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Weekly dynamics of phytoplankton functional groups under high water level fluctuations in a subtropical reservoir-bay

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Abstract In reservoirs, water level fluctuations strongly influence phytoplankton development. However, studies on the response of phytoplankton in the reservoir-bay to water level fluctuations are very scarce, especially in the highly dynamic reservoir system, for instance, the Three Gorges Reservoir (TGR) on the Yangtze River in China. Therefore, we carried out weekly monitoring in a typical tributary bay—Xiangxi Bay of the TGR from March 2008 to March 2009, to analyze the dynamics of phytoplankton functional groups, as well as their response to the water level fluctuations and other environmental conditions. The phytoplankton functional groups G (short, nutrient-rich water columns with high light and without nutrient deficiency), M (dielly mixed layers of small eutrophic, low latitude with high insolation and without flushing and low total light) and Lo (summer epilimnia in mesotrophic lakes with segregated nutrients and without prolonged or deep mixing) were the most important in biomass, mainly represented by *Pandorina morum* and *Eudorina elegans*, *Microcystis aeruginosa*, *Peridiniopsis niei* and *Ceratium hirundinella*, respectively. The dominant functional groups had close relationships with the water level fluctuations, light and nutrient, etc. Principal components analysis and redundancy analysis indicated that phytoplankton functional groups in Xiangxi Bay were restricted by the mixing regime and other abiotic variables under the influences of the mixing regime. In Xiangxi Bay, the water level fluctuation showed significant correlations with many physico-chemical variables, including the mixing depth ($r = 0.97$, $p < 0.001$) and the relative water column stability ($r = -0.80, p < 0.001$). The study implied that water level fluctuations had complex influence on environmental changes and selecting for phytoplankton functional groups in a highly dynamic reservoir-bay. The important characteristics of the dominant phytoplankton functional groups in Xiangxi Bay were also discussed.

Keywords Water level fluctuations · Functional groups · Phytoplankton dynamics · Redundancy analysis · Three Gorges Reservoir · Xiangxi Bay

Introduction

As an important physical factor for aquatic ecosystems, hydrodynamics can be regarded as the interfaces between aquatic ecology, biomechanics and

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environmental fluid mechanics (Nikora 2009). Water level fluctuations, emerging as a significant element of hydrodynamics, is a natural phenomenon that occurs in almost all aquatic ecosystems. For instance, in a giant subtropical reservoir—the Three Gorges Reservoir (TGR) of China, the water level varies between 145 m (flood season) and 175 m (dry season) because the operation pattern is storing clear water after the flood season and releasing muddy water by lowering the water level of the reservoir during the flood season, according to complex benefits including flood control, power generation and shipping, and seasonal changes in suspended particles along with its seasonal flooding (Shao et al. 2008). The effects of drastic water level fluctuations have caused a wide range of attention.

Water level fluctuations have important effects on estuary (Costa et al. 2009), wetland (Chow-Fraser et al. 1998), lake (Osborne et al. 1987; Gulati et al. 2008; Coops et al. 2003), reservoir (Naselli-Flores and Barone 1997; Donagh et al. 2009; Arfi 2005; Cott et al. 2008) and other ecosystems. It has been reported that water level was the main factor controlling phytoplankton biomass, species diversity, evenness and community change rate in the river, and in the lake, different phytoplankton groups (C- to S-strategists and R-strategists) responded to different water level phases (de Emiliani 1997). In reservoirs ecosystems, variations in water level may affect plankton biomass and species composition (Naselli-Flores and Barone 1997; Donagh et al. 2009). In a tributary bay (Xiangxi Bay) of the Three Gorges Reservoir, the longitudinal patterns of phytoplankton distribution were under the influence of water level fluctuations (Wang et al. 2010a).

Temporal variability, structure and dynamics of phytoplankton community are the most important to aquatic ecosystems' metabolism; furthermore, phytoplankton can be used as a monitoring tool to determine the water quality and help to understand the characteristics and variations in aquatic ecosystems (Costa et al. 2009; Crossetti and Bicudo 2008). Traditionally, phytoplankton composition was studied considering the biomass variations in the major taxonomic classes; however, such approach cannot actually reflect the functioning of an ecosystem (Reynolds 1997; Costa et al. 2009). It seems to be helpful to solve the problem that functional groups approach was developed and applied. Reynolds (1997) defined several phytoplankton functional groups that potentially, and alternately, may dominate or co-dominate in a given environment, based on Grime's (1979) seminal work on terrestrial vegetation and using physiological, morphological and ecological attributes of the phytoplankton species (Reynolds et al. 2002; Kruk et al. 2002). Nowadays, the phytoplankton functional groups approach uses 38 assemblages according to their sensitivities and tolerances, identified by alpha-numeric codes (Padisák et al. 2009) and have been triumphantly applied in estuary, lake and reservoir ecosystems (Costa et al. 2009; Mieleitner et al. 2008; Becker et al. 2009; Crossetti and Bicudo 2008).

The studies of phytoplankton in TGR were focusing on comparisons of before and after impoundment (Kuang et al. 2005), rainy and dry seasons (Zeng et al. 2006), and some were in terms of algal bloom events (Xu et al. 2009, 2010; Wang et al. 2010b). The phytoplankton functional groups approach has not been applied in TGR until now. Moreover, the studies of phytoplankton in a reservoir such as the TGR after the final stage of impoundment with drastic water level fluctuations and complex hydrodynamic characteristics are still scarce. Additionally, there was a higher frequency of algal bloom and level of eutrophication in reservoir-bays, compared with the main axis of the reservoir (Cai and Hu 2006). However, the response of phytoplankton in reservoir-bays to water level fluctuations was poorly documented. So it is of great theoretical and practical importance to carry out related investigations. In the present study, we firstly determined the driving factors influencing the changes in phytoplankton functional groups in the TGR with high water level fluctuations due to artificial management, by analyzing the weekly variations in phytoplankton functional groups in biomass, and then discussed the effect of water level fluctuations and main characteristics of dominant functional groups in the highly dynamic Xiangxi Bay, with the purpose of supplying helpful information to water quality management and reservoir operation in the similar reservoir systems.

