

Spatiotemporal variation of planktonic and sediment bacterial assemblages in two plateau freshwater lakes at different trophic status

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Received: 5 December 2015 / Revised: 12 December 2015 / Accepted: 14 December 2015 / Published online: 28 December 2015
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Abstract Both planktonic and sediment bacterial assemblages are the important components of freshwater lake ecosystems. However, their spatiotemporal shift and the driving forces remain still elusive. Eutrophic Dianchi Lake and mesotrophic Erhai Lake are the largest two freshwater lakes on the Yunnan Plateau (southwestern China). The present study investigated the spatiotemporal shift in both planktonic and sediment bacterial populations in these two plateau freshwater lakes at different trophic status. For either lake, both water and sediment samples were collected from six sampling locations in spring and summer. Bacterioplankton community abundance in Dianchi Lake generally far outnumbered that in Erhai Lake. Sediment bacterial communities in Erhai Lake were found to have higher richness and diversity than those in Dianchi Lake. Sediments had higher bacterial community richness and diversity than waters. The change patterns for both planktonic and sediment bacterial communities were lake-specific and season-specific. Either planktonic or

sediment bacterial community structure showed a distinct difference between in Dianchi Lake and in Erhai Lake, and an evident structure difference was also found between planktonic and sediment bacterial communities in either of these two lakes. Planktonic bacterial communities in both Dianchi Lake and Erhai Lake mainly included *Proteobacteria* (mainly *Alpha*-, *Beta*-, and *Gammaproteobacteria*), *Bacteroidetes*, *Actinobacteria*, *Cyanobacteria*, and *Firmicutes*, while sediment bacterial communities were mainly represented by *Proteobacteria* (mainly *Beta*- and *Deltaproteobacteria*), *Bacteroidetes*, *Chlorobi*, *Nitrospirae*, *Acidobacteria*, and *Chloroflexi*. Trophic status could play important roles in shaping both planktonic and sediment bacterial communities in freshwater lakes.

Keywords Bacteria · Biomass · High-throughput sequencing · Microbial community · Freshwater · Trophic status

Yu Dai and Yuyin Yang contributed equally to this work.

Electronic supplementary material The online version of this article (doi:10.1007/s00253-015-7253-2) contains supplementary material, which is available to authorized users.

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Introduction

Bacteria are the important components of aquatic ecosystems. They are responsible for biogeochemical cycling of nutrients and biotransformation of organic matter (Liu et al. 2009; Martins et al. 2011). Bacterial assemblages are sensitive to environmental perturbations and might be used as an indicator to aquatic environmental conditions (Marshall et al. 2008; Wu et al. 2009). So far, molecular biology techniques have been extensively used to investigate planktonic bacterial communities in freshwater lakes. Bacterioplankton community structure might be influenced by a variety of environmental factors including organic matter, nitrogen, phosphorus, pH, and temperature (Crump et al. 2003; Lindstrom 2000; Pearce 2005; Wu et al. 2009; Zhang et al. 2014). Multiple influential factors

might collectively shape freshwater lake bacterioplankton community (Wei et al. 2008; Wu et al. 2009). Recently, investigating sediment bacterial community has aroused increasing attention. A few environmental factors have been proposed to be the potential determinants to sediment bacterial community structure in freshwater lake, including organic matter, phosphorus, pH, nitrogen, and heavy metal (Bai et al. 2012; Song et al. 2012; Yu et al. 2015; Zeng et al. 2009; Zhang et al. 2015a; Zhao et al. 2011). However, the compositions of planktonic or sediment bacterial assemblages in freshwater lake ecosystems and their driving forces remain still elusive, given the heterogeneity of habitats in space and time. Moreover, our current knowledge on freshwater lake bacterial assemblages was obtained mainly based on the intra-lake investigation on a single lake, much less attention has been drawn to the inter-lake investigation. In addition, information on the comparison of bacterial assemblages in water column and sediment is still very limited (Ye et al. 2009). Although the seasonal shift in bacterioplankton community structure in freshwater lake has been well-documented (Kent et al. 2004; Lymer et al. 2008; Tjeldens et al. 2008), little is known about the seasonal variation of sediment bacterial community (Chen et al. 2015; Steger et al. 2011; Szabo et al. 2011).

Compared to the structure of bacterial community, information on its abundance in freshwater lake and its regulating factors is much more fragmentary. So far, only several previous studies have investigated the spatial heterogeneity of bacterial abundance in freshwater lake sediments (Liu et al. 2015; Thevenon et al. 2011; Zhang et al. 2015a). These studies suggested that sediment bacterial abundance might be influenced by sediment organic matter and nutrients (Liu et al. 2015; Thevenon et al. 2011; Zhang et al. 2015a). However, the seasonal effect on sediment bacterial abundance has not been addressed. Moreover, although a number of previous studies have investigated bacterial abundance in water columns of freshwater lakes (Almeida et al. 2015; Brek-Laitinen et al. 2012; Pirlot et al. 2005; Vila-Costa et al. 2013), the environmental factors regulating the distribution of bacterioplankton community abundance in freshwater lake remain largely unclear.

Although traditional low-profiling molecular biology tools (e.g., automated ribosomal intergenic spacer analysis (ARISA), denaturing gradient gel electrophoresis (DGGE), and clone library analysis) have made a great contribution to our understanding of bacterial assemblages in freshwater lake ecosystem, the recent emergence of high-throughput sequencing technologies can offer a new opportunity to yield more comprehensive information on the spatiotemporal variation of planktonic and sediment bacterial assemblages. High-throughput sequencing analysis has found applications to characterize bacterial communities in water columns or sediments from a variety of freshwater ecosystems, such as lake (Bai et al. 2012; Bashenkhaeva et al. 2015; Zhang et al.

2015a), river (Lu and Lu 2014a, b, c; Su et al. 2015; Xie et al. 2014; Yang et al. 2015a), and reservoir (Zhang et al. 2015b). Dianchi Lake (309 km², at 1886 m above sea level) and Erhai Lake (251 km², at 1972 m above sea level) are the largest two freshwater lakes on the Yunnan Plateau (southwestern China).

Dianchi Lake extends 39 km length in north–south direction with a width of 13.5 km, while Erhai Lake stretches 40 km long from north to south with a width of 7–8 km. The average water depths of Dianchi Lake and Erhai Lake were 4.4 and 10 m, respectively. They are characterized as eutrophic and mesotrophic, respectively (Wang et al. 2015a; Yang et al. 2015b). So far, only fragmentary knowledge existed on sediment bacterial community in these two lakes (Bai et al. 2012; Xiong et al. 2015), and its spatiotemporal shift and the influential factors remain poorly understood. Information on planktonic bacterial community in these two freshwater lakes is still lacking. Moreover, the difference of bacterial community abundance and structure between in Dianchi Lake and in Erhai Lake remains unknown. Therefore, the main aim of the present study was to investigate the spatiotemporal variation of both planktonic and sediment bacterial populations in these two freshwater lakes at different trophic status. The abundance and structure of bacterial assemblages were characterized using quantitative PCR (qPCR) assay and Illumina-based high-throughput sequencing, respectively.

Materials and methods

Study sites and sampling

Six different sampling locations were selected from either of Dianchi Lake (D1–D6) and Erhai Lake (E1–E6) (Fig. S1). Triplicate water samples (30 cm depth below water surface) and sediment cores were collected from these two freshwater lakes in April (spring) and August (summer) in 2015, using plexiglass water sampler and core sampler, respectively. After collection, these lake water samples and sediment cores were immediately transported to the laboratory. The sediment cores were sliced into layers, and the upper layer (0–10 cm) was used for further chemical and molecular analyses. The physicochemical properties of lake water and sediment samples were determined according to the literatures (China Environmental Protection Agency 2002; Wang 2012) and were listed in Tables S1 and S2, respectively. The levels of Dianchi Lake water pH, temperature, ammonia nitrogen (NH₄⁺-N), nitrate nitrogen (NO₃⁻-N), total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), and ratio of TOC to TN (C/N) were 8.45–8.91, 18.4–21.3 °C, 0.204–0.5 mg/L, 0.02–0.13 mg/L, 0.59–2.96 mg/L, 0.044–0.152 mg/L, 10–58 mg/L, and 5.03–32.4, respectively. The

levels of Erhai Lake water pH, temperature, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TN, TP, TOC, and C/N were 8.6–8.89, 21.1–23.3 °C, 0.094–0.593 mg/L, 0.041–0.486 mg/L, 0.47–2.68 mg/L, 0.021–0.344 mg/L, 6.5–20.9 mg/L, and 4.59–24.79, respectively. Moreover, the levels of Dianchi Lake sediment pH, temperature, oxidation and reduction potential (ORP), $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TN, TP, TOC, and C/N were 6.41–7.48, 18.4–21.7 °C, –19.9–32.3 mv, 11.22–65.79 mg/kg, 1.48–3.53 mg/kg, 878.18–1268.57 mg/kg, 249.23–482.25 mg/kg, 3.33–11.66 g/kg, and 2.85–11.41, respectively. The levels of Erhai Lake sediment pH, temperature, ORP, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TN, TP, TOC, and C/N were 6.07–7.88, 17.5–22.5 °C, –52.6–55.3 mv, 6.12–25.49 mg/kg, 0.14–8.25 mg/kg, 504.09–1043.68 mg/kg, 86.33–251.49 mg/kg, 3.32–3.39 g/kg, and 4.16–6.64, respectively.

