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ORIGINAL ARTICLE

Multi-year succession of cyanobacteria blooms in a highland reservoir with changing nutrient status, Guizhou Province, China

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ABSTRACT

Over the last 22 years significant phytoplankton changes in Hongfeng lake reservoir have been observed with multiple years of harmful cyanobacteria blooms (cHABs). Fish farming and other anthropogenic activities from 1994-2001 triggered the harmful blooms. Nine years after the cessation of aquaculture, a conversion from problematic species (*Microcystis* spp, *Aphanizomenon flos-aquae*) to the less problematic species *P. limnetica* and other associated non-cyanobacteria taxa was recorded. Through this period of change, trophic factors (bottom-up) were re-examined, and correlations between cHABs and selected environmental variables were observed. Higher temperatures, nutrients [total nitrogen (TN), total phosphorus (TP)] and available light significantly favored the development of *Microcystis* spp blooms. With declining nutrient loads, and a decline in TP relative to TN there was a competitive shift from *Microcystis* summer blooms to the growth of *Pseudanabaena limnetica* and other non-cyanobacteria. *Pseudanabaena limnetica* was favored over *Microcystis* spp when temperatures were <20°C and TP was <0.03 mg L⁻¹. The apparent species succession to *P. limnetica* was enhanced by a competitive advantage under varied light conditions. Multiple environmental and biotic conditions (not always nutrients) were driving cHABs. Although only a selected number of environmental variables were examined, the CCA analysis supports observations that temperature and nutrients were associated with the species shift. The replacement of cHABs with the growth of less toxic cyanobacteria like *P. limnetica*, and other algae creates an interesting scenario (new community condition) for the removal of problematic taxa in reservoir systems. Diverting or controlling blooms will have direct implications on water quality and economic remediation initiatives in reservoir and lake management.

Key words: *Aphanizomenon*; competitive succession; cyanobacteria blooms; *Microcystis*; nitrogen and phosphorus; *Pseudanabaena*.

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INTRODUCTION

Cyanobacteria are the most ancient primary producers on the planet and can form harmful algal blooms (cHABs) in freshwater, estuarine and marine ecosystems (O'Neil *et al.* 2012; Reynolds and Walsby, 1975). Harmful algal blooms have been reported in the scientific literature for more than 130 years (Francis, 1878; O'Neil *et al.*, 2012) and are presently increasing in occurrence events across freshwater systems (Hallegraeff, 1993; Paerl and Huisman, 2009). These blooms are associated with poor water quality, accumulation of aquatic biomass and low saturated oxygen levels (Jonas *et al.*, 2014; Wiegand and Pflugmacher, 2005). Cyanobacteria under certain conditions can also produce toxins which along with taste and odor compounds have negative biological and human health effects (Jonas *et al.*, 2014; Pick, 2016; Wiegand

and Pflugmacher, 2005). Massive proliferations of harmful algae in freshwater and marine ecosystems have caused losses to natural resources, national economies, and resulted in human sickness and death worldwide (Bláha *et al.*, 2009; Lewitus *et al.*, 2012; Ma *et al.*, 2014). A previous study has shown that biological and economic losses due to HABs were estimated at US\$82 million annually in the United States and nearly US\$813 million annually in Europe (Hoagland and Scatista, 2006).

Two contributors to cHABs, *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault and *Microcystis* spp have been correlated to increased nutrient inputs, especially phosphorus and nitrogen (Liqiang *et al.*, 2003; Conley *et al.*, 2009; Ma *et al.*, 2015; O'Neil *et al.*, 2013). Paerl and Huisman (2009) and Pick (2016) also attributed climate change (warmer temperatures) to changes in hydrological cycles and blooms. Further, Knoll *et al.* (2008) have associated cHABs to invasive species events.

Blooms are complex events, typically not caused by a single environmental driver but rather a series of factors occurring concurrently (Heisler *et al.*, 2008; O'Neil *et al.*, 2012). The reservoir with cHABs concern in this study, Hongfeng Lake (Guizhou Province), is a typical Karst plateau deep water reservoir. The reservoir has been a water source for the City of Guiyang since 1960 with presently no public, industrial or recreational use. In 1994, fish cages for aquaculture were deployed in Hongfeng Lake reservoir and remained until 2001. This aquaculture practice caused extensive cHAB blooms (*Aphanizomenon flos-aquae* and *Microcystis* spp) during and after the period of fish culturing. This single anthropogenic impact has dramatically changed the quality of this economic water source.

