

# Benthic Bacteria Community Changes in Responses to Different Organic Resources from Macrophyte- and Algae-Dominated Areas of Lake Taihu, China

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## Abstract

Carbon resources play an important role in affecting the benthic bacterial community in shallow lakes. In this study, pyrosequencing was applied to compare bacteria phylogenic profile in incubated sediments with normal and exchanged organic detritus in macrophyte-dominated East Lake Taihu and algal-dominated Meiliang Bay. We observed significant bacteria species variations in sediments from two bays, regardless of treatments. RDA (Redundancy Analysis) analysis showed that sediment characteristics, especially concentrations of total nitrogen might account for this differentiation. Besides, algal-dominated Meiliang Bay sediment with addition of Vallisneria detritus exhibited higher bacterial species variations than the sediment amended with Microcystis detritus. To the contrary, sediments from macrophytedominated East Lake Taihu shared similar bacteria profile at all taxonomic levels and grouped together in MDS (multidimensional scaling) plots over the treatments with Vallisneria or Microcystis detritus addition into the sediment. We speculated that the different degradability of macrophyte detritus and algal detritus led to varied bacterial responses to exchanged organic resources and ultimately, the amounts, nutrient availability and degradability of organic resources may be main reasons for benthic bacteria community structure differentiation between the two states in shallow lakes.

## **Keywords**

Macrophyte-Dominated Lake, Algal-Dominated Lake, Benthic Bacteria, Pyrosequencing, Organic Resources

## 1. Introduction

Shallow lakes can have two alternative equilibria: a clear state dominated by aquatic vegetation, and a turbid state characterized by high algal biomass [1] [2]. These two aquatic ecosystems differ dramatically from the very beginning of the food web-producers as macrophyte or phytoplankton respectively [3] [4]. The producers support the lives including bacteria in water column, causing significant differences in bacterioplankton community composition between two ecological states [5] [6]. The detritus of dead phytoplankton and macrophyte would also sink into the sediment, and serve as important carbon resources supporting benthic bacteria growth [7] [8] [9] [10], accompanying with benthic bacteria community differentiation. Shao et al. [11] explored these benthic bacteria community structure varied both in the surface sediment and also across vertical gradients in two ecological states [12], using denaturing gradient gel electrophoresis (DGGE) in conjunction with sequence analysis (phylogenetic analysis). However, the low resolution of phylogenetic information revealed by DGGE cannot give a reasonable explanation. Pyrosequencing, using the detection of released pyrophosphate (PPi) during DNA synthesis, is an alternative technology for much more detailed characterization of nucleic acids than DGGE [13] [14].

Besides, Jones and Lennon developed a theoretical model demonstrating the microbial dormancy strategy. They reported that even if a huge range of microbial types are present, only few of them are adapted to local organic resource in most ecosystems, the remaining majority of species stay rare as dormant [15]. Those rare species generate a seed bank, which comprises individuals prepared to be resuscitated following environmental changes [16], in our case, the input of different organic resources. For the above information, we assume that the dominant benthic bacteria from these two alternative equilibria are acclimatized to their different local organic resources as mainly phytoplankton detritus and macrophyte detritus, and eventually result in benthic bacteria community composition differentiation. In that way, if we exchange their carbon resources, dramatically bacterial species variation with exchanged dominant species would be observed.

To testify this hypothesis, we sampled sediment cores from these two ecological ecosystems and incubated them with exchanged organic resources as *Vallisneria* sp. detritus and *Microcystis* sp. detritus, respectively. Pyrosequencing was carried out for the benthic bacteria inventory. Over 9000 16S rRNA gene fragment sequences from each of four sediment samples were obtained. This lab experiment will help us understanding how functional benthic bacteria shift during Lake Regime shift from a clear state dominated by aquatic vegetation to a turbid state characterized by high algal biomass and give us hints for lake management.

