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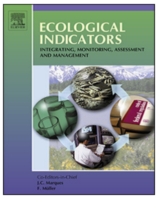

Water-level fluctuations are key for phytoplankton taxonomic communities and functional groups in Poyang Lake

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ABSTRACT

Biological species can be assembled into functional groups based on functional traits, which are keys to understanding the response of phytoplankton to environmental factors, such as the physical and chemical characteristics of aquatic systems. Here, we studied the taxonomic and functional communities of phytoplankton over three years in Poyang Lake and further examined the effect of water-level on these groups. Phytoplankton were generally dominated by diatoms across seasons, followed by cyanobacteria and green algae. Functional groups were mainly composed of organisms tolerant to fluctuating mixing intensities, such as group **P**, which was mainly composed of filamentous *Aulacoseira granulata* and showed a typical seasonal variation. Compared to the other physical and chemical variables of the lake, water-level showed a greater influence on seasonal variations in phytoplankton total biomass, taxonomic communities and functional groups. The influence of water-level on phytoplankton communities included two aspects: direct effects of biomass dilution and mixing and indirect effects of nutrient dilution and underwater light availability. Our results also indicated that the functional groups were more sensitive to water-level than the taxonomic communities, which was supported by the higher variation of functional groups explained solely by water-level. Collectively, these findings illustrate the direct and indirect effects of water-level on phytoplankton taxonomic communities and functional groups, and providing insights into how water-level can alter phytoplankton communities in a larger complex floodplain system.

1. Introduction

Water-level fluctuations, typical characteristic of floodplain lakes, are dominant forces controlling the function of lacustrine ecosystems by both direct and indirect effects. These effects include biotic and abiotic factors, such as biological components (Yang et al., 2016) and physical and chemical variables (Leira and Cantonati, 2008). For example, fluctuations in the water-level can alter the lake morphometry and transform the characteristics of the sedimentation zones, such as erosion, transportation and accumulation (Håkanson, 1977). Declining water-levels may cause contaminated sediments to be suspended and have the potential to fundamentally change littoral sediments and biogeochemical characteristics in floodplain lakes (Furey et al., 2004). However, the relative effects of water-level fluctuations on biological communities are less clear than the effects of other physical and chemical variables.

As an important biological component in floodplain lakes, phytoplankton communities show significant temporal fluctuations in response to the hydrological regime by both direct and indirect effects (Bovo-Scomparin and Train, 2008). Regarding indirect effects, water-level reduction could increase sediment resuspension and turbidity, decrease light availability (da Costa et al., 2016), and finally change the phytoplankton community structure (Evtimova and Donohue, 2016). For example, lowering the water-level could increase nutrient concentrations and enhance the proliferation and dominance of cyanobacteria (Tian et al., 2015). Regarding direct effects, water-level fluctuations could not only have a mixing disturbance (Liu et al., 2012) but also have a strong dilution effect (Lobo et al., 2018; Stevic et al., 2013) on phytoplankton community dynamics.

Although water-level fluctuations represent one of the primary

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drivers in aquatic ecosystems globally, understanding of the ecological impacts of altered water-level regimes in lakes lags far behind the understanding of impacts from other human disturbances (e.g., eutrophication). Specifically, the influence of water-level fluctuations on the phytoplankton is still not fully understood (Coops et al., 2003; Evtimova and Donohue, 2016). Previous studies have been conducted to determine the responses of phytoplankton to water-level fluctuations in floodplain lakes, such as lakes in Paraguay River (Oliveira and Calheiros, 2000), Araguaia River (Nabout et al., 2006), Mary River (Townsend, 2006), and Murray River (Butler et al., 2007). Those studies indicate that phytoplankton dynamics are hydrologically driven and that water-level fluctuations influence the community composition and population densities of the phytoplankton. Thus, we expect that water-level plays an important role in phytoplankton communities in floodplain lakes.

Compared to traditional taxonomic communities, the classification of functional groups could better identify the environmental variables and anthropogenic disturbances (Abonyi et al., 2012; Abonyi et al., 2014). This approach assembles species with similar morphological (Török et al., 2016) and ecological characteristics (Padisák et al., 2009), or morpho-functions (Kruk and Segura, 2012) and has become widely used in phytoplankton studies (Becker et al., 2010; Xiao et al., 2011; Yu et al., 2017). Previous studies have found that light, mixing regime and nutrient availability were the driving factors of the seasonal variation in phytoplankton functional groups (Becker et al., 2010). For example, permanent mixing, low transparency and nitrogen limitation contributed to the dominance of the group **SN** (represented by *Cylindrospermopsis catemaco* and *C. philippinensis*) in a deep Mediterranean reservoir (Komárková and Tavera, 2003). In addition, water-level has also been identified as the principal factor limiting phytoplankton development and functional group variation (Wang et al., 2011; Zhu et al., 2013). Thus, we may expect functional groups to better respond to water-level and other environmental variables than taxonomic communities.

Poyang Lake shares similar characteristics to rivers and lakes (Wu et al., 2013; Wu et al., 2014); hence, it is beyond the traditional lotic or lentic categories of aquatic ecology. The spatial and temporal distribution and structure of phytoplankton in Poyang Lake have been frequently reported, but information on functional groups and their relationship with hydrologic characteristics is scarce. For example, the studies of this lake have focused on eutrophication (Zhang et al., 2016), the effects of water-level on water quality characteristics (Liu et al., 2016; Wu et al., 2018), phytoplankton succession (Qian et al., 2016), seasonal dynamics of phytoplankton composition and the mechanism of algal bloom formation (Wu et al., 2013). To date, only one study has examined the phytoplankton functional groups in the northern part of the lake from May to December, which is the conversion period from the river phase to the lake phase (Liu et al., 2015). However, regarding phytoplankton functional groups, little information is available at the seasonal and inter-annual scale.

In the present study, we evaluated the effects of water-level on the dynamics of the phytoplankton taxonomic communities and functional groups in Poyang Lake. We addressed the following hypotheses: (1) water-level fluctuations are the primary determinant for phytoplankton community, high water-level favors cyanobacterial dominance (Fig. 1); (2) the influences of water-level on phytoplankton seasonal variation include both direct and indirect effects; (3) phytoplankton functional groups may better characterize hydrological conditions than taxonomic communities.

