



# Changes in planktonic and sediment bacterial communities under the highly regulated dam in the mid-part of the Three Gorges Reservoir

Yu Qin<sup>1</sup> · Qiong Tang<sup>1</sup> · Lunhui Lu<sup>2</sup> · Yuchun Wang<sup>3,4</sup> · Irina Izaguirre<sup>5</sup> · Zhe Li<sup>2</sup>

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## Abstract

Bacterial communities play an important role in the biogeochemical cycle in reservoir ecosystems. However, the dynamic changes in both planktonic and sediment bacterial communities in a highly regulated dam reservoir remain unclear. This study investigated the temporal distribution patterns of bacterial communities in a transition section of the Three Gorges Reservoir (TGR) using Illumina MiSeq sequencing. Results suggested that in comparison to the planktonic bacteria, sediment bacteria contributed more to the reservoir microbial communities, accounting for 97% of the 7434 OTUs. The Shannon diversity index in the water (3.22~5.68) was generally lower than that in the sediment (6.72~7.56). In the high water level period (January and March), *Proteobacteria*, *Actinobacteria*, *Cyanobacteria*, and *Firmicutes* were the most abundant phyla, whereas in the low water level period (May, July, and September), the dominant phyla were *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes*. Sediment samples were dominated by *Proteobacteria*, *Chloroflexi*, and *Acidobacteria*. Principal coordinate analysis of the bacterioplankton communities showed greater sensitivity to monthly changes than that of the sediment bacterial communities. Network analysis suggested that in comparison to planktonic bacterial communities, sediment bacterial communities were more complex and stable. The linear relationship between the CH<sub>4</sub>/CO<sub>2</sub> ratio, water level, and relative abundance of methanotrophs highlighted the potential methane-oxidizing process in the mid-part of the TGR. Moreover, the potential impact of dam regulation on the bacterial communities was revealed by the significant relationship between abundant phyla and the inflow of the TGR.

## Key points

- *Bacterioplankton communities showed great sensitivity to monthly changes.*
- *Potential methane-oxidizing process was revealed in this representative area.*
- *Water inflow regulated by dam has significant effects on dominant bacterioplankton.*

**Keywords** Bacterial communities · Water · Sediment · Three Gorges Reservoir · Community structure

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Yu Qin and Qiong Tang contributed equally to this work.

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✉ Lunhui Lu  
lulunhui@cigit.ac.cn

<sup>1</sup> Key Laboratory of Hydraulic and Waterway Engineering of the Ministry of Education, Chongqing Jiaotong University, Chongqing 400074, China

<sup>2</sup> Key Laboratory of Reservoir Aquatic Environment, Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences, Chongqing 400714, China

<sup>3</sup> State Key Laboratory of Simulation and Regulation of Water Cycle in River Basin, Beijing 10038, China

<sup>4</sup> China Institute of Water Resources and Hydropower Research, Beijing 100038, China

<sup>5</sup> Departamento de Ecología, Genética y Evolución-IEGEB (UBA-CONICET), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

## Introduction

The influence of large dams is a hot topic in the environmental field (Winton et al. 2019). Dams are built for flood control, hydroelectricity generation, irrigation, navigation, etc., contributing to economic growth in a local region (Lehner et al. 2011). These ecosystems also play an important role in coupling biogeochemical cycles between land and rivers (Ruiz-Gonzalez et al. 2013). Water flow carries living and nonliving matter, while sediment is the source or sink of nutrient circulation (Zhang et al. 2019). The establishment of dam reservoirs impedes the flow of basic nutrients including carbon (C), phosphorus (P), nitrogen (N), and silicon (Si), along a river network, and promotes the enhanced transformation and elimination of nutrients (Maavara et al. 2020). In addition, a dam reservoir acts as an “in-stream” reactor, hindering the flow of nutrients and thus increasing residence time along the land-ocean aquatic continuum. These increases in the retention time of nutrients enhance the transition of nutrients from the dissolved to particulate forms through primary productivity or adsorption, precipitation, and retention, as well as the gaseous removal and/or atmospheric fixation of nutrients in a reservoir (Maavara et al. 2020). Sedimentation of particulate matters and the increase of light transmittance under water supported the increase of primary production, leading to the development and change of food web (Lu et al. 2020). These changes result in differences in hydrology or limnology between reservoirs and natural water bodies and further influence microbial communities and related biogeochemical cycles (Zeglin 2015). Microorganisms are ecologically important and functionally diverse components of freshwater environments, supporting a range of ecosystem processes and functions. Meanwhile, they drive all major biogeochemical cycling, so they have an incredible impact on ecosystem services (Clark et al. 2018).

Bacteria contribute greatly to biogeochemical processes and nutrient circulation in reservoir ecosystems (Madsen 2011; Xu et al. 2011). Sediment bacterial communities degrade organic matter in sediments by mineralization (Chen et al. 2017). Planktonic bacterial communities are the aggregate of a variety of upstream bacterial sources that grow in soil, stormwater, lakes, and groundwater (Liu et al. 2018). They play a key role in the decomposition of dissolved organic matter in the water and depositing the metabolites of the degraded bacteria into sediments in the form of particle organic matter (Marshall 1981; Winton et al. 2019). The composition and structure of planktonic bacterial communities are highly responsive to changes in the environment (Wang et al. 2020). Sediment bacterial community establishes in a habitat that is the result of a long-term sediment erosion and accumulation process (Liu et al. 2018). River or reservoir bacterial communities of planktonic and sediment environments have recently been demonstrated to be highly diverse and variable (Chen et al. 2017; Crump et al. 2009; Liu et al. 2019b; Nyirabuhoro et al. 2020; Yan

et al. 2015). Crump et al. (2009) reported that synchronous changes in bacterial communities were largely correlated with periodic changes in river systems. However, it was indicated that spatial variability would be more important than temporal trends in the sediments of Miyun Reservoir, China (Chen et al. 2017). In aquatic ecosystem, methane is mainly produced by methanogens in anoxic sediments (Ferry and Lessner 2010). Methanotrophs are microbes that oxidize methane into carbon dioxide. They are classified into type I and type II (Bowman 2006). Arguably, methane oxidation in the water column is an important methane sink before it is released from the aquatic system into the atmosphere (Bussmann et al. 2017). Therefore, methane oxidation is not only a vital process of carbon migration and transformation in water, but also an important way to reduce the greenhouse effect of reservoir (Murrell and Jetten 2009).

