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Research Article

Seasonal succession of phytoplankton functional groups in Lake Fuxian and its driving factors

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Abstract – The concept of phytoplankton functional groups was proposed based on data from numerous European lakes and has been widely used in lakes, reservoirs, rivers worldwide. However, the application of this concept to subtropical plateau lakes has rarely been reported. In this study, 16 sampling sites were selected across the entirety of Lake Fuxian, Yunnan, China. Eighteen phytoplankton functional groups (F, G, J, X2, X1,T, P, MP, D, C, H1, L_O, S1, M, Y, E, W1 and W2) were classified according to the investigation of surface water and gradient depth samples. Nine of these groups, namely L_O, H1, C, MP, P, T, X1, J and F, were identified as dominant species (>5% total biomass). Furthermore, L_O, H1 and T were considered predominant (accounting for the maximum percentage of biomass in each month). The sampling showed that the seasonal succession of predominant assemblages in surface water was T (October) to H1 (January) to H1 (April) to Lo (July) and T+Lo (October) to T (January) to H1 (April) to Lo (July) in the gradient depth water. Redundancy analysis (RDA) combined with the indicator function of the phytoplankton groups suggested that WT and TN/TP were important factors in driving the succession of predominant assemblages all year around.

Keywords: Redundancy analysis / functional assemblages / subtropical plateau lake / nutrition level / water temperature

1 Introduction

Phytoplankton have a relatively short lifespan and can respond rapidly to subtle environmental changes. Given these characteristics, phytoplankton are commonly used to indicate environmental conditions or changes in aquatic ecosystems. Studies have focused on the standing crops (Chla content) of phytoplankton (Elliott *et al.*, 2006; Staehr and Sand-Jensen, 2006; Wang *et al.*, 2011; Elliott, 2012) when evaluating the nutrition level of aquatic ecosystems. However, the content of Chla do not necessarily reflect the whole ecosystem function (Costa *et al.*, 2009). Instead, phytoplankton structure is correlated with the adaptive strategies of different kinds of algae (Reynolds, 1998; Padisák *et al.*, 2003; Cao *et al.*, 2018). Therefore, phytoplankton community structure is considered to be more precise for evaluating ecosystem function than biomass or Chla content and is commonly used as an important sensitive indicator for detecting environmental changes in water regions (Reynolds *et al.*, 1993; Hering *et al.*, 2006; Yang *et al.*, 2016).

In traditional studies, phytoplankton composition has been classified on the basis of Linnaean phylogenetic taxonomic affiliation (Wang *et al.*, 2011). However, the utilisation of taxonomy in describing certain environmental conditions has numerous drawbacks, because taxonomic classification might include species with diverse morphological characteristics that represent different properties and adaptive strategies (Huszar and Caraco, 1998; Kruk *et al.*, 2010). For example, *Microcystis* sp. and *Anabaena* sp. have distinct adaptive strategies even if they belong to the same taxa, Cyanobacteria. The latter possesses heterocysts that enable nitrogen fixation and domination under nitrogen-deficient conditions. Reynolds *et al.* (2002) firstly proposed the concept of phytoplankton functional groups based on morphological, physiological and ecological characteristics. In that concept, assemblages occurring simultaneously under similar conditions are usually classified into one functional group. In comparison with phylogenetic representation, the importance and usefulness of functional groups in species prediction and condition description are well appreciated (Huszar *et al.*, 2000;

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Kruk *et al.*, 2002; Salmaso and Padisák, 2007). Further classification and modification by Padisák *et al.* (2009) led to the identification of 39 phytoplankton functional groups, and the tolerance and sensitivity of each phytoplankton functional group were described. Habitat characteristics could be speculated in accordance with phytoplankton functional group composition. The phytoplankton functional group structure could be obtained on the basis of habitat characteristics.

The initial concept of phytoplankton functional groups was proposed according to the data from numerous European temperate lakes (Reynolds *et al.*, 2002; Padisák *et al.*, 2009). Thereafter, the functional group concept has been widely applied to researches on phytoplankton in lake and reservoir ecosystems worldwide (Xiao *et al.*, 2011; Dantas *et al.*, 2012; Costa *et al.*, 2015; Tian *et al.*, 2015; Ongun Sevindik *et al.*, 2017). Nevertheless, knowledge about functional groups in subtropical plateau lakes remains limited (Cao *et al.*, 2018). Lake Fuxian (24°21′–24°38′ N, 102°49′–102°57′ E, 1722 m a.s.l), an oligotrophic freshwater plateau lake located in central Yunnan Province, is the second deepest lake of China. It has maximum and mean depths of 155.0 and 89.6 m, respectively. This lake is in a subtropical zone with a monsoon climate and faces several challenges of eco-environmental protection (Zhou *et al.*, 2018). So far, the temporal dynamics and succession of phytoplankton functional groups in this lake have received limited attention (Zhang *et al.*, 2007; Dong *et al.*, 2014). Moreover, the key driving factors that influence the temporal and vertical distribution of phytoplankton functional groups have rarely been studied.

The purpose of this study was to (1) systematically demonstrate the structure of phytoplankton functional groups in the surface and deep water regions of Lake Fuxian and (2) identify the key environmental factors involved in structuring phytoplankton functional groups.

2 Sampling and analysis

Water samples were taken seasonally, that was October 2014 (autumn), January 2015 (winter), April 2015 (spring) and July 2016 (summer) at 16 sampling sites in Lake Fuxian (Fig. 1). To illustrate the vertical distribution characteristics (physicochemical variables and phytoplankton data), samples were collected at a series of gradient depths from the surface to the bottom (0.5, 5, 10, 20, 30, 50, 80 and 130 m) at sampling site $8^{\#}$ (center and deepest of the lake). Only surface water (0.5 m) was collected at the other 15 sampling sites. Water temperature (WT), pH and conductivity (Con) were recorded in situ with a YSI-6600 (Xylem Inc., USA) at a surface depth of 0.5 cm and gradient depth at sampling site $8^{\#}$.