Materials and methods

Study site and sampling

The Three Gorges Reservoir (TGR) is the largest water conservancy and hydropower project reservoir in China, located in 29°16′–31°25′ N, 106°–110°50′ E (Huang et al. 2006; CRAES Report 2004). A subtropical monsoon climate prevails (Jiang et al. 2006), with average annual rainfall 1,000–1,300 mm, characterized as warm winter and hot summer, early spring and cold autumn, heavy rain and scant frost, high humidity, a lot of clouds and light winds (CRAES Report 2004). It is more than 600 km long and 1.1 km wide, with normal water level of 175 m, surface area of 1,080 km^2 and capacity of 3.93×10^{10} m^3 (Huang et al. 2006).The Xiangxi River is the largest tributary of the TGR in Hubei Province, located in 38 km upstream of the Three Gorges Dam, with a length of 94 km in the mainstream, a watershed area of 3,099 km^2, the natural fall of 1,540 m and the average annual discharge of 65.5 m^3/s (Wang et al. 1997). The lower 20–40 km stretch of Xiangxi River featured as subcritical flow similar to natural lake after impoundment of TGR, and since then it was called Xiangxi Bay (Cai and Hu 2006; Ye et al. 2007). In the present study, the sampling site was located at the Xiangxi Ecosystem Station of the Institute of Hydrobiology, Chinese Academy of Sciences/China Three Gorges Corporation, 25 km upstream of the mouth stretch of Xiangxi Bay (Fig. 1).

Samplings were performed at weekly intervals from March 14, 2008, to March 13, 2009, at a depth of 0.5 m beneath the water surface using a 5 L Van Dorn sampler. Samples for analyses of nutrients were stored in a pre-cleaned plastic bottle and acidified with sulfuric aid for laboratory analysis. Samples for phytoplankton analyses were fixed with neutral Lugol's solution.

Biotic and abiotic variable measurements

A sedimentation method was used for taxon identification and counting (Cai 2007; Huang et al. 2000). Phytoplankton was quantitatively analyzed in a Fuchs-Rosental slide, with an Olympus CX21 microscope (Olympus Corporation, Japan) at 400× magnification. Taxonomic identification of phytoplankton species was done according to Hu and Wei (2006) and John et al. (2002).

Vertical profiles of water temperature (WT) were recorded by the EcoTech Monitoring Stations (Eco-Tech Umwelt-Meßsysteme GmbH, Germany). Conductivity (Cond), pH, dissolved oxygen (DO, %) and turbidity (NTU) of the water surface were measured with Environmental Monitoring Systems (YSI 6600EDS, USA). The photosynthetic active radiation (PAR) through the water column was obtained from an underwater quantum sensor (Li-192SA, USA).

The concentrations of ammonium nitrogen (NH_4-N), nitrate nitrogen (NO_3-N), phosphate phosphorus (PO_4-P) and silicate silicon (SiO_2-Si) were measured with a segmented flow analyzer (Skalar San^{++}, Netherlands), according to Protocols for Standard Observation and Measurement in Aquatic Ecosystems of Chinese Ecosystem Research Network (CERN) (Cai 2007; Huang et al. 2000).

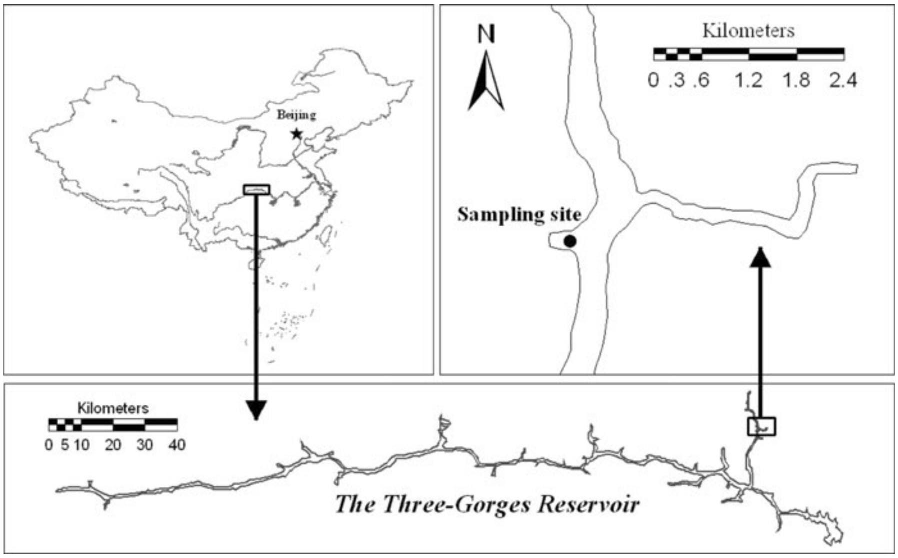


Fig. 1 Location of sampling site in Xiangxi Bay of the Three Gorges Reservoir, China

Data analysis

Euphotic zone was calculated as the depth of the 1% light level. Mixing depth was evaluated equal to the epilimnetic zone when the reservoirs showed stratification; otherwise, it was taken equal to the actual depth at the sampling site (Naselli-Flores 2000). The lower boundary of the epilimnion was determined by a thermocline, i.e., a change of 1°C per 1 m depth change. The ratio between the euphotic and mixing depths (Zeu/Zmix) was used as a measure of light availability (Jensen et al. 1994). Water level fluctuations (WLF) were measured by the difference between daily average water level and the lowest water level, i.e., water level in June 12, 2008, 145.15 m. The real-time data of water level were obtained from the China Three Gorges Corporation.

The dimensionless parameter relative water column stability was calculated by comparing the density gradient of the whole water column to the density difference between 4 and 5°C pure water using the following formula (Padisák et al. 2003):

$$\mathrm{RWCS} = \frac{D_b - D_S}{D_4 - D_5}$$

where D_b, D_s, D_4 and D_5 are the density of the bottom waters, the density of the surface water, the densities of water at 4 and 5°C, respectively. In this study, the depth of 1 m was considered as “surface”, the depth of 10 m was considered as “bottom” in light of 10 m as the water depth at the sampling site when the TGR reached the lowest water level.

Algal biovolume was calculated using formulae for geometric shapes, and assuming the fresh weight unit as expressed in mass, where $1\ \mathrm{mm}^3/\mathrm{L} = 1\ \mathrm{mg/L}$ (Huang et al. 2000; Wetzel and Likens 2000). Based on the criteria proposed by Reynolds et al. (2002), species contributing more than 5% to the total biomass were grouped into functional groups.

Principal components analysis (PCA) was used to determine temporal patterns of physical and chemical variables. The PCA analysis was performed in the software Statistica 6.0, on the variables including WT, Cond, DO (%), NTU, Zeu/Zmix, NH_4-N, NO_3-N, PO_4-P and SiO_2-Si, which were all transformed by Log $(x + 1)$.

