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Seasonal variation in functional phytoplankton groups in Xiangxi Bay, Three Gorges Reservoir*

YANG Min (杨敏)[1, 2, 3], BI Yonghong (毕永红)[1], HU Jianlin (胡建林)[1],
ZHU Kongxian (朱孔贤)[1], ZHOU Guangjie (周广杰)[1], HU Zhengyu (胡征宇)[1, **]

[1] *State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*

[2] *Graduate University of Chinese Academy of Sciences, Beijing 100049, China*

[3] *Chongqing Academy of Environmental Sciences, Chongqing 401147, China*

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Abstract We describe the phytoplankton dynamics and structure in Xiangxi Bay, Three Gorges Reservoir. Samples were collected monthly in the surface waters between August 2007 and July 2008. We identified 10 principle functional groups. C-strategists and S/R-strategists with a wide range of tolerance dominated the phytoplankton assemblage. Seasonal variation was related to water column stability because of changes in hydraulic operation in October, January, and May. Functional group C (*Asterionella formosa*) and P (*Aulacoseria granulata*) dominated in August and September, whereas group Lo (*Peridiniopsis niei*) was the most abundant between February and April, forming a dinoflagellate bloom. Group B (*Stephanodiscus hantzschii*), X2 (*Komma acudata*), and Y (*Cryptomonas erosa*) were present throughout most of the year but were most abundant in late spring. A cyanobacterial bloom occurred from June to July, during which group M (*Microcystis aeruginosa*, *M. wesenbergii*) and H_1 (*Anabaena flos-aquae*) were dominant. Green algae, characterized by group G (*Eudorina* sp., *Pandorina* sp., *Pyramidomonas* sp.) and J (*Pediastrum* spp., *Coelastrum* spp., *Scenedesums* spp.), were abundant after the bloom degraded. This sequence was corroborated by canonical correspondence analysis (CCA). The summary sequence of functional groups resulting from CCA was: C/P→Lo→H1/M/J/G. The dynamics of the phytoplankton community may be explained by the stability of water column, irradiance, water temperature, and nutrient structure.

Keyword: phytoplankton; functional group; Xiangxi Bay; Three Gorges Reservoir

1 INTRODUCTION

Seasonal succession of phytoplankton is generally assumed to be a function of changing physical, chemical and biological variables (Sommer et al., 1986). Models have been developed to understand the regulatory influence on phytoplankton of environmental factors acting upon phytoplankton assemblages (Moss et al., 1996). Most of the predictive models treat phytoplankton either as single entity or by major taxonomic divisions. According to Hu and Wei (2006), the freshwater phytoplankton fauna consists of organisms drawn from thirteen classes, with a high degree of morphological diversity. The traditional view, which examines taxonomic control at division level, has been used to predict the relative abundance of phytoplankton with some success. However, the morphological-functional framework has performed better than the taxonomic approach in simulating compositional changes (Huszar and Caraco, 1998; Huszar et al., 2000).

Based on this approach, lakes and reservoirs are characterized by groups of phytoplankton species which share strategies that are advantageous. Following Grime's (1977) seminal work on terrestrial vegetation, Reynolds (1997) separated phytoplankton

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** Corresponding author: huzy@ihb.ac.cn

into subdivisions based on species strategies (C-invasive, S-acquisitive, R-attuning). According to this scheme, C-strategists are small phytoplankton with a high surface/volume (S/V) ratio and rapid growth. These species are dominant under conditions of high light and high nutrients. S-strategists are slow-growing, large unicells or colonies with a low S/V ratio that tend to dominate under conditions of high light and low nutrients. R-strategists are generally elongated unicells, colonies, or filaments, with a high S/V ratio, and are adapted to low light incumbent upon frequent fluctuations of light levels in the turbid layers.

