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Do the regular annual extreme water level changes affect the seasonal appearance of *Anabaena* in Poyang Lake?

Kuimei Qian^{Corresp., 1}, Martin Dokulil², Yuwei Chen³

¹ College of Environmental Engineering, Xuzhou University of Technology, Xuzhou, Jiangsu, China

² Research Department for Limnology, Mondsee, University of Innsbruck, Mondsee, Austria, Mondsee, Austria

³ Nanchang Institute of Technology, Nanchang, China

Corresponding Author: Kuimei Qian

Email address: qiankuimei@xzit.edu.cn

Background. Poyang Lake is an exceptional system exhibiting a water level change of up to 14 m every year. In the years 2013 and 2014 water level changes were 8.03 m and 11.22m respectively. The biomass of *Anabaena* and heterocyst frequency increased in the summers of recent years.

Methods. A weekly or bi-weekly monitoring period from June to November 2013 and 2014 was set up to explain the reason for this phenomenon.

Results. *Anabaena* was observed throughout the year. The average relative biomass of *Anabaena* in the study period was over 40%, being most abundant in summer. The average heterocyst frequency was 0.226% in 2013 and 0.760% in 2014. The SPSS analysis indicated a positive correlation of *Anabaena* biomass with water temperature and water level and negative one with TN, which is the reason for the increase of heterocyst frequency from 2013 to 2014. It also indicated that heterocyst frequency of *Anabaena* was positively correlated with water temperature, water level and PO₄-P, and negatively with DIN/DIP, NO₃-N and TN. At the same time, water temperature and DIN/DIP were significantly correlated with water level, which means that water level changes have a direct effect on *Anabaena* and its heterocyst formation in Poyang Lake.

Conclusions. The results of the study support the hypothesis that increasing biomass and heterocyst formation of *Anabaena* were primarily caused by changes in the environmental parameters, such as high water temperature and suitable nutrients in summer and autumn, driven by the regular annual extreme water level change of Poyang Lake. The results can provide a theoretical basis for the management and utilization of Lake Poyang.

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Kuimei Qian¹, Martin Dokulil², Yuwei Chen³

¹ College of Environmental Engineering, Xuzhou University of Technology, Jiangsu Laboratory of Pollution Control and Resources Reuse, Xuzhou, Jiangsu Province, China

² Research Department for Limnology, Mondsee, University of Innsbruck, Mondsee, Austria

³ Nanchang Institute of Technology, Nanchang, Jiangxi Province, China

Corresponding Author:

Kuimei Qian¹

Lishui Road, Xuzhou City, Jiangsu Province, 221018, China

Email address: qiankuimei@xzit.edu.cn

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² Research Department for Limnology, Mondsee, University of Innsbruck, Mondsee, Austria

³ Nanchang Institute of Technology, Nanchang, Jiangxi Province, China

Corresponding Author:

Kuimei Qian¹

Lishui Road, Xuzhou City, Jiangsu Province, 221018, China

Email address: qiankuimei@xzit.edu.cn

Abstract

Background. Poyang Lake is an exceptional system exhibiting a water level change of up to 14 m every year. In the years 2013 and 2014 water level changes were 8.03 m and 11.22m respectively. The biomass of *Anabaena* and heterocyst frequency increased in the summers of recent years.

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Conclusions. The results of the study support the hypothesis that increasing biomass and heterocyst formation of *Anabaena* can be primarily caused by seasonal changes in water level of Poyang Lake.

Introduction

Water level change is a key element of hydrology and has a significant effect on lake ecology and management affecting environmental factors such as turbidity and transparency (Coops, Beklioglu & Crisman, 2003; Lopes, Bicudo & Ferragut, 2005; Mihaljević & Stević,

2011). Such water level changes are usually moderate, multi-annual or annual (Zohary & Ostrovsky, 2011; Casali et al. 2011) where else Poyang Lake changes once every year by up to 14 meters (Zhang et al., 2014). Water level change has an important role in the exchange of organisms and nutrients among the main channel, tributaries, and lakes along the water flow. Phytoplankton presents temporal patterns related to environmental changes (Huszar et al., 1998) and is an important ecological tool to obtain short-term responses (Reynolds, 2002; Rodrigues et al., 2002). Cyanobacterial N₂ fixation is of ecological importance in aquatic environments (Karl et al., 2002). In nitrogen-deficient water, Cyanobacterial N₂ fixation provides new combined nitrogen to the pelagic ecosystem and hence supports new planktonic production (Capone & Carperter, 1982).

Water level change initiatives the confrontation of organisms and nutrients among the main channel, tributaries, and lakes. Each environment associated with floodplain has different factors that influence the structure and dynamic of aquatic communities. Poyang Lake is one of the only two lakes that are still freely connected with Changjiang (Yangtze) River, having great effects on the maintaining the unique biota of the Yangtze floodplain ecosystem. Poyang Lake could be classified as highly eutrophic, due to the excessive agricultural chemical and industrial inputs, and waste discharges during intensive economic activities and growing human population in recent decades (Yang et al., 2015). Nutrients in Poyang Lake caused the proliferation of algae (Deng et al., 2011; Zhen et al., 2011, Liu et al., 2016a). Total phytoplankton biomass and Cyanobacteria biomass in autumn of years 2010-2013 were obviously high, confirming the Cyanobacteria bloom in some regions of Poyang Lake in these years (Qian et al., 2016b). There were visible buoyant migration of existing populations of *Anabaena spp.* and *Microcystis spp.* to the lake surface in some lentic regions, and even in the surface of the channel of Poyang Lake. Therefore not only the buoyant Cyanobacteria but also the nutrients flow to this area along with the water current. There is a clear shift of the dominant Cyanobacteria species from *Microcystis spp.* to *Anabaena spp.* in the late summer and early autumn. *Anabaena*, as a nitrogen-fixing species, formed heterocyst in this time.

