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ABSTRACT

We investigated dynamics of the phytoplankton community and abiotic factors in Xiangxi Bay of the Three-Gorge Reservoir, China, by daily sampling a specific site during a spring algal bloom (February 23–April 28, 2005). Among the 76 taxa observed, *Asterionella formosa* and *Cyclotella* spp. were the dominants, accounting for 47.2% and 29.9% of the total abundance, respectively. We determined the five distinct developing phases of the bloom by analyzing the dissimilarity of physicochemical parameters. Simultaneously, six phytoplankton community groups were distinguished by TWINSPAN classifications. The pattern for algal community succession was similar to that for the bloom phase shift, and the structural complexity of communities significantly decreased over time. Water temperature and silicate were the main factors that related to the development of the bloom and the shifts of the phytoplankton community.

INTRODUCTION

Phytoplankton blooms can cause loss of aquatic biodiversity and interfere with use of the water for fisheries, recreation, industry, agriculture, and drinking (Paerl 1988, Carpenter et al. 1998, Verspagen et al. 2006). Therefore, studies of phytoplankton blooms in regulated rivers have drawn much attention. Long-term observations have shown that increased nutrient inputs, coupled with reduced flow velocity and prolonged water retention time, were the main reasons for the increases in phytoplankton biomass in many regulated rivers (Ha et al. 2002). Similarly, such a phenomenon was also observed in Three-Gorge Reservoir (TGR) after damming of the Yangtze River. In the mainstream of the Yangtze River and its upstream tributaries, no algal blooms were reported before the construction of Three-Gorge Dam. The impoundment changed the downstream stretches of inflow tributaries into reservoir-bays, and algal blooms often occur in these bays, especially during warm spring periods (Cai and Hu 2006).

The Xiangxi River is the largest tributary of the TGR in Hubei Province. After impoundment, the lower 25-km stretch of this river became Xiangxi Bay, with current velocity of 0.002-0.0041 m s^{-1} (Zeng et al. 2006). Xiangxi Bay can be considered as representative of most eutrophic bays of the TGR (Cai and Hu 2006). Monthly monitoring over two years revealed mean concentrations of total nitrogen, total phosphorus, and chlorophyll *a* in Xiangxi Bay of 1.29 mg L^{-1}, 0.153 mg L^{-1}, and 11.7 µg L^{-1}, respectively, and the maximum chlorophyll *a* concentration reached 60 µg L^{-1} in spring (Cao et al. 2006). Previous studies performed in Xiangxi Bay on the seasonal or monthly succession of phytoplankton showed that the bloom-forming phytoplankton included *Asterionella formosa*, *Cyclotella* spp., *Cryptomonas* spp., *Peridiniopsis* spp., and *Rhodomonas* spp., and the maximum algal density occurred in April (Zeng et al. 2006, Zhou et al. 2006).

In temperate regions, the development of spring blooms has been the focus of many investigations (Tiselius and Kuylenstierna 1996). The initiation, development, and

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termination of spring diatom blooms are controlled by various factors, such as water warming, nutrient limiting, zooplankton grazing, and cell sinking (Kasai et al. 1997, Yin et al. 1997). However, the relative importance and interplay of these factors show much variation in different aquatic systems and climates (Iriarte and Purdie 2004). The climate of the TGR is subtropical monsoon (Jiang et al. 2006). In subtropical systems, the underlying mechanisms that control the timing of the onset, the magnitude, and the duration of a spring bloom may be very different from those in temperate regions.

In most previous studies, there was no detailed monitoring of bloom dynamics, especially in subtropical regions. Most of the interpretations of bloom phenomena were made from monthly or weekly sampling studies (e.g., Kasai et al. 1997, Ha et al. 2003, Iriarte and Purdie 2004, Zeng et al. 2006). However, phytoplankton populations respond so rapidly and sensitively to their environment that conventional study methods fail to obtain more subtle and interesting aspects of their dynamic ecology (Ryther 1954). Obviously, it is necessary to make intensive observations at frequent intervals to study the mechanisms controlling the major bloom events. Thus, the aim of the present study was to examine the initiation, development, and termination of a spring bloom in Xiangxi Bay, and to explore environmental factors that might govern algal composition.