#### 2. Experimental

### 2.1. Materials and Methods

#### 2.1.1. Study Area

Lake Taihu, as the third biggest lake in China, holds a surface area of ~2338 km<sup>2</sup> and an

average depth of 1.9 m. Besides, it exhibits spatial heterogeneity in physicochemical conditions and plankton community structure, with macrophyte- and alage-dominated zones separated by clearly defined boundaries, creating the right model for studying these two aquatic ecosystems. The lake is located in the Yangtze Delta in eastern China (30°55'N - 31°32'N, 119°52'E - 126°36'E). The two sampling sites are located in East Lake Taihu (31°10'02'', 120°22'57'') and Meiliang Bay (31°28'39'', 120°12'35'') in Wuxi. East Lake Taihu is a typical submerged macrophyte-dominated zone with high biomass of *Vallisneria* sp., while Meiliang Bay, located in the northern part of the lake, is characterized by high densities of *Microcystis* sp. and an absence of submerged macrophytes [17].

#### 2.1.2. Experimental Settings

Six intact sediment cores (inner diameter = 15 cm) including 3 form East Lake Taihu and the other 3 from Meiliang Bay were sampled at a depth of 20 cm and transported to the laboratory on August 22, 2012. The coreliners used for sampling consisted of transparent acrylic cylinders ( $15 \times 33$  cm, inner diameter  $\times$  height; sediment surface equivalent to 176.7 cm<sup>2</sup>) that were capped at both ends with rubber stoppers. After the acclimation and sediment stabilization period of 24 h, each core from two different lake areas was taken out of the system and sampled to provide an initial state (regarded as EB and MB), others were used as incubation chambers. We added Microcystisdetritus to one sediment chamber from Meiliang Bay and Vallisneria detritus to one sediment chamber from East Lake Taihu as normal state and the control (regarded as Meiliang Bay sediment with Microcystisdetritus, MM and East Lake Taihu sediment with Vallisneriadetritus, EV respectively). The rest two chambers were added with exchanged detritus (Meiliang Bay sediment with Vallisneriadetritus, MV and East Lake Taihu sediment with Microcystis detritus, EM respectively). The biomass added was all 24.2 g to reflect the natural phytoplankton biomass deposition found in Lake Taihu and to be comparable. All the chambers were incubated at 28.5°C for 5 days. Both *Vallisneria* sp. and Microcystis sp. were collected from Lake Taihu in according sampling sites and prepared as detritus by freeze-drying and grinding.

#### 2.1.3. Analysis of Environmental Parameters

After incubation, pH was measured immediately for surface sediments (0 - 1 cm). We also sampled the surface sediments (0 - 1 cm). The freeze-dried sediments were homogenised with a mortar and pestle and passed through a No. 10 sieve (2 mm sieve mesh openings). Chlorophyll *a* (Chl *a*) was extracted from freeze dried samples of approximately 1 g by leaching for 24 h in 90% acetone at 4°C in the dark. Chl *a* content was then analyzed using an ultraviolet spectrophotometer [18] [19]. Analysis of sediment total organic carbon concentrations (TOC), total nitrogen concentrations (TN) and total phosphorus concentrations (TP) were processed using an elemental analyzer (EA3000, EuroVector).

#### 2.1.4. DNA Extraction, 16 S rRNA Construction and Pyrosequencing

The MoBioUltraClean Soil DNA isolation kit (MoBio Laboratories, USA) was used to

extract total microbial community DNA from approximately 1 g of material per sample following the protocol of the manufacturer. DNA concentrations were qualified using NanoDrop spectrophotometer (NanoDrop Technologies Inc, DE). The V3-V5 region of the 16S rRNA gene (E. coli position 357 to 926) was targeted by barcoded primers for their high variability [20]. The sequences of the partial 16S rRNA genes were detected using a GS-FLX 454 sequencer (Roche). Fastaq files containing sequences were submitted to NCBI Sequence Read Achive (SRX 1283592).