Based on their growth strategies, Reynolds defined several phytoplankton into 31 functional groups that potentially may dominate or co-dominate in a given environment (Reynolds et al., 2002), each being more likely to occur under particular environmental conditions. These share adaptive features, based on the physiological, morphological, and ecological attributes of the species. The presence of these groups can be used to infer recent environmental conditions more accurately than phylogenetic representatives. The application of the phytoplankton functional-group approach to aquatic systems provides important information for understanding species dynamics in pelagic communities in temperate, subtropical, and tropical regions (Huszar et al., 2003; Leitão et al., 2003; Sarmento et al., 2007; Lopes et al., 2005; Fabbro and Duivenvoorden, 2000; Kruk et al., 2002). The functional phytoplankton groupings can be applied to certain types of reservoirs given the small spatial and temporal scales at which phytoplankton exist (Marinho and Huszar, 2002; Becker et al., 2009). These groupings may also be applied to rivers (Devercelli, 2006), although they were initially described for European lakes (Reynolds, 2002).

Since the construction of the Three Gorges Dam, a number of studies have evaluated the impact of the dam on the aquatic ecosystem, including the phytoplankton assemblages, in the impounded lake (Zeng et al., 2006, 2007; Ye et al., 2006, 2007; Xing et al., 2008). These studies have, for the most part, treated phytoplankton as a single entity (e.g., chlorophyll *a*) to evaluate the relationship between biotic and abiotic variables. However, in some instances, researchers have generalized the identification of recurrent taxa and noted the seasonal dynamics of phytoplankton groups and species. However, the general patterns of phytoplankton species/group succession are poorly understood in the Three Gorges Reservoir and its tributaries.

Our primary objectives were to describe the temporal variation of phytoplankton during the second stage of impoundment in Xiangxi Bay. In addition, we evaluated the relationship between abiotic factors and seasonal variation of phytoplankton. We used a morphological/functional approach to investigate the phytoplankton dynamics in the Three Gorges Reservoir. The intermediate control hypothesis proposed by Elser and Goldman (1991) suggested that the zooplankton grazing pressure on phytoplankton is low in both oligotrophic and eutrophic lakes.

2 MATERIAL AND METHOD

2.1 Study site

Xiangxi River, located 38 km upstream of the Three Gorges Dam, is the largest tributary of the Three Gorges Reservoir (TGR) in Hubei Province. Since impoundment in 2003, the lower 25 km stretch of this river has been named Xiangxi Bay. During the second water storage stage of the TGR (altitude = 156 m), Xiangxi Bay has increased in length to ~33 km. Xiangxi Bay is representative of eutrophic regions within the TGR. Since in the river was dammed in 2003, dinoflagellate and diatom blooms have occurred regularly during the spring in Xiangxi Bay. In addition, a large scale cyanobacterial bloom was documented in the summer of 2008.

2.2 Sampling and analysis

2.2.1 Sample collection

We collected samples at monthly intervals in the surface waters at 8 sampling sites in Xiangxi Bay using a 5 L sampler from July 2007 to August 2008 (Fig.1).

2.2.2 Physicochemical analysis

We measured physical and chemical factors such as temperature, water transparency, dissolved oxygen, pH, conductivity and turbidity in situ. Temperature was measured using a thermometer. Dissolved oxygen and conductivity were measured with a JPB-607 DO meter (Leici Instrument, Shanghai, China) and a DDB-3 (Leici Instrument) meter respectively. pH and turbidity were measured using a HI 98128 pH meter (HANNA Instrument, Woonsocket, RI, USA) and a WGZ-B turbidimeter (Xinrui, Shanghai, China), respectively. Transparency was measured using a Secchi disk.