2. Materials and methods

2.1. Study area

Poyang Lake (28°22′ − 29°45′N, 115°47′ − 116°45′E) is located in the middle and lower catchment of the Yangtze River in Jiangxi Province, China (Fig. 2). It is the largest freshwater lake in China with a catchment area of 1.62×10^5 km^2 and is freely connected with Yangtze River (Liu et al., 2015). The size of Poyang Lake shrinks extensively associated with the seasonal change in the water-level, i.e., from less than 1000 km^2 in the dry season, fall or winter, to approximately 4000 km^2 in the summer rainy season (Baumgärtner et al., 2008; Feng et al., 2012; Hui et al., 2008; Shankman et al., 2006). It receives water inputs mainly from five rivers: Xiushui, Ganjiang, Fuhe, Xinjiang, and Raohe Rivers, and discharges into the Yangtze River from a narrow outlet in the north (Ye et al., 2013). The Ganjiang River is the largest river in the region, extending 750 km, and contributes almost 55% of the total discharge into Poyang Lake (Shankman et al., 2006). Headwaters of these rivers are located to the east, south and west of the Jiangxi Province, which is surrounded by high mountains (Shankman et al., 2006; Ye et al., 2013).

As a connected lake located at the junction of the middle and lower catchment of the Yangtze River, Poyang Lake exhibits large seasonal water-level fluctuations. It is determined primarily by the water surface elevation of the Yangtze River and, to a lesser extent, by the discharge from the five rivers (Shankman et al., 2006). The highest water-levels generally range from approximately 18 to 21 m a.s.l during the summer rainy season, and the lowest levels usually range from 8.8 to 11.4 m a.s.l during the fall or winter dry season. Because of its abundant resources (water, sand, wind, etc.), the lake plays a critical role in the local economic development.

2.2. Sampling and analyses

We sampled seasonally (January, April, July, October) at fifteen sites by a Ruttner sampler between January 2012 and October 2014 (Fig. 2). At each site, one mixed sample was obtained from three depths, that is the surface, middle and bottom layers of water column. Sampling was finished within 1–2 days. Water temperature (WT), specific conductance (Cond) and dissolved oxygen (DO) were measured at the study sites using a Hydrolab Datasondae 5 sensor. Water depth was determined by a hand held Speedtech Depthmate portable sounder. The secchi depth (SD) was determined at the same time with a Secchi disc. Suspended solids (SS), chemical oxygen demand (COD_{Mn}), total nitrogen (TN), total phosphorus (TP), phosphate (PO_4^--P), nitrate (NO_3^--N), nitrite (NO_2^--N), and ammonium (NH_4^--N) analyses were carried out following the standards of the American Public Health Association (1998). All measurements were completed within 24 h of sampling. Dissolved inorganic nitrogen (DIN) was the sum of nitrate, nitrite and ammonium concentrations. The nitrogen to phosphorus ratio (N:P) was the ratio between total nitrogen and total phosphorus. Chlorophyll *a* (Chl *a*) was extracted in hot 90% ethanol and measured by spectrophotometry after filtering 500 mL samples through GF/F filters (47 mm, Whatman) according to Lorenzen (1967). The water-level at Xingzi station was obtained from the website of the Water Resources Department of Jiangxi Province (http://www.jxsl.gov.cn/slxxhw/jhsq/index.html) and Poyang Lake Laboratory for Wetland Ecosystem Research.

One-liter phytoplankton samples were fixed with Lugol's iodine solution (1% v/v) and settled in a column bottle for 48 h. After the supernatant was siphoned off with a 2 mm diameter hose, the residue (25 mL) was collected and used for counting phytoplankton by light microscopy (Chen et al. 2003); Phytoplankton were classified according to Hu and Wei (2006). The mean algal biovolume was calculated using the appropriate geometric configurations and volume formulae according to Hillebrand et al. (1999), and a specific gravity of 1 mg mm^{-3} was assumed for calculating algae biomass (Chen et al., 2003; Xiao et al., 2011).

There are three widely used phytoplankton functional classifications: functional groups proposed by Reynolds et al. (2002) and revised by Padisák et al. (2009); morpho-functional groups proposed by Salmaso and Padisák (2007); and morphology-based functional groups

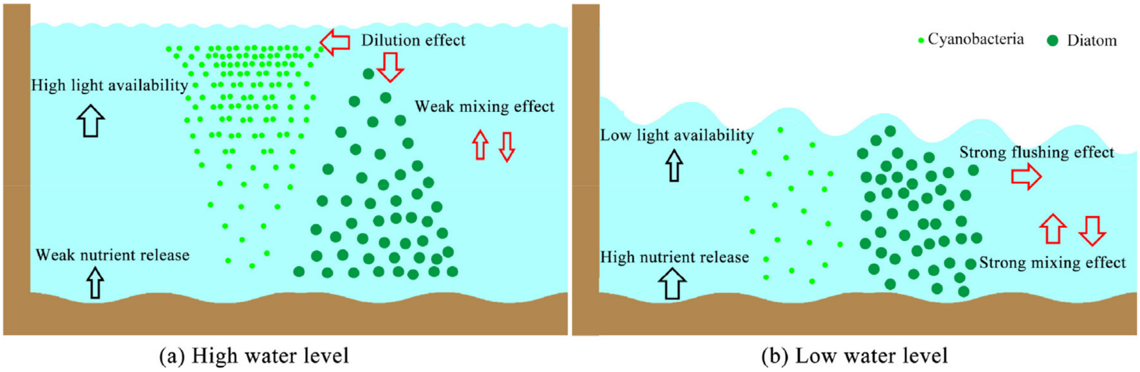

Fig. 1. Conceptual figures for the effects of water-level on phytoplankton assemblages. High-water-level scenarios (**a**) associated with weak mixing conditions and high dilution. The weak mixing makes cyanobacterial cells apt to float in the water column, and diatom cells sink to the bottom. Weak mixing condition also results in low nutrient release and high light availability. However, low-water-level scenarios (**b**) consist of strong mixing conditions, which are much more in favorable for diatom than cyanobacteria. Moreover, strong mixing is associated with high nutrient release and low light availability.