#### 2.2. Sequences and Statistic Analysis

Raw sequence reads were retrieved and subjected to the PyroNoise algorithm for removal of 454 sequencing errors [21]. Furthermore, primer sequences were trimmed and reads only between 200 bp (not including primer sequences) to 1000 bp were included. Sequences with chimeras were excluded using the UChime algorithm on the Mothur platform [22] [23]. Pairwise distances between aligned sequences were calculated. Sequences lower than 97% similarity (or 0.03 distance) were clustered into unique operational taxonomic units (OTUs) in Mothur. RDP Classifier was used to assign taxonomy [24]. Alpha diversity analysis like Shannon index and rarefaction curve was performed by QIIME [25]. Beta diversity was calculated based on Bray-Curtis similarity matrix [26], and the resulting matrix was used for multidimensional scaling (MDS) of the samples by PRIMER v5.0 software. To evaluate the influences of environmental variables on OTU variation in sediment samples, redundancy analyses (RDA) were performed using CANOCO 5.0 (SCIENTIA Software), for Detrended Correspondence Analysis (DCA) run on species variables indicated that the longest gradient was <3. Forward selections were performed for a selection of restrictive factors. The significance of the canonical axes together was assessed in permutation tests with 499 unrestricted Monte Carlo permutations.

#### 3. Results

#### **3.1. Microbial Diversity**

A total of 45,438 effective reads was produced by pyrosequencing analysis of 16 S rRNA gene amplicons. 5270 operational taxonomic units (OTUs) at 97% sequence similarity were finally obtained. The rarefaction curves constructed on the basis of 16S rRNA gene sequences nearly reached saturation level for the samples, suggesting that nearly entire microbial community was well covered (**Figure 1**).

The phylogenetic affiliation of microbes was assigned to 17 bacterial phyla, 3 candidate divisions at the phylum level (Figure 2) and distributed into 65 categories at class level, 182 categories at family level and 314 categories at genus level. All the sediments shared the same dominant species at phylum level as *Proteobacteria* (33.0% - 44.2%), *Acidobacteria* (8.5% - 13.3%), *Actinobacteria* (2.5% - 10.1%), *Choloflexi* (2.4% - 5.1%), *Nistrospira* (0.9% - 2.6%), *Firmicutes* (0.8% - 2.3%).Those are common phyla in lake sediments [27] [28]. Bar chart displaying the bacterial community composition of each sample at class level was also showed below (Figure 3). East Lake Taihu sediment



**Figure 1.** Diversity of microbial communities in sediment samples. EB represents non-incubated sediment sample from East lake Taihu. EV represents incubated sediment sample from East lake Taihu with *Vallisneria detritus*. EM represents sediment sample from the East lake Taihu incubated with *Microcystis* detritus. MB represents non-incubated sediment sample from Meiliang Bay. MM represents incubated sediment sample from Meiliang Bay with *Microcystis* detritus. MV represents sediment sample from Meiliang Bay incubated with *Vallisneria* detritus.



**Figure 2.** Visual representation of microbial distribution in samples at the phylum level, giving the 20 recognized taxa in all samples with unidentified taxa included as 'Other'. EB represents non-incubated sediment samples from East lake Taihu. EV represents incubated sediment sample from East lake Taihu with *Vallisneria* detritus. EM represents sediment sample from the East lake Taihu incubated with *Microcystis* detritus. MB represents non-incubated sediment from Meiliang Bay. MM represents incubated sediment from Meiliang Bay with *Microcystis* detritus. MV represents sediment from Meiliang Bay incubated with *Vallisneria* detritus.