The collected water samples were taken to the laboratory immediately for nutrient analysis and phytoplankton numeration. Total phosphorus (TP), total nitrogen (TN), ammonia (NH_4^+–N), nitrate (NO_3^-–N), soluble total phosphorus (STP), chemical oxygen demand (COD_{Mn}) and suspended substance (SS) were determined according to Editorial Board of Water and Wastewater Monitoring and Analysis Methods of the Ministry of Environmental Protection of the People's Republic of China (ed) (2002). The fixation and concentration of phytoplankton samples were performed according to the reference mentioned above. Then, algal density was enumerated in a 0.1 mL counting chamber under a Nikon microscope with 10 × 40 magnification. Algae were counted using the Utermöhl (1931) method (Lund *et al.*, 1958; Paxinos and Mitchell, 2000), and the counting error was approximately ±10% (Venrick, 1978).

Phytoplankton taxa were classified in accordance with Hu and Wei (2006) and identified to the species or genus level. Algal biomass was calculated using the method reported by Hillebrand *et al.* (1999) and Sun and Liu (2003). In this method, each alga was fitting to a geometric shape (such as *Microcystis* fit as a sphere); Then, by measuring the parameters (such as diameter of *Microcystis*), we could obtain the volume of the target alga and according to 1 mm^3/L being equivalent to 1 mg/L, we could get the biomass of each alga. Finally, the identified algae were classified into functional groups in accordance with Reynolds *et al.* (2002) and Padisák *et al.* (2009). Functional groups that contribute to more than 5% of total phytoplankton biomass for at least 1 month were classified as dominant groups (Xiao *et al.*, 2011). Furthermore, the predominant functional groups were identified as the species with biomass values at maximum percentages every month, as stated in the data obtained by Cao *et al.* (2018).

Canoco 4.5 for Windows was used to analyse the relationship between the composition of dominant phytoplankton functional groups and physicochemical parameters. In canonical correspondence analysis (CCA), data were transformed to log $(x+1)$. Species biomass data were subjected to detrended correspondence analysis (DCA) to calculate single-peak response value (SD) and to decide whether a linear or unimodal ordination method should be applied (Lepš and Šmilauer, 2003). CCA analysis was performed if SD > 2. Otherwise, redundancy analysis (RDA) was applied. The significance of environmental variables was evaluated using the Monte Carlo test. Variables were considered to be significant when $p < 0.05$ (Ter Braak *et al.*, 1986; Dong *et al.*, 2006).

3 Results

3.1 Environmental variables

The surface water temperature of Lake Fuxian ranged between 13.77 and 22.89 °C. The temperature variation between each sampling site was small. Pronounced thermal stratification was observed during the summer at sampling site $8^{\#}$, where the maximum water temperature difference between the surface (0.5 m) and bottom (80 m) was 9.26 °C (Fig. 2). The water of Lake Fuxian was generally alkaline, and its pH varied from 8.220 to 8.940. No obvious differences were observed amongst sampling sites and seasons. The conductivity of the water fluctuated in the range 0.316–0.346. Water conductivity was highest in the spring (January) and lowest in the summer (July) (Fig. 3).

Seasonal variations in COD_{Mn} and SS were detected at all sampling sites. COD_{Mn} and SS varied from 1.115–1.990 and 0.400–1.980 mg/L, respectively (Fig. 4). The highest values were observed in October (autumn) and the lowest in April (spring). NH_4^+–N, NO_3^-–N and TN concentrations varied in the respective ranges of 0.002–0.047, 0.007–0.152 and