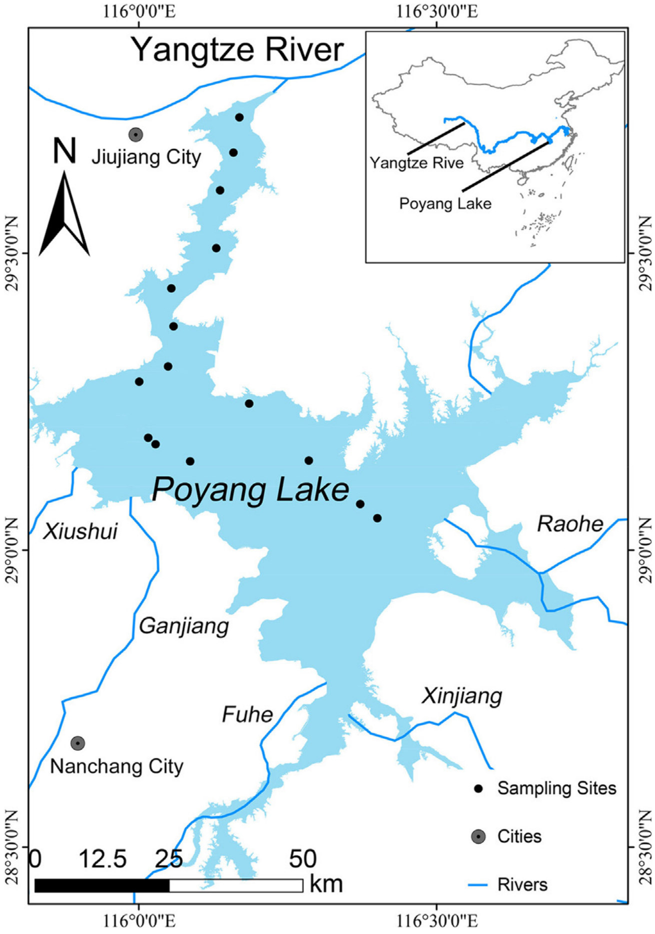

Fig. 2. Location of Poyang Lake, China. Sampling sites were shown in black dots.

proposed by Kruk et al. (2010). Compare to morpho-functional groups and morphology-based functional groups, however, the functional groups have been shown to provide a more detailed description of phytoplankton (Izaguirre et al., 2012, Stanković et al., 2012). Moreover, functional groups have been widely used in the analyses of different aquatic ecosystems around the world, such as reservoirs (e.g., Xiao et al., 2011; de Souza et al., 2016), rivers (e.g., Abonyi et al., 2012; Zhu et al., 2013), and floodplain lakes (e.g., Bovo-Scomparin and Train, 2008; Mihaljević et al., 2009). Thus, due to the more information it provides and its wide usage in multiple aquatic ecosystems, we applied functional groups here to evaluated the dynamics of phytoplankton in response to water level fluctuations in Poyang Lake.

2.3. Statistical analyses

We tested for seasonal differences in phytoplankton biomass and environmental variables using the Kruskal-Wallis test. Due to the lack of normality, Spearman's rank correlations were used to explore the relationships of water-level, Chl *a*, SD and nutrients (Wu et al., 2014). Linear and quadratic models were used to explore the relationships between water-level and environment factors or functional groups by the *trendline* function in the R package basicTrendline (Mei et al., 2018). The more appropriate model was selected based on a lower value of Akaike's information criterion, and the F-statistic was used to test the significance of regression.

The relationships between taxonomic communities and environmental factors or functional groups and environmental factors were analyzed by detrended correspondence analysis (DCA) and redundancy analysis (RDA). We used variance inflation factors (VIF) to identify the collinearity between environmental variables with the function *envfit*, and the redundant environmental variables with VIF > 20 were removed before the RDA. RDA models were selected by the *ordistep* function. Phytoplankton communities were Hellinger transformed prior to RDA analyses, and the environment data were standardized by scaling to zero mean and unit variance. Variation partitioning was used to test the pure effects of nutrient concentration, light availability and hydrological condition with the function of *varpart*.

Moreover, we examined the relationships between temperature, water-level, light condition, nutrient enrichment, and phytoplankton communities using partial least squares path modeling (PLS-PM) in the R package plspm (Sanchez, 2013). This method is known as the partial least squares approach to structural equation modeling and allows for the estimation of complex cause-effect relationship models with latent variables, which was especially suitable for our sampling data. Seven latent variables were used: temperature, water-level, underwater light availability (SD and SS), nutrients (TN, DIN and NO_3^--N), total biomass, taxonomic communities (the first axis of PCoA), and functional groups (the first axis of PCoA). Path coefficients represent the direction and strength of the linear relationships between variables or the direct effects. Indirect effects are the multiplied path coefficients between a predictor and a response variable, adding the product of all possible paths excluding the direct effect. Models with different structures were evaluated using the goodness of fit statistic. More details can be found in Sanchez (2013) and Wang et al. (2016). In addition, random forest analysis was used to identify the most important predictors for phytoplankton seasonal variations (Elith et al., 2008; Feld et al., 2016). All of the above analyses were performed in R (R version 3.5.2).

