Hydrobiologia (2014) 732:61–70
DOI 10.1007/s10750-014-1844-2

PRIMARY RESEARCH PAPER

Spatial distribution of chlorophyll *a* and its relationship with the environment during summer in Lake Poyang: a Yangtze-connected lake

Zhaoshi Wu · Hu He · Yongjiu Cai · Lu Zhang · Yuwei Chen

Received: 15 November 2013 / Revised: 26 January 2014 / Accepted: 22 February 2014 / Published online: 6 April 2014

Abstract Lake Poyang, a Yangtze-connected lake that is the largest freshwater lake in China, was studied in summer from 2009 to 2012. The primary objective was to investigate the spatial variability of chlorophyll *a* (chl *a*) on a whole-lake scale and to identify the key factors affecting phytoplankton growth. Stepwise multiple linear regression and Spearman's rank correlation analyses showed that the shade index is the major factor determining the spatial distribution of chl *a*; nutrients don't explain much variation in chl *a*, except in the east. The relationships between shade index and chl *a* varied regionally. Chl *a* varied inversely with the variation of the shade index, especially in the north and south, reflecting light limitation. However, the correlation was positive in the east due to high chl *a* concentration negatively affecting light availability, which was promoted by sufficient nutrients. In the center, no factor was found to have an obvious effect on phytoplankton growth, most likely because of human activities and high heterogeneity. These new data on the spatial variability of chl *a* and its relationship with light availability in Lake Poyang will be crucial to understand chl *a* regulation and contribute to the knowledge regarding phytoplankton in the Yangtze Basin.

Keywords Lake Poyang · Yangtze-connected · Chl *a* · Shade index · Region

Handling editor: Judit Padisák

Z. Wu · H. He · Y. Cai · L. Zhang · Y. Chen (✉)
Poyang Lake Laboratory for Wetland Ecosystem Research, State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, 73 East Beijing Road, Nanjing 210008, People's Republic of China
e-mail: fdzs4444@sina.com

Z. Wu
e-mail: zswu1987@163.com

H. He
e-mail: hehuabc@tom.com

Y. Cai
e-mail: caiyj@niglas.ac.cn

L. Zhang
e-mail: luzhang@niglas.ac.cn

H. He
Graduate University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

Introduction

Because of its fundamental role in aquatic food chains and sensitivity to environmental changes, phytoplankton is important for various bodies of water (Reynolds, 1984a, b). To adequately understand the phytoplankton life cycle and its response to ecological change, many studies have focused on phytoplankton distribution through time and space (Reynolds, 1984a; Dokulil & Padisak, 1994; Valdes-Weaver et al., 2006). Generally, the spatial distribution of phytoplankton biomass is related to identifiable limnological characteristics of the ecosystems concerned (Reynolds, 1984a). Various environmental factors are associated with phytoplankton biomass [measured as chlorophyll *a* (chl *a*)] in freshwater lakes, such as nutrients (total phosphorus, total nitrogen, or the ratio of TN: TP) and light (Dillon & Rigler, 1974; Wang et al., 2008; Xu et al., 2010; Zhang et al., 2012). Of these factors, nutrient conditions have received particular attention and are generally regarded as the primary limiting factor of algal growth.

There are hundreds of shallow lakes in the Yangtze Basin. The limnological conditions of these lakes vary widely (Wang et al., 2008). Because of human activity during the 1950s–1970s, only two large Yangtze-connected lakes remain, namely, Lake Poyang and Lake Dongting, the largest and second largest freshwater lakes in China, respectively; these lakes are extremely different from the Yangtze-isolated lakes, especially with regard to hydrological conditions. These two types of lakes are both important for providing drinking water, sightseeing, and economic development, among other human uses. As a consequence, these lakes are damaged by human activities and are experiencing accelerated eutrophication, resulting in increased phytoplankton biomass and toxic algal blooms (Jin, 2003; Wang et al., 2008). However, greater attention has been focused on chl *a* regulation in Yangtze-isolated lakes, such as Lake Taihu and Lake Chaohu (Chen et al., 2003; Deng et al., 2007). As a result of their completely different limnological characteristics, the theories of chl *a* regulation derived from Yangtze-isolated lakes are not applicable to Yangtze-connected lakes.

Lake Poyang, a Yangtze-connected lake, is the largest freshwater lake in China, but research on chl *a* distribution and regulation in Lake Poyang is still at an early stage. For such a large and complex lake ecosystem, investigations must have a sufficient spatial extent (especially in areas less well studied) to detect the spatial variability of chl *a* and its relationships with environmental factors. However, previous surveys of chl *a* have had limited spatial and temporal coverage (Pan et al., 2009). Furthermore, few experimental or empirical studies are available to elucidate the principal factors influencing phytoplankton biomass (Wu et al., 2013, 2014). Additionally, no modeling efforts have been undertaken to establish the relationship between chl *a* concentration and the responsible environmental variables.

The primary objectives of this study were (1) to obtain a broader understanding of chl *a* distribution in Lake Poyang on a whole-lake scale and (2) to explore the key environmental variables regulating phytoplankton in Lake Poyang and establish primary models of chl *a* concentration. Our study will provide a basis for understanding chl *a* regulation in Lake Poyang that is crucial for monitoring ecological changes in the lake. Additionally, our research will contribute to the knowledge of phytoplankton in the Yangtze Basin and in shallow lakes worldwide.

