

中国江苏太湖和阳澄湖细菌群落组成、多样性和时空动态比较研究

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摘要: 为了调查与比较太湖和阳澄湖浮游细菌群落的分布、多样性及动态, 采用密集时间(每周)采样法于2012年6月至10月采集了85个样品, 并通过16S rRNA基因高通量测序分析了其菌群组成。原始读长序列经过过滤后, 共获得142 354条高质量读长序列, 归属于4 589个运算分类单元(operational taxonomic units, OTUs), 其中变形菌门(主要包括 γ -变形菌门)和拟杆菌门是两个湖泊的主要类群。两个湖泊的菌群共同拥有19.55%的OTUs, 这些OTUs占总读长序列条数的95.01%, 表明它们之间存在高度重叠。阳澄湖的群落 α -多样性高于太湖, 这可能主要归因于两个湖泊的稀有菌群。有趣的是, 我们观察到浮游细菌群落的组成随时间急剧波动, 推测在极浅湖泊中菌群抵抗外来干扰的能力较低。综上所述, 本研究结果对人们更好地理解湖泊菌群的组成差异及时空动态具有重要参考价值。

关键词: 细菌群落; 16S rRNA基因; 454焦磷酸测序; 太湖; 阳澄湖

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Comparison of the Composition, Diversity and Spatiotemporal Dynamics of Bacterial Communities in Lake Taihu and Lake Yangcheng, Jiangsu, China

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Abstract: To investigate and compare the distribution, diversity and dynamics of bacterioplankton communities in Lake Taihu and Lake Yangcheng in Jiangsu Province, China, the bacterial community composition was analyzed from 85 samples using 454-pyrosequencing of 16S rRNA genes. The samples were taken weekly within an intensive time period from June to October 2012. A total of 142 354 clean reads were ge-

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nerated that were assigned to 4 589 operational taxonomic units (OTUs), with Proteobacteria (mainly γ -Proteobacteria) and Bacteroidetes being the dominant taxa in both lakes. In addition, 19.55% of OTUs, accounting for 95.01% of the total reads, were shared by bacterial communities in the two lakes, which indicated a high degree of overlap between them. The communities in Lake Yangcheng had a higher α -diversity than those in Lake Taihu, which may be mainly attributed to the rare taxa found in both lakes. Interestingly, the results showed that the bacterioplankton composition profile dramatically fluctuated over time. This may be explained by the low capability of the communities to resist external disturbances in extremely shallow lakes. Our study provides information for better understanding of the spatiotemporal dynamics in bacterial communities and differences in their compositions between two related lakes.

Key words: bacterial community; 16S rRNA gene; 454-pyrosequencing; Lake Taihu; Lake Yangcheng

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Bacterial communities are key components in aquatic ecosystems, and play a crucial role in biogeochemical cycles and profoundly impact water quality^[1]. The composition and diversity of bacterioplankton are closely related to spatial, temporal and environmental factors in water systems, such as ecological habitats, seasonality, and nutrient concentrations^[2-6]. For example, elevation showed strong influence on bacterioplankton community composition, and the dissimilarity of bacterioplankton community increased with increasing differences in elevation^[4]; bacterioplankton community dissimilarity strongly adheres to geographic distance decay relationship in 42 lakes and reservoirs across China^[6].

Lake Taihu is the third largest freshwater lake in China, covering an area of 2 338 km² with a mean depth of 1.9 meters^[7]. Lake Yangcheng, part of the Taihu basin, has a similar depth and is about one-nineteenth the size of Lake Taihu. Two lakes are in close proximity and are the key freshwater resources for residents in the surrounding areas. In recent decades, both lakes have undergone increasingly serious eutrophication as a result of human activities^[8-9]. In recent years, with high-throughput sequencing of the 16S rRNA gene, many studies have been performed to investigate the diversity and composition of bacterioplankton, as well as its relationship to environmental factors^[10-11]. Several studies revealed that seasonal succession caused significant differences in bacterial communities, and temporal variation of the microbial community was significant-

tly greater than spatial variation in Lake Taihu^[10-13]. However, to date, sampling in an intensive time period to investigate the composition and dynamics of bacterioplankton communities in Lake Taihu has rarely been documented.

Studies of the bacterioplankton community in Lake Yangcheng are scarce, except for that Bai *et al.*^[14] investigated in 2013 the bacterial community structure, especially the Cyanobacteria composition, and compared the community similarity between Lakes Taihu and Yangcheng at temporal scale. However, the understanding of bacterial community responding to environmental factors in this lake remains poor. More importantly, the two adjacent lakes share similar geographic and climatic conditions, so they can be ideally used to explore the determinants leading to the divergence of the bacterial profiles between these two lakes.

Therefore, by collecting water samples weekly from June to October 2012 at each of three sites in the two lakes, we characterized and compared the diversity and composition of their bacterioplankton communities, explored the spatiotemporal dynamics of bacterial composition profiles, and determined the linkages within the bacterial communities in response to changing environmental parameters.

1 Materials and methods

1.1 Sampling sites

Water samples were collected from total six sites in Lake Taihu and Lake Yangcheng, Jiangsu,

China. The sampling sites are shown in Fig.1. Sampling site T1 (Jinsu port) is a water source area of Suzhou City, which is less affected by pollution than the other two sampling sites, T2 (beacon No. 4) and T3 (Xintang port). The latter two sites are located in areas subjected to industrial wastewater discharge (Fig.1A). Lake Yangcheng is divided into three parts, and water samples were collected from the Y1 (western), Y2 (middle) and Y3 (eastern) parts of the lake (Fig.1B).

1.2 Sampling and environmental factors

Triplicate water samples were collected weekly 0.5 m below the surface from six sites from June to October 2012. Some samples were not collected due to bad weather. A total of 85 samples were obtained from the two lakes for processing and analysis. For each sample, water temperature (Tem), pH, dissolved oxygen (DO), chlorophyll-a (Chl-a) and algal density were simultaneously measured *in situ* using a Multi-Parameter Water Quality Sonde (6600V2-00, YSI Inc., America). Total nitrogen (TN), total phosphorus (TP), ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N) and chemical oxygen demand (COD) were determined using the standard methods^[15]. The eutrophication evaluation was performed with the trophic level index (TLI) method^[16].

1.3 DNA extraction, amplification, and 454-pyrosequencing

The samples were transported to the laboratory on ice for DNA extraction immediately. A 100 mL volume of water from each sample was centrifuged using a high-speed freezing centrifuge at 12 000 r/min

for 15 min at 4 °C. The supernatant was discarded and the precipitate was resuspended with ddH₂O. DNA was extracted using Universal Genomic DNA Extraction Kit Ver.3.0 (DV811A, TaKaRa Bio Inc., China) according to the manufacturer's instructions. DNA was extracted from the triplicate samples of each site and was mixed together. The primer pair 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 533R (5'-TTACCGCGGCTGCTGGCAC-3') was used to amplify the V3 region of the 16S rRNA gene^[17]. The PCR products were purified and sequenced on the 454 GS FLX Titanium (SinoGenoMax Co., Ltd., Beijing, China). The raw pyrosequencing data generated in the present study were submitted to the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under accession number SRP092336.

1.4 Sequence processing and bacterial population analyses

Pyrosequencing reads were analyzed with MOTHUR following the standard operating procedure (SOP) suggested by Schloss *et al.*^[18]. After removing the primer sequences and barcodes, low-quality reads were trimmed, including reads with an ambiguous base, less than 200 bp, or with homopolymers longer than 8 bp. Chimeras were removed through the "chimera.uchime" method, using the preclustered sequences as their own reference. Reads affiliated with chloroplasts or mitochondria were excluded from the subsequent analysis. Finally, clean reads were aligned and clustered into OTUs with a threshold value of 97% sequence similarity.