The aim of the study was to find factors affecting the seasonal appearance of *Anabaena* in Poyang Lake. We hypothesize that the transition in water level is responsible for shifts in species domination within the Cyanobacteria population from *Microcystis* to *Anabaena* and back. We further hypothesize that increasing biomass and heterocyst formation of *Anabaena* can be

primarily caused by seasonal changes in water level. Such fluctuations alter the physical and chemical parameters of a system, such as Poyang Lake.

Materials & Methods

Study area

Poyang Lake (28°22' N–29°45' N, 115°47' E–116°45' E) is located in northern Jiangxi Province and south of the middle and lower reaches of the Yangtze River. The lake flows from south to north to discharge into the Yangtze River through a narrow outlet at Hukou (Fig. 1). The lake level and its annual change is determined by discharges from the five sub-tributaries and the climatic variability in the region. Precipitation increases rapidly from March to August and decreases after September. In response to the annual cycle of precipitation, Poyang Lake has four obvious different phases: low water level phase, increasing water level phase, high water level phase and decreasing water level phase. The water level will increase to higher than 14 m above sea level at Wu Song at Xingzi in the high water level phase, with the maximum between 16 to 20 m. It disperses into several smaller water bodies in the low water level phase when the water level decreases to 13 m, the point “S” in Fig. 1. It is divided into two parts by Songmenshan Mountain. The northern part is the water channel joining the Yangtze River, with the length of 40 km and the width of 3-5 km (the narrowest point is about 2.8 km). Water area in the northern part between Duchang and Xingzi counties of Poyang Lake, were selected for the study (Fig. 1). This area forms a narrow meandering channel in the low water level phase during the winter. Cyanobacteria (mostly *Anabaena*, *Microcystis* and *Planktothrix*) gathered in this area in summer and autumn.

Methods

Samples were collected weekly or bi-weekly during the period May to November in 2013 and June to December 2014. Five stations were selected to sample in the water area in the northern part between Duchang and Xingzi counties of Poyang Lake (Fig. 1). Water depth was measured using a hand held Speedtech Depthmate portable sounder. Water transparency was estimated using a ~30 cm Secchi disc. Water temperature and pH were measured in situ with multiparameter profiler YSI 6600 V2. The water samples were collected by a 'Ruttner'-sampler at three depths (surface, middle and bottom layers of the lake) and combined in a clean bucket to form the final sample directly at each point. Phytoplankton sub-samples (1000 mL) were immediately fixed with 10 mL Lugol's Iodine solution. The phytoplankton taxon was identified

and enumerated by the inverted-microscope Nikon TS100-F following the sedimentation and inverted-microscope method of Utermöhl (1958). The algal division, taxa, genus, and species were identified according to Hu and Wei (2006) and the biomass estimated by volume. Heterocyst frequency, the number of heterocyst per unit length of filament (Chan et al., 2004), can be used as an indicator of the N_2 fixation capacity of the Cyanobacteria (Laamanen & Kuosa, 2005). Water column nutrient (NO_2 -N, NO_3 -N, NH_4 -N, and PO_4 -P) samples were filtered with 0.2 μm syringe filters before determined. Total N (TN) and total P (TP) were determined by persulfate oxidation and spectrophotometry (Jin & Tu, 1990). Total P was oxidized to PO_4^{3-} at 120°C. Dissolved inorganic nitrogen (DIN) is the sum of concentrations of NO_2 -N, NO_3 -N and NH_4 -N. The chlorophyll a concentration (chl a) was determined according to Lorenzen (1967). Water level data for the period January 2013 to December 2014 were obtained from the hydrology of the Jiangxi Province website (http://www.jxsl.gov.cn/id_jhsq201404101112508271/column.shtml).

All calculations were completed with the statistical package SPSS for Windows (version 17.0). One-way analysis of variance tests (ANOVA) were used to determine if the mass concentrations of dissolved nutrients in water (NH_4^+ -N, NO_3^- -N, and PO_4^{3-} -P) differed among the sampling periods (Kar et al., 2015). A Spearman rank correlation test was performed to detect correlations between measured physico-chemical parameters and the flooding regime to *Anabaena* heterocyst frequency in Poyang Lake. Graphs were generated with SigmaPlot 12.0 (Systat Software Inc.).

Results

Water level changed from 8.67 m to 16.70 m in 2013 and from 7.37 m to 18.59 m in 2014 (Fig. 2 and Table 1). Water temperature ranged from 15 to 33°C in 2013 and 12 to 30°C in 2014. It was the coincidence that the water level was high in summer when the temperature was high. Water transparency was about 0.5-0.7 m in May and June at the beginning of the increasing water level phase and it decreased to 0.3-0.4 m in August of 2013. Water transparency ranged between 0.25-0.5m in 2014.

