Phytoplankton dynamics and their relationship with environmental variables of Lake Poyang
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ABSTRACT
Field investigations were conducted to identify environmental variables influencing phytoplankton dynamics in Lake Poyang. The results showed that diatoms predominated in the phytoplankton community. Concentrations of nutrients were high, and levels of phytoplankton biomass and chlorophyll a were low. During the low water level period (WLP), from January to May 2013, phytoplankton biomass was low. It increased from July 2013 and peaked in September 2013 during the high WLP. From October 2013 to January 2014, phytoplankton biomass decreased again. Highest values were generally measured in the middle district and lowest in the northern district. It decreased from October 2013 to January 2014. Redundancy analysis showed that water temperature and suspended solids (SS) concentrations were the principal factors regulating the growth of phytoplankton. The variations in SS were contrary to the biomass variations at the spatial level. During the high WLP, the blocking effect of the Yangtze River led to decreased water velocity and prolonged water retention time in Lake Poyang. Due to both the SS sedimentation and increase in water temperature, phytoplankton grew rapidly. Based on these findings, the variety of phytoplankton dynamics was caused by the combined effects of the Yangtze River effect, water temperature, and SS.

Key words | environmental variables, Lake Poyang, phytoplankton dynamics, suspended solids, Yangtze River

INTRODUCTION
Phytoplankton is the main primary producer of water ecosystems and plays an important role in food chains (Reynolds 1984). Alterations in phytoplankton composition and distribution characteristics in water reflect a changing environment and indicate the trophic status (Reynolds et al. 1993; Chen et al. 2005; Wu et al. 2011). The dynamics of phytoplankton communities are influenced by a complex array of biotic and abiotic factors operating through direct and indirect pathways (Vanni & Tente 1990; Carrillo et al. 1995; Burford & Davis 2011). The nutrient content, structure, and dynamics have received particular attention in the world's northernmost temperate lakes. When compared to other macronutrients required by biota, phosphorus is the least abundant and commonly the first element to limit biological productivity (Wetzel 2001). However, the nutrient–chlorophyll a (Chl a) relationship is generally nonlinear, and suggests that other factors, e.g., physical (water level, water flow, light) and biotic (predation, competition) also limit algal growth (Millard et al. 1996; Schernewski et al. 2005).

With regard to lotic lakes, hydrological factors such as water level, water flow, and water retention time are thought...
to be of greater importance to phytoplankton development (Pace et al. 1992; Lázár et al. 2012). Many studies have addressed patterns of phytoplankton variation in floodplain ecosystems, rivers, and estuaries, where the water level strongly affects the ecosystem (Zinabu 2002; Huang et al. 2004; Burford et al. 2012). High levels of phytoplankton biomass have been observed during periods of low water levels, when more light and nutrients are available in temperate lakes (Nõges et al. 2003). Tockner et al. (1999) showed that Chl a concentration was usually influenced more strongly by water flow than by nutrients in rivers and their associated waters. Decreases in flow velocity accelerate freshwater phytoplankton growth, while increases inhibit phytoplankton growth (Sabater et al. 2008; Palijan 2012). Water retention time is also a crucial factor affecting algal growth, and a longer water retention time will benefit phytoplankton growth (Soballe & Kimmel 1987; Emiliani 1997). Additionally, phytoplankton Chl a concentrations may vary with discharge, catchment area, water depth, or other physical factors (Kilkus et al. 1975; Soballe & Kimmel 1987).

As one of the largest floodplains in the world, the Yangtze River floodplain is characterized by numerous shallow lakes which are freely connected to the Yangtze River (Pan et al. 2009). Lake Poyang, which is the largest freshwater lake in China and connected to the Yangtze River, is characterized by complex hydrographic conditions. Nitrogen and phosphorus concentrations of Lake Poyang have increased in the last 30 years (Zhen 2010). The concentrations of nitrogen and phosphorus were 0.684 mg/L and 0.076 mg/L in 1998, but were 2 times and 0.2 times higher, respectively, in 2013. However, the Chl a content of Lake Poyang increased slowly relative to other eutrophic lakes, such as Taihu and Chaohu in the mid-lower regions of the Yangtze River.

