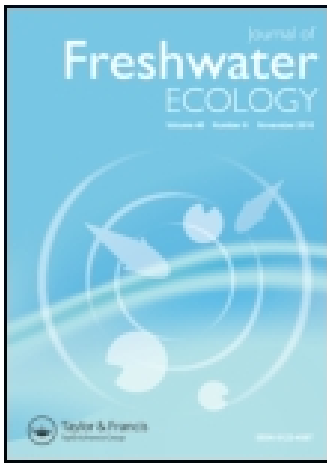


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Journal of Freshwater Ecology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjfe20>

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Published online: 18 Mar 2011.

To cite this article: Lin Ye & Qinghua Cai (2011) Spring phytoplankton blooms in Xiangxi Bay of Three-Gorges Reservoir: spatiotemporal dynamics across sharp nutrient gradients, *Journal of Freshwater Ecology*, 26:1, 11-18, DOI: [10.1080/02705060.2011.553815](https://doi.org/10.1080/02705060.2011.553815)

To link to this article: <http://dx.doi.org/10.1080/02705060.2011.553815>

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Spring phytoplankton blooms in Xiangxi Bay of Three-Gorges Reservoir: spatiotemporal dynamics across sharp nutrient gradients

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(Received 16 September 2010; final version received 8 November 2010)

After the impoundment of Three-Gorges Reservoir, the specific hydrodynamics created sharp nutrient gradients in Xiangxi Bay. To discover how spring blooms in Xiangxi Bay respond to sharp nutrient gradients, we investigated the phytoplankton community composition and dynamics along nutrient gradients and analyzed the strategies of different types of phytoplankton in filling their niches. We observed a total of 148 taxa of 59 genera belonging to seven phyla. Phytoplankton concentration ranged from 0.03×10^7 to 3.74×10^7 cell L^{-1} with two pulses during the spring bloom period. Bacillariophyta was the predominant group, which accounted for 75.4% of total abundance. Canonical correlation analysis (CCA) revealed that phytoplankton occurred in optimal niches for their growth across the nutrient gradients. Specifically, species of Bacillariophyta were found in the region with Si:DIN > 1, and species of Cryptophyta, Chrysophyta, Euglenophyta, Pyrrophyta, and some of Chlorophyta were most abundant in the region with DIN:PO₄P < 16. High abundances of Cyanophyta and some Chlorophyta were observed in the region where DIN:PO₄P > 16. The CCA also indicated a potential nutrient limitation of Si on Bacillariophyta, of DIN on Cyanophyta and some Chlorophyta, and of PO₄P on Cryptophyta, Euglenophyta, Pyrrophyta, and some Chlorophyta. Moreover, as a complement for the traditional Redfield ratio of 16N:1P in determining whether N or P limits a system, our study revealed that the stoichiometric ratio of 1Si:1DIN is an important criterion to determine limitation for diatoms.

Keywords: Eutrophication; phytoplankton blooms; limiting factor; nutrient gradients

Introduction

Three-Gorges Reservoir (TGR) is one of the biggest reservoirs in the world with a storage capacity of 39.3 billion m^3 . It serves as the main water source for the Middle–Lower Yangtze Plain downstream, which is the most developed and heavily populated region in China. However, since the impoundment of the TGR in June 2003, the reservoir has experienced eutrophication problems (Cai and Hu 2006), and phytoplankton blooms have been frequently observed in many tributary bays of TGR (Ye, Xu, et al. 2006; Xu et al. 2009). Effective water resource management and

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algal bloom control will require the knowledge of how phytoplankton responds to the environmental factors and understanding the limiting factors for phytoplankton growth.

According to the Redfield (1958) ratio, the stoichiometric ratio of 16N: 1P (in atoms) is a widely used criterion in determining the nutrient limitation in aquatic ecosystems (OECD 2006). This theory assumes that phosphorus is the potential limiting factor where $N:P > 16:1$, whereas nitrogen will be the potential limiting factor when $N:P < 16:1$. Generally, phosphorus has been considered to be the primary nutrient limiting phytoplankton growth in freshwater ecosystems (OECD 2006).

