The high resilience of the bacterioplankton community in the face of a catastrophic disturbance by a heavy Microcystis bloom

Huabing Li¹,², Peng Xing¹ & Qinglong L. Wu¹

¹State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography & Limnology, Chinese Academy of Science, Nanjing, China; and ²Graduate School of Chinese Academy of Science, Beijing, China

Abstract

The accumulation and breakdown of cyanobacterial blooms often causes catastrophic changes in the aquatic fauna of lakes. Recovery from these changes is always prolonged. However, little is known about the resilience and recovery of the bacterioplankton community composition (BCC) after this type of disturbance. In this study, we examined the resistance and resilience of the BCC following a Microcystis bloom disturbance with in situ mesocosm experiments with varying levels of Microcystis biomass ranging from 75 to 13 012 μg L⁻¹, as measured by the chlorophyll-a concentration, over 13 days. The BCC was assessed with denaturing gradient gel electrophoresis of 16S rRNA genes, followed by cloning and sequencing of the selected samples. We observed a strong shift of the BCC from the control on the first day of the bloom disturbance. The most dramatic change in the BCC occurred in the mesocosm with the highest Microcystis biomass, in which the dissolved oxygen varied strongly. However, we observed a rapid recovery of the BCC from day 7, when most of the investigated environmental factors had also recovered. On day 12, the BCC in the different mesocosms resembled the control at day 0 to a greater extent than during the accumulation and breakdown of the Microcystis bloom. Our study indicated that although the resistance of the BCC is low, the resilience is high, even following a catastrophic disturbance by a Microcystis bloom in a freshwater lake.

Introduction

Bacteria are important for biogeochemical cycling and are subject to different types of disturbances. It is interesting to know how the bacterial community composition (BCC) responds to disturbances as this could help to predict the responses of ecosystem processes to environmental changes on the basis of the microbial community composition (Allison & Martiny, 2008). While the topic of disturbance responses of BCC is attracting more attention, few studies have produced consistent results. Certain studies suggest that disturbed microbial communities cannot recover or that the recovery is slow (Dorigo et al., 2010; Dethlefsen & Relman, 2011). Other research shows that the BCC in grass soils is resistant to drying–rewetting regimes, whereas the BCC in oak soils is not (Fierer et al., 2003). However, additional studies have shown that the responses of aquatic bacterial communities to disturbance, which disrupts chemical and physical parameters, such as the concentrations of dissolved oxygen (DO) and nutrients (nitrogen and phosphorus) in the water column, vary with the initial community composition (Yannarell et al., 2007; Jones et al., 2008; Shade et al., 2008, 2010a, b) and that all of the bacterial communities can recover rapidly (Shade et al., 2011).

Owing to eutrophication, cyanobacterial blooms, especially Microcystis blooms, are becoming a widespread problem in many lakes (Paerl et al., 2001; Lehman, 2007; Wu et al., 2007). The accumulation and breakdown of cyanobacterial blooms often causes changes in the BCC within in situ enclosures through the production of dissolved organic matter (DOC), decreased pH,
and decreased DO in the water column; these differences were also evident with different levels of Microcystis biomass (Li et al., 2011). However, little is known about the recovery of the BCC after the recession of Microcystis blooms in the natural environment. Unlike other experiments on disturbance focusing on one or two specific factors, the pulse effect of Microcystis blooms on lake ecosystems represents a type of natural disturbance. We analysed the BCC before, during the breakdown and after the recession of a Microcystis bloom using in situ near-natural mesocosm (50 × 180 m and 1.3 m in average depth) experiments with varying levels of Microcystis biomass ranging from 75 to 13 012 µg L⁻¹ chlorophyll-a (Chl a). The highest Microcystis biomass represents a catastrophic disturbance, as this biomass causes anaerobic conditions that result in the death of other planktonic species. The BCC was assessed with PCR–denaturing gradient gel electrophoresis (PCR-DGGE) of the 16S rRNA genes, followed by cloning and sequencing of the selected samples. We observed the low resistance and high resilience of the bacterioplankton community during a disturbance caused by a catastrophic Microcystis bloom.