METHODS AND MATERIALS

We sampled the surface water of Xiangxi Bay daily between 1000 and 1100 h from February 23 to April 28, 2005 at a site ca. 5 km upstream from the mouth of the bay. Water temperature (WT), dissolved oxygen (DO), and pH were measured *in situ* with a Horiba U-20 meter (Horiba Advanced Techno, Japan). Transparency (SD) was determined with a 20-cm Secchi disc. Water for analysis of other parameters was collected with a 5-L Van Dorn bottle. A 300-600 mL subsample was filtered through a microfilter (0.8 μm), and the filter was packed in ice in a dark cooler and sent to the laboratory for spectrophotometric analysis of chlorophyll *a* (chl *a*) according to the standard method of APHA (1989). Water for dissolved substances analysis was acidified with sulfuric acid (Huang et al 2000) and transported to the laboratory. The concentrations of dissolved inorganic nitrogen [DIN (NO_2-N + NO_3-N + NH_4-N)], dissolved inorganic phosphorus [DIP (PO_4-P)], and dissolved silicon [DSi (SiO_2-Si)] were measured with a segmented flow analyzer (Skalar SAN++, Netherlands). Dissolved organic carbon (DOC) concentration was measured with a total organic carbon analyzer (Shimadzu TOC-$V_{CPH/CPN}$, Japan)

A 1.5-L water sample was preserved on site with standard Lugol's solution (Huang et al. 2000). Subsequently, phytoplankton was concentrated by sedimentation and preserved with 5% neutral formalin. From each concentrated sample, a 0.1 mL quantitative subsample was examined in a Fuchs-Rosenthal counting chamber under magnification (400X). Most phytoplankters were identified to species or genus according to Hu et al. (1980). Small centric diatoms, mainly of the genus *Cyclotella*, were combined as one group (*Cyclotella* spp.) (Zeng et al. 2006).

We analyzed abiotic environmental factors and chl *a* concentrations to group samples using hierarchical cluster analysis (HCA). The bloom phases were determined by comparing the chl *a* concentration of each HCA group with the critical value of algal bloom (30 μg L^{-1}; Prepas 2003) with a one-sample t - test. We classified algal samples and defined phytoplankton assemblage types using two-way indicator species analysis (TWINSPAN). Canonical correspondence analysis (CCA) was utilized to relate phytoplankton assemblage types to environmental gradients. Furthermore, we tested differences in phytoplankton community type among bloom phases with multi-response permutation procedures (MRPP). Prior to multivariate analyses, abundance data of

phytoplankton were transformed into relative abundance to better approximate normality. All multivariate analyses (HCA, TWINSPAN, CCA, and MRPP) were run using PC-ORD 4.0 with default options. In addition, we examined significant differences among bloom phases for algal density and environmental variables using one-way analysis of variance (ANOVA). All data for the ANOVA were $\log_{10}(y+1)$ transformed to improve normality and homoscedasticity (Levene's test t, $p > 0.05$). If the between-subjects effects of ANOVAs were significant, we performed multiple comparisons among bloom phases. These comparisons were carried out following the procedure of Beckmann et al. (2005). In short, Tukey's honestly significant difference (HSD) *post hoc* tests were performed, except in cases of persistent heteroscedasticity where we performed Games-Howell tests. Both one-sample student's t-test and one-way ANOVA were run with SPSS13.0.

RESULTS

Algal cell concentrations varied substantially during the observation period and ranged from 0.69×10^6 to 26.0×10^6 cells L^{-1}. The phytoplankton assemblage comprised 76 taxa, which included Bacillariophyta (19), Chlorophyta (33), Chrysophyta (3), Cryptophyta (4), Cyanophyta (7), Euglenophyta (3), Pyrrophyta (6), and Xanthophyta (1). Diatoms accounted for 87.2% of the total abundance. Among them, *Asterionella formosa* and *Cyclotella* spp. were the dominant taxa, accounting for 47.2% and 29.9% of the total abundance, respectively. The other common taxa with over 1% of the total abundance were *Chroomonas* sp. (5.7%), *Melosira* sp. 1 (5.6%), *Cryptomonas ovata* (3.0%), *Rhodomonas lacustris* (2.9%), *Melosira* sp. 2 (1.6%), and *Synedra* sp. (1.6%).

Based on abiotic factors and algal biomass, we divided the spring bloom into the following five phases using HCA: *pre*-bloom (February 23–March 10), *early*-bloom (March 12–20), *trans*-bloom (March 21–April 2), *mid*-bloom (April 3–16), and *late*-bloom (April 17–28). The most serious bloom was observed in the *mid*-bloom period, when the concentrations of chl *a* were significantly ($p < 0.01$) higher than 30 µg L^{-1} (Table 1).