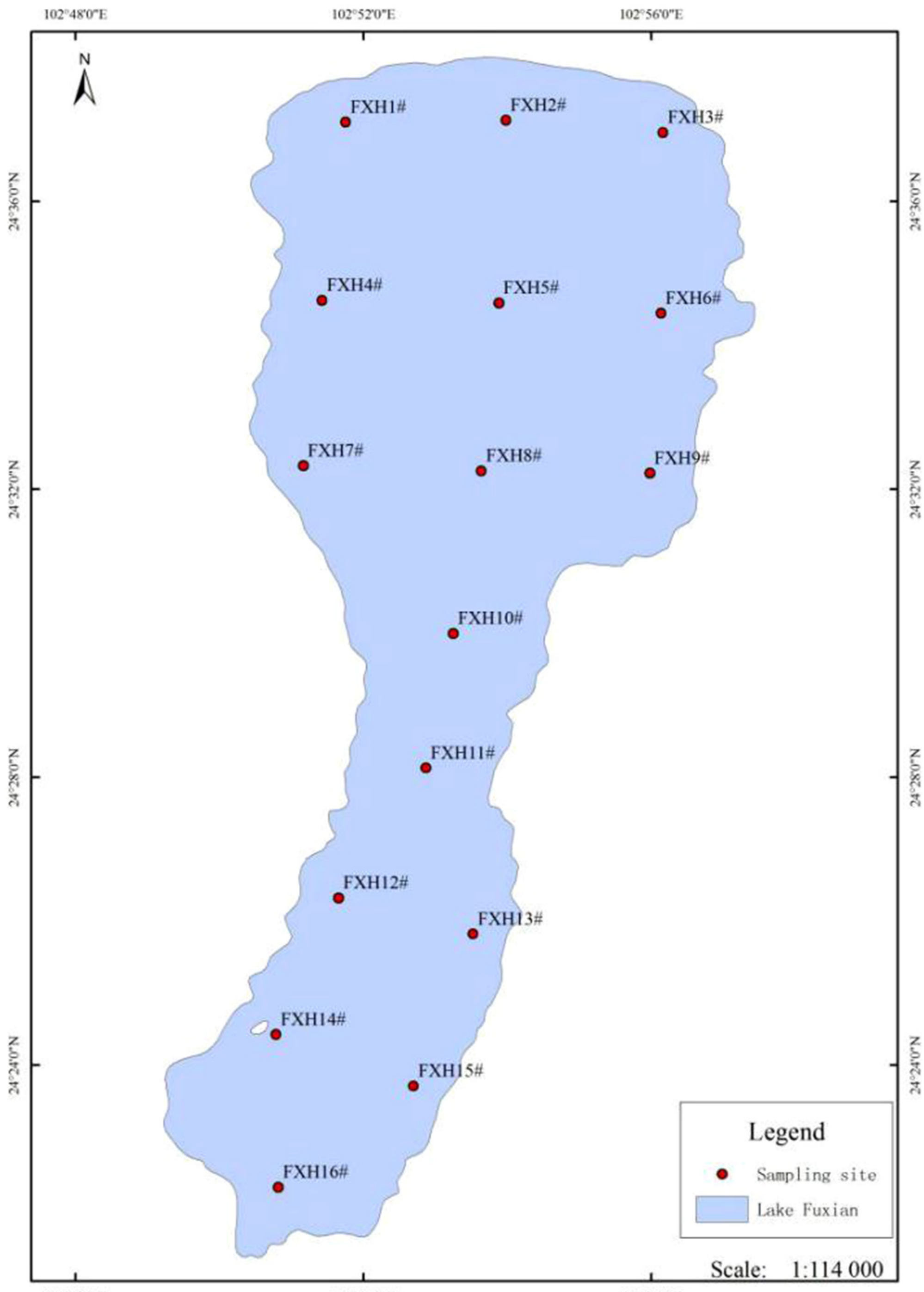

Fig. 1. Sampling sites of Lake Fuxian (FXH), Yunnan, China.

0.028–0.188 mg/L. Seasonal changes in NO_3^-–N and TN concentrations were detected, and the highest value was observed in January (winter) and July (summer). STP and TP concentrations varied in the ranges of 0.003–0.028 and 0.007–0.051 mg/L, respectively. Seasonal variations were also detected, and the highest value occurred in October (autumn) and January (winter). Moreover, TN/TP analysis demonstrated that TN/TP fluctuated between 1.030 and 14.050, and the highest value was observed in July (summer) (Fig. 5).

3.2 Composition of phytoplankton functional groups

Overall, 66 species (genera) belonging to seven taxonomic categories (Chlorophyta, Cryptophyta, Bacillariophyta, Cyanophyta, Pyrrophyta, Chrysophyta and Euglenophyta) were identified during the experimental periods. In total, eighteen phytoplankton functional groups were classified (Tab. 1), namely, assemblages F, G, J, X2, X1,T, P, MP, D, C, H1, L_O, S1, M, Y, E, W1 and W2.

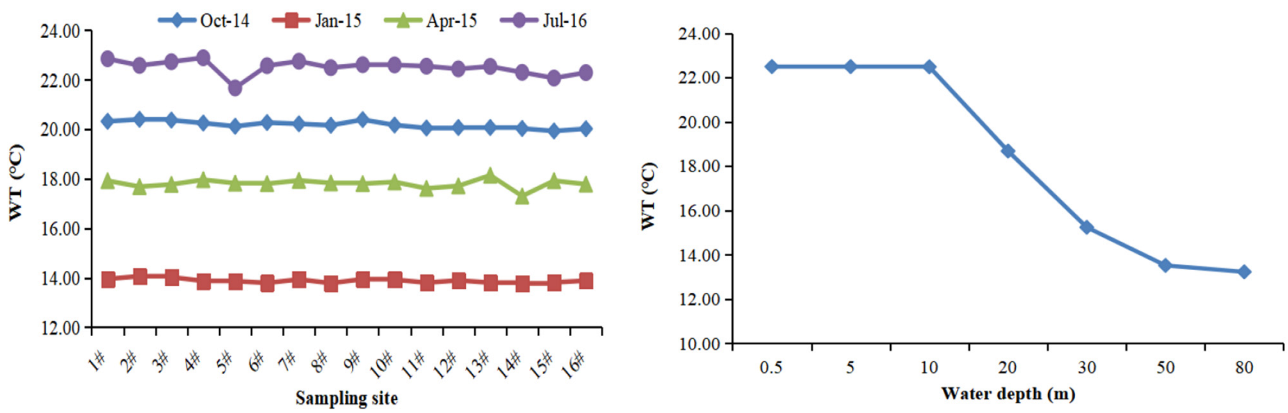

Fig. 2. Seasonal dynamics of water temperature at the surface (16 sampling sites) and gradient depth (sampling site $8^{\#}$) of Lake Fuxian in summer.

