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Dynamics of dissolved organic carbon after a cyanobacterial bloom in hypereutrophic Lake Taihu (China)

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ABSTRACT

To establish the influence of the cyanobacterial bloom collapse on the characteristics of dissolved organic carbon (DOC) in Lake Taihu, high-molecular-weight dissolved organic matter (HMW-DOM), with sizes between 1 kDa and 0.5 μm, were collected using cross-flow ultrafiltration, from three different eutrophic regions. Isolated HMW-DOM was further characterized by atomic carbon to nitrogen ratio and neutral sugars composition by gas chromatography and mass spectrometry. The results indicated that the cyanobacterial cell lysis induced by nitrate depletion is the likely mechanism for DOC release. The relatively high DOC level was associated with the high chlorophyll *a* concentration in Meiliang Bay, one of the most eutrophic bays in the northern part of the lake. However, no significant correlations were observed between chlorophyll *a* concentration and HMW-DOC concentration during the demise of the cyanobacterial bloom in Lake Taihu. No significant differences were found in the HMW-DOC concentration among the three sampling sites, which were selected to represent different eutrophic status. However, a significant difference in the HMW-DOC concentration was found between October 2009 and January 2010 in all three sampling sites ($p = 0.02$). The HMW-DOC release may be attributed to the cyanobacterial cell lysis after the peak of summer bloom. The similarity in neutral sugar composition between the HMW-DOM and cyanobacterial exopolysaccharides suggests that the cyanobacterial bloom is the source of HMW-DOM. However, the significant correlation between the carbon to nitrogen ratio in HMW-DOM and chlorophyll *a* concentration was only observed in Meiliang Bay, which implies that apart from the cyanobacteria-derived DOC, a fraction of DOC was from riverine input. The decline of the cyanobacterial bloom also changed the overall DOM pool, leading to a shift in the component of HMW-DOM from a C-enriched material to an N-enriched material, as revealed by the variation in the carbon to nitrogen ratios. Overall, these results demonstrate that the quantitative and qualitative DOM is affected by the post-cyanobacterial bloom in Lake Taihu.

Introduction

Bloom-forming cyanobacteria have been observed in Lake Taihu for more than a decade, which is most pronounced from spring to autumn, with maximal chlorophyll *a* (Chl *a*) concentrations in summer (Xu et al., 2010). van Boekel et al. (1992) reported that phytoplankton cell lysis events occur after blooms when large phytoplankton blooms deplete inorganic nutrients. Wetz and Wheeler (2003) also observed a significant accumulation of dissolved organic matter (DOM) after nitrate depletion of the phytoplankton. Consequently, a large amount of DOM is released during phytoplankton cell lysis, which represents an important carbon and nitrogen pool in the microbial food web (Cherrier and Bauer, 2004). Aoki et al. (2008) reported that the algal DOM released from *Microcystis aeruginosa* considerably contributes to the organic matter in Lake Biwa. Understanding the effects of the cyanobacterial bloom on the Lake Taihu ecosystem is important for future predictions and controls of the affected regions. The main objective of this study is to determine if the DOM quality and quantity in Lake Taihu is affected by the cyanobacterial bloom collapse.

DOM can be separated by cross-flow ultrafiltration, resulting in a number of different molecular weight size fractions, such as high and low molecular weight dissolved organic matter (HMW-DOM: >1 kDa; LMW-DOM: <1 kDa) (Benner et al., 1997; Kepkay et al., 1997a). The two most important components of DOM are dissolved organic carbon (DOC) and dissolved organic nitrogen (DON); and phytoplankton blooms have a greater effect on DOC pools relative to DON (Gobler and Sañudo-Wilhelmy, 2003; Wetz et al., 2008). DOC from dead cells mainly consists of high-molecular-weight (HMW) compounds, whereas DOC exported from live cells