Materials and methods

Study area

Lake Poyang (28°22′–29°45′N, 115°47′–116°45′E) is located in Jiangxi Province in China in the downstream region of the Yangtze River (Fig. 1). With a watershed area of 1.622×10^5 km^2, Lake Poyang is the largest freshwater lake in China. The annual discharge and storage capacity of the lake are approximately 1.457×10^{11} and 2.95×10^{10} m^3, respectively (Zhu & Zhang, 1997). There are five main river tributaries, including the Gan River, Fu River, Xin River, Xiu River, and Rao River, that flow into Lake Poyang. The limnology of Lake Poyang is strongly affected by seasonal differences in the water level. Consistent with the variation in the water level, the lake area changes seasonally and reaches its peak in the summer. With abundant resources, such as water, sand, and wind, Lake Poyang plays an important role in local economic development and has been heavily exploited for sand extraction, transport, fishing, tourism, and other uses. As a result, Lake Poyang has exhibited a rising trend in phytoplankton biomass (Wu et al., 2013).

In such a large and complex lake, the relationship between chl *a* and environmental variables may be region dependent. To determine the relationship between chl *a* concentration and environmental factors more accurately, the study area was divided into four regions: northern, middle, eastern, and southern Lake Poyang, referred to as North LPY, Middle LPY, East LPY, and South LPY, respectively (Fig. 1). These spatial delineations reflect the different hydrological conditions of Lake Poyang. North LPY, which connects the lake with the Yangtze River, is relatively narrow, and the environmental factors vary within a

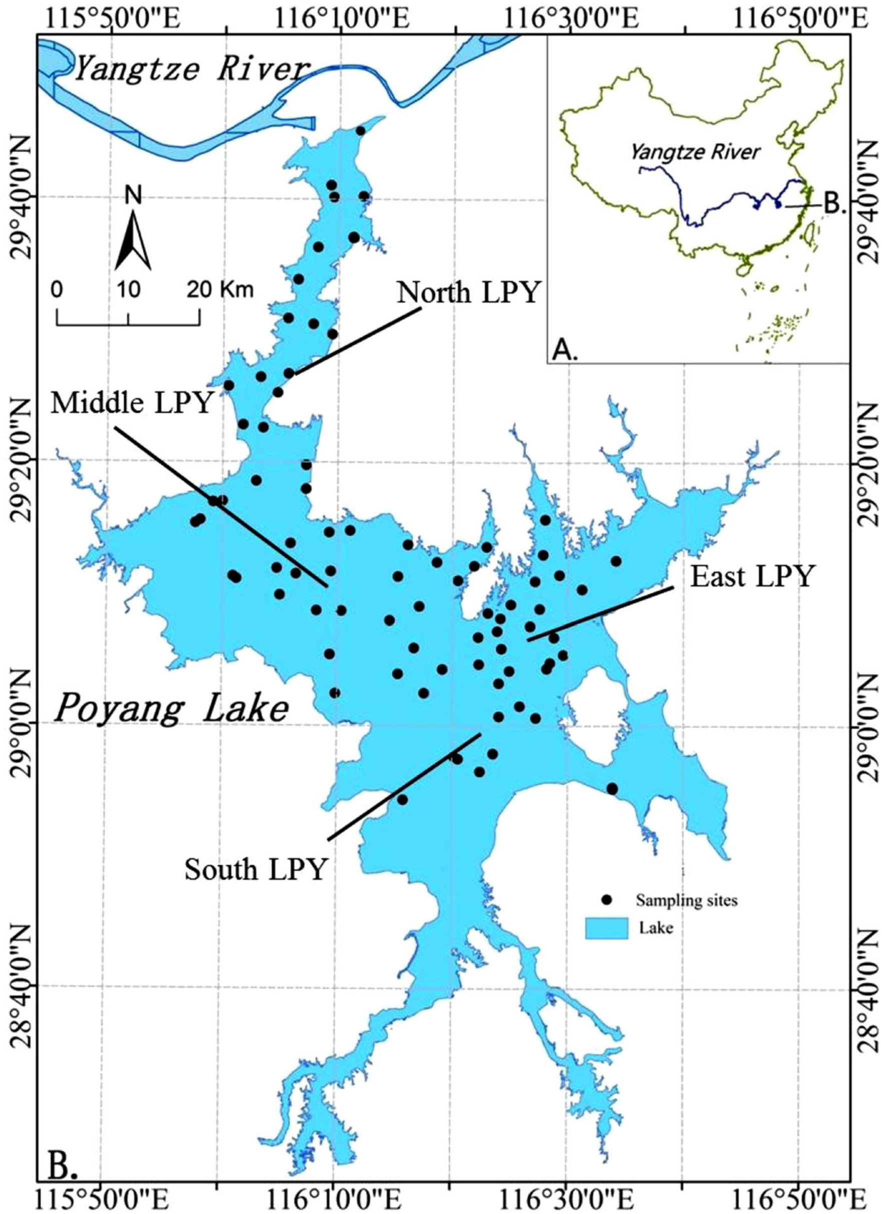

Fig. 1 Location of Lake Poyang, delineating the four regions: North LPY (North Lake Poyang), Middle LPY (Middle Lake Poyang), East LPY (East Lake Poyang), and South LPY (South Lake Poyang)

narrow range (Wu et al., 2013). Middle LPY covers the largest area in our study, with moderate water depth and nutrient concentrations. The water flow rate in Middle LPY is lower than in South LPY or North LPY (Dou & Jiang, 2003). East LPY is located in a relatively calm environment, and the hydrological conditions are much different from the other three regions. South LPY receives large amount of water from inflows in its southern portion.

In Lake Poyang, it is ideal to investigate the spatial distribution and regulation of chl *a* in summer because of the intrinsic variability of the lake area. The lake area is approximately 4,000 km^2 in summer, much larger than in the dry seasons (Zhu & Zhang, 1997; Shankman et al., 2006), which enables sampling to be more extensive and comprehensive. In addition, the lake ecosystem is relatively stable due to the balance of water levels between the Yangtze River and Lake Poyang, which excludes some effects of complex hydrological conditions and is beneficial for exploring the relationship between chl *a* concentration and environmental factors.