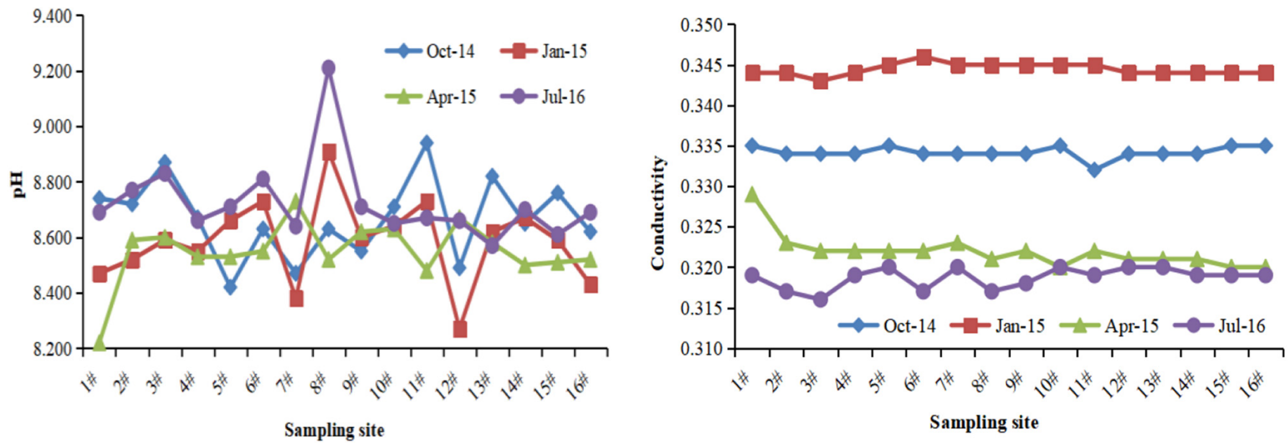

Fig. 3. Seasonal dynamics of pH and conductivity at the surface water (16 sampling sites) of Lake Fuxian.

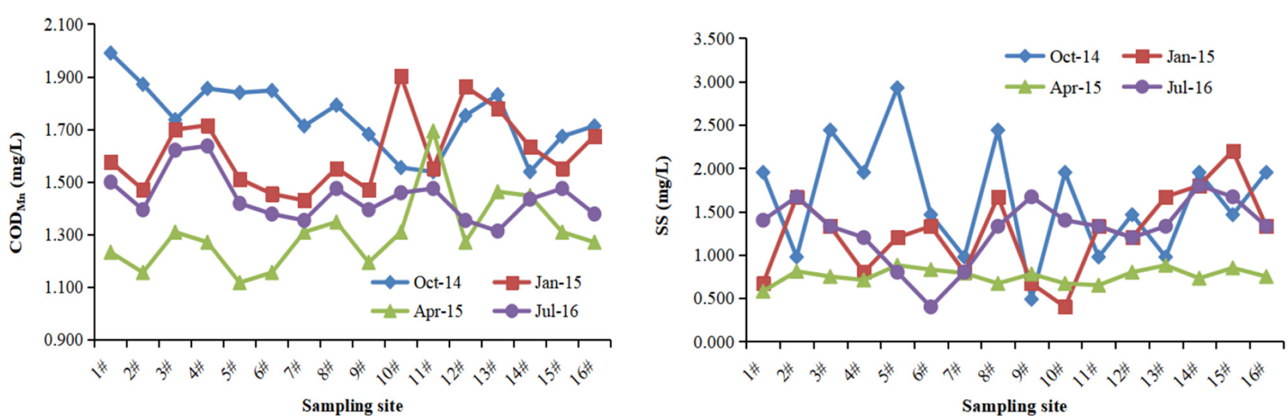

Fig. 4. Seasonal dynamics of COD_{Mn} and SS at the surface water (16 sampling sites) of Lake Fuxian.

3.3 Biomass of dominant phytoplankton functional groups

Assemblage biomasses exceeding 5% of the total phytoplankton biomass, which corresponded to the abundant functional group, were considered. Nine groups were recognised, namely groups L_O, H1, C, MP, P, T, X1, J and F. The dominant groups detected in samples collected from the surface and gradient depths of Lake Fuxian showed seasonal variations (Figs. 6 and 7). During autumn and winter, the dominant assemblages were diversified and consisted of Lo, H1, C, MP, P, T, X1, J and F. By contrast, during spring and summer,