Molecular analyses

In the present study, 0.22- μm pore-size membrane (diameter 50 mm; Millipore) was used to retain lake water microbial cells. Water DNA and sediment DNA were extracted using E.Z.N.A. Water DNA kit (Omega, USA) and Powersoil DNA extraction kit (Mobio Laboratories, USA), respectively. The density of bacterial 16S ribosomal RNA (rRNA) gene was determined using the primer sets 341F (5'-CCTACGG GAGGCAGCAG-3')/534R (5'-ATTACCGCGGCTGC TGGCA-3'), as previously described (Jung et al. 2011; Liu et al. 2014). One-way analysis of variance (ANOVA) followed by Student-Newman-Keuls test was used to check the significant difference ($P < 0.05$) in the bacterial 16S rRNA gene copy number among samples. Moreover, bacterial primer set 515F (5'-GTGCCAGCMGCCGCGG-3')/R907 (5'-CGTCAATTCMTTTRAGTTT-3') was used for the construction of PCR amplicon libraries for Illumina MiSeq high-throughput sequencing, as previously described (Guan et al. 2015; Wang et al. 2015b). The raw Illumina reads were deposited in the NCBI short-read archive under accession numbers SRP066731 for water and SRP066467 for sediment, respectively. The quality filtering of the Illumina sequences was processed according to the protocol (Caporaso et al. 2010), and then chimeric reads were removed using UCHIME (Edgar et al. 2011). Chimeric-free sequences were grouped into operational taxonomic units (OTUs) with a maximum distance of 3 %, and then OTU-based community richness (Chao1 estimator) and alpha diversity (Shannon and Simpson indices) were further calculated using the UPARSE pipeline (Edgar 2013). The Ribosomal Database Project (RDP) classifier was used to assign the taxonomic identity of the representative sequence from each OTU (Wang et al. 2007). In addition, OTU-based beta diversity was obtained using UniFrac analysis. To describe the relationship of bacterial communities among samples, unweighted UniFrac using the Quantitative Insights into Microbial Ecology (QIIME)

program was used for unweighted pair group method with arithmetic mean (UPGMA) clustering.

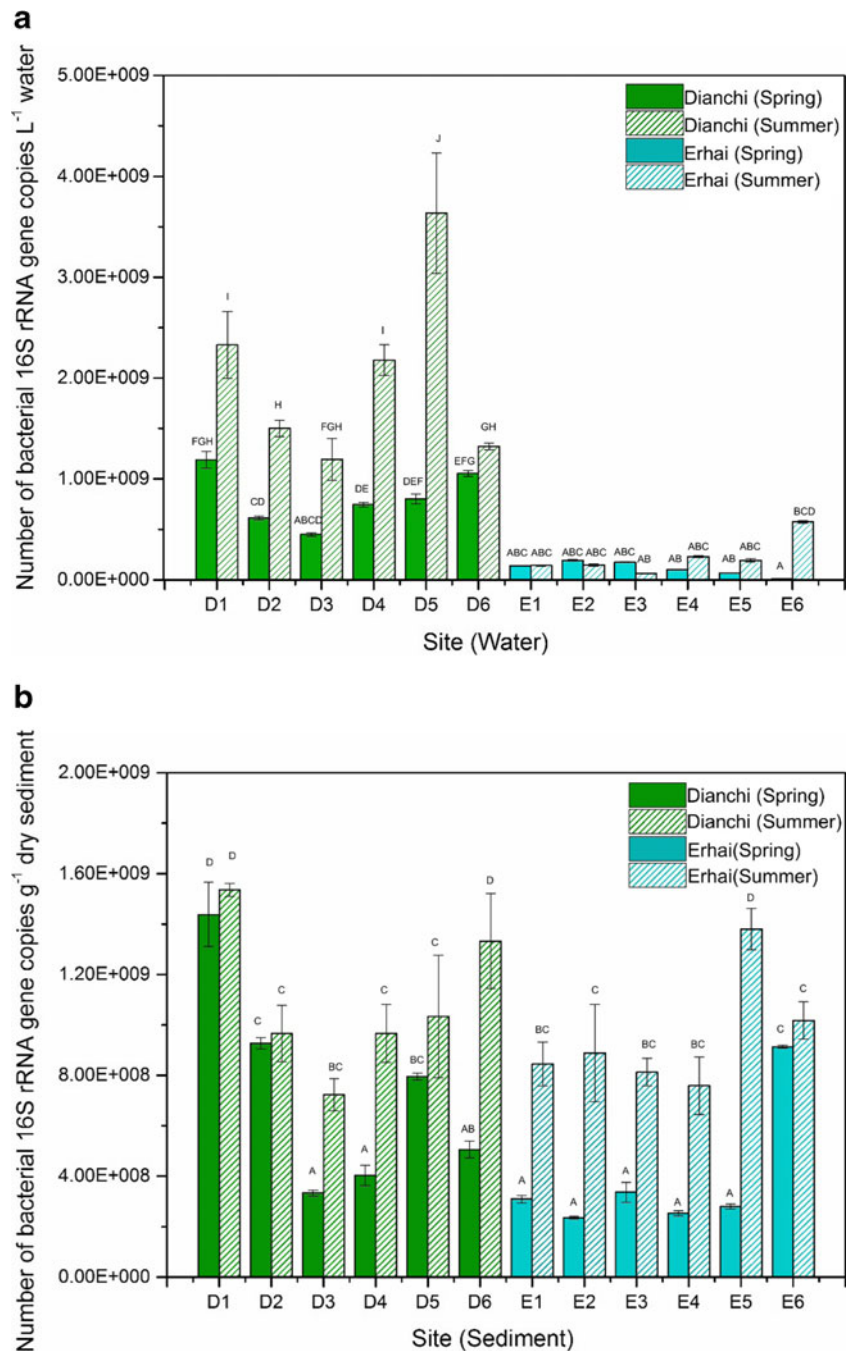
The relationship between bacterial assemblages and lake water or sediment properties was assessed with Spearman rank correlation analysis using the software SPSS 20.0. Detrended correspondence analysis (DCA) was also used to determine the suitable ordination analysis method. Since the longest DCA axis had a gradient length less than 3 standard deviation units, the correlations between bacterial community OTU composition and the environmental factors were explored with redundancy analysis (RDA) using CANOCO 4.5 (Lepš and Šmilauer 2003). In this study, the sequence number in each major bacterial OTU (defined at 50 sequences cutoff) was used as species input, while the determined lake water or sediment physicochemical properties were assigned as environmental input (Zhang et al. 2015a). The significance tests of Monte Carlo permutations were conducted to select the suitable model of the bacteria–environment relationships.

Results

Bacterial community abundance

The density of bacterial 16S rRNA gene ranged from 4.5×10^8 to 1.19×10^9 copies per liter water in the spring water samples from Dianchi Lake, while the summer water samples from Dianchi Lake had the bacterioplankton community size of 1.19×10^9 to 3.64×10^9 16S rRNA gene copies per liter water (Fig. 1a). In either spring or summer, the abundance of Dianchi Lake bacterioplankton community at one sampling site was generally different from that at other sampling sites ($P < 0.05$). This indicated the remarkable spatial variation of bacterioplankton abundance in Dianchi Lake. At a given sampling site in Dianchi Lake, the summer water sample had higher bacterioplankton abundance than the corresponding spring one ($P < 0.05$), suggesting the evident seasonal effect on bacterioplankton abundance in Dianchi Lake. Moreover, the spring water samples from Erhai Lake illustrated the bacterial abundance of 8.01×10^6 to 1.93×10^8 16S rRNA gene copies per liter water, while the number of bacterial 16S rRNA gene ranged from 6.14×10^7 to 5.74×10^8 copies per liter water in the summer water samples from Erhai Lake. No significant difference in bacterioplankton abundance was found among the spring water samples at sampling sites E1, E2, and E3 or between those at sampling sites E4 and E5 ($P > 0.05$). The summer water samples at sampling sites E1, E2, E4, and E5 also showed no significant difference in bacterioplankton abundance ($P > 0.05$). These results suggested the relatively slight spatial change of bacterioplankton abundance in Erhai Lake. The trend for the seasonal variation of bacterioplankton abundance in Erhai Lake was not apparent. At sampling sites E4, E5, or E6, the summer water sample

Fig. 1 Abundance of bacterial 16S rRNA gene in spring and summer water samples (a) and sediment samples (b) from different sampling sites in Dianchi Lake and Erhai Lake. Different letters above the columns indicate significant differences ($P < 0.05$)



had higher bacterioplankton abundance than the corresponding spring one ($P < 0.05$), while an opposite trend was observed at sampling site E3. No significant difference in bacterial abundance was found between the spring and summer water samples at sampling sites either E1 or E2 ($P > 0.05$). In addition, the water samples from Dianchi Lake generally had much higher bacterial abundance than those from Erhai Lake ($P < 0.05$).