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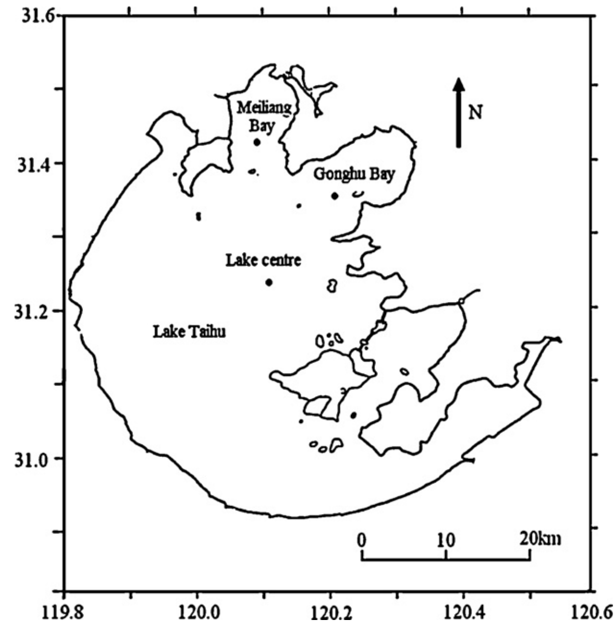

Fig. 1. Location of the sampling sites in Lake Taihu.

are largely made up of low-molecular-weight (LMW) compounds (Lee and Rhee, 1997). Compared to LMW-DOC, HMW-DOC reportedly contains more carbohydrates and is highly bioreactive in the carbon cycle (Amon and Benner, 1994; Pakulski and Benner, 1994; Engelhaupt and Bianchi, 2001). Furthermore, the neutral sugars that are hydrolyzed from more complex carbohydrate structures are known to be major components of fresh DOC from phytoplankton, which is used to fuel heterotrophic bacterial growth (Biersmith and Benner, 1998; Skoog et al., 1999).

To ascertain how the composition of DOC is affected by the decline of cyanobacterial bloom, the DOC characteristics after a pelagic bloom in 2009 were studied in three different eutrophic regions in Lake Taihu. The concentrations of Chl *a*, DOC, and HMW-DOC were analyzed and HMW-DOM was characterized in terms of neutral sugar composition and carbon to nitrogen ratio (C:N). The resulting data provides insight into the dynamics, sources, molecular composition, and degradability of the DOC released from cell lysis of the cyanobacterial bloom induced by nitrate depletion.

Materials and methods

Site description

Lake Taihu is one of the largest freshwater lakes in China and it is located in the southeastern part of the Yangtze River Delta (latitude 30°55′40″–31°32′58″N; longitude 119°52′32″–120°36′10″ E), with an area coverage of 2340 km^2. An annual serious cyanobacterial bloom occurs in late May or early June, and the large volume of cyanobacteria colonies is driven to the western and northern areas of the Lake Taihu by the high frequency of southwest winds (Wu and Kong, 2009). In this study, surface water samples from Lake Taihu were taken monthly from August 2009 to March 2010. The sampling sites were categorized into the following regions: (1) Meiliang Bay, one of the most eutrophic bays in the northern part of the lake, with a high density of *Microcystis* scum in summer (Chen et al., 2003); (2) Lake centre, an open lake without serious pelagic blooms during summer; and (3) Gonghu Bay, a bay used to be dominated by submerged macrophytes (Zhang et al., 2006), and is now less eutrophic than Meiliang Bay (Fig. 1).

In the present study, the results of microscopical analysis indicates that cyanobacteria account for more than 95% of the phytoplankton biomass for the three sampling sites during all sampling periods. Chl *a* concentrations were used to represent the biomass of cyanobacteria. Although *Microcystis* is the dominant cyanobacterial species (Chen et al., 2003), *Anabaena* appear from November 2009 to January 2010. Lower biomass (<5%) of Bacillariophyta and Cryptophyta occur in January and Chlorophyta in March 2010, respectively.

Analytical procedures

Three replicate measurements of each sample were performed. Chl *a* collected on a GF/F filter and extracted with 90% acetone, was measured using the method described by Yan et al. (2004). Ultrafiltration was performed with a Millipore Pellicon standard system using a 1 kDa regenerated cellulose PLAC filter cartridge (filter area 0.5 m^2), which is suitable for applications during plankton blooms (Guéguen et al., 2002). Water samples were filtered through a 0.5-μm pore size filter prior to ultrafiltration. The ultrafiltration procedure for the collected samples has been described by Guo and Santschi (1996). HMW-DOM is defined as the fraction between 1 kDa and 0.5 μm. DOC (<0.5 μm) and HMW-DOC (1 kDa to 0.5 μm) were analyzed by high temperature catalytic oxidation method using a total organic carbon analyzer (Shimadzu TOC-V CPN, Japan) (Zhang et al., 2006). After ultrafiltration, aliquots of both retentate and ultrafiltrate were sampled for a DOC mass balance (Guo et al., 1995; Guo and Santschi, 1996). The HMW-DOM concentrate was freeze-dried to yield a powdered sample and stored in a freezer (<−20 °C) until further analysis.