Studies examining the decline and termination of cyanobacteria blooms have primarily focused on the effects of nutrients and other environmental factors, particularly on the decrease of available phosphorus. In contrast, studies looking at biological interactions related to algal blooms are rare (*e.g.* Proulx *et al.* 1996). The objective of this study was to evaluate the temporal and spatial occurrence of cHAB competitive succession in Hongfeng Lake reservoir in relation to nutrients and environment. Specifically what temporal scale of change was observed and the implications for recovery and improvement of water quality in other manipulated reservoir systems.

METHODS

Study site

Hongfeng Lake reservoir (26°24'-26°34'N, 106°20'-106°26'E), is located in Guiyang City, Guizhou Province, southwest China (Fig. 1). This is one of many reservoirs built on the Maotiao River, its closest neighbor is Baihua Reservoir (~20 km downstream). Hongfeng reservoir is a deep-water impoundment (45 m) with limestone and dolomite as the dominant bedrock. The local soils are calcareous, with high pH (Liu *et al.*, 2012). Water storage in the reservoir was initiated in 1960, providing local communities with hydropower, fisheries, irrigation, drinking water, and recreation resources. The five main fish species are *Cyprinus carpio* L (Common carp), *Carassius auratus* L. (Goldfish), *Ctenopharyngodon idella* Valenciennes (Grass Carp) *Aristichthys nobilis* (Richardson) (Bighead Carp), and *Hypophthalmichthys molitrix* Valenciennes (Silver Carp). The regional watershed surface area is 1596 km², reservoir water surface area 57.2 km², reservoir mean depth of 24 m, and maximum depth of 45 m (Fang and Li, 2009; Liu *et al.*, 2012; Lu *et al.*, 2007).

We utilized reported studies (our work and others) over the past 35 years from Hongfeng Lake reservoir, including new data collected by our group from 2007-2014, in this study. The dataset included physical and chemical factors as well as phytoplankton community