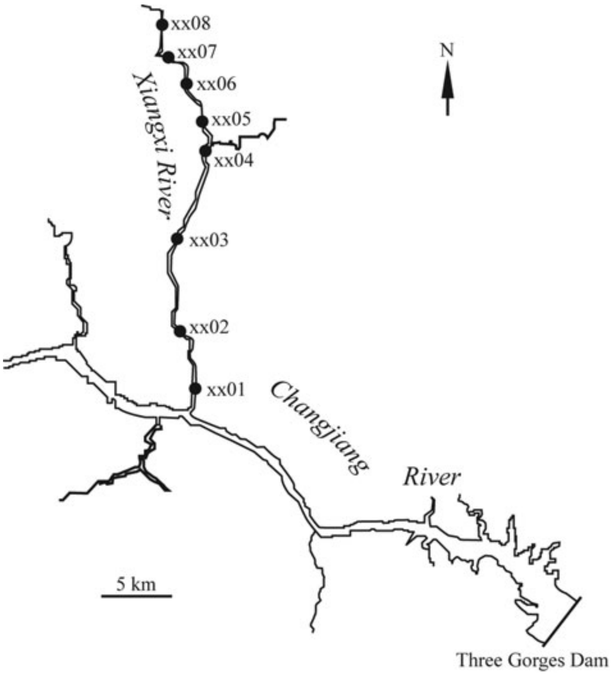

Fig.1 Distribution of sampling sites in Xiangxi Bay

We measured the levels of orthophosphate (PO_4^{3-}-P), nitrate (NO_3^--N), and ammonium (NH_4^+-N) in water samples that were filtered through a 0.45 μm pore-size Whatman GF/F filter. Unfiltered water samples were digested for the analysis of total nitrate (TN) and total phosphorus (TP). The levels of all nutrients were quantified by spectrophotometry, following SEPB (2002), using an ultraviolet spectrophotometer (UV-1700, Shimadzu, Kyoto, Japan). Orthophosphate was analyzed using the ammonium molybdate method. Nitrate was determined by colorimetric analysis and ammonium by the Napier solution method. Total phosphorus concentration was measured by colorimetry after digestion of the unfiltered samples with potassium peroxydisulfate ($K_2S_2O_8$) and (NaOH) to the orthophosphate phase. TN was digested with 5% $K_2S_2O_8$ and measured as nitrate.

2.2.3 Quantitative analysis of phytoplankton

The phytoplankton samples were fixed in Lugol's solution and preserved with 4% formalin after sedimentation for 48 h. We quantified the number of phytoplankton following the method of Utermöhl (1958). The supernatant was removed using a siphon and the samples were concentrated to a final volume of 30 mL. After complete mixing, 0.1 mL of the concentrated sample was counted directly in a counting chamber under a standard light microscope (Olympus CX41) at a magnification of 400×. An algal count, including the colonial forms, was obtained by enumerating single cells.

Phytoplankton species were identified according to Hu and Wei (2006). We divided the dominant species of phytoplankton into functional groups according to Reynolds et al. (2002). The dominant species were those that contributed at least 5% of the relative abundance in at least one sample.

2.2.4 Data analysis

We used a principal component analysis (PCA) to determine which physicochemical variables contributed to the temporal changes in phytoplankton species abundance. We performed a canonical correspondence analysis (CCA) to determine which of the primary environmental variables were responsible for the variation in the phytoplankton community. We selected the environmental variables from the PCA results which had the greatest correlation with the first 2 axes, thus avoiding redundant variables. Prior to conducting the multivariate analysis, the phytoplankton abundance data were transformed to relative abundance to better approximate normality. The ability of the environmental variables to explain the variance in species data in the CCA was tested using Monte Carlo simulation with unrestricted permutations. Variables were considered to be significant when $P<0.05$. PCA and CCA were performed using CANOCO 4.5.

3 RESULT

3.1 Hydrodynamics

As a consequence of hydraulic operations in October, January, and May, the water level changed significantly within a short period (days) causing turbulence and mixing. The water column was more stable during the period between these rapid changes (i.e., from August to September, February–April, and June–July) (Fig.2) which likely favored algae development.

3.2 Physical and chemical variables

The physical and chemical variables are presented in Table 1. Of all the indices, temperature varied the most among the four phases. The chemical indices were more variable than the physical indices. The concentrations of N and P were relatively high, and exceeded the international threshold for eutrophication (TN > 0.2 mg/L, TP > 0.02 mg/L). The seasonal variation in TN was consistent with the