The neutral sugar composition of HMW-DOM was determined according to Handa and Yanagi (1969). For the acid hydrolysis of HMW-DOM, 100–200 mg of dry samples were dissolved in 1 mL of 2 M trifluoroacetic acid. This mixture was heated in a tightly capped glass vial at 121 °C for 2 h (Aluwihare et al., 2002). Neutral sugars were then quantified as alditol acetates by gas chromatography and mass spectrometry (Agilent 7890-5975C). The contribution of individual neutral sugars to the total neutral sugars is expressed in mole percentage (mol%). The isolated HMW-DOM samples were analyzed for C:N ratio using a EuroVector elemental analyzer (Guo et al., 2009).

Statistical analysis

The SPSS 16.0 software package was used for statistical analysis. Mean differences were determined using a two-tailed *t*-test. Differences were considered significant at $p < 0.05$. The Chl *a*, NO_3^-, DOC, HMW-DOC, neutral sugar composition, and C:N ratio data are presented as mean ± standard deviation.

Results

Chl a and nitrate concentration

The average Chl *a* concentration was higher in Meiliang Bay than in Gonghu Bay and Lake centre from June to October. The Chl *a* concentration peaked in July in all the three lake regions, which then decreased and maintained at low levels. In January, the Chl *a* concentration increase, particularly in Meiliang Bay and Gonghu Bay, but then returned to relatively low levels in March (Fig. 2a). The nitrate concentrations increased continuously in all three lake regions, but an obvious drop occurred in October, when the lowest nitrate concentration was observed in Lake centre and Gonghu Bay (Fig. 2b).

DOC and HMW-DOC concentration

The DOC concentration showed a clear increase at the sampling sites, with the maximum DOC concentration being higher in Meiliang Bay than of both other sites. In Meiliang Bay, the maximum

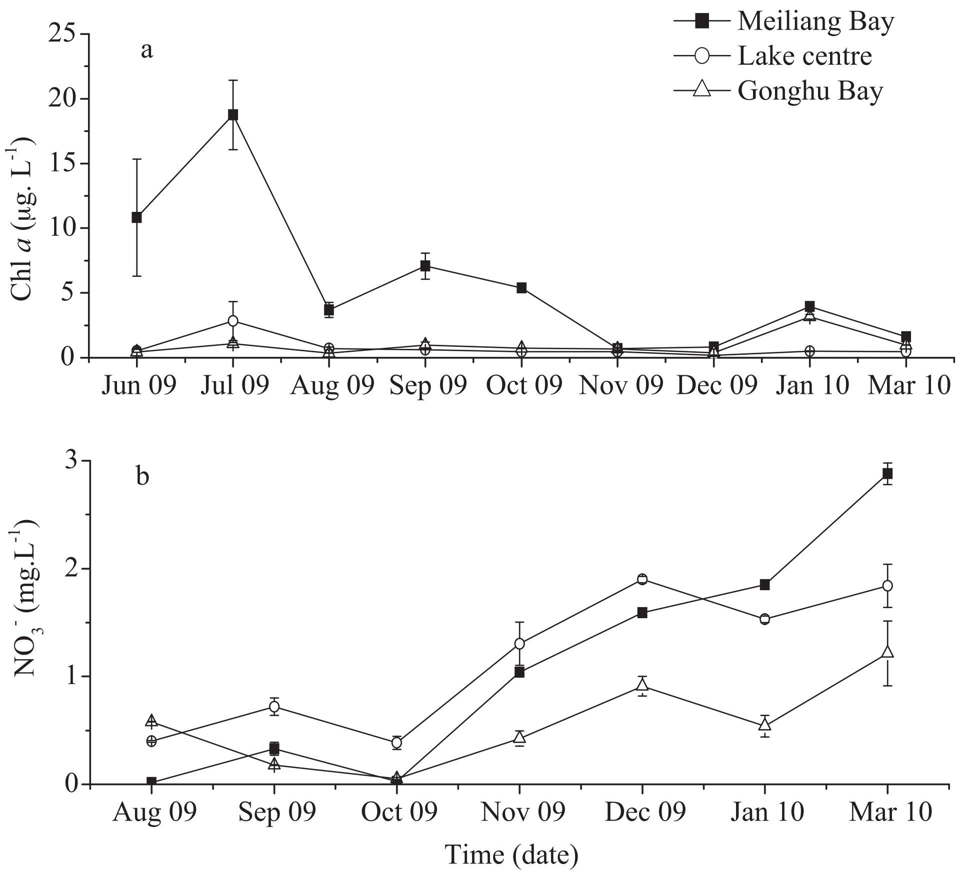

Fig. 2. Chl *a* (a) and nitrate (b) concentration from August 2009 to March 2010 in Lake Taihu.