Based on algal composition, TWINSPAN classified the 62 daily observations into seven groups with characteristic species. Since two groups occurring in the mid-bloom phase had the same characteristic species, we combined them as one group. Thus, six distinct community groups (a through f) of phytoplankton were identified (Table 2), and the pattern for the algal community group succession was similar to that for the bloom phase shift.

The comparisons of community types by MRPP further confirmed that the shifts in phytoplankton composition were significant between the bloom phases, as shown by the strong chance-corrected within-group agreement and test statistic. First, the marked changes of phytoplankton composition from the *pre*-bloom to the *early*-bloom phase were the absence of characteristic species *Chroomonas* sp., *Rhodomonas lacustris*, *Cryptomonas ovata*, and *Melosira* sp. 2, the decline of the dominance of *A. formosa* and *Melosira* sp.1, and the presence of one dominant *Cyclotella* spp. Second, the dynamic characteristics of the phytoplankton community from the *early*-bloom to the *trans*-bloom phase included the presence of the characteristic species *Chroomonas* sp., *R. lacustris*, and *C. ovata*, and the increase of the dominance of *A. formosa*. In the *mid*-bloom phase, phytoplankton community was characterized by the co-dominant species *A. formosa* and *Cyclotella* spp. Finally, the species *A. formosa* had an advantage over its competitor *Cyclotella* spp. in the *late*-bloom phase. In addition, total density of phytoplankton significantly declined from the *trans*-bloom phase but remained high during the last two phases, with a peak of 2.6×10^7 cells L^{-1} in the *mid*-bloom phase (Fig. 1). The ebb and

flow of the density of the dominant *Cyclotella* spp. was apparent across all phases. The *early-* and the *mid*-bloom phases had significantly higher *Cyclotella* spp. density than the remaining phases. The pattern for another dominant species *A. formosa* was relatively simple, and the last two phases had significantly higher density than the first three phases (one-way ANOVA, $p < 0.01$ in all cases).

When overlaid on the CCA sample ordination in Fig. 2, the six community groups were well separated in the environmental space. The phytoplankton community of the *pre*-bloom phase shifted from group a to group b, and occupied the right hand side of the ordination diagram. All the remaining types ranged in sequence along the first CCA dimension. In the present CCA ordination, the first ordination axis, with an eigenvalue of 0.303, was the only one with statistical significance (Monte Carlo test, $p = 0.001$) and explained 28.1% of the variance in the species data. Axis 1 was positively correlated ($p < 0.01$) with DSi ($r = 0.91$) and transparency ($r = 0.55$) and negatively correlated ($p < 0.01$) with water temperature ($r = - 0.95$), pH ($r = - 0.70$), and DOC ($r = - 0.68$).

Table 1. Means (standard deviation) of chl *a* and environmental variables of the five phases during the spring bloom, derived from HCA grouping. Within a variable, values with the same letters are not significantly different ($p > 0.05$).

Bloom phase	Pre-	Early-	Trans-	Mid-	Late-
Date	23 Feb–10 Mar	12–20 Mar	21 Mar–2 Apr	3–16 Apr	17–28 Apr
	N = 16	N = 9	N = 12	N = 13	N = 12
Chl *a* (μg L^{-1})	6.66 (4.38)	24.48 (17.44)	13.25 (7.67)	62.30 (16.32)	32.42 (10.24)
pH (1-14)	8.15 (0.14)^a	8.38 (0.23)^{ab}	8.39 (0.26)^b	8.93 (0.23)^c	8.92 (0.27)^c
DO (mg L^{-1})	11.03 (1.39)^a	11.37 (1.03)^a	10.85 (0.86)^a	13.13 (1.66)^b	11.27 (0.92)^a
SD (cm)	305 (78)^a	256 (102)^a	332 (81)^a	122 (27)^b	134 (40)^b
DOC (mg L^{-1})	1.01 (0.09)^a	1.40 (0.39)^{ab}	1.07 (0.09)^a	1.73 (0.25)^b	1.74 (0.23)^b
WT (°C)	11.46 (1.03)^a	12.53 (0.39)^b	13.10 (0.87)^b	16.42 (0.87)^c	20.41 (1.58)^d
DIN (mg L^{-1})	1.26 (0.05)^a	1.31 (0.11)^a	1.11 (0.22)^{ab}	0.91 (0.17)^{bc}	1.17 (0.41)^{ac}
DIP (mg L^{-1})	0.10 (0.01)^{ac}	0.08 (0.02)^a	0.13 (0.02)^b	0.11 (0.03)^c	0.08 (0.02)^a
DSi (mg L^{-1})	2.97 (0.13)^a	2.29 (0.32)^b	1.81 (0.35)^c	0.61 (0.49)^d	0.27 (0.25)^d