Ordination analysis was performed using CANOCO version 4.5 (Ter Braak and Šmilauer 2002), and all the abiotic and biological data were transformed by Log $(x + 1)$ at first. Detrended correspondence analysis (DCA) for the species data was employed to decide whether linear or unimodal ordination methods should be applied (Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Redundancy analysis (RDA), which is a constrained ordination method, was applied to examine the relationships between the environmental variables and phytoplankton functional groups and to select the best variable describing the functional groups distribution (Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Monte Carlo simulations with 499 permutations were used to test the significance of the environmental variables to explain the functional groups data in the RDA (Lepš and Šmilauer 2003). Kruskal–Wallis *H* test was employed for comparisons among the physical and chemical conditions of the different periods. Nonparametric correlation analysis (Pearson correlation) was used to determine the relationships between the biomass of dominant groups and the environmental factors, as well as the relationships between WLF and the other environmental variables. Kruskal–Wallis *H* test and correlation analysis were performed in the software SPSS 16.0.

Results

Temporal patterns of physical and chemical factors

Water level fluctuations of the TGR in the study period are shown in Fig. 2, varied between 144.66 m and 172.80 m, with the range of 28.14 m. The water level kept in median water level and then varied to the lowest water level rapidly from March 14 to June 5, 2008. It remained lowest near the water level of 145 m, with the variation range of not more than 1.2 m in the flood season, from June 6 to September 28, 2008. The water level rose rapidly from September 29 to November 11, 2008, and then descended slowly from November 12, 2008, to March 13, 2009.

According to the temperature vertical profiles in the upper 10-m water column (Fig. 3), three different patterns were distinguished based on weekly surveys: transition period (from March 14 to May 23, 2008, when the water column condition was transformed from mixing to stratification), stratification period (from May 30 to September 26, 2008, when

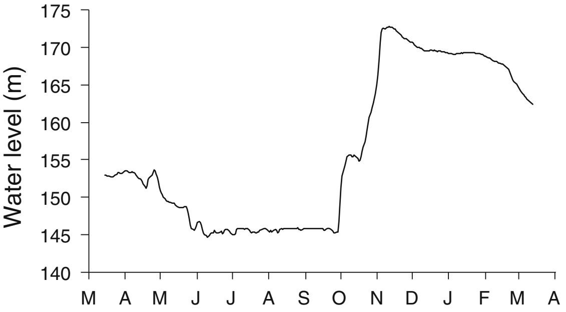


Fig. 2 Water level fluctuations of the Three Gorges Reservoir in the monitoring period

stratification condition could be observed discontinuously) and mixing period (from October 3, 2008, to March 13, 2009, when water column was totally mixed). The retention time of water in Xiangxi Bay was 117, 64 and 440 days, respectively for the three periods (Wang, unpublished data). Mean and ranges of water level fluctuations, some limnological variables and concentrations of nutrients are listed in Table 1.

The mean of water level fluctuations in stratification period was much smaller than transition period and mixing period; they were 0.5, 6.3 and 21.2 m, respectively. The relative water column stability reached the highest values in stratification period, and then the transition period, while mixing period had the lowest values (not more than 11.73). In terms of the availability of light in the water column, Zeu/Zmix ratio was biggest in the stratification period, while the values of Zeu and Zmix showed

Fig. 3 Depth-time isopleths of water temperature in Xiangxi Bay of the Three Gorges Reservoir

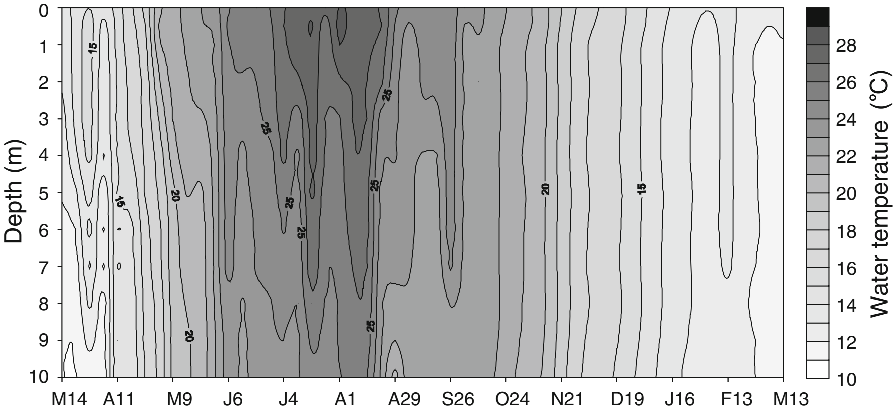


Table 1 Mean and ranges of some environmental variables

	Transition period		Stratification period		Mixing period		*p*
	Mean	Range	Mean	Range	Mean	Range	
WLF	6.3	3.3–8.5	0.5	0.0–0.7	21.2	8.6–27.4	<0.001
RWCS	48.99	9.39–87.20	71.48	25.73–120.06	5.24	0.00–11.73	<0.001
Zeu	3.9	1.1–5.9	3.5	2.2–7.2	7.6	3.6–11.2	<0.001
Zmix	16.2	2.0–19.5	9.0	1.0–11.7	32.2	19.6–38.4	<0.001
Zeu/Zmix	0.27	0.11–0.53	0.68	0.22–3.54	0.23	0.16–0.32	0.001
WT	17.7	13.3–23.0	26.0	23.1–28.4	16.7	12.0–23.2	<0.001
Cond	317	281–362	286	179–342	261	172–308	<0.001
pH	8.56	8.27–9.05	8.66	8.17–9.12	8.36	8.18–8.63	0.001
DO (%)	121.17	95.70–174.20	140.39	93.10–213.10	90.93	82.20–110.30	<0.001
NTU	18.2	0.8–94.7	10.4	4.4–20.0	4.6	0.9–14.0	0.001
NH_4-N	0.10	0.001–0.26	0.13	0.02–0.57	0.05	0.001–0.22	0.002
NO_3-N	1.04	0.35–1.82	1.10	0.71–1.36	1.40	0.95–1.76	0.001
PO_4-P	0.12	0.03–0.32	0.02	0.001–0.06	0.07	0.03–0.09	<0.001
SiO_2-Si	2.22	1.21–2.90	3.79	2.51–7.66	3.77	3.24–8.22	<0.001

the smallest in this period. It indicated that water column stratification conditions provided good availability of light for phytoplankton development in the stratification period of Xiangxi Bay. Temporal variations in five water quality parameters showed that stratification period had higher values of WT, pH and DO (%), while Cond and NTU were relatively small in the transition period.