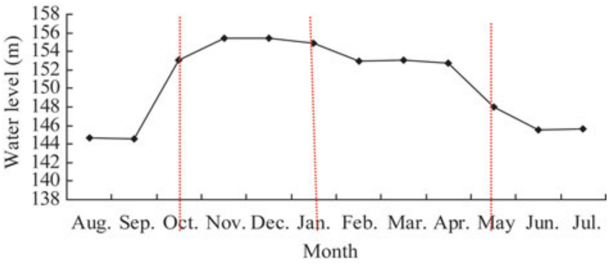

Fig.2 Changes in water level between August 2007 and July 2008 in Xiangxi Bay

changes in NO_3^--N which was lowest in March. There was a peak in TP during spring (February–April) resulting in the lowest TN:TP ratio. The concentration of TP increased significantly in February and peaked in March (0.55 mg/L). The TN:TP ratio decreased (<7) between January–May and March (1.41). The nutrient concentrations varied depending on the regulation of the reservoir.

3.3 Phytoplankton dynamics

The phytoplankton cell density was highest in June (8.89×10^8 cell/L) and lowest in January (1.92×10^5 cell/L). The phytoplankton taxa in Xiangxi Bay were grouped into 6 phyla (Bacillariophyta, Cyanophyta, Cryptophyta, Dinophyta, Chlorophyta, and Euglenophyta). The most common taxa were *Peridiniopsis niei*, *Stephanodiscus hantzschii*, *Komma caudata*, *Cryptomonas erosa*, *Pyramidomonas* sp., *Pandorina* sp., *Eudorina* sp., *Mircocystis* spp., *Asterionella formosa*, and *Aulacoseria granulata*.

We identified 10 functional groups: B, C, P, M, H1, X2, J, G, Y, and Lo (Table 2) These groups accounted for >90% of total abundance. Groups B, X2, and Y were present throughout the year, while the remaining groups were dominant during certain period (Fig.3).

Table 2 List of phytoplankton in Xiangxi Bay based on taxonomy, functional group, and life strategy

Species	Taxonomic group	Functional group	Growth strategist
Stephanodiscus hantzschii	Bacillariophyceae	B	C
Asterionella formosa	Bacillariophyceae	C	R
Aulacoseria granulata	Bacillariophyceae	P	R
Microcystis spp.	Cyanophyceae	M	S
Microcystis aeruginosa	Cyanophyceae	M	S
Microystis wesenbergii	Cyanophyceae	M	S
Anabaena sp.	Cyanophyceae	H1	CS
Closterium sp.	Zygnematophyceae	P	S
Staurastrum sp.	Zygnematophyceae	P	S
Pediastrum simplex var. *duodenarium*	Chlorophyceae	J	C
Pediastrum biradiatum	Chlorophyceae	J	C
Coelastrum reticulatum	Chlorophyceae	J	C
Coelastrum microporum	Chlorophyceae	J	C
Scenedesmus arcuatus	Chlorophyceae	J	C
Scenedesmus spp.	Chlorophyceae	J	C
Pyramidomonas sp.	Chlorophyceae	G	C
Eudorina sp.	Chlorophyceae	G	S
Pandorina sp.	Chlorophyceae	G	S
Cryptomonas erosa	Cryptophyceae	Y	C
Cryptomonas sp.	Cryptophyceae	Y	C
Komma acudata	Cryptophyceae	X2	C
Peridiniopsis niei	Dinophyceae	Lo	S
Peridiniopsis penadii	Dinophyceae	Lo	S

3.4 Ordination

All 12 environmental indices were involved in the initial CCA analysis. Forward selection revealed

Table 1 Physicochemical characterization of Xiangxi Bay (mean±SD)