**Figure 3.** Bar chart displaying the bacterial community composition at class level. "Other" refers to unidentified class with no previous report of former taxa. EB represents non-incubated sediment sample from East lake Taihu. EV represents incubated sediment sample from East lake Taihu with *Vallisneria* detritus. EM represents sediment sample from the East lake Taihu incubated with *Microcystis* detritus. MB represents non-incubated sediment from Meiliang Bay. MM represents incubated sediment from Meiliang Bay with *Microcystis* detritus. MV represents sediment from Meiliang Bay incubated with *Vallisneria* detritus.

bacteria profiles with different treatments and with time showed similar patternat class level. However, bacteria constitution from Meiliang Bay incubated sediment with *Vallisneria* detritus showed distinct pattern with that from the other two Meiliang Bay originated sediments.

A hierarchical cluster tree and a multidimensional scaling (MDS) plot was drawn using PRIMER 5.0 (Figure 4). These two figures showed a visual representation of the similarity of sediments based on their bacterial community composition at the 97% OTU level. The hierarchical cluster tree showed that sediments from the different ecological state were separated to different clusters (Figure 4(a)). Meiliang Bay sediment

sample incubated with Vallisneria sp. took another branch, apart from the other two Meiliang Bay sediment samples. In MDS plot (Figure 4(b)), we also noticed that all sediment samples from macrophyte-dominated East Lake Taihu were grouped together and dramatic species variations occurred among algae-dominated Meiliang Bay sediment samples incubated with exchanged organic resources.

## 3.2. Redundancy Analysis

We prepared a RDA biplot of the samples based on OUT level and 4 environmental variables (TN, TP, Chla, pH) to reveal the relationships between bacteria community changes and environmental parameters (Figure 5). We observed significant differences in environmental characteristics in sediments originated from the two ecological sites (P < 0.05). Sediments originated from algal-dominant area hold a higher average of TOC, TN, TP and Chla contents and a lower pH content than submerged macrophytedominated sediments.

In the graph, sediment samples from algae-dominated Meiliang Bay plotted on the right of axis 2, while Sediment samples from macorphyte-dominated Meiliang Bay plotted on the other side of axis 2. This RDA graph also demonstrated that TN played a significant role in the bacterial community variation in all sediments (p < 0.05). The eigenvalues of the first and second axis were 0.3946 and 0.2334, respectively, and these 2 axes explained 63.8% of the bacterial OTU variation in sediments. Permutation test on all axes showed that pseudo-F = 1.8, p = 0.054.

#### **3.3. OTU Variations**

At OTU level, 30% sequences was assigned to no more than 1% of the OTUs at 97% similarity levelin each sediment, other OTUs were found less than 20 sequences (<0.37%). The large number of highly diverse, low-abundance OTUs constitutes a "rare biosphere" that might be inactive as a seed bank. SIMPER analysis was used to identify OTU variations in different sediment samples. OTUs contributed most to between-site



Figure 4. Visual representation of the similarity of sediments based on their bacterial community composition at the 97% OTU level, including a. a MDS plot and b. a hierarchical cluster tree. Circles represent sediment samples from East lake Taihu. Triangles represent sediment samples from Meiliang Bay. Whites represent sediments without incubation. Blacks represent sediments incubated with Vallisneria detritus, and slashes represents incubated with Microcystis detritus.





**Figure 5.** Redundancy analysis of biplots showed variable composition of bacteria in relation to the important environmental factors in different sediment samples. Circles represent sediment samples from East lake Taihu. Triangles represent sediment samples from Meiliang Bay. Whites represent sediments without incubation. Blacks represent sediments incubated with *Vallisneria* detritus, and slashes represents incubated with *Microcystis* detritus. Environmental variable marked with asterisks was significant (p < 0.05).

differentiation and their population densities based on phylogenetic information in each sediment sample were showed in **Table 1**. Similar species differentiations were observed in our incubated control sediment samples. Some of these OTUs stayed as top 1% OTUs in both two sediments at different ecological state, however in a distinct population density based on phylogenetic information. We also noticed that OTU00021 and OTU00019 stayed as rare species in Meiliang Bay sediment, and as dominant species in East Lake Taihu sediment. OTU00020 and OTU00024, to be opposite, stayed as rare species in East Lake Taihu sediment, and as dominant species in Meiliang Bay sediment.

