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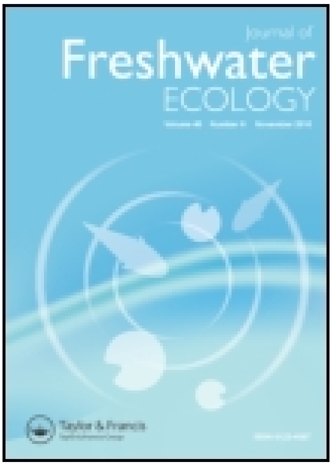

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EDITOR'S CHOICE ARTICLE

Phytoplankton dynamics and their equilibrium phases in the Yanghe Reservoir, China

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Phytoplankton species composition, seasonal dynamics, and spatial distribution were studied during 2009 along with key physical and chemical variables in Yanghe Reservoir, a temperate eutrophic reservoir with a long water residence time of 284 days. In the northern part of the reservoir, *Microcystis wesenbergii* dominated throughout the summer but no steady-state phases were found, as periods of equilibrium lasted for only two weeks each. In the southern part, the first steady-state phase occurred in spring, lasted for four weeks, and was dominated by *Cryptomonas erosa*. The second phase was dominated by *M. wesenbergii* in late summer and persisted for four weeks. The results suggest that steady-state phases establish more readily in deep areas with longer residence times and more dominant species compared to shallow areas. Thermal stratification in the deep area and fluctuation of nitrogen and phosphorus concentrations in the shallow area were considered to be responsible for such differences. Canonical correspondence analysis indicated that *M. wesenbergii* was more strongly related to NO_x–N than to temperature in both areas of the reservoir. We conclude that in eutrophic lakes, a high concentration of nutrients such as NO_x–N is more important than temperature in the establishment of a steady state.

Keywords: equilibrium phase; steady state; phytoplankton dynamics; thermal stratification; eutrophic lakes

Introduction

Terms such as ecological equilibrium, steady state, and stable state have been frequently used in ecosystem ecology. When describing a community, a steady state is a dynamic equilibrium because there are losses and additions to the community through time, the result of which is an invariant assemblage (Rojo & Alvarez-Cobelas 2003). In phytoplankton ecology, the equilibrium/steady-state concept emerged to describe a situation of little variability of species dominance and total biomass over time. For formally and accurately defining the concept, it was previously suggested to be no more than three species dominating the assemblage and contributing to 80% or more of the total biomass for at least three weeks without considerable variation in total biomass (Sommer et al. 1993). This concept has useful applications in discussions of the diversity–disturbance relationship and for explaining long-lasting successional phases dominated by one or several

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*Corresponding author. Email: xieping@ihb.ac.cn species, especially because such species are often a nuisance and can interfere with water use (Naselli-Flores et al. 2003).

A number of studies have dealt with steady-state phytoplankton assemblages in various types of lakes leading to a better understanding of the equilibrium concept in phytoplankton ecology (Allende & Izaguirre 2003; Mischke & Nixdorf 2003; Morabito et al. 2003; Naselli-Flores & Barone 2003; Nixdorf et al. 2003). Steady-state conditions are expected to occur more frequently in deep lakes than in shallow, mixed ones (Mischke & Nixdorf 2003) as stratification in deep lakes is considered to facilitate phytoplankton steady states (Dokulil & Teubner 2003; Leitao et al. 2003; Becker et al. 2008) with the competitive exclusion process reaching completion, resulting in the establishment of the equilibrium stage (Morabito et al. 2003). Comparison of steady-state phases between deep and shallow lakes appear to be difficult due to the differing phytoplankton compositions and environmental factors, including climate and nutrients. This study eliminates some of these confounding variables by studying one reservoir which has both shallow and deep areas.

Yanghe Reservoir is a temperate, eutrophic reservoir in north China with increasingly serious blooms of cyanobacteria in recent years. It was built in 1961 as an important drinking water source for Qinhuangdao and Beidaihe. Due to an increasing population, intensification of agriculture, domestic sewage inputs, and industry, water quality has deteriorated rapidly since the 1990s. Especially in the late autumn each year, wastewater from starch production in the upper reaches of the reservoir's catchment brings a great deal of organic nutrients into the reservoir. In the early summer of 2007, *Anabaena spiroides* was the dominant species of a blue-green algae bloom with a significant outbreak of odorous compounds which caused a drinking water crisis (Li et al. 2009). Despite the frequency of these algal blooms, research on phytoplankton composition, succession and distribution in the reservoir are rare.

In this paper, phytoplankton temporal and spatial variations in Yanghe Reservoir in 2009 are presented. Steady-state phases were identified according to Sommer et al. (1993) in order to understand the succession of phytoplankton assemblages and to investigate the environmental conditions which promote the establishment of a steady-state phase.

Methods

Study site

Yanghe Reservoir (39° 45′ to 40° 13′ N, 119° 00′ to 119° 25′ E) has a capacity of 3.58×10^8 m^3, an average depth of 5.8 m, average water area of 13 km^2, volume of 7.6×10^7 m^3 and controlling watershed of 755 km^2 (Figure 1). The average annual rainfall was 750 mm (1961–2009) with 56% falling during July and August and the water residence time was estimated as 284 days (provided by local weather bureau). In summer, water in the reservoir's southern part (near the dam) experiences thermal stratification, which does not exist in the northern part due to its relatively shallow water depth (Li 1999). In winter, the entire reservoir surface is ice covered (Wang & Zheng 2013).