**Materials and methods**

**Experimental design**

The in situ mesocosm experiment was conducted in 3 large enclosures (each 50 × 180 m and 1.3 m in average depth, Supporting information, Fig. S1) in Gonghu Bay (31°27′40.5″N, 120°21′32.7″E), in the northeastern part of Lake Taihu. The experiment was performed from 16 July through 28 July 2009. Each of the three enclosures was constructed from high-density nylon. The top of each was enclosed with floats extending approximately 35 cm in water depth. The bottom was secured with iron chains embedded at a depth of approximately 20 cm above the lake surface, and the bottom was secured with other large particles (Li et al., 2011). The enclosures were also evident with different levels of Microcystis biomass (97 µg L⁻¹ of chl a). The treatment C enclosure was attached to its 5-m polycarbonate filter (Millipore) to remove phytoplankton and other large particles (Li et al., 2011). The filters were stored at −80 °C prior to nucleic acid extraction. The total nucleic acids were extracted and purified from the bacteria as described previously (Li et al., 2011).

**Measurement of physiochemical parameters**

During the experiment, the concentrations of DO, pH, conductivity (COND) and water temperature (T) in the experimental enclosures were determined daily using a Multi-Parameter Water Quality Sonde (YSI 6600) at three sites located along a vertical transect in each of the three enclosures. Depth-integrated water samples (5 L) for the analysis of other chemicals and the characterisation of the bacterial community were collected daily during the first 2 days and then every 2 days until day 9. The two final samples were collected 3 days apart. Specifically, the samples were collected on 16 July (day 0, at approximately 10:00 hours), 17 July (day 1), 19 July (day 3), 21 July (day 5), 23 July (day 7), 25 July (day 9), and 28 July (day 12). All samples in each of the three enclosures were collected at the three sites and mixed. The water samples were stored at 4 °C and taken to the laboratory within 2 h for further processing. The total phosphorus (TP), total nitrogen (TN), DOC, ammonium (NH₄-N), nitrate (NO₃-N), nitrite (NO₂-N), ortho-phosphorus (PO₄-P), and Chl a concentrations were measured according to standard methods (Greenberg et al., 1992).

**Bacterial biomass collection and DNA extraction**

The bacterial biomass was collected from a 200-mL subsample of water onto 0.2-µm polycarbonate filters (Millipore) after prefiltration through a 5-µm polycarbonate filter (Millipore) to remove phytoplankton and other large particles (Li et al., 2011). The filters were stored at −80 °C prior to nucleic acid extraction. The total nucleic acids were extracted and purified from the bacteria as described previously (Li et al., 2011).

**Bacterial community analysis by 16S rRNA gene-based PCR-DGGE analysis**

We used the mixed DNA from the samples collected from the three respective enclosures at day 0 as the PCR template for day 0 in the subsequent DGGE analysis. The bacterial 16S rRNA genes were amplified and assessed with PCR-DGGE according to previously described methods (Muyzer et al., 1993). In brief, the 16S rRNA genes were amplified using the universal bacterial primers 341f (5′-CCTACGGGAGGCAGC AG-3′) with a GC clamp attached to its 5′-end and 907r (5′-CGGTCAATTCMTT- GAGTTT-3′; Muyzer et al., 1993). The PCR amplifications...
were performed in a total volume of 50 μL containing the following reagents (final concentrations): 0.5 mM of each primer, 1× buffer, 2.0 mM MgCl₂, 250 mM dNTPs, 2.5 U of Taq DNA polymerase (TaKaRa, Japan), 10 ng of extracted DNA, and DNase- and RNase-free water. The amplification was performed in an automated thermocycler (PTC 200-cycler, MJ Research) using the following touchdown protocol: one cycle at 94 °C for 5 min, 30 cycles of 1 min at 94 °C, 1 min at 65–55 °C (reducing the temperature by 1 °C cycle⁻¹ for 10 cycles plus 20 cycles at 55 °C), and 1 min at 72 °C, followed by a final extension at 72 °C for 5 min (Muyzer et al., 1993). The sizes of PCR products were verified on a 1.2% agarose gel and quantified using PicoGreen (Molecular probes, Invitrogen, Shanghai, China). Approximately 800 ng of DNA was loaded onto a 6% (w/v) polyacrylamide gel (acrylamide and N,N'-methylene bisacrylamide at a ratio of 37.5 : 1), with a denaturing gradient that ranged from 45% to 70% (where 100% is defined as 7 M urea and 40% deionised formamide). The electrophoresis was performed in a DGGE-2001 system (CBS Scientific) in 1× TAE running buffer [40 mM Tris (pH 7.4), 20 mM sodium acetate, and 1 mM EDTA] at 100 V and 60 °C for 16 h. The gels were stained with SYBR Green I (1 : 10 000 dilution; Molecular Probes) for 30 min and photographed in a Fluor-S MultiImager (Bio-Rad). The DGGE banding patterns were analysed using the GelCompare II software package (Applied Maths, Kortrijk, Belgium) after digitalisation of the DGGE gels.