Sample collection and lab analysis

Sampling was conducted in July (2009–2011) in Lake Poyang at 19 regular sampling sites. To obtain more spatial data on the entire lake, we added two additional surveys in August 2011 and July 2012, with 36 and 48 additional sites, respectively. The sampling in North LPY, Middle LPY, and South LPY was continuous starting in 2009, with a larger area sampled in August 2011 and July 2012. The monitoring of East LPY was started in August 2011.

Selected environmental parameters, including water temperature (T), pH, and electrical conductivity (con), were obtained using a Hydrolab Datasonde 5 sensor in situ. Water depth was measured using a Speedtech SM-5 Portable Depth Sounder. Water transparency was determined using a Secchi disk. The shade index (SI) was also used to represent underwater light conditions. The SI is defined as the ratio of water depth to water transparency (Scheffer, 1998; Kosten et al., 2012).

The vertically integrated water samples were collected with acid-cleaned 10-l plastic buckets and kept cool and shaded prior to transport to the laboratory. Chemical oxygen demand (COD_{Mn}) and nutrient concentrations, namely, total nitrogen (TN), total phosphorus (TP), dissolved nitrogen (DTN), dissolved phosphorus (DTP), ammonium (NH_4), nitrite (NO_2), nitrate (NO_3), and orthophosphate (PO_4), were analyzed according to APHA (1998).

Chlorophyll *a* (chl *a*) concentration was filtered through GF/F filters (47 mm; Whatman) and measured according to Lorenzen (1967) with spectrophotometric measurements after extraction in hot 90% ethanol.

Data analysis

The approximate spatial distribution of chl *a* concentration and the shade index in Lake Poyang during summer were based on the averaged data of all samplings. Chl *a* concentration data were also averaged among the four study regions. To detect relationships between underwater light conditions (Secchi depth and shade index) and chl *a*, Spearman's rank correlations were conducted, precluding the lack of normality of the data. Significance analyses were performed using a Kruskal–Wallis nonparametric test.

Stepwise multiple linear regressions were used to explore the relationship between chl *a* concentration and the responsible environmental variables, including TN, TP, pH, conductivity, Secchi depth, and shade index. The value of R^2 was used to identify the best model. The percentage model error (PE) was employed to evaluate the predictive ability of the model. PE was calculated by $PE = \sum\left|\frac{P}{O} - 1\right| \times 100/n$ according to Canfield & Bachmann (1981). In the formula above, P is the predicted chl *a* concentration with no transformation and O is observed chl *a* concentration. With regard to regional differences, the shade index was chosen to explore the relationship with chl *a* concentration among the four regions in a first round of stepwise linear regression. In a second round, we added total nitrogen, total phosphorus, pH, conductivity, and Secchi depth as dependent variables. All data were log $(x + 1)$-transformed prior to analysis to meet the conditions of normality and homogeneity of variance in the residuals.

The statistical package SPSS for Windows (version 17.0) was used for analyses of Spearman's rank correlation and regression statistics. We tested the significant difference for the data among all four regions with PAST software (Paleontological Statistics v2.15) (Hammer et al., 2001).

Results

Spatial distribution of chl *a*

During the period 2009–2012, the average chl *a* concentration during summer in Lake Poyang was 10.42 μg l^{-1}. The spatial difference in chl *a* concentrations was obvious (Fig. 2). Chl *a* concentration peaked in the eastern section of Lake Poyang, up to 34.37 μg l^{-1}. The lowest value of chl *a* concentration (2.11 μg l^{-1}) was observed in the northern section of Lake Poyang, close to the connecting point between Lake Poyang and the Yangtze River.

Regionally, the average chl *a* concentration was significantly higher in East LPY (14.99 μg l^{-1}) than in the other three regions (Fig. 3). The mean chl *a* concentration in Middle LPY was second highest and was also significantly different from that in North LPY ($P < 0.001$) and South LPY ($P = 0.016$). The lowest value of average chl *a* concentration (5.61 μg l^{-1}) was found in North LPY, which was not significantly different from the value in South LPY ($P = 0.067$).

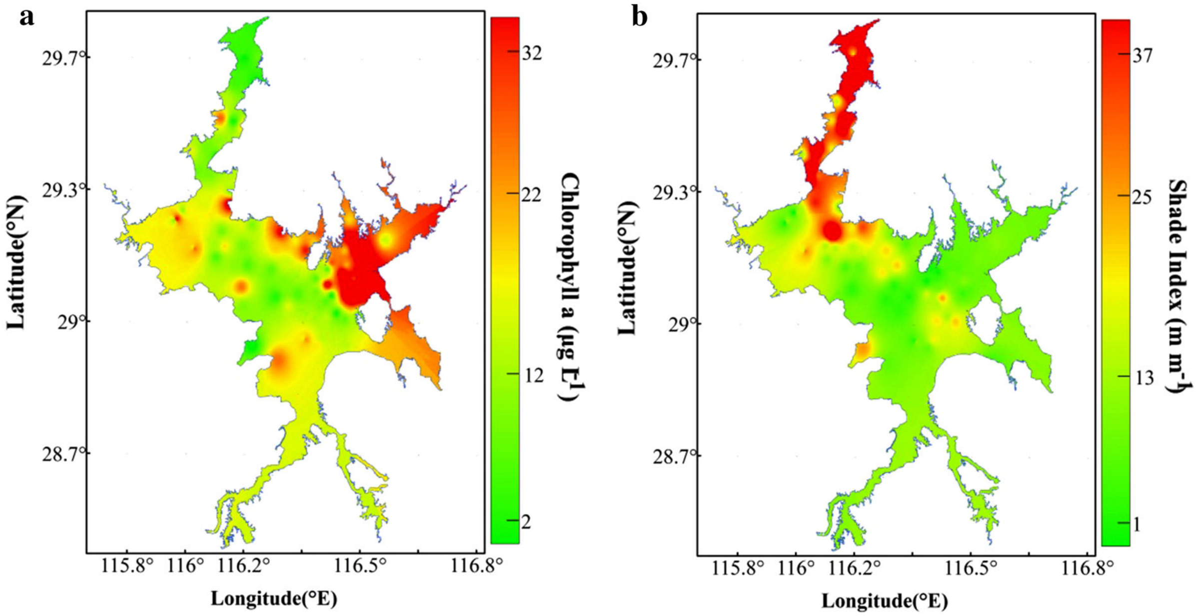

Fig. 2 Approximate spatial distribution of chl *a* concentration and shade index in Lake Poyang during summer (**a** chlorophyll *a*, **b** shade index). The data for chl *a* and shade index were averaged for all samplings (2009–2012)