The number of bacterial 16S rRNA gene ranged from 3.33×10^8 to 1.54×10^9 copies per gram dry sediment in the sediment samples from Dianchi Lake, while the sediment

samples from Erhai Lake showed the bacterial abundance of 2.35×10^8 to 1.38×10^9 16S rRNA gene copies per gram dry sediment (Fig. 1b). In spring, the bacterial abundance of Dianchi Lake sediment community at one sampling site was generally different from that at other sampling sites ($P < 0.05$). In contrast, no significant difference in bacterial abundance was found among the summer sediment samples at sampling sites D1, D4, and D5 or between those at sampling sites D1 and D6 ($P > 0.05$). This suggested the spatial variation of Dianchi Lake sediment bacterial abundance was relatively slight in summer, compared to spring. At most of the sampling

sites in Dianchi Lake, the sediment samples had higher bacterial abundance than the corresponding spring ones ($P < 0.05$), suggesting the apparent seasonal effect on sediment bacterial abundance in Dianchi Lake. Moreover, most of the spring sediment samples from Erhai Lake (five out of six) showed no significant difference in bacterial abundance ($P > 0.05$). No significant difference in bacterial abundance also occurred among the summer sediment samples at sampling sites E1, E3, and E4 or between those at sampling sites E2 and E6 ($P > 0.05$). These results suggested only a slight spatial fluctuation of sediment bacterial abundance in Erhai Lake in both seasons. However, the seasonal effect on sediment bacterial abundance in Erhai Lake was evident. The summer sediment samples usually had much higher bacterial abundance than the corresponding spring ones ($P < 0.05$).

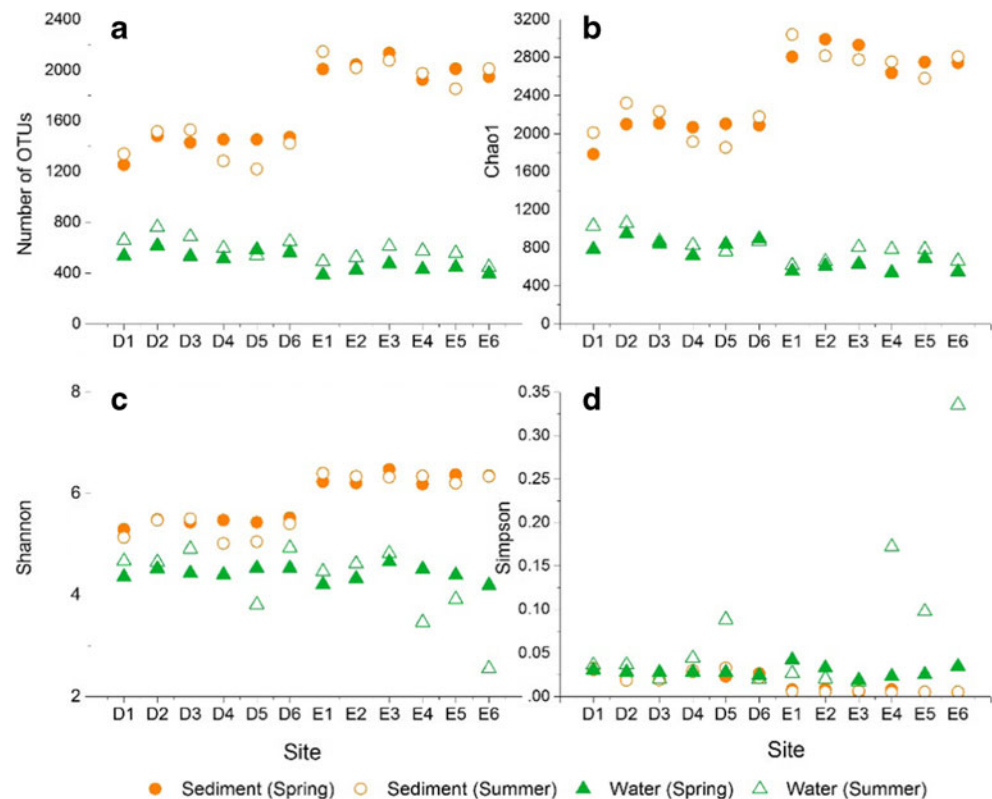
Bacterial community richness and diversity

In the present study, the obtained valid bacterial reads from each lake sample ranged between 18,307 and 49,967, normalized to 18,300 to compare bacterial community richness and alpha diversity. High Good's coverage ($\geq 94.7\%$) indicated that the OTUs of each bacterial library were well captured. Dianchi Lake water bacterial libraries were composed of 511–759 OTUs, while Erhai Lake water bacterial libraries included 384–611 OTUs (Fig. 2a, b). The Chao1 richness estimators of bacterioplankton communities in Dianchi Lake and Erhai

Lake were 714–1059 and 538–803, respectively. An evident spatial variation of bacterioplankton OTU number and Chao1 estimator was observed in these two lakes. The summer water sample generally had higher OTU number and Chao1 estimator than the corresponding spring one at a given sampling site in either Dianchi Lake or Erhai Lake, indicating the evident seasonal effect on bacterioplankton community richness in these two lakes. Lake sediment samples had much higher OTU number and Chao1 estimator (bacterial community richness) than water samples. Sediment samples from Dianchi Lake had 1221–1528 OTUs and the Chao1 estimator of 1781–2318, while those from Erhai Lake had more OTUs (1852–2146) and higher Chao1 estimator (2635–3039). However, although an evident spatial variation of sediment bacterial OTU number and Chao1 richness estimator was observed in these two lakes, the trend for the seasonal change of sediment bacterial community richness was not clear.

The Shannon diversity indices of bacterioplankton communities in Dianchi Lake and Erhai Lake were 3.81–4.93 and 2.55–4.82, respectively. Compared to spring water samples, summer ones showed a relatively large spatial fluctuation of Shannon diversity in either Dianchi Lake or Erhai Lake (Fig. 2c). At a given sampling site, the bacterioplankton Shannon diversity in Dianchi Lake generally increased from spring to summer, yet the trend for the seasonal variation of bacterioplankton diversity in Erhai Lake was not clear. Lake sediment samples were found to have higher bacterial

Fig. 2 Bacterial community OTUs (a), Chao1 estimator (b), Shannon index (c), and Simpson index (d)



community diversity than water ones. Sediment samples from Dianchi Lake had the Shannon diversity indices of 5.01–5.5, while those from Erhai Lake had relatively higher diversity (6.18–6.47). Only the summer sediment samples from Dianchi Lake showed a considerable spatial variation of Shannon diversity. At a given sampling site, the sediment Shannon diversity in Dianchi Lake generally decreased from spring to summer, yet the trend for the seasonal change of sediment bacterial diversity in Erhai Lake was not clear. In addition, the Simpson indices of planktonic and sediment bacterial communities were 0.017–0.335 and 0.004–0.033, respectively (Fig. 2d). At a given sampling site, water sample was usually found to have higher Simpson index (evenness) than sediment one. Sediment samples from Dianchi Lake showed higher bacterial community evenness than those from Erhai Lake.

UPGMA clustering analysis of bacterial communities

The result of UPGMA clustering illustrated that lake water samples were distantly separated from sediment samples, indicating the distinct structure difference between planktonic and sediment bacterial communities (Fig. 3). Water samples could be further divided into four distinct groups. The water samples from Dianchi Lake were separated from those from Erhai Lake, suggesting that bacterioplankton community structure was lake-specific. For either of the two lakes, spring water samples were separated from summer ones. This indicated an apparent seasonal shift in bacterioplankton community structure.

The sediment samples from Dianchi Lake were distantly separated from those from Erhai Lake, suggesting that sediment bacterial communities differed sharply in these two lakes. The sediment samples from Dianchi Lake could be further divided into three distinct groups. Sample DSAp1 was distantly separated from other Dianchi Lake sediment samples. Samples DSAu2, DSAu3, DSAu4, and DSAu6 were grouped together. At a given sampling site (except for site D5), the sediment samples in spring and summer were clearly separated, suggesting the evident seasonal effect on sediment bacterial community structure in Dianchi Lake. In addition, the sediment samples from Erhai Lake could also be further divided into three distinct groups. However, the trend for the seasonal change of sediment bacterial community structure in Erhai Lake was not apparent. Samples ESAP5, ESAu5, ESAP6, and ESAu6 were grouped together, and samples ESAP1 and ESAu1 were also clustered.