The seasonal change in water level triggers variable nutrient concentrations largely due to dilution (Table 1 and Fig. 3). Total nitrogen concentrations varied from 0.49 to 3.07 mg L^{-1} in the increasing water level phase, averaging 1.70 mg L^{-1} , and varied from 1.21 to 3.44 mg L^{-1} in the high water level phase, averaging 1.85 mg L^{-1} . Nitrate concentrations varied from 0.24 to

1.52 mg L⁻¹ in the increasing water level phase, averaging 0.87 mg L⁻¹, and varied from 0.66 to 1.63 mg L⁻¹ in the high water level phase, averaging 0.95 mg L⁻¹. Nitrite concentrations varied from 0.019 to 0.053 mg L⁻¹ in the increasing water level phase, averaging 0.037 mg L⁻¹, and varied from 0.012 to 0.067 mg L⁻¹ in the high water level phase, averaging 0.037 mg L⁻¹. Ammonium concentrations varied from 0.076 to 0.182 mg L⁻¹ in the increasing water level phase, averaging 0.129 mg L⁻¹, and varied from 0.016 to 0.161 mg L⁻¹ in the high water level phase, averaging 0.089 mg L⁻¹. PO₄-P concentrations varied from 0.003 to 0.191 mg L⁻¹ in the increasing water level phase, averaging 0.038 mg L⁻¹, and varied from 0.011 to 0.217 mg L⁻¹ in the high water level phase, averaging 0.045 mg L⁻¹ (Fig. 3). Total phosphorus concentrations varied from 0.011 to 0.621 mg L⁻¹ in the increasing water level phase, averaging 0.108 mg L⁻¹, and varied from 0.038 to 0.252 mg L⁻¹ in the high water level phase, averaging 0.108 mg L⁻¹. DIN/DIP varied from 4.41 to 506.78 in the increasing water level phase, averaging 104.02, and varied from 4.43 to 88.76 mg L⁻¹ in the high water level phase, averaging 42.73 (Table 1). The difference in nutrient concentrations between the low and high water level are clearly revealed for NH₄-N, NO₂-N, PO₄-P, as well as for transparency by one-way ANOVA, Values were significantly different (p<0.05) among the two water level phases.

Associated with water level changes and the resulting shift in nutrient concentrations are significant alterations in phytoplankton community composition. During the high-water level phase of 2013, Cyanobacteria contributed 78.5% to the average 11.1 mg L⁻¹ of total phytoplankton biomass (Fig. 4A & B). Main genera were *Microcystis*, *Planktothrix* and *Anabaena* (Fig. 4C). Among the six species of *Anabaena* identified, namely *Anabaena affinis*, *A. planctonica*, *A. smithii*, *A. circinalis*, *A. spiroides* and *A. azotica*, the last two were the most prominent ones. The average relative biomass of *Anabaena* was 43.6% during the study periods. Higher contributions occurred in May, July and August of 2013 and were over 40% during most of 2014.

Anabaena abundance ranged from 5 cells mL⁻¹ to 9500 cells mL⁻¹ (Fig. 5A) but was around 50-150 cells mL⁻¹ most of the time, except for the high values of 3000-9500 cells mL⁻¹ in May and August 2013 and 300-500 cells mL⁻¹ in August and September 2014. The mean filament size was 50 cells, ranging from 25 to 171 cells in 2013, while the mean filament size ranged from 25 cells to 58 cells in 2014. The average heterocyst frequency was 3.42% and 9.63% in August of 2013 and 2014, respectively (Fig. 5B). The heterocyst frequency was 3.65% in the increasing

water level phase, and 3.82% in the high water level phase averaged for both years. The greater percentages of heterocysts during high water level are an indirect indication of possible N-fixation which is supported by the low nitrogen concentration and the DIN/DIP ratio.

To evaluate the interdependence between all variables and the parameters of *Anabaena* a Spearman Rank Correlation was used (Table 2). The measured environmental variables were significantly correlated with water level. *Anabaena* biomass was positively correlated with water temperature and water level, and negatively correlated with TN. Heterocyst frequency of *Anabaena* was positively correlated with water temperature, water level and $\text{PO}_4\text{-P}$, and negatively with DIN/DIP, $\text{NO}_3\text{-N}$ and TN.

Discussion

Water level changes were 8.03 m and 11.22 m in 2013 and 2014, respectively, which were much more than in other studies (Zohary T & Ostrovsky I., 2011; Nöges, Nöges & Laugaste, 2003; Casali et al., 2011). Water level changes intensely influence nutrient cycling and mixing processes, which led to the variations of the aquatic biota and phytoplankton dynamics (Zohary and Ostrovsky, 2011; Bakker & Hilt, 2016). Regular annual extreme water level change of Poyang Lake is the foremost driver for environmental parameters in this floodplain lake ecosystem (Liu, Teubner & Chen, 2016b). Total nitrogen and total phosphorus concentrations show a clear seasonal pattern in Poyang Lake.

Total nitrogen concentration was 1.5 mg L^{-1} on average and mean total phosphorus concentrations was 0.13 mg L^{-1} in Poyang Lake. The high nutrient concentration was propitious to the propagation and proliferation of algae (Deng et al. 2011; Zhen et al. 2011). Buoyant migration of Cyanobacteria blooms to the lake surface was observed during summer and autumn in 2012-2013 in some regions of Poyang Lake indicating the Cyanobacteria bloom in some regions and the highly eutrophic status of the lake (Liu et al., 2016a; Qian et al., 2016a). Cyanobacteria were usually subdominant in Lake Poyang. Cyanobacteria temporarily became the dominant species accounting for about 57% of total phytoplankton biomass and replacing diatoms in August 2013. The Cyanobacterial biomass was significantly greater in the Eastern Bay (lentic region) than in the lotic region of Northern Poyang Lake (Liu et al., 2016a). The higher nutrient concentrations in the northern part seem to be the result of nutrients and phytoplankton biomass coming from the southern part of the lake (Liu et al., 2016a; Liu, Qian & Chen, 2015). These results may indicate the transportation of Cyanobacteria with the water

current from the southern part to the northern part of Poyang Lake because of the buoyant characteristics of Cyanobacteria.