Sampling and analyses

Due to the different physical conditions between the northern and southern parts of the reservoir, three sampling stations were set up in each, in order to investigate the spatial variation of phytoplankton. In the north, sampling stations S1, S2, and S3 had an average water depth of 3.8 ± 0.8 m during the sampling period, while in the south, sampling

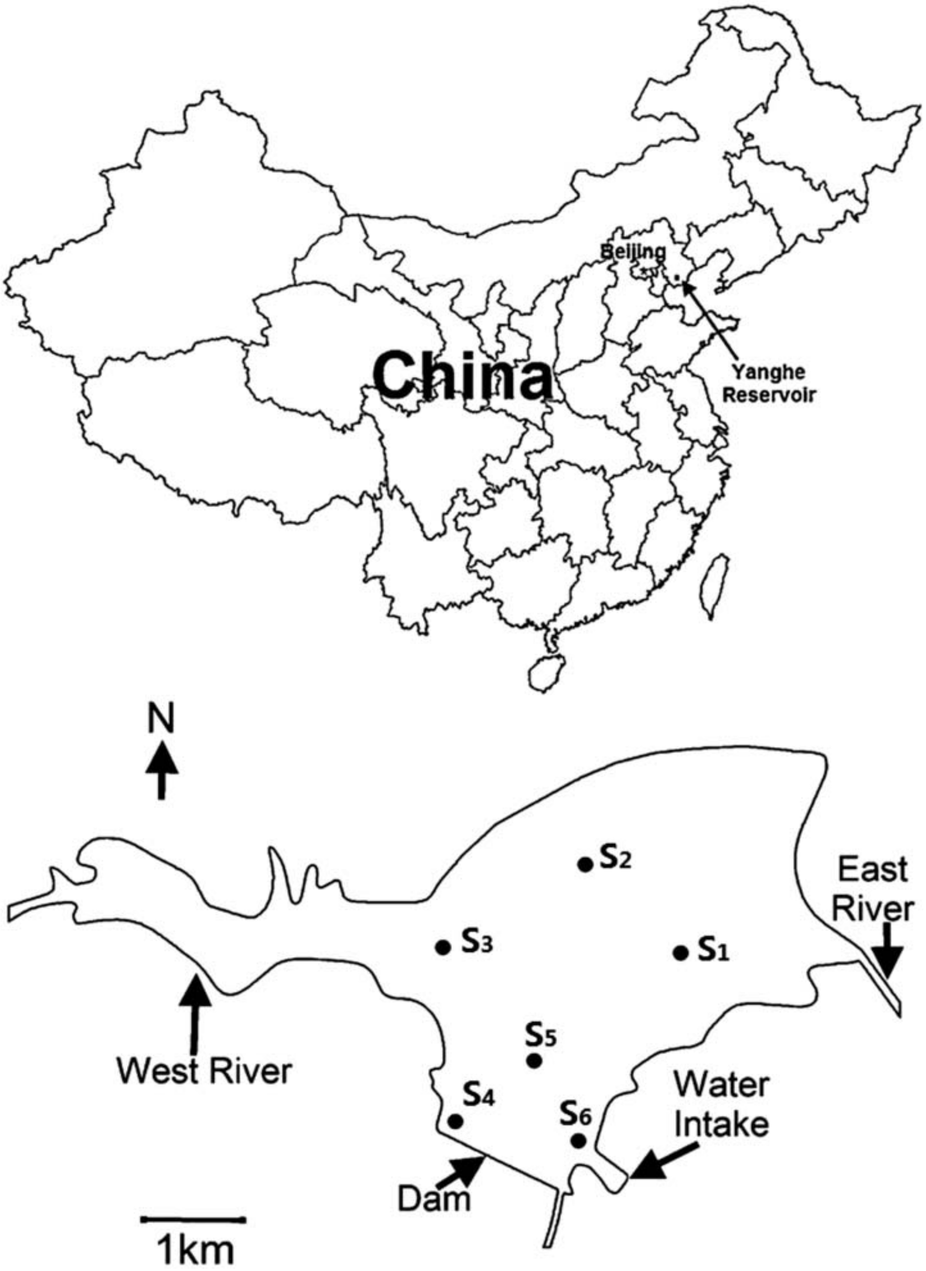

Figure 1. Location and map of Yanghe Reservoir showing the locations of the sampling stations.

stations S4, S5, and S6 had an average depth of 8.6 ± 0.9 m. Water samples were collected from March to November 2009, on a weekly basis during the summer cyanobacterial bloom (June–August), fortnightly in April, May, and September, and monthly in March, October, and November. Each water sample composed of a mixture of surface, middle, and deep water (1:1:1) was collected using a 5-L Schindler sampler.

Values for temperature, dissolved oxygen (DO), and water transparency were obtained *in situ*. Temperature was measured by a WMY-01 digital thermometer (Medical Instrument, Shanghai, China). DO was measured by a JPB-607 DO meter (Leici Instrument, Shanghai, China) and transparency was measured by Secchi disk.