Bacterial community composition

In the present study, a total of 18 bacterial phyla or candidate divisions were frequently identified from Dianchi

Lake and Erhai Lake, including *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, *Chlorobi*, *Cyanobacteria*, *Planctomycetes*, *Nitrospirae*, *Chloroflexi*, *Firmicutes*, *Acidobacteria*, *Spirochaetae*, *Deferribacteres*, *Armatimonadetes*, *Gemmatimonadetes*, *WS3*, *OP8*, *TA06*, and *OP3* (Fig. 4). *Proteobacteria* (accounting for 19.7–66.7 %) was usually the largest bacterial phylum in the water samples from both Dianchi Lake and Erhai Lake. Compared with the spring water samples, the summer water samples from either of the two lakes illustrated a relatively large spatial shift in the proteobacterial proportion. Moreover, *Proteobacteria* (34.4–47.1 %) was always the largest phylum in the sediment samples from Dianchi Lake and Erhai Lake. A relatively slight spatiotemporal variation of sediment proteobacterial organisms occurred in either of these two lakes. However, at a given sampling site, sediment samples generally had higher proteobacterial proportion than water ones. In addition, the proteobacterial communities of the spring and summer water samples from Dianchi Lake were mainly composed of *Alphaproteobacteria*, *Betaproteobacteria*, and *Gammaproteobacteria* (Fig. 5). *Alphaproteobacteria* and *Betaproteobacteria* dominated the proteobacterial communities in the spring water samples from Erhai Lake, while *Betaproteobacteria* and *Gammaproteobacteria* showed the dominance in the proteobacterial communities in the summer water samples from Erhai Lake. In contrast, the sediment proteobacterial communities in both Dianchi Lake and Erhai Lake mainly consisted of *Betaproteobacteria* and *Deltaproteobacteria*.

Bacteroidetes was usually the second largest bacterial phylum in the spring water samples from both Dianchi Lake (22.8–30.2 %) and Erhai Lake (17.9–27.2 %). However, the proportion of planktonic *Bacteroidetes* organisms in the two lakes showed an evident decrease in summer. The proportion of *Bacteroidetes* organisms in sediments (3.1–12.6 %) was generally much lower than that in waters. At a given site in Dianchi Lake (except for D5), the proportion of sediment *Bacteroidetes* was lower in summer than in spring. Moreover, *Actinobacteria* and *Cyanobacteria* were the two major components of bacterioplankton community in Dianchi Lake (*Actinobacteria* 10.1–25.3 %, *Cyanobacteria* 11.5–22.9 %) and Erhai Lake (*Actinobacteria* 1.4–23.4 %, *Cyanobacteria* 4.5–20 %) but became the minor bacterial groups in sediments of these two lakes. In summer, at a given site, the proportion of planktonic *Actinobacteria* organisms usually increased in Dianchi Lake but decreased in Erhai Lake, while the proportion of planktonic *Cyanobacteria* organisms usually showed an increase in both lakes. In addition, *Firmicutes* showed relatively high proportion in two summer water samples from Dianchi Lake and one from Erhai Lake (14.9–40.3 %) but became much less abundant in other lake water samples (0.6–

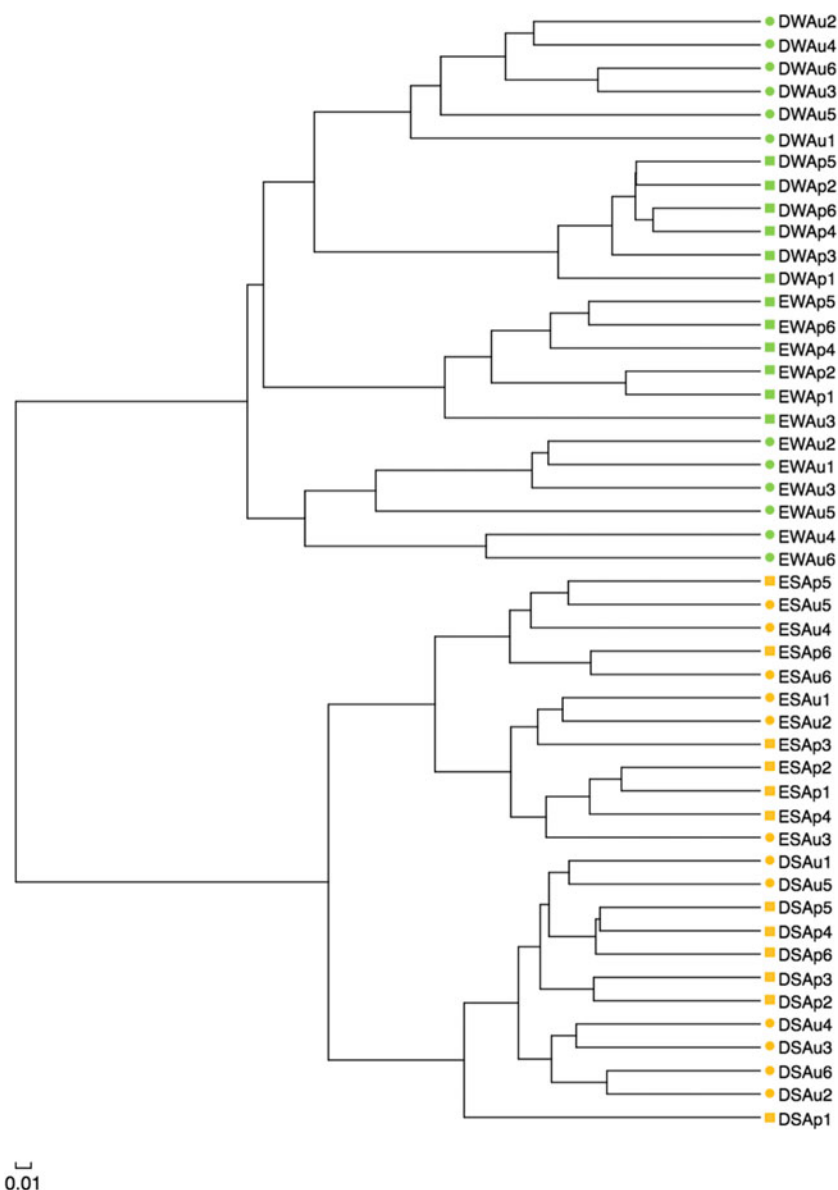


Fig. 3 UPGMA clustering of water and sediment samples from Dianchi Lake and Erhai Lake. Samples DWAp1, DWAp2, DWAp3, DWAp4, DWAp5, and DWAp6 represent the April water samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DWAu1, DWAu2, DWAu3, DWAu4, DWAu5, and DWAu6 represent the August water samples from sites D1 to D6 in Dianchi Lake, respectively. Samples EWAp1, EWAp2, EWAp3, EWAp4, EWAp5, and EWAp6 represent the April water samples from sites E1 to E6 in Erhai Lake, respectively. Samples EWAu1, EWAu2, EWAu3, EWAu4, EWAu5, and EWAu6 represent the August water samples from sites E1 to E6 in Erhai Lake, respectively.

Samples DSAp1, DSAp2, DSAp3, DSAp4, DSAp5, and DSAp6 represent the April sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DSAu1, DSAu2, DSAu3, DSAu4, DSAu5, and DSAu6 represent the August sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples ESAp1, ESAp2, ESAp3, ESAp4, ESAp5, and ESAp6 represent the April sediment samples from sites E1 to E6 in Erhai Lake, respectively. Samples ESAu1, ESAu2, ESAu3, ESAu4, ESAu5, and ESAu6 represent the August sediment samples from sites E1 to E6 in Erhai Lake, respectively

7.4 %). *Firmicutes* was also a minor bacterial group in sediments of Dianchi Lake and Erhai Lake.

Chlorobi was a major bacterial group in sediments of Dianchi Lake (8.5–16.5 %), but its proportion was relatively low in sediments of Erhai Lake (4.6–8.5 %). In contrast, sediment *Nitrospirae* and *Acidobacteria* species generally showed higher proportion in Erhai Lake (*Nitrospirae* 4–

13.2 %, *Acidobacteria* 6.28.4 %) than in Dianchi Lake (*Nitrospirae* 3.7–10.7 %, *Acidobacteria* 3.1–5.3 %). *Chloroflexi* was also a major component of sediment bacterial communities in these two freshwater lakes (3.1–9.8 %). However, microorganisms within phyla *Chlorobi*, *Nitrospirae*, *Acidobacteria*, and *Chloroflexi* were the minor bacterial groups in lake waters.