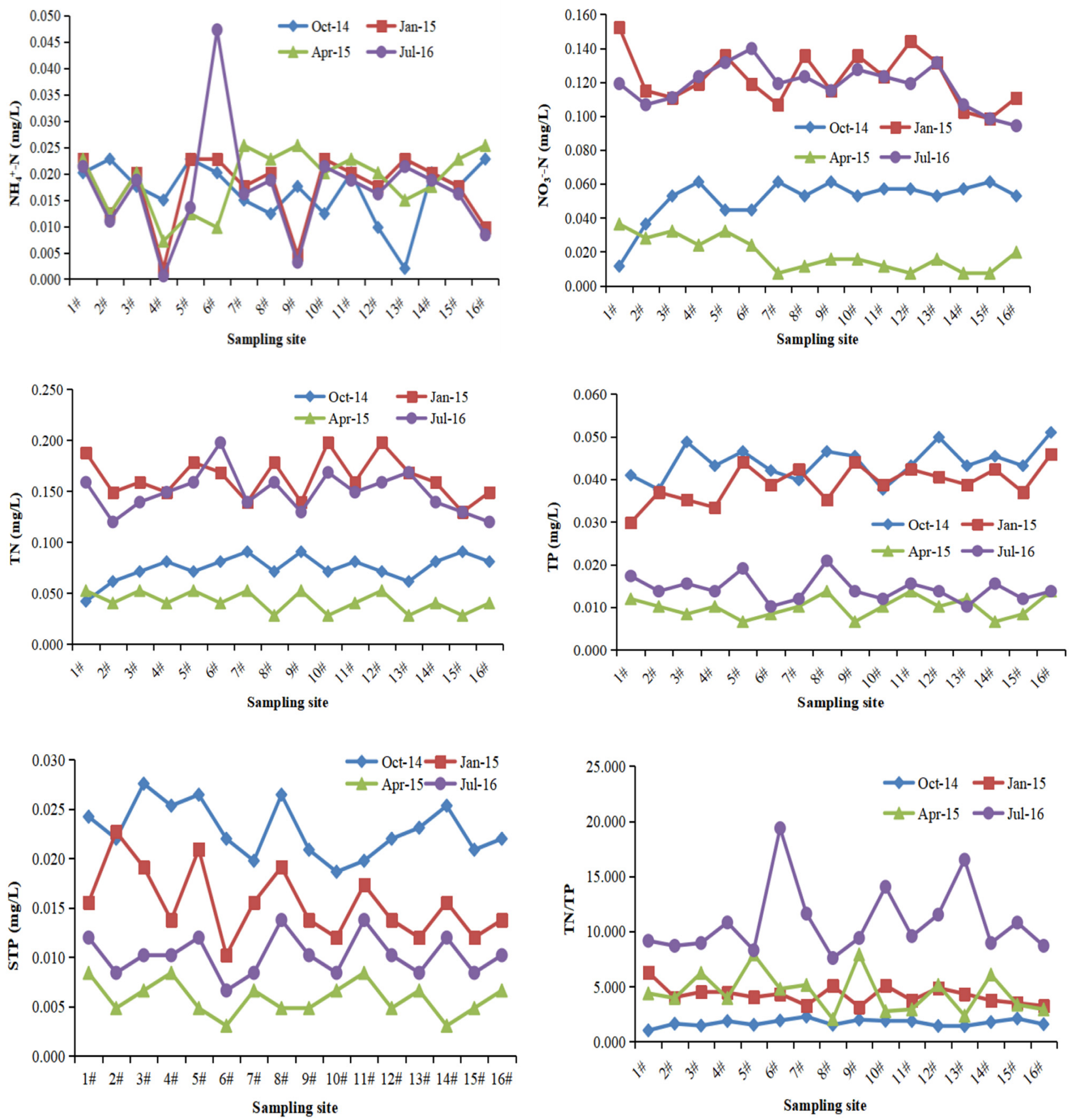

Fig. 5. Seasonal dynamics of nutrition (NH_4^+-N, NO_3^--N, TN, TP, STP, TN/TP) at the surface water (16 sampling sites) of Lake Fuxian.

Lo, H1, T and C were especially dominant. Furthermore, the predominant assemblage (the maximum percentage of each season) in the surface water samples shifted from T (October) to H1 (January) to H1 (April) to L_o (July) (Fig. 6).

The gradient depth sampling of site $8^{\#}$ in Lake Fuxian revealed similar seasonal distribution dynamics as that of the surface water. In autumn and winter, the dominant assemblages were diversified and consisted of Lo, H1, C, MP, P, T, X1, J and F. However, during spring and summer, the groups Lo, H1, T and C were especially dominant. The predominant assemblage, i.e. the maximum percentage of each season, also shifted from T+Lo (October) to T (January) to H1 (April) to L_o (July) (Fig. 7). The maximum biomass values were detected in the samples collected from 0.5 to 5 m depth, especially in October, during which the maximum biomass values were detected from a depth of 130 m.

3.4 Relationships between phytoplankton functional group composition and environmental variables

For the statistical analysis of data, eleven abiotic environmental variables (TP, TN, NH_4^+–N, NO_3–N, STP,

Table 1. All taxonomic and functional groups composition across the Lake Fuxian during our study period.

Species	Taxonomic group	Functional group	Habitat characteristics
Chlorococcum Fries *Kirchneriella contorta* (Schm.) Bohl. *Nephrocytium* agardhianum Näg. *Selenastrum* Reinsch *Dictyosphaerium* Näg. *Quadrigula chodatii* (Tan-Ful) G. M. Smith *Oocystis elliptica* W. West *Oocystis lacustis* Chod.	Chlorophyta	F	Clear, deeply mixed meso-eutrophic lakes
Pleodorina californica Shaw *Eudorina elegans* Ehr.	Chlorophyta	G	Stagnating water columns in small eutrophic lakes, reservoirs and stable phases in larger river-fed basins
Coelastrum microporum Näg. *Coelastrum reticulatum* (Dang.) Senn. *Golenkinia* Chod. *Actinastrum* Lag. *Chodatella longiseta* Lemm. *Tetraedron minimum* (A. Br.) Hansg. *Tetraedron trilobulatum* (Reinscch.) Hansg. *Scenedesmus bijuba* (Turp.) Lag. *Scenedesmus brasiliensis* Bohl. *Scenedesmus obliquus* (Turp.) Kütz. *Scenedesmus quadricauda* (Turp.) Bréb. *Scenedesmus* Mey. Crucigenia Morr.	Chlorophyta	J	Shallow, mixed, highly enriched regions
Pteromonas Sel. *Chlamydomonas* Ehr.	Chlorophyta	X2	Shallow, meso-eutrophic regions
Chroomonas acuta Uterm.	Cryptophyta		
Chlorella Beij. *Schroederia robusta* Korsch. *Schroederia spiralis* (Printz) Korsch. *Ankistrodesmus angustus* Bern. *Ankistrodesmus acicularis* (A. Br.) Korsch. *Ankistrodesmus falcatus* (Cord.) Ralfs	Chlorophyta	X1	Eutrophic and hypertrophic regions
Mougeotia Ag.	Chlorophyta	T	Persistently mixed layers, in which light is increasingly the limiting constraint and thus optically deep, mixed environments including clear epilimnia of deep lakes in summer
Melosira granulata (Ehr.) Ralfs *Fragilaria* Lyngby.	Bacillariophyta	P	Eutrophic thermocline
Closterium gracile Bréb. *Staurastrum gracile* Ralfs	Chlorophyta		
Nitzschia Hass. *Navicula* Bory, *Achnanthes* Bory. *Gomphonema* Ag. *Cocconeis* Ehr. *Frustulia* Ag. *Cymbella perpusilla* Cl. *Cymbella tumida* (Greg.) Cl.	Bacillariophyta	MP	Frequently stirred up, inorganically turbid shallow lakes
Ulothrix Kütz.	Chlorophyta		
Synedra acus Kütz	Bacillariophyta	D	Shallow, turbid regions including rivers
Cyclotella Kütz.	Bacillariophyta	C	Eutrophic small- and medium-sized lakes
Aphanizomenon flos-aquae (L.) Ralfs. *Aphanizomenon* Morr. *Anabaena azotica* Ley *Anabaena osicellariordes* Bory.	Cyanophyta	H1	Eutrophic, both stratified and shallow lakes

Table 1. (continued).