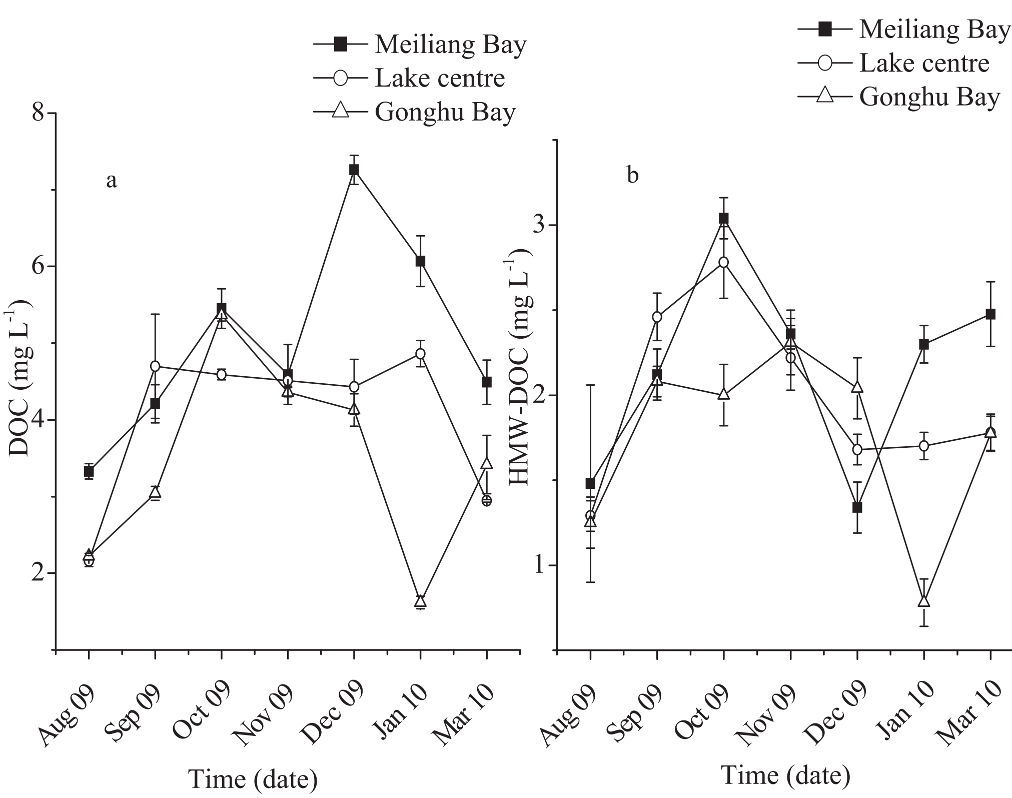

Fig. 3. Variation of DOC (a) and HMW-DOC (b) from August 2009 to March 2010 in Lake Taihu.