The Three Gorges Reservoir (TGR) was formed in 2003 after the construction and impoundment of the Three Gorges Dam (TGD). The reservoir covers the main stem of the Yangtze River from Chongqing upstream to Yichang City, the dam site. The full length of the TGR is approximately 660 km, and the full reservoir surface area at its normal operation level is approximately 1080 km<sup>2</sup>. According to the operation scheme, the water level of the TGR is impounded to 175 m in October for hydro-power generation and gradually decreases to 145 m for flood control in March (Li et al. 2016). Thus, the operation of the TGD leads to distinctive limnological characteristics in the main stem of the Yangtze River (Liu et al. 2012), especially in the mid-part of the reservoir. Typically, the longitudinal axis of the TGR can be divided into a lacustrine zone, transition zone, and riverine zone (Li et al. 2017). The transition zone is the most sensitive among these three zones (Thornton et al. 1990). Meanwhile, this zone received bulk deposition of upstream sediments and was the hotspot of methane accumulation (Li et al. 2020). The transition zones are characterized by the higher productivity and biomass of phytoplankton, due to the increase in water residence time and the light penetration, and the deposition of sediment and clay particles in near-surface water. As a result, the transition zone may be the most fertile part of the reservoir since light and nutrients both favor photosynthesis by algae (Straskraba 1999; Thornton et al. 1990). These characteristics make suspended sediment more abundant and easier to deposit, and further results in different responses of bacterial community between water and sediment to the unstable environments in typical transition zone. Moreover, hydrology conditions not only alter water chemistry (such as dissolved oxygen and water temperature) (Li et al. 2010) but also change physical and chemical factors in sediments (such as total organic carbon concentration and saturated water capacity) (Xu et al. 2011), resulting in dynamic changes in the biogeochemical cycles of aquatic environments (Martins et al. 2011). Several researches of bacterial communities have been conducted in the TGR (Li et al. 2019; Li et al. 2017; Liu et al. 2018), and most publications emphasize on the diversity and composition of planktonic or sediment bacterial

communities. However, the responses of planktonic and sediment bacterial communities to the environmental disturbances still remain largely uncovered in the typical transition zones.

Therefore, it is hypothesized that the responses in the water and sediment of bacterial communities at different periods (high and low water level) under the regulated dam would be different in the mid-part of the TGR. The purpose of this study was to (i) analyze the diversity and temporal distribution patterns of planktonic and sediment bacterial communities; (ii) investigate the effects of environmental and hydrological factors on the bacterial communities; (iii) explore the potential methane-oxidizing process in the water and sediment; and (iv) reveal the changes of planktonic and sediment bacterial communities under the influence of the TGD. This study will lay a theoretical foundation for the micro-ecological process in the river-reservoir ecosystems.

## Materials and methods

### Study sites and sampling

The sampling sites of this study generally cover the whole transition zones in the TGR, including Fuling (FL), Zhongxian (ZX), and Wanzhou (WZ) (Fig. 1). Water and sediment samplings were synchronously conducted in January, March, May, July, and September of 2018. According to the

dam regulation, January and March were in the period of high water level, and May, July, and September were in the period of low water level. Total 30 samples were collected, including 15 water samples and 15 surface sediment samples. Sample information was provided in Table S1.

For water sampling, 5 L of water was collected in a clear polypropylene container for each site and transported to the laboratory within 6 h. Then, 1 L of water was filtered through 0.22- $\mu\text{m}$  pore size membrane filters (Millipore, Bedford, MA). The membranes were transported in liquid nitrogen and then stored at  $-86\text{ }^{\circ}\text{C}$  in the laboratory until DNA extraction. The remaining water samples were pretreated based on standard methods for the physico-chemical analysis. A dredger was used to collect the surface sediment samples. The sediment samples were kept in sterilized polypropylene tubes for microbial analysis and self-sealing bags for physico-chemical analysis in coolers, and then transported to the laboratory. In addition, the overlying water of each sediment sample was obtained to analyze the headspace concentrations of  $\text{CH}_4$  and  $\text{CO}_2$  to characterize the mineralization of the sediments.

### Physical and chemical analyses

Water temperature (T) and dissolved oxygen (DO) were determined by a YSI® ProODO dissolved oxygen meter, and the pH was determined by a YSI® 63 pH meter. Total organic carbon (TOC) was determined by a Shimadzu® TOC-VWP

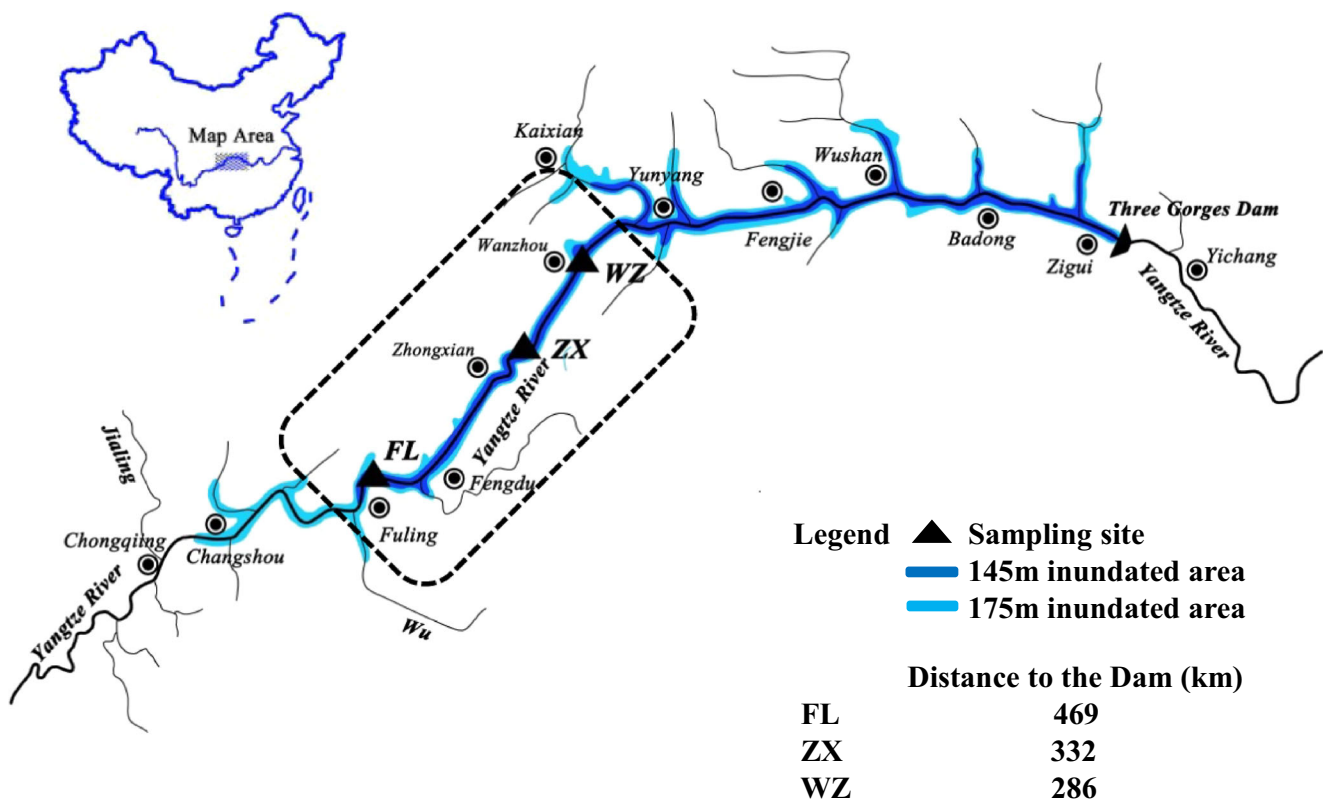


Fig. 1 Map of the Three Gorges Reservoir area (TGR) showing the location of the sampling sites

analyzer ((Shimadzu®, Japan); total nitrogen (TN) was determined by the Kjeldahl nitrogen method (Society 1982); nitrate nitrogen (NO<sub>3</sub>-N) and ammonium nitrogen (NH<sub>4</sub>-N) were measured by potassium chloride solution-spectrophotometric methods (Protection 2012); and the concentration of CH<sub>4</sub> and CO<sub>2</sub> in water was determined by the headspace equilibrium method and gas chromatography (Qin et al. 2018).