OTUs contributed most to incubated Meiliang Bay sediments with *Microcystis* detritus and *Vallisneria* detritus and their population density in each sediment sample were showed in **Table 2**. OTU00005, OTU00004, OTU00001, OTU0008 and OTU00021, which had high contribution to between-site bacteria species differentiation, also contributed significantly to Meiliang Bay sediments added with varied organic resources. There are some OTUs stayed a relatively high population density in sediment from both sites and got an even higher population density in Meiliang Bay sediments with altered organic resources.

We didn't analyze the species variations between East Lake Taihu sediments with exchanged organic resourse for Bray-curtis dissimilarity calculated between them was less than the dissimilarity between the control and the background value.

#### 4. Discussion

Our bacteria inventory by pyrosequencing demonstrated significant between-origin

**Table 1.** SIMPER analysis results displaying 10 OTUs contributes most to bacterial community differentiation between macrophyte-dominant East lake Taihu and algal-dominant Meiliang Bay and their population density based on phylogenetic information in different sediment samples. EB represents non-incubated sediment sample from East lake Taihu. EV represents incubated sediment sample from East lake Taihu. By represents non-incubated sediment sediment from Meiliang Bay. MM represents incubated sediment from Meiliang Bay with *Microcystis* detritus.

OTU	Assignation	EB (%)	MB (%)	Contribution (%)	EV (%)	MM (%)
OTU00001	Acidobacteria Gp17	3.53	1.25	2.03	2.39	0.90
OTU00005	Unidentified Bacteria	1.05	2.27	1.25	0.79	2.08
OTU00021	Actinobacteria	1.50	0.19	1.20	1.52	0.24
OTU00020	Betaproteobacteria	0.34	1.50	1.15	0.25	0.68
OTU00004	Desulfobacteraceae	0.81	1.83	1.03	1.34	1.39
OTU00008	Proteobacteria	1.79	0.70	0.96	1.30	0.76
OTU00019	Unidentified Bacteria	1.14	0.22	0.83	1.27	0.46
OTU00016	Betaproteobacteria	0.42	1.23	0.81	1.23	2.71
OTU00024	Betaproteobacteria	0.36	1.09	0.73	0.18	0.47
OTU00022	Betaproteobacteria	0.63	1.33	0.71	0.68	0.90

**Table 2.** SIMPER analysis results displaying OTUs contributes most to bacterial community differentiation between algal-dominant Meiliang Bay sediment incubated with *Vallisneria* detritus and with *Microcystis* detritus and their population density based on phylogenetic information in different sediment samples. EB represents non-incubated sediment sample from East lake Taihu. EV represents incubated sediment sample from East lake Taihu with *Vallisneria* detritus. MB represents non-incubated sediment from Meiliang Bay. MM represents incubated sediment from Meiliang Bay with *Microcystis* detritus. MV represents sediment from Meiliang Bay incubated with *Vallisneria* detritus.

OTU	Assignation	MV	ММ	Contribution	MB	EB	EV
		(%)	(%)	(%)	(%)	(%)	(%)
OTU00005	Unidentified Bacteria	2.92	2.08	1.40	1.25	3.53	2.39
OTU00004	Desulfobacteraceae	2.11	1.39	1.05	1.83	0.81	1.34
OTU00001	<i>Acidobacteria</i> Gp17	1.56	0.90	0.86	1.25	3.53	185
OTU00014	Acidobacteria Gp6	0.99	0.51	0.54	1.04	0.81	0.52
OTU00028	Acidobacteria Gp6	1.02	0.59	0.53	0.79	0.65	0.28
OTU00078	Unidentified <i>Bacteria</i>	0.81	0.39	0.44	0.29	0	0.12
OTU00008	Proteobacteria	0.97	0.76	0.44	0.70	1.79	1.30
OTU00052	Unidentified <i>Bacteria</i>	0.77	0.39	0.42	0.56	0.43	0.56
OTU00011	Unidentified <i>Bacteria</i>	1.01	0.24	0.41	1.05	1.18	0.41
OTU00021	Actinobacteria	0.60	0.24	0.36	0.19	1.50	1.52