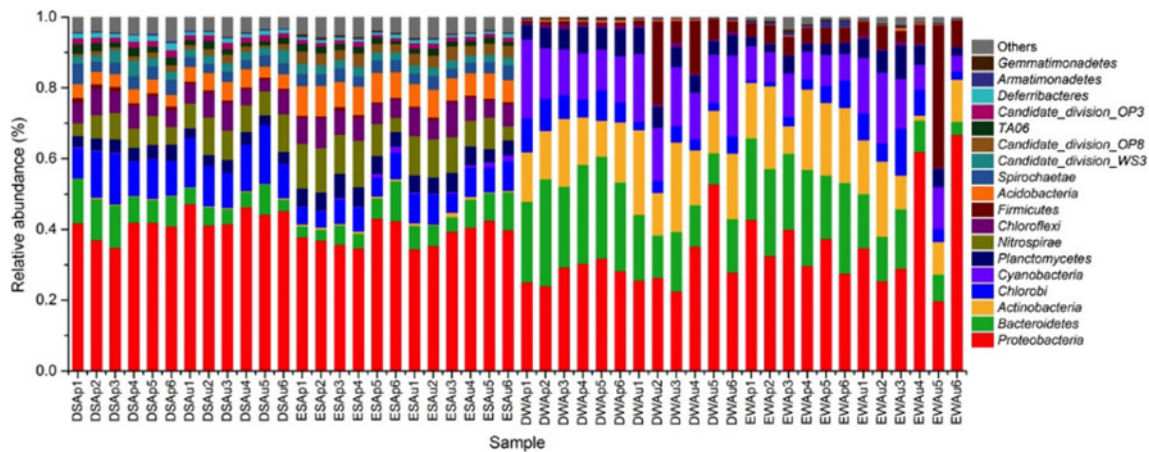


Fig. 4 Comparison of the quantitative contribution of the sequences affiliated with different bacterial phyla to the total number of sequences from a given lake water or sediment sample. Others include unclassified *Bacteria* and the bacterial phyla with the largest relative abundance less than 1 % in each sample. Samples DWAp1, DWAp2, DWAp3, DWAp4, DWAp5, and DWAp6 represent the April water samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DWAu1, DWAu2, DWAu3, DWAu4, DWAu5, and DWAu6 represent the August water samples from sites D1–D6 in Dianchi Lake, respectively. Samples EWAp1, EWAp2, EWAp3, EWAp4, EWAp5, and EWAp6 represent the April water samples from sites E1 to E6 in Erhai Lake, respectively. Samples

EWAu1, EWAu2, EWAu3, EWAu4, EWAu5, and EWAu6 represent the August water samples from sites E1 to E6 in Erhai Lake, respectively. Samples DSAp1, DSAp2, DSAp3, DSAp4, DSAp5, and DSAp6 represent the April sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DSAu1, DSAu2, DSAu3, DSAu4, DSAu5, and DSAu6 represent the August sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples ESAp1, ESAp2, ESAp3, ESAp4, ESAp5, and ESAp6 represent the April sediment samples from sites E1 to E6 in Erhai Lake, respectively. Samples ESAu1, ESAu2, ESAu3, ESAu4, ESAu5, and ESAu6 represent the August sediment samples from sites E1 to E6 in Erhai Lake, respectively

Influential factors regulating bacterial community

Spearman rank correlation analysis indicated that the abundance, OTU number, and Chao1 richness estimator of bacterioplankton community were positively correlated to the levels of water $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TN, and TP ($P < 0.05$

or $P < 0.01$) but negatively correlated to C/N ($P < 0.01$) (Table 1). Bacterioplankton community Shannon diversity illustrated a significant positive correlation with the level of water $\text{NO}_3^-\text{-N}$ ($P < 0.05$). *Alphaproteobacteria* and *Bacteroidetes* showed a significant negative correlation with water temperature ($P < 0.01$) but were positively correlated to

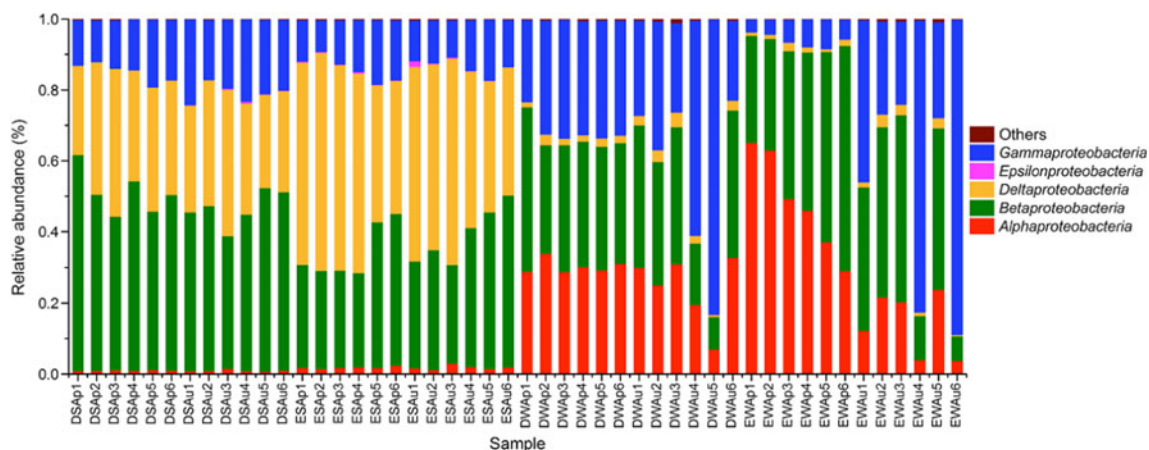


Fig. 5 Comparison of the quantitative contribution of the sequences affiliated with different proteobacterial classes to the total number of proteobacterial sequences from a given lake water or sediment sample. Unclassified *Proteobacteria* was included as others. Samples DWAp1, DWAp2, DWAp3, DWAp4, DWAp5, and DWAp6 represent the April water samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DWAu1, DWAu2, DWAu3, DWAu4, DWAu5, and DWAu6 represent the August water samples from sites D1 to D6 in Dianchi Lake, respectively. Samples EWAp1, EWAp2, EWAp3, EWAp4, EWAp5, and EWAp6 represent the April water samples from sites E1 to E6 in Erhai Lake, respectively. Samples EWAu1, EWAu2, EWAu3,

EWAu4, EWAu5, and EWAu6 represent the August water samples from sites E1 to E6 in Erhai Lake, respectively. Samples DSAp1, DSAp2, DSAp3, DSAp4, DSAp5, and DSAp6 represent the April sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples DSAu1, DSAu2, DSAu3, DSAu4, DSAu5, and DSAu6 represent the August sediment samples from sites D1 to D6 in Dianchi Lake, respectively. Samples ESAp1, ESAp2, ESAp3, ESAp4, ESAp5, and ESAp6 represent the April sediment samples from sites E1 to E6 in Erhai Lake, respectively. Samples ESAu1, ESAu2, ESAu3, ESAu4, ESAu5, and ESAu6 represent the August sediment samples from sites E1 to E6 in Erhai Lake, respectively

Table 1 Spearman rank correlation analysis of water environmental factors with the abundance, richness, and diversity of bacterioplankton community or the proportion of planktonic bacterial groups

Parameter	pH	Temperature	NH ₄ ⁺ -N	NO ₃ ⁻ -N	TN	TP	TOC	C/N
Abundance	0.22	0.208	0.793^b	0.911^b	0.701^b	0.679^b	0.216	-0.622^b
OTUs	0.015	0.335	0.523^b	0.791^b	0.432^a	0.405^a	-0.066	-0.568^b
Chao1 richness	0.142	0.088	0.614^b	0.784^b	0.643^b	0.531^b	0.112	-0.604^b
Shannon diversity	0.033	0.183	0.365	0.437^a	0.265	-0.004	0.181	-0.184
<i>Proteobacteria</i>	0.18	0.138	-0.23	-0.365	-0.206	-0.032	0.147	0.366
<i>Alphaproteobacteria</i>	0.277	-0.565^b	0.193	-0.253	0.3	0.046	0.689^b	0.221
<i>Betaproteobacteria</i>	-0.209	-0.206	-0.384	-0.502^a	-0.327	-0.404	-0.043	0.349
<i>Gammaproteobacteria</i>	0.236	0.357	0.154	0.409	0.185	0.337	-0.242	-0.359
<i>Bacteroidetes</i>	0.215	-0.697^b	0.153	-0.191	0.39	0.211	0.448^a	-0.046
<i>Actinobacteria</i>	0.112	0.058	0.258	-0.062	0.171	0.02	0.247	0.061
<i>Cyanobacteria</i>	-0.045	0.356	0.406^a	0.708^b	0.296	0.164	-0.01	-0.429^a
<i>Firmicutes</i>	-0.432^a	0.467^a	-0.134	-0.079	-0.425^a	-0.412^a	-0.302	0.176