Lake Poyang has five tributaries and connects to the Yangtze River (Pan et al. 2009). Water exchange between Lake Poyang and the five tributaries, the Yangtze River, or the upstream reservoirs is closely related and determines the unique seasonal fluctuation of inflow discharge, water level, and flow velocity of the lake (Jiang & Huang 1997; Guo et al. 2012; Zhang et al. 2014). These characteristics have made phytoplankton dynamics and environmental factors very complicated. Wu et al. (2013) found that the biomass of major algal groups (i.e., Bacillariophyta, Cryptophyta, and Chlorophyta) and the total biomass of Lake Poyang were significantly and positively correlated with the average transparency determined from seasonal data. The annual trends in phytoplankton Chl a were associated with nutrient concentrations and temperature, but few significant correlations between Chl a and the nutrient concentrations were observed in the dry and mid-dry seasons of Lake Poyang (Wu et al. 2015; Wang et al. 2015), and light (or turbidity) and water retention time is more important than nutrients for restricting phytoplankton biomass (Wu et al. 2014a, 2014b). Pan et al. (2009) showed that phytoplankton Chl a was closely related to certain environmental factors, especially water velocity (U) at lotic sites. Regression analyses in lotic regions revealed that a higher amount of variance in log10 Chl a was accounted for by U0.5 (r2 = 0.34), and that U was the major factor influencing Chl a.

However, under the complicated variations in the river–lake relationship, especially the blocking effect of the Yangtze River to Lake Poyang during the high water level period (WLP), the dynamics of phytoplankton and the associated environmental variables during water level changes remain unclear. Therefore, we conducted field investigations at 17 sites of Lake Poyang during the high, normal, and low level period in 2012 and 2013, and during water level changes from July 2013 to January 2014 to illustrate the phytoplankton composition and the temporal–spatial distribution of phytoplankton in Lake Poyang. We also considered some environmental variables that are responsible for alterations in phytoplankton composition and distribution, such as suspended solids (SS), velocity, transparency, total nitrogen (TN), total phosphorus (TP), and temperature to explain the key factors influencing phytoplankton dynamics of the lakes connected to the Yangtze River.

**MATERIALS AND METHODS**

**Study area**

Lake Poyang (28°22′–29°45′N, 115°47′–116°45′E) is located in Jiangxi Province of southeast China in the downstream portion of the Yangtze River (Figure 1). The lake contains five tributaries (Xiu River, Gan River, Fu River, Xin River, Rao River) and connects in the
north to the Yangtze River in Hukou (Pan et al. 2009). The lake undergoes seasonal fluctuations in level under the combined action of the five tributaries and the Yangtze River (Shankman et al. 2006; Ye et al. 2011). However, these fluctuations are inconsistent during different WLPs. Specifically, in the high WLP, annual discharge of the lake is approximately $6 \times 10^{12}$ m$^3$. However, in the low WLP, annual discharge of the lake is 2.4 times lower than during the high WLP (Wang et al. 2013). The average water level of Lake Poyang is 12.86 m; however, the water level fluctuates greatly. The highest water level of 22.50 m was observed in 1998, while the lowest water level of 5.90 m was observed in 1963 (Xingzi Hydrological Station).

**Sample collection and analysis**

Samples were collected during the high WLP (June 2012 and July 2013), the normal WLP (September 2012 and October 2013), and the low WLP (November 2012 and December 2013) at 17 sites covering the lake. In addition, we added another sampling period from July 2013 to January 2014 to obtain data during the period of dramatic water level changes using the same sites. To determine the
spatial variations in phytoplankton, the study area was divided into three regions, the northern district (sites 1–5), the middle district (sites 6–11), and the southern district (sites 12–17) (Figure 1).