	Phase 1 (Aug.–Sep.)	Phase 2 (Nov.–Dec.)	Phase 3 (Feb.–Apr.)	Phase 4 (Jun.–Jul.)
TN (mg/L)	1.554±0.687	1.160±0.169	1.311±0.377	1.582±0.569
TP (mg/L)	0.088±0.043	0.103±0.054	0.456±0.246	0.177±0.092
P-PO_4^{3-} (mg/L)	0.104±0.088	0.090±0.037	0.112±0.056	0.044±0.050
N-NO_3^- (mg/L)	0.896±0.142	1.340±0.145	0.973±0.320	1.195±0.301
N-NH_4^+ (mg/L)	0.163±0.058	0.109±0.043	0.125±0.033	0.119±0.036
TN:TP	18.87±4.31	17.38±5.41	3.25±2.09	9.80±1.26
Trans (m)	1.2±0.3	2.0±0.5	1.7±0.7	1.3±0.5
Cond (μs/cm)	278.5±19.1	282.5±10.3	239.9±44.3	292.5±35.9
pH	8.2±0.3	7.9±0.2	8.5±0.3	8.5±0.4
Temp (°C)	24.7±1.8	14.4±0.8	15.9±1.6	25.5±2.2
DO (mg/L)	7.3±0.9	5.5±0.8	9.6±1.8	8.9±1.1
Turb (NTU)	8.5±3.6	2.9±2.3	6.1±3.7	9.8±7.8

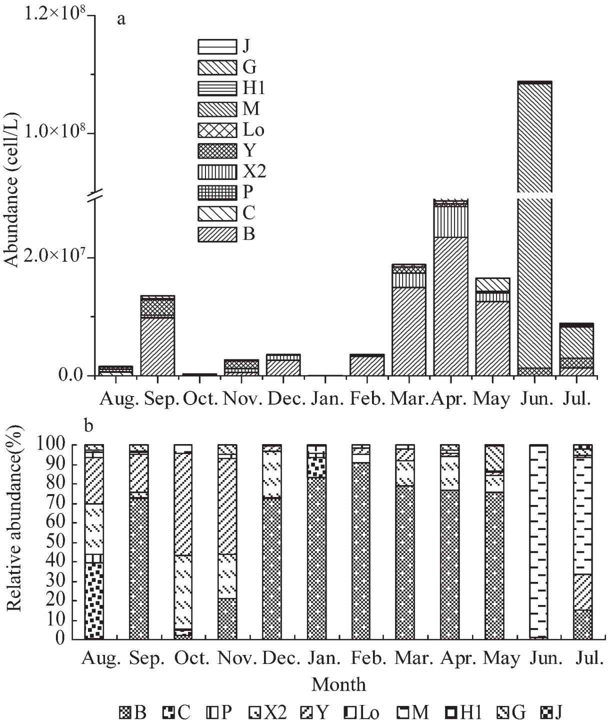

Fig.3 Temporal variation of phytoplankton taxa (a) and principal groups (b) in Xiangxi Bay

that 6 of the 12 variables made independent and significant contributions to the variation in the phytoplankton data (Fig.4). The eigenvalues for CCA axis 1 (0.398) and axis 2 (0.185) accounted for 85.6% of the variance in the phytoplankton-environment relationship. The species-environment correlation for CCA axis 1 (0.704) and axis 2 (0.521) (Table 3) indicated a strong relationship between 10 functional groups and 6 major environmental variables. Temperature was the most important variable to axis 1 ordination, associated with a gradient from low (left side) to high (right side). Axis 2 represented differences in TN:TP ratio with a gradient from low (bottom) to high (up). Phytoplankton functional groups were divided into 4 groups according to CCA (Fig.4).

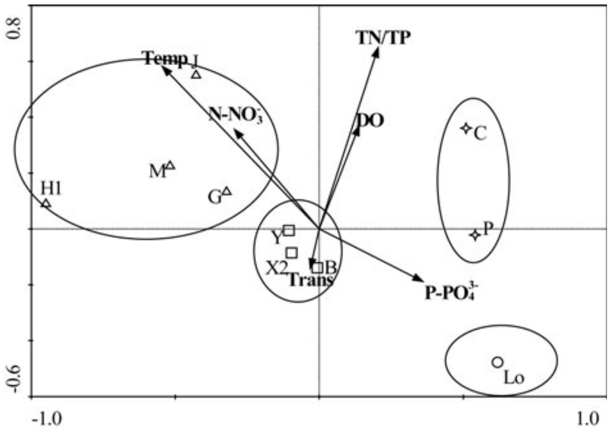

Fig.4 Bioplot of CCA for 6 abiotic variables and 10 phytoplankton functional groups

Table 3 CCA analysis for 6 abiotic variables and 10 principle groups in Xiangxi Bay