### DNA extraction, PCR amplification, and sequencing

Genomic DNA of both the filters and sediment samples was extracted using the FastDNA spin kit for soil (MP Biomedicals, USA) in duplicate, according to the manufacturer's recommended protocol. The quality of the extracted DNA was checked by 1% agarose gel electrophoresis. PCR and sequencing experiments were performed using the combined duplicate DNA extracts. The V3–V4 region of the bacterial 16S rRNA gene was amplified using the primer pair 515F/806R (Walters et al. 2016). The PCR mixture contained 4 µL of 5×FastPfu Buffer, 2 µL of 2.5 mM dNTPs, 0.8 µL of each primer (5 µM), 0.4 µL of FastPfu polymerase, and 10 ng of template DNA. All reactions were performed in triplicate. Finally, the purified PCR products were combined and then sequenced on the Illumina MiSeq PE250 platform (Majorbio Biotechnology Company, Shanghai, China) (Liu et al. 2019c).

### Bioinformatics and statistical analysis

QIIME version 1.8 was used to quality-filter the raw sequences of the amplicons (Caporaso et al. 2010). The bioinformatics analyses were all based on operational taxonomic units (OTUs), which were clustered with a 97% similarity cutoff by UPARSE (version 7.1). The chimeric sequences were identified and then removed by UCHIME (Edgar 2013). The RDP Classifier against the Greengenes database was then used to obtain the taxonomy of the sequences (Liu and Wong 2013). Quality controls, species annotations, and statistical calculations were carried out using the standard QIIME2 pipeline. The raw sequencing data were submitted to the NCBI Sequence Read Archive (SRA, <http://trace.ncbi.nlm.nih.gov/Traces/sra/sra.cgi>) under accession number PRJNA635208.

Alpha diversity indices (richness, ACE, Shannon index, Simpson index, etc.) and dissimilarity-related calculations were calculated in R Studio using the vegan and OTU table packages. Stackplot of taxonomy composition was analyzed using R studio. Bray-Curtis distance-based principal coordinate analysis (PCoA) was used to analyze the differences between samples. Analysis of similarity (ANOSIM) statistics was conducted to detect the significance of the differences between different months and sites based on Bray-Curtis dissimilarity of species using 999 permutations. PCoA, ANOSIM statistics, Wilcoxon rank-sum test, and Kruskal-Wallis H test were visualized and calculated using the Majorbio Cloud platform online ([www.](http://www.majorbio.com)

[majorbio.com](http://www.majorbio.com)). The linear discriminant analysis effect size (LEfSe) biomarker discovery suite was to compare the abundance of the bacterial composition at each taxonomic level (from kingdom to genus) and to identify taxa differentially abundant among groups (Segata et al. 2011) between the water and sediment samples in different months. Significant taxa were applied to generate taxonomic cladograms and explain the monthly differences. R studio was used to calculate the data required for linear discriminant analysis, and then, the graph was constructed on the website [www.ehbio.com/ImageGP/](http://www.ehbio.com/ImageGP/). The relationships between the environmental factors and the alpha diversity index were analyzed by Pearson correlation analysis using R v3.6.1. Moreover, the linear relationship between the CH<sub>4</sub>/CO<sub>2</sub> concentration, water level, and the relative abundance of aerobic methanotrophs and the boxplot of month and aerobic methanotrophs relative abundance were also calculated using R v3.6.1. In addition, the linear regressions between the relative abundance of dominant phyla and water inflow were performed using Origin (version 2018) to show the potential dam regulation on the microbiota.

Microbial correlation network analysis is an increasingly popular tool for the study of microbial community structure and internal interactions (Rottjers and Faust 2018). Two networks were constructed from water and sediment, respectively. In order to reduce noise and false positive predictions, we selected OTUs that had 100% occurrence for further analysis in each network (Liu et al. 2019a). Only Spearman's rank correlation coefficients ( $|r| > 0.6$ ) and statistically significant ( $p < 0.05$ ) correlations were accepted for network analyses. Topological analysis, modular analysis, and visualization were calculated by the igraph package of R Studio and Gephi (version 0.91). The size of the node was determined by the degree (the number of edges attached to the nodes) in the network.

## Results

### Environmental factors of water and sediments

The physiochemical properties of the water and sediment samples are showed in Table S2. The pH values of the water samples were between 7.78 and 8.33, indicating that the water is weakly alkaline. The lowest TOC concentrations in FL were observed in September and the highest in January, ranging from 0.29 to 2.61 mg/L in the water, and from 0.01 to 0.06 g/kg (average 0.03 g/kg) in the sediment. TN concentrations ranged from 0.45 to 4.81 mg/L in the water, being higher in January and March (average 2.75 mg/L) than in May, July, and September (average 0.65 mg/L); in the sediment TN ranged from 0.28 to 4.56 g/kg. NH<sub>4</sub>-N concentrations varied between 0.03 and 0.45 mg/L in the water and reached its peak in ZX in July, whereas the difference in the sediment was more obvious among the 5 months. The NO<sub>3</sub>-N concentrations fluctuated at

each site and ranged from 0.45 to 0.76 mg/L (average 0.62 mg/L) in the water. The concentrations of CH<sub>4</sub> in water samples varied from 0.02 to 0.34 μM/L, whereas from 0.03 to 0.65 μM/L in overlying water of the sediment.