The data in bold indicates that they have statistical significance

^a Correlation is significant at the 0.05 level

^b Correlation is significant at the 0.01 level

TOC ($P < 0.05$ or $P < 0.01$). *Betaproteobacteria* was negatively correlated to NO₃⁻-N ($P < 0.05$). Moreover, *Cyanobacteria* showed significant correlations with NH₄⁺-N, NO₃⁻-N, and C/N ($P < 0.05$ or $P < 0.01$), while *Firmicutes* was correlated to water pH, temperature, TN, and TP ($P < 0.05$). The water environmental factors in the first two RDA axes respectively explained 36.6 and 28.6 % of the total variance for bacterioplankton OTU composition (Fig. 6). In this study, water environmental factors including temperature ($F = 5.66$, $P = 0.002$, 499 permutations), NO₃⁻-N ($F = 5.27$, $P = 0.002$, 499 permutations), NH₄⁺-N ($F = 4.97$, $P = 0.002$, 499 permutations), TN ($F = 4.10$, $P = 0.002$, 499 permutations), C/N ($F = 2.94$, $P = 0.004$, 499 permutations), and TOC ($F = 2.06$, $P = 0.038$, 499 permutations) were found to significantly contribute to the planktonic bacterial assemblage–environment relationship.

Sediment community abundance was positively correlated to sediment temperature, ORP, TOC, and C/N ($P < 0.05$ or $P < 0.01$) but negatively to pH ($P < 0.05$) (Table 2). Sediment NH₄⁺-N, NO₃⁻-N, TN, TP, and TOC showed negative correlations with bacterial OTUs, Chao1 estimator, Shannon diversity, *Deltaproteobacteria*, and *Acidobacteria* ($P < 0.05$ or $P < 0.01$) but were positively correlated to *Chlorobi* ($P < 0.05$ or $P < 0.01$). Moreover, Shannon diversity, *Chlorobi*, and *Acidobacteria* also showed significant correlations with pH and ORP ($P < 0.05$ or $P < 0.01$), while Chao1 estimator was correlated to pH ($P < 0.05$). *Proteobacteria* was positively correlated to TN ($P < 0.05$) and TOC ($P < 0.01$). *Betaproteobacteria* showed positive correlations with NH₄⁺-N, NO₃⁻-N, TN, TP, and TOC ($P < 0.05$ or $P < 0.01$) but a negative correlation with pH ($P < 0.05$). In addition, *Nitrospirae* was negatively correlated to NH₄⁺-N, NO₃⁻-N, and TN ($P < 0.05$ or $P < 0.01$), while *Chloroflexi* only showed

a negative correlation with NO₃⁻-N ($P < 0.01$). The sediment environmental factors in the first two RDA axes respectively accounted for 28.5 and 10.8 % of the total variance for sediment bacterial OTU composition (Fig. 7). Sediment environmental factors including NH₄⁺-N ($F = 5.92$, $P = 0.002$, 499 permutations), TP ($F = 5.57$, $P = 0.002$, 499 permutations), TN ($F = 5.44$, $P = 0.002$, 499 permutations), and TOC ($F = 2.84$, $P = 0.006$, 499 permutations) significantly

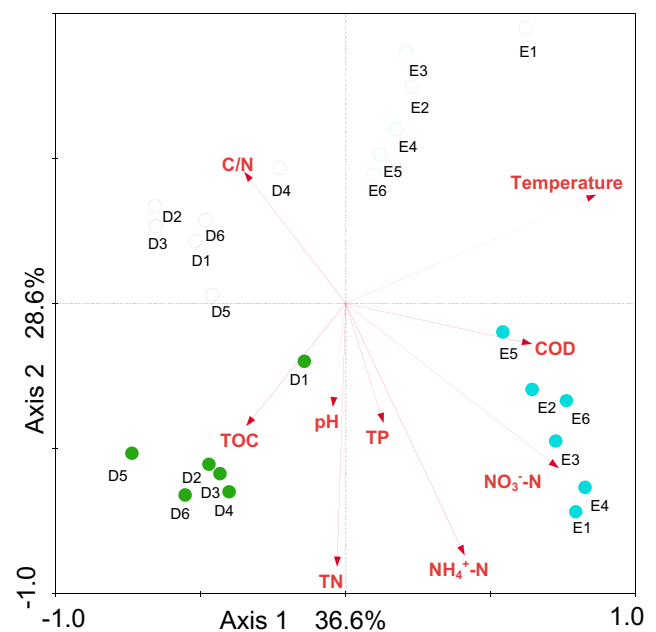


Fig. 6 RDA ordination plot for the first two principal dimensions of the relationships between bacterioplankton OTU composition and lake water parameters. Green-filled and open circles indicate the spring and summer water samples at sites D1–D6 in Dianchi Lake, respectively. Blue-filled and open circles indicate the spring and summer water samples at sites E1–E6 in Erhai Lake, respectively

Table 2 Spearman rank correlation analysis of sediment environmental factors with the abundance, richness, and diversity of sediment bacterial community or the proportion of sediment bacterial groups

Parameter	pH	Temperature	ORP	NH ₄ ⁺ -N	NO ₃ ⁻ -N	TN	TP	TOC	C/N
Abundance	-0.482^a	0.445^a	0.462^a	0.17	0.303	0.209	-0.022	0.492^a	0.527^b
OTUs	0.386	0.046	-0.324	-0.719^b	-0.595^b	-0.777^b	-0.694^b	-0.631^b	-0.184
Chao1 richness	0.445^a	0.084	-0.382	-0.79^b	-0.548^b	-0.797^b	-0.704^b	-0.559^b	-0.091
Shannon diversity	0.47^a	-0.019	-0.441^a	-0.622^b	-0.461^a	-0.661^b	-0.718^b	-0.610^b	-0.257
<i>Proteobacteria</i>	-0.157	0.033	0.193	0.328	0.388	0.444^a	0.222	0.593^b	0.342
<i>Betaproteobacteria</i>	-0.42^a	0.052	0.316	0.525^b	0.496^a	0.653^b	0.397	0.562^b	0.233
<i>Deltaproteobacteria</i>	0.362	0.046	-0.232	-0.671^b	-0.55^b	-0.776^b	-0.543^b	-0.508^a	-0.083
<i>Bacteroidetes</i>	-0.129	-0.067	-0.058	0.309	0.408^a	0.385	0.035	0.02	-0.197
<i>Chlorobi</i>	-0.51^a	0.193	0.509^a	0.599^b	0.704^b	0.568^b	0.61^b	0.509^a	0.286
<i>Nitrospirae</i>	0.285	0.138	-0.179	-0.503^a	-0.466^a	-0.581^b	-0.203	-0.39	-0.038
<i>Chloroflexi</i>	0.092	0.057	0.056	-0.209	-0.614^b	-0.391	-0.083	-0.218	0.03
<i>Acidobacteria</i>	0.531^b	0.029	-0.455^a	-0.703^b	-0.498^a	-0.73^b	-0.685^b	-0.479^a	-0.079

The data in bold indicates that they have statistical significance

^a Correlation is significant at the 0.05 level

^b Correlation is significant at the 0.01 level

contributed to the sediment bacterial assemblage–environment relationship.

Discussion

Bacterial abundance in freshwater lake

There have been a few reports on the spatiotemporal variation of planktonic bacterial assemblages in freshwater

lake. Brek-Laitinen et al. (2012) showed the considerable seasonal change of bacterioplankton abundance at one sampling site in Lake Vesijärvi. The profound seasonal change of bacterioplankton abundance was also observed in Crystal Bog Lake (Kent et al. 2004) and in Lake Loosdrecht (Tijdens et al. 2008). Pirlot et al. (2005) and Wei et al. (2008) illustrated the both seasonal and spatial fluctuation of bacterioplankton abundance in Lake Tanganyika and Chaohu Lake, respectively. In these previous studies, bacterioplankton abundance was not quantified using qPCR. In the present study, qPCR targeting bacterial 16S rRNA gene was applied to estimate bacterial abundance in waters and sediments of Dianchi Lake and Erhai Lake. A remarkably spatial and evidently seasonal variation of bacterioplankton abundance was found in Dianchi Lake. This was in agreement with the results reported in the previous studies (Brek-Laitinen et al. 2012; Pirlot et al. 2005; Wei et al. 2008). In contrast, the spatial change in Erhai Lake was relatively slight, and the trend for the seasonal change of bacterioplankton abundance in Erhai Lake was not clear. This suggested that the seasonal shift in bacterioplankton abundance might be lake-specific. In addition, the bacterioplankton abundance in Dianchi Lake generally far outnumbered that in Erhai Lake. Two previous studies also indicated that the substantial difference of bacterioplankton abundance could exist in different lakes (Almeida et al. 2015; Vila-Costa et al. 2013). To date, the influential factors regulating bacterioplankton abundance remain essentially unclear. Almeida et al. (2015) indicated that bacterial abundance increased with the level of water dissolved organic carbon (DOC). However, in this study, the result of Spearman rank correlation analysis suggested that bacterioplankton abundance might be influenced by water NH₄⁺-N, NO₃⁻-N, TN, TP, and C/N. Therefore, lake trophic