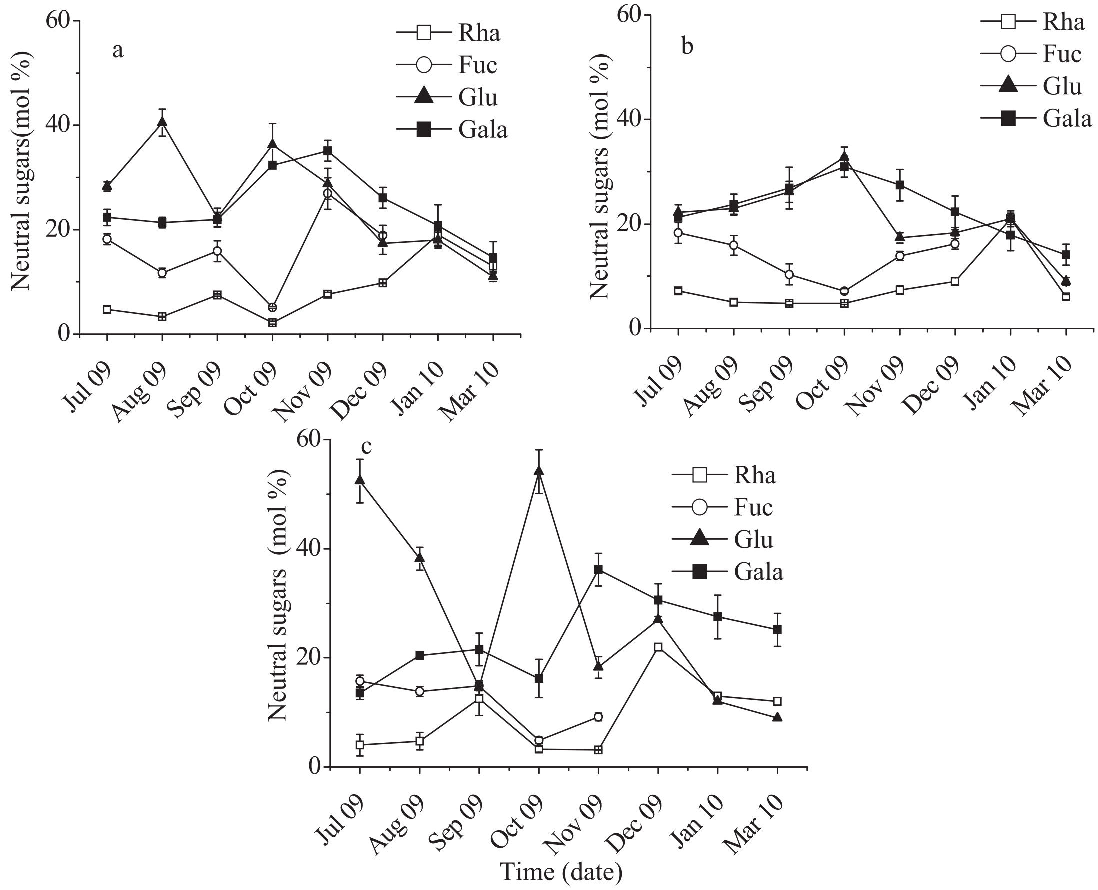

Fig. 4. Variation of mol% of rhamnose, fucose, glucose, and galactose from July 2009 to March 2010 in HMW-DOM samples from Lake Taihu (a: Meiliang Bay; b: Lake centre; c: Gonghu Bay. In Meiliang Bay and Lake centre, fucose was not detected in January and March. From December to March, fucose was not detected in Gonghu Bay).

DOC concentrations were observed in December whereas for Lake centre, the DOC concentration increased from 2.2 ± 0.1 mg L^{-1} in August to 4.7 ± 1.2 mg L^{-1} in September. Then, the concentrations remained constant but decreased after next January. Meanwhile, in Gonghu Bay, the highest DOC concentration (5.4 ± 0.08 mg L^{-1}) was observed in October (Fig. 3a). No significant differences were found in the HMW-DOC concentration among the three sampling sites ($p > 0.05$). The HMW-DOC concentration increased from August, reaching its maximum at around October, followed by fluctuations (Fig. 3b). In all the three sampling sites, significant differences in HMW-DOC concentrations were found between October and January ($p = 0.02$, $n = 3$).

Neutral sugar composition of HMW-DOM

The neutral sugar composition of HMW-DOM was dominated by glucose and galactose. The mol % of glucose showed fluctuations but reached a relatively low value in March at all sampling sites. From July to December, the mol % of fucose fluctuated whereas that of rhamnose showed an increase at all three sampling sites from July to March (Fig. 4).

Atomic carbon to nitrogen ratio of HMW-DOM

The C:N ratio of HMW-DOM ranged from 6 to 27, which increased from August and reached its maximum in September. Then, the ratios decreased significantly; however, no significant differences were observed among the three lake regions ($p > 0.05$) (Fig. 5).