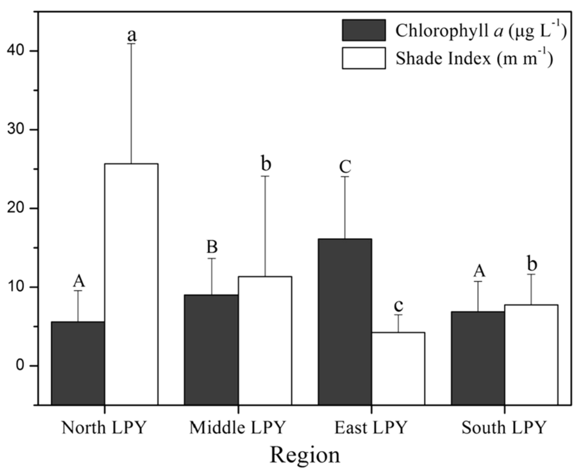

Fig. 3 Mean and standard deviation of chl *a* concentration and SI in all four regions of Lake Poyang. *Uppercase* (*A*, *B*, *C*) and *lowercase letters* (*a*, *b*, *c*) are used to distinguish differences in the chl *a* concentration and the shade index, respectively. Means with *different letters* are significantly different ($P < 0.05$)

Key factor analyses and light-chl *a* models

Lake Poyang exhibits a wide range of environmental parameters (Table 1). Shade index, for example, varied by approximately 80-fold spatially, showing that underwater light conditions changed greatly on a spatial level. In contrast with chl *a*, the spatial variability of the shade index was higher in the northern portion of Lake Poyang and lower in the east and south (Fig. 2). Regionally, relatively abundant chl *a* was generally found, with a low-shade index in the East LPY, whereas in the North LPY, where the shade index was extremely high, the chl *a* concentrations were the lowest (Fig. 3).

Stepwise multiple linear regressions performed for the responsible variables, including nutrients (TN and TP), pH, conductivity, Secchi depth, and shade index, showed that shade index entered first and contributed the greatest to explaining chl *a* concentration on a whole-lake scale (Table 2, Model 1). With regard to regional differences, chl *a* was also significantly correlated with underwater light indictors (Table 3). In each of these four regions, the relationship between the chl *a* concentration and the shade index was stronger than that between chl *a* concentration and Secchi depth. Therefore, the shade index was the key factor in regulating the spatial distribution of chl *a* concentration. Furthermore, the relationship between chl *a* concentration and shade index differed regionally. In North LPY and South LPY, there were significant ($P < 0.001$ and $P = 0.002$, respectively) and inverse correlations between the chl *a* concentration and the shade index, whereas in East

Table 1 Environmental variables summarized as the mean values and ranges in Lake Poyang during summer from 2009 to 2012

Parameter	North LPY	Middle LPY	East LPY	South LPY
Water depth (m)	8.65 (1.50–17.20)	5.28 (0.60–18.10)	2.99 (0.50–5.50)	4.42 (1.00–9.00)
Secchi depth (m)	0.37 (0.20–0.70)	0.67 (0.10–2.10)	0.75 (0.30–1.50)	0.66 (0.20–1.15)
Suspended solids	30.10 (13.00–80.40)	32.77 (0.80–517.00)	15.31 (2.50–100.25)	23.46 (2.67–89.25)
Temperature (°C)	30.10 (26.59–33.33)	30.83 (28.13–33.42)	31.03 (28.99–32.08)	30.74 (28.60–33.90)
pH	7.83 (6.85–8.93)	8.04 (7.03–9.30)	8.42 (7.57–9.23)	7.75 (6.97–8.99)
Conductivity ($\mu S\ cm^{-1}$)	119.6(62.10–351.60)	107.92 (60.50–190.40)	97.38 (67.90–188.60)	106.15 (56.10–188.20)
TN ($mg\ l^{-1}$)	1.24 (0.80–2.40)	1.33 (0.67–5.37)	1.33 (0.37–6.81)	1.38 (0.73–2.76)
TP ($mg\ l^{-1}$)	0.05 (0.03–0.17)	0.08 (0.02–1.18)	0.12 (0.02–0.90)	0.07 (0.02–0.21)
DTN ($mg\ l^{-1}$)	1.07 (0.69–1.68)	1.25 (0.55–2.32)	1.23 (0.19–2.61)	1.33 (0.57–2.56)
DTP ($mg\ l^{-1}$)	0.03 (0.01–0.07)	0.04 (0.00–0.08)	0.07 (0.04–0.13)	0.06 (0.02–0.16)
NO_2 ($mg\ l^{-1}$)	0.02 (0.00–0.03)	0.03 (0.00–0.27)	0.03 (0.00–0.22)	0.06 (0.01–0.33)
NO_3 ($mg\ l^{-1}$)	0.78 (0.00–1.91)	0.7 (0.10–1.52)	0.37 (0.01–1.73)	0.67 (0.17–1.76)
NH_4 ($mg\ l^{-1}$)	0.09 (0.02–0.22)	0.13 (0.01–0.55)	0.16 (0.01–0.60)	0.25 (0.02–0.74)
PO_4 ($mg\ l^{-1}$)	0.01 (0.00–0.09)	0.01 (0.00–0.06)	0.01 (0.00–0.04)	0.01 (0.00–0.08)
COD_{Mn} ($mg\ l^{-1}$)	2.73 (1.52–4.20)	2.92 (1.34–5.43)	3.72 (1.28–5.79)	3 (1.55–5.61)