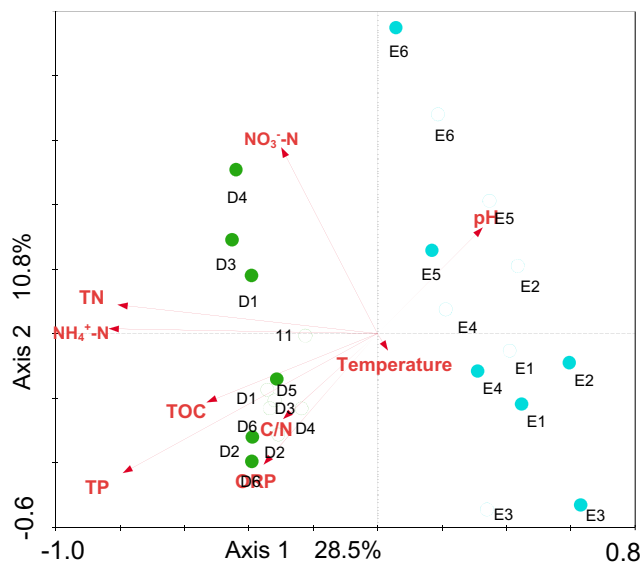


Fig. 7 RDA ordination plot for the first two principal dimensions of the relationships between sediment bacterial OTU composition and sediment parameters. Green-filled and open circles indicate the spring and summer sediment samples at sites D1–D6 in Dianchi Lake, respectively. Blue-filled and open circles indicate the spring and summer sediment samples at sites E1–E6 in Erhai Lake, respectively

status might be a key determinant to bacterioplankton abundance in freshwater lake. An earlier study also indicated that bacterioplankton biomass was positively correlated to variables associated with lake trophic status (Lindstrom 2000).

So far, several previous studies have investigated the spatial pattern of bacterial abundance in freshwater lake sediment (Liu et al. 2015; Thevenon et al. 2011; Zhang et al. 2015a). These previous studies indicated the striking fluctuation of sediment bacterial abundance in freshwater lakes. However, the seasonal effect on sediment bacterial abundance has not been well explored. Only Schwarz et al. (2007) reported a slight temporal fluctuation of bacterial abundance in profundal sediment in Lake Kinneret. In this study, the densities of bacterial 16S rRNA gene in sediments of Dianchi Lake and Erhai Lake were 3.33×10^8 – 1.54×10^9 and 2.35×10^8 – 1.38×10^9 copies per gram dry sediment, respectively, comparable to that in sediments of small freshwater lakes on the Yunnan Plateau (1.12×10^8 – 5.83×10^8) (Zhang et al. 2015a), but lower than that in profundal lake sediment of Lake Kinneret (average 1.88×10^{10}) (Schwarz et al. 2007). Moreover, in spring, a remarkable spatial variation of sediment bacterial abundance occurred in Dianchi Lake. This was consistent with the results of previous investigations on sediments of other freshwater lakes (Liu et al. 2015; Thevenon et al. 2011). In contrast, a relatively slight fluctuation of bacterial abundance was found in the spring and summer sediment samples from Erhai Lake and in the summer sediment samples from Dianchi Lake. Therefore, the spatial change pattern of sediment bacterial abundance might be lake-specific and also depend on sampling date. In addition, in this study, the seasonal effect on sediment bacterial abundance in both Dianchi Lake and Erhai Lake was evident. This was different from the result reported on the profundal sediment of Lake Kinneret (Schwarz et al. 2007). So far, little is known about the influential factors regulating sediment bacterial abundance in freshwater lake. Some previous studies suggested that sediment bacterial abundance in freshwater lake might be influenced by sediment organic matter and nutrients (Liu et al. 2015; Thevenon et al. 2011; Zhang et al. 2015a). A previous study revealed that Dianchi Lake sediment bacterial abundance showed a significant positive correlation with TOC (Bai et al. 2012). In this study, the result of Spearman rank correlation analysis suggested that sediment bacterial abundance in freshwater lake could be influenced by a number of sediment physicochemical parameters including pH, temperature, ORP, TOC, and C/N.

Bacterial richness and diversity in freshwater lake

The remarkable seasonal or/and spatial change of bacterioplankton community richness and diversity has been observed in a number of freshwater lakes (Crump et al. 2003; Kent et al. 2004; Konopka et al. 1999; Li et al. 2015;

Lindstrom and Bergstrom 2005; Wei et al. 2008; Wu et al. 2009; Yannarell et al. 2003; Zwirgmaier et al. 2015), yet these previous studies mainly applied traditional low-profiling molecular biology tools, which could underestimate the bacterial richness and diversity in waters of freshwater lakes. High-throughput sequencing is more suitable to describe the overall bacterial community richness and diversity of complicated environmental samples (Guan et al. 2015; Ju and Zhang 2014; Liao et al. 2015; Wu et al. 2015; Zhang et al. 2015a). In this study, Illumina MiSeq high-throughput sequencing was applied to reveal the bacterial community richness and diversity in freshwater Dianchi Lake and Erhai Lake. The Chao1 richness estimator and Shannon diversity index of bacterioplankton communities in Dianchi Lake and Erhai Lake were 714–1059 and 3.81–4.93 and 538–803 and 2.55–4.82, respectively, usually much higher than the previous reported values based on the application of traditional low-profiling molecular biology tools (Crump et al. 2003; Kent et al. 2004; Konopka et al. 1999; Li et al. 2015; Wei et al. 2008; Wu et al. 2009; Yannarell et al. 2003). A recent study using high-throughput sequencing analysis also revealed relatively high bacterioplankton richness and diversity in freshwater lakes (Bashenkhaeva et al. 2015). In this study, the evident spatial and seasonal change of bacterioplankton community richness occurred in either Dianchi Lake or Erhai Lake. Although the seasonal effect on bacterioplankton Shannon diversity in Dianchi Lake was also obvious, the trend for the seasonal change of bacterioplankton community diversity in Erhai Lake was not clear. This suggested the lake-specific seasonal change pattern of bacterioplankton community diversity. In addition, the studied two lakes showed a more remarkable spatial fluctuation of Shannon diversity in summer than in spring, suggesting that the spatial change pattern of bacterioplankton community diversity was dependent on sampling date. Numerous previous studies indicated that the richness and diversity of bacterioplankton community in freshwater lake might be influenced by a number of factors, such as water temperature, pH, dissolved oxygen, alkalinity, organic carbon, and nutrients (Li et al. 2015; Lymer et al. 2008; Martinez-Alonso et al. 2008; Pearce 2005; Wei et al. 2008; Wu et al. 2009). In this study, the result of Spearman rank correlation analysis suggested that the variables associated with the trophic status might be an important driving force for bacterioplankton community richness and diversity.

Tšertova et al. (2013) reported the homogeneous bacterial diversity in the upper sediment layers of a shallow lake, while many other previous studies showed the evident spatial heterogeneity of bacterial community richness and diversity in freshwater lake sediment (Bai et al. 2012; Chen et al. 2015; Liu et al. 2009; Shao et al. 2013; Song et al. 2012; Yu et al. 2015). These previous studies focused on the intra-lake investigation, yet the inter-lake difference of bacterial richness and