Anabaena biomass was positively correlated with water temperature and water level, and negatively correlated with TN. Similar as in the floodplain lakes of the Paraná basin during the warm season (Emiliani 1990, 1993), high biomass of N₂-fixing *Anabaena* were documented in Poyang Lake. Warm water is necessary for the growth of diazotrophic organisms (Stal, 2009). The development of the *Anabaena* population was strongly correlated with water temperature and the highest biomasses were at the times of the temperature maxima similar to what has been reported elsewhere (Laamanen & Kuosa, 2005). *Anabaena* can be recorded in the water column of Poyang Lake throughout the year, but it had its annual biomass peak in summer in Poyang Lake (Qian *et al.*, 2016a). *Anabaena* biomass varied synchronously with the change water temperature and was therefore significantly correlated temperature.

Cyanobacterial N₂ fixation is of ecological importance in aquatic environments (Karl *et al.*, 2002). When N/P ratios are low and phosphate concentrations are high, as is the case in floodplain lakes, phytoplankton communities can become dominated by heterocyst-bearing Cyanobacteria capable of N₂ fixation (Lewis & Wurtsbaugh, 2008). It resulted the dominance of N-fixing Cyanobacteria of the phytoplankton community composition in a mesocosm experiment when N/P ratio was low (Schindler, 1977; Smith, 1983; Levine & Schindler, 1999; Smith & Bennett, 1999; Vrede *et al.*, 2009). *Anabaena* developed quickly when N/P dropped in spring and ranked the first in terms of biomass in summer in Chaohu Lake (Deng *et al.*, 2007). *Anabaena* is one of the genera of filamentous Cyanobacteria that can exist as plankton and is known for its nitrogen fixing abilities. The formation of the heterocysts is induced by the lack of combined nitrogen in the medium (Schindler, 1977). The number of heterocysts correlates with the N₂ fixation activity of the population (Lindahl, Wallström & Brattberg, 1980; Riddolls, 1985). When DIN concentration is at limiting levels the ability to fix N₂ is a clear advantage for heterocyst bearing Cyanobacteria (Smith, 1983; Hense & Beckmann, 2006; Piehler *et al.*, 2009). In the present study, heterocyst frequency of *Anabaena* was positively correlated with water temperature, water level and PO₄-P, and negatively with DIN/DIP, NO₃-N and TN, which is the reason for the increase of heterocyst frequency at high water level in both years. Therefore, *Anabaena* was able to propagate with low nitrogen concentration.

In addition, buoyancy provided by the gas vesicles of *Anabaena* enables it to float to the surface to make the most of the available light (Walsby *et al.*, 1989) and atmospheric nitrogen. This is the reason why visible buoyant migration to the lake surface of Cyanobacteria blooms occurred during summer and autumn in 2013 -2014 in some regions of Poyang Lake when *Anabaena* was the dominant species (Qian *et al.*, 2016b). *Anabaena* can fix atmospheric nitrogen at such low levels of nitrogen that nitrogen would not necessarily limit their growth in Poyang Lake during the high water level phase. *Anabaena* biomass was positively correlated with water temperature and water level, and negatively correlated with TN, which is the reason for the increase of heterocyst frequency in the present study.

Water level fluctuations exert an overall impact on phytoplankton community composition, through affecting the physical and chemical environmental parameters in Poyang Lake (Qian *et al.*, 2016a). Low and high-water level periods differed in several water quality characteristics in Poyang Lake, such as NO₂-N, NO₃-N, TN and TP. The water level change coincided with the season in Poyang Lake. The summer population of *Anabaena* usually contains heterocysts, while filaments were usually devoid of heterocysts in winter and early spring (Laamanen, 1996). The average relative contribution of *Anabaena* to Cyanobacterial biomass was 43.55% and heterocyst frequency was higher than 3% in high-water level phases in Poyang Lake. We conclude that variations in environmental parameters related to both seasonal variations and water level changes triggered the variations in *Anabaena* biomass and heterocyst frequency.

Conclusions

Cyanobacteria biomass accounted for about 57% of total phytoplankton biomass, temporarily becoming the dominant species even replacing diatoms in August in 2013. The dominant species of Cyanobacteria were nitrogen-fixing *Anabaena*, which was present throughout the year. The average relative biomass of *Anabaena* during the study period was over 40%, being most abundant in summer. When water level increased, *Anabaena* became the dominant species, produced a high number of heterocysts, reflecting relatively nitrogen deficiency in Lake Poyang during this period. The results of the study support the hypothesis that increasing biomass and heterocyst formation of *Anabaena* were primarily triggered by variations in the environmental factors, such as high water temperature and suitable nutrients in summer and autumn, driven by the regular annual extreme water level change of Poyang Lake. The results can provide a theoretical basis for the management and utilization of Lake Poyang.

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Figure 1

Map of Poyang Lake indicating Songmen Mountain and the reference point 'S' (refer to the text).

The insert shows the area at 13 m water level in dark grey and at 20 m water level in light grey. The locations of the sampling stations are indicated by numbers #1-5.