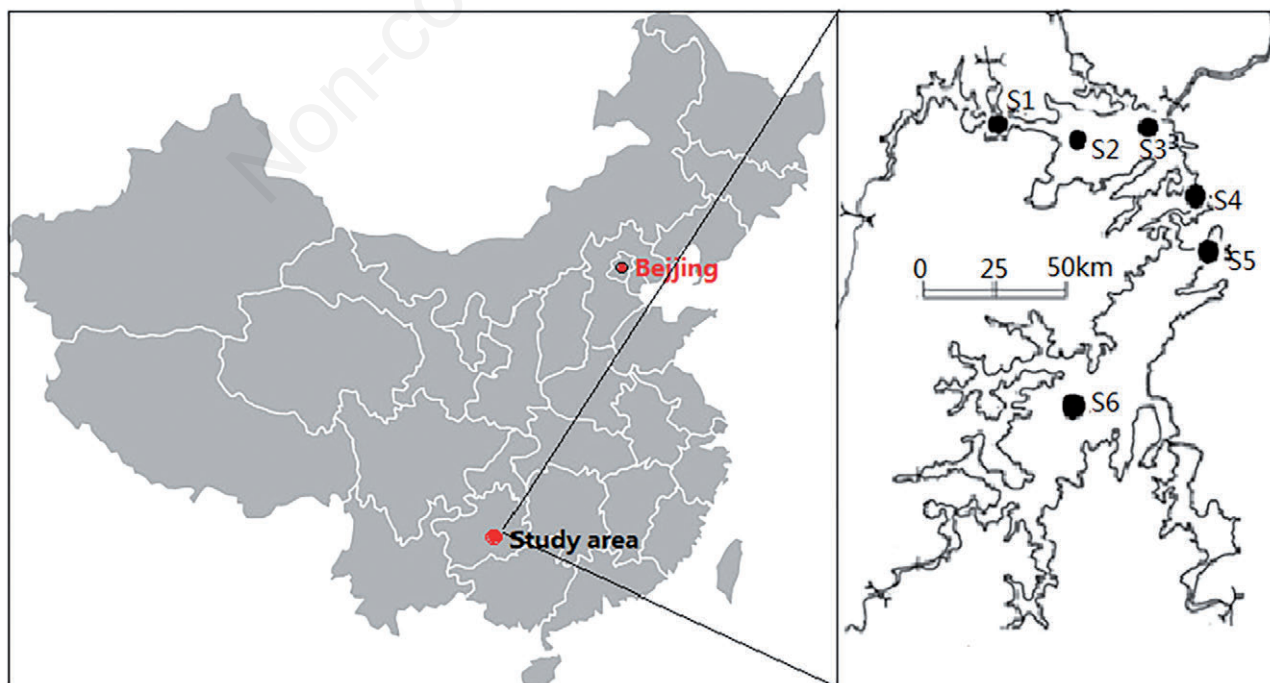


Fig. 1. Lake Hongfeng. Locations of the study sites in the reservoir, sites S1 to S6.

composition. In this study, a cyanobacteria bloom was defined as a dense blue-green colored surface layer with chlorophyll-*a* concentrations in excess of $10 \mu\text{g L}^{-1}$, or with cell densities that exceed $1.510^7 \text{ cells L}^{-1}$ (Australian and New Zealand Environment and conservation council, Canberra, 1992). Air temperatures around Guiyang have shown no significant annual differences from 1961-2011, with winter temperatures $13.9\text{-}16.5^\circ\text{C}$, and a mean of 22.5°C in the summer (Guiyang City, June-August, $25\text{-}30^\circ\text{C}$) (Li *et al.*, 2013). Water levels in the reservoir from 1961-1979 were on average 1237.3 units and during the study period from 2008-2010, 1237.2 units ($\text{SD}\pm 1.8$).

Sampling sites from 2005-2014 were along six transects ($n=12$) perpendicular to the longitudinal axis of the lake [S1 ($26^\circ33'18''\text{N}$, $106^\circ21'20''\text{E}$); S2 ($26^\circ32'49''\text{N}$, $106^\circ23'01''\text{E}$); S3 ($26^\circ32'47''\text{N}$, $106^\circ25'34''\text{E}$); S4 ($26^\circ31'38''\text{N}$, $106^\circ26'03''\text{E}$); S5 ($26^\circ30'50''\text{N}$, $106^\circ26'20''\text{E}$); S6 ($26^\circ29'09''\text{N}$, $106^\circ25'17''\text{E}$)] (Fig. 1).

Samples preparation and analysis

Sampling for phytoplankton and water quality was once every week from August 2008 to December 2009 (Tab. 1). In other years (2010 - 2014) phytoplankton samples were collected once every season (Tab. 1). Phytoplankton sampling included two parts. First, samples for qualitative species analysis were collected as follows: a phytoplankton net ($64 \mu\text{m}$ mesh) was submerged to 50 cm under the water surface in “∞” formation. The net was lifted slowly from the water vertically to limit backwash.

The samples were then fixed using methanol: glycerin:distilled water=1:1:8. Phytoplankton were identified according to the alga-flora of Hu *et al.* (1980). Part two, 1 L bottles of phytoplankton were collected from the water surface (0.5 m), mid-depth (8 m) and bottom (16 m) to determine community composition, abundance and biomass. Phytoplankton samples were preserved with Lugol's iodine solution, then isolated through sedimentation for 48h and concentrated to a final volume of 30 mL. The density of individual cells for each taxon was measured with a Sedgwick-Rafter counting chamber under magnifications of $200\text{-}400\times$. Total algal biovolumes for each species were calculated from cell numbers and cell size measurements. Biomass was calculated from species shapes converted to biovolumes (Hillebrand *et al.*, 1999). The final conversion to biomass assumed that 1 mm^3 of volume was equivalent to 1 mg of fresh weight biomass (Papista *et al.*, 2002).

Physico-chemical parameters, including water temperature (WT), dissolved oxygen (DO), and pH were measured in situ with a Yellow Springs Instruments (YSI) 6600 multi-sensor sonde (Yellow Springs Inc, Yellow Springs, OH, USA). Light intensity was measured using a ZDS-10W underwater light meter (lux) and converted to photosynthetic photon density using the following formula: $1000 \text{ lux} \approx 19.53 \mu\text{mol m}^{-2} \text{ s}^{-1}$. In the lab, TN, TP and $\text{NH}_3\text{-N}$ were quantified using the alkaline potassium persulfate oxidation method (Ma *et al.*, 2014). Chlorophyll-*a* (chl-*a*) was analyzed by spectrophotometry after extraction in 90% acetone (Ma *et al.*, 2014).