### Alpha diversity analysis of planktonic and sediment bacterial communities in the mid-part of the TGR

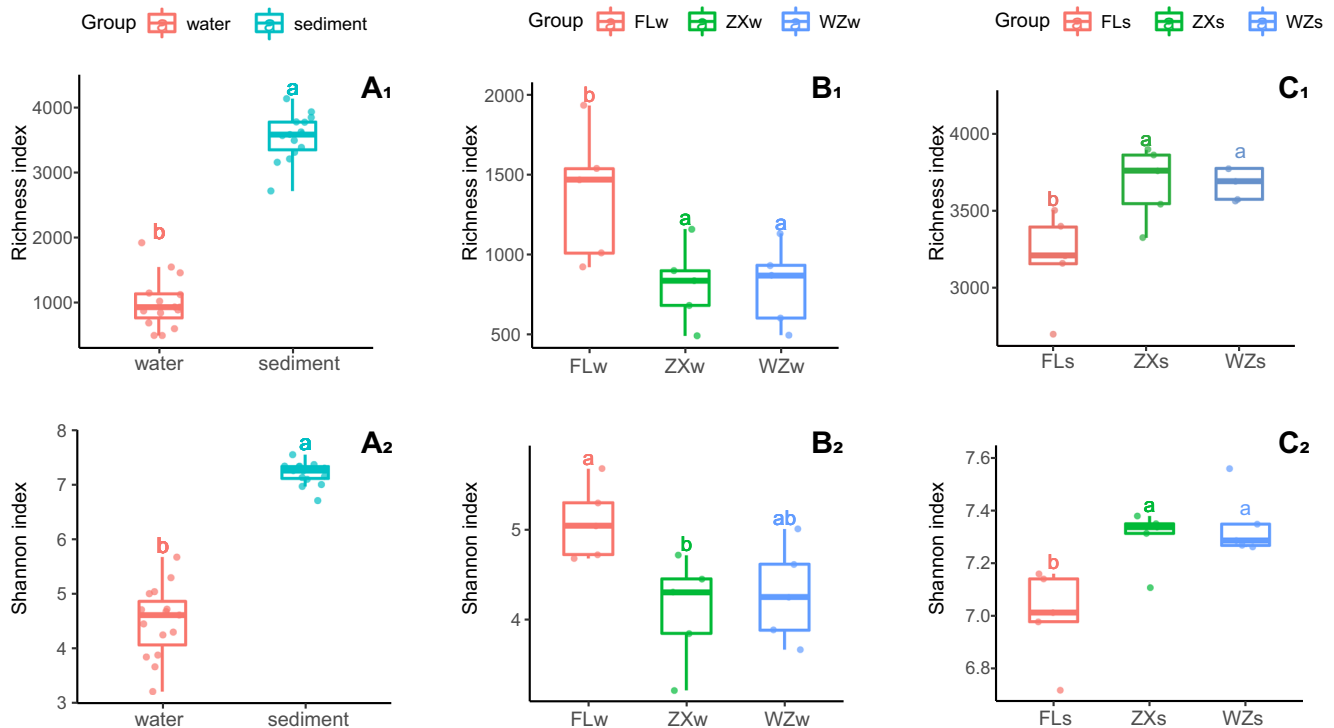
A total of 1,365,739 high-quality bacterial 16S rRNA gene sequences and 7434 OTUs were obtained from 30 samples (15 water and 15 sediment samples) by high-throughput sequencing. A total of 4063 OTUs were obtained in the water and 7212 OTUs in the sediment. OTUs in the sediment samples accounted for 97.0% of the total OTUs, among which 45.3% were unique for this habitat. Water subgroup OTUs accounted for only 54.7% of the total OTUs. The Shannon diversity was higher in the sediment, varying from 6.72 to 7.56 in the sediment and 3.22 to 5.68 in the water. Rarefaction curves showed that the bacterial OTUs obtained were sufficient to represent the bacterial communities in the water and sediment samples (Fig. S1). The Good's coverage mean values of the sediment samples were 0.971 (Table S3), indicating that the sediment bacterial community was well represented by the current bacterial profile. The OTU richness and Shannon diversity of water samples and sediment samples were compared. Overall richness and Shannon index values were significantly higher for the sediment bacterial communities than for the water samples (Fig. 2A<sub>1</sub>, A<sub>2</sub>).

Multiple different indices also indicated this trend (Table S3). As shown in Fig. 2B<sub>1</sub>, C<sub>1</sub>, there were significant differences in the richness index between the water samples (FLw vs. ZXw and WZw) and sediment samples (FLs vs. ZXs and WZs). Significant differences were observed in the Shannon diversity between the sediment samples (FLs vs. ZXs and WZs), whereas in the case of the water samples, significant differences were found between FLw and ZXw (Fig. 2B<sub>2</sub>, C<sub>2</sub>).

### Taxonomic composition and beta diversity of bacterial community in the water and sediment samples

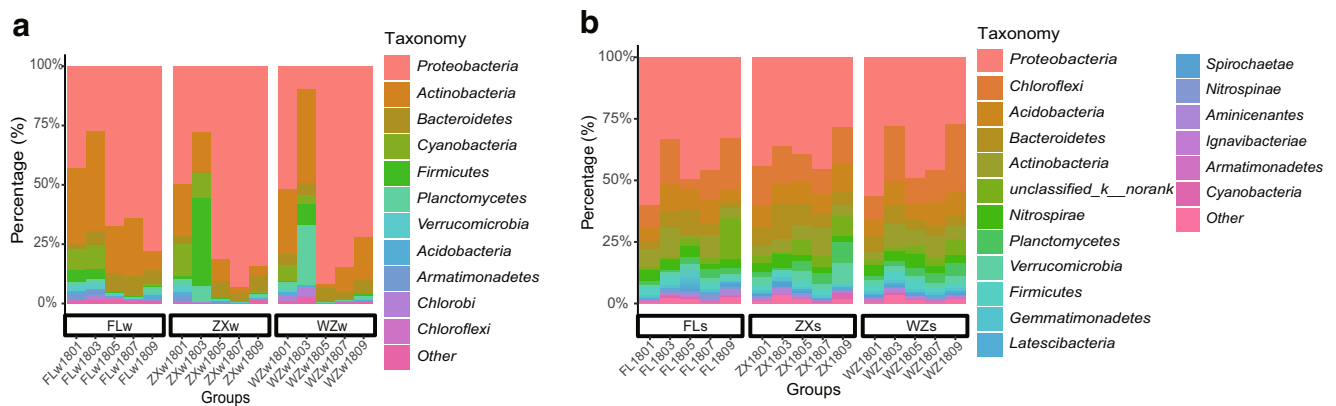
Of the 7434 clustered bacterial OTUs, 91.9% (6832) were at the phylum level, followed by 82.7% (6150), 64.9% (4824), 54.5% (4054), 28.2% (2094), and 5.2% (384) at the class, order, family, genus, and species levels, respectively. The bacterial communities in the water were dominated by *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Cyanobacteria*, with these phyla accounting for 62%, 18%, 5%, and 4% respectively. The sediment samples were dominated by *Proteobacteria*, *Chloroflexi*, and *Acidobacteria*, accounting for 41%, 14%, and 9%, respectively.

The bacterial communities exhibited remarkable temporal heterogeneity (Fig. 3). The relative abundance of *Proteobacteria* at three sites (FLw, ZXw, and WZw) greatly decreased in March, as shown in pink. At the same time,



**Fig. 2** Comparison of the richness and Shannon indices between water and sediment samples (A<sub>1</sub> and A<sub>2</sub>). Comparison of the richness and Shannon indices among FL, ZX, and WZ (B<sub>1</sub>, B<sub>2</sub>, C<sub>1</sub>, C<sub>2</sub>). FLw, ZXw,

and WZw represent all the water samples in Fuling, Zhongxian, and Wanzhou, respectively. FLs, ZXs, and WZs represent all the sediment samples in Fuling, Zhongxian, and Wanzhou, respectively



**Fig. 3** Histograms of phylum abundances across the sampling period as measured at the three sites in water (a) and sediment (b). FLw, ZXw, and WZw represent all the water samples in Fuling, Zhongxian, and

Wanzhou, respectively. FLs, ZXs, and WZs represent all the sediment samples in Fuling, Zhongxian, and Wanzhou, respectively

except for ZXw, the proportions of *Actinobacteria* in FLw and WZw in March were substantially higher than those in the other months. The proportion of *Firmicutes* was highest in ZXw in March. Changes in the proportion of the different bacterial phyla in the sediment are shown in Fig. 3b. The diversity of the bacterial communities was significantly higher than that of the water. Compared with the water samples, *Chloroflexi* were the second highest abundant in the sediment samples. *Proteobacteria* were present in all samples, being highest in number in May and July. In summary, these results indicated that the bacterial community of the sediments was more varied and complex than that of the water samples.