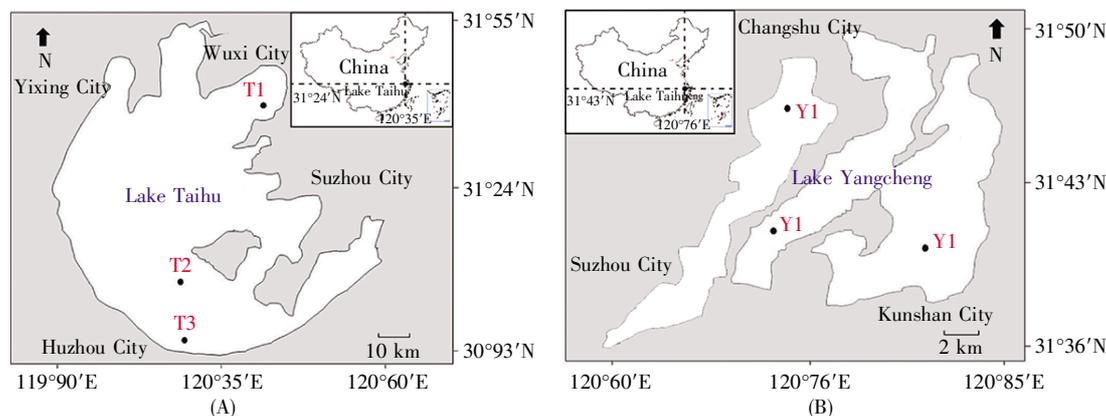


Fig.1 Sampling locations in Lake Taihu (A) and Lake Yangcheng (B)

1.5 Bacterial diversity and statistical analyses

To avoid biases generated by differences in sequencing depth, samples were normalized to the same depth, based on the sample that had the lowest number of sequences prior to downstream bioinformatics analysis. The α -diversity indices (Shannon, Simpson and Chao1) were calculated using the "summary.single" command implemented in MOTHUR, and displayed as a boxplot for both two lakes. The β -diversity measure was used to analyze bacterial community differences between samples and sites. The microbial community structures in different samples were compared using UniFrac^[19] based on the phylogenetic relationship of representative reads from different samples. Weighted UniFrac distance calculations and the corresponding significant test were performed between pairs of samples using the Fast UniFrac pipeline^[20].

Statistical analysis of metagenomic profiles (STAMP) was employed to test for significant differences in bacterial community abundances between Lake Taihu and Lake Yangcheng^[21]. Statistical significance of differences between samples (q value) was assessed using the two-sided Fisher's exact test with Storey's false discovery rate method of multiple test correction within STAMP. The confidence intervals were determined using the Newcombe-Wilson method. Features with a q value of less than 0.05 were deemed significant.

1.6 Relationships between bacterial communities and environment

The vegan 2.3-0 package implemented in R (<http://www.r-project.org/>) was used to explore the relationship between changes in community structure and measured environment variables. The detrended correspondence analysis (DCA) values of the gradient length along the longest axis of Lake Taihu and Lake Yangcheng were 3.18 and 3.66, respectively. Therefore, redundancy analysis (RDA) was chosen for ordination analysis. As some environment variables were missing for some samples, only 59 samples (29 for Lake Taihu, 30 for Lake Yangcheng) were included in RDA analysis. Environmental factors were log-transformed and standard-

ized as explanatory variables. The significance of the environmental factors was tested with 999 Monte Carlo permutations, and only factors that were found to be significant ($P < 0.05$) were included in the subset of forward selected variables.

2 Results

2.1 Sequencing data and diversity analysis

Pyrosequencing yielded a total of 336 341 raw reads from the 85 samples collected from the two lakes. After removing low quality reads, 142 354 clean reads remained from the 85 samples (71 027 reads in 42 Lake Taihu samples and 71 327 reads in 43 Lake Yangcheng samples). These clean reads were aligned and clustered into 4 589 unique OTUs (2 368 in Lake Taihu and 3 118 in Lake Yangcheng) at 97% sequence similarity. The numbers of OTUs varied from 1 031 to 3 489 in all samples.

The α -diversity indices (Shannon, Simpson and Chao1) were calculated using a subset of 1 031 reads per sample, selected randomly based on the sample with the smallest sequencing effort. The sequencing effort was sufficient to capture the relative complete diversity of these communities, which were confirmed by the high Good's coverage index, ranging from 88.1% to 96.5% in each sample (Table S1). Differences in the indices between the two lakes are present in Fig.2 with the P values of paired sample t -test shown on the top of each boxplot. Overall, the community diversity in Lake Yangcheng was higher than that in Lake Taihu. While the former had a greater Shannon index and a smaller Simpson index than the latter (Figs.2A and 2B, $P < 0.01$ for Shannon index, $P < 0.02$ for Simpson index). On average, the Chao1 index of Lake Yangcheng showed ~1.36 times the community richness index in Lake Taihu (Fig.2C, $P < 0.001$).

Among the 4 589 OTUs, 19.55% were shared by the two lakes, while 32.05% and 48.40% were unique to samples from Lake Taihu and Lake Yangcheng, respectively (Fig.3A). When the abundance of each OTU was accounted for, 95.01% of the total reads occurred in both lakes, 1.86% were exclusive to the Lake Taihu, and 3.13% to the Lake

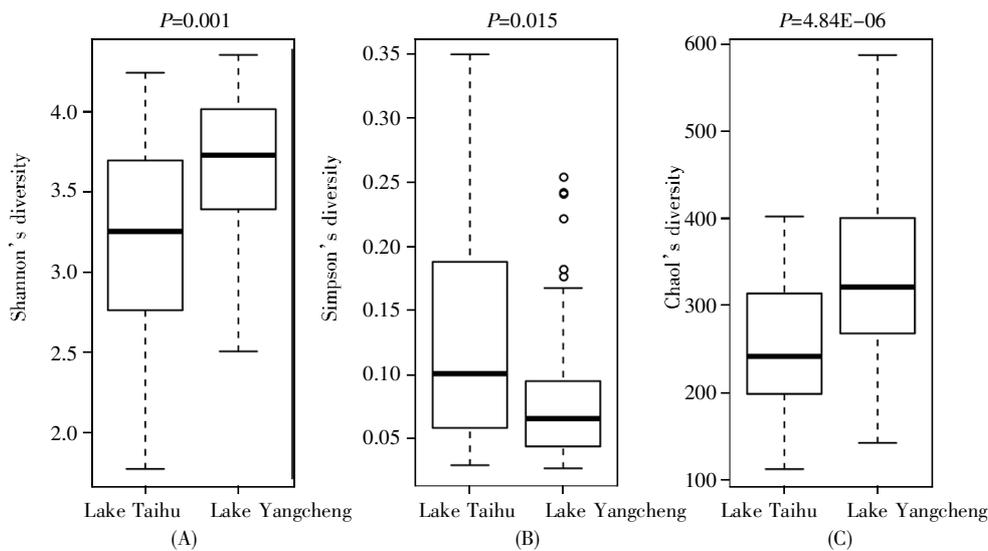


Fig.2 Boxplot of diversity indices in Lake Taihu and Lake Yangcheng

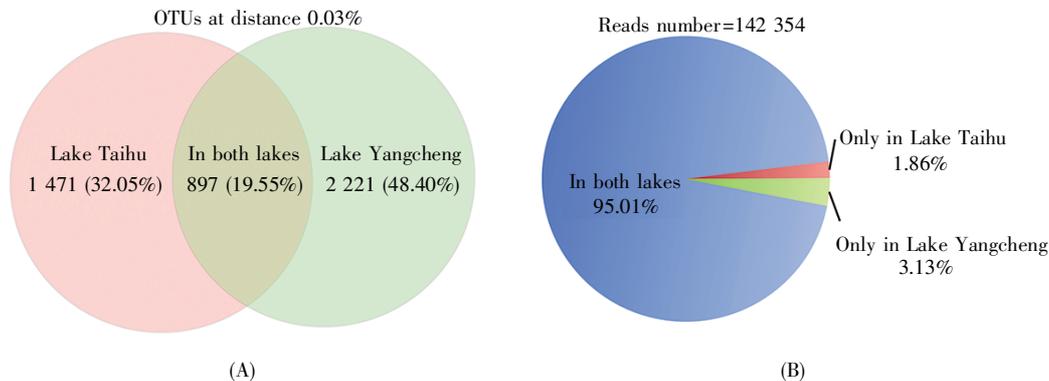


Fig.3 Comparison of bacterial community structure between Lake Taihu and Lake Yangcheng

(A) Venn diagram showing OTUs distribution between the two lakes; (B) Pie plot showing the percentage of reads from each lake exclusively and shared by both lakes.

Yangcheng (Fig.3B).