Axes	1	2
Eigenvalues	0.398	0.185
Species-environment correlations	0.704	0.521
of species-environment relation	58.4	85.6

4 DISCUSSION

The role of morphological and physiological plasticity in maintaining phytoplankton populations under different environmental conditions has been thoroughly evaluated in the recent literature (Naselli-Flores and Barone, 2003; Naselli-Flores et al., 2007; Stoyneva et al., 2007; Dokulil et al., 2007). According to Naselli-Flores et al. (2007), morphological variability is recognizable both at the population and assemblage level. The same population is maintained when the extent of an environmental parameter does not exceed the morphological adaptive capacity of that single population. If environmental changes are strong enough, species replacement will occur, leading to further adaptation at a higher organizational level.

In general, nutrients, water temperature, and light are the key factors regulating phytoplankton dynamics (Cetinic et al., 2006; Chapman et al., 1998). In addition, biotic factors and other physicochemical factors, such as water movement, have some effect on the growth of phytoplankton. Water hydraulics affects the composition and abundance of phytoplankton and influences the availability of two resources that are important for growth: light and nutrients (Reynolds, 2006). Water retention time, a function of water inflow and the reservoir hydraulic regulation scheme, is considered to be a measurable variable describing the hydraulics of a reservoir. Water level changes in a reservoir reflect changes in the hydrodynamics.

Phases 1, 2, 3, and 4 were defined based on four periods of water column stability and were consistent with phytoplankton community data, supporting the utility of the functional group concept in describing the seasonal variation of phytoplankton, as shown in the CCA.

A community consisting of unicell diatoms (group B) and Cryptophyta (groups X2 and Y) dominated during all four phases. In addition to the groups that were dominant throughout the year, we observed other groups during the different phases. During phase 1 (August–September), there was a marked increase in the abundance of colonial diatoms (groups C and P). There were no obvious dominant groups in phase 2. Phase 3 was characterized by dinoflagellates (group Lo). From June to July (phase 4), a more diverse community composed of cyanobacterial species (groups H1 and M) and Chlorophytes (groups J and G) was established. Excluding the groups that were present year round, the temporal sequence of functional groups derived by CCA was: C/P → Lo → H1/M/J/G (Fig.5).

The CCA revealed that water temperature and the TN/TP ratio explained a highly significant proportion of the functional group variation. During August and September (rainy season), the water column was turbid as a result of increases in the suspended load of non-living particles, introduced by runoff. *Aulacoseria granulata* (group P) and *Asterionella formosa* (group C), both R-strategists (stress tolerant), outcompeted other species during this phase, which was characterized by low transparency and high turbulence. Becker et al. (2009) reported that a decrease in SRP constituted a competitive advantage for group C in Faxinal Reservoir, a meso-eutrophic reservoir in South Brazil. The PO_4^{3-}-P concentration was never lower than 0.035 mg/L during our study, suggesting that this nutrient was not correlated with the dominance of group C. The phytoplankton morphology was characterized by a predominance of filaments or chains, which provide extensive light absorbing surfaces (Gómez et al., 2004) and are advantageous in environments with a high concentration of suspended solids (Gómez et al., 2004). Conversely, they are more likely to sink to the bottom because of their heavy silic sheath, so depend upon water turbulence for resuspension (Hötzel and Croome, 1996; O'Farrell et al., 2001; Becker et al., 2009). The development of these morphological types was constrained when the discharge decreased during the drought phase (Devercelli, 2006).