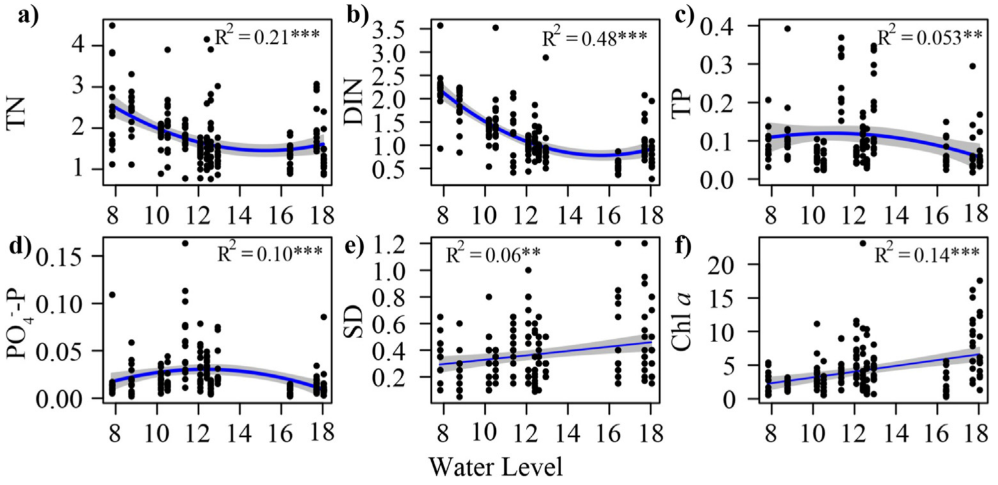

Fig. 3. The relationships between water-level and physicochemical variables or Chlorophyll *a*. The samples were collected from 2012 to 2014 in Poyang Lake. Solid lines indicate significant ($P < 0.05$) relationships, and dotted lines indicate non-significant ($P < 0.05$) relationships. A linear or quadratic model was selected based on the lower value of Akaike's information criterion. TN: total nitrogen; DIN: dissolved inorganic nitrogen; TP: total phosphorus; PO_4^--P: phosphate, SD: Secchi depth; Chl *a*: Chlorophyll *a*. The units of TN, DIN, TP, PO_4^--P and Chl *a* are mg L^{-1}, whereas SD and water-level are meter.

3. Results

3.1. Relationships between water-level and environmental factors

The water-level in Poyang Lake ranged from 7.5 to 18 m and exhibited significant seasonal differences across the four seasons, with the highest level in summer and the lowest level in winter (Fig. S1). The average water-level fluctuations were 7.33 and 8.75 m for intra- and inter-annually, respectively. Levels were higher in spring and autumn than in summer and winter. Water temperatures, SD and Chl *a* had strong seasonal oscillations, all of which peaked in summer and lowest in winter (Fig. S2a–b). However, other physical and chemical factors, such as SS, COD_{Mn}, DO, Cond and nutrient concentrations, showed different seasonal patterns (Fig. S2). For example, concentrations of COD_{Mn} and TN were higher in winter than in summer (Fig. S2d, g). The phytoplankton total biomass, TP and PO_4^--P were shared similarly seasonal variation, all of which were higher in spring and autumn than summer and winter (Fig. S2i–l).

Both of nitrogen and phosphorus nutrient levels showed significant ($P < 0.01$) seasonal variation (Fig. S2g–j), which was significantly ($P < 0.05$) associated with the water-level (Fig. 3a–d). TN and DIN concentrations were significantly ($P < 0.01$) and negatively correlated with water-levels (Fig. 3a–b). The TP and PO_4^--P concentrations were unimodal distributed with water-level, both peaking at 12.5 m (Fig. 3c–d). The significantly ($P < 0.01$) positive correlation between water-level and SD was also observed (Fig. 3e). Moreover, we also observed a significant ($P < 0.01$) and positive correlation between water-level and Chl *a* (Fig. 3f).

3.2. Phytoplankton functional groups and their relationships with water-level

Seventy-two phytoplankton genera or species, which could be coded into twenty-four functional groups, were identified from the samples collected over three years (Table 1). Diatoms contributed 16.66% to 78.81% to the total biomass and dominated during the sampling period: *Aulacoseira granulata* was the dominant species (Fig. S3). Cyanobacteria increased in spring and contributed significantly to the total biomass in summer and autumn. *Microcystis* sp. and *Anabaena* sp. were the dominant species among cyanobacteria. Regarding the functional group, groups **P**, **Y**, **MP**, **H1** and **M** were the dominant groups, and each showed seasonal dynamics (Fig. S4). Group **P**, represented by the large filamentous *Aulacoseira granulata* and meroplanktonic green algae, comprised more than 40% of the phytoplankton biomass, especially during the period of rising water-level. Group **Y** peaked in winter and was lowest in summer. Groups **H1** and **M** were generally dominant during the highest water-level periods, at 10.61% and 6.75% of the phytoplankton total biomass, respectively. Groups **Lo**, **B**, **G** occurred occasionally as dominant or codominant groups.

The relationships between group **P** or **MP** and water-level were quadratic and unimodal, both of which peaked at the water-level of 12.5 m (Fig. 4a-b). Group **P** had a significant ($P < 0.01$) relationship with water-level, but there was no significant ($P > 0.05$) relationship between group **MP** and water-level (Fig. 4a-b). There was also a similar quadratic model with group **M** and water-level, and the biomass of group **M** increased with water-level (Fig. 4c). Group **H1** had a significant ($P < 0.01$) and positive linear relationship with water-level (Fig. 4d). In contrast, groups **Y** and **Lo** did not have a significant ($P > 0.05$) relationship with water-level (Fig. 4e–f).

3.3. Effect of water-level on phytoplankton taxonomic and functional communities

We found a close and significant relationship between phytoplankton taxonomic or functional compositions and environmental parameters based on RDA ordination (Fig. 5). All selected environmental factors accounted for 15.24% of the variation of phytoplankton taxonomic communities, while for functional groups, environmental factors explained 17.39%. Regarding phytoplankton taxonomic composition, environmental variables, such as water-level, SD, pH, DIN, Cond, DO and Chl *a*, had significant ($P < 0.05$) influences; water-level was the most important. For phytoplankton functional groups, water-level, SD, pH, Cond, DIN, Chl *a* and N:P ratio had significant ($P < 0.05$) influences, and water-level was also the most critical environmental variable. Groups **M**, **H1**, **N** and **Lo** were related to high water-level and high SD, while group **MP** were found to be negatively related to WL or SD and positively to Cond or DIN. Group **P** was positively related to pH value and negatively correlated with SD and the N:P ratio.