2.2 Bacterial community composition

The 4 589 OTUs were assigned into 23 known phyla covering 193 genera based on MOTHUR – modified RDP taxonomy. At the phylum level, Lakes Taihu and Yangcheng shared all of the top ten major phyla (assayed as average relative abundance) (Fig.4A). The dominant phyla included Proteobacteria (65.26%), Bacteroidetes (13.52%), Actinobacteria (1.28%), Firmicutes (1.30%) and Cyanobacteria (0.98%) for Lake Taihu, and Proteobacteria (57.92%), Bacteroidetes (18.43%), Cyanobacteria (2.33%), Actinobacteria (2.00%), Verrucomicrobia (1.18%) for Lake Yangcheng (Fig.4A). In both lakes, γ -Proteobacteria (37.95% in Lake Taihu vs. 31.16% in Lake Yangcheng), followed by β -Proteobacteria (19.20%

vs. 20.15%) and α -Proteobacteria (4.61% vs. 3.17%), was the dominant subdivisions of Proteobacteria. The top five major phyla occupied 82.34% and 81.86% of the total bacterial composition in Lakes Taihu and Yangcheng, respectively. In more detail, bacterial composition of each sample at the phylum level is shown in Figs.4B and 4C. Overall, both lake bacterial communities displayed a similar composition. However, the relative abundances of all the phyla, except for Firmicutes and Gemmatimonadetes, were significantly distinct ($P < 0.05$) between the two lakes based on STAMP analysis (Fig.5A).

At the genus level, the most abundant genera (average relative abundance $> 0.1\%$) made up 55.29% and 50.98% of the total bacterial composition in Lakes Taihu and Yangcheng, respectively (the details

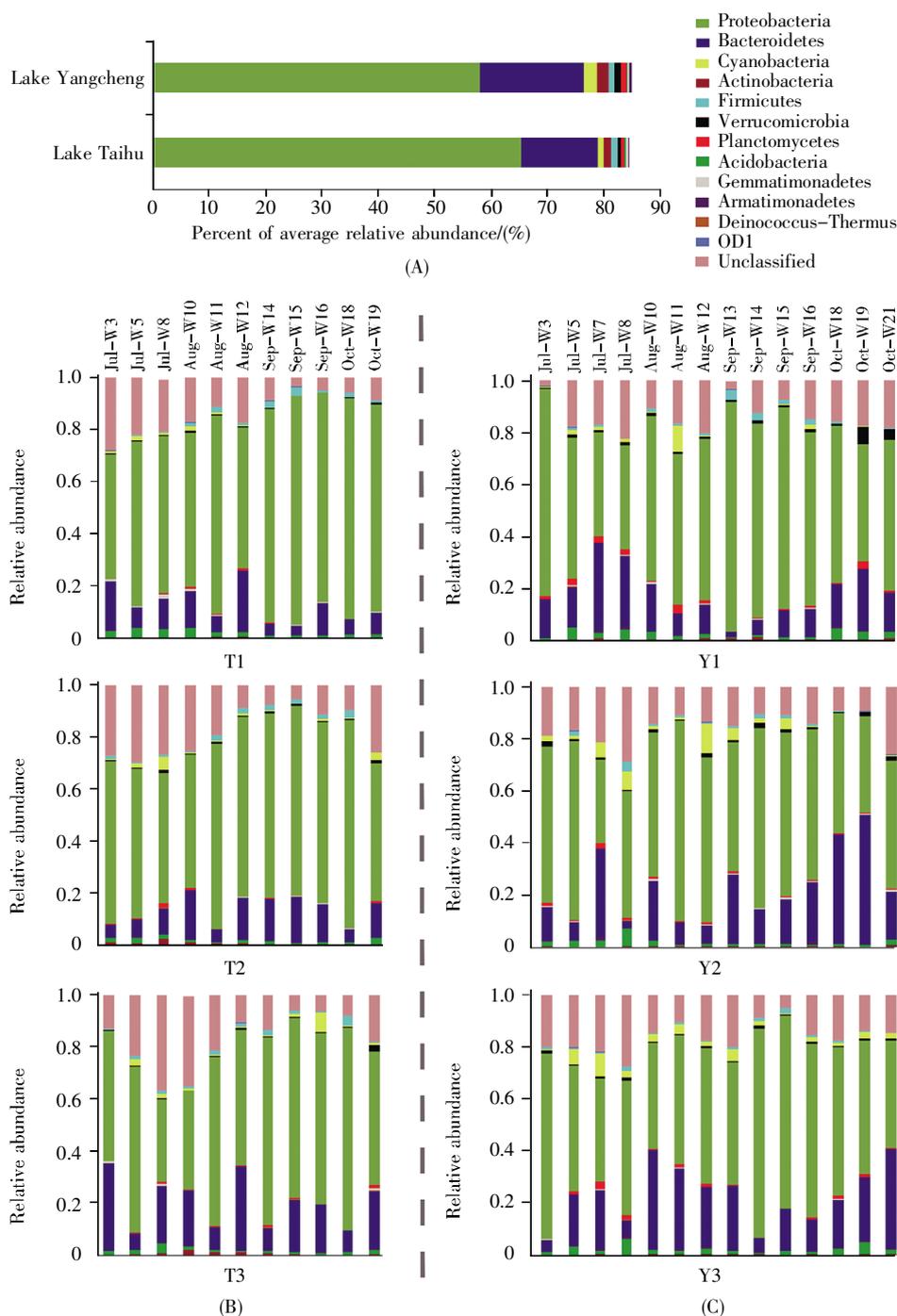


Fig.4 Relative abundances of bacteria within the community at the phylum level in Lake Taihu and Lake Yangcheng (A) The average relative abundance (>0.1%) in Lake Taihu and Lake Yangcheng (the unclassified OTUs are not included); (B) Detailed relative abundance of 33 samples in Lake Taihu; (C) Detailed relative abundance of 44 samples in Lake Yangcheng.

are listed in Table S2). Genera with average relative abundance > 1% included *Escherichia_Shigella* (23.24% in Lake Taihu vs. 18.26% in Lake Yangcheng), *Serratia* (10.98% vs. 8.19%), *Limnohabitans* (7.72% vs. 5.52%), *Flavobacterium* (3.96% vs. 6.83%), *Algoriphagus* (1.46% vs. 0.87%), *Polynucleobacter* (1.34% vs. 2.83%), *Rhodobacter* (1.33% vs. 1.19%),

and *Gp II a* (0.49% vs. 1.42%) (Table S2). Accordingly, the two lakes had similar profiles of bacterial community composition. Two genera of Enterobacteriaceae, containing *Escherichia* and *Serratia*, represented the dominant bacterial groups across all samples. Among seven top abundant genera, *Polynucleobacter* and *Gp II a* showed statistically marked