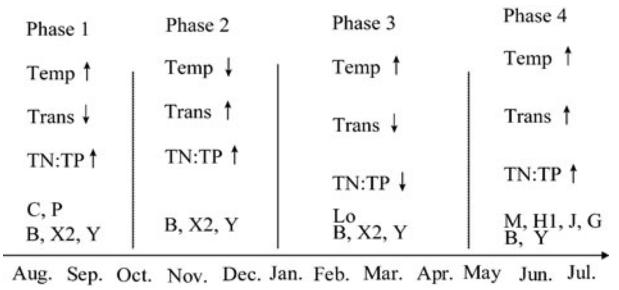

Fig.5 Synthesis of the primary abiotic and functional groups between Aug. 2007 and Jul. 2008

Groups B, X2, and Y were present throughout the year but were most abundant in late spring. Group B was characterized by *Stephanodiscus hantzschii*. The resistance to sinking was improved by this diatom's high surface area-to-volume ratio (Padisák, 2003) as a consequence of its small size (diameter 3–5 μm). Groups Y and X2 were represented by *Cryptomonas erosa* and *Komma acudata*, respectively. X2 was plotted in the CCA showing a positive loading on transparency, which was consistent with observations in the Middle Paraná River (Devercelli, 2006). The development of these small unicellar phytoplankton (C-strategists) was a consequence of their SA/V ratio and metabolic activity, which favored light-harvesting, nutrient uptake and, subsequently, enhanced growth rates. Moreover, they are able to counteract sedimentation in slow flowing waters and in patches of low turbulence (Reynolds, 1984). The increased levels of organic matter and decreased light levels benefited heterotrophic feeding and boosted the mixotrophic Cryptomonas (Devercelli, 2006). Although this is not a direct assumption validated by CCA, Unrein (2002) and O'Farrell et al. (2003) suggested that an alternative nutritional option constituted a competitive advantage in water bodies of the Paraná River floodplain. Members of Cryptophyta were more abundant at sites xx07 and xx08, which receive domestic sewage from Gaoyang Town. We speculate that this explains why Cryptophyta out competed other species at these sites.

The water column was also relatively stable between February–April, coincident with an increase in solar radiation and water temperature (to ~15.9°C). These conditions were conducive for dinoflagellate cyst germination in the shallower regions of the bay (Kawabata and Ohta, 1989) and resulted in a dinoflagellate bloom, dominated by *Peridiniopsis niei* (group Lo). The surface water was colored brown by accumulation of this species. In contrast to the low levels of nutrients available in Lo dominated areas in the TAG Reservoir, TN and TP concentration increased to 0.46 and 1.31 mg/L, respectively, in Xiangxi Bay, which was consistent with Liu et al. (2008). It was likely that Lo was able to grow well under a broad range of nutrient concentrations. The abundance of *P. niei* decreased in late spring when the water temperatures increased to 20°C, and the dinoflagellate bloom degraded. Lo was much more susceptible to higher temperatures than to changes in nutrient concentrations. The competitive ability of this species appears to be favored by ample light, a stable water column, and lower water temperatures.

Following the release of water in May, the water level remained relatively constant at 145.5 m. Water column stability is essential for the development of Cyanobacteria (Zohary and Breen, 1989; Reynolds, 1993). An increase in temperature (above 25°C) and an increase of turbidity caused by precipitation also favored an increase of Cyanobacteria density in the bay. High water temperatures along with an increase in irradiance and water stability tended to favor *Microcystis* growth. Heterocytic cyanobacteria tend to dominate at low levels of NO_3^--N (McQueen and Lean, 1987). However, the peak in cyanobacterial abundance in Xiangxi Bay coincided with high levels of NO_3^--N (1.14–1.22 mg/L). Nitrogen tends to be a limiting nutrient when TN:TP <7.2, based on N:P theory by Redfield. The lower TN:TP ratio (<7.0) during late May likely favored the outcompetition of other taxa and the formation of the cyanobacterial bloom. During the initial period of the bloom, characterized by high nutrient concentrations and high light, group G (*Eudorina*) phytoplankton were most abundant. We observed a shift in dominance from Microcystis to green algae and diatoms (Toetz, 1981; Visser et al., 1996) in late July, coincident with an increase in precipitation.

In conclusion, this functional approach provides a synthesis of the temporal variability in the abundance of individual phytoplankton species. Of the species and functional groups present throughout the study, C-strategists and S- and R-strategists that have a wide range of tolerance dominated the phytoplankton assemblage in Xiangxi Bay between August 2007 and July 2008. The dynamics of the phytoplankton community may be explained by water column stability, irradiance, water temperature, and nutrient structure.

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