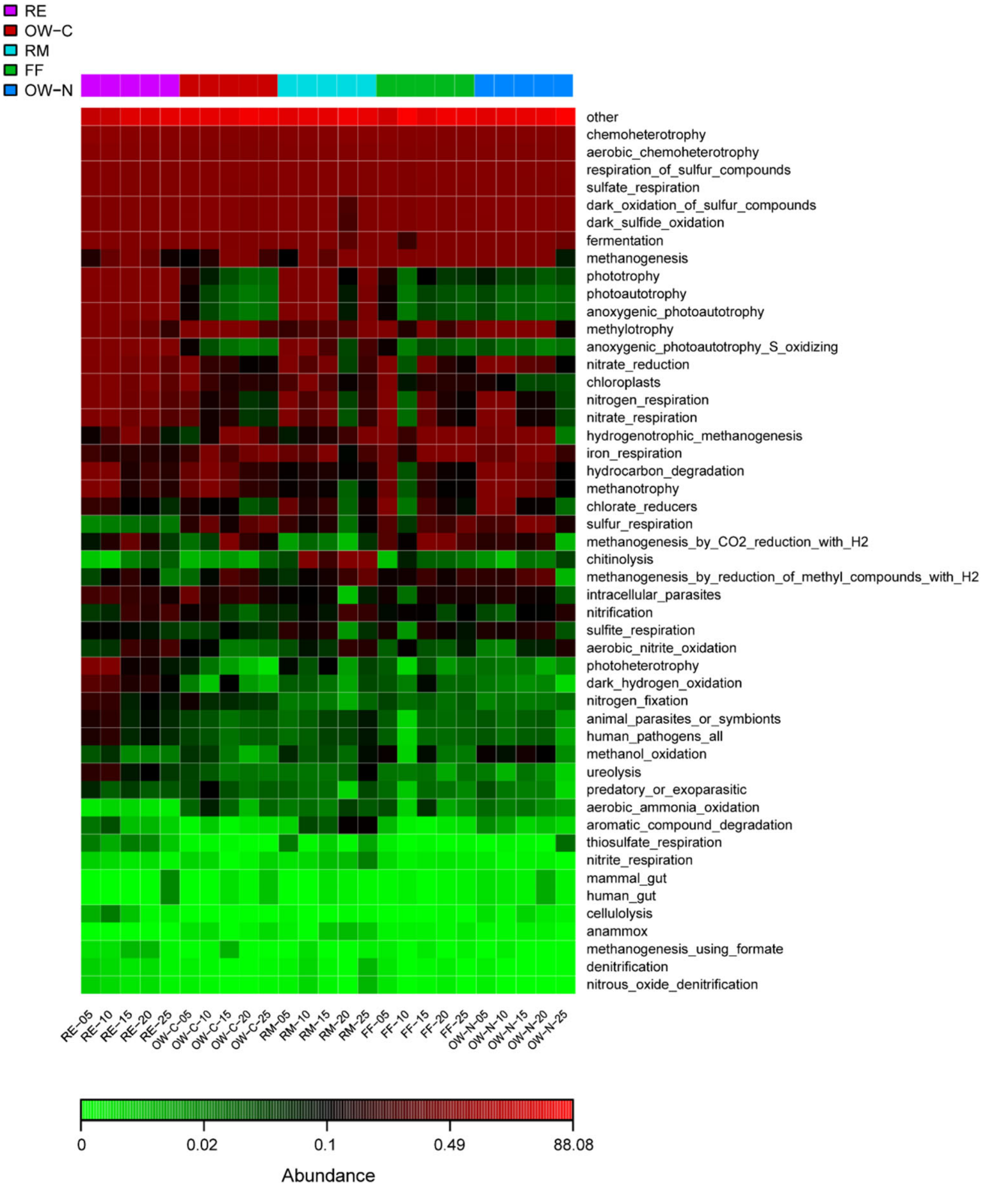


Fig. 3 Significant difference in abundance of dominant species on **a** phylum and **b** genus

Fig. 4 Distribution of bacterial function in the FAPROTAX database for different habitats of Baiyangdian Lake