DISCUSSION

For many oligotrophic waters, algal growth is usually assumed to be mainly influenced by the nutrient availability, whereas in eutrophic ones the effects of hydrophysical environmental conditions determined by the local climate are much more influential (Horn 2003). Generally, nitrogen (N) and phosphorus (P) are essential elements contributing to eutrophication (Carpenter et al. 1998). The concentrations of total N and total P in Xiangxi Bay already exceeded the threshold values of the eutrophic state (Cai and Hu 2006), although they fluctuated appreciably during the shifts of the bloom phases. Thus, neither N nor P should be considered as the primary factors limiting the onset of the spring bloom in Xiangxi Bay. This conclusion is further supported by the results of CCA, because neither DIN nor DIP significantly correlated with Axis 1.

Temperature can promote phytoplankton growth rate and plays a critical role in

Table 2. Algal community groups with their characteristic species.

Community group	Characteristic species
a	*Asterionella formosa, Chroomonas* sp., *Melosira* sp. 1, *Cyclotella* spp., *Rhodomonas lacustris, Cryptomonas ovata, Melosira* sp. 2
b	*Cyclotella* spp., *Asterionella formosa, Melosira* sp. 1, *Synedra* sp.
c	*Cyclotella* spp., *Asterionella formosa, Melosira* sp. 1, *Synedra* sp.
d	*Asterionella formosa, Cyclotella* spp., *Chroomonas* sp., *Cryptomonas ovata, Rhodomonas lacustris, Melosira* sp. 2
e	*Asterionella formosa, Cyclotella* spp.
f	*Asterionella formosa*

the timing of a phytoplankton bloom (Goldman 1977, Yin et al. 1997). For example, when the major bloom events occurred at Calshot, surface temperature was greater than 12 °C (Iriarte and Purdie 2004). Surface temperature (12.53 ± 0.39 °C) of the *early*-bloom phase was significantly higher than that of the *pre*-bloom phase (11.46 ± 1.03 °C) when the spring bloom event began to occur in Xiangxi Bay. It could also be the case that in Xiangxi Bay a threshold temperature was necessary for the increase of chl *a* concentrations to reach the critical value of blooms (30 µg L^{-1}), although major spring blooms occurred at temperatures of other regions lower than that of Xiangxi Bay (Townsend 1994). Further, CCA indicated that the surface temperature significantly influenced the shifts of the phytoplankton assemblages during the diatom bloom. Hence, it is reasonable to believe that the occurrence of the bloom in the *early*-bloom phase could be triggered by the increase of water temperature.

The spring bloom will terminate because of depletion of a certain nutrient, usually silicate (Tsunogai and Watanabe 1983). Diatoms have high requirements for DSi to form
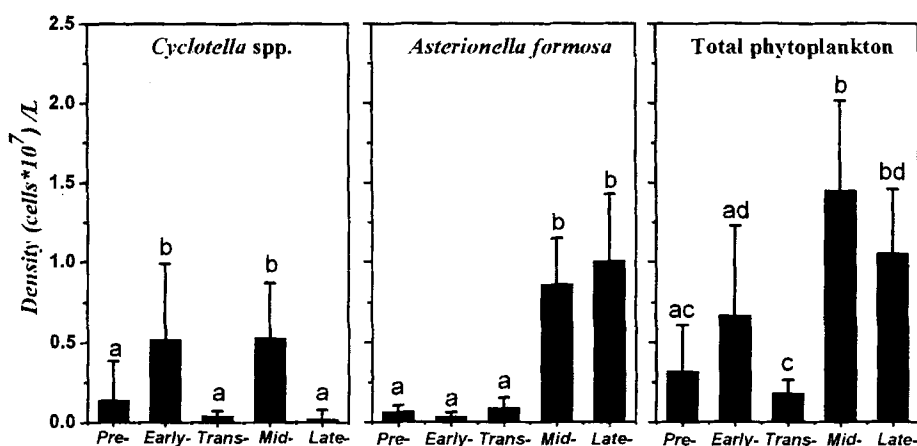

Figure 1. Algal density of the five phases during the spring bloom, derived from HCA grouping. Values with the same letters are not significantly different ($p >$ 0.05).