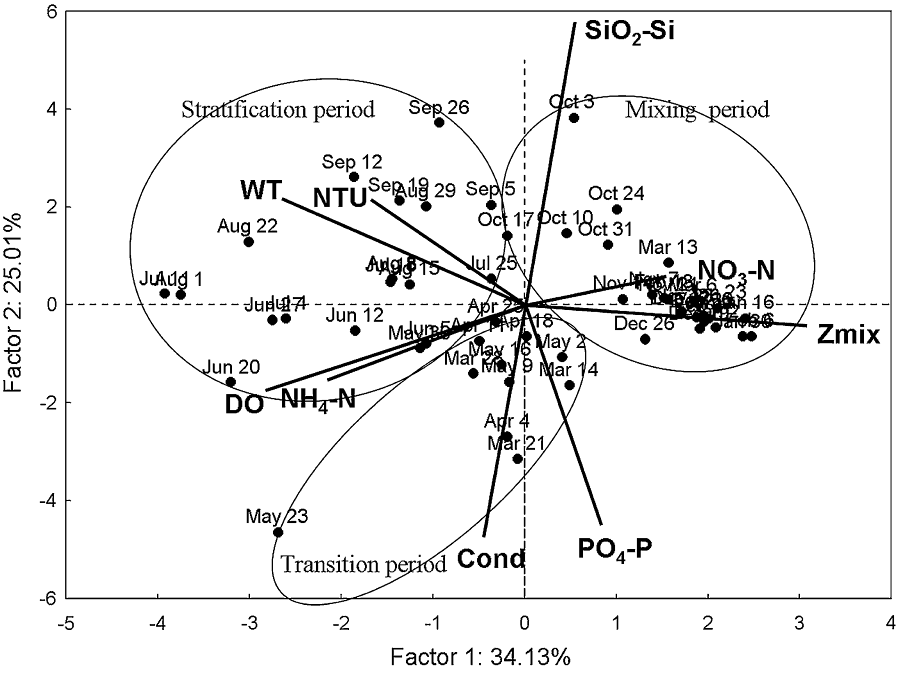
Nutrients concentrations also showed differences between the three periods (Table 1). NH_4-N concentrations reached maximum on June 20, 2008 (0.57 mg/L). NO_3-N concentrations increased from stratification to mixing period, indicating a nitrification process. PO_4-P concentrations were relatively small in the stratification period. SiO_2-Si concentrations were higher in stratification and mixing periods than in transition period. The differences in nutrients concentrations in three different periods indicated the complex influences of mixing regime on the plankton and nutrient dynamics. With respect to stratification, though it was related to the thermal effect, its formation reflected the impact of water level fluctuations in the TGR, because it was very hard to generate stratification environment in the dynamic conditions with high variations in water level fluctuations.

The PCA explained 59.14% of the data variations in the first two axes by using 9 abiotic variables (Fig. 4). The first axis (34.13%) reflected mixing regime, with the most important variables for its ordination were Zmix (0.90), DO (−0.83) and WT (−0.78). The second axis (25.01%) showed the gradient of the salinity, with the most important variables for its ordination were SiO_2-Si (0.91), Cond (−0.74) and PO_4-P (−0.70). On the positive side of axis 1, samples in the mixing period were correlated with the highest values of Zmix and NO_3-N, whereas on its negative side, samples in the stratification period were correlated with the highest values of DO, NH_4-N, WT and NTU. On the positive side of axis 2, samples in the stratification and mixing periods were ordered with the highest values of SiO_2-Si, whereas on its negative side, samples in the transition period were correlated with the highest values of Cond and PO_4-P. In general, the first two components of PCA expressed a temporal gradient of mixing regime and abiotic variables under the influences of the mixing regime.

Temporal variations in phytoplankton functional groups

Seventy-nine taxa of phytoplankton species were identified, distributed in six major taxonomic categories, i.e., Cyanophyta (9), Bacillariophyta (13), Cryptophyta (6), Dinophyta (5), Euglenophyta (2)

Fig. 4 Principal components analysis in Xiangxi Bay of the Three Gorges Reservoir



and Chlorophyta (44). The 32 descriptive species (more than 5% to the total biomass) were in 5 major taxonomic categories and belonged to 12 functional groups (Table 2). The typical trait of these functional groups was exhibited in Table 3.

The G, M and Lo phytoplankton functional groups were the most important in biomass (Fig. 5a), mainly represented by *Pandorina morum* and *Eudorina elegans*, *Microcystis aeruginosa*, *Peridiniopsis niei* and *Ceratium hirundinella*, respectively. The species as *Cyclotella* spp (C), *Chroomonas acuta*, *Rhodomonas lacustris* and *Rhodomonas* sp. (X2), *Cryptomonas ovata* and *Cryptomonas* sp. (Y), *Aulacoseira granulate*, *A. granulata* var. *angustissima* and *Aulacoseira* sp. (P) were also important in biomass.

The temporal variations in relative biomass of the main phytoplankton functional groups are shown in Fig. 5b. In spring 2008, it changed from the Y (*Cryptomonas ovata* and *Cryptomonas* sp.) and X2 (*Chroomonas acuta*) functional groups dominated to Lo (94.0%, and *Peridiniopsis niei* occupied 93.7%) dominated, with the maximal value of total biomass as 16.70 mg/L (Mar 28, 2008). X2 and C functional groups became important after the relative biomass of Lo decreased. From April 18, the total biomass kept on the low level till May 16, 2008. The water column stratification in the sampling site was firstly observed on May 23, 2008, with the maximal total biomass in the study period of 80.08 mg/L. At that time, the G functional group was the most important with the relative biomass of 99.8%, including two species as *Pandorina morum* (68.2%) and *Eudorina elegans* (31.6%). The biomass of G functional group suddenly decreased on May 30, while *Microcystis aeruginosa* (M) and *Anabaena flos-aquae* (H1) began to emerge in the investigation. Then, the total biomass started to increase till the *Microcystis aeruginosa* bloom broke up on June 20 (total biomass of 21.64 mg/L, and *M. aeruginosa* occupied 87.8%). The relative biomass of *M. aeruginosa* reached its maximum of 94.1% on June 27, when the total biomass decreased to 11.85 mg/L. Afterward, the total biomass and the relative biomass of *M. aeruginosa* continued to decrease, while the relative biomass of *Pandorina morum* increased. The total biomass varied between 0.41 and 3.11 mg/L from July 18 to September 5, when M, C, G, X2, P, Lo, Y and D functional groups were dominant or co-dominant alternately. Then, *Peridiniopsis niei* (Lo) became the most important on September 12, when the total biomass reached 12.0 mg/L and Y group (*Cryptomonas ovata* and *Cryptomonas* sp.) were also important. The last observation of stratification was on September 26. Afterward, it was a very long period with high variations in water level for rapid impoundment and recession of the TGR till February 6, 2009. During this period, the water column was totally mixed, with the low level of biomass, i.e., varied between 0.01 and 0.20 mg/L with the mean of 0.08 mg/L. On February