Phytoplankton samples were collected from the surface water (0.5 m) in cleaned 1 L plastic containers. Samples were fixed in situ with Lugol’s iodine solution (1.5% v/v) and allowed to settle for 24 h, after which they were concentrated to 50 mL. Enumeration of the algae was done using a Leica microscope (DM750, Leica). Taxa were classified according to Hu & Wei (2006) and identified to the genus level. We used a 0.1 mL counting box containing 100 horizons at 10 × 40 magnification to calculate the algal cell density (SEPA 2012). This value was then converted into biomass (Bio) and the mean volume was calculated using appropriate geometric configurations (Hillebrand et al. 1999). Volume values were converted to biomass assuming that 1 mm³ of volume was equivalent to 1 mg of fresh-weight biomass. Samples were analyzed using Duncan’s (D) test after one-way analysis of variance (one-way ANOVA) and redundancy analysis (RDA) conducted with CANOCO (version 4.5) (Liu et al. 2010; Wang et al. 2011).

Selected environmental parameters, including water temperature (T), pH, and dissolved oxygen (DO), were obtained using a Hydrolab Data Sonde 5 sensor in situ. Water samples were obtained and placed into acid-cleaned 1 L plastic containers and kept cool and shaded before being transported to the laboratory for analysis, which was conducted in 24 hours. TN was measured by the alkaline potassium persulfate digestion-UV spectrophotometric method, while ammonia nitrogen (NH₃-N) was analyzed by Nessler’s reagent spectrophotometry. TP was measured using the ammonium molybdate method, SS were analyzed using the weighing method (105 °C) and water transparency (Tran) was determined using a Secchi disk. All of the above methods are described in detail in the Water and Waste-water Monitoring Analysis Method of the Standard Methods (SEPA 2012). Chl a was determined by the acetone extraction-spectrophotometric method (Arar 1997).

A depth-averaged two-dimensional numerical model was applied based on high resolution lake survey data in 2010 to study the hydrodynamics of Lake Poyang. The computational domain is about 98 km × 124.25 km covering the whole lake with the mesh size 250 m × 250 m. There are four national flood storage and detention basins separated from the main lake by the embankment in the south and eastern part of Lake Poyang. The northern boundary is set up as water levels at Hukou which is the confluence of Lake Poyang and the Yangtze River. There are five tributaries flowing into the lake, which were treated as mass and momentum source term in the simulation.

RESULTS

Phytoplankton community structure and dominant species

Overall, 81 genera belonging to eight phyla were identified during 2013 (Appendix and Table 1; the Appendix is available with the online version of the paper). Chlorophyta (40 genera) were the largest group, representing 49.38% of the total number of genera, followed by Cyanophyta (17), Bacillariophyta (13), Euglenophyta (4), Pyrrophyta (2), Cryptophyta (2), Chrysophyta (2), and Xanthophyta (1). The average biomass of phytoplankton in all sampling sites during the investigation time was 0.488 mg/L. Bacillariophyta were the dominant groups (0.142 mg/L), accounting for 29.10% of the total biomass. The biomass of Cryptophyta (0.089 mg/L), Chlorophyta (0.088 mg/L), and Euglenophyta (0.080 mg/L) was slightly lower than that of Bacillariophyta, contributing 18.24%, 18.03%, and 16.39% of the total biomass, respectively. The biomass of other phyla such as Chrysophyta and Xanthophyta

| Phylum           | Average biomass (mg/L) | Percentage (%) | Average density (cells/L) | Percentage (%) |
|------------------|------------------------|----------------|---------------------------|----------------|
| Cyanophyta       | 0.043                  | 8.88           | 3.78 × 10⁵                 | 38.68          |
| Chlorophyta      | 0.088                  | 18.07          | 1.73 × 10⁵                 | 17.67          |
| Bacillariophyta  | 0.142                  | 29.00          | 2.15 × 10⁵                 | 22.02          |
| Cryptophyta      | 0.089                  | 18.19          | 5.07 × 10⁴                 | 5.18           |
| Pyrrophyta       | 0.036                  | 7.30           | 1.98 × 10⁴                 | 2.02           |
| Euglenophyta     | 0.080                  | 16.46          | 8.35 × 10⁴                 | 8.54           |
| Chrysophyta      | 0.010                  | 2.00           | 5.64 × 10⁴                 | 5.78           |
| Xanthophyta      | 0.001                  | 0.10           | 1.02 × 10³                 | 0.10           |
| Total            | 0.488                  | 100            | 9.77 × 10⁵                 | 100            |
was much lower than that of the phyla listed above. The order of magnitude of cell density was not the same as that of the phytoplankton biomass. *Cyanophyta*, *Bacillariophyta*, and *Chlorophyta* accounted for most of the cells (78.37%).