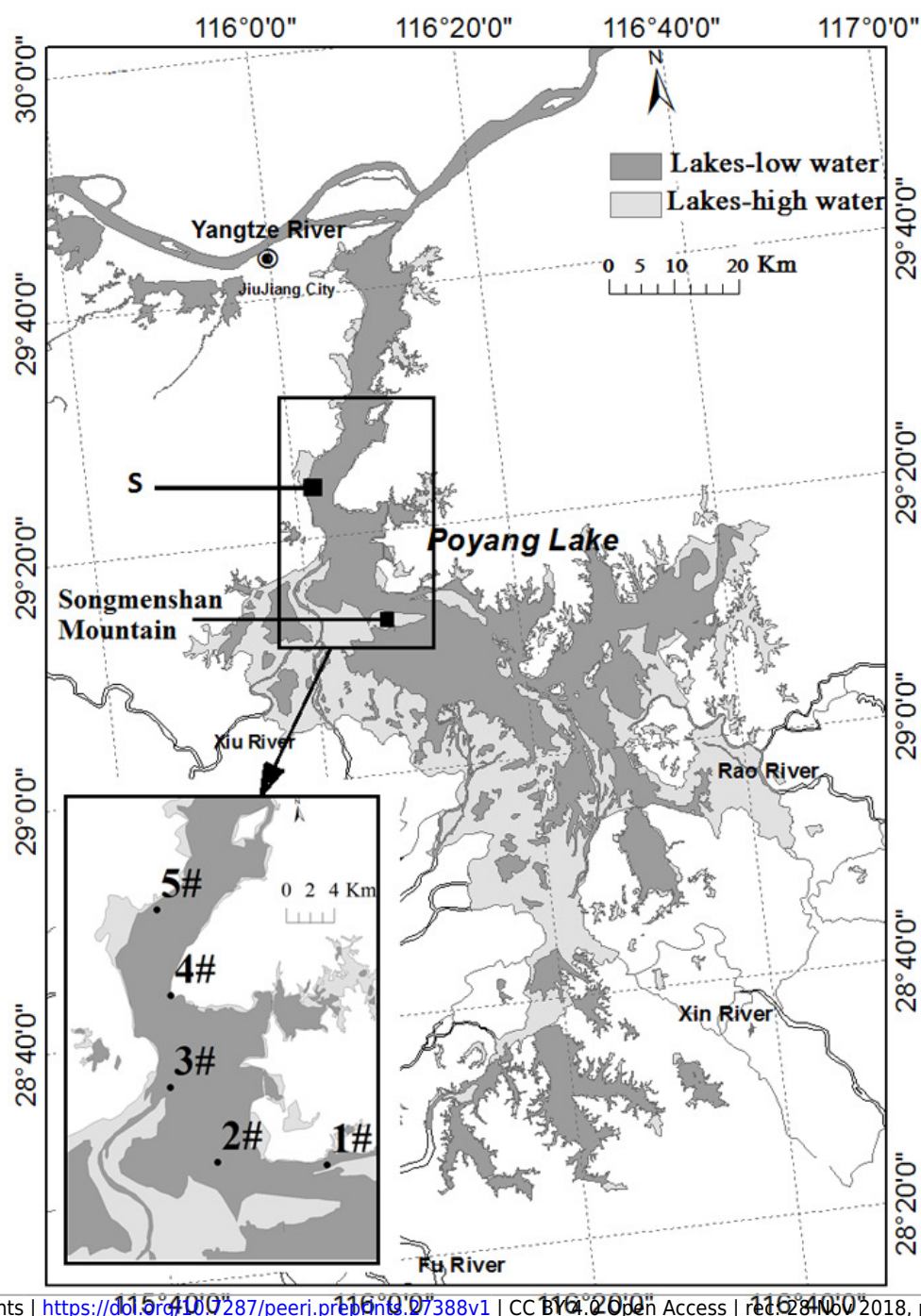


Figure 2

Water level fluctuations of Poyang Lake in the years 2013 and 2014

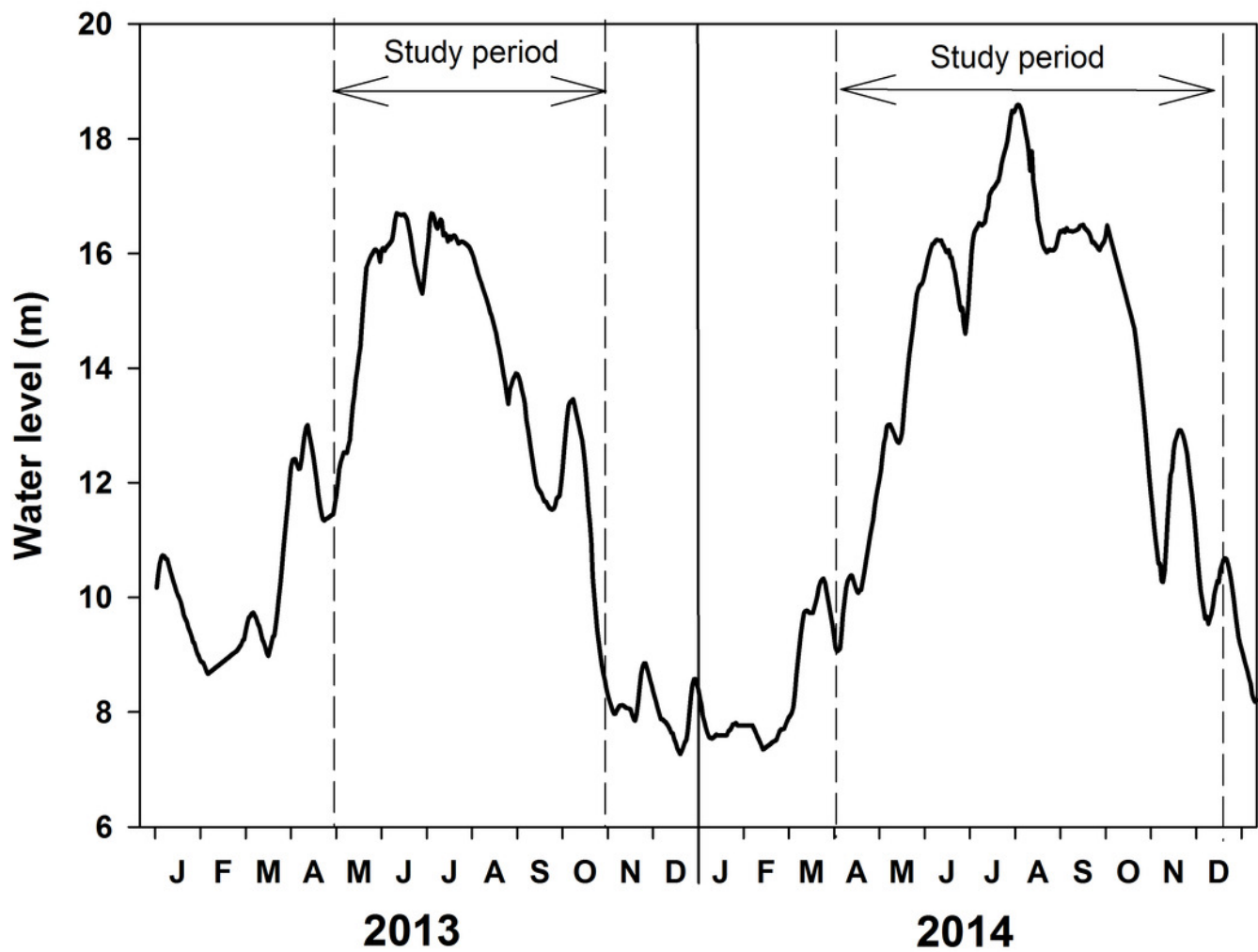


Figure 3

Variations of the masured environmental parameters in the years 2013 and 2014

(A) water temperature and water level, (B) suspended solids (SS) and transparency, (C) conductivity and pH, (D) total phosphorus (TP-P) and phosphate ($\text{PO}_4\text{-P}$), (E) total nitrogen (TN-N), nitrite ($\text{NO}_2\text{-N}$), nitrate ($\text{NO}_3\text{-N}$) and ammonium ($\text{NH}_4\text{-N}$) and (F) DIN and DIN/DIP

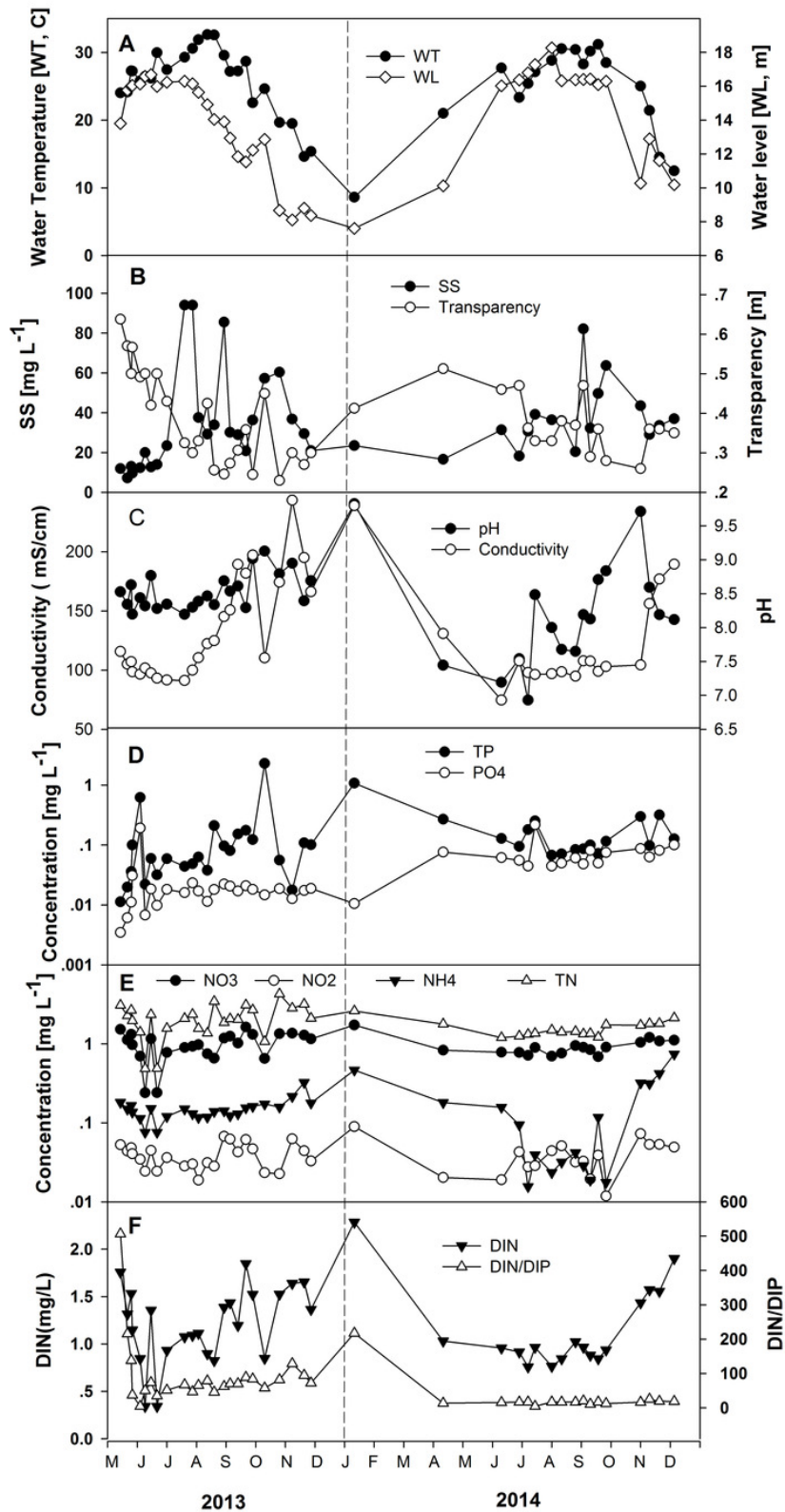


Figure 4

Variations of the phytoplankton biomass and chlorophyll-a in the years 2013 and 2014

(A) Phytoplankton biomass and chlorophyll-a. (B) Percent of Cyanobacteria in the total phytoplankton biomass. (C) The relative biomass of the dominant Cyanobacteria genera. For references, the water level changes from Figure 2 is inserted as a grey line in panel B.