Table 2 Descriptor phytoplankton species (> 5% to the total biomass) in Xiangxi Bay

Species	Taxonomic group	Functional group
Microcystis aeruginosa	Cyanophyta	M
Anabaena flos-aquae	Cyanophyta	H1
Chroomonas acuta	Cryptophyta	X2
Cryptomonas ovata	Cryptophyta	Y
Cryptomonas sp.	Cryptophyta	Y
Rhodomonas lacustris	Cryptophyta	X2
Rhodomonas sp.	Cryptophyta	X2
Aulacoseira granulata	Bacillariophyta	P
Aulacoseira granulata var. *angustissima*	Bacillariophyta	P
Aulacoseira sp.	Bacillariophyta	P
Melosira varians	Bacillariophyta	T_B
Cyclotella spp	Bacillariophyta	C
Synedra acus	Bacillariophyta	D
Synedra sp.	Bacillariophyta	D
Asterionella formosa	Bacillariophyta	C
Peridiniopsis niei	Dinophyta	Lo
Peridiniopsis sp.	Dinophyta	Lo
Ceratium hirundinella	Dinophyta	Lo
Pyramimonas nanella	Chlorophyta	X2
Chlamydomonas reinhardtii	Chlorophyta	X2
Chlorogonium sp.	Chlorophyta	X2
Pandorina morum	Chlorophyta	G
Eudorina elegans	Chlorophyta	G
Quadrigula chodatii	Chlorophyta	F
Oocystis elliptica	Chlorophyta	F
Oocystis lacustris	Chlorophyta	F
Gloeocystis gigas	Chlorophyta	F
Sphaerocystis schroeteri	Chlorophyta	F
Pediastrum duplex	Chlorophyta	J
Coelastrum microporum	Chlorophyta	J
Coelastrum reticulatum	Chlorophyta	J
Closterium venus	Chlorophyta	P

Table 3 Trait of phytoplankton functional groups detected in Xiangxi Bay (quoted from Padisák et al. 2009 and Reynolds et al. 2002)

Functional group	Habitat template	Typical representatives	Tolerances	Sensitivities
M	Eutrophic to hypertrophic, small- to medium-sized water bodies.	*Microcystis* *Sphaerocavum*	High insolation	Flushing, low total light
H1	Eutrophic, both stratified and shallow lakes with low nitrogen content.	*Anabaena flos-aquae* *Aphanizomenon*	Low nitrogen	Mixing, poor light, low phosphorus
X2	Shallow, meso-eutrophic environments.	*Plagioselmis* *Chrysochromulina*	Stratification	Mixing, filter feeding
Y	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*	Low light	Phagotrophs
P	Continuous or semi-continuous mixed layer of 2–3 m in thickness. This association can be represented in shallow lakes of high trophic states where the mean depth is of this order or greater, as well as in the epilimnia of stratified lakes of high trophic states when the mixing criterion is satisfied.	*Fragilaria crotonensis* *Aulacoseira granulate* *Closterium aciculare* *Staurastrum pingue*	Mild light and C deficiency	Stratification Si depletion
T_B	Highly lotic environments (streams and rivulets).	*Nitzschia* *Navicula*		
C	Eutrophic small- and medium-sized lakes with species sensitive to the onset of stratification.	*Asterionella Formosa* *Aulacoseira ambigua* *Stephanodiscus rotula*	Light, C deficiencies	Si exhaustion stratification
D	Shallow turbid waters including rivers.	*Synedra acus* *Nitzschia* spp *Stephanodiscus hantzschii*	Flushing	Nutrient depletion
Lo	Deep and shallow, oligo to eutrophic, medium to large lakes.	*Peridinium* *Woronichinia* *Merismopedia*	Segregated nutrients	Prolonged or deep mixing
G	Nutrient-rich conditions in stagnating water columns; small eutrophic lakes and very stable phases in larger river-fed basins and storage reservoirs.	*Eudorina* *Volvox*	High light	Nutrient deficiency
F	Clear, deeply mixed meso-eutrophic lakes.	*Colonial Chlorophytes* *e.g. Botryococcus* *Pseudosphaerocystis* *Coenochloris* *Oocystis lacustris*	Low nutrients high turbidity	?CO2 deficiency
J	Shallow, mixed, highly enriched systems (including many low-gradient rivers).	*Pediastrum, Coelastrum* *Scenedesmus* *Golenkinia*		Settling into low light

13, 2009, the total biomass reached 3.02 mg/L, dominated by Y (*Cryptomonas ovata*, 28.8% and *Cryptomonas* sp., 28.1%) and C (*Cyclotella* spp, 24.5% and *Asterionella Formosa*, 0.8%) functional groups. Then, the C functional group kept on high relative biomass.