**Temporal–spatial distribution of phytoplankton**

The biomass varied greatly in different WLPs. The average biomass was highest in the high WLP (0.562 mg/L), which was much higher than in the normal and low WLPs (0.187 mg/L, 0.102 mg/L) (Figure 2). However, phytoplankton biomass had a similar spatial distribution pattern in the three WLPs. Phytoplankton biomass was higher in the middle district (0.144 mg/L) than in the southern district (0.103 mg/L), and both were much higher than in the northern district (0.037 mg/L).

The phytoplankton community structure changed significantly in different WLPs. The dominant phytoplankton was *Bacillariophyta* in the high WLP, and *Cryptophyta* or *Bacillariophyta* in the normal and low WLP. In the mid-east part of the lake (sites 8–10) in the high WLP, when biomass was highest, the dominant phytoplankton was *Bacillariophyta*, but *Cyanophyta* comprised a greater proportion than at other sampling sites. The *Cyanophyta* cell density (4.03 \times 10^5 cells/L) was higher than that of *Bacillariophyta* (2.80 \times 10^5 cells/L). *Anabaena*, *Aphanizomenon*, and *Pseudanabaena* were the most important genera of *Cyanophyta*.

**Yearly variations in phytoplankton biomass**

Phytoplankton biomass was low from January 2013 to May 2013 and increased from July 2013 to obtain its maximum in September 2013, while it decreased from October 2013 to January 2014 (Figure 3). In the first stage (January to May), phytoplankton biomass increased as water level increased. From July to August, the biomass continued to increase but the water level began to decrease. From August 2013 to January 2014, the decrease in biomass coincided closely with decreases in water level. *Bacillariophyta* biomass showed little change from January 2013 to January 2014. *Cryptophyta* and *Pyrrophyta* prevailed in May. *Chlorophyta* prevailed in July and *Bacillariophyta* prevailed in August. *Euglenophyta* dominated in September and *Bacillariophyta* dominated from October 2013 to January 2014. *Cyanophyta* biomass changed markedly with variations during the water level changes period, with the highest value in July and August.

**Environmental parameters**

Water quality data for Lake Poyang from samples collected at the 17 stations are presented in Figure 4. The TN and TP concentration of Lake Poyang were high, with a mean value of 1.45 mg/L and 0.051 mg/L, and wide ranges of 0.32–14.22 mg/L and 0.005–0.499 mg/L, respectively. The highest concentration of TN and TP both occurred during the low WLP. NH3-N concentration did not vary significantly between the three WLPs and tended to decrease from the high WLP to the low WLP. The water transparency was low in Lake Poyang, with a mean value of 0.53 m and the range of 0.1–0.9 m. SS concentrations were high (52.32 mg/L), and varied greatly (9.4–153.5 mg/L), showing the opposite trend of water transparency. During the three WLPs, Chl a concentration was between 2.65 and 5.38 μg/L, and this value decreased as the water level decreased. Chl a variation was similar to the variations of phytoplankton biomass. There were no significant differences (p > 0.05) in DO and pH.

RDA (Figure 5) indicated that phytoplankton biomass was significantly positively correlated with transparency and temperature and significantly negatively correlated with TP and SS. Phytoplankton biomass was negatively correlated with velocity (Table 2). The distributions of *Cyanophyta*, *Chlorophyta*, *Bacillariophyta*, and *Euglenophyta* were mainly related to temperature, while *Pyrrophyta* and *Chrysophyta* were influenced by transparency (Figure 5; Table 2).