After the impoundment of TGR, the specific hydrodynamics have created an inverse pattern of nitrogen and phosphorus in Xiangxi Bay (Ye, Xu, Cai 2006; Ye et al. 2007). As a result, the N:P ratio decreases quickly from downstream to upstream in Xiangxi Bay, which may lead to a heterogeneous phytoplankton community composition and nutrient limitation along the bay. Therefore, it is interesting to discover how phytoplankton dynamics respond to the sharp nutrient gradients. In this study, we investigated the phytoplankton community composition and dynamics across sharp nutrient gradients and analyzed the responses of different types of phytoplankton to these nutrient gradients.

Materials and methods

Sampling site and data

Xiangxi Bay, the former Xiangxi River prior to the construction of TGR, is located in the northwestern Hubei Province. Fourteen sites from the mouth to the upstream of Xiangxi bay were sampled every 6 days from 26 February to 28 April 2005 (Figure 1). The water samples were collected, preserved, and analyzed according to the standard methods, and details of these analyses can be found in previous papers (Ye, Xu, Han, et al. 2006; Ye and Cai 2009). The analyzed environmental variables included pH, dissolved oxygen (DO), water temperature (WT), phosphate phosphorus (PO_4P), dissolved inorganic nitrogen ($DIN = NH_4N + NO_2N + NO_3N$), and dissolved silicate (Si).

Another sample was collected from the surface water and preserved immediately with Lugol's solution in each site for phytoplankton study. Cells were counted and identified at $400\times$ magnification with the guidance of John et al. (2003) and Hu and Wei (2006), with most taxa being identified at species level. In this study, species of *Cyclotella* and *Stephanodiscus* were merged as *Cyclotella* spp. because they could not be distinguished clearly under $400\times$ magnification.

Data analysis

Canonical correlation analysis (CCA) was employed to assess the effects of physical and chemical variables on the spatial and temporal dynamics of the phytoplankton community during the bloom period at the most detailed taxonomic level. To reduce the effects of rare species on the ordination, only species which contributed $\geq 1\%$ of total phytoplankton abundance (TPA) on at least five occasions were selected for the CCA (Muylaert et al. 2000). All species data (relative abundance) in the CCA were $\log(x + 1)$ transformed to obtain a normal distribution. The CCA was performed by

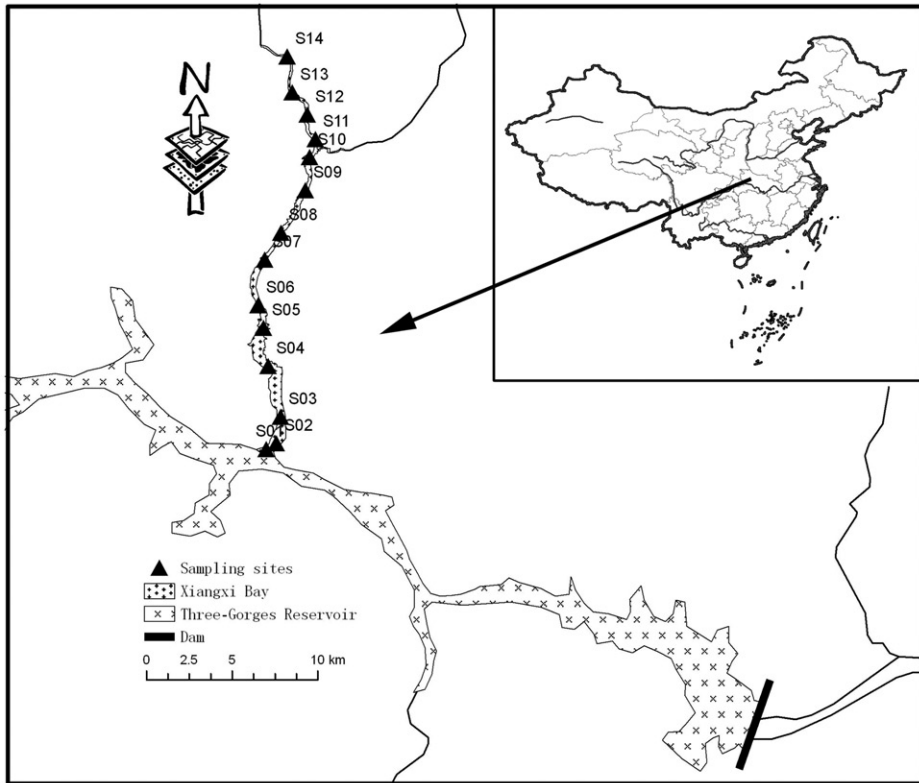


Figure 1. Location of Xiangxi Bay and the spatial distribution of sampling sites.