Furthermore, variation partitioning showed that the three main environmental groups, that is nutrients, light availability and hydrological conditions, explained 13%, 7%, and 8.8% of the variation in phytoplankton total biomass, taxonomic communities and functional groups, respectively (Fig. 6a–c). For total biomass, the variation explained by nutrient concentration was much higher than light availability and hydrological conditions (Fig. 6a). For taxonomic and functional communities, the variation explained by hydrological conditions was the highest, and the joint explanation by nutrient concentrations and hydrological conditions was higher than those explained by light and hydrological conditions or nutrient and light (Fig. 6b–c). Interestingly, the joint effects of nutrient and light was very low for total biomass, taxonomic communities and functional groups (Fig. 6a–c).

Finally, we conducted PLS-PM to illustrate the effects of water-level on phytoplankton biomass, taxonomic communities or functional

Table 1
Main functional groups and representative species from Poyang Lake.

Group code	Genus included	Habitat template
P	*Aulacoseira granulata*, *A. g. var.angustissima*, *Closteriopsis* sp., *Closterium* sp.	Eutrophic epilimnia
Y	*Cryptomonas ovata*, *Cryptomonas erosa*, *Chroomonas acuta*	Lentic ecosystems, enriched lakes
M	*Microcystis* sp.	Eutrophic to hypertrophic, small- to medium-sized water bodies
MP	*Oscillatoria* sp., *Cymbella* sp., *Gomphonema* sp., *Navicula* sp., *Gyrosigma* sp., *Surirella* sp., *Surirella robusta*, *Ulotrix* sp.	Frequently stirred up, inorganically turbid shallow lakes
Lo	*Merismopedia* sp., *chroococcus* sp., *Peridinium* sp., *Ceratium hirundinella*	Deep and shallow, oligo to eutrophic, medium to large lakes
H1	*Anabaenopsis* sp., *Anabaena* sp., *Aphanizomenon* sp.	Eutrophic, both stratified and shallow lakes with low nitrogen content
B	*Cyclotella* sp., *Fragilaria* sp., *Synedra* sp.	Mesotropher, Senstivities to stratification
G	*Eudorina* sp. *Pandorina* sp., *Volvox* sp.	Nutrient-rich conditions in stagnating water columns
J	*Scendesmus* sp., *Pediastrum tetras*, *Pediastrum duplex*, *Pediastrum simplex*, *Crucigenia* sp., *Ankistrodesmus* sp., *Tetraedron* sp., *Tetrastrum* sp., *Coelastrum* sp., *Selenastrum* sp., *Actinastrum* sp., *Coelastrum reticulatum*, *Golenkinia* sp.	Mixed, eutrophic lakes
C	*Asterionella* sp.	Mixed, eutrophic small-medium lakes
N	*Cosmarium* sp., *Staurastrum* sp.	Mesotrophic epilimnia

groups via nutrients and underwater light conditions. The water-level had both direct and indirect effects on phytoplankton total biomass, taxonomic communities and functional groups. For total biomass, temperature and nutrient concentration had dominant negative effects (Fig. 6d). The water-level had a strong effect on underwater light conditions and nutrient concentrations and an indirect effect on phytoplankton. However, for taxonomic and functional communities (Fig. 6e-f), the direct effect of water-level was much higher than that of total biomass. The water-level had a strong negative direct effect on taxonomic communities and a positive direct effect on functional groups. The indirect effect of water-level was mainly through altering the underwater light condition and nutrient concentration, although the underwater light effects were weaker than other factors. Furthermore, random forest analysis supported the pivotal effects of water-level on phytoplankton seasonal variations (Fig. S5), which indicated the less importance role of nutrient and temperature compared to water-level.

4. Discussion

Our study showed that water-level was a key environmental factor for both biotic and abiotic conditions in Poyang Lake. It not only affected physical and chemical factors but also further influenced the phytoplankton communities at the taxonomic and functional levels. Compared to taxonomic communities, functional groups showed more advantages in revealing the effects of water-level. Interestingly, water-level affected phytoplankton assemblages both directly through dilution and mixing effect of biomass and indirectly via modifications in nutrient concentrations and underwater light availability. To the best of our knowledge, this is the first study to explicitly show the both direct and indirect effects of water-level on functional groups of phytoplankton.

We find that environmental variables had a greater explanatory power for functional groups than for taxonomic communities. This was well supported by redundancy analyses and variation partitioning, which further showed that water-level explained the highest unique variation of both functional and taxonomic communities. This finding indicated that the classification of functional groups was much more sensitive to environmental factors than taxonomic communities, which was also observed in previous studies (e.g., Abonyi et al., 2012). A study in Pampa Plain shallow lakes showed that the classification of functional groups could provide more information than taxonomic communities for a detailed description of the phytoplankton assemblages (Izaguirre et al., 2012). Compared to functional groups, the taxonomic approach has at least three drawbacks in phytoplankton ecology. First, there are a large number of taxonomic species in an aquatic ecosystem; only a few of them are dominant, and the rare species could increase the functional redundancy of the phytoplankton community (Kruk et al., 2016; Xiao et al., 2018). Second, many broad taxonomic groups include species with different ecological characteristics, and the

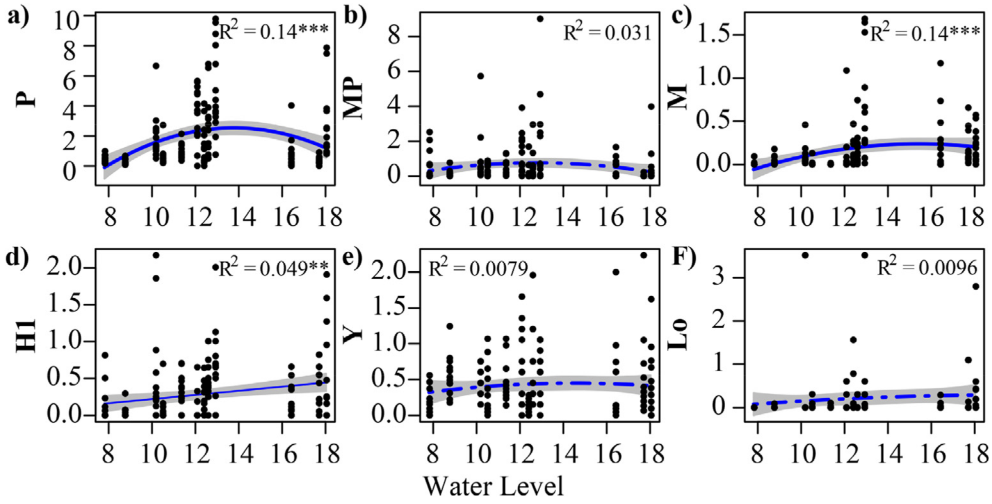

Fig. 4. The relationships between water-level and phytoplankton functional groups. The solid lines indicate significant relationships ($P < 0.05$), and dotted lines indicate nonsignificant ($P < 0.05$) relationships. A linear or quadratic model was selected based on a lower value of Akaike's information criterion. The unit of functional groups and water-level are mg L^{-1} and meter, respectively.