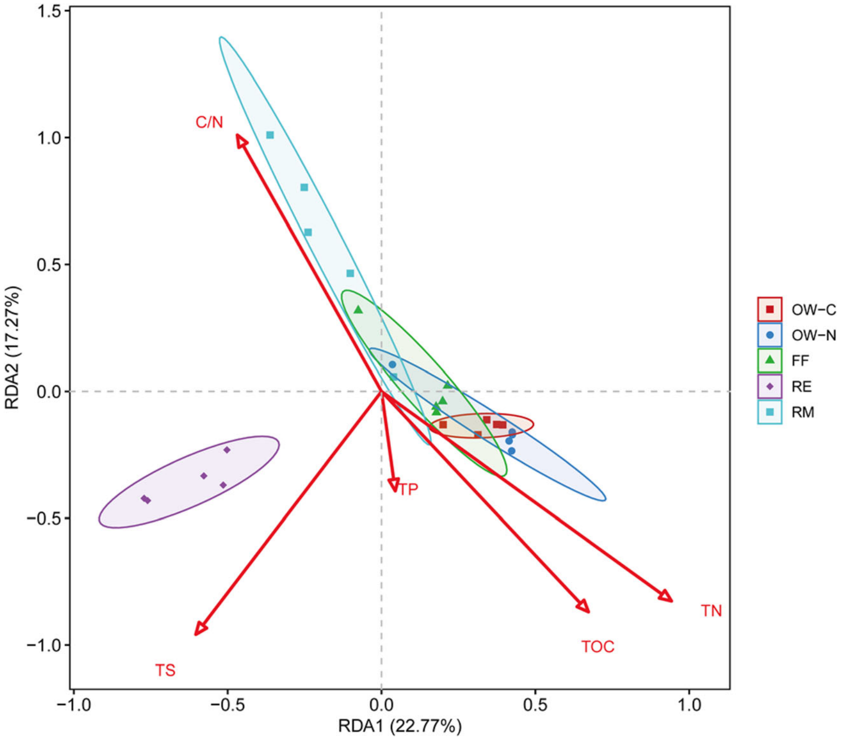


Fig. 5 RDA analysis of the relationship between bacterial community structures with environmental influencing factors in different habitats on OTU level

for reed marshes, and TN and TOC were the dominant influencing factors for open water habitats. Bioenv analysis showed that the best single parameter for explaining the composition of bacterial community structure at OTU level was TS (Table S3). The subset (TN, TP, TS, and C/N ratio) of environmental variables could best explain the variations of bacterial community structures at OTU level.

4 Discussion

4.1 Bacterial diversity change in surface sediments

As we all know, the richness of bacterial community is a valuable research indicator. In Baiyangdian Lake, the richness of bacterial community of reed marshes was higher than other habitats. The reason for that could be the highest C/N ratio of sediments in reed marshes habitat, which promoted the growth of bacteria (Table S2). Meanwhile, a large number of plant roots provided a more complex living environment for bacteria. For example, the root system of reed plants has strong oxygen transport and pollutant purification capacities (Tanaka et al. 2012). Plants can transform carbon dioxide in the atmosphere into biological organic carbon through photosynthesis, and form specific bacterial communities around roots through humification of plant litter and root exudation (Tanaka et al. 2012; Zhai et al. 2013; Liu et al. 2016).

Besides, the bacterial community diversity of Baiyangdian Lake showed differences within different habitats. River estuary had the highest bacterial diversity, followed by reed marshes and fish farms, and open water habitats had the lowest bacterial diversity. The reason for that could be the utilization of water in different areas affected the physical and chemical properties of surface sediments (Geist and Hawkins 2016). In addition, Franklin and Mills (2003) found that in the small-scale space of 2.5 cm–11 m, the similarity between microbial species showed a downward trend with the increase of distance. Therefore, there were certain spatial differences between different habitats, which might also affect the diversity of bacterial communities. In this research, for the two open water habitats from different geographic locations, there was no significant difference in abundance and diversity of bacterial communities. This result indicated the spatial differences were not the dominant driving factors for these two areas. Because in Caiputai and Nanliuzhuang areas, the water contamination was more serious than in other areas for the emission of wastewater which produced by human activities. The driving effect of heavy contaminants was greater than spatial differences on the diversity of bacterial communities.

4.2 Changes in bacterial community structures and environmental influencing factors among different habitats

The bacterial community structures of Baiyangdian Lake could be divided into two categories, the first category was river estuary and the second one was fish farms, reed marshes, and open water habitats, by using PCA analysis and hierarchical clustering on OTU level. These results indicated that the different habitats had important influence on the bacterial community structures of surface sediments. Compared with other habitats, the bacterial community structures of river estuary were unique. River estuary habitat was directly affected by the Tang River. There were residential areas along the upper reaches of the Tang River, which brought a lot of pollutants into the lake. The river ecosystem is an open system which carries out energy and material flows among river flows to lake ecosystem (Zeng et al. 2010). River flow brings water, sediment, and wastes into lake ecosystem. As for the hydrodynamic effect, it was stronger than internal lake areas, and pollutants in the lake might combine with particles brought by river flows, through adsorption and sedimentation, causing difference in nutrient distribution between sediment and water of the lake (Zhang et al. 2019b). Additionally, the single parameter that could best explain the difference of bacterial community structures in different habitats was TS. As is shown in Table S3, the concentration of TS was the highest in river estuaries.