the CANOCO (Ver. 4.51), with forward selection to identify the environmental variables that best explained the phytoplankton variations. The significance of environmental variables was tested using Monte Carlo permutation testing (9999 permutations) implemented in CANOCO.

Results

Environmental variables

The detailed descriptions of the variation of selected environmental variables can be found in a previous paper (Ye et al. 2007). Briefly, nitrogen and phosphorus had a clear inverse pattern along the bay, with tendencies for a decrease in nitrogen and an increase in phosphorus from the mouth to the upstream region of the bay. The depletion of DIN and Si was observed in the upper and middle regions of Xiangxi Bay, respectively. As a result, there was a wide range of nutrient ratios during the spring bloom period. The DIN:PO₄P ratio ranged from 0.33 to 55.26 (by atomic mass). The variations of Si:DIN and Si:PO₄P ranged from 0.02 to 7.96 and from 0.28 to 42.58, respectively.

Spatiotemporal dynamics of phytoplankton

A total of 148 taxa of 59 genera belonging to seven phyla were observed during the bloom period. In general, phytoplankton concentration ranged from 0.03×10^7 to

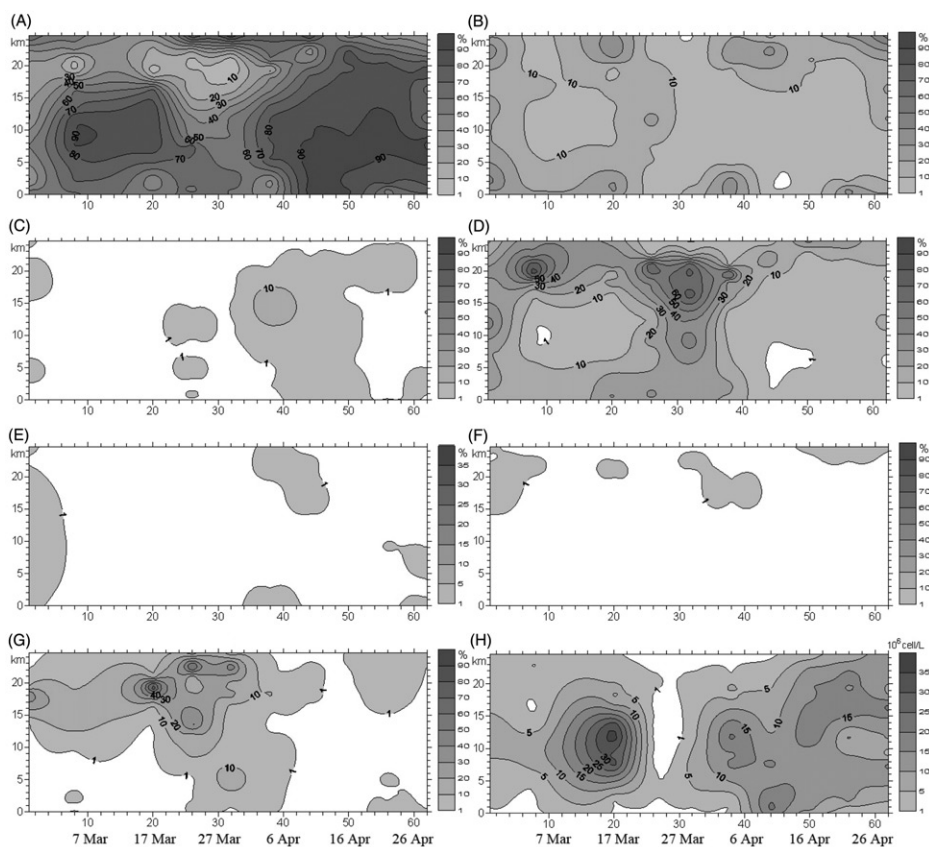


Figure 2. The spatiotemporal dynamics of phytoplankton in Xiangxi Bay during the spring phytoplankton bloom period. Relative abundance of (A) Bacillariophyta, (B) Chlorophyta, (C) Chrysophyta, (D) Cryptophyta, (E) Cyanophyta, (F) Euglenophyta, (G) Pyrrophyta, and (H) the TPA. The x-axis is the day number starting on 26 February, and the y-axis the distance to the mouth of the bay.

$3.74 \times 10^7 \text{ cell L}^{-1}$ with two pulses (Figure 2). Specifically, Bacillariophyta was the predominant group with broadest distribution in Xiangxi Bay, which accounted for 75.4% of TPA. *Cyclotella* spp. was the most abundant group, which accounted for 45.2% of TPA. *Asterionella formosa* was the secondary dominant species accounting for 29.3% of TPA.