Significant differences in the top 15 phyla among the different groups were statistically observed based on Wilcoxon rank-sum test and Kruskal-Wallis H test (Fig. S2). The species difference analysis demonstrated that the abundance of bacterial communities differed significantly between water and sediment at phylum level ( $p < 0.05$ ). There were significant differences in *Firmicutes*, *Cyanobacteria*, *Planctomycetes*, and *Chlorobi* for the water samples in March ( $p < 0.05$ ), whereas 4 phyla (i.e., *Proteobacteria*, *Planctomycetes*, *Gemmatimonadetes*, and *unclassified\_k\_norank*) were significantly different for the sediment samples in March ( $p < 0.05$ ). A cladogram depicted the phylogenetic distribution of all detected bacterial composition types in Fig. S3. LEfSe identified *Acidobacteria*, *Verrucomicrobia*, *Armatimonadetes*, and *Cyanobacteria* as discriminative groups in January for the water samples. *Planctomycetes*, *Firmicutes*, *Deinococcus-Thermus*, and *Chlorobi* were discriminated in March. However, there was only significant difference of *Proteobacteria* in the sediments. Five different color groups were evident for water samples, whereas four color groups were shown for sediment samples. These different enrichment groups showed the clear performance of the main characteristics of bacterial community structure in the water, corresponding to the 5 months. Compared with the water samples, the sediment samples did not show obvious significant changes.

Principal coordinate analysis (PCoA) was applied to determine the community composition of each sample (Fig. 4). The first two axes explained 34.87% and 17.63%. The first axis showed that the bacterial communities of the water samples differ from the corresponding sediment samples, regardless of sampling site and month. The bacterial communities of the water samples exhibited distinct temporal groups, whereas the bacterial communities in the sediment samples did not form separated clusters by month. Furthermore, the analysis of similarity (ANOSIM) confirmed the correlation between different month groups and distinct microbial communities for the water and sediment samples ( $r = 0.793$ ,  $p = 0.001$ ).

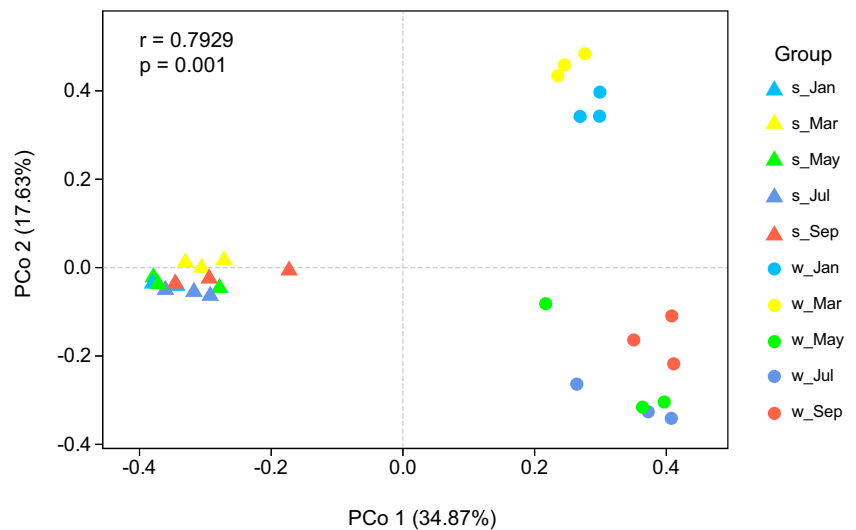
### Effects of environmental factors on the bacterial community

The relationships between the  $\alpha$ -diversity index and the environmental factors were determined by Pearson correlation (Fig. 5). The  $\alpha$ -diversity index of sediment and water samples both showed a significant positive or negative correlation with each other. Interestingly, the water level (Fig. 5a) showed a positive correlation with dissolved oxygen (DO), but a negative relationship with water temperature (T). The concentration of  $\text{CO}_2$  had a strong positive correlation with  $\text{NH}_4\text{-N}$  (Fig. 5b). Furthermore, four environmental factors (TN, DO, T, and water level) had significant effects on planktonic bacterial community based on the canonical correspondence analysis (CCA) (Table S4, Fig. S4). For the sediment bacterial community, the concentrations of  $\text{NH}_4\text{-N}$  and  $\text{CO}_2$  were significant variables based on redundancy analysis (RDA) ( $p < 0.05$ ).

### Network analysis of bacterial communities

The topological structures of the bacterial communities based on the OTU level are displayed in Fig. 6. The two networks were defined according to the same threshold,

**Fig. 4** Principal coordinate analysis (PCoA) diagram illustrating the bacterial composition of the water and sediment samples. s\_Jan, s\_Mar, s\_May, s\_Jul, and s\_Sep represent the sediment samples in January, March, May, July, and September, respectively; w\_Jan, w\_Mar, w\_May, w\_Jul, and w\_Sep represent the water samples in January, March, May, July, and September, respectively