Chemical analyses of water samples in the laboratory included chemical oxygen demand (COD), total phosphorus (TP), total nitrogen (TN), nitrate–N (NO_3–N), ammonium–N (NH_4–N) and nitrite–N (NO_2–N). All the measurements and analyses followed the Chinese standard methods for the lake eutrophication survey (Jin & Tu 1990). TP was measured by colorimetry after digestion with H_2SO_4. TN was determined by the Kjeldahl method. NO_3–N was analyzed using the automated Korolev/cadmium reduction method. Ammonium (NH_4–N) was determined by the Nessler method, and nitrite (NO_2–N) was determined by the naphthylamine method. NO_3–N and NO_2–N concentrations were summed to give total oxidized inorganic nitrogen (NO_x–N). Chlorophyll *a* was determined spectrophotometrically (Lorenzen 1967) after filtration on Whatman GF–C glass filters and 24-h extraction in 90% acetone.

One-liter phytoplankton samples were fixed *in situ* with acetic Lugol's solution according to Parsons et al. (1984) and concentrated to approximately 50 mL after sedimentation for 48 h. The concentrated samples were counted in a 0.1-ml counting chamber using an Olympus microscope under ×400 magnification after intensive mixing. Colonial *Microcystis* cells were separated using an ultrasonic crusher (JY88-II, Scientiz, Ningbo, China) and the individual cells counted. Phytoplankton species were identified with reference to the methods detailed by Hu and Wei (2006).

Data analysis

Phytoplankton functional groups were established according to Reynolds et al. (2002) and Padisak et al. (2003). Steady-state phases were identified according to Sommer et al. (1993). All results from sampling stations S1, S2, and S3 were averaged to represent the northern part of the reservoir, while the southern part was represented by the averaged results from S4, S5, and S6.

The CANOCO v.4.5 computer program was used for all multivariate and ordination analyses (ter Braak & Smilauer 1998). The first gradient length of detrended correspondence analysis (DCA) was used to select the appropriate model (ordination procedure) for the constrained ordinations. Standard deviations of 2.0 units or greater (which are representative of a relatively long gradient) indicated that numerical analyses assuming unimodal species distributions, such as canonical correspondence analysis (CCA), would be the most appropriate for this data-set. In the present study, mean physicochemical variables and the most prominent algal taxa in both parts of Yanghe Reservoir were subjected to DCA and CCA. Before performing the analysis, the data were $\ln(x+1)$ transformed. To determine the variables best related to the phytoplankton dynamics, a Monte Carlo permutation test was applied.

Results

Physical and chemical variables

Means and ranges of the physical and chemical variables for the northern and southern parts of the reservoir are presented in Table 1. Water depth and transparency in the north were lower than that in the south during the whole sampling period, and accordingly,

Table 1. Mean, standard deviation, minimum, and maximum values for five environmental factors measured during sample collection in the northern end and southern end of Yanghe Reservoir, China.

Environmental factors	North			South		
	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Secchi depth (m)	1.3 ± 0.6	0.5	4.5	1.8 ± 1.08	0.6	6.8
Depth (m)	3.8 ± 0.8	1	6.3	8.6 ± 0.9	5.3	10.5
Temperature (°C)	19.2 ± 7.84	0.3	28	20.2 ± 7.89	0.0	27.8
Dissolved oxygen (mg/L)	10.1 ± 1.82	5.8	14.82	9.85 ± 1.76	5.9	14.49
COD_{Mn} (mg/L)	3.42 ± 0.62	2.1	5.1	3.17 ± 0.58	1.9	4.8

COD and chlorophyll *a* in the north were higher than those in the south. Dissolved oxygen varied little between the two areas. Nutrient and water temperature dynamics for the reservoir are shown in Figure 2. TN and TP had obvious increases in concentration on August 5 and October 27 in both the northern and the southern parts of reservoir, respectively (Figure 2(a) and 2(b)). Total inorganic oxidized nitrogen (NO_x–N) was higher in the north than the south only in late summer, whereas NH_4–N was the opposite (Figure 2(c) and 2(d)). Temperature varied between 0 and 28 °C throughout the year for the two locations.

Phytoplankton species composition and seasonal succession

A total of 48 phytoplankton species were identified throughout the sampling period (Table 2). The greatest number of species were contributed by Chlorophyta (21) followed by Bacillariophyta (11), Cyanophyta (5), Euglenophyta (3), Dinophyta (3), Cryptophyta (2), Chrysophyta (2), and Haptophyta (1). Functional group J had the largest allocation of species followed by functional group P (Table 2).

Seasonal variations of dominant phytoplankton species are shown in Figures 3 and 4. In the northern part of the reservoir, no steady-state phases were found during the whole sampling period. In summer, the average total phytoplankton biomass was 18 mg/L. In early summer, *Oocystis borgei* (24.4%) was the dominant species, while in late summer, *M. wesenbergii* was the dominant species. There were two occasions when *M. wesenbergii*, along with two other species, contributed more than 80% of the total biomass but these persisted for only two-week periods (as shown by the vertical gray bars in Figure 3(a) and 3(c)) and so did not meet the criteria outlined by Sommer et al. (1993) for steady-state determination.

A. spiroides was the second dominant species in August constituting 13.7% of the total biomass. In spring and autumn in the northern section, the total biomass of phytoplankton was below 10 mg/L and *Cryptomonas erosa* was the dominant species.