The dominances of Chlorophyta, Cryptophyta, and Pyrrophyta were also observed briefly in some upstream sites. The peak of Chlorophyta even achieved $7.1 \times 10^6 \text{ cell L}^{-1}$ at site S14 on 28 April, which was 55% of the total abundance of that sample. Chlorophyta became the dominant group in the upstream region of the bay in later spring after the decline of the Bacillariophyta bloom (Figure 2). The dominant species of Chlorophyta were *Chlorella pyrenoidosa* (3.6% of TPA), *Chlamydomonas ovalis* (1.8%), *Actinastrum hantzschii* (1.1%), *Chlamydomonas globosa* (0.9%), and *Chlorella vulgaris* (0.9%).

The Cryptophyta accounted for 9.6% of TPA on average with its highest density of $5.0 \times 10^6 \text{ cell L}^{-1}$ at S11 on 4 April. This group was represented by three species,

Table 1. The phytoplankton taxa contributed to $\geq 1\%$ of TPA in each site and at least have five occasions during the spring bloom period.

Phylum	Species
Bacillariophyta	<i>A. formosa</i> , <i>Cocconeis placentula</i> , <i>Cyclotella</i> spp., <i>Cymbella</i> sp. 1, <i>Diatoma vulgare</i> , <i>Fragilaria crotonensis</i> , <i>Fragilaria</i> sp. 1, <i>Gomphonema</i> sp. 1, <i>Mastogloia smithii</i> var. <i>amphicephala</i> , <i>Melosira granulata</i> var. <i>angustissima</i> , <i>Melosira granulata</i> , <i>Navicula minima</i> , <i>N. Salinarum</i> , <i>N. simplex</i> , <i>Synedra acus</i> , <i>S. ulna</i> , and <i>S. vaucheriae</i>
Chlorophyta	<i>A. hantzschii</i> , <i>C. globosa</i> , <i>Chlamydomonas microsphaera</i> , <i>C. ovalis</i> , <i>C. pyrenoidosa</i> , <i>C. vulgaris</i> , <i>Kirchneriella obesa</i> , <i>Scenedesmus bijuga</i> , and <i>Westella botryoides</i>
Chrysophyta	<i>Chromulina ovalis</i>
Cryptophyta	<i>C. acuta</i> , <i>C. erosa</i> , and <i>C. ovata</i>
Cyanophyta	<i>Chroococcus limneticus</i>
Euglenophyta	<i>Euglena geiculata</i>
Pyrrophyta	<i>Peridiniopsis</i> sp. 1

which were *Chroomonas acuta* (4.7% of TPA), *Cryptomonas ovata* (2.6%), and *Cryptomonas erosa* (2.4%). Pyrrophyta only accounted for 2.8% of TPA; however, it was a predominant group in the upstream region of the bay (Figure 2). The observed peak of Pyrrophyta was in site S11 on 17 March with 7.7×10^6 cell L⁻¹, which accounts for 83.8% of that sample. *Peridiniopsis* sp. 1 was the absolutely dominant Pyrrophyta, representing 96.7% of this group.