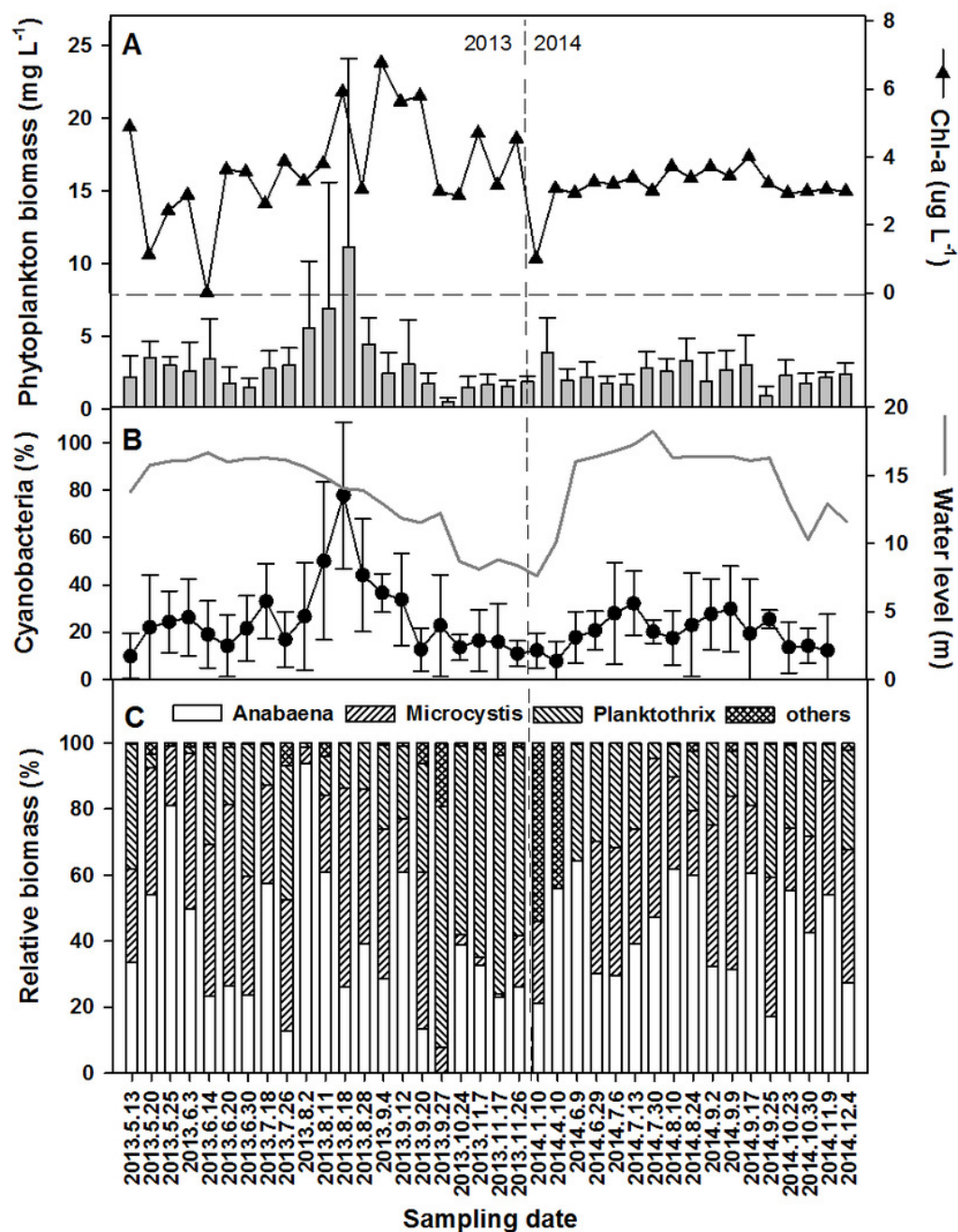


Figure 5

Variations of *Anabaena* abundance and *Anabaena* heterocyst frequency in the years 2013 and 2014

(A) *Anabaena* abundance. (B) Mean filament length and heterocyst frequency.