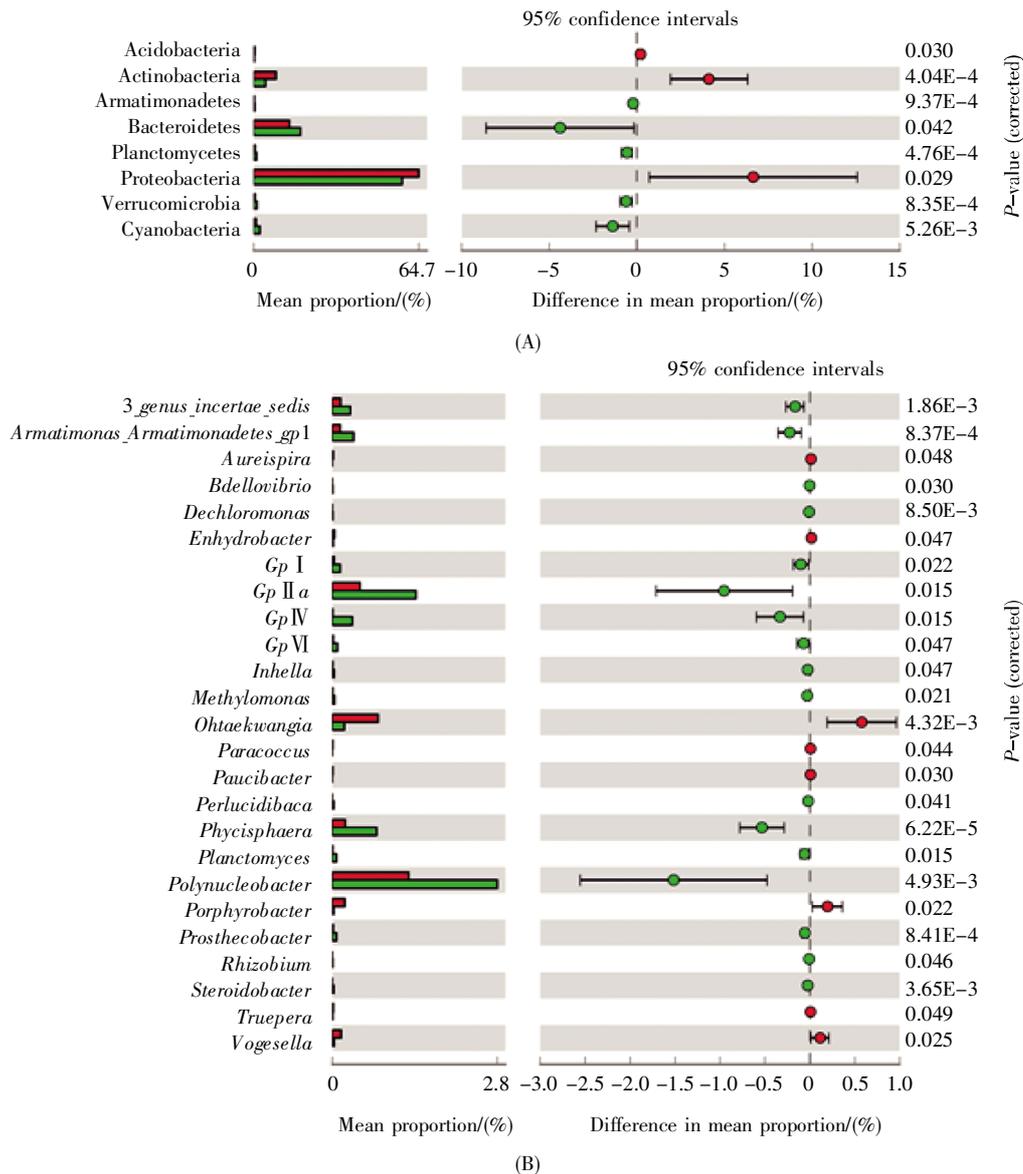


Fig.5 Comparison of bacterial composition profiles for Lake Taihu (red) and Lake Yangcheng (green) at the phylum (A) and the genus (B) levels using STAMP analysis

Only phyla and genera with significant difference are listed; differences in mean proportions = Lake Taihu – Lake Yangcheng.

differences ($P < 0.05$) between two lakes based on STAMP analysis (Fig.5B).

2.3 Temporal variations of bacterial composition within each lake

Samples obtained from three different sites in each lake at the same time point were chosen to compare their bacterioplankton composition temporally. Clearly, bacterial abundances varied at the phylum level over time among samples at each site of Lake Taihu (Fig.4B) and Lake Yangcheng (Fig.4C). For example, among 11 samples from the T1 site, the abundances of Bacteroidetes (bright blue) fluctuated widely, ranging from 3.71% to 23.15%, with a medium value of 6.20%. In addition, the weighted UniFrac distance analysis showed significant changes in the distance values between all pairs of samples collected from these two lakes ($P < 0.05$; Fig.6).

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2.4 Spatial variation of bacterial community and its responses to the environmental parameters

RDA was performed to determine the relationship between environmental factors and bacterial community. In Lake Taihu, the first two axes showed 14.84% and 12.29% of the total variance for bac-

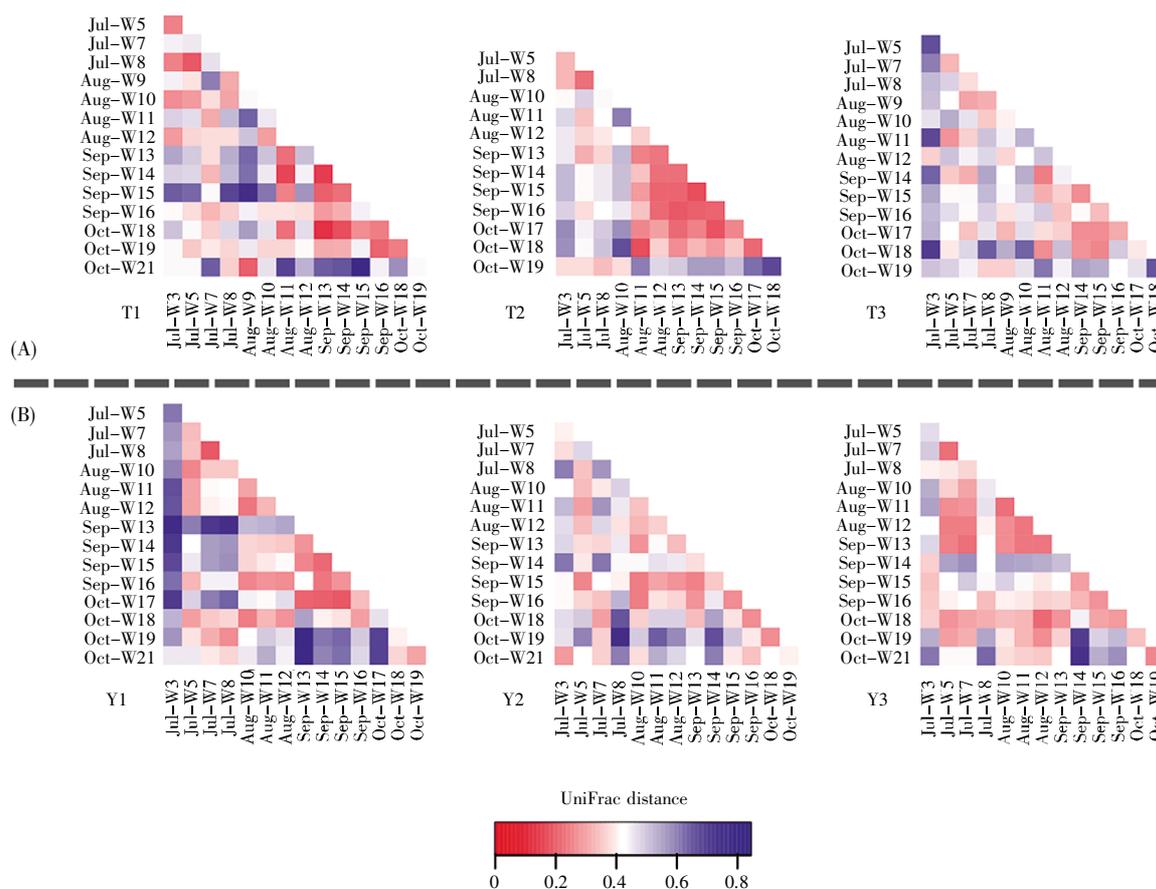


Fig.6 Heatmap showing the weighted UniFrac distances between a pair of samples from six sampling sites in Lake Taihu (T1~3) (A) and Lake Yangcheng (Y1~3) (B)

Statistical significance was observed between all pairs of samples ($P < 0.001$). Color key represents the UniFrac distance.

tertoplankton OTUs composition (Fig.7A). Sampling site T1 (Jinsu port) is a water source area of Suzhou City, which is less affected by pollution than the other two sampling sites. All samples collected from T1 clustered together and could be distinctly discriminated from the samples collected from T2 and T3 by RDA ordination (Fig.7A). Based on the Monte Carlo permutation tests in redundancy analysis, seven environment variables including $\text{NO}_3\text{-N}$ ($P=0.001$), TN ($P=0.005$), TP ($P=0.001$), Tem ($P=0.035$), pH ($P=0.001$), Chl-*a* ($P=0.001$), and algal density ($P=0.004$) showed significant influences on bacterial communities ($P < 0.05$); other three environment variables ($\text{NH}_4^+\text{-N}$, COD, and DO) had P values greater than 0.05. In Lake Yangcheng, the first two axes explained 14.85% of the cumulative variance in the species-environment correlation with 9.7% in Axis 1 and 5.15% in Axis 2. Y3 had a smallest trophic level index (TLI) among three sites (Fig.S1). There

was a separation between groups from Y3 and the Y1 and Y2 sites (Fig.7B). In contrast to Lake Taihu, only three environmental factors (TP, $P=0.025$; Tem, $P=0.002$; algal density, $P=0.016$) in Lake Yangcheng were found to significantly contribute to the planktonic bacterial assemblage environment relationship (Fig.7B).