In the southern part of the reservoir, two steady-state phases occurred during the sampling period. The first phase occurred from April 21 to May 22 when *C. erosa* (59.1%) and *O. borgei* (21.3%) co-dominated and made up 80.4% of the total biomass. The second phase lasted from August 12 to September 9 when *M. wesenbergii* was the dominant species, constituting 77.3% of the total biomass with *C. erosa* (3.2%) and *Ceratium hirundinella* (3.5%). Together the three species contributed a total of 84% to the total biomass.

Seasonal succession of the total number of phytoplankton species is shown in Figure 4. In the southern section, the number of species showed varying degrees of decrease during the steady-state phases outlined above (Figure 3(b)). In the northern

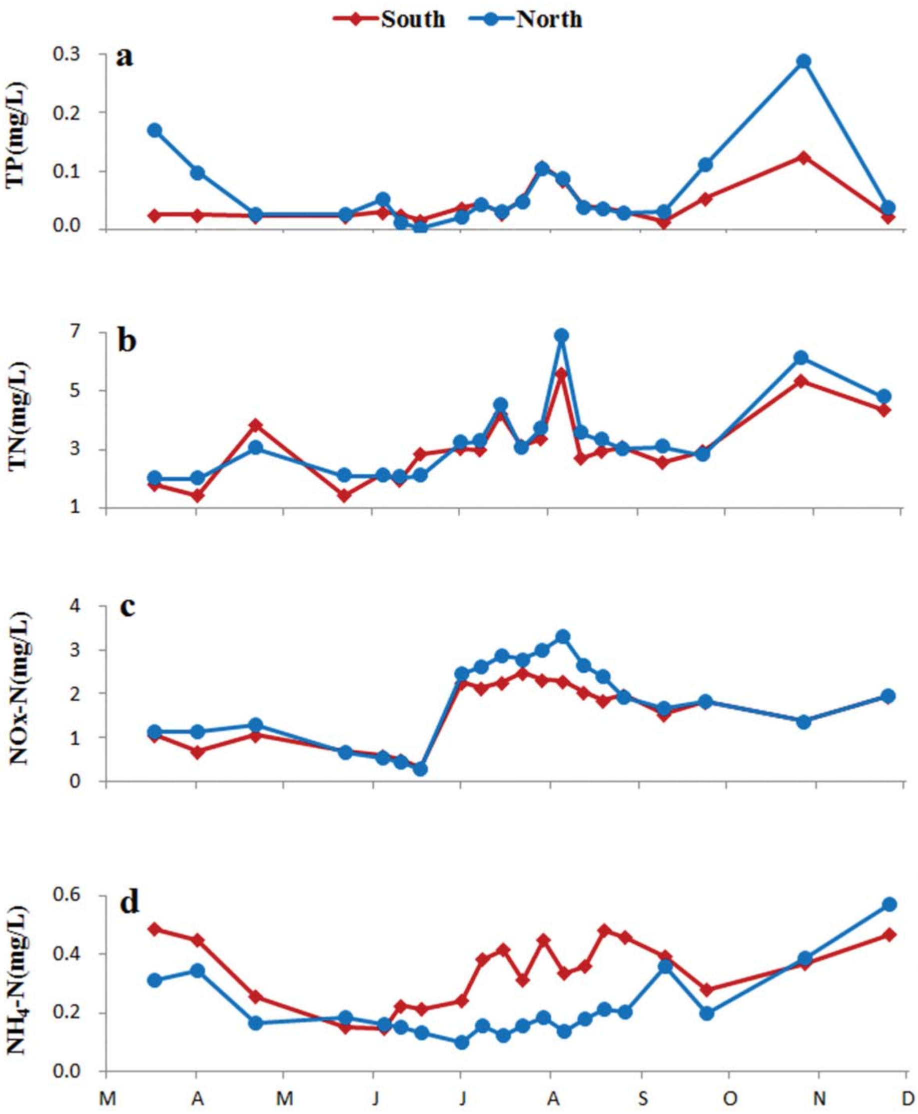

Figure 2. Nutrient and water temperature dynamics in Yanghe Reservoir during March–November 2009. NO_x is the sum of NO_3–N and NO_2–N representing total oxidized inorganic nitrogen.

section, the species' numbers rapidly increased and no steady state was identified during the first southern steady-state period. Interestingly, no steady state was observed in the north during the second southern steady-state period, despite the species' numbers having a similar decrease as in the southern location.

CCA comparison

The length of the first gradient in the DCA was 2.37 in the northern section and 2.23 in the southern section (not shown); therefore, CCA was appropriate for the data-set (ter Braak & Smilauer 1998). In the north, all environmental variables considered for the analysis

Table 2. List of phytoplankton taxa along with their respective functional group and relative abundance for all samples collected in the study from Yanghe Reservoir, China.