The DGGE patterns were subjected to a hierarchical cluster analysis with PRIMER 5 software (http://www.primer-e.com/).

Sequence data and phylogenetic analysis
To analyse the recovery of BCC following Microcystis blooms, seven clone libraries were generated from the obtained bacterial 16S DNA templates (one at day 0, three at day 3, and three at day 12), which were selected according to the changes in the chemical parameters and BCC. The bacterial amplifications for sequence analysis were generated from 16S rRNA gene using the primers 341F and 907r. The PCR amplification was conducted as described above. The purified PCR products were ligated into the pGEM-T Easy Vector (Promega) and then transformed into Escherichia coli DH5α according to the manufacturer’s instructions. Subsequent to verification using PCR amplification (M13F and M13R primers), the positive clones were randomly selected for sequencing, which was performed at the Invitrogen Company (Shanghai, China).

All sequences were compared against chimeras with Mallard (Ashelford et al., 2006). The remaining sequences were clustered in operational taxonomic units (OTUs) with a 0.03 cut-off value using the ‘cluster’ command in the MOTHUR software (Schloss et al., 2009). The sequence of each OTU was chosen as a representative and was blasted against the NCBI (http://www.ncbi.nlm.nih.gov/BLAST/) and the RDP databases (Wang et al., 2007) to assign a phylogenetic affiliation to the 16S rRNA gene sequences.

Statistical analysis
Based on the PCR-DGGE and Clone library results, the Bray–Curtis distance between the communities before (day 0) and after (days 1, 3, 5, 7, 9 and 12) the accumulation of the Microcystis bloom (day 0) in each of the three enclosures was used to estimate the bacterial community resistance (Shade et al., 2011). Here, the BCC on day 0 (A0, the mixed DNA from the three samples at day 0) was used as a reference. For each enclosure, we calculated the difference in similarity between day 0 and every other day. To summarise the overall recovery at the end of the experiment, the Bray–Curtis similarity of each enclosure from day 12 to day 0 was compared using PRIMER 5 software (http://www.primer-e.com/).

The slopes of the linear regression analyses between all pairwise Bray–Curtis similarity indices and the observation days were calculated to determine the bacterial community rate of change (resilience; Shade et al., 2011) in each enclosure after the accumulation of the Microcystis bloom.

The canonical correspondence analysis (CCA) was used to reveal the relationships between BCC and the environmental parameters because the length of the first detrended correspondence analysis (DCA) axis was more than 2. All the measured environmental variables were log(1+x) transformed except for temperature and pH. In the case of the DGGE results, a binary matrix was constructed by scoring the presence (1) and absence (0) of particular bands. The environmental factors significantly describing parts of variation in BCC were identified using forward selection with 499 unrestricted Monte Carlo permutations. The CCA was calculated with CANOCO 4.5 software (ter Braak & Šmilauer, 2002).

The differences between the clone libraries constructed were statistically assessed using the ‘libshuff’ command in the MOTHUR software (Schloss et al., 2009).

Nucleotide sequence accession numbers
The obtained 16S rRNA gene sequences were available at GenBank under the accession numbers JN371170–JN3717670.
Results

The physiochemical parameters of the water column in enclosures

At the beginning and end of this experiment, all the measured environmental variables except nitrite and nitrate were similar among the three enclosures. At other times, these variables differed (Fig. 1). The water temperature, which ranged from 27 to 34 °C, was similar among the three enclosures during the present experiment (Fig. 1a). With the development of this *Microcystis* bloom, the Chl a concentration increased and then drastically decreased on day 3 (2 days after the accumulation of the bloom) in all enclosures. The Chl a level returned to its initial value by day 9 (Fig. 1c). Similarly, the conductivity in the three enclosures was similar before and after this *Microcystis* bloom (days 0 and 12) but increased in C enclosures during anoxic phase. Although the concentrations of nitrite and nitrate did not recover by day 12, similar trends of variation were found in the other environmental factors, especially in the concentration of DO. The DO concentration in enclosure C decreased markedly from 5.3 mg L$^{-1}$ on day 0 to 0.2 mg L$^{-1}$ on day 2 and maintained this low level until day 9 (Fig. 1k).