The other phytoplankton – Chrysophyta, Cyanophyta, and Euglenophyta was seldom observed during the spring bloom period. Chrysophyta, accounting for 2.0% of TPA, was only seen for several days in sites S07, S08, and S09 with abundance over 1×10^6 cell L⁻¹. The abundances of Cyanophyta and Euglenophyta were extremely low. They only accounted for 0.3% and 0.2% of TPA, respectively.

Phytoplankton community changes in relation to environmental factors

A total of 33 taxa, which contributed to $\geq 1\%$ of TPA on at least five occasions, made up 95.2% of total abundance during the whole spring period. The selected phytoplankton taxa for the CCA consisted of 17 Bacillariophyta, 9 Chlorophyta, 3 Chrysophyta, 1 Chrysophyta, 1 Cyanophyta, 1 Euglenophyta, and 1 Pyrrophyta (Table 1). According to the results of forward selection procedure in CCA, all selected environmental variables (pH, DO, WT, Secchi depth, DIN, PO₄P, and Si) were significantly correlated with the phytoplankton community (Figure 3), and explained 27.5% of the variations in the species composition. The *p*-value for DO was 0.03; the others were <0.001 .

Specifically, axis 1 [eigenvalue (e.v.) 0.374] explained 13.6% of the species variation. This axis was strongly determined by WT, Si, and PO₄P. Axis 2 (e.v. 0.204) explained 7.4% of the variation in the species data, which was determined by the DIN Secchi depth, pH, and DO. According to the bi-plot of community composition and environmental variables (Figure 3), the species of Bacillariophyta were positively correlated with Si and negatively with WT. This suggests that diatoms thrive the best in the regions of high concentration of Si and low WT. Cryptophyta and

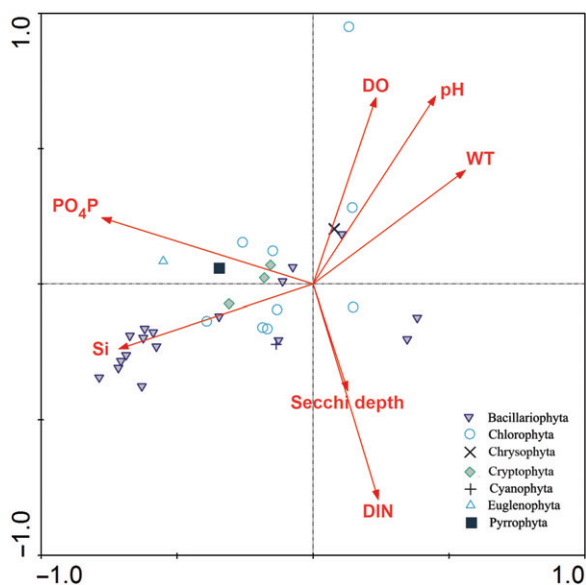


Figure 3. Canonical correspondence analysis ordination of environmental variables and phytoplankton community relative abundance for all sites. All vectors are significant ($p < 0.05$; Monte Carlo permutation test).

Euglenophyta as well as Pyrrophyta correlated with PO_4P positively and WT negatively. Chrysophyta had a positive relationship with WT, pH, and DO and a negative relationship with DIN and Si; Cyanophyta had the opposite species–environmental relationship as Chrysophyta. Chlorophyta had a wide distribution in the ordination diagram, which indicated that different species of Chlorophyta had different nutrient requirements.

Discussion

Because diatoms have a higher competition for nutrients than other species in spring with the cold water (Lampert and Sommer 2007), it is not surprising that diatoms constituted the predominant group in Xiangxi Bay during the spring bloom period. The significant negative correlation between relative abundance of diatom species and WT confirmed that diatom species have greater competitive ability than other species in cold waters. CCA also revealed that Si was the most important nutrient factor for diatom species. Si is a necessary element for diatoms to synthesize the silica shells (Turner et al. 1998). By comparing the spatiotemporal pattern of Si in a former study (Ye et al. 2007), we observed clear depletions of Si after two peaks of diatom blooms. This phenomenon was also observed after diatom blooms in a Korean reservoir (Ha et al. 2003).