Species	Taxonomic group	Functional group	Habitat characteristics
Merismopedia Mey.	Cyanophyta	Lo	Deep or shallow, oliotrophic or eutrophic, medium to large lakes
Chroococcus Näg.			
Peridinium gutwinskii Ehr.	Pyrrophyta		
Peridinium volzii Lemm.			
Peridinium pusillum (Pen.) Lemm.			
Ceratium hirundinella (Müll.) Schr.			
Phormidium Kütz.	Cyanophyta	S1	Turbid mixed environments (shade-adapted cyanoprokaryotes)
Pseudoanabaena			
Microcystis Kütz.	Cyanophyta	M	Eutrophic to hypereutrophic, small to medium lakes
Cryptomons ovata Ehr.	Cryptophyta	Y	This codon, mostly including large cryptomonads but also small dinoflagellates, refers to a wide range of habitats, which reflect the ability of its representative species to live in almost all lentic ecosystems when grazing pressure is low
Cryptomonas erosa Ehr.			
Dinobryon Ehr.	Chrysophyta	E	Usually small, shallow, base-poor lakes or heterotrophic ponds
Phacus Duj.	Euglenophyta	W1	Ponds, even temporary, rich in organic matter from husbandry or sewages
Trachelomonas Ehr. Em. Defl.	Euglenophyta	W2	Mesoeutrophic ponds, even temporary, shallow lakes

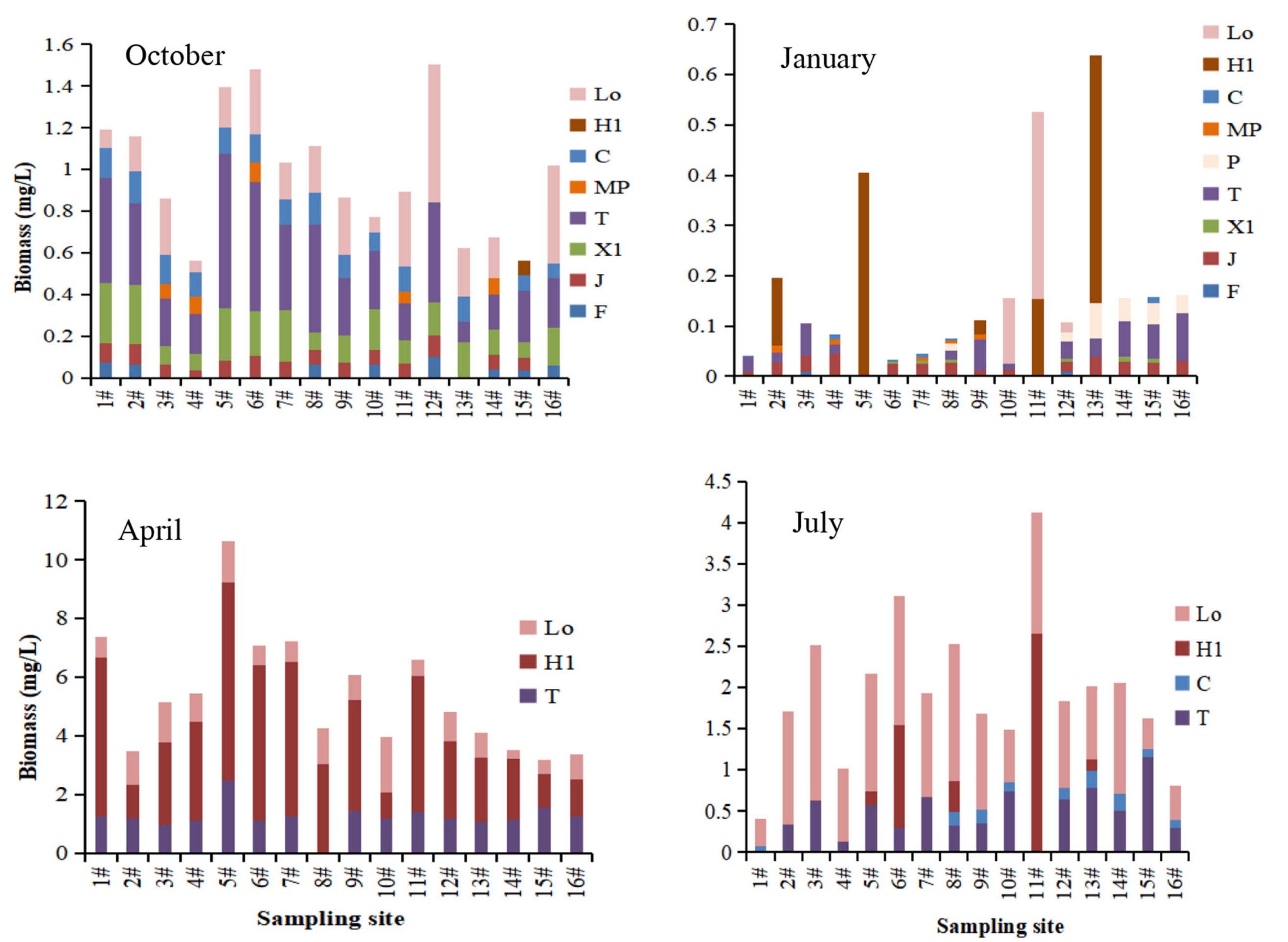

Fig. 6. Seasonal changes of dominant phytoplankton functional groups composition at the surface water of Lake Fuxian during the experimental period.