Table 2 Linear models explaining the chl *a* concentration (log(chl-*a* + 1) in $\mu g\ l^{-1}$) based on whole-lake data

	Linear model	R^2	P
1	1.203*** − 0.271***log(SI + 1)	0.155	<0.001
2	1.986*** − 0.280***log(SI + 1) − 0.384**log(con + 1)	0.196	<0.001
3	0.408# − 0.231***log(SI + 1) − 0.396**log(con + 1) + 1.630*log(pH + 1)	0.217	<0.001

The models result from a stepwise selection procedure using the following independent factors: total nitrogen (log(TN + 1) in $\mu g\ l^{-1}$), total phosphorus (log(TP + 1) in $\mu g\ l^{-1}$), pH, conductivity (log(con + 1) in $\mu S\ cm^{-1}$), Secchi depth (log(Secchi + 1) in m), and shade index (log(SI + 1) in $m\ m^{-1}$)

$n = 169$. The significance of the regression coefficients is indicated by *** $P < 0.001$; ** $0.001 < P < 0.01$; * $0.01 < P < 0.05$; and # $P > 0.05$

Table 3 Spearman correlation coefficients and *P* values for the relationship between underwater light condition (SD and SI) and chlorophyll *a* concentration in different regions of Lake Poyang during summer

Region	Coefficient		*P* value	
	SD	SI	SD	SI
North LPY	0.473	−0.716	0.003	0
Middle LPY	0.055	−0.153	0.657	0.218
East LPY	−0.392	0.451	0.024	0.008
South LPY	0.563	−0.577	0.003	0.002

LPY, the concentration of chl *a* was significantly ($P = 0.008$) and positively related to the shade index. With regard to Middle LPY, there was no significant correlation between the chl *a* concentration and the Secchi depth or shade index.

Separate SI-chlorophyll *a* regressions were analyzed in all four regions (Fig. 4). The coefficients of determination of the regression were highest in North LPY (0.589), suggesting that the chl *a* concentration was largely affected by its shade index. R^2 was also relatively high in the regression of East LPY (0.436) and South LPY (0.309). The PE of the regressions was no larger than 50%, and *P* values were all lower than 0.05 in North LPY, East LPY, and South LPY. With regard to Middle LPY, R^2 of the regression was lower than 0.02, indicating that the shade index could not explain the variation of chl *a* concentration.

Effects of other factors on light-chl *a* models

In addition to the shade index, conductivity and pH also contributed to the chl *a* variation on a whole-lake scale but explained much less than the shade index

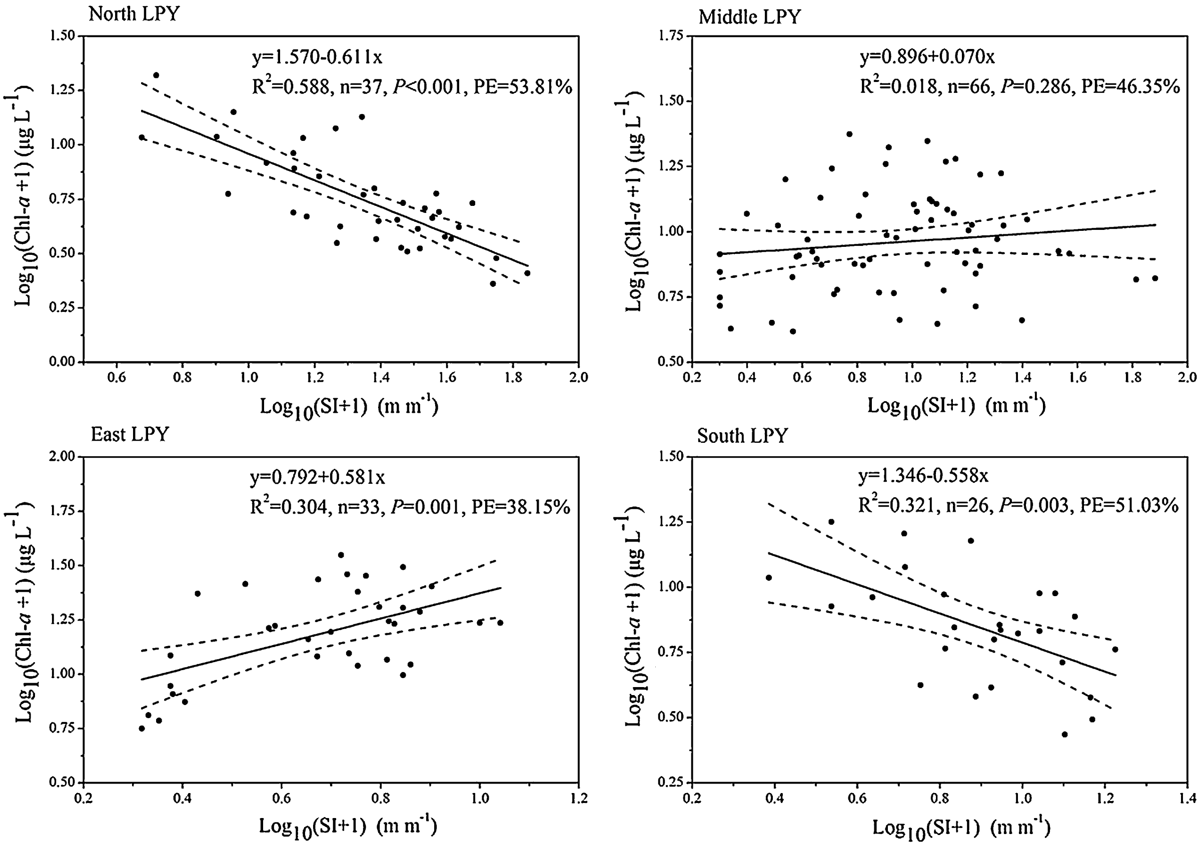

Fig. 4 Relationships between chlorophyll *a* (chl *a*) and shade index (SI) in all four regions of Lake Poyang during summer. *Dashed lines* indicate the 95% confidence limits