Taxa	Functional group	Relative abundance (%)
Cyanophyta		
Microcystis wesenbergii	M	35.23
Anabaena spiroides	H1	1.45
Oscillatoria spp.	MP	<1
Chroococcus spp.	K	<1
Merismopedia tenuissima	Lo	<1
Cryptophyta		
Chroomonas spp.	X2	<1
Cryptomonas erosa	Y	10.07
Bacillariophyta		
Synedra spp.	D	<1
Fragilaria crotomensis	P	8.75
Cyclotella meneghiniama	C	2.44
Melosira granulata	P	2.70
M. granulata var. angustissima	P	<1
M. granulata var. angustissima f. spiralis	P	<1
Pinnularia spp.	\	<1
Cymbella spp.	MP	<1
Navicula spp.	MP	<1
Surirella spp.	MP	<1
Asterionella spp.	C	<1
Chlorophyta		
Scenedesmus spp.	J	1.23
Pediastrum simplex	J	1.24
P. simplex var. duodenarium	J	2.39
P. duplex	J	<1
P. boryanum	J	<1
P. tetras	J	<1
P. integrum	J	<1
Oocystis borgei	F	9.50
Tetrahedron spp.	G	<1
Chlamydomonas spp.	X2	2.29
Crucigenia spp.	J	<1
Coelastrum spp.	J	<1
Cosmarium circulare	N	<1
Staurastrum cernulatum	P	<1
Eudorina elegans	G	<1
Pandorina morum	G	<1
Ankistrodesmus spp.	X1	<1
Nephrocytium spp.	F	<1
Closterium spp.	P	<1
Closteriopsis longissima	P	<1
Dictyosphaerium pulchelum	F	<1
Euglenophyta		
Euglena spp.	W1	<1
Trachelomonas spp.	W2	<1
Phacus spp.	W1	<1
Chrysophyta		
Mallomonas spp.	E	<1
Dinobryon spp.	E	<1
Dinophyta		
Peridinium spp.	Lo	7.91
Ceratium hirundinella	Z_{MX}	2.41
Gymnodinium spp.	Y/Lo	<1
Haptophyta		
Chrysochromulina parva	\	<1

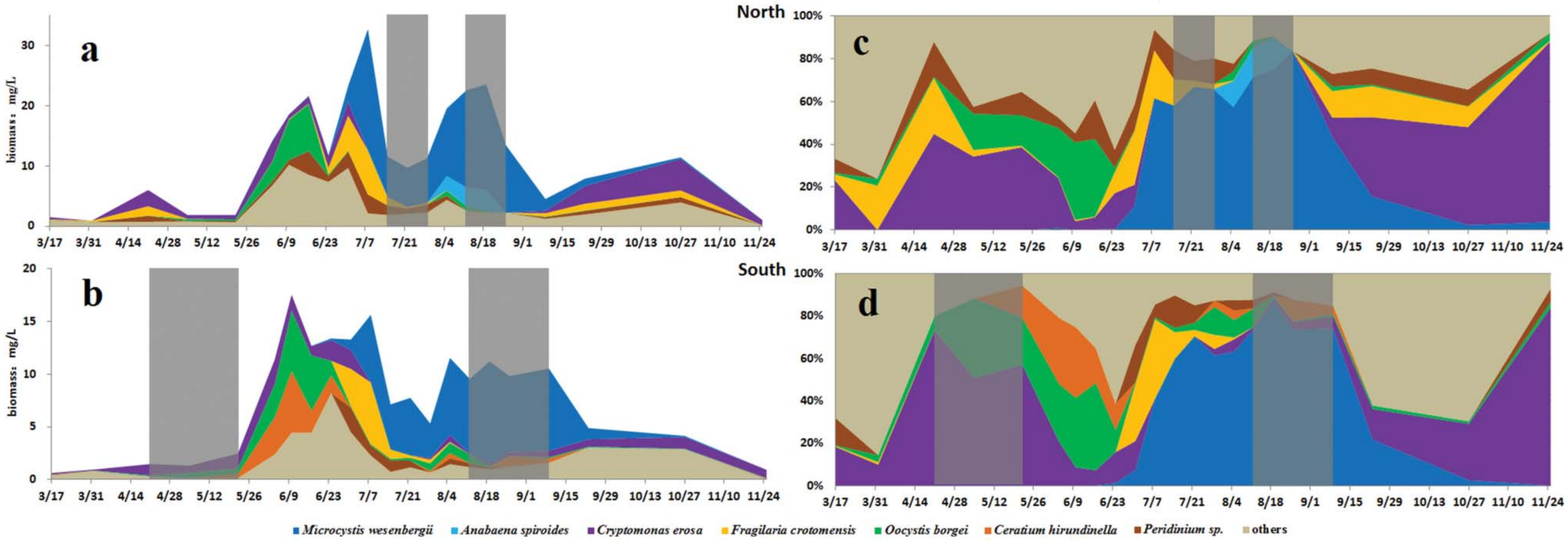

Figure 3. Seasonal variation of dominant phytoplankton species and their relative abundances in 2009 in the northern section (panels (a) and (c)) and the southern section (panels (b) and (d)). Periods when no more than three species contributed more than 80% of the biomass are shown in gray in the northern section. Steady-state phases are shown in gray in the southern section.