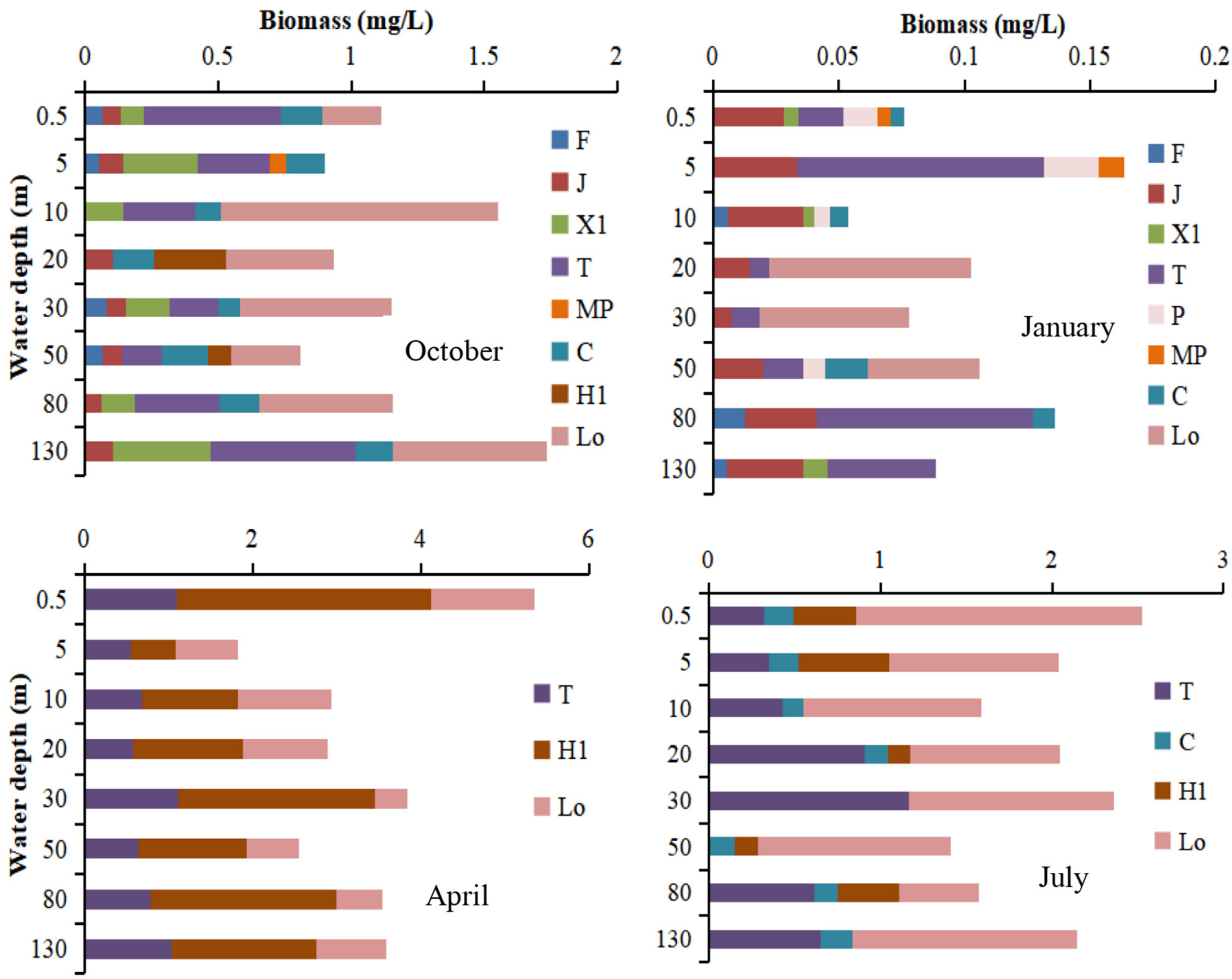

Fig. 7. Seasonal changes of dominant phytoplankton functional groups composition at the gradient depth water (Sampling site 8#) of Lake Fuxian during the experimental period.

TN/TP, SS, COD, Con, pH and WT) and nine abundant phytoplankton functional groups (L_O, H1, C, MP, P, T, X1, J and F) were considered. The correlated factors that influenced the dominant functional groups of the surface water samples and the assemblages of the gradient depth samples were considered. DCA showed that the SD value for the surface sample was 0.627 (<2). Thus, RDA was applied, and the significance of environmental variables was detected through the Monte Carlo test ($F=98.585$; $p=0.0020$). As shown in Figure 8, the functional groups L_O, C, H1 and T were significantly negatively correlated with STP, COD, TP and Cond. Groups C and L_O were positively correlated with WT and TN/TP, and groups T and H1 were positively correlated with NH_4^+–N. The functional group MP was significantly positively correlated with NO_3^-–N, TN and SS. Groups J, X1, F and P were significantly positively correlated with Con but were negatively correlated with WT and TN/TP.