Discussion

Nitrate depletion, phytoplankton cell lysis, and DOC release

Nutrient deficiency has been described to directly affect phytoplankton cell death in both laboratory and field studies (Lee and Rhee, 1997). Nitrogen limitation is particularly important for the occurrence of cell lysis. In N-limited continuous cultures free of

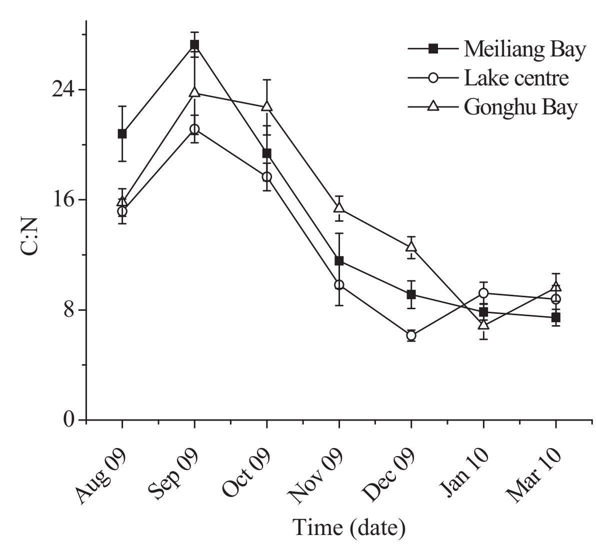

Fig. 5. C:N ratio of HMW-DOM from August 2009 to March 2010 in Lake Taihu.

viruses and bacteria, *Ditylum brightwellii* exposes a specific lysis rate of 0.014 d^{-1} (Brussaard et al., 1997). Additionally, termination of *Phaeocystis* bloom is induced by nitrate depletion (van Boekel et al., 1992).

Nitrate is the primary form of inorganic N in Lake Taihu, and the peak of cyanobacteria biomass is associated with the highest nitrate concentration (McCarthy et al., 2007). From August to October, nitrate concentrations in Lake Taihu decreased to its minimum values due to cyanobacteria utilization, denitrification, and decreased input caused by the dry season (Xing et al., 2001). In situ nutrient addition experiments suggest that N is the primary limiting nutrient during the summer and autumn bloom periods in Lake Taihu (Xu et al., 2010). Thus, cyanobacterial bloom cell lysis is induced by nitrate depletion.

In Lake Taihu, cyanobacterial blooms occur as colonial morphologies under natural conditions with high amounts of extracellular polysaccharides (Yang et al., 2008). Hence, cyanobacteria are able to excrete copious amounts of carbohydrates, which is the major contributor to the DOC pool (Zhang et al., 2009). In all three sampling sites, the occurrence of maximum DOC concentrations lagged after July when the cyanobacterial bloom was present, indicating that the elevated DOC originated from the cyanobacteria, which was released during the decline phase of the cyanobacterial bloom. The increased concentration of DOC after phytoplankton blooms has also been observed in other studies (Meon and Kirchman, 2001). The excretion of DOC from phytoplankton lysis represents up to 70% of the net primary production in the eastern tropical North Atlantic (Agustí et al., 2001). The results implied that the cell lysis of cyanobacteria induced by nitrate is an important DOC source in Lake Taihu.

The relationship among DOC, HMW-DOC, and Chl a

The correlation between DOC concentration and Chl *a* concentration is still controversial. In the mid-Atlantic coastal bay, a dramatic increase in DOC concentration was observed after a brown tide bloom but no correlation between DOC and Chl *a* was reported (Minor et al., 2006). However, a significant correlation between DOC concentration and Chl *a* was observed after a bloom of the Pelagophyte *Aureococcus anophagefferens* (Simjouw et al., 2004). In the present study, the maximum DOC concentration was observed in Meiliang Bay, situated at the north end of Lake Taihu. The bay is well known as one of the most eutrophic bays in China, where the Chl *a* concentrations are much higher than the other two regions. The result indicates that Chl *a* and DOC may be linked, but no significant correlation was concluded. Many different biotic and abiotic processes are involved in DOC dynamics, such as grazing, photochemical oxidation, and adsorption to sinking particles (Chin et al., 1998). Furthermore, the exogenous sources of DOC, i.e., riverine and off-shore water, may be important in DOC production in Lake Taihu. Large amounts of untreated wastewater from factories and residential areas are discharged to Liangxi and Zhihu Gang Rivers, then the two rivers empty into Meiliang Bay.