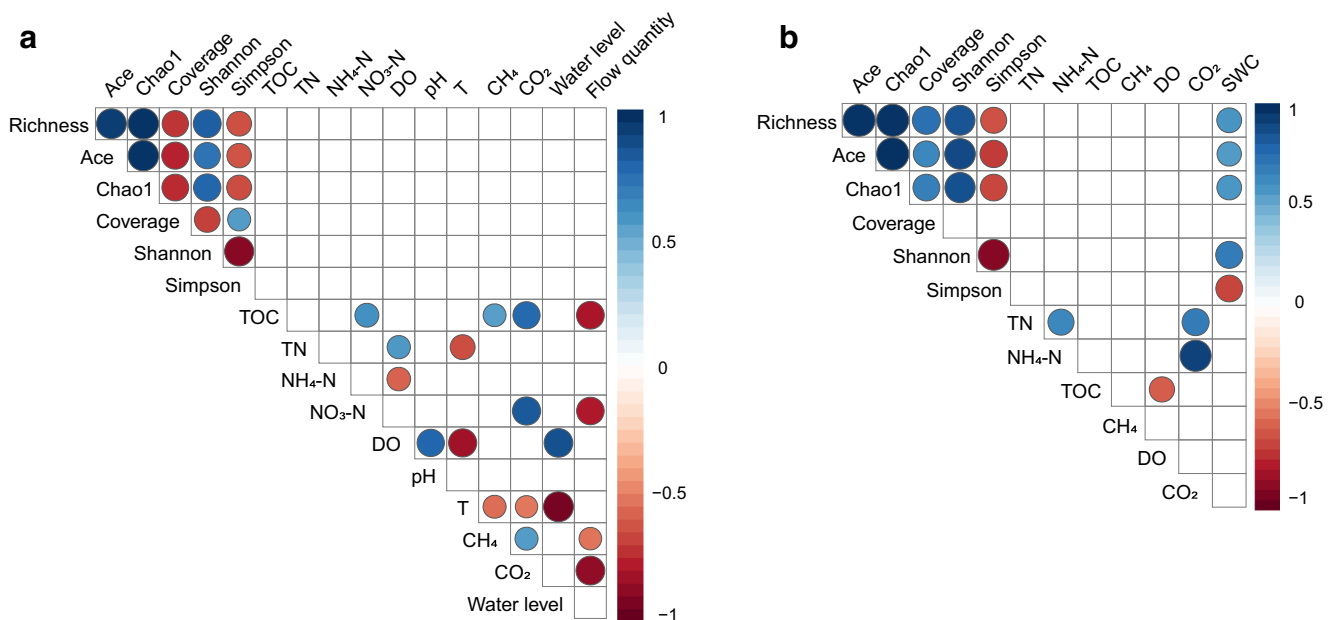


and the corresponding statistical results are showed in Table 1. Total 53 of 4063 OTUs in the water and 412 of 7212 OTUs (100% occurrence) in the sediment were selected for the further analysis. The network in the water contained 53 nodes and 201 edges, whereas 412 nodes and 5638 edges were included in the sediment network. Interestingly, positive correlations (edges) were obviously more than negative correlations both in the two networks (Table 1). However, the percentage of negative links was slightly higher in the sediment (31.3%) than in the water (26.9%), indicating that sediment bacterial network showed greater competition among species than planktonic bacterial network. Each network of the community had a

high modularity (> 0.4). However, the modularity of planktonic bacterial network (1.059) was lower than that of sediment bacterial network (1.139). Furthermore, the network of sediment bacterial communities was obviously complex (linkage density among those taxa) (Table 1) than that of the planktonic bacterial communities.

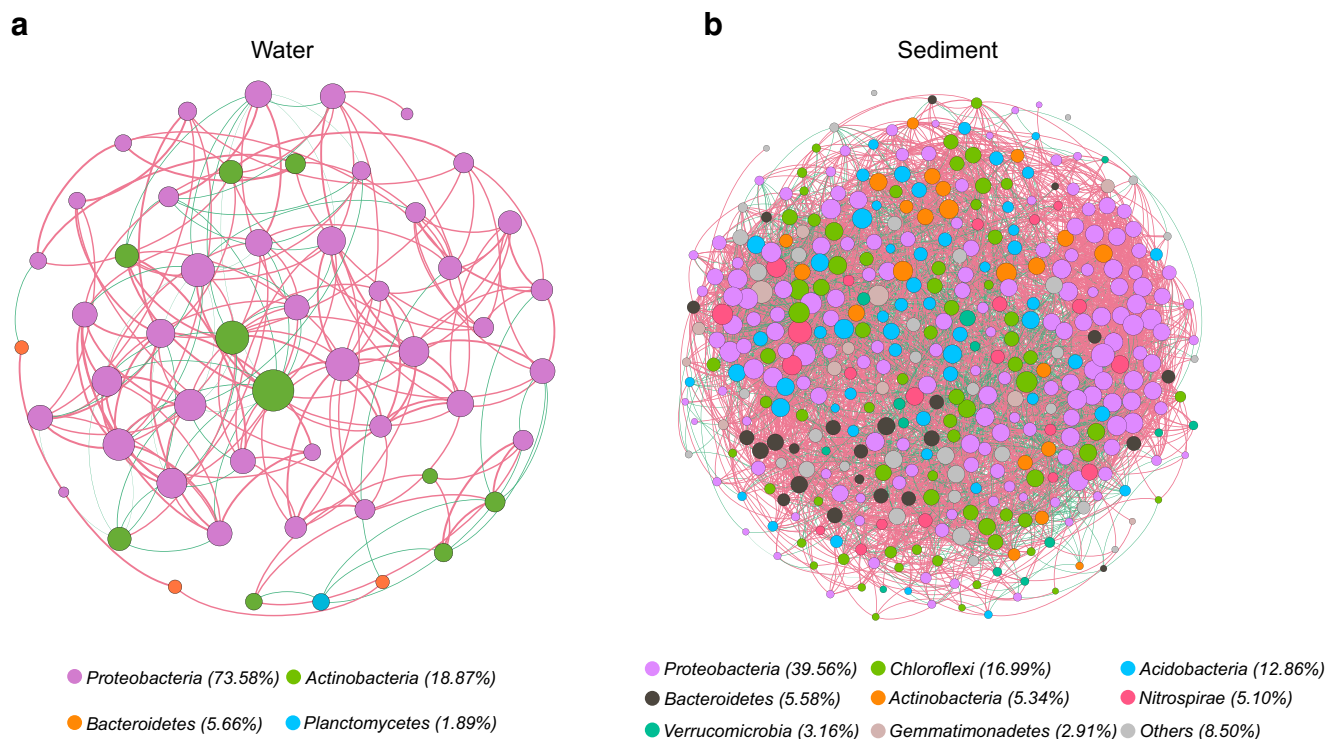
**Aerobic methanotrophic bacteria in the water and sediment samples**

Aerobic methanotrophic bacteria play an important role in the mineralization of sediments, directly affecting the concentration of CH<sub>4</sub> and CO<sub>2</sub> in overlying water. Aerobic



**Fig. 5** Pearson correlation between the bacterial  $\alpha$ -diversity indices (Richness, ACE, Chao1, Simpson, Shannon index, and Coverage) and environmental factors in the water (a) and sediment samples (b). SWC,

saturated water capacity of sediment samples. This diagram with blank implies no significant coefficient ( $p > 0.05$ )



**Fig. 6** Networks of different bacterial communities in the water and sediment. Each node represents one OTUs and its size corresponds to the degree of connectivity (the number of nodes directly connected to other nodes). Only connections between species that were statistically

significant ( $p < 0.05$ ) and strongly ( $|r| > 0.6$ ) correlated were performed. The pink and green lines represent positive and negative correlation, respectively. The thickness of the line is proportional to the value of absolute Spearman's correlation coefficient

methanotrophic bacteria in the water and sediment samples were identified according to relevant species information. There were mainly two dominant genera of aerobic methanotrophic bacteria, *Methylococcaceae* (*Gammaproteobacteria*, type I) and *Methylocystaceae* (*Alphaproteobacteria*, type II), respectively. The relative abundance of aerobic methanotrophs in the water and sediment accounted for approximately 0.8% of the total

community, respectively. In order to evaluate the dam regulation effect on the aerobic methanotrophic bacteria, the correlation between relative abundance of aerobic methanotrophs and water level was analyzed. The relative abundance of aerobic methanotrophs in the period of high water level was higher than that in May, July, and September (low water level) (**Fig. S5**, **Fig. S6**). The  $\text{CH}_4/\text{CO}_2$  ratio showed a negative correlation with the abundance of aerobic methanotrophic bacteria in the sediment. There was a significant positive correlation between the water level and the relative abundance of planktonic aerobic methanotrophs ( $r^2 = 0.546$ ,  $p = 0.001$ ).

**Table 1** Topological parameters of different bacterial community network

Communities	Water $n = 15$	Sediment $n = 15$
Nodes	53	412
Edges (positive edges/negative edges)	201 (147/54)	5638 (3873/1765)
Average degree	7.585	27.369
Network diameter	7	5
Linkage density	3.792	13.684
Modularity	1.059	1.139
Average clustering coefficient	0.504	0.393
Average path length	2.719	2.501

## Discussion

The planktonic and sediment bacterial communities were influenced by the regulation of the dam. In this study, three representative sampling sites in the mid-part of the TGR were selected for analyzing the planktonic and sediment bacterial communities at different regulation times. This study aims to provide important comparative information about the bacterial communities of water and sediment samples in the TGR, demonstrating difference in diversity and temporal patterns between the two habitats.