4 Discussion

4.1 Environmental variables

Lake Fuxian is a subtropical plateau lake located in Yunnan, China. According to our gradient depth sampling, it was demonstrated that the water temperature in Lake Fuxian decreased with water depth. The largest temperature difference between the surface and bottom water was detected in July. This result was in agreement with the description provided by Zhang *et al.* (2007), who indicated that in Lake Fuxian, a thermocline is initiated in late March and gradually enhances until August (Zhang *et al.*, 2007). The gradient water temperature from the surface to bottom layer of the water could affect phytoplankton distribution, just as studies by Litchman and Klausmeier (2008), Cellamare *et al.* (2016) who also indicated that temperature was a major force in structuring communities. As shown in Figure 7, the low temperature at the

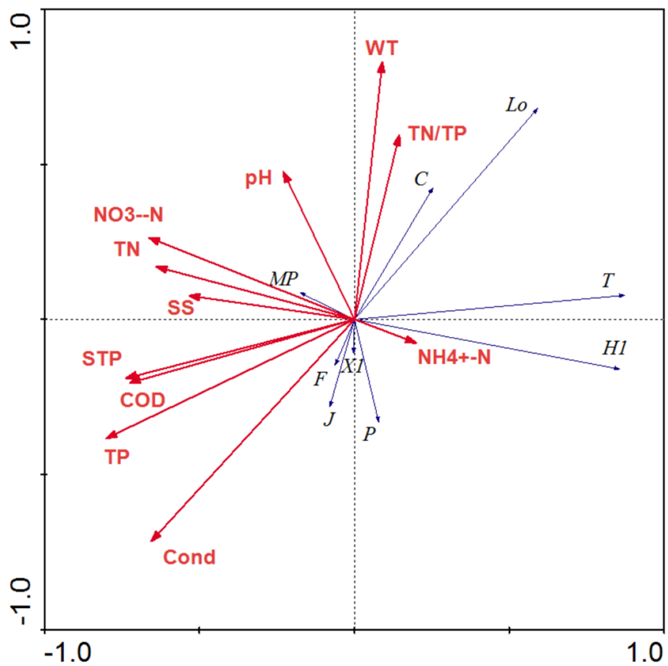

Fig. 8. Dominant functional groups (MP, C, Lo, T, H1, P, X1, J, F)-environment biplot RDA of Lake Fuxian.

deep water might play important roles in the dominance of assemblage Lo.

Besides, in the present study, it was demonstrated that the fluctuation of TN/TP in Lake Fuxain was from 1.03 to 14.05. Reynolds (1984) indicated that nitrogen tends to be a limiting nutrient when TN/TP < 7.23 (mass ratio). Based on this theory and combined with our survey data, it was suggested that nitrogen might be a limiting factor in Lake Fuxian all year around except for July. However, the further researches should be conducted to verify whether this speculation was rational. In addition, Reynolds *et al.* (2000) proposed that phosphorus is not a limiting factor for most phytoplankton when soluble reactive phosphorus (SRP) concentration is >10 μg/L, but it is a limiting factor for some phytoplankton organisms when SRP concentration is between 3 and 10 μg/L. In our study, the SRP in Lake Fuxian was <10 μg/L all year around (the data were not shown), which also might suggest that phosphorus could be a limiting factor in this lake.

4.2 Phytoplankton functional group structure and related environmental variables

Numerous studies have reported that phytoplankton community structure could be affected by nutrients, water temperature, water level and light. The key driving factors are diversified amongst lakes, reservoirs, ponds and other aquatic ecosystems worldwide. In the present study, we observed a clear relationship between phytoplankton functional group succession and environmental variable dynamics in Lake Fuxian. The dominant functional group succession was comprehensively regulated by nutrition and water temperature.

As shown in Figures 6 and 7, the functional group T (consisting of *Mougeotia* sp.) was dominant in the surface water during the whole year. This group was especially dominant during October and January. Gradient sampling at site 8# demonstrated that group T was dominant even in deep water. In addition to Lake Fuxian, this filamentous green algae is also dominant in European deep lakes (Sommer, 1986) or reservoirs (Li *et al.*, 2017) and subtropical freshwater lakes, such as Lake Taihu and Lake Erhai (Song *et al.*, 2010; Cao *et al.*, 2018). The distribution of group T is dependent on their characteristics of sensitivity to nutrient deficiency and tolerance for low light. The gradual dominance of Group T in Lake Fuxian since the 1990s (Dong *et al.*, 2014) indicates that nutrient levels in the lake have increased since then. However, the relative importance of phosphorus and nitrogen in influencing Group T is controversial. Mccormick and O'dell (1996) suggested that assemblage T favours conditions of phosphorus enrichment. Li *et al.* (2017) recently indicated that group T is significantly associated with nitrogen. We also demonstrated that group T was significantly and positively correlated with NH_4^+–N.

Our present work suggested that group H1 was also dominant during the whole year, but it was especially dominant during April. The succession of dominant functional groups from H1 (April) to Lo (July) in Lake Fuxian might be correlated with water temperature and nutrient concentration. This result coincided with the report of Li *et al.* (2017), who also indicated that nitrogen-fixing *Anabaena* sp. (group H1) often dominated the phytoplankton community during spring under relatively poor nutrient conditions.

Reynolds (2000) and Padisák *et al.* (2009) suggested that group L_o (comprising large dinoflagellates represented by the motile *Peridinium*) could easily obtain additional nutrients from the hypolimnion and is suitable for growth and dominance in the thermotropic layer during summer. This finding is in agreement with our investigation in Lake Fuxian. Assemblage L_O was particularly prevalent during the hot season from July and October. The present result was also in accordance with that reported by Huang *et al.* (2018), who demonstrated that assemblage Lo was dominant during stratification periods in summer and autumn. Water temperatures between 20 °C and 27 °C are favourable for the growth and development of Group L_O (Grigorszky *et al.*, 2006). However, temperature reductions could disrupt the dominance of L_O. Our RDA analysis results for Lake Fuxian also suggested that the functional group L_O was significantly and positively associated with WT and TN/TP.

5 Conclusion

According to surface and gradient depth sampling of Lake Fuxian, it was suggested that the concept of phytoplankton functional groups was well applicable in this subtropical plateau lake. The predominant assemblages succession was demonstrated as T (October) to H1 (January) to H1 (April) to Lo (July) in Lake Fuxian. Furthermore, according to RDA analysis, it was suggested that WT and TN/TP might be key driving factors in the phytoplankton changes of Lake Fuxian.

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