Fig. 1. Changes in water temperature (a), conductivity (b), Chl a (c), dissolved organic carbon (d), TN (e), TP (f), nitrite (g), nitrate (h), ammonium (i), ortho-phosphorus (j), DO (k) and pH (l) in the enclosures during the development of this *Microcystis* bloom. A was the control without *Microcystis* addition, B had low biomass addition of *Microcystis* (97 μg L$^{-1}$ Chl a), and C had an extremely high addition of *Microcystis* (13 012 μg L$^{-1}$ Chl a).
DGGE analysis of the bacterial community

In a manner similar to that exhibited by the environmental variables, the DGGE profiles of the bacterial DNA extracted from the three enclosures showed highly similar patterns at the beginning and end of the experiment but diverged on separate trajectories during the breakdown phase of the *Microcystis* bloom. These trajectories varied with the levels of *Microcystis* biomass (Figs S2 and S3). On day 0, the BCC was similar among the three enclosures; from days 1 to 9, there was much variation in the BCC among the three enclosures. On day 12, the BCC in the three enclosures was similar and showed patterns similar to those observed on day 0 and in enclosure A on day 7 (Figs S2 and S3).

To measure the resistance of the bacterial communities to different levels of *Microcystis* spp. biomass, we compared the average and the minimum daily Bray–Curtis values obtained before (day 0) and after the accumulation of *Microcystis* bloom communities (Table 1). The results showed that the bacterial communities in the three enclosures changed immediately after the accumulation of the *Microcystis* bloom. However, the communities in the control (A) and B enclosures were slightly resistant, showing higher average and minimum daily Bray–Curtis similarities (Table 1), whereas enclosure C was least resistant.

This enclosure showed the lowest average and minimum daily Bray–Curtis similarity (Table 1).

Although the resistance of the bacterial communities in the three enclosures was low, the recovery was relatively strong and rapid. The community in each enclosure after the recession of the *Microcystis* bloom (day 12) was more similar to the control at day 0 (>57% similarity) than during the accumulation and breakdown of the *Microcystis* bloom (days 1 through 9), suggesting that all of the communities ultimately achieved a degree of recovery by the end of the experiment (Table 1, Fig. 2a).

A linear regression analysis revealed that the rate of change, or resilience, of the bacterial community in enclosure C was the most rapid, approximately 2 and 1.5 times higher than that in the control (A) and enclosure B, respectively (Fig. 3).

Phylogenetic analysis of the bacterial community

To identify the BCC, a total of 785 16S rRNA gene sequences (120 prior to the breakdown phase of the *Microcystis* bloom, 345 during the breakdown phase of the bloom, and 320 after the bloom) were analysed (Table 2). These sequences contained a total of 281 OTUs. The samples from enclosures A and B on day 3 contained the most OTUs (73 and 80, respectively), whereas the sample from enclosure A on day 0 contained the fewest (45) (Table 2). A comparison of the observed number of OTUs revealed that libraries A3 and B3 had lower coverage values (32.4% and 35.5%, respectively), whereas library A0 had the highest (62.5%). This comparison indicated that the A3 and B3 samples had higher diversity, whereas the A0 sample had the lowest diversity (Shannon indices were 4.07, 4.19, and 3.34, respectively; Table 2).

**Table 1.** Resistance and recovery of bacterial communities for each treatment

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<th>Resistance:</th>
<th>Recovery:</th>
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<tr>
<td></td>
<td>minimum</td>
<td>average</td>
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<td>similarity to day 0 control</td>
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<tr>
<td>Enclosure A</td>
<td>42.1</td>
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</tr>
<tr>
<td>Enclosure B</td>
<td>45.8</td>
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</tr>
<tr>
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<td>42.1</td>
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</table>

**Fig. 2.** Recovery was calculated as the difference in Bray–Curtis similarity determined on PCR-DGGE (I) and Clone library (II) results for each treatment to the control on day 0.

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The NCBI (http://www.ncbi.nlm.nih.gov/BLAST/) and RDP databases (Wang et al., 2007) were used to determine the phylogenetic affiliations of the various clone sequences (Fig. 4, Fig. S4). In general, the 785 sequences comprised Betaproteobacteria, Actinobacteria, Bacteroidetes, Alphaproteobacteria, Firmicutes and unidentified bacterial groups (with relative abundances of 25.1%, 22.8%, 13.0%, 7.9%, 6.6%, and 7.9%, respectively), but the BCCs in the enclosures at the three stages of the Microcystis bloom were not the same (Figs 4 and S4).