species variations in algal-dominant Meiliang Bay originated sediments and macrophyte-dominant originated East Lake Taihu sediments, regardless of their different treatments. That result was possibly due to the different sediment characteristics between the two states. In the macrophyte-dominated state of East Lake Taihu, the organic fractions of the sediment mainly formed from the detritus of large vascular plants [11] [12]. In contrast, cyanobacteria detritus is also an important organic resource in sediment from algal-dominated lake area [29]. The higher primary production in cyanobacteria dominated areas of the lake increases the amount of organic resources. Besides, macrophytes were characterized as low N concentrations relatively to those of phytoplankton [30], which means their differences in nutrient availability. RDA analysis also showed that TN concentrations changes might have significantly impact on this between-origin differentiation.

There were no significant differences in sediment characteristics in incubated and non-incubated sediments, indicating that the nutrients we added into the sediments was much smaller compared to the intrinsic nutrients of sediments. All sediment samples from macrophyte-dominated East Lake Taihu also shared similar bacteria profile at all taxonomic levels and grouped together in MDS plots. However, in spite of similar sediment characteristics, the addition of Vallisneria detritus to algal-dominated Meiliang Bay sediment caused relatively large bacterial community changes comparing to the control and the background. Two main reasons may account for these different benthic bacteria responses. First is the different food quality of macrophyte and phytoplankton to bacteria. Comparing to labile phytoplankton, macrophyte was a less degradable resource for their complex tissue and high contents of lignin and fiber [31]. Certain bacteria are mores specialized at complex substrate decomposition with a more complex process, eg. The excretion of extracellular enzymes like cellulose [32] [33]. The addition of Vallisneria detritus to Meiliang Bay sediment made them more competitive, resulting in a elevated population density. Second, besides macrophyte-derived material, phytoplankton also contributed to sediment organic fraction in macrophyte dominated area [34] [35]. The identity and importance of the source materials that drive bacteria mineralization in sediments likely depends on a combination of their relative amounts and degradability [36]. In that case, phytoplankton detritus is also an accustomed small fraction of substrate for benthic bacteria in East Lake Taihu, and small amount of Microcystis detritus was regarded as normal condition. Therefore, we observed low bacteria community composition dissimilarity between non-incubated sediment, incubated sediment with Microcystis detritus and with Vallisneria detritus.

Detailed OTUs variations furtherly demonstrated how benthic bacteria in Meiliang Bay responses to *Vallisneria* detritus amendment. OTU00005, OTU00004 and OTU0008, which had high contribution to between-origin bacteria species, became higher in population density based on phylogenetic information with input of *Vallisneria* detritus, possibly for their better use of macrophyte derived organic resources. OTU00021, dominant in East Lake Taihu but rare in Meiliang Bay sediment, was triggered into activity with the amendment of *Vallisneria* detritus. Rest OTUs staying as top 1% dominant bacteria in both Meiliang Bay and East Lake Taihu sediment might be able to decomposing both macrophyte detritus and phytoplankton detritus, while the addition of macrophyte detritus made them more competitive. We speculated that these OTUs were potentially specialized at macrophyte detritus degradation and their enhanced activity might responsible for the whole bacteria community composition changes with regard to macrophyte detritus addition in Meiliang Bay sediment.

## 5. Conclusion

In all, at least part of our hypothesis was true. The amounts, nutrient availability and the degradability of organic resources might have a profound effect on benthic bacteria community composition and ultimately caused benthic bacteria community differentiation in two ecological states.

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