## Influence of environmental factors on the bacterial communities

In this study, water level, T, DO, and TN were significantly related with variations in the planktonic bacterial communities (Table S4). Water temperature was significantly lower at high water level than low water level, whereas dissolved oxygen at high water level was significantly higher than at low water level ( $p < 0.01$ , Fig. S7). Previous research revealed that bacterioplankton communities in large river reservoirs were directly or indirectly affected by impoundment and discharge (Li et al. 2017; Ruiz-González et al. 2013). Water temperature is a potential limiting factor because each microorganism has its particular optimal temperature requirement (Pomeroy and Wiebe 2001). Since the optimum temperature range of each phylotype is different, the composition of microbial community composition may vary with the fluctuation in water temperature (Pomeroy and Wiebe 2001). It has also previously been proved that temperature had a significant impact on the dynamics and composition of bacterioplankton in rivers (Chen et al. 2013; Crump and Hobbie 2005) and other aquatic ecosystems, such as lakes (Ju et al. 2014) and marine environments (Fuhrman et al. 2008). Similarly, previous studies in the Yangtze River have recently indicated that water temperature and dissolved oxygen influence the temporal distribution of bacterial communities (Liu et al. 2018). Nutrient concentrations (such as TN and  $\text{NH}_4\text{-N}$ ) were also considered to be important environmental factors affecting bacterial community composition, as they were vital for bacterial growth and development (Wang et al. 2015). Even though there were temporal differences in physiochemical properties, the temporal distribution of bacterial communities in the sediments of the reservoir could be attributed to the annual cycle of impoundment and discharge (Stegen et al. 2012), and sediment bacterial communities showed little difference among these 5 months.

## Potential methane-oxidizing process in the mid-part of the TGR

In a river-reservoir system,  $\text{CH}_4$  is mainly produced by methanogens in sediments. The generated  $\text{CH}_4$  is then oxidized to  $\text{CO}_2$  by methanotrophs (Crevecoeur et al. 2019). Methanotrophs are also the only bacteria that use methane as their sole source of energy and carbon (Crevecoeur et al. 2017). Thus, it is very important to study the  $\text{CH}_4/\text{CO}_2$  ratio to investigate the current situation of methane oxidation in the water and sediments. Methane oxidation was greatly influenced by  $\text{CH}_4$  concentration, which in turn is strongly affected by water level fluctuations, so it could be said that the methane oxidation rate mirrored the distribution of methane (Matoušů et al. 2016). A large amount of organic carbon from upstream and terrestrial sources was absorbed

during the period of low water level, which was a sufficient condition for  $\text{CH}_4$  accumulation at the bottom of the mid-part of the TGR (Li et al. 2020). Fig. S5 shows that the relative abundance of methanotrophs decreased more obviously in the sediments than in the water, indicating that the environment in the sediments was more suitable for the growth of methanotrophs and the gradual consumption of methane. Crevecoeur et al. (2017) also demonstrated a negative relationship between methane concentration and methanotrophs in bottom samples. In addition, many investigations have revealed that 66–95% of the  $\text{CH}_4$  diffused from the anoxic zone is oxidized on surface sediment (Borrel et al. 2011; Bosse et al. 1993; Frenzel et al. 1990). The significant change in the water level of the TGR from impoundment to discharge seems to directly influence the relative abundance of methanotrophic bacteria in the water (Fig. S5). One possible reason is that the fluctuation of water level affects dissolved oxygen and temperature in the water (Fig. S7), and some studies have indicated that these two factors may influence the abundance of methanotrophic bacteria in the water (Kraemer et al. 2017; Roland et al. 2017). The effect of oxygen on microorganisms generally depends on the tolerance of enzymes in microbial cells (Roland et al. 2017), while the influence of temperature on methanotrophic bacteria relies mainly on the temperature tolerance and activity of enzymes in microorganisms (Kraemer et al. 2017). The monthly changes also suggest this trend (Fig. S6). Interestingly, Wang et al. (2014) detected that  $\text{CH}_4$  consumption was greatly affected by the water level of the TGR in the range of 30 m from 145 to 175 m, indicating that it was related to temperature. He et al. (2012) reported that different types of methanotrophs had their suitable growth temperature; the relative abundance of type I and type II methanotrophs changed with not only temperature but also the composition of type I methanotrophs community were also affected by temperature. Variations in  $\text{CO}_2$  and  $\text{CH}_4$  concentrations, as well as in temperature, would determine the activity and community composition of methanotrophs (Horz et al. 2005; Knoblauch et al. 2008). These taxonomic changes will in turn bring about changes in the community of metabolic partners, which may potentially cause cascading effects throughout the microbial community and alter the dynamics of  $\text{CH}_4$  (Dean et al. 2018). Changes in the  $\text{CH}_4$  cycle are associated with climate change, and increased methane production warms the planet, which in turn leads to increased methane production (Dean et al. 2018).

## Changes of planktonic and sediment bacterial communities under the regulated dam

An increasing number of studies based on high-throughput sequencing technology have demonstrated that there is