(Table 2, Models 2 and 3). TN and TP did not add to the variance in chl *a* concentration explained by the shade index. When we added more variables to explain chl *a* variation in the four regions, we found that the shade index was also the most explanatory factor in the North LPY, East LPY, and South LPY regions. Conductivity explained a portion of the chl *a* variation in the Middle LPY ($R^2 = 0.077$) and also added to the model in the South LPY region. TP played a role in the East LPY region (Table 4).

Discussion

Our large-scale investigations provide a broader understanding of chl *a* distribution and contribute to the knowledge of chl *a* regulation in the Yangtze-connected Lake Poyang. The mean value of chl *a* is much larger than that identified by a previous study with limited coverage (2.11 $\mu g\ l^{-1}$) (Pan et al., 2009). According to the analyses of stepwise multiple regressions and Spearman's rank correlations based on summer data, the shade index mediates the chl *a* distribution, and its role differs regionally. Nutrient availability does not explain much variation of chl *a*, except in the South LPY region. Other factors, such as freshwater input and human activity, also regulate phytoplankton chl *a* in Lake Poyang.

Light, which provides energy for photosynthesis, is attenuated below the surface of lakes by particulate matter (phytoplankton and non-phytoplankton particles) and chromophoric-dissolved organic matter (Dokulil, 1984; Zhang et al., 2007). In a turbid and well-mixed lake, phytoplankton is under insufficient in light conditions much of the time, and underwater light conditions are commonly a limiting factor in regulating phytoplankton chl *a* concentration (Cole et al., 1992). Lake Poyang is a turbid lake, with an average Secchi depth and shade index of 0.67 m and 12.60 $m\ m^{-1}$ during summer, respectively. The lake is always well

Table 4 Regional linear models explaining the chl *a* concentration (log(chl-*a* + 1) in μg l^{-1})

Area	Linear model	*n*	*P*	R^2	PE (%)
North LPY	1.570*** − 0.611***log(SI + 1)	37	<0.001	0.588	53.81
Middle LPY	1.903*** − 0.466*log(con + 1)	70	0.014	0.077	41.66
East LPY	0.792*** + 0.581**log(SI + 1)	33	0.001	0.304	38.15
	0.150# + 0.795***log(SI + 1) +0.269**log(TP + 1)	33	<0.001	0.481	31.91
South LPY	1.346*** − 0.558**log(SI + 1)	26	0.003	0.321	51.03
	2.420*** − 0.597**log(SI + 1) − 0.517*log(con + 1)	26	0.001	0.443	36.80

The models result from a stepwise selection procedure using the independent factors: total nitrogen (log(TN + 1) in μg l^{-1}), total phosphorus (log(TP + 1) in μg l^{-1}), pH (log (pH + 1)), conductivity (log(con + 1) in μS cm^{-1}), Secchi depth (log(Secchi + 1) in m), and shade index (log(SI + 1) in m m^{-1})

The significance of the regression coefficients is indicated by *** $P < 0.001$; ** $0.001 < P < 0.01$; * $0.01 < P < 0.05$; and # $P > 0.05$

mixed and continuously turbid due to its connection with the Yangtze River, water currents, frequent winds, and human activities (such as sand extraction and transportation), which cause sediment particles (especially sand) to be resuspended. Our study, based on a large spatio-temporal scale, suggests that underwater light conditions (indicated by the shade index) profoundly affect the phytoplankton chl *a* concentration in the lake, which is consistent with the findings of a previous study (Wu et al., 2013, 2014). Overall, a more favorable underwater light climate (low shade index) was associated with an elevated chl *a* concentration in Lake Poyang based on the average shade index and chl *a* concentrations in all four regions.

Light-limited algal chl *a* concentration was especially evident in two regions of our study area, the North LPY and South LPY regions, where non-algal turbidity is high, with average shade indexes of 25.66 and 7.76 m m^{-1}, respectively. According to unpublished data, the mean inorganic matter/total suspended solids in the North LPY and South LPY regions was 85.05 and 80.95%, respectively, demonstrating that the insufficiency of underwater light conditions is mainly caused by non-algal particles, especially sand. The effect of non-algal turbidity on phytoplankton was first studied by Murphy (1962), who suggested that turbidity negatively affects the productivity of an aquatic environment by controlling the effective energy available for photosynthesis. With a higher water flow rate than the other two regions (Middle LPY and East LPY) (Dou & Jiang, 2003), our study also supports previous findings by Reynolds & Descy (1996) that suggest that the availability of light primary controls riverine phytoplankton populations.

The effect of nutrient on phytoplankton chl *a* regulation in Lake Poyang was not obvious, which is consistent with previous studies (Wu et al., 2013, 2014). However, in the East LPY, TP was the second most important parameter in the light-environment model and explained 17.7% of the chl *a* variability. Capblancq (1990) noted that phosphorus limited most freshwater ecosystems, and it has been reported that in lakes with low phosphorus concentrations (TP < 0.2 mg l^{-1}), phytoplankton biomass is linearly related to the P concentration (Seip, 1994). In river-connected lakes, TP plays a more important role in lentic regions than in lotic regions (Pan et al., 2009). Located in the eastern bay of the lake, the East LPY region was characterized by calm conditions, indicated by the significantly (all values of $P < 0.001$) lowest shade index among the four regions. Additionally, submersed macrophytes, such as *Vallisneria* sp. and *Hydrilla verticillata*, were mainly observed in this region during the surveys, which may have reduced the water-flow velocity (Madsen et al., 2001). Therefore, TP might regulate chl *a* in the East LPY but not in the other three regions.