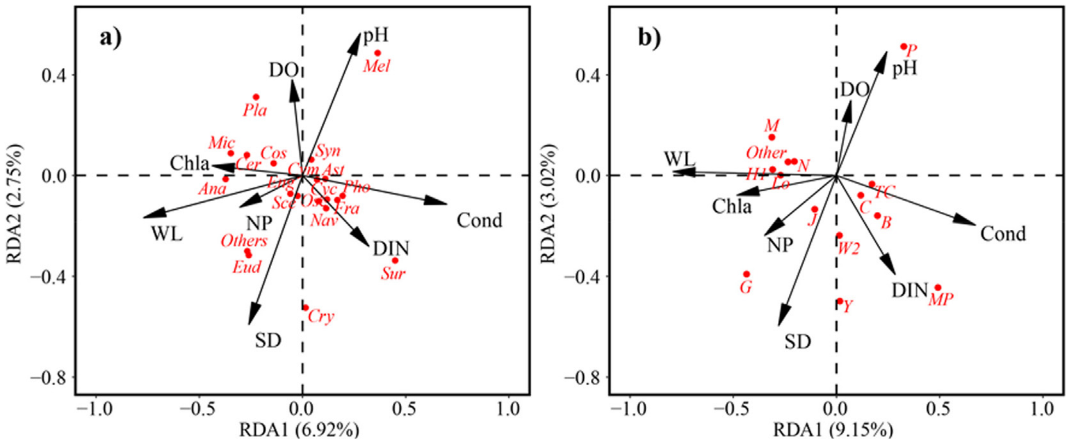

Fig. 5. Redundancy analysis of environment variables and phytoplankton taxonomic communities (**a**) or functional groups (**b**). Solid lines with arrowheads represent environmental variables, while red dots representing taxonomic communities (**a**) and functional groups (**b**), respectively. The percentages of the total variance explained are shown in brackets. There were eight environmental variables selected: WL, water-level; SD, Secchi depth; Cond, specific conductance; DO, dissolved oxygen; NP, nitrogen to phosphorus ratio; DIN, dissolved inorganic nitrogen; Chla, Chlorophyll *a*; Taxonomic groups: *Aul*, *Aulacoseria granulata*; *Cry*, *Cryptomonas ovata*; *Sur*, *Surirella* sp.; *Ana*, *Anabaena* sp.; *Cer*, *Ceratium hirundinella*; *Mic*, *Microcystis* sp.; *Fra*, *Fragilaria* spp.; *Cyc*, *Cyclotella* spp.; *Pho*, *Phormidioideae* sp.; *Ast*, *Asterionella* sp.; *Cym*, *Cymbella* sp.; *Cos*, *Cosmarium* sp.; *Syn*, *Synedra* sp.; *Eud*, *Eudorina* sp.; *Osc*, *Oscillatoria* sp.; *Eng*, *Englena acus*; *Sce*, *Scendesmus* sp.; *Nav*, *Navicula* sp.; *Pla*, *Planktothrix* sp.. Functional groups are shown in Table 1.

taxonomic communities may not well represent their ecological habitat. Third, due to convergent evolution, distantly related species could share similar ecological characteristics (Salmaso et al., 2015). The classification of functional groups, however, assembles species into a few groups with similar ecological, morphological, or morpho-functional characteristics (Kruk et al., 2016), and each group includes phenological, habitat and trophic information (Salmaso et al., 2015). In addition, by considering relatively few groups, the functional redundancy of phytoplankton communities can be significantly reduced (Xiao et al., 2018). Functional groups can be explained by ecological