3 Discussion

One of the main objectives of the present study was to determine whether bacterial communities in Lakes Taihu and Yangcheng differed in diversity and composition. Our results revealed a higher α -diversity of bacterial communities in Lake Yangcheng compared to Lake Taihu using Shannon, Simpson and Chao1 indices (Fig.2). This result matches those from the previous investigation that Lake Yangcheng had larger bacteria diversity than Lake Taihu at phylum level^[4]. Previous studies showed that

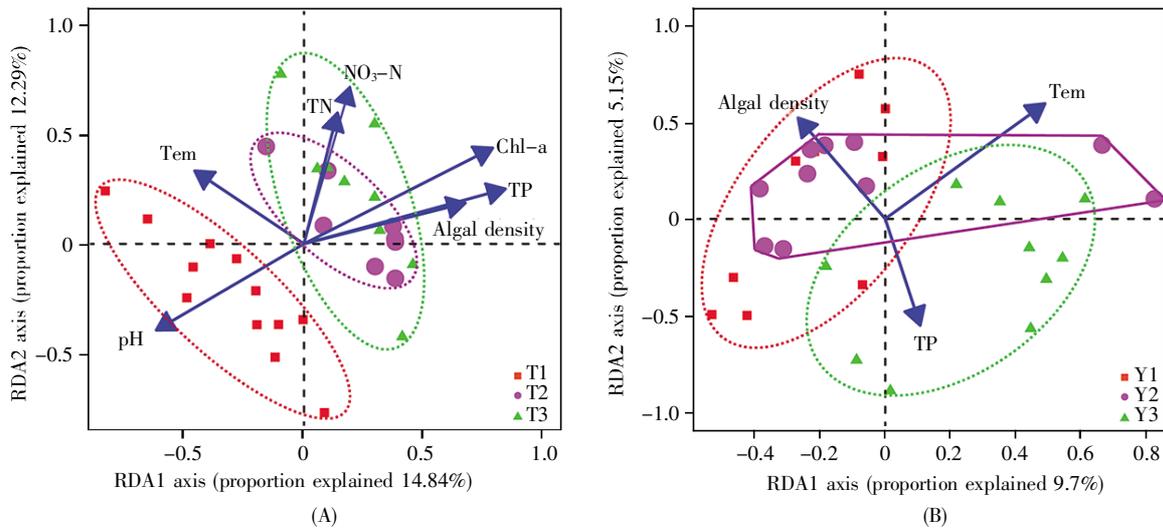


Fig.7 RDA ordination analysis of the distribution of bacterial community related to the significant environment variables ($P < 0.05$) in Lake Taihu (A) and Lake Yangcheng (B)

Blue arrows represent environment variables. TP, total phosphorus; pH, potential of hydrogen; Chl-a, chlorophyll-a; Tem, water temperature; NO₃-N, nitrate nitrogen; TN, total nitrogen.

biodiversity was negatively correlated with a lake area, as bacterial communities in small lakes with large catchment area are easily and frequently influenced by the unpredictable input of bacteria from their surrounding catchments or sediments^[4,22-23]. Thus, a higher biodiversity in Lake Yangcheng was probably due to the smaller lake area than that of Lake Taihu. Additionally, Li *et al.*^[4] reported in 2017 that the rare taxa govern the overall bacterial community diversity pattern. There were 1 471 and 2 221 OTUs unique to Lake Taihu and Lake Yangcheng, respectively (Fig.3A). Hence, the greater number of specific OTUs identified in Lake Yangcheng compared with that in Lake Taihu, was potentially an important reason resulting in significant difference of bacterial community diversity between the two lakes.

An interesting finding in this study, however, was that 19.55% of the OTUs, occupying 95.01% of the total reads, were shared between bacterial communities of the two lakes (Fig.3). We speculated that high degree of overlap between these two lakes was probably shaped by their similar geography and climate, as they are close to each other in distance and both originate from the Taihu basin^[6]. It has been reported that geographic distance showed a stronger correlation with the similarities of the bacterial community in Lake Taihu^[24]. In contrast to our fin-

dings, distinct or significant differences were observed in bacterioplankton community composition among closely situated lakes, e.g. three high-elevation tropical lakes located within the Lauca basin^[25], two sub-alpine lakes in Taiwan^[26], and two saline meromictic lakes (lakes Shunet and Shira)^[27].

The overlap of OTUs between two lakes was attributed to the top shared dominant phyla (Fig.4A). In accordance with our results, numerous studies showed that five phyla (Proteobacteria, Actinobacteria, Bacteroidetes, Cyanobacteria and Verrucomicrobia) were the most abundant bacterial taxa in common lineages of freshwater lake bacteria^[1, 7, 14, 28-29]. Although all five subdivisions of Proteobacteria were identified in two lakes, γ -Proteobacteria was the dominant subphylum, followed by β -Proteobacteria and α -Proteobacteria. This was inconsistent in some ways with the findings from previous studies that β -Proteobacteria was considered to be the dominant subphylum of the Proteobacteria^[1, 7, 10, 30]. However, Huang *et al.*^[31] reported in 2019 that γ -Proteobacteria followed by β -Proteobacteria was the most abundant class in the lake, lake wetland and estuary sediment samples. Therefore, we speculated that bacterial component exchange between sediments and water column may lead to this result.

At temporal scale, our results reveal a remar-

kable weekly fluctuation of bacterial communities at each site with sampling in an intensive time period. This phenomenon could be interpreted as that the bacterial community diversity in extremely shallow lake was instable, and was susceptible to climate and other factors, such as storms, rainfall, winds, and water diversion^[10, 13, 32]. Unlike in a deep reservoir or an ocean where water stratification is benefit for maintaining the stability of microbial community^[33-34], wind-induced sediment resuspension represents a major characteristic in shallow turbid lake systems^[30, 35]. Sediment resuspension can push bacteria to be released from sediments and incorporated into water column^[31]. For instance, the diversity and structure of bacterioplankton communities significantly varied in a wind wave turbulence experiment^[30]. In addition, two lakes probably suffer from frequent storms in summer due to the East Asian monsoon^[32].

At spatial scale, RDA ordination analysis showed a distinct separation of taxonomic composition between the T1 site and the other two sampling sites (T2 and T3) in Lake Taihu. Previous studies reported that trophic status displayed significant correlation with community composition, and had indirect effects by altering the composition of bacterioplankton^[3, 36-37]. It has been reported that the discharge of domestic and industrial wastewater led to an increased level of the nutrient loading^[38]. The seven environmental factors ($\text{NO}_3\text{-N}$, TN, TP, Tem, pH, Chl-a, and algal density) influencing bacterial community compositions in Lake Taihu are related to trophic status except the time-related factor Tem. The T1 sample points are distributed at the lower left corner of Fig.7A. This is consistent with the fact that T1 is a crucial drinking water source and has milder eutrophication than the T2 and T3 sites, both of which are located in areas subjected to industrial wastewater discharge according to trophic level index (TLI) evaluation (Fig.S1). Similarly, the three factors affecting bacterial community changes in Lake Yangcheng were also related to trophic status (TP and algal density) and seasonality (Tem). Bacterial community in the site Y3 was distinct from those in the other two sampling sites (Y1 and

Y2) in Lake Yangcheng, possibly due to the lower TP in the former site (Table S3). Thereby, the significant differences in spatial distribution of community composition in two lakes can be explained mostly by eutrophication degree and are highly related to the spatiotemporal changes of environmental factors.

Our RDA analysis showed seven environment factors ($\text{NO}_3\text{-N}$, TN, TP, Tem, pH, Chl-a, and algal density) in Lake Taihu and Lake Yangcheng were significantly correlated with bacterial communities. These results are partly consistent with those findings in recent studies, which showed that there are strong linkages between bacterial community composition and water temperature, pH, $\text{NO}_3\text{-N}$, and Chl-a in Lake Taihu^[12, 30, 38]. It is increasingly apparent that the composition and diversity of bacterioplankton are closely related to the surrounding environmental factors. Nutrient bioavailability (e.g., $\text{NO}_3\text{-N}$ and phosphorus) and water properties (e.g., temperature and pH) play critical roles in driving the activities and large-scale distribution of freshwater bacterial communities because they are playing a crucial role in the growth and development of bacteria^[39-41]. For example, phosphorus concentration was found to be one of the most important factors influencing change of bacterioplankton communities^[39]. Previous studies revealed that temperature has a significant effect on the dynamics and composition of plankton communities in rivers^[40]. As the range of optimal growth temperature for each phenotype is different, water temperature changes can result in variation in microbial community composition. In addition, it is well known that Chl-a can be used as a measure of algal biomass, which is a biological disturbance to lake bacterial communities. Various investigations have reported that Chl-a is significantly related to bacterial community composition^[40, 42].