HMW-DOC contributes a significant fraction to DOC, which is distinct in chemical composition of LMW-DOC and can be separated by cross-flow ultrafiltration from the DOC pool (Gustafsson and Gschwend, 1997). Phytoplankton blooms are a direct source of HMW-DOC (Gobler and Sañudo-Wilhelmy, 2003), but the occurrence of the highest HMW-DOC (1 kDa to 0.2 μm) concentration usually lags behind the development of the Chl *a* maximum (Kepkay et al., 1993), which may be due to the decomposition and cell lysis of phytoplankton (Wang and Guo, 2001; Floge and Wells, 2007). A laboratory experiment implied that a great amount of HMW-DOC (>1 kDa) is released during the decomposition of cyanobacteria in Lake Taihu (Sun et al., 2007). Thus, we suggest that the release of HMW-DOC is attributed to the cell lysis after the cyanobacterial peak.

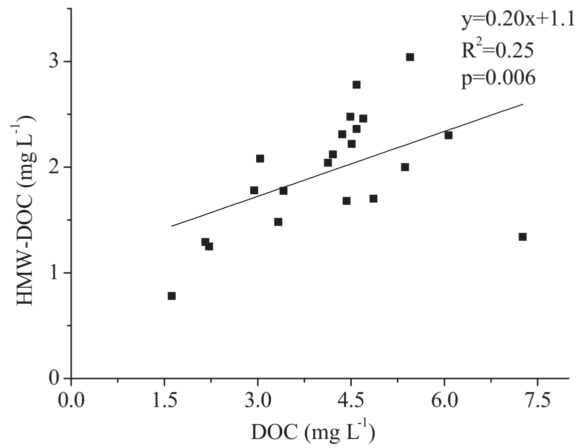

Fig. 6. Relationship between DOC and HMW-DOC from August 2009 to March 2010 in Lake Taihu (N = 21).

Plots of HMW-DOC vs. DOC concentrations show a positive linear relationship in all the study regions (Fig. 6). Thus, HMW-DOC seems partitioned in a predictable way, with DOC concentration as the main variable. In Lake Taihu, the slope of the correlation line is 0.20, implying that 20% of the variation in the DOC pool is from the HMW-DOC fraction (1 kDa to 0.5 μm).

Gobler and Sañudo-Wilhelmy (2003) reported that HMW-DOC strongly correlates with Chl *a* during an estuarine phytoplankton bloom. In Lake Taihu, a correlation between HMW-DOC concentration and Chl *a* has been observed (Zhang et al., 2008), which cannot be concluded from the present study due to the following possible reasons: First, HMW-DOC reportedly has a rapid turnover and a portion of it is remineralized by microbial respiration after the collapse of algal blooms (Amon and Benner, 1996; Gobler and Sañudo-Wilhelmy, 2003). The maximum bacterial abundance lag behind the maximum phytoplankton biomass in Lake Taihu, which suggests that the HMW-DOC released from the phytoplankton cell lysis is an important carbon source that fuels heterotrophic bacterial growth (Gao et al., 2007). Second, humic substances derived from the diagenesis of structural materials in soils are an important source of HMW-DOC in freshwater systems (Gustafsson and Gschwend, 1997; Engelhaupt and Bianchi, 2001). In Lake Taihu, wind-induced resuspension of sediments occurs frequently, thus the materials released from sediments largely affect the concentration of HMW-DOC in this large shallow lake (Sun et al., 2007). Finally, the HMW-DOC defined in this study can be further separated into very high dissolved organic carbon (VH-DOC: 30 kDa to 0.2 μm) and high dissolved organic carbon (H-DOC: 1–30 kDa). The biochemical composition of VH-DOC is suggested to resemble living biomass (primarily plankton) more closely than high H-DOC (Harvey and Mannino, 2001). Therefore, VH-DOC may be closely related to Chl *a*, instead of HMW-DOC.

Chemical characteristics of HMW-DOM

Neutral sugar composition of HMW-DOM

Seven major neutral sugars (glucose, galactose, rhamnose, fucose, mannose, xylose, and arabinose) were detected in all HMW-DOM samples from Lake Taihu. This result is consistent with previous studies, which have also found similar neutral sugar composition in freshwaters (Repeta et al., 2002). The changes in neutral sugar composition are likely due to the release of extracellular polymeric substances (EPS) by the cyanobacteria. Glucose and galactose are known to dominate the high-molecular-mass