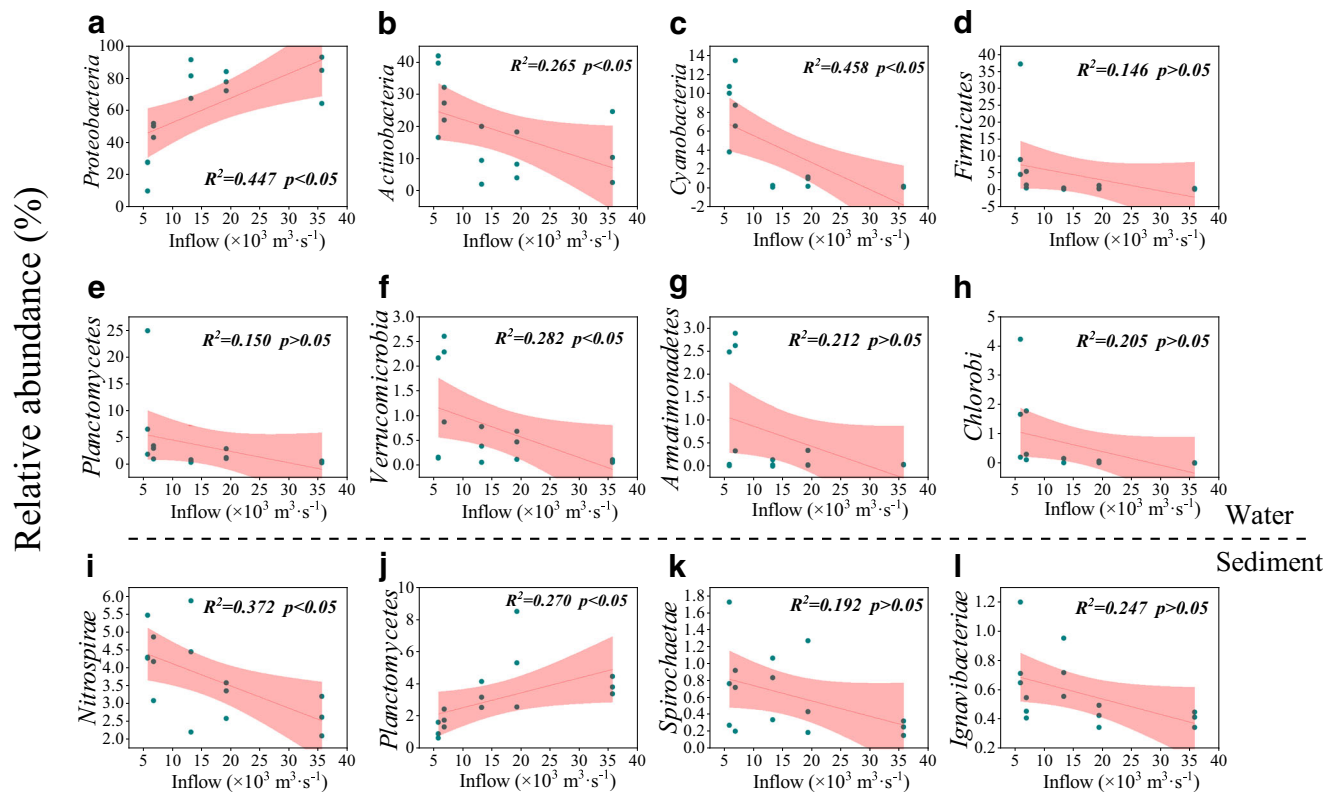
enormous diversity in the microbial communities harbored in aquatic environments (Henson et al. 2018; Li et al. 2019; Liu et al. 2015; Sun et al. 2014). The results of this study evidenced that  $\alpha$ -diversity in the sediment including richness, Shannon, Ace, and Chao1 were all higher than those in the water (Table S3). Bacterial communities in the sediment were the primary contributors to the bacterial diversity of the TGR. Only 3% of the total OTUs were unique to the water sample, and the planktonic bacterial populations are more likely to fluctuate than that in the sediment samples. In previous studies, Liu et al. (2018) and Feng et al. (2009) also found that the sediment samples had higher  $\alpha$ -diversity than the water in the Yangtze River. The distinctness of bacterial communities in the water and sediment may be attributed to the differences in the microgeochemical environment and the influence of the regulated dam (Cole et al. 2013; Klaver et al. 2007). Moreover, the network of sediment bacterial was more complex than that of planktonic bacterial network (Table 1), indicating that the species within sediment were more closely related (Landi et al. 2018). The negative connection ratio of sediment bacterial network was slightly higher than that of planktonic bacterial network, suggesting that the competition among species in sediment bacterial network was greater than that of planktonic bacterial network. Previous studies have proved that more negative interactions within a community may improve the stability of the network under interference (Coyte et al. 2015).

The dominance of *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Cyanobacteria* in the planktonic bacterial communities of TGR coincides with the results of some previous researches (Liu et al. 2018; Xiang et al. 2018). *Proteobacteria* was the most abundant phylum, and some studies have shown that this group plays an important role in bacterioplankton communities in the water, owing to its high substrate absorption and growth rate (Kasalicky et al. 2013). The second most abundant phylum was *Actinobacteria*, a Gram-positive bacteria that can absorb nutrients and is ubiquitous in freshwater habitats (Li et al. 2017). Interestingly, the *Bacteroidetes* phylum was predominantly observed at the low water level in May, July, and September (Fig. 3). The relative abundance of *Cyanobacteria* in January and March was higher than that in May, July, and September. Furthermore, LEfSe identified *Cyanobacteria* as discriminative groups in January for the water samples (Fig. S3). This phenomenon could be explained by the following reasons. First, TN concentrations in January and March were higher than those in May, July, and September (Table S2), which may stimulate the growth of *Cyanobacteria*, as *Cyanobacteria* abundance has been reported to be positively correlated with nitrogen content in the water (Gkelis et al. 2014). Second, water level after impoundment remained high during January and March, and the increasing water residence time favored *Cyanobacteria* growth, preventing them from dispersing into

new habitats. Contrarily, during the discharge period (May, July, and September), the relative abundance of *Cyanobacteria* was low due to large water flow and short water residence time.

The results of this study showed that in contrast to the sediment communities, the planktonic communities were separated into two groups (w\_Jan and w\_Mar; w\_May, w\_Jul, and w\_Sep) according to sampling months (Fig. 4), indicating that the planktonic bacterial community displayed a more sensitive and complex response to different months. Different factors could account for this result. First, differences in environmental and hydrographic conditions between the two habitats (Liu et al. 2018). Second, the alternate impoundment and discharge periods (Xu et al. 2011). A succession of planktonic bacterial community composition was observed during the different months (Fig. 3). It was speculated that the structure and functional patterns of bacterioplankton communities may be influenced by the regulation of the TGD. We found that there was a significant correlation between inflow and the relative abundance of the dominant phyla in the water, such as *Proteobacteria*, *Actinobacteria*, and *Cyanobacteria*, while only two dominant phyla in the sediment (*Nitrospirae* and *Planctomycetes*) had a significant correlation (Fig. 7). This result indicated that in comparison to the sediment communities, the planktonic bacterial communities were more easily influenced by TGD operation. Third, the differences in the community distributions from different sites indicated that dispersal and drift influenced bacterial community assemblages (Li et al. 2019). In addition, the reservoir system has an unusually large boundary with other ecosystems, such as vegetation (Ren et al. 2018) and surrounding soil (Xiang et al. 2018) in the watershed. The seasonal or periodic (impoundment and discharge) water level fluctuations can flush out microorganisms from surrounding systems, which also results in different levels of community diversity and composition and increased variation in the bacterial community in the TGR. Therefore, in comparison to the sediment communities, the planktonic bacterial communities were more vulnerable to TGD regulation and environmental conditions.

The diversity, temporal distribution patterns, and methane-oxidizing processes of both planktonic and sediment bacterial communities were analyzed in the mid-part of the TGR. The sediment subgroup accounted for 97% of the total OTUs, indicating that bacteria in the sediment played a more important role in the bacterial diversity of the reservoir. In comparison to the sediment bacterial communities, the planktonic bacterial communities were more sensitive to monthly variation of environmental conditions, and the temporal distribution patterns of the bacterial communities were explained by environmental factors. Sediment bacterial network was more complex and stable than that of planktonic bacterial network. The potential methane-oxidizing process in the water and sediment was revealed in the mid-part of the TGR. The results of our study provide a valuable



**Fig. 7** The linear relationship between inflow and the relative abundance of dominant phyla in the water (a–h) and sediment (i–l)

comparative information about the bacterial communities of water and sediment samples in the TGR, evidencing contrasting diversity and temporal patterns between the two habitats. A comprehensive understanding of planktonic and sediment bacterial communities is necessary for any large reservoir ecosystem.

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**Authors' contributions** YQ and QT investigated, studied, and wrote the original manuscript. LL provided the frame, the research goal of article, and supervised this work. YW revised the manuscript and supervised this work. II revised the manuscript. ZL was responsible for proofreading and reviewed article. All authors read and approved the manuscript.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with human participants or animals performed by any of the authors.

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