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frustules, and a diatom bloom deprived of Si will deteriorate faster than if deprived of P or N (Hecky et al. 1973, Golterman 1975). The *early*-bloom phase in Xiangxi Bay, accompanied by the higher DSi concentration than the *mid-* and the *late*-bloom phases, consisted of fast growing species [r-strategists; e.g., small centric diatoms (*Cyclotella* spp.)]. In the *mid*-bloom phase, the increased phytoplankton was co-dominated by small centric diatoms and larger pinnate diatoms (*A. formosa*), which substantially contributed to the peak of the bloom. In this phase, the most dramatic variation was the significant depletion of DSi accompanying the most serious bloom. Thereafter, the elimination of small centric diatoms in the *late*-bloom phase signaled the end of the bloom peak, and the obvious decline of the bloom in this phase also suggested the silicate limitation. It seemed that *A. formosa* was the superior competitor under silicate limitation. An experiment for resource competition between planktonic algae (Tilman 1977) also demonstrated that *Asterionella formosa* had a slight advantage over *Cyclotella meneghiniana* when both species were silicate limited.

The metabolism and production of zooplankton will increase with increasing temperature and food supply in spring (Montagnes and Lessard 1999), and grazing by zooplankton is generally regarded as an important factor for loss phytoplankton (Kasai et al. 1997). Among zooplankton of Xiangixi Bay in spring, the most dominant group was rotifers rather than larger-bodied zooplankters (Crustacea). The rotifer density during the study period ranged from 10 to 13,230 ind. L^{-1}, with a mean of 1,482 ind. L^{-1} ($n = 62$), whereas the mean density of Crustacea was 8 ind. L^{-1} ($n = 62$), ranging from 0 to 98 ind.
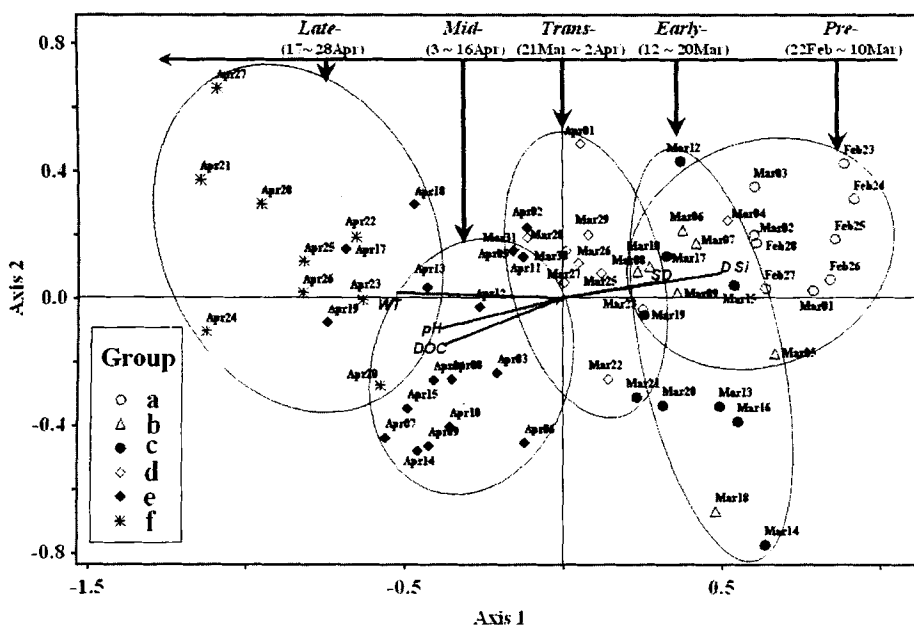

Figure 2. CCA sample ordination with the community types derived from TWINPAN grouping. The vectors represent environmental variables. The vector length is proportional to its importance and the angle between two vectors reflects the degree of correlation between variables. The angle between a vector and each axis is related to its correlation with the axis. Variables with correlation coefficients over 0.50 are presented. Different symbols indicate different community groups, and related sample scores are enclosed with ellipses.

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L^{-1} (data provided by Xiangxi River Ecosystem Station, CAS). According to regression analyses of rotifer density and algal biomass (expressed as chl *a*), Zhou (2007) attributed the increase in spring rotifer density to the algal bloom and discussed the importance of rotifer grazing for initiating clear water. However, rotifers could only be important grazers on small centric diatoms, not larger-colony diatoms like *A. formosa*. As the larger diatom species were the more dominant species in the last two phases, zooplankton grazing would likely be incapable of improving water clarity of Xiangxi Bay due to the low density of larger-bodied zooplankton.

ACKNOWLEDGEMENTS

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