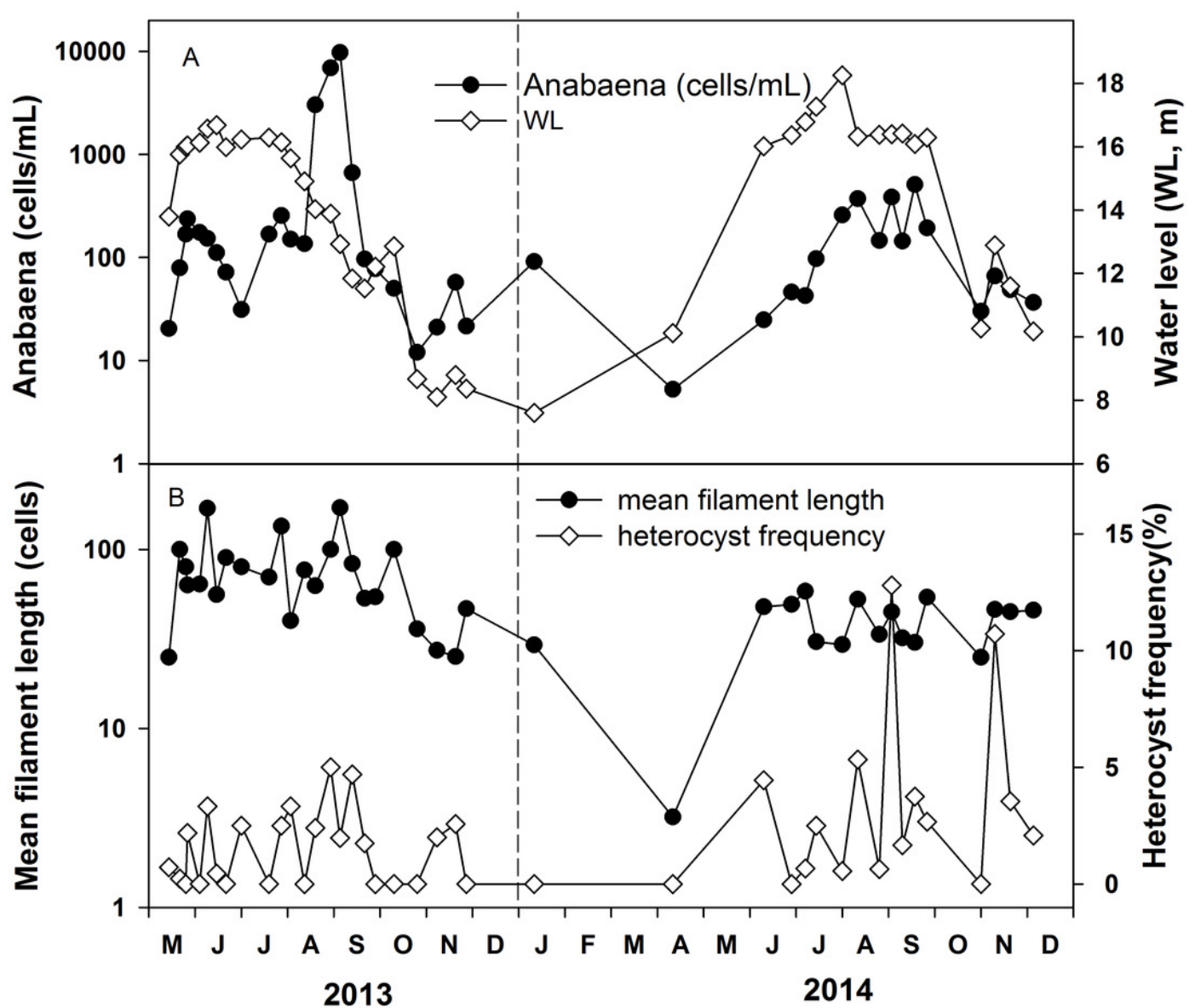


Table 1 (on next page)

Summary of statistical data for the measured variables

1

Table 1 Summary of statistical data for the measured variables

	Mean	Max	Min	Std Dev
WL(m)	13.789	18.26	7.6	3.091
WT(°C)	25.508	33.31	10.03	5.408
Transparency (m)	0.374	1.0	0.1	0.17
SS(mg L ⁻¹)	35.897	203.3	1.4	33.707
Turbidity(NTU)	45.223	418	2.4	37.841
pH	8.378	10.38	6.72	0.565
Conductivity(ms cm ⁻¹)	130.127	495.7	37.9	49.713
TN(mg L ⁻¹)	1.984	7.3	0.04	1.07
NO3-N(mg L ⁻¹)	0.991	2.17	0.07	0.343
NO2-N(mg L ⁻¹)	0.0388	0.18	0.0001	0.0255
NH4-N(mg L ⁻¹)	0.157	1.33	0.001	0.157
TP(mg L ⁻¹)	0.122	3.63	0.01	0.299
PO4-P(mg L ⁻¹)	0.05	0.85	0.001	0.0668
DIN/DIP	43.559	172.43	0.8	38.163

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Table 2 (on next page)

Correlation coefficients (Spearman's rho) between environmental variables and parameters of *Anabaena*

1 **Table 2 Correlation coefficients (Spearman's rho) between environmental variables and parameters of *Anabaena***

	herocyst	Anabaena	Cyanobacteria	phytoplankton	Chla	WL
WL	0.327**	0.171*	0.215**	0.132	0.172*	1.000
WT	0.167*	0.315**	0.384**	0.292**	0.409**	0.539**
transparency	-0.016	0.012	-0.063	0.219**	-0.106	0.181*
SS	-0.019	0.005	0.021	-0.259**	0.048	-0.068
Turbidity	-0.049	-0.111	-0.099	-0.245**	-0.070	-0.310**
pH	-0.063	0.034	0.054	-0.043	-0.001	-0.297**
Conductivity	-0.187*	-0.193*	-0.137	-0.145	-0.174*	-0.658**
TN	-0.157*	-0.160*	-0.174*	-0.150*	-0.118	-0.507**
NH ₄ -N	-0.055	-0.049	-0.106	0.017	-0.220**	-0.561**
NO ₃ -N	-0.188*	-0.132	-0.128	-0.120	-0.175*	-0.476**
TP	0.099	-0.111	-0.065	-0.151*	-0.055	0.072
PO ₄ -P	0.247**	-0.057	-0.148	-0.042	-0.164*	0.440**
DIN/DIP	-0.255**	0.020	0.093	0.023	0.043	-0.642**

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

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