**DISCUSSION**

Nutrients such as TN and TP were relatively high, while phytoplankton biomass and Chl a levels were relatively low and *Bacillariophyta* still dominated in Lake Poyang. These findings suggest that phytoplankton dynamics in Lake Poyang were affected not only by the nutrients, but also by other factors.
Figure 2 | Phytoplankton biomass variations in Lake Poyang: (a) high WLP, (b) normal WLP, (c) low WLP (left, 2012; right, 2013).
Phytoplankton biomasses and environmental variables

Being connected to five tributaries and the Yangtze River, all of which had large water flow, Lake Poyang exhibits strong hydrodynamic conditions and high SS concentrations. Figure 5 shows that SS and velocity may be the important factors affecting phytoplankton biomass. Increases in SS not only reduce light transmission (Carlson 1992), but also cause algae cells to sink by flocculation (Cao et al. 2015a, 2015b). Dong et al. (2011) showed that the percentage of cohesive sediment of Lake Poyang was 35.95–85.76%. These cohesive sediments have a flocculating effect on phytoplankton. Some other lakes in these areas, such as Lake Taihu and Lake Chaohu, had low SS concentrations (35.8 mg/L in Taihu Meiliang Bay, 20–50 mg/L in Lake Chaohu) (Chen et al. 2003; Jin et al. 2010). Chl a contents were much higher when TN and TP reached the same values as Lake Poyang a few years ago (Kun & Pu 2011; Wang et al. 2014). The water volume of the five tributaries into Lake Poyang is large, and water exchange between Lake Poyang and the Yangtze River is frequent, which may be important factors causing the high SS concentrations. Moreover, frequent shipping traffic and heavy sand exploitation in northern Lake Poyang have led to sediments’ resuspension and are the main factors responsible for increased SS concentrations.
Dynamics of phytoplankton biomass

From January to May (the normal WLP), the phytoplankton biomass of Lake Poyang increased slowly. From July to August (the high WLP), the phytoplankton biomass increased rapidly in the static lake water. After October (the normal and low WLP), the biomass began to decline.

The water level and water volume of Lake Poyang increased gradually from January to May. During this time, phytoplankton biomass increased with an increase in the amount of light (Figure 6), which suggested that increases in radiant energy are conducive to the growth of phytoplankton. In July, water level and water volume increased to maximum values of 16.71 m and 13,000 m$^3$/s, respectively. Phytoplankton biomass increased rapidly from July, and peaked in August. At this time, the water velocity of Lake Poyang decreased (Figure 7), the water retention time was prolonged (25.5 d) (Wu et al. 2014) and the SS sedimentation increased. The five tributaries carried high volumes of nutrients into the lake, which, when coupled with the higher water temperature, accelerated the growth of the phytoplankton. However, the amount of radiant energy cannot explain the increase in biomass (Figure 6).

Table 2 | Correlation coefficient of phytoplankton biomass and environmental parameters

|     | Chl a  | TN  | TP   | NH$_3$N | T    | pH   | DO   | SS   | Tran | V    |
|-----|--------|-----|------|---------|------|------|------|------|------|------|
| Bio | 0.647**| −0.060 | −0.223* | −0.162 | 0.246* | −0.211 | −0.082 | −0.271* | 0.262* | −0.114 |
| Chl a | 0.175 | 0.004 | −0.055 | 0.084 | 0.000 | 0.044 | −0.225* | 0.199 | −0.203 |
| TN | 0.557** | 0.428** | −0.078 | 0.133 | −0.112 | 0.132 | −0.275* | 0.098 |
| TP | 0.703** | 0.031 | 0.217* | −0.175 | 0.310** | −0.380* | 0.106 |
| NH$_3$N | 0.062 | −0.045 | −0.205 | 0.160 | −0.338** | −0.020 |
| T | −0.276* | −0.854** | 0.044 | 0.161 | 0.094 |
| pH | 0.332** | 0.138 | −0.085 | −0.068 |
| DO | −0.066 | 0.044 | −0.069 | −0.135 |
| SS | −0.542** | 0.432** |

Table 3 | Abbreviations of phytoplankton species for RDA

| Taxon | Abbreviations | Taxon | Abbreviations |
|-------|---------------|-------|---------------|
| Cyanophyta | Cya | Pyrrophyta | Pyr |
| Chlorophyta | Chl | Euglenophyta | Eug |
| Bacillariophyta | Bac | Chrysophyta | Chr |
| Cryptophyta | Cry | Xanthophyta | Xan |