In conclusion, we monitored the spatiotemporal dynamics of bacterial communities in the two lakes by sampling weekly within an intensive time period and through 454-pyrosequencing of 16S rRNA genes. In bacterial compositions, Lakes Taihu and Yangcheng shared the most abundant taxa and had

no significant differences. However, Lake Yangcheng harbored significantly higher α diversity than Lake Taihu. A higher percentage of unique reads in Lake Yangcheng compared with that in Lake Taihu implied that the differences in bacterial diversity were mainly caused by the presence of rare taxa. Importantly, we observed remarkable fluctuation in the bacterial communities over time in both lakes. This suggested the low capability of the communities to resist external disturbances in extremely shallow lakes. In addition, the linkages within the bacterial communities in response to changing environmental parameters were documented for both lakes.

Supplement data

The following materials are available in the online version of this article.

Table S1 454–sequencing parameter statistics of clean reads

Table S2 Genera with an average relative abundance >0.1%

Table S3 Summary of environment variables

Fig.S1 Trophic level index for six sites in the two lakes

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Supporting information for:

Comparison of the Composition, Diversity and Spatiotemporal Dynamics of Bacterial Communities in Lake Taihu and Lake Yangcheng, Jiangsu, China

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Table S1 454-sequencing parameter statistics of clean reads

Label	Sample	Nseqs	Community richness		Community diversity		Sequencing depth
			Chao1 (95% CI)		Shannon (95% CI)		Coverage
0.03	T1_Jun-W3	1 272	198.125 (153.664~290.034)		3.401 (3.313~3.489)		0.949
0.03	T1_Jul-W5	1 462	156.045 (131.429~207.68)		3.395 (3.306~3.484)		0.955
0.03	T1_Jul-W7	1 644	256.615 (206.949~347.429)		3.4 (3.288~3.512)		0.926
0.03	T1_Jul-W8	1 420	221.938 (167.992~330.799)		3.374 (3.279~3.469)		0.943
0.03	T1_Aug-W9	1 592	168.833 (125.362~265.743)		2.345 (2.218~2.472)		0.957
0.03	T1_Aug-W10	1 194	327.923 (276.369~414.741)		4.005 (3.9~4.11)		0.903
0.03	T1_Aug-W11	1 989	232.773 (181.204~330.032)		2.714 (2.59~2.837)		0.932
0.03	T1_Aug-W12	1 430	234 (183.815~330.983)		3.524 (3.428~3.619)		0.937
0.03	T1_Sep-W13	2 183	148.563 (112.727~224.874)		2.113 (2.006~2.22)		0.954
0.03	T1_Sep-W14	2 251	268.214 (191.388~422.306)		2.613 (2.49~2.735)		0.936
0.03	T1_Sep-W15	2 077	112 (88.176~167.05)		1.772 (1.659~1.884)		0.965
0.03	T1_Sep-W16	1 679	257.789 (195.57~376.467)		2.899 (2.784~3.014)		0.931
0.03	T1_Oct-W18	1 606	137.75 (102.851~218.01)		2.164 (2.056~2.272)		0.962
0.03	T1_Oct-W19	1 496	177.667 (134.712~268.284)		2.793 (2.69~2.897)		0.952
0.03	T1_Oct-W21	3 076	320.111 (206.826~565.94)		2.897 (2.786~3.009)		0.94
0.03	T2_Jun-W3	1 373	163 (134.127~222.605)		3.38 (3.295~3.465)		0.952
0.03	T2_Jul-W5	1 699	195.65 (154.677~276.903)		3.247 (3.152~3.342)		0.944
0.03	T2_Jul-W8	1 461	249.387 (207.384~325.071)		3.748 (3.652~3.844)		0.925
0.03	T2_Aug-W10	1 131	264.778 (226.521~332.589)		4.177 (4.091~4.262)		0.922
0.03	T2_Aug-W11	1 873	213.105 (161.458~313.735)		2.359 (2.239~2.478)		0.938
0.03	T2_Aug-W12	1 618	224.048 (180.305~309.111)		3.353 (3.241~3.466)		0.94
0.03	T2_Sep-W13	1 444	276 (208.21~405.716)		3.027 (2.906~3.147)		0.93
0.03	T2_Sep-W14	2 005	264.913 (208.082~369.891)		3.095 (2.973~3.217)		0.926
0.03	T2_Sep-W15	1 857	236 (176.252~357.029)		2.824 (2.7~2.947)		0.942
0.03	T2_Sep-W16	1 093	203.25 (165.96~278.162)		3.252 (3.135~3.369)		0.947
0.03	T2_Oct-W17	1 920	241.625 (188.659~339.364)		2.527 (2.397~2.657)		0.927
0.03	T2_Oct-W18	1 511	188.588 (142.652~281.781)		2.184 (2.06~2.308)		0.946
0.03	T2_Oct-W19	2 647	378.563 (305.248~501.995)		4.238 (4.149~4.327)		0.895
0.03	T3_Jun-W3	1 116	277.176 (228.289~362.118)		3.692 (3.592~3.792)		0.914
0.03	T3_Jul-W5	1 562	208.55 (162.419~298.632)		3.115 (3.015~3.215)		0.94
0.03	T3_Jul-W7	1 637	401.438 (318.252~539.869)		3.806 (3.699~3.913)		0.887
0.03	T3_Jul-W8	1 031	317.156 (263.912~409.823)		4.186 (4.092~4.28)		0.913
0.03	T3_Aug-W9	1 310	351 (282.208~468.979)		4.041 (3.947~4.136)		0.903
0.03	T3_Aug-W10	1 072	313.278 (264.604~396.995)		4.171 (4.072~4.269)		0.911
0.03	T3_Aug-W11	1 792	240.714 (174.2~376.142)		2.759 (2.644~2.874)		0.941
0.03	T3_Aug-W12	1 468	240.625 (193.74~328.415)		3.492 (3.391~3.593)		0.932