Tab. 1. Sample dates for this study from 2007 to 2014.

Sample	Date	Sample	Date	Sample	Date	Sample	Date
SA1-5	Aug.-Dec. 2007	SA6-11	Feb.-Jul. 2008	SA13-22	Mar.-Dec. 2010	SA23, SA24, SA25,	Jan. 2013 Apr. 2013 Jan. 2014
S 0	29/07/2008	S 15	15/11/2008	S 30	17/05/2009	SA26,	Aug. 2014
S 1	05/08/2008	S 16	29/11/2008	S 31	24/05/2009	S 45	30/08/2009
S 2	12/08/2008	S 17	13/12/2008	S 32	30/05/2009	S 46	05/10/2009
S 3	19/08/2008	S 18	27/12/2009	S 33	07/06/2009	S 47	11/12/2009
S 4	26/08/2008	S 19	09/01/2009	S 34	14/06/2009	S 48	03/01/2010
S 5	02/09/2009	S20	11/02/2009	S 35	21/06/2009	S 49	05/01/2011
S 6	06/09/2009	S 21	28/02/2009	S 36	28/06/2009	S 50	07/04/2011
S 7	13/09/2009	S 22	14/03/2009	S 37	05/07/2009	S 51	06/07/2011
S 8	20/09/2008	S 23	22/03/2009	S 38	12/07/2009	S 52	15/12/2011
S 9	29/09/2008	S 24	26/03/2009	S39	17/07/2009	S 53	09/01/2012
S 10	04/10/2008	S 25	04/04/2009	S 40	26/07/2009	S 54	10/04/2012
S 11	11/10/2008	S 26	19/04/2009	S 41	03/08/2009	S 55	08/07/2012
S 12	18/10/2008	S 27	25/04/2009	S 42	10/08/2009	S 56	15/07/2013
S 13	25/10/2008	S 28	05/05/2009	S 43	18/08/2009	S 57	15/11/2013
S 14	01/11/2008	S 29	10/05/2009	S 44	25/08/2009	S58	05/04/2014

Additional data from 1980-2004 was also examined using previous research (Chen *et al.*, 1998; Chen *et al.*, 2008; Li, 2001; Liang *et al.*, 1998; Liang *et al.*, 1999; Liao *et al.*, 2004; Long *et al.*, 2013; Pang and Pang, 2007; Shen *et al.*, 2006; Shi and Wu, 1982; Wu *et al.*, 2004; Zhou *et al.*, 1987).

Statistical analysis

Statistical analyses were conducted using the software SPSS 18.0 (PASW), Origin 8.0, and Canoco for windows 4.5. Phytoplankton biomass, Chl-*a* along with physical and chemical parameters (TN, TP, NH₃-H, pH and water temperature) were averaged (n=12) for sites and depths (S1-S6) on each sampling date. SPSS 18.0 was used to analyze environment and species associations using P values before Canonical Correspondence Analysis (CCA). CCA analysis examined relationships between species and environmental factors. Canoco for windows 4.5 was used for principal component analysis (PCA) and detrended correspondence analysis (DCA). Principal component analysis was performed to detect major gradients among the environmental variables (Ter Braak and Prentice, 1988) as well as to detect outliers (Birks *et al.*, 1990). Detrended correspondence analysis with detrending by segments and down-weighting of rare taxa was performed to examine patterns in the data, and to determine the maximum amount of variation within the species composition data. The gradient length of the main

DCA ordination axes (2.0-4.0) determined that CCA unimodal models would be applied (Ter Braak and Prentice, 1988).