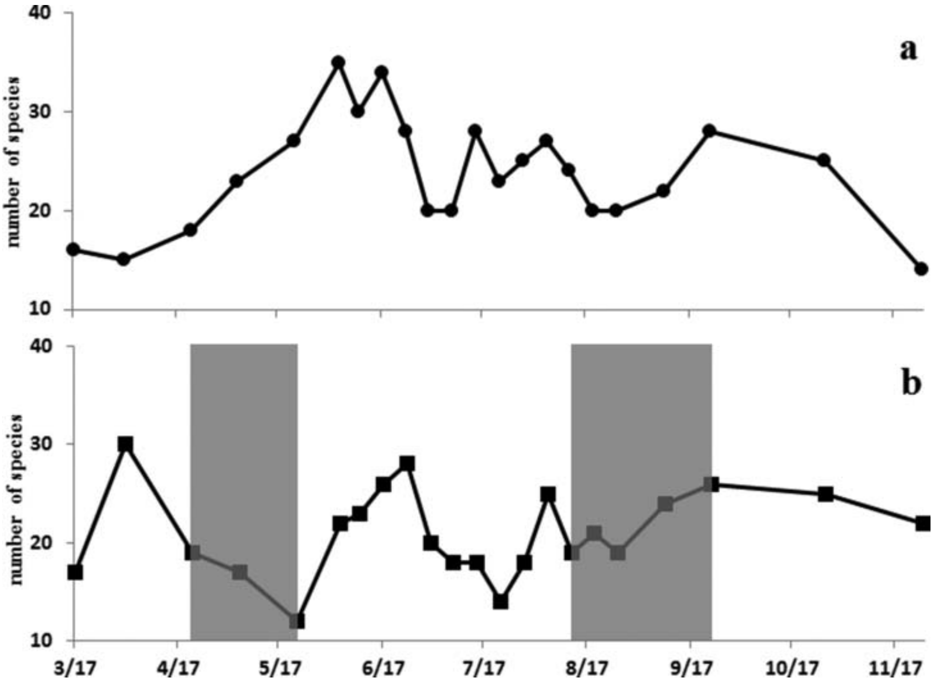

Figure 4. Variation in total number of phytoplankton species in (a) the northern section and (b) in the southern section of the Yanghe Reservoir in 2009. Steady-state phases are shown in gray.

(Table 3) accounted for 56.5% of the total variation of the phytoplankton assemblage. Axis 1 was strongly associated with Secchi depth, temperature, COD, and NH_4–N, whereas axis 2 was associated with NO_x–N (Figure 5(a)). Axes 1 and 2 combined explained a large proportion of variance in the phytoplankton–environment relationship (88.7%). In the north, *Peridinium* spp. was positioned near the center of the ordination diagram and *M. wesenbergii* was positioned on the positive side of axis two (Figure 5(a)).

In the south, all the environmental variables considered for the analysis accounted for 56.9% of the total variation of the phytoplankton assemblage (Table 3) and axes 1 and 2 combined explained 89% of variance in the phytoplankton–environment relationship. Axis 1 was strongly associated with temperature and COD, while axis 2 was mainly associated with NO_x–N, NO_4–N, and DO.

Discussion

Since the criteria were established by Sommer et al. (1993) for identifying an equilibrium phase, research has been focused increasingly on the steady-state phases in phytoplankton seasonal succession in various types of lakes (Dokulil & Teubner 2003; Leitao et al. 2003; Stoyneva 2003; Celik & Ongun 2008). In theory, deep lakes are considered to experience steady-state phases more readily in comparison with shallow lakes due to stratification (Mischke & Nixdorf 2003). Actually, such phases, dominated by cyanophytes, are often seen in hypertrophic conditions in stressed shallow water bodies and usually occur in summer or late summer (Mischke & Nixdorf 2003; Nixdorf et al. 2003; Padisak et al. 2003; Stoyneva 2003). Trophic state, disturbance, and stress factors also play important

Table 3. Eigenvalues for CCA axes (1–4) and correlation coefficients between environmental factors and CCA ordination axes.

	North					South				
	1	2	3	4	Total inertia	1	2	3	4	Total inertia
Eigenvalues	0.328	0.125	0.051	0.007		0.375	0.095	0.048	0.01	
Species–environment correlations	0.906	0.714	0.527	0.311		0.927	0.702	0.513	0.299	
Cum.% variance of species	36.2	50.1	5.7	56.5		40.5	50.7	55.8	56.9	
Cum.% variance of species–environment	64.2	88.7	98.5	100		71.1	89	98	100	
Sum of all eigenvalues					0.906					0.927
Sum of all canonical eigenvalues					0.512					0.528
Secchi depth	−0.129	0.312	0.318	0.068		0.267	0.188	0.224	0.066	
Temperature	−0.400	−0.556	−0.118	0.054		−0.385	−0.543	−0.116	−0.105	
Dissolved oxygen	0.148	−0.012	−0.025	−0.033		0.523	−0.109	−0.079	−0.009	
TN:TP	0.232	−0.324	−0.098	0.032		−0.013	0.144	−0.278	0.216	
NO_x–N	−0.851	0.116	−0.061	−0.022		−0.850	0.129	0.032	−0.04	
NH_4–N	0.036	0.366	0.355	−0.026		−0.462	−0.014	0.109	0.101	
Chemical oxygen demand	−0.360	−0.338	0.056	−0.22		−0.342	−0.345	0.179	0.139	