There were abundant bacterial species of surface sediments in Baiyangdian Lake. The total relative abundance of dominant phylum was up to 75.60%, which could represent the bacterial community structure of surface sediments in the Baiyangdian Lake well. The kinds of dominant phylum were similar to that in freshwater lake sediments studied by other researchers (Han et al. 2020; Pan et al. 2020; Sun et al. 2020). On phylum level, *Proteobacteria*, *Chloroflexi*, *Firmicutes*, and *Planctomycetes* had significant differences (p <0.05) in different habitats. *Proteobacteria*, *Chloroflexi*, and *Firmicutes* were the richest in open water habitats. These phyla are known to function in the nutrient cycle in the water-sediment environment. For example, *Proteobacteria* play an important role in carbon metabolism and decomposition of soluble sugars (Xu et al. 2017), and many bacteria in this phylum have been functionally identified as organisms that relating to carbon and nitrogen cycles (Zhou et al. 2019). *Planctomyces* was the richest in river estuary; a previous research reported that *Planctomyces* could remove organic matter pollutants (Liu et al. 2018). This might be the water flows from the Tang River brought a large number of organic materials due to the wastewater emission. On the genus level, *Desulfatiglans* and *Clostridium sensu stricto* had significant differences (p <0.05). *Desulfatiglans*, a sulfate-reducing bacterium (SRB), was related to the sulfur cycle. Balk et al. found that sulfate-reducing bacteria could be used to treat heavy metals and hydrocarbon pollution, which could indicate that there were heavy hydrocarbon and heavy metals pollution in Caiputai and Nanliuzhuang areas than other areas (Balk et al. 2008). This conclusion was consistent with the findings of other studies on the presence of heavy metals and hydrocarbon pollution in Baiyangdian Lake and the spatial heterogeneity of pollution (Zhang et al. 2018a; Zhang et al. 2018b). *Clostridium sensu stricto*, the dominant genus of *Firmicutes*, could hydrolyze carbohydrate and protein, producing certain toxins. This result indicated that the surface sediments of Caiputai and Nanliuzhuang areas might have certain biotoxicity.

4.3 Variations of ecological functions among different habitats

By using FAPROTAX to functional annotation prediction, there were 17 dominant ecological function genes whose relative abundance was above 1%. The 17 dominant ecological function genes participated extensively in the biogeochemical circulation of carbon, nitrogen, sulfur, and phosphors. The relative abundance of ecological function genes related to carbon and sulfur was the highest, indicating that the carbon cycle and sulfur cycle in the surface sediments of Baiyangdian Lake were stronger than other nutrient cycles. Among different habitats, the kinds of dominant ecological function genes were consistent, but the relative abundance was different. In detail, the relative abundance of sulfur oxidation genes and sulfite respiration genes showed the highest abundance at the river estuary and the least abundance in the open water habitats. Combined with the physicochemical properties of surface sediments (Table S3), it corresponded to the concentration of TS in the surface sediments of river estuary was higher than open water habitats. Because the river estuary was affected by the Tang River, the water from the Tang River could bring a certain amount of sulfur-containing substances. Hence, the high concentration of sulfur materials made the environment of river estuary available for sulfur-connected bacteria to grow. Furthermore, the relative abundance of nitrate reduction genes, nitrification genes, and nitrite oxidation genes in river estuary habitat was also higher than other habitats, but the concentration of TN was lower than other habitats, because the relative abundance of nitrate reduction genes was higher than nitrification genes and nitrite oxidation genes, which translated nitrates into nitrite, ammonia, or nitrogen which could be released into water bodies.

5 Conclusions

The bacterial species in the surface sediments of different habitats in Baiyangdian Lake were typical freshwater lake bacteria, which were widely involved in the nutrient circulations. The bacterial community structures and composition and ecological functions were significantly different in different habitats. They could be divided into two groups of bacterial community structures: one was a river estuary and the other comprised reed marshes, fish farms, and open water habitats. As for open water habitats located in different areas, there was no significant difference, indicating that in heavily polluted areas, the influence of spatial differences was weaker than other environmental factors. The river estuary contained abundant bacterial species, with the most evenness distributed and the richest relative abundance of ecological functions related to carbon and sulfur cycle. Because the river estuary was affected directly by the Tang River and the hydraulic disturbance was more frequent than other habitats. Further analysis found the environmental influencing factors of bacterial community structures were different among different habitats. Sulfur was the key influencing factor in the river estuary, C/N ratio was the key influencing factor in the reed marshes; and nitrogen and organic carbon were the influencing factors in open water habitats. For further study in the future, we will focus on the bacterial community structures of sediments on the depth, in order to build a systematic study of Baiyangdian Lake. This work not only laid a solid foundation for future research but also provided a guidance to assess the ecological management in Baiyangdian Lake.

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Declarations

Conflict of interest The authors declare no competing interests.

Human and Animal Rights and Informed Consent The article does not contain any studies with human participants or animals.

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