RESULTS

Environmental conditions 1980-2015

Total nitrogen and TP concentrations were vastly different from 1980 to 2015 ($P < 0.0001$). In 1980, TN concentrations were approx. 1.0 mg L^{-1} (Fig. 2b) while TP concentrations were $< 0.02 \text{ mg L}^{-1}$ (Fig. 2c). Prior to 1994, cyanobacterial blooms were not reported. In 1994, large-scale fish cages for aquaculture were deployed in Hongfeng Lake reservoir. The use of feedstock with high P and N (4.5% and 7%, respectively, Zhong *et al.*, 2004) increased nutrient loads in the reservoir. At the peak of additions, TP levels were 0.14 mg L^{-1} and TN reached 4.9 mg L^{-1} . Seasonal cyanobacterial blooms consistently occurred from 1994 - 2009 and were associated with elevated TP and TN (Fig. 2, Tab. 1). In order to better understand annual bloom dynamics in Hongfeng Lake reservoir, water quality measurements were collected biweekly (total 59 sample dates) from August 2007 to December 2009. Cyanobacterial blooms occurred when mean surface and mid-water concentrations of TN were 1.15 mg L^{-1} or greater and TP concentrations were 0.054 mg L^{-1} or greater (Figs. 3-6). The bottom waters during periods of cyanobacterial blooms had a mean TN concentration of 1.32 mg L^{-1} and mean TP concentration of 0.079 mg L^{-1} (Fig. 7). Chlorophyll-*a* concentrations ($> 10 \mu\text{g L}^{-1}$) during bloom periods in surface waters were significantly higher than concentrations in mid- and bottom waters (Figs. 5a, 6a, 7a). After 2009, *Microcystis* and *Aphanizomenon* blooms declined, with significant reductions in TP (mean 0.033 mg L^{-1} surface waters, 0.028 mg L^{-1} mid-depths and 0.036 mg L^{-1} in bottom waters) (Figs. 5c, 6b, 7b). In contrast mean TN levels increased slightly (mean 1.59 mg L^{-1} in surface waters, 1.57 mg L^{-1} in mid-depth, and 1.50 mg L^{-1} in bottom waters) (Figs. 5b, 6b, 7b). The nitrogen-phosphorus (N:P) ratio ranged from 4-114 with a mean of 40 between 1980-2014; there was no significant relationship between cyanobacterial bloom and TN:TP ratio (Figs. 2a, 3a).

Water temperatures were important for phytoplankton growth (Fig. 8a). Annually, temperatures in Hongfeng Lake reservoir ranged from Summer $>$ Autumn $>$ Spring $>$ Winter. *Microcystis* biomass increased with increasing water temperatures and to a lesser extent increasing TP and NH₃-N (Fig. 9). Chlorophyll-*a* concentrations exceeded $10 \mu\text{g L}^{-1}$ when surface water temperatures were $> 11^\circ\text{C}$ (exceptions Jan. 2012 and Apr. 2014) (Fig. 5a). In general, chlorophyll-*a* concentrations increased when water temperatures increased ($R^2 = 0.3$, $P < 0.0001$, $n = 58$) (Fig. 8a). Chlorophyll-*a* exceeded $20 \mu\text{g L}^{-1}$ when temperatures were

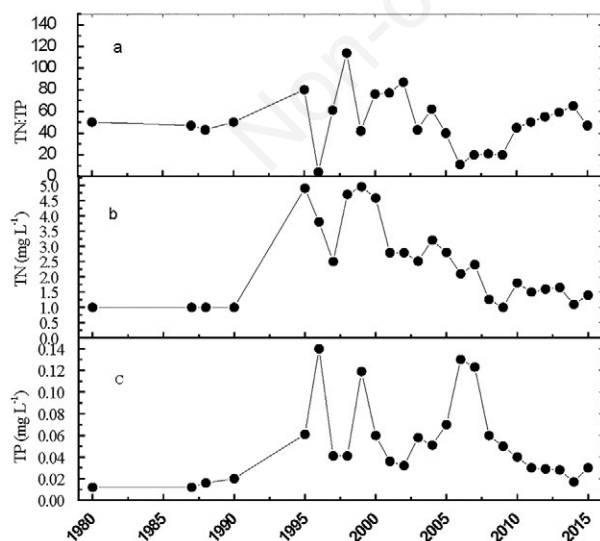


Fig. 2. TP, TN and TN:TP (mean of all sample sites) in Lake Hongfeng reservoir, China from 1980-2015. Additional data obtained from Zhou *et al.* (1987), Chen *et al.* (1998), Liang *et al.* (1998), Liang *et al.* (1999), Li (2001), Liao *et al.* (2004), Wu *et al.* (2004), Shen *et al.* (2006), Long *et al.* (2013).

above 17°C. There was also a significant relationship between Chlorophyll-*a* concentration and higher water temperatures in mid- and bottom waters (Figs. 6a, 7a).