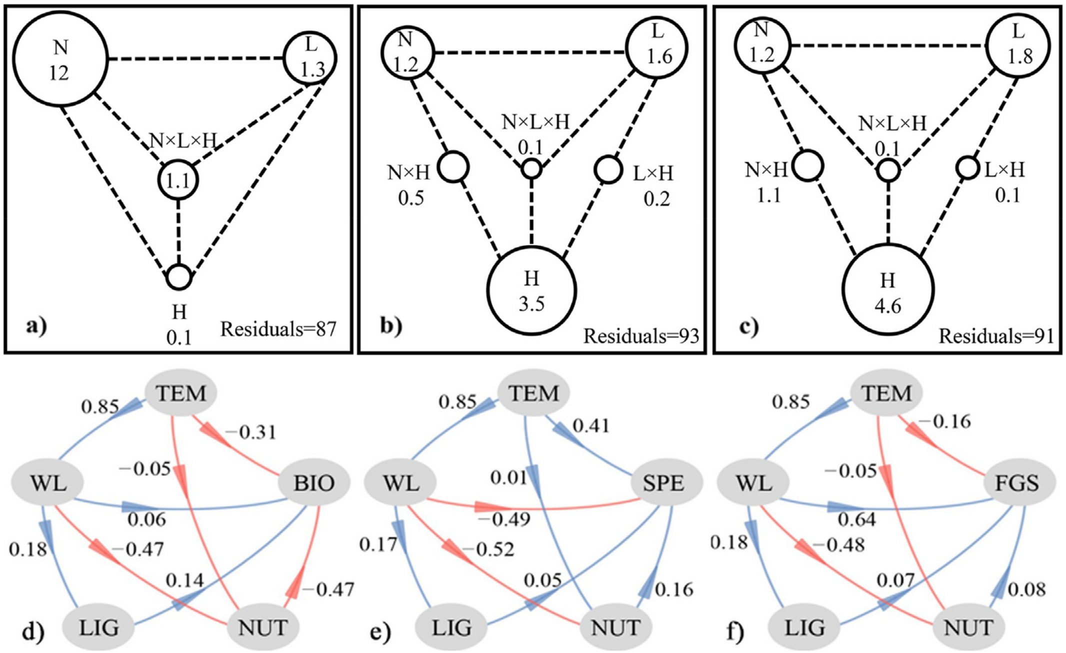

Fig. 6. The effects of environmental variables on phytoplankton characteristics. These effects were quantified with variation partitioning (**a**, **b**, **c**) and partial least squares path modeling (PLS-PM, **d**, **e**, **f**), respectively. Three phytoplankton characteristics are included: total biomass (**a, d**), taxonomic communities (**b, e**), and functional groups (**c, f**). For variation partitioning, the proportion of the variance in phytoplankton characteristics explained by the nutrients (N: nitrogen to phosphorus ratio and dissolved inorganic nitrogen), light availability (L: Secchi depth and suspended solids) and hydrological conditions (H: water-level and water depth). Each roundness represents a given biological variation partitioned into the relative effects of each factor or combination of factors, where geometric areas are proportional to the respective percentages of explained variation. The edges of the triangle depict the variation explained by each factor along. Percentages of variation explained by interactions of two or all of three factors are indicated on the sides and in the middle of the triangles, respectively. For PLS-PM, there were seven latent variables were included: water-level (WL), temperature (TEM), underwater light availability (LIG), nutrients (NUT), total biomass (BIO), taxonomic communities (SPE), and functional groups (FGS). The total biomass and first axis of PCoA of taxonomic communities and functional groups were used as observed variables. The underwater light availability included secchi depth and suspended solids, while the nutrients included total nitrogen, dissolved inorganic nitrogen, nitrate. WL, TEM and LIG were all included in the final models of three characteristics. However, for the NUT, the dissolved inorganic nitrogen was selected for all characteristics, total nitrogen was selected only for total biomass, nitrate was selected for total biomass and functional groups. Models were assessed using goodness of fit (GoF) statistics. The GoFs for **d**, **e** and **f** are 0.490, 0.478 and 0.523, respectively.

attributes, environmental tolerance and trophic states rather than taxonomic communities (Salmaso et al., 2015), and its advantages were confirmed by comparing with other functional classifications, such as morphologically-based functional groups (Kruk and Segura, 2012) and morpho-functional groups (Izaguirre et al., 2012). For example, using a functional group approach, a higher portion of the variance of phytoplankton communities is explained by environmental variables than that of phytoplankton taxonomic communities in a subtropic reservoir in China (Xiao et al., 2018). Thus, compared to taxonomic communities, functional classification can provide a better understanding of the response of phytoplankton communities to environmental variables, such as water-level fluctuations in Poyang Lake.

Interestingly, water-level had a direct effect on both taxonomic and functional communities of phytoplankton by mixing and dilution effects during low and high water-level periods, respectively. For taxonomic communities, we found that cyanobacteria and diatoms responded differently to these effects. The biomass of cyanobacteria increased substantially during the high-water-level period, while diatom biomass increased during the middle-water-level period (e.g., approximately 12.5 m). These different patterns between cyanobacteria and diatoms could be partly explained by their morpho-physiological traits. For cyanobacteria, *Microcystis* sp. and *Anabaena* sp. are two common genera in Poyang Lake. Both have advantageous characteristics in the stratified water column, such as large colony or filaments and buoyancy regulation (Brookes and Ganf, 2001; Brookes et al., 1999). Their large size, for instance, can prevent them from being consumed by most zooplankton, and buoyancy regulation can provide rapid adjustment of their vertical positions in the euphotic layer (Soares et al., 2009). These characteristics could facilitate a rapid increase in a stable water column, although there was a strong dilution effect during the high-water-level period in Poyang Lake. However, these advantages are eclipsed in a mixing conditions during low-water-level periods. This may be due to water-level fluctuations, which could increase physical stresses, such as turbulence, shear flow (Berdalet, 1997), flow velocity (Wu et al., 2010), and sediment flocculation (Peng et al., 2018). This observation is consistent with those in subtropical floodplain lakes (Domitrovic, 2003), where a rapid increase in water-level led to a domination of cyanobacteria. Furthermore, the low water-level associated with low water temperature can also limit the cyanobacteria growth (Liu et al., 2015). However, for diatoms with heavy frustule, the large filamentous *Aulacoseira granulata* was dominant in Poyang Lake. Compared to cyanobacteria, diatoms favor relatively stronger mixing for water flow suspension and thus avoid sinking. For example, *Aulacoseira granulata* has a good adaptability in a well-mixed and destratified water column and achieves higher biomass during regular hydrological fluctuation (Wang et al., 2011). Previous studies also showed that mixing and suspension may be more critical to the growth of diatom than water temperature in water bodies with high flow rate (Liu et al., 2015; Kilham and Kilham, 1975). Thus, the strong mixing effect during the low-water-level period could promote the growth of diatoms in Poyang Lake, while the sinking rate of diatoms is high during the high-water-level periods due to the stable water column.