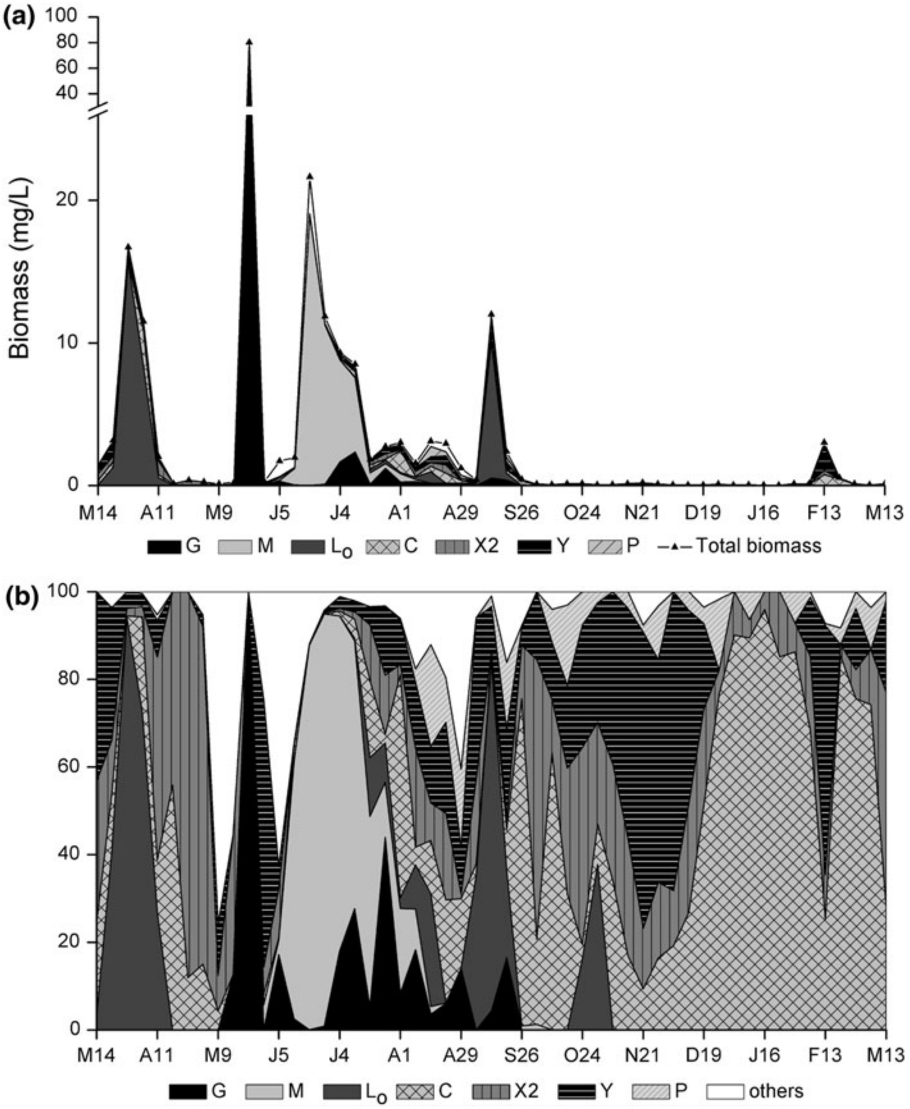


Fig. 5 **a** Weekly variations in total biomass (mg/L) and the biomass of the main functional groups (mg/L) of phytoplankton in Xiangxi Bay. **b** Weekly variation in the relative biomass of the main phytoplankton functional groups in Xiangxi Bay

The significant relationships between the biomass of main functional groups and abiotic variables including water level fluctuations, light and nutrient are shown in Table 4. The biomass of G group was positively correlated with DO and PO_4-P. The M group was positively correlated with WT, pH, DO and NH_4-N and negatively correlated with WLF and Zeu. The Lo group was negatively correlated with NO_3-N. The C group was positively correlated with Zeu/Zmix and pH and negatively correlated with NO_3-N. The X2 group was positively correlated with NTU and negatively correlated with WLF, Zeu, Zmix and NO_3-N. The Y group was negatively correlated with Zeu and NO_3-N. The P group was positively correlated with RWCS and WT and negatively correlated with WLF, Zeu, Zmix and PO_4-P.

Phytoplankton community ordinations based on functional groups

The results of DCA based on species data showed the relatively short gradient lengths of the first two axes (3.197 and 2.766 standard deviation units, respectively), so the linear ordination method—RDA was chosen for analyzing the relationships between the biotic data and environmental variables (Lepš and Šmilauer 2003).

Table 4 Pearson correlation between abiotic variables and the main phytoplankton functional groups ($p < 0.05$)

	G	M	Lo	C	X2	Y	P
WLF		−0.29			−0.34		−0.29
RWCS							0.35
Zeu		−0.28			−0.40	−0.28	−0.27
Zmix					−0.32		−0.31
Zeu/Zmix				0.46			
WT		0.31					0.33
Cond							
pH		0.52		0.33			
DO (%)	0.28	0.55					
NTU					0.44		
NH_4-N		0.70					
NO_3-N			−0.48	−0.44	−0.34	−0.43	
PO_4-P	0.69						−0.32
SiO_2-Si							

Fig. 6 shows the redundancy ordination diagram performed on WT, pH, Zeu/Zmix, NH_4-N, NO_3-N, PO_4-P and the main phytoplankton functional groups. The first two redundancy axes accounted for 35.0% of the variability in phytoplankton data (axis 1 = 25.4%, axis 2 = 9.6%) and accounted for 81.2% of the variability in the species–environment relation (axis 1 = 58.8%, axis 2 = 22.4%). The first axis of RDA was mainly positively correlated with pH (0.78), WT (0.76) and NH_4-N (0.59). The second axis was mainly positively correlated with NO_3-N (0.62). The test for significance of all canonical axes by Monte Carlo simulation showed that all canonical axes were significant ($F = 5.819$, $p = 0.002$, 499 permutations under reduced model). All the chose environmental variables explained 43.1% of the total variability in phytoplankton data. The three significant environmental variables screened by automatic forward selection of RDA were pH ($F = 10.84$, $p = 0.002$), WT ($F = 8.94$, $p = 0.002$) and NO_3-N ($F = 5.35$, $p = 0.004$).

The temporal dynamics of phytoplankton functional groups in Xiangxi Bay of the TGR were well described by the distributions of samples in the RDA ordination diagram (Fig. 6), following the mixing regime. The samples in the stratification period with weak WLF and mixing period with strong WLF were in the positive and negative sides of the first RDA axis, respectively. The stratification period showed higher values of WT, pH, Zeu/Zmix and NH_4-N concentration, while the samples with higher NO_3-N and PO_4-P concentrations appeared in the mixing period. By comparison, the M, G and Lo functional groups showed best performance in the stratification period, while the C, X2 and P groups contributed high biomass in the mixing period. The Y group showed high biomass in the transition phase of the above two periods. The samples of the transition period distributed between the stratification and the mixing period indicating the high variations in environmental factors and the composition of phytoplankton functional groups in the transition period.

Discussions

According to Reynolds (1999), the limits for phytoplankton growth and the accumulation of biomass are mainly set by available solar energy flux, available carbon and available phosphorus and nitrogen, all of which may be strongly constrained by water movements, the morphology and hydrology of the water body and by its food web structure ultimately (Reynolds 1999; Naselli-Flores and Barone 2000). The remarkable shifts in composition and biomass of phytoplankton in a tropical estuary occurred due much more to the river discharge than to nutrient availability such as nitrogen, phosphorus and silica (Costa et al. 2009). In some man-made lakes characterized by conspicuous water level fluctuations, the annual and interannual variability in the abundance and composition of phytoplankton may be strongly influenced by