Hongfeng Lake reservoir was alkaline with mean pH values of 8.4, 8.3 and 8.0 in surface, mid-depths and bottom waters respectively (Figs. 5a, 6a, 7a). In surface waters, pH values increased when chlorophyll-*a* increased ($R^2=0.23$, $P<0.0001$, $n=58$) (Fig. 8d). No significant pH changes were associated with enhanced chlorophyll-*a* in mid- and bottom waters ($P>0.05$).

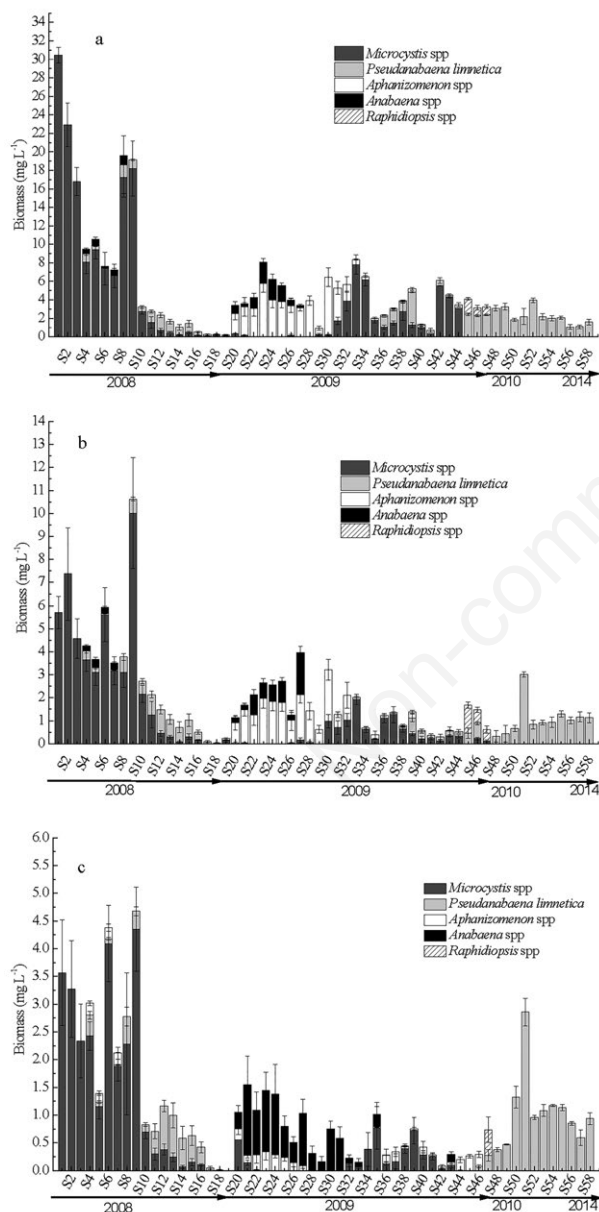


Fig. 3. Biomass of Cyanophyta (a surface, b middle, c bottom water) in Lake Hongfeng reservoir, China, 2008-2014. Each datum represents the mean of six sample sites with standard errors).

Dissolved oxygen levels in surface waters were consistently higher than mid-depth and bottom waters, with mean levels of 7.6, 7.1 and 5.1 mg L⁻¹ respectively. Since oxygen was present in bottom waters the reservoir was mixed (Figs. 5a, 6a, 7a). There was no DO correlation with total phytoplankton biomass throughout the water column. However, there was a DO correlation with the biomass of diatoms and *Pseudanabaena limnetica* (Lemmermann) Komárek (Fig. 9c).