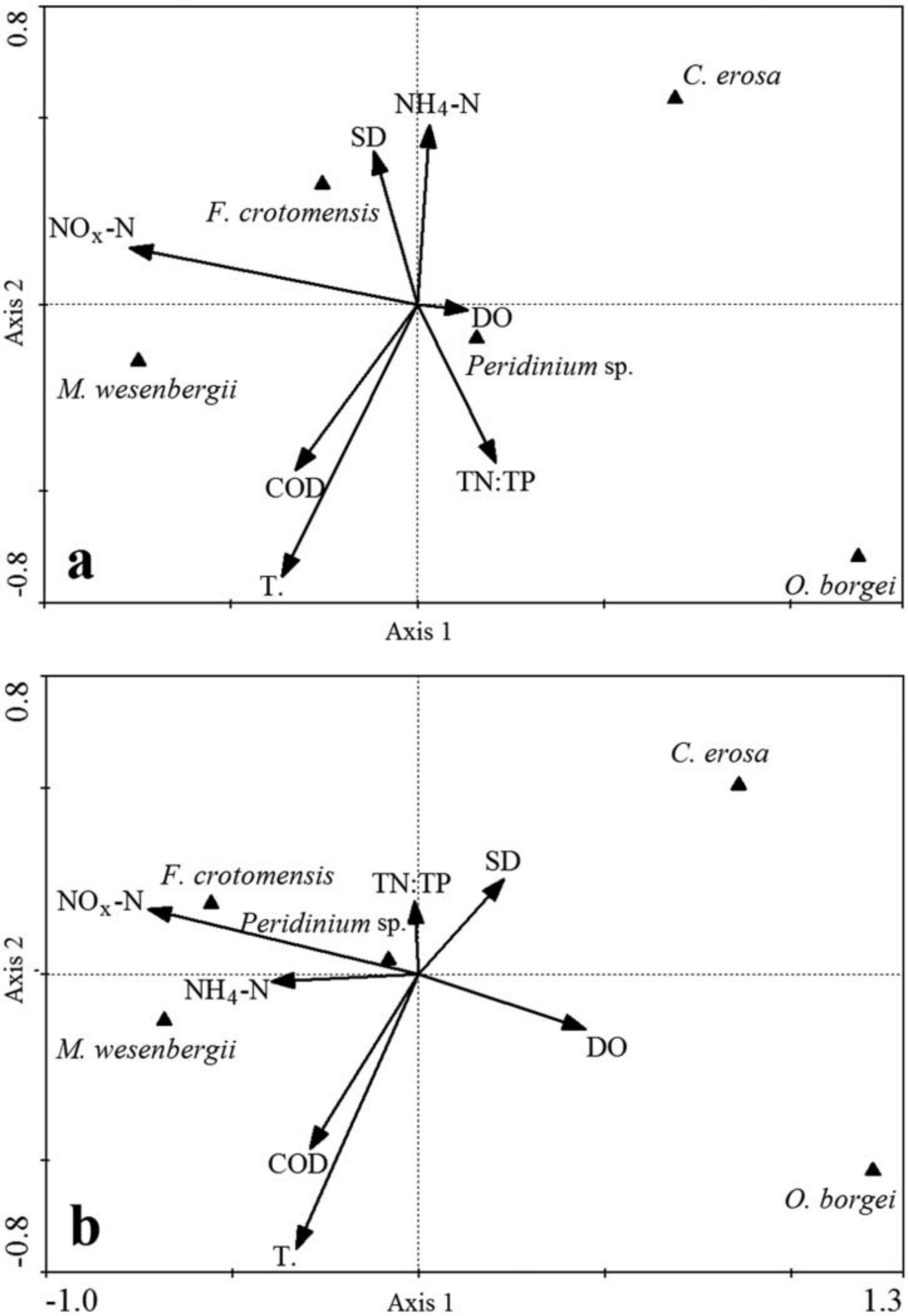

Figure 5. Species–environmental variables biplot of canonical correspondence analysis for (a) the northern section and (b) in the southern section. The triangles represent dominant species and the arrows represent environmental variables.

roles in the establishment of steady-state phases and the development of phytoplankton equilibrium (Naselli-Flores et al. 2003).

Yanghe Reservoir is completely ice covered in winter, from December to February, while in summer, the southern part of the reservoir is thermally stratified (Gao et al. 2010). According to the criteria set by Sommer et al. (1993), either steady- or non-steady-state phases of phytoplankton assemblages were observed in both parts of the Yanghe Reservoir. By comparing the deep and shallow areas, we suggest that in summer, stratified regions have more dominant species that persist longer, resulting in the achievement of a steady-state system, compared to non-stratified regions where steady states may not occur.

In the middle of spring, the first steady-state phase was found in the southern part where *C. erosa* (59.1%) and *O. borgei* (21.3%) were co-dominant (Figure 3(d)). The lowest value of total species number was also during this period (Figure 4). Meanwhile, no steady-state phase occurred in the northern section (Figure 3(a)) and the number of species increased (Figure 4). Cyanobacterial steady states are always accompanied by low diversity and have been described in many eutrophic lakes in the northern temperate zones (Elliott et al. 2000; Mischke & Nixdorf 2003; Morabito et al. 2003). This is an expected result because during the equilibrium conditions either the environmental factors may not be suitable for the growth of other species or they are inhibited by dominant species (Reynolds et al. 1993). Padisak et al. (2003) found that the total number of species clearly increased in 10 Hungarian lakes when they were not in equilibrium state. The comparison of the two areas in the Yanghe Reservoir in the middle of spring supports the findings of Padisak et al. (2003) as an increase in the numbers of species resulted in no steady-state formation in the polymictic shallow area.