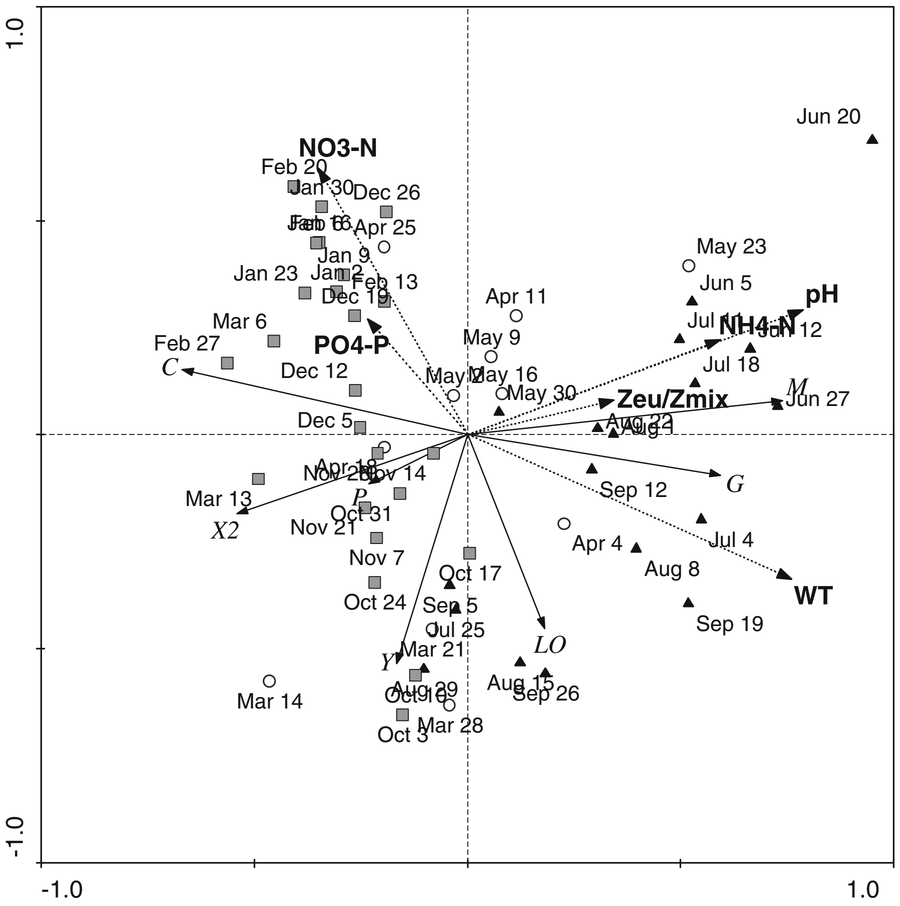


Fig. 6 RDA ordination diagram of the main functional groups and environmental variables in Xiangxi Bay. *Circle* indicates transition period samples, *up-triangle* indicates stratification period samples, and *square* indicates mixing period samples, respectively

their peculiar hydraulic regimes rather than by nutrient availability (Naselli-Flores 2000). In reservoirs, although both internal and external variables determine the structure of the plankton community, physical variables generally predominate (Wilk-Wožniak and Pociecha 2007).

Hydrodynamics play an active role in the formation of water quality and the bio-productivity of reservoirs, determining the movement of suspended and dissolved matter; heat; intensity of their circulation inside the ecosystem; stipulation of the speed of contaminating processes; the self-purification of the reservoirs and finally providing the conditions of the ecosystem function (Dubnyak and Timchenko 2000).

Water level fluctuations were strongly associated with many environmental variables in Xiangxi Bay of the TGR (Table 5). It was noteworthy that WLF significantly positively correlated with Zmix ($r = 0.97$, $p < 0.001$), suggesting the deeper mixing layer in high WLF period and the lower one under small WLF with stratification conditions. The latter situation could be expressed by the significantly negatively correlation between WLF and RWCS ($r = -0.80$, $p < 0.001$). The correlation between WLF and stability of stratification was mainly influenced by the seasonal changes in water body characteristic in the bay as well as the artificial regulation of TGR. Pearson correlation analysis also showed that WLF was positively correlated with Zeu, NO_3-N and PO_4-P ($p < 0.05$) and negatively correlated with Zeu/Zmix, WT, pH, DO and NH_4-N ($p < 0.05$). These results indicated that WLF had direct or indirect effects on physical and chemical conditions including the mixing regime.

Table 5 Pearson correlations between water level fluctuations and environmental variables

Environmental variable	Pearson correlation coefficient	p
RWCS	−0.80	<0.001
Zeu	0.84	<0.001
Zmix	0.97	<0.001
Zeu/Zmix	−0.31	0.022
WT	−0.74	<0.001
Cond	−0.14	0.331
pH	−0.46	0.001
DO (%)	−0.65	<0.001
NTU	−0.24	0.079
NH_4-N	−0.40	0.003
NO_3-N	0.50	<0.001
PO_4-P	0.27	0.048
SiO_2-Si	0.02	0.909

The second axis of the RDA separated the samples in the stratification and mixing periods which had distinct mixing regime, while in the transition period, high variations in phytoplankton and environmental factors indicated the seasonal characteristics as well as the effects of mixing regime. The study in Faxinal Reservoir (Brazil) revealed that the mixing regime was the main determining factor of the seasonal dynamics of the phytoplankton community (Becker et al. 2009). In Xiangxi Bay of the TGR, temporal dynamics of phytoplankton functional groups were influenced by the mixing regime as well as the environmental variables under its effect. Water level fluctuations were seasonally regulated; on the other hand, WLF might affect the mixing regime and other environmental factors, so there was complex impact of WLF on phytoplankton dynamics.

From the perspective of the most important species when the total phytoplankton biomass in surface water reached peak values, the succession process of phytoplankton in Xiangxi Bay of the TGR could be summarized as Lo (*Peridiniopsis niei*) → G (*Pandorina morum*) → M (*Microcystis aeruginosa*) → Lo (*Peridiniopsis niei*) → Y (*Cryptomonas ovata* and *Cryptomonas* sp.). In term of the relative biomass, the C and Y functional groups had high values in different seasons and under different WLF patterns, showing their wide adaptability to the environment changes in the TGR. However, there were potential uncertainties of these results caused by the limitation to surface samples, so more information about the vertical distribution of phytoplankton could help to improve the conclusions.