Before the accumulation of the Microcystis bloom (day 0), the 16S rRNA gene sequences of bacteria in the three enclosures comprised Actinobacteria (Acidimicrobidae incertae sedis, Micrococineae, and unclassified Actinomycetales, with relative abundances of 11.7%, 23.3%, and 25%, respectively), followed by Alphaproteobacteria (Sphingomonadaceae and unclassified Rhizobiales, with relative abundances of 2.5%, and 3.3%, respectively) and Betaproteobacteria (Burkholderiaceae and Comamonadaceae, both with relative abundances of 3.3%; Fig. 4).

Two days after the accumulation of the Microcystis bloom (day 3), the bacterial populations in the enclosures had all changed. These populations varied with the levels of Microcystis biomass (Fig. 4). In the control enclosure (A), the relative abundance of Comamonadaceae increased to 17.6%. This group became the most abundant group. The unclassified Actinomycetales remained among the dominant populations (Fig. 4), but their relative abundance decreased to 12.0%. The other dominant groups in this enclosure were Flavobacteriaceae (Bacteroidetes),

<table>
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<tr>
<th>Sample</th>
<th>No. of Sequences</th>
<th>No. of OTUs</th>
<th>Coverage (%)</th>
<th>Shannon index</th>
<th>Simpson index</th>
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Micrococcineae, Rhodocyclaceae, and other unclassified Betaproteobacteria (with relative abundances of 5.6%, 5.6%, 4.6%, and 4.6%, respectively; Fig. 4). Similarly, all of these dominant groups were among the most abundant in enclosure B. However, their relative abundances varied. Chitinophagaceae and other unclassified bacterial populations affiliated with Bacteroidetes (with relative abundances of 4.0% and 6.5%, respectively) were among the other dominant groups in enclosure B (Fig. 4). However, in enclosure C, Clostridiales (with relative abundances of 11.5% and 14.2%, respectively) became the most abundant group. Other abundant groups included Ruminococcaceae, Clostridiales, Flavobacteriaceae, and unclassified Bacteroidetes (with relative abundances all more than 7%; Fig. 4).

After the recession of the Microcystis bloom (day 12), the BCCs in the three enclosures changed but were very similar to each other. The BCCs in the three enclosures comprised Rhodocyclaceae, Burkholderiaceae, Comamonadaceae, Acidimicrobiidae incertae sedis, Micrococcineae, Caulobacteraceae, unclassified Burkholderiaceae, and unclassified Actinomycetales, with relative abundances > 7% (Fig. 4). In addition, the bacterial population in enclosure C also included Sphingomonadaceae.

The LIBSHUFF analysis of the clone library clearly indicated that the BCCs in the three enclosures at the three stages of the Microcystis bloom differed significantly except on day 12, which showed an increased number of OTUs (Table 3).

Factors related to BCC changes

The CCA model showed that the concentrations of Chl a, NO3-N, NO2-N, DOC, DO, and T contributed most to the variance in the bacterial community (for all canonical axes, $P < 0.05$, Fig. 5). The eigenvalues of the first and second axes were 0.96 and 0.97, respectively, indicating that both axes were important. The first two axes contributed to 21.5% of the observed variation in the composition of the bacterial community, and the full set of four canonical axes contributed to 33.2% of the observed variation. The first axis showed a high canonical correlation with the NO2-N and DOC concentrations ($r = -0.78$ and 0.65, respectively), followed by NO3-N, T, Chl a, and DO ($r = -0.52$, 0.41, 0.14 and −0.11, respectively), whereas the second axis was correlated with the DOC and DO concentrations ($r = 0.70$ and −0.62, respectively), followed by T, NO2-N, Chl a, and NO3-N ($r = -0.54$, 0.33, −0.26 and −0.09, respectively). This CCA plot clearly showed a stronger influence of the DOC and DO during the accumulation and breakdown phases of the Microcystis bloom than of the other measured environmental variables on the BCCs in the three enclosures. Subsequent to the recession of the Microcystis bloom, most of the environmental factors investigated returned to their original values; the BCCs in the different mesocosms were similar to the control on day 0 and the NO2-N and NO3-N concentrations contributed to most of the differences observed among these bacterial communities (Fig. 5).