NH₃-H concentrations in Hongfeng Lake reservoir

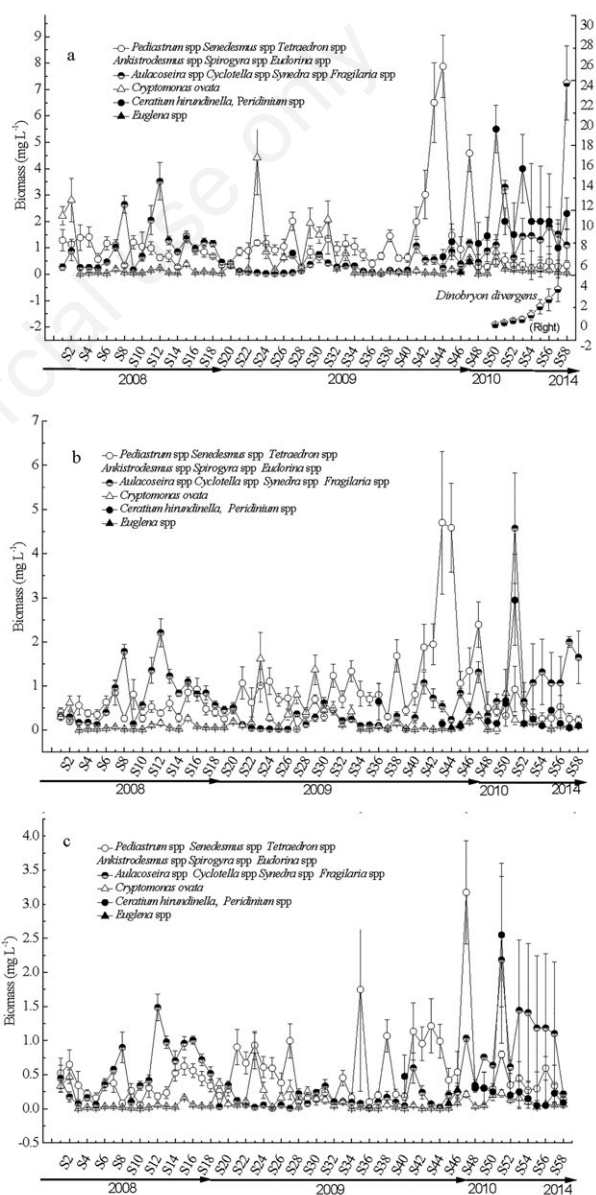


Fig. 4. Biomass of phytoplankton (a surface, b middle, c bottom water) in Lake Hongfeng reservoir, China, 2008-2014. Each datum represents the mean of six sample sites with standard errors).

limnetica, *Anabaena* spp (including *Dolichospermum* spp), *A. flos-aquae*, and *Raphidiopsis* spp.

In intensive monitoring (2008 - 2009), phytoplankton biomass fluctuated showing a seasonal occurrence of cyanobacterial blooms in Hongfeng Lake reservoir (Fig. 3). Cyanobacteria biomass during this period exceeded 2.0 mg L^{-1} at least 80% of the time. Total cyanobacteria biomass was correlated with total phytoplankton biomass ($R^2=0.3$, $P<0.05$, $n=58$) (Fig. 8b), and Chlorophyll-*a* ($R^2=0.3$, $P<0.0001$, $n=58$) (Fig. 8c). The biomass of *Microcystis* spp contributed 57-100% to the total cyanobacterial biomass from July 2008 to January 2009, and May to August 2009. *Aphanizomenon flos-aquae* and *Anabaena* spp were prominent from February to April 2009. *Pseudanabaena limnetica* appeared in June 2009, and was the dominant species after January 2010 (Fig. 3a). At this time, phytoplankton biomass in mid-depth and bottom waters were significantly lower than in surface waters (Fig. 3b, c). Chlorophyll-*a* concentrations were not correlated with the biomass of *P. limnetica* ($P>0.05$), even when densities were high.

Chlorophyta were represented by *Scenedesmus* spp, *Tetraedron* spp, *Pediastrum* spp, *Ankistrodesmus* spp, *Spirogyra* spp and *Staurastrum* spp. Chlorophytes contributed from 1.5-66% of the total biomass from 2008 to 2014, with an average of 18%. Chlorophyte biomass had a positive association with TN concentrations in mid-depth and bottom waters (Fig. 9 b,c). Diatom populations, were mainly composed of *Aulacoseira* spp, *Synedra* spp