There was only one species observed in the monitoring period belonged to M group, *Microcystis aeruginosa*, which kept the dominant status of more than 50% in relative biomass from June 12 to July 11, 2008, in Xiangxi Bay. The RDA ordination diagram showed high values of WT, pH and Zeu/Zmix when dominated by M group, indicating its good adaptability to the water column stratification conditions in summer influenced by weak WLF. Many factors promote *Microcystis* dominance, including resource competition, light conditions, pH/CO_2 conditions, buoyancy, high-temperature tolerance, avoidance by herbivores, superior cellular nutrient storage, ammonium nitrogen exploitation, competition for trace elements and water exchange (Yoshinaga et al. 2006). In this study, *M. aeruginosa* dominated when the temperature varied between 25.21 and 27.41°C. It was positively correlated with pH, in accordance with the literature (Fonseca and Bicudo 2008). The M group adapts to high light availability expressed as high values of Zeu/Zmix when M group dominated, and there are other studies suggesting that the species in M groups such as *M. aeruginosa* occur in enriched lakes and are tolerant to low light availability (Reynolds et al. 2002; Bovo-Scomparin and Train 2008). In Xiangxi Bay of the TGR, high phytoplankton biomass contributed to low concentrations of soluble reactive phosphorus and nitrate nitrogen, in accordance with the study in Foz do Areia reservoir (da Silva et al. 2005).

The habitat template for G group was nutrient-rich conditions in stagnating water columns; small eutrophic lakes and very stable phases in larger river-fed basins and storage reservoirs (Padisák et al. 2009). In the present study, the species involved in G group included *Pandorina morum* and *Eudorina elegans*. *P. morum* became the dominant algae as long as nutrients are not yet depleted in the end of clear-water phase (Sommer 1986; Köhler and Hoeg 2000). In Xiangxi Bay of the TGR, the biomass of G group reached its maximum of 80.0 mg/L on May 23, 2008, when the concentration of PO_4-P reached the maximum in the study period as 0.32 mg/L. Jensen et al. (1994) explained the selection of chlorophytes at the highest phosphorus concentration by the continuous input of nutrients and carbon from the external loading and the sediment in shallow lakes that favoured the fast-growing species (Romo and Villena 2005).

Lo groups include large dinoflagellates usually found in summer epilimnia in mesotrophic lakes with segregated nutrients and without prolonged or deep mixing (Reynolds et al. 2002). The presence of flagella contributes to the organism's motility and the water renovation around the organism, therefore easing its contact with nutrients by breaking gradients around the cell (Lopes et al. 2005). However, decreasing temperature and deepening of mixing zone favored the disruption of the Lo dominance (Huszar et al. 2003). The Lo group dominated in transition and stratification period, not in mixing period in Xiangxi Bay of the TGR.

The representative species of C group were *Cyclotella* species, which are commonly found in reservoirs and are cited as a reference diatom used for indication of primary productivity in oligo-mesotrophic water bodies (Gurbuz et al. 2003). During the whole study period, *Asterionella Formosa* of C group appeared only in the mixing period (except for 19% on March 14, 2008), with quite low relative biomass (no more than 8%), whose competition ability is not as good as the small and light *Cyclotella* spp. Not considering atelomixis, growth of the species of *Cyclotella* is better in mixed waters (Reynolds 1997; Lopes et al. 2005), and these species are also adapted to low light availability (Reynolds 1997). So they can compete favorably with other algae in well mixed waters of spring, autumn and winter in Xiangxi Bay of the TGR characterized by low Zeu/Zmix ratios. Additionally, the C group showed high biomass in March and April when the temperature ranged from 13.5 to 14.5°C, indicating its good adaptability to the low water temperature. Actually, diatoms were inversely related to temperature, and they occurred preferentially in temperatures below 18°C and were directly related to higher discharge and a deeper mixing layer (da Silva et al. 2005).

Y group mostly includes large cryptomonads but also small dinoflagellates, living in almost all lentic ecosystems when grazing pressure is low (Padisák et al. 2009). *Cryptomonas* spp. are common in moderately enriched systems, characterized as high surface: volume ratio (Bovo-Scomparin and Train 2008), rapid phosphorus uptake rates and relatively fast growth (Albay and Akçaalan 2003). In the present study, the samples that had high relative biomass of Y group were correlated with low concentrations of NO_3-N and PO_4-P. According to Kruk et al. (2002), Y group is tolerant to high light attenuation coefficient values, indicating its adaptation to light deficient environments. In this study, Y group dominated in the low light available environment expressed as low Zeu/Zmix ratios. There are other literatures suggesting that they have abilities to improve their nutrient uptake by mixotrophy, which allows them to develop in light-limited conditions (Jones 2000), and furthermore, they enhance the competitiveness by the possession of flagella that allow vertical migration between water layers of optimal light conditions and nutrient concentrations (Bovo-Scomparin and Train 2008).

In Ömerli reservoir of Istanbul, *Cryptomonas* spp. were the most important species in late winter and early spring, accounting for 96.14–98.6% of the total biomass in March of maximum biomass (Albay and Akçaalan 2003). However, Y group was very common all year round in Xiangxi Bay. Studies in Brazilian reservoirs showed that their survival strategies lie between those of the colonizing (C-strategists) and tolerant species (R-strategists) (Dos Santos and Calijuri 1998). This fact would explain they exist for long periods in the water column. They increase the relative density closely following some disturbance that simultaneously causes the decline of another species (Crossetti and Bicudo 2005). The dominance of the Y group in high and low water periods and low light availability environments denotes its opportunistic feature (Bovo-Scomparin and Train 2008; Borges et al. 2008). In Xiangxi Bay, their permanence in the transitional stage of stratification period and mixing period was the most typical in the RDA ordination diagram, and they also have high relative biomass in the other time, for instance, May 30, 2008 (61.1%), June 27, 2008 (57.1%), December 12, 2008 (44.1%) and February 13, 2009 (56.9%).

X2 group was comprised by *Rhodomonas lacustris*, *Rhodomonas* sp., *Chroomonas acuta* in this study, and it appeared in all the surveys. They are sensitive to mixing and to light depletion, with a rapid reproduction rate and less susceptible to settling (Reynolds 1997; Devercelli 2006). In the mixing period of Xiangxi Bay, Cryptophyceans (including Y and X2 groups) and diatom were dominated, may be explained by the hydrodynamics environment, which favors the nanoplanktonic species with high reproductive rate which recycle the nutrients in the epilimnetic layer (Reynolds 1997; Reynolds et al. 2002; Borges et al. 2008).

The habitat template for P group is shallow lakes and the epilimnia of stratified lakes with higher trophic states (Padisák et al. 2009). It comprises filamentous diatoms, very common in large mesotrophic lakes in low latitudes (Huszar et al. 2000). It is characterized as a high adaptability to light decrease and water disturbance (Reynolds et al. 2002; da Silva et al. 2005). The large filamentous *Aulacoseira granulate* depends upon turbulence for suspension and required an inoculum from adjacent water bodies to develop in the main river flow, thus achieving higher abundance during periods of regular hydrological fluctuations (Devercelli 2006). In Xiangxi Bay of the TGR, the P group dominated in the mixing period may be correlated with its good adaptability to high water turbulence.

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