Figure 6 | Variations in the amount of radiant energy in Lake Poyang in 2013.
From October to November, the water level (8–12 m) and water volume (990–5,980 m$^3$/s) decreased, and the water retention time was reduced (12.5 d); however, the water velocity, SS concentrations increased and amount of radiant energy decreased, which led to decreased phytoplankton growth. From December to the following February or March, the water level (7–9 m) and water volume (21.1–3,680 m$^3$/s) decreased continuously, and the lake was transformed from lacustrine status to river status. This drastic water level fluctuation resulted in the lowest water retention time (2.7 d) and the highest water velocity (Figure 7). The SS concentrations were relatively high. Furthermore, water temperature and the radiant energy (Figure 6) were decreasing rapidly, which was not beneficial to phytoplankton growth (Wang et al., 2015). In addition, the opposite trend was observed on the spatial level for phytoplankton biomass with SS (Figure 8). Specifically, the biomass decreased as the SS increased. The relationship between phytoplankton biomass and SS was more pronounced on the spatial level than on the temporal level.

**Dominant phytoplankton of Lake Poyang**

Although TN and TP of Lake Poyang were relatively high, *Bacillariophyta* (mainly for *Melosira*, *Cyclotella*, and *Navicula*) were dominant for the entire WLP. This may have been because of the strong hydrodynamic conditions and high SS concentrations of Lake Poyang during the WLP. Simulation analysis showed that the average flow velocity of Lake Poyang ranged from 0.005 to 0.858 m/s and the percentage above 0.1 m/s was greater than 50% during the three WLPs (Figure 7). Cocquyt & Vyverman (2005) argued that the phytoplankton community is dominated by diatoms in good hydrodynamic condition or well-mixed water columns. For example, *Bacillariophyta* dominate in typical river systems (Gosselain et al., 1994; Ha et al., 2002). Diatoms also have the highest algae density in
phytoplankton, and strong water hydrodynamic forces can reduce settlement losses of diatoms. Furthermore, the buoyancy regulation mechanism of Cyanobacteria is restricted by water mixing. Other studies have shown that water mineral particles were beneficial to diatoms. This is because the flocculation sedimentation effect of the particles was greater on Cyanobacteria than diatoms (Cao et al. 2015a, 2015b). In addition, a moderate amount of SS is helpful for phytoplankton diatoms’ growth because SS are rich in silicate, which is necessary for diatom proliferation (Zhang 2006; Ding et al. 2013). Therefore, the heavy SS concentrations in Lake Poyang (52.32 mg/L) may be the primary cause of the dominance of diatoms.

Cyanobacterial risk in local area

Despite diatoms being the dominant group in Lake Poyang, Cyanobacteria accounted for a relatively high proportion in local areas of Lake Poyang during the high WLP, such as sites 8–10 in the mid-east area and sites 13 and 15 in the entrance of the five tributaries into the lake. Field investigations conducted in August 2007 and October 2012 revealed large Cyanobacterial blooms that lasted almost two months (Dai et al. 2015). RDA revealed that Cyanobacteria biomass was positively correlated with temperature ($r = 0.216$) and showed a negative relationship with velocity ($r = -0.159$) (Figure 5). Increases in water temperature and decreases in velocity can accelerate Cyanobacteria growth. In the high WLP, the blocking effect of the Yangtze River induced elevated water levels in Lake Poyang, which prolonged the water retention time. During this time, the water velocity and SS concentrations were very low (Figure 7), water temperature was high, Cyanobacteria grew fast and Cyanobacterial blooms’ risk increased.

CONCLUSION

The phytoplankton community of Lake Poyang was found to be composed of 8 phyla and 81 genera. The biomass was much higher in the high WLP than in the normal WLP and the low WLP. During the high WLP, phytoplankton biomass increased rapidly; however, after the high WLP it decreased greatly. Phytoplankton biomass was generally highest in the middle district and lowest in the northern district. Nutrients in Lake Poyang were high, while phytoplankton biomass and chlorophyll a contents were low and the phytoplankton community was still dominated by Bacillariophyta, which may be the reason for the strong hydrodynamic condition and high SS concentrations. The relationship between biomass and SS mainly reflected on the spatial distribution. Phytoplankton biomass was extremely high in the high WLP, which was caused by the combined effects of the blocking effect of the Yangtze River, water temperature, and SS.

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