Nutrient also contributed to the inverse relationship between chl *a* concentration and light availability in the East LPY, which is totally opposite from the pattern observed in the North and South LPY. Nutrient concentrations were relative high (particularly phosphorus) in this region. Additionally, with the relatively calm location and submersed macrophytes, which contributed to a greater underwater light climate (Barko et al., 1991; Fonseca, 1996), we hypothesized that cause and effect are reversed in this region, where light limitation is minimized or nonexistent, and dense phytoplankton negatively affects light availability.

The pH (8.42) in the East LPY region was significantly (all values of $P < 0.005$) higher than in the other three regions, with a reduction in available free CO_2, indicating that phytoplankton and submersed macrophytes actively photosynthesized (Wetzel, 1983). Although macrophytes compete with phytoplankton for light and nutrients, some cyanobacteria can become dominant in the presence of macrophytes (Guseva & Goncharova, 1965; Wetzel, 1983). As with non-algal particles, dense algal cells enhance light scattering and create a turbid environment, especially in eutrophic lakes (Carlson, 1977; Tilzer, 1988; Sterner et al., 1997). Moreover, cyanobacterial blooms were commonly observed in the East LPY during summer. Thus, our hypothesis supports the consistent relationship between the shade index and chl *a* concentration in the East LPY region.

In addition, freshwater inputs may decrease chl *a* concentration on some levels. The shade index explained more chl *a* variance in the North LPY than in the South LPY region. The North LPY region is the area connecting to the Yangtze River, and the hydrological and nutrient conditions are highly similar (Wu et al., 2013). However, environmental conditions, especially hydrological conditions (such as water flow rate), are more complex in the South LPY region, which receives water flow from upper tributaries. Freshwater inputs resulting in a decreased chl *a* concentration in the water column were observed by Burford et al. (2012). This phenomenon might explain why the chl *a* concentration was not significantly ($P = 0.067$) greater in the South LPY region than in the North LPY region, with a significant ($P < 0.001$) difference in shade index between the two areas.

With regard to the Middle LPY region, no significant relationship between chl *a* and environmental factors was observed in our research. Although conductivity was considered in a stepwise multiple regression, the explanatory power of this variable was limited. The inherent characteristics of the Middle LPY region provide an explanation as to why no environment was significantly related to chl *a* concentration. The Middle LPY region covered the largest area in our study, and its higher heterogeneity was reflected in a wider range of most environmental factors we examined. Similar to the South LPY, there are also tributaries flowing into the Middle LPY region, which may reduce the correlation between the shade index and chl *a*. Human activities also play an important role in regulating phytoplankton in this area; sand excavation is more frequent in the Middle LPY region, especially in summer. In such a complex region, many more variables may contribute to the explanation of chl *a* variance, such as tributary runoff, wind, and sand extraction, which requires further study.

In Lake Dongting, another Yangtze-connected lake, underwater light conditions also play an important role in explaining chl *a* variation (Xu et al., 2005); the effects of nutrients are not obvious in Lake Poyang or in Lake Dongting (Xu et al., 2005; Wu et al., 2013). These results improve our understanding of phytoplankton chl *a* concentration responses to light availability in Yangtze-connected lakes and stress the importance of the shade index as an important factor in management. Additionally, our study provides baseline data for future assessments of ecological change and a means for monitoring phytoplankton biomass regionally.

Acknowledgments We thank the Lake Poyang Laboratory for Wetland Ecosystem Research (PLWER) for providing the foundation for the experiment. We are also grateful to Dr. Jinlong Gao and Dr. Xingwang Fan for making the interpolation map. This study was financially supported by the National Basic Research Program of China (Grant 2012CB417005) and Science and Technology Major Project of Jiangxi Province (Grant 20114ABG01100).

References

APHA (American Public Health Association), 1998. Standard Methods for the Examination of Water and Waste Water, 20th ed. American Public Health Association, Washington, DC.

Barko, J. W., D. Gunnison & S. R. Carpenter, 1991. Sediment interactions with submersed macrophyte growth and community dynamics. Aquatic Botany 41: 41–65.

Burford, M. A., I. T. Webster, A. T. Revill, R. A. Kenyon, M. Whittle & G. Curwen, 2012. Controls on phytoplankton productivity in a wet–dry tropical estuary. Estuarine, Coastal and Shelf Science 113: 141–151.

Canfield Jr, D. E. & R. W. Bachmann, 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. Canadian Journal of Fisheries and Aquatic Sciences 38: 414–423.

Capblancq, J., 1990. Nutrient dynamics and pelagic food web interactions in oligotrophic and eutrophic environments: an overview. Hydrobiologia 207: 1–14.

Carlson, R. E., 1977. A trophic state index for lakes. Limnology and Oceanography 22: 361–369.

Chen, Y. W., C. X. Fan, K. Teubner & M. T. Dokulil, 2003. Changes of nutrients and phytoplankton chlorophyll-*a* in a large shallow lake, Taihu, China: an 8-year investigation. Hydrobiologia 506: 273–279.

Cole, J. J., N. F. Caraco & B. L. Peierls, 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? Limnology and Oceanography 37: 1608–1617.

Deng, D. G., P. Xie, Q. Zhou, H. Yang & L. G. Guo, 2007. Studies on temporal and spatial variations of phytoplankton in Lake Chaohu. Journal of integrative plant biology 49: 409–418.

Dillon, P. J. & F. H. Rigler, 1974. The phosphorus–chlorophyll relationship in lakes. Limnology and Oceanography 19: 767–773.