After the decline of the Bacillariophyta bloom in later spring, the abundance of Chlorophyta increased significantly in the upstream region of Xiangxi Bay. This Bacillariophyta–Chlorophyta succession pattern in later spring is a general pattern, which has been observed in reservoir (Ostojic et al. 2005) and estuarine systems (Domingues et al. 2005). In the upstream region dominated by Chlorophyta,

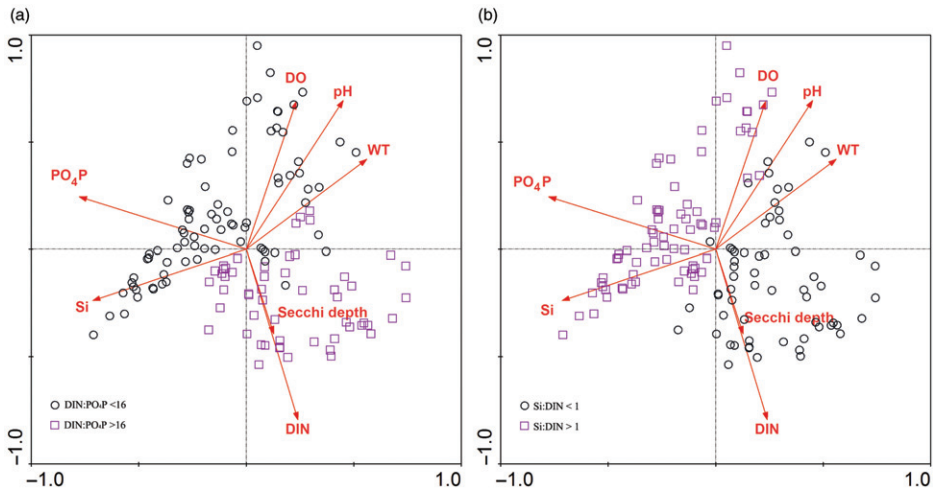


Figure 4. Biplot of the sampling sites and environmental variables in CCA diagram. The sites were categorized by 16DIN:1PO₄P (A) and 1Si:1DIN (B).

an obvious depletion of nitrogen was also observed, with the lowest DIN concentration of 4.28 μM at S13 on 28 April. This phenomenon indicates that Chlorophyta can grow faster and have a higher affinity for nutrients than other phytoplankton groups under low nitrogen conditions (Graneli and Moreira 1990; Postius and Ernst 1999).

When the sampling sites were partitioned by 16N:1P ratio (Figure 4(a)), there was a clear niche selection by different types of phytoplankton. Cyanophyta and some Chlorophyta species appeared in the region where $\text{DIN:PO}_4\text{P} > 16$. When the $\text{DIN:PO}_4\text{P}$ ratio decreased below 16, Cyanophyta and some Chlorophyta species lost their dominance because DIN became the limiting factor for their growth. Similarly, PO_4P would be the limiting factor for Cryptophyta, Euglenophyta, Pyrrophyta, and other Chlorophyta species dominant in regions where $\text{DIN:PO}_4\text{P} < 16$.

Because the diatoms have a 1Si:1N atomic ratio in their biomass (Brzezinski 1985), we also sorted all sampling sites by 1Si:1DIN to investigate the relationships between the occurrence of diatom species and Si:DIN ratio. The highest relative abundance of diatoms was observed in the region where the Si:DIN ratio was above 1, and these species had a positive relationship with Si. Similarly, when the Si:DIN ratio decreased to a value below 1, the diatoms lost their dominance; dissolved silicate would be the limiting factor for diatom growth. This phenomenon suggests that 1Si:1DIN (Figure 4) is a good criterion to determine potential limitation for the growth of diatoms.

Acknowledgements

The authors thank D. Li, X. Shao, S. Zhou, X. Han, Y. Xu, X. Jia, and F. Li for their assistance in the field sampling. This study was funded by Major Projects for Water Pollution Control and Remediation of China (2009ZX07528-003), National Natural Science Foundation of China (No. 40671197), and the Key Project of Knowledge Innovation Program of CAS (Nos. KZCX2-YW-427 and KSCX2-SW-111).

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