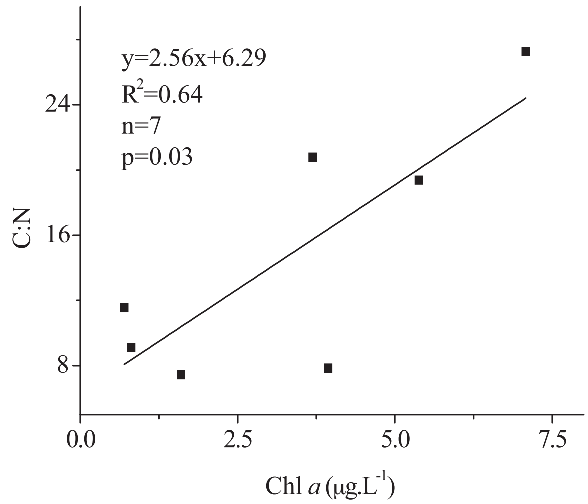

Fig. 7. Relationship between Chl *a* and C:N ratio of HMW-DOM from August 2009 to March 2010 in Meiliang Bay (N = 7).

heteropolysaccharides (Nicolaus et al., 1999; Pereira et al., 2009). These results suggest that cyanobacteria may be the major source for HMW-DOM in Lake Taihu. In the present study, there was an increase in deoxysugars (rhamnose plus fucose) and a decrease in glucose after the bloom, which is indicative of organic matter decomposition (Hedges et al., 1994; Ogier et al., 2001). Thus, neutral sugars contribute to the semi-labile HMW-DOM pool in Lake Taihu.

Carbon to nitrogen ratio of HMW-DOM

The C:N ratios in the HMW-DOM samples collected from Lake Taihu ranged from 6 to 27, which is similar to the C:N ratio of HMW-DOM (1 kDa to 0.2 μm) in freshwater lakes Nobska pond (6) and Lake Superior (18), as observed by Repeta et al. (2002). The high polysaccharide and carbon content of HMW-DOM exert a large influence on the carbon cycling in the microbial food web and the C:N ratio (Kepkay et al., 1997b; Gobler and Sañudo-Wilhelmy, 2003). This is the case for Lake Taihu, where C:N ratios of HMW-DOM reached its maximum value in September, when cyanobacterial cell lysis resulted in a large release of phytoplankton-derived carbohydrates, which has a C:N ratio that is significantly higher than the Redfield ratio (Amon and Benner, 1994; Williams, 1995). The C:N ratio in Lake Taihu returned to pre-bloom levels due to respiration as C is preferentially degraded compared with N in the DOM pool (Wetz et al., 2008). Thus, a significant difference was found in the ratio of C:N between September and January (p = 0.018, n = 3). Furthermore, the decrease in C:N can be due to an increase in DON produced from nitrate by N-fixing cyanobacteria and heterotrophic bacteria (Wetz and Wheeler, 2003; Simjouw et al., 2004; Yamanoti et al., 2004; Mei et al., 2005; McCarthy et al., 2007) because a depleted nitrate concentration was observed around October in all three sampling regions. This result indicates that HMW-DOM changed from a C-enriched to an N-enriched component after the bloom.

The strong, positive correlation between the C:N ratios of HMW organic matter and algal biomass (Chl *a*; p = 0.03, R^2 = 0.64, n = 7) in Meiliang Bay suggests that the cyanobacterial bloom were the primary source of HMW-DOM (Fig. 7). However, no significant relationship can be observed in Gonghu Bay and Lake centre. Furthermore, bacterial activity usually degrades the phytoplankton-derived DOC fairly rapidly (in weeks) (Søndergaard et al., 2000), but the C:N ratio of HMW-DOM decreased after September. Therefore, apart from the labile bloom-derived DOC pool, another part of DOC may be recalcitrant, with a terrestrial origin.

This study allows the observation of changes in DOC characteristics during the decline of cyanobacterial blooms in Lake Taihu. The results indicate that nitrate depletion is responsible for the cyanobacterial bloom cell lysis in Lake Taihu. Furthermore, a bloom collapse releases and changes the overall DOM pool, in which the HMW-DOM changes from a C-enriched to an N-enriched component after the bloom. In addition, the HMW-DOC enriched in carbohydrates and hence with a higher carbon to nitrogen ratio might be released due to cell lysis following the peak of cyanobacterial blooms. No significant differences were found in the HMW-DOC concentration among the three sampling sites. Furthermore, HMW-DOC is highly bioreactive, and bacterial respiration is responsible for the decline in C:N ratio. Future studies are required to elucidate the precise mechanism of the cyanobacterial release and bacterial assimilation in the different molecular weight DOC using ^{13}C tracer and cross-flow ultrafiltration methods.

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