0.03	T3_Sep-W14	1 889	331.667 (270.438~434.349)	3.209 (3.076~3.341)	0.148 (0.13~0.166)	0.898
0.03	T3_Sep-W15	1 920	253 (188.716~380.169)	2.834 (2.709~2.958)	0.185 (0.164~0.205)	0.937
0.03	T3_Sep-W16	1 690	336.067 (241.843~518.329)	3.602 (3.503~3.7)	0.064 (0.056~0.072)	0.925
0.03	T3_Oct-W17	1 550	348.154 (289.26~445.907)	3.736 (3.616~3.856)	0.084 (0.072~0.097)	0.895
0.03	T3_Oct-W18	1 724	145.286 (119.444~199.61)	2.343 (2.219~2.466)	0.256 (0.233~0.28)	0.955
0.03	T3_Oct-W19	3 263	347.538 (276.549~472.399)	4.187 (4.096~4.277)	0.036 (0.03~0.042)	0.91
0.03	Y1_Jun-W3	1 458	188.391 (152.062~259.396)	2.764 (2.647~2.881)	0.176 (0.155~0.196)	0.943
0.03	Y1_Jul-W5	1 428	384.575 (317.777~493.556)	4.098 (3.994~4.202)	0.046 (0.039~0.053)	0.886
0.03	Y1_Jul-W7	1 222	391.387 (312.908~523.465)	4.064 (3.965~4.163)	0.041 (0.036~0.046)	0.893
0.03	Y1_Jul-W8	1 235	288.154 (246.772~359.699)	4.162 (4.07~4.254)	0.033 (0.029~0.037)	0.915
0.03	Y1_Aug-W10	1 165	216.136 (179.164~288.926)	3.725 (3.625~3.824)	0.063 (0.054~0.072)	0.944
0.03	Y1_Aug-W11	1 171	277.903 (226.988~367.517)	3.413 (3.298~3.529)	0.097 (0.085~0.11)	0.917
0.03	Y1_Aug-W12	1 468	321.292 (253.745~442.678)	3.846 (3.745~3.947)	0.053 (0.046~0.06)	0.917
0.03	Y1_Sep-W13	2 259	448.214 (300.616~728.152)	2.503 (2.371~2.635)	0.241 (0.218~0.264)	0.909
0.03	Y1_Sep-W14	1 744	263.636 (217.965~344.093)	3.038 (2.906~3.169)	0.167 (0.148~0.186)	0.919
0.03	Y1_Sep-W15	1 381	391 (271.211~621.842)	2.761 (2.626~2.895)	0.221 (0.197~0.245)	0.919
0.03	Y1_Sep-W16	1 230	452.667 (348.561~628.282)	3.668 (3.547~3.789)	0.09 (0.078~0.103)	0.886
0.03	Y1_Oct-W17	1 361	377.5 (281.511~547.491)	2.611 (2.469~2.753)	0.253 (0.229~0.278)	0.904
0.03	Y1_Oct-W18	1 353	231.048 (183.477~322.58)	3.531 (3.434~3.629)	0.067 (0.058~0.075)	0.937
0.03	Y1_Oct-W19	2 651	384.778 (315.169~500.025)	4.349 (4.261~4.436)	0.027 (0.023~0.031)	0.89
0.03	Y1_Oct-W21	2 116	463.261 (349.231~660.52)	4.193 (4.107~4.279)	0.027 (0.024~0.03)	0.891
0.03	Y2_Jun-W3	1 560	271.281 (228.838~347.185)	3.97 (3.873~4.068)	0.044 (0.038~0.05)	0.923
0.03	Y2_Jul-W5	1 504	232.885 (189.899~312.899)	3.4 (3.293~3.507)	0.084 (0.074~0.094)	0.932
0.03	Y2_Jul-W7	1 125	496.889 (384.709~685.01)	4.284 (4.187~4.382)	0.036 (0.03~0.041)	0.881
0.03	Y2_Jul-W8	1 530	142 (119.966~189.632)	2.962 (2.859~3.065)	0.112 (0.102~0.123)	0.959
0.03	Y2_Aug-W10	1 198	423.886 (341.693~558.574)	4.096 (3.993~4.2)	0.043 (0.037~0.048)	0.882
0.03	Y2_Aug-W11	1 508	271.619 (211.675~383.886)	3.406 (3.299~3.514)	0.084 (0.074~0.093)	0.928
0.03	Y2_Aug-W12	1 598	360.219 (288.097~481.834)	3.691 (3.582~3.8)	0.065 (0.057~0.073)	0.896
0.03	Y2_Sep-W13	1 699	259.04 (209.579~350.264)	3.653 (3.551~3.755)	0.066 (0.057~0.075)	0.928
0.03	Y2_Sep-W14	2 357	288.44 (226.545~399.739)	2.915 (2.785~3.046)	0.181 (0.161~0.202)	0.919
0.03	Y2_Sep-W15	1 511	254 (213.826~325.927)	3.769 (3.664~3.875)	0.068 (0.057~0.078)	0.924
0.03	Y2_Sep-W16	1 449	308.6 (258.42~395.053)	4.103 (4.006~4.199)	0.039 (0.034~0.044)	0.911
0.03	Y2_Oct-W18	1 415	281.714 (218.84~398.859)	3.597 (3.495~3.699)	0.068 (0.059~0.078)	0.926
0.03	Y2_Oct-W19	2 652	426.25 (322.901~604.87)	3.797 (3.695~3.9)	0.053 (0.047~0.059)	0.894
0.03	Y2_Oct-W21	3 178	445.12 (339.894~625.215)	3.97 (3.871~4.07)	0.043 (0.038~0.049)	0.89
0.03	Y3_Jun-W3	1 310	238.844 (197.327~313.3)	3.113 (2.991~3.236)	0.149 (0.13~0.168)	0.924
0.03	Y3_Jul-W5	1 549	346.05 (261.323~500.935)	3.79 (3.693~3.886)	0.049 (0.044~0.055)	0.916
0.03	Y3_Jul-W7	1 192	320.636 (266.121~414.712)	4.126 (4.03~4.222)	0.038 (0.033~0.043)	0.91
0.03	Y3_Jul-W8	1 528	314.438 (231.029~475.122)	3.375 (3.265~3.485)	0.092 (0.081~0.103)	0.927
0.03	Y3_Aug-W10	1 718	586.563 (406.077~913.732)	3.925 (3.826~4.024)	0.045 (0.04~0.051)	0.889
0.03	Y3_Aug-W11	1 531	328.122 (276.73~413.935)	4.051 (3.95~4.152)	0.042 (0.037~0.046)	0.9
0.03	Y3_Aug-W12	1 529	408.2 (324.116~549.71)	4.107 (4.008~4.205)	0.039 (0.034~0.045)	0.891
0.03	Y3_Sep-W13	1 817	473.75 (356.269~674.742)	3.947 (3.845~4.049)	0.05 (0.043~0.057)	0.887
0.03	Y3_Sep-W14	1 959	275.731 (218.942~377.979)	2.606 (2.468~2.745)	0.24 (0.217~0.263)	0.92
0.03	Y3_Sep-W15	1 476	244 (193.354~337.147)	2.88 (2.758~3.001)	0.159 (0.142~0.177)	0.927
0.03	Y3_Sep-W16	1 357	387.935 (313.203~514.283)	3.845 (3.721~3.968)	0.091 (0.077~0.105)	0.896
0.03	Y3_Oct-W18	1 342	260.276 (216.162~340.318)	3.802 (3.699~3.904)	0.059 (0.051~0.067)	0.926
0.03	Y3_Oct-W19	3 489	448 (306.188~717.75)	3.71 (3.619~3.802)	0.049 (0.043~0.055)	0.911

Notes: T1~3, samples from Lake Taihu; Y1~3, samples from Lake Yangcheng; CI, confidence interval.

Table S2 Genera with an average relative abundance >0.1%

Lake Taihu		Lake Yangcheng	
Genus	Average relative abundance	Genus	Average relative abundance
<i>Escherichia_Shigella</i>	23.24%	<i>Escherichia_Shigella</i>	18.26%
<i>Serratia</i>	10.98%	<i>Serratia</i>	8.19%
<i>Limnohabitans</i>	7.72%	<i>Flavobacterium</i>	6.83%
<i>Flavobacterium</i>	3.96%	<i>Limnohabitans</i>	5.52%
<i>Algoriphagus</i>	1.46%	<i>Polynucleobacter</i>	2.83%
<i>Polynucleobacter</i>	1.34%	<i>GpIIa</i>	1.42%
<i>Rhodobacter</i>	1.33%	<i>Rhodobacter</i>	1.19%
<i>Rheinheimera</i>	0.66%	<i>Rheinheimera</i>	0.89%
<i>Pelomonas</i>	0.51%	<i>Algoriphagus</i>	0.87%
<i>GpIIa</i>	0.49%	<i>Phycisphaera</i>	0.76%
<i>Bacillus</i>	0.47%	<i>Pseudomonas</i>	0.60%
<i>Streptococcus</i>	0.40%	<i>Opitutus</i>	0.41%
<i>Pseudomonas</i>	0.36%	<i>Pelomonas</i>	0.40%
<i>GpXI</i>	0.35%	<i>Armatimonas_Armatimonadetes_gp1</i>	0.36%
<i>Gemmatimonas</i>	0.32%	<i>Bacillus</i>	0.34%
<i>Fluviicola</i>	0.30%	<i>GpIV</i>	0.34%
<i>Opitutus</i>	0.27%	<i>3_genus_incertae_sedis</i>	0.30%
<i>Ohtaekwangia</i>	0.24%	<i>Streptococcus</i>	0.29%
<i>Phycisphaera</i>	0.23%	<i>Limnobacter</i>	0.29%
<i>3_genus_incertae_sedis</i>	0.14%	<i>Gemmatimonas</i>	0.24%
<i>Vogesella</i>	0.14%	<i>Aquabacterium</i>	0.14%
<i>Armatimonas_Armatimonadetes_gp1</i>	0.14%	<i>Fluviicola</i>	0.14%
<i>OD1_genus_incertae_sedis</i>	0.12%	<i>GpI</i>	0.13%
<i>Gp4</i>	0.12%	<i>Undibacterium</i>	0.13%
		<i>Luteolibacter</i>	0.11%