diversity has yielded poor attention. Our previous study showed a large difference of bacterial community richness and diversity among the profundal sediments of many small freshwater lakes on the Yunnan Plateau (Zhang et al. 2015a). Moreover, a few previous studies also revealed the marked seasonal change of bacterial community richness and diversity in freshwater lake sediment (Bai et al. 2012; Chen et al. 2015; Song et al. 2012). In the present study, the result of Illumina MiSeq high-throughput sequencing analysis indicated that the OTU number, Chao1 richness estimator, and Shannon diversity index of sediment bacterial communities in Dianchi Lake were 1221–1528, 1781–2318, and 5.01–5.5, respectively, while sediment bacterial communities in Erhai Lake had more OTUs (1852–2146) and higher Chao1 richness (2635–3039) and Shannon diversity (6.18–6.47). The large difference of sediment bacterial OTUs and Shannon diversity was also observed among small freshwater lakes on the Yunnan Plateau (Zhang et al. 2015a). The observed values of sediment bacterial OTUs and Shannon diversity in Dianchi Lake and Erhai Lake were much higher than those in other freshwater lakes based on low-profiling biology techniques (Chen et al. 2015; Nam et al. 2008; Lim et al. 2011; Song et al. 2012; Shao et al. 2013; Tšertova et al. 2013). Other previous studies using high-throughput sequencing analysis also revealed relatively high bacterial sediment community richness and diversity in freshwater lakes (Bai et al. 2012; Zhang et al. 2015a). The present study indicated no clear trend for the seasonal change of sediment bacterial community richness, although an evident spatial variation of bacterial richness was observed in these two lakes. In addition, a remarkable spatial variation of bacterial Shannon diversity occurred in summer Dianchi Lake sediments but not in spring Dianchi Lake sediments. In either spring or summer, only a slight spatial variation of bacterial Shannon diversity was found in Erhai Lake sediments. Therefore, the spatial change pattern of sediment bacterial diversity might be lake-specific and also depend on sampling date. To date, little is known about the influential factors regulating the sediment bacterial richness and diversity in freshwater lake. Yu et al. (2015) suggested that lake sediment bacterial richness and diversity might be influenced by TP and heavy metal. Our previous studies suggested that sediment NO_3^- -N might be a key determinant to sediment bacterial richness and diversity in small freshwater lakes on the Yunnan Plateau (Zhang et al. 2015a). Xiong et al. (2015) indicated that organic matter directly affected sediment bacterial diversity in Erhai Lake, while Bai et al. (2012) identified no links between sediment properties and bacterial richness or diversity in Dianchi Lake. In this study, the result of Spearman rank correlation analysis suggested that sediment bacterial richness and diversity might be influenced by a number of environmental factors including pH, ORP, NH_4^+ -N, NO_3^- -N, TN, TP, and TOC. So far, information on the comparison of bacterial richness and diversity in water columns and

sediments is very limited. Only an earlier study using DGGE analysis revealed higher bacterial richness in sediment than in water column in Lake Taihu (Ye et al. 2009). In this study, in both Dianchi Lake and Erhai Lake, bacterial richness and diversity were found to be higher in sediments than in water columns.

Bacterial community structure in freshwater lake

Numerous previous studies have shown the seasonal or/and spatial change of bacterioplankton community structure in freshwater lakes (Bashenkhaeva et al. 2015; Crump et al. 2003; Kent et al. 2004; Li et al. 2015; Pearce 2005; Tjndens et al. 2008; Wei et al. 2008; Wu et al. 2009; Zhang et al. 2014). In this study, the results of UPGMA clustering and phylogenetic analysis of bacterial communities also indicated an apparent spatial and seasonal change of bacterioplankton community structure in either Dianchi Lake or Erhai Lake. Moreover, a large difference of bacterioplankton community structure was found between in Dianchi Lake and Erhai Lake. A few previous studies also reported the remarkable difference of bacterioplankton community structure among freshwater lakes at different trophic status (Lindstrom 2000; Wu et al. 2009; Yannarell et al. 2003; Zwirgmaier et al. 2015). The links between freshwater lake bacterioplankton community structure and environmental factors have not been fully understood. A number of factors might collectively influence bacterioplankton community structure (Wei et al. 2008; Wu et al. 2009). However, trophic status was widely accepted as a key determinant of bacterioplankton community structure (Lindstrom 2000; Pearce 2005; Wei et al. 2008; Wu et al. 2009; Zhang et al. 2014; Zwirgmaier et al. 2015). In the present study, the result of RDA showed that nutrients as well as water temperature mainly accounted for the variation of bacterioplankton community structure. The result of Spearman rank correlation analysis also indicated that water temperature was significantly correlated to three major bacterial groups, *Alphaproteobacteria*, *Bacteroidetes*, and *Firmicutes*, while the level of nutrients showed significant correlations with *Cyanobacteria*, *Betaproteobacteria*, and *Firmicutes*. Hence, nutrients and water temperature might play crucial roles in shaping bacterioplankton community structure in freshwater lake.

The evident spatial heterogeneity of bacterial community structure in freshwater lake sediment has been well-documented (Bai et al. 2012; Bouzat et al. 2013; Chen et al. 2015; Haller et al. 2011; Liu et al. 2009; Song et al. 2012; Xiong et al. 2015; Yu et al. 2015; Zeng et al. 2008), while much fewer literatures existed on the seasonal change of bacterial community structure in freshwater lake sediment (Bai et al. 2012; Chen et al. 2015; Song et al. 2012; Schwarz et al. 2007). To date, the inter-lake bacterial community structure

difference remains poorly understood. Our recent study revealed the distinct sediment bacterial community structures in small freshwater lakes on the Yunnan Plateau (Zhang et al. 2015a). In this study, the result of phylogenetic analysis of bacterial communities illustrated an obvious spatial heterogeneity of sediment bacterial community structure in either Dianchi Lake or Erhai Lake, while the result of UPGMA clustering further confirmed distinct sediment community structure in these two lakes. Moreover, an evident seasonal effect on sediment bacterial community structure occurred in Dianchi Lake, but the trend for its seasonal change in Erhai Lake was not clear. This suggested that the spatial change pattern of sediment bacterial community structure might be lake-specific. The environmental factors driving freshwater lake sediment bacterial community structure remain largely unclear, although previous studies suggested that it might be affected by one or two sediment parameters, including pH (Zeng et al. 2008, 2009; Zhao et al. 2011), ORP (Zeng et al. 2008), organic matter (Liu et al. 2015), nitrogen (Chen et al. 2015; Liu et al. 2015), phosphorus (Song et al. 2012; Yu et al. 2015; Zeng et al. 2009), and heavy metal (Yu et al. 2015). Our previous study indicated that the level of sediment NO_3^- -N might contribute to the difference of bacterial community structure among small freshwater lakes on the Yunnan Plateau (Zhang et al. 2015a). Bai et al. (2012) indicated that TOC was the main force driving the variability of sediment bacterial community structure in Dianchi Lake. Xiong et al. (2015) also indicated that organic matter played an important role in structuring sediment bacterial community in Erhai Lake. In the present study, the result of RDA suggested that four sediment parameters (NH_4^+ -N, TP, TN, and TOC) mainly accounted for the change of sediment bacterial community structure in these two lakes. The result of Spearman rank correlation analysis indicated that these four sediment parameters also had significant correlations with *Proteobacteria* (including *Beta*- and *Deltaproteobacteria*), *Chlorobi*, *Nitrospirae*, and *Acidobacteria*. Hence, NH_4^+ -N, TP, TN, and TOC might collectively structure sediment bacterial community in Dianchi Lake and Erhai Lake.

So far, very limited information existed on the bacterial community structure difference between in water column and in sediment. Only an earlier study using DGGE analysis revealed that planktonic and sediment bacterial communities in Lake Taihu had distinct structures (Ye et al. 2009). In this study, the result of UPGMA clustering illustrated the distinct structure difference between planktonic and sediment bacterial communities in both Dianchi Lake and Erhai Lake. Planktonic bacterial communities in these two lakes were mainly composed of *Proteobacteria* (mainly *Alpha*-, *Beta*-, and *Gammaproteobacteria*), *Bacteroidetes*, *Actinobacteria*, *Cyanobacteria*, and *Firmicutes*, while sediment bacterial communities were dominated by *Proteobacteria* (mainly *Beta*- and *Deltaproteobacteria*), *Bacteroidetes*, *Chlorobi*,

Nitrospirae, *Acidobacteria*, and *Chloroflexi*. However, an earlier study using pyrosequencing indicated that *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, and *Chloroflexi* were the major bacterial phyla in sediments of Dianchi Lake, while proteobacterial communities were mainly composed of *Beta*-, *Gamma*-, and *Epsilon-proteobacteria* (Bai et al. 2012). Moreover, DGGE analysis showed that *Chloroflexi*, *Deltaproteobacteria*, and *Firmicutes* were dominant in sediments of Erhai Lake (Xiong et al. 2015). These results in the previous studies were different from those obtained in the current study.

In conclusion, the change pattern of planktonic and sediment bacterial communities in freshwater lake was lake-specific and season-specific. Planktonic and sediment bacterial communities showed an evident structure difference. Bacterial community structures differed greatly in Dianchi Lake and Erhai Lake. Trophic status might be a key force driving planktonic and sediment bacterial communities in freshwater lake.

Acknowledgments This work was financially supported by the National Natural Science Foundation of China (No. 41571444), National Basic Research Program of China (2015CB458900), and special fund of State Key Joint Laboratory of Environment Simulation and Pollution Control (15L02ESPC).

Compliance with ethical standards The work has not been published previously and not under consideration for publication elsewhere.

Conflict of interest The authors declare that they have no competing interests.

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