C. erosa (group Y), a micro-algal food source for zooplankton, has been found co-dominating with other species during a steady-state phase only twice previously (Padisak et al. 2003; Rojo & Alvarez-Cobelas 2003). In the present case, *C. erosa* was co-dominant with *O. borgei* (group F), a green alga. A possible explanation is that the assemblage was formed by species with different rates of resource-uptake, mobility and light-intensity requirements (Levins 1979; Salmaso 2003). According to the functional classification of phytoplankton summarized by Reynolds et al. (2002), group Y species are tolerant to low light, while green algae of group F seem to have a higher light threshold and are tolerant of low nutrients. So here, *C. erosa* and *O. borgei* likely co-dominated because they have different niches and did not compete. Furthermore, a peak value of TN (3.81 mg/L) on April 21 also indicated adequate nutrients for both species to avoid competition.

In late summer, both parts of the reservoir experienced a cyanobacterial bloom dominated by *M. wesenbergii* from the end of June to the beginning of September (Figure 3). The second steady-state phase in the southern part was dominated by *M. wesenbergii*, which constituted 77.3% of the total biomass and lasted for four weeks (Figure 3(d)). *M. wesenbergii* biomass fluctuated substantially in the northern part but dominated throughout the summer (Figure 3(a)). There was an absence of a steady-state phase due to the short duration of species co-domination, based on criteria by Sommer et al. (1993).

CCA is an intuitive expression of the relationship between phytoplankton species and environmental factors (ter Braak & Verdonschot 1995). In this context, CCA showed that *M. wesenbergii*, the primary component of the steady-state assemblages, was closely related to NO_x–N in the ordination diagram in both parts of the reservoir (Figure 5). *M. wesenbergii* is a non-nitrogen-fixing cyanobacteria and its growth strongly depends on the concentration of nitrogen in the water (Gerloff & Skoog 1957; Xu et al. 2010). Maximum and average values of TN and NO_x–N in the northern part were higher than the southern part (Table 1) primarily in summer and late autumn (Figure 2(b) and 2(c)). These disparities were probably attributed to both internal and external nutrients.

Every year in the late autumn, wastewater from starch production in the upper reaches of the Yanghe Reservoir catchment brings a great deal of organic nutrients into the reservoir, from the north to the south. This caused an abrupt rise in TN and TP concentrations in October 2009 (Figure 2(a) and 2(b)). Since little of the inorganic nitrogen is utilized at this time, the long water residence time of 284 days made it possible to have a large proportion of the external TN deposited in sediments. Once the temperature rises in the summer, the nitrogen in the sediments is released to the overlying water (Li et al. 2007), leading to a high concentration of NO_x–N (Figure 2(c)). However, due to stratification this may not cause disturbance in the surface waters (Becker et al. 2008), resulting in a lower NO_3–N concentration in surface waters in the southern location.

External nutrients from storm runoff in the upper catchment transported by inflowing rivers may also increase the nutrient concentrations in the reservoir as demonstrated by a sudden rise in TN (6.84 mg/L) on August 5 and TP (0.105 mg/L) on July 29 (Figure 2(a) and 2(b)). During this time, *A. spiroides* became the secondary dominant species in the northern area but disappeared after TP fell below the average level (0.039 mg/L) on August 12 (Figure 3(a) and 3(c)). Consequently, a steady state was not established as in the southern reservoir because the bloom was broken into two parts due to the sudden change in phytoplankton community composition (Figure 3). *A. spiroides* (group H1) is tolerant of low nitrogen levels, as it relies on its nitrogen-fixing capabilities and can outcompete *Microcystis* in growth rates in low N:P ratio conditions (Nalewajko & Murphy 2001). Considering the phosphorus concentration in Yanghe Reservoir was below 0.05 mg/L for most of the year in 2009 (Figure 2(a)), the sudden rise in TP concentration could be the factor that caused the appearance of *A. spiroides* and thereby inhibited the formation of a steady-state phase.

Steady-state phases in deep lakes seem to have different dominant species in different seasons (Naselli-Flores & Barone 2003; Becker et al. 2008) but shallow lakes frequently have only one steady-state phase or several steady-state phases with the same dominant species during the year (Mischke & Nixdorf 2003; Moustaka-Gouni et al. 2007; Celik & Ongun 2008). These differences were also apparent in our study. It was clearly shown that thermal stratification and the stable nutrient concentrations aided the deep area of Yanghe Reservoir to form steady-state phases more readily than the shallow area, which was manifested in the presence of more dominant species and a longer duration. In the shallow area, although the high nitrogen and temperature in summer allowed *M. wesenbergii* to become the dominant species and form the beginnings of a steady-state phase, turbulent factors such as nitrogen released from sediments and phosphorus from storm runoff reduced the duration of the equilibrium.

A steady state occurs less frequently in temperate-climate phytoplankton (Naselli-Flores et al. 2003) in comparison with tropical (Ganf 1974; Rott 2002) and polar (Allende & Izaguirre 2003) phytoplankton where the steady-state phase development is more likely and long lasting. This can be attributed to longer individual seasons and narrower seasonal temperature variation. In Yanghe Reservoir, temperature ranged from 0 to 28 °C during the sampling period (Table 1) and the CCA showed that temperature was the most important factor that influenced the distribution of phytoplankton in axis 1 (Figure 5). Steady states were still found in the deep section despite temperature varying widely at the same time in spring (Figure 3(b) and 3(d)). We conclude that in eutrophic lakes, high concentrations of nutrients such as NO_x–N are more influential in the establishment of the steady state than temperature.

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