Dokulil, M. T., 1984. Assessment of components controlling phytoplankton photosynthesis and bacterioplankton production in a shallow, alkaline, turbid lake (Neusiedlersee, Austria). Internationale Revue der gesamten Hydrobiologie und Hydrographie 69: 679–727.

Dokulil, M. T. & J. Padisak, 1994. Long-term compositional response of phytoplankton in a shallow, turbid environment, Neusiedlersee (Austria/Hungary). Hydrobiologia 275: 125–137.

Dou, H. S. & J. J. Jiang, 2003. The Five Freshwater Lake in China, Press of University of Science &Technology of China (in Chinese).

Fonseca, M. S., 1996. The role of seagrasses in nearshore sedimentary processes: a review. In Nordstrom, K. & C. T. Roman (eds), Estuarine Shores: Evolution, Environments and Human Alterations. Wiley, London: 261–286.

Guseva, K. A. & S. P. Goncharova, 1965. O vliianii vysshei vodnoi rastitel 'nosti na razvitie planktonnykh sinezelenykh vodoroslei. Ekologiia i Fiziologiia Sinezelenykh Vodoroslei: 230–234.

Hammer, Ø., D. Harper & P. Ryan, 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 9.

Jin, X. C., 2003. Analysis of eutrophication state and trend for lakes in China. Journal of Limnology 62: 60–66.

Kosten, S., V. L. Huszar, E. Becares, L. S. Costa, E. Donk, L. A. Hansson, E. Jeppesen, C. Kruk, G. Lacerot, N. Mazzeo, L. D. Meester, B. Moss, M. Lürling, T. Nõges, S. Romo & M. Scheffer, 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biology 18: 118–126.

Lorenzen, C. J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnology and Oceanography 12: 343–346.

Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71–84.

Murphy, G. I., 1962. Effect of mixing depth and turbidity on the productivity of fresh-water impoundments. Transactions of the American Fisheries Society 91: 69–76.

Pan, B. Z., H. J. Wang, X. M. Liang & H. Z. Wang, 2009. Factors influencing chlorophyll *a* concentration in the Yangtze-connected lakes. Fresenius Environmental Bulletin 18: 1894–1990.

Reynolds, C. S., 1984a. The Ecology of Freshwater Phytoplankton. Cambridge University Press, London.

Reynolds, C. S., 1984b. Phytoplankton periodicity - the interactions of form, function and environmental variability. Freshwater Biology 14: 111–142.

Reynolds, C. S. & J. P. Descy, 1996. The production, biomass and structure of phytoplankton in large rivers. Archiv für Hydrobiologie. Supplementband. Large rivers 10: 161–187.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman and Hall, London.

Seip, K. L., 1994. Phosphorus and nitrogen limitation of algal biomass across trophic gradients. Aquatic Sciences - Research Across Boundaries 56: 16–28.

Shankman, D., B. D. Keim & J. Song, 2006. Flood frequency in China's Poyang Lake region: trends and teleconnections. International Journal of Climatology 26: 1255–1266.

Sterner, R. W., J. J. Elser, E. J. Fee, S. J. Guildford & T. H. Chrzanowski, 1997. The light: nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. The American Naturalist 150: 663–684.

Tilzer, M. M., 1988. Secchi disk–chlorophyll relationships in a lake with highly variable phytoplankton biomass. Hydrobiologia 162: 163–171.

Valdes-Weaver, L. M., M. F. Piehler, J. L. Pinckney, K. E. Howe, K. Rossignol & H. W. Paerl, 2006. Long-term temporal and spatial trends in phytoplankton biomass and class-level taxonomic composition in the hydrologically variable Neuse-Pamlico estuarine continuum, North Carolina, USA. Limnology and Oceanography 51: 1410–1420.

Wang, H. J., X. M. Liang, P. H. Jiang, J. Wang, S. K. Wu & H. Z. Wang, 2008. TN:TP ratio and planktivorous fish do not affect nutrient–chlorophyll relationships in shallow lakes. Freshwater Biology 53: 935–944.

Wetzel, R. G., 1983. Limnology. Saunders, Philadelphia.

Wu, Z. S., Y. J. Cai, X. Liu, C. P. Xu, Y. W. Chen & L. Zhang, 2013. Temporal and spatial variability of phytoplankton in Lake Poyang: the largest freshwater lake in China. Journal of Great Lakes Research 39: 476–483.

Wu, Z. S., X. J. Lai, L. Zhang, Y. J. Cai & Y. W. Chen, 2014. Phytoplankton chlorophyll a in Lake Poyang and its tributaries during dry, mid-dry and wet seasons: a 4-year study. Knowledge and Management of Aquatic Ecosystems. http://dx.doi.org/10.1051/kmae/2013088.

Xu, H., H. W. Paerl, B. Q. Qin, G. W. Zhu & G. Gao, 2010. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. Limnology and Oceanography 55: 420–432.

Xu, M., G. M. Zeng, X. Y. Xu, G. H. Huang, W. Sun & X. Y. Jiang, 2005. Application of Bayesian regularized BP neural network model for analysis of aquatic ecological data - a case study of chlorophyll-*a* prediction in Nanzui water area of Dongting Lake. Journal of Environmental Sciences 17: 946–952.

Zhang, M., Y. Yu, Z. Yang, X. L. Shi & F. X. Kong, 2012. The distribution of phytoplankton along trophic gradients and its mediation by available light in the pelagic zone of large eutrophic lakes. Canadian Journal of Fisheries and Aquatic Sciences 69: 1935–1946.

Zhang, Y. L., B. Zhang, X. Wang, J. S. Li, S. Feng, Q. H. Zhao, M. L. Liu & B. Q. Qin, 2007. A study of absorption characteristics of chromophoric dissolved organic matter and particles in Lake Taihu, China. Hydrobiologia 592: 105–120.

Zhu, H. H. & B. Zhang, 1997. The Poyang Lake. Press of University of Science & Technology of China, Hefei. (in Chinese).