![Fig. 5. Correspondence canonical analysis (CCA) biplots showed variable composition of bacteria in relation to the strongest environmental factors in the enclosures with different biomass of Microcystis spp.](https://academic.oup.com/femsec/article-abstract/82/1/192/566770)
**Discussion**

The change in Chl a in the C enclosure indicated a rapid decomposition of the Microcystis biomass in our experiment (Fig. 1c), which produced drastic changes in the environmental factors in the water column (Fig. 1). The high concentrations of DOC, TP, TN, NH₄-N, PO₄-P and low DO and pH in the enclosure amended with the highest addition of Microcystis have also been found in some other experiments (Li et al., 2011). The increase in conductivity in the C enclosure from day 2 to day 7 could be due to the release of some ions including the Mg, Fe, and phosphorus from sediment into the water column during the anoxic condition (Li et al., 2012). However, we observed that all of the measured environmental factors in the water column, except nitrate and nitrite, could recover in a short time (within 12 days).

Interestingly, the disturbed BCC also recovered from day 7 following the recovery of the investigated environmental factors (especially the DOC and DO concentrations, Fig. 1d and k). At day 12, the BCCs in the different enclosures, comprising Rhodocyclaceae, Burkholderiaceae, Comamonadaceae, Acidimicrobiidae incertae sedis, Micrococccineae, and Caulobacteraceae, were similar to each other (Fig. 4) and also more similar to the control at day 0 than to the BCCs occurring during the breakdown of the Microcystis bloom (Table 2, Fig. 2i and 5, Fig. S2 and S3). Some other studies also demonstrated that the aquatic bacterial communities could recover rapidly following disruption disturbances of the concentrations of DO and nutrients (nitrogen and phosphorus) in the water column (Shade et al., 2010a, b, 2011). Unlike the above-mentioned experiments focusing few specific factors, the pulse effect of Microcystis blooms on lake ecosystems represents a type of natural disturbance. Still, we found a rapid recovery of BCC in lakes even in face of catastrophic disturbance. These results suggest that BCCs may be deterministic by environmental factors in lakes.

There are several potential reasons for the high resilience of the BCC to the natural pulse of Microcystis blooms. Firstly, the BCC may possess multiple dormant states or seed banks allowing them to survive under unfavourable environmental conditions (Lennon & Jones, 2011). Secondly, high growth rates and high phenotypic flexibility of bacteria may allow the disturbed BCC to return to its pre-disturbance state in a short time after environment improved (Allison & Martiny, 2008). Thirdly, cyanobacterial blooms, especially Microcystis blooms, have occurred regularly during the summer in Lake Taihu since 1980 (Qin et al., 2007), and the resulting physiological adaptation and rapid evolution might have contributed to the adaptation of the lake's bacteria to the natural pulse of Microcystis blooms. Finally, the rich resources including the high concentration of algal-derived DOC might favour certain opportunists (Eiler & Bertilsson, 2004; Li et al., 2011) and might then improve the resilience of the BCC to the effects of the Microcystis blooms.

Although the BCC in each enclosure achieved a degree of recovery by the end of the experiment (Table 2, Fig. 2i), the LIBSHUFF analysis showed that the compositions of these communities were still a bit different from the BCC of the control on day 0 (Table 2). This result indicated that the recovery was not complete. The dynamics of the free-living bacterial communities in lakes are shaped by various factors (e.g. Šimek et al., 2005, 2008; Kent et al., 2007; Grossart et al., 2008; Berdjeb et al., 2011; Zeng et al., 2012). In the present study, not all of the environmental factors recovered after the recesion of the Microcystis bloom. The concentrations of nitrite and nitrate did not recover. In addition, it is not known whether biotic variables, such as heterotrophic nanoflagellate, exert an important influence on the bacterial community composition (e.g. Šimek et al., 2005, 2008; Kent et al., 2007) in our experiment. Chen found a significant change of zooplankton community during this 13-day experiment, but no obvious recovery on the 13th day (unpublished data). This is probably the reason why the four axes in the CCA model explained only 33.2% of the observed variation in the composition of bacterial community (Fig. 5). Thus, the BCCs in the present work achieved a degree of recovery immediately, but they did not recover completely.

In conclusion, we explored the pulse effect of Microcystis blooms on BCC and we found that the BCCs showed low resistance, but high resilience even in the face of a catastrophic disturbance by a Microcystis bloom.

**Acknowledgements**

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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** Map of Gonghu Bay in Lake Taihu, China, showing the location of experiment site.

**Fig. S2.** Figure of PCR-DGGE profile of bacterial community composition in the enclosures during the experiment.

**Fig. S3.** Clustering analysis of PCR-DGGE profile of bacterial community composition in the enclosures during the experiment.

**Fig. S4.** The composition of dominated bacterial 16S rRNA gene amplicons recovered from the three stage of this *Microcystis* bloom.

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