Table S3 Summary of environment variables

Site	Sample name	NH ₄ ⁺ -N (mg/L)	NO ₃ -N (mg/L)	TN (mg/L)	TP (mg/L)	COD (mg/L)	Tem (°C)	pH	DO (mg/L)	Chl- <i>a</i> (mg/L)	Algal density (cells/L)
T1	Jun-W3	0.327	0.153	0.58	0.009 5	16	26	9.73	9.5	0.002 8	315
T1	Jul-W5	0.161	0.136	0.3	0.021 33	11.11	31.1	9.8	8.27	0.002 1	365
T1	Jul-W7	0.147	0.17	1.41	0.013 5	13.19	30.9	9.51	7.92	0.001 7	227
T1	Jul-W8	0.186 8	0.12	1.73	0.005 6	12	29.1	8.89	8.14	0.003	424
T1	Aug-W9	0.055 2	0.195	0.41	0.009 5	12	31.1	9.74	8.65	0.002 5	252
T1	Aug-W10	0.169 1	0.053	0.96	0.052 8	11.43	31.5	8.91	8.46	0.002 9	155
T1	Aug-W11	0.199 9	0.195	0.7	0.009 5	7.69	32.7	9.3	9.5	0.001 3	70
T1	Aug-W12	0.158 9	0.254	1.32	0.068 89	19.23	31	8.8	9	0.001 7	328
T1	Sep-W13	0.223 9	0.203	1.42	0.073	13.46	26.2	8.82	8.48	0.002 4	274
T1	Sep-W14	0.244 4	0.271	1.34	0.020 1	9.49	25.8	8.45	7.31	0.002 5	224
T1	Sep-W15	0.155 4	0.135	0.6	0.036 4	21.43	23.7	9.26	9.79	0.001 8	112
T1	Sep-W16	0.108 5	0.109	0.83	0.044 5	17.65	23.1	8.9	7.9	0.001 9	67
T2	Jun-W3	0.172 8	1.542	1.68	0.033 1	7.27	26.4	8.35	8.55	0.003 2	230
T2	Aug-W10	0.153 7	0.993	1.36	0.076 4	11.43	29.1	8.83	6.97	0.007 9	650
T2	Aug-W11	0.126 3	0.852	1.32	0.052 8	11.54	30.9	8.41	7.27	0.003 9	440
T2	Aug-W12	0.128 1	0.664	0.91	0.077	23.08	28.7	8.72	8.95	0.006 2	990
T2	Sep-W13	0.097 2	0.126	0.75	0.081 1	11.48	26.2	8.64	8.66	0.006 2	640
T2	Sep-W14	0.179 4	0.263	0.81	0.073	6.32	25.5	8.34	8.22	0.005 5	1 100
T2	Sep-W15	0.222 2	0.289	0.75	0.072 96	8.77	23.9	8.55	8.82	0.008 2	1 080
T2	Sep-W16	0.065 5	0.34	1.39	0.097 4	11.76	24.4	8.56	8.7	0.006 8	1 200
T3	Jun-W3	0.279 8	2.773	3.56	0.127 7	7.27	26.3	7.93	7.46	0.009 6	380
T3	Jul-W7	0.176	0.278	0.75	0.111 9	8.79	29.5	8.83	7.84	0.009	1 620
T3	Aug-W8	0.197 6	0.086	1.36	0.151 3	28	29.4	7.76	7.51	0.018	254
T3	Aug-W10	0.242 7	1.592	2.1	0.104	17.14	31	8.83	8.93	0.007 8	400
T3	Aug-W11	0.100 7	1.124	1.67	0.068 6	7.69	31.5	8.58	7.59	0.005 4	550
T3	Aug-W12	0.138 3	0.954	1.36	0.077	3.85	29	8.68	8.9	0.003 6	680
T3	Sep-W14	0.133 2	0.553	1	0.056 7	6.32	26.4	8.59	8.25	0.006 5	2 500
T3	Sep-W15	0.237 6	0.041	0.65	0.085 1	14.04	23.5	8.69	9.08	0.008 7	2 340
T3	Sep-W16	0.097 7	0.254	3.25	0.174 6	23.5	24.2	8.53	9.37	0.007 7	640
Y1	Jun-W3	0.179 8	0.469	1.11	0.064 65	25.46	25.5	7.67	4.35	0.022	500
Y1	Jul-W5	0.318 4	0.818	3.62	0.151 3	14.16	30.1	7.99	6.49	0.024 9	710
Y1	Jul-W7	0.187	0.877	3.16	0.064 6	4.4	30.2	8.22	7.63	0.018 3	740
Y1	Aug-W8	0.035 4	0.902	1.71	0.115 8	20	31	8.59	8.92	0.030 2	1 120
Y1	Aug-W10	0.170 8	0.053	1.89	0.135 5	11.43	30.5	7.97	6.75	0.016 4	500
Y1	Aug-W11	0.087	0.587	0.77	0.123 7	15.38	27	7.86	6.54	0.008 1	360
Y1	Aug-W12	0.089 23	0.92	1.74	0.166 5	15.38	27.6	7.91	7.2	0.009 8	360
Y1	Sep-W13	0.057 9	0.869	1.1	0.109 6	13.4	27.2	8.01	6.92	0.007 2	300
Y1	Sep-W15	0.302 6	0.92	1.33	0.121 8	14.04	23.8	8.52	10.1	0.014 4	520
Y1	Sep-W16	0.151 5	0.928	1.19	0.162 4	13.73	22.9	7.86	7.37	0.011 4	378
Y2	Jun-W3	0.228 9	0.053	0.91	0.048 9	21.82	24.9	8.09	5.75	0.005 2	172
Y2	Jul-W5	0.262 5	0.719	2.16	0.178 8	12.39	29.8	8.33	5.98	0.014 6	397
Y2	Jul-W7	0.117	0.244	1.51	0.127 7	17.58	30.1	8.76	8.52	0.027 9	682
Y2	Aug-W8	0.185	0.893	1.49	0.190 7	16	30.8	8.3	6.33	0.011 5	466
Y2	Aug-W10	0.164	0.04	1.63	0.198 5	15.24	31	8.66	7.99	0.028 1	489
Y2	Aug-W11	0.121 2	0.749	0.56	0.111 9	11.54	32.4	8.57	9.18	0.013 1	473
Y2	Aug-W12	0.169 1	1.414	1.97	0.170 6	15.38	28.9	8.82	9.03	0.019 1	572
Y2	Sep-W13	0.194 8	1.208	1.91	0.207 2	15.38	26.2	8.45	6.8	0.013 9	263
Y2	Sep-W15	0.14	1.355	1.59	0.154 3	12.5	24	8.44	9.2	0.021 6	475
Y2	Sep-W16	0.104 9	1.602	1.63	0.150 2	11.76	24	8.59	8.95	0.018 3	445
Y3	Jun-W3	0.271	0.694	1.11	0.017 88	14.55	24.6	8.17	6.09	0.014 1	512
Y3	Jul-W5	0.053 42	0.053	0.86	0.084	10.62	30.1	8.16	6.97	0.013 9	1 515
Y3	Jul-W7	0.171	0.12	1.21	0.060 7	8.79	29.9	8.72	8.39	0.022 5	1 682
Y3	Aug-W8	0.066	0.045	0.95	0.080 4	32	30.4	8.37	6.89	0.016 5	1 273
Y3	Aug-W10	0.122 9	0.046	1.04	0.111 9	15.24	31.2	8.56	7.6	0.017 4	1 750
Y3	Aug-W11	0.087	0.169	0.34	0.037 1	15.38	31.8	8.36	6.03	0.015	1 108
Y3	Aug-W12	0.165 7	0.203	0.68	0.072 9	19.23	28	8.72	6.43	0.012	599
Y3	Sep-W13	0.152	0.22	0.98	0.081 1	15.38	25.6	8.39	7.56	0.024 7	1 572
Y3	Sep-W15	0.155 4	0.169	0.72	0.073	19.61	24.2	8.4	10.8	0.048 3	720
Y3	Sep-W16	0.149 7	0.544	1.85	0.072 9	15.69	23.5	8.64	8.24	0.014 1	974

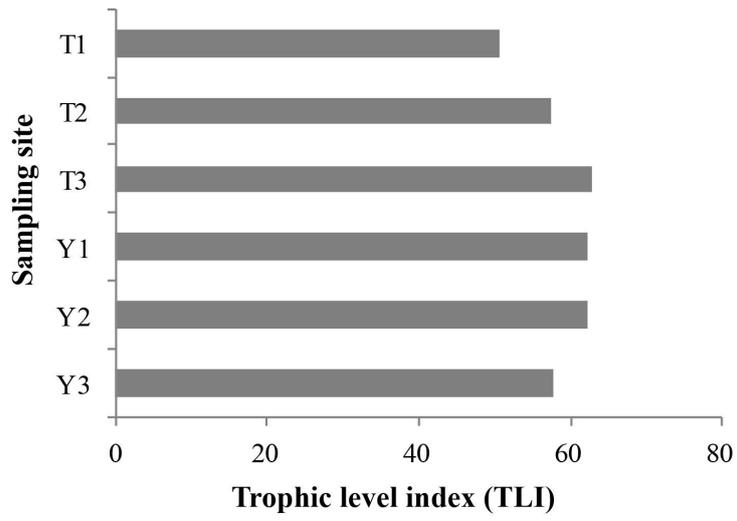


Fig.S1 Trophic level index for six sites in the two lakes