For functional groups, we also observed a direct effect of water-level, which was more pronounced in groups **M**, **H1** and **P**. Despite these groups being common in Poyang Lake, their responses to environmental factors were different, especially those to water-level. For example, the biomass of group **P** was negatively correlated with water-level, while groups **M** and **H1** were positively correlated. These different patterns observed among groups are mainly related to their own biological characteristics, e.g., tolerance and sensitivity, and habitat characteristics, e.g., mixing or stratification of the water column. Poyang Lake is a continuously disturbed aquatic ecosystem (Liu et al., 2015; Wu et al., 2013), and persistent flushing is the primary factor influencing the dynamics of phytoplankton functional groups (Hu et al., 2013). Thus, functional groups tolerant to flushing were usually dominant throughout the seasons, particularly in the low-water-level periods. Groups **M** and **H1** are both multicellular and produce buoyant colonies. For instance, group **M** was comprised of large colonial *Microcystis* sp., and group **H1** consisted of filamentous *Anabaena* sp., *Aphanizomenon* sp. and *Anabaenopsis* sp. The large colony and buoyancy of both groups keep them in the euphotic layer with a low sedimentation rate in the water column (Reynolds, 2006). Moreover, another common trait for groups **H1** and **M** is their tolerance to stratification and sensitivity to water flush conditions (Padisák et al., 2009). These characteristics of groups **H1** and **M** thus led to their dominance in stable water columns and to their decreased biomass during high-water-level and low-water-level periods, respectively, in Poyang Lake. Group **P**, however, were in favor of habitats with physical mixing and a continuous or semi-continuous mixed layer of 2–3 m in thickness (Padisák et al., 2009). Different from the species in groups **H1** and **M**, group **P** is mainly characterized by their tolerance to mixing conditions and sensitivity to stratification condition. These characteristics facilitated a reduced flushing loss through mixing and maintenance of a high biomass during low-water-level period in Poyang Lake. However, during high-water-level period, the high sedimentation rate can reduce the biomass of this group in a stratified or stable water columns (Liu et al., 2012).

In addition to the above direct effects, we found indirect effects of water-level on both phytoplankton taxonomic and functional communities. These indirect effects occurred via both physical and chemical variables. For example, there were positive relationships between water-level and Secchi depth, indicating that there were higher underwater light conditions during high-water-level period. Moreover, water-level and nutrients showed strong negative correlations across the seasons, and thus higher water-levels were frequently associated with lower nutrient concentrations. These negative correlations between water-level and nutrients may be largely due to dilution effects or sediment resuspension associated with water-level fluctuations. These findings of the indirect effects of water-level are consistent with other aquatic systems. For instance, the reduced water-level increased water turbidity, nutrient concentration, and even changed the phytoplankton community in tropical shallow lakes (da Costa et al., 2016) and subtropical reservoirs (Yang et al., 2016).

For taxonomic communities, we found that water-level indirectly affected the phytoplankton community via the alteration of nutrient concentrations. Obviously, the response of phytoplankton to these indirect effects vary among species, especially for cyanobacteria and diatoms. Cyanobacteria biomass showed a significant and negative correlation with TN but not with TP. The dominant species, *Anabaena* sp. and *Microcystis* sp., accounted for 36% and 22%, respectively, of the total cyanobacterial biomass. Both species are better competitors for nutrients than centric diatoms due to efficient nutrient-uptake strategies when nutrients are deficient (Nalewajko and Murphy, 2001). For instance, the nitrogen-fixing system of *Anabaena* sp. can be helpful in tolerating nitrogen deficiency (De Nobel et al., 1998). Thus, cyanobacteria are highly competitive during high-water-level periods with relatively lower nutrient concentrations. However, for other phytoplankton in Poyang Lake, *Aulacoseira granulata* was the dominant species and generally peaked during the low-water-level periods. It showed a significant and positive correlation with TN, which indicates that nutrient conditions, especially TN, are the limiting factors for diatom dominance in Poyang Lake. Similar results were also found in other aquatic ecosystems with (Li et al., 2018) or without (Yang et al., 2017; Zhu et al., 2015) extensive water-level fluctuations. For instance, after hydrological disturbance, the domination of cyanobacteria can cause some sensitive non-cyanobacteria species to disappear due to nutrient and light limitations (Yang et al., 2017).

For functional groups, the indirect effects of water-level were caused by nutrient limitation and light availability, especially for groups **H1**, **M** and **P**. The biomass of groups **H1** and **M** peaked in high-water-level periods with low nutrient concentrations, while the biomass of group **P** was lower. Such observations may be mainly due to their functional traits relevant to nutrient cycling and light conditions. Groups **H1** and **M** are composed of species associated with eutrophic and eutrophic-hypereutrophic environments, respectively (Padisák et al., 2009; Reynolds et al., 2002). Group **H1**, mainly composed of nitrogen-fixing cyanobacteria, can adapt well to nitrogen deficient conditions. For filamentous *Anabaena* sp. of group **H1**, the high ratio of surface to volume facilitates the rapid uptake of nutrients and light (Reynolds, 2006). Group **M** in Poyang Lake was mainly dominated by *Microcystis* sp., which has an efficient nutrient-uptake system. Group **P**, which was negatively correlated with light availability (e.g., Secchi depth), has a low light tolerance (Padisák et al., 2009; Reynolds et al., 2002), which is helpful for its dominance in low-light conditions during mixing periods in Poyang Lake and Gaozhou Reservoir, China (Xiao et al., 2015). Therefore, functional groups, such as **H1**, **M** and **P**, showed a sensitive response to environmental variations associated with water-level fluctuations in Poyang Lake. This indicates that functional groups could be used as an alternative approach to taxonomic communities to examine environmental effects on community assemblages.

It should be noted that the unexplained variations for taxonomic and functional communities were relatively high, which might be due to some unmeasured yet important environmental factors, such as nutrient limitation or grazing pressure. Phytoplankton in Poyang Lake was dominated by diatom, which was generally affected by silicate limitation when nitrogen and phosphorus were sufficient (Reynolds, 2006) and by high grazing pressure (Odate and Imai, 2003). Moreover, stochastic processes due to natural or anthropogenic disturbance may also have influences on phytoplankton communities. Thus, it is possible, and perhaps likely, that unmeasured variables, such as nutrient silicate, zooplankton grazing and stochastic processes, contribute in part to the seasonal variations of phytoplankton taxonomic and functional community.

5. Conclusion

Phytoplankton taxonomic and functional compositions were driven by both direct and indirect effects of water-level fluctuations. Direct effects, included biomass dilution and mixing effects in high and low water-level periods, respectively, while indirect effects included nutrient variation and underwater light availability. In addition, we also found that functional groups were more sensitive to water-level fluctuations than taxonomic communities, which indicates that functional groups could be used as an alternative approach to taxonomic communities to examine environmental effects on community assemblages. In summary, water-level plays a key role in determining environmental conditions, such as nutrient concentrations and light availability, and also biological variability, such as phytoplankton taxonomic and functional communities, in floodplain lakes, and it could be a useful indicator for the prediction of phytoplankton community variations.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.05.021.

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