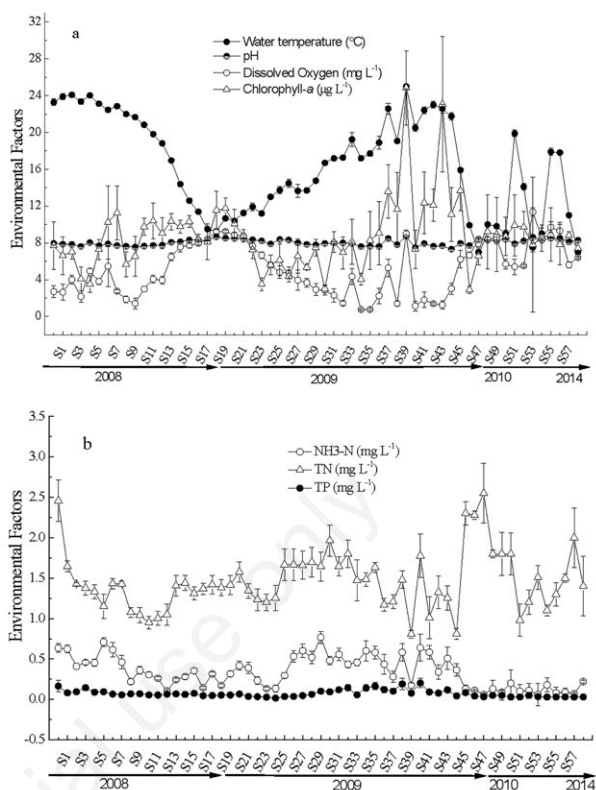


Fig. 7. Environmental Factors (a: water temperature, pH, dissolved oxygen and chlorophyll-*a*; b: $\text{NH}_3\text{-N}$, TN, TP) for the bottom waters in Lake Hongfeng reservoir, 2008-2014. Each datum represents the mean of six sample sites with standard errors.

Tab. 2. Phytoplankton densities (L^{-1}) in Lake Hongfeng reservoir from 1980 to 2007.

Sampling	Phytoplankton counts (with references)					
May to Oct. 1980	Total phytoplankton density $<2.1 \times 10^6$ (Shi and Wu, 1982).					
April 1987	Total phytoplankton density $<10^7 \text{ L}^{-1}$ (Zhong and Shi, 1992)					
July 1990	Total phytoplankton density $<10^7 \text{ L}^{-1}$ (Zhong and Shi, 1992)					
Sept. to Oct. 1994	Cyanobacteria blooms across lake; large number of fish killed (Pang and Pang, 2007)					
Spring of 1995	Total phytoplankton density $1.0793 \times 10^8 \text{ L}^{-1}$ (Chen <i>et al.</i> , 1998)					
Summer of 1995	Total phytoplankton density $5.8254 \times 10^8 \text{ L}^{-1}$ (Chen <i>et al.</i> , 1998)					
September 1996	22.97 mg m^{-3} (Pang and Pang, 2007)					
Spring of 1997	<i>Aphanizomenon flos-aquae</i> bloom. Average $9.332 \times 10^7 \text{ L}^{-1}$ (Chen <i>et al.</i> , 2008)					
March to April 1998	Slurry of <i>A. flos-aquae</i> concentrated at 0.5 m near surface (Pang and Pang, 2007)					
June 20 th 1999	<i>Microcystis</i> bloom (Pang and Pang, 2007)					
2000	No reported the occurrence of algal bloom					
2001 to 2004	Mean density 2.63×10^6 (Cyanobacteria bloom in local area) (Pang and Pang, 2007)					
Sampling	Cyanophyta	Chlorophyta	Diatoms	Pyrrhophyta	Cryptophyta	Chrysophyta
April 2005	7.2×10^6	2.15×10^6	0.65×10^6	0.016×10^6	0.79×10^6	-
August 2005	124.51×10^6	7.77×10^6	0.562×10^6	-	0.74×10^6	-
March 2006	29.69×10^6	7.13×10^6	1.49×10^6	0.011×10^6	0.15×10^6	-
August 2006	54.1×10^6	4.37×10^6	0.43×10^6	-	0.57×10^6	-
July 2007	149.6×10^6	4.84×10^6	0.858×10^6	0.044×10^6	0.506×10^6	-

-, not detected.

(*sensu lato*), *Cyclotella* spp (*sensu lato*), and *Fragilaria* spp (*sensu lato*). Diatoms contributed on average 17% to the total biomass from 2008-2014. Biomass of cryptophytes (mainly *C. erosa*) represented an average 5.8% of the total biomass from 2008 - 2014; there was a positive association between pH and biomass of cryptophytes in mid-depth waters (Fig. 9a). Pyrrophyta biomass (predominantly *Peridiniopsis* spp and *C. hirundinella*) increased between 2010-2014 mainly because of minor increases in cell numbers and large cell biovolumes. Chrysophytes were rare in 2008-2013. *Dinobryon divergens* increased in 2014, and became the most prominent taxon; its biomass reaching 24.3 mg L⁻¹ (Fig. 4a, right y-axis scale).

Biomass levels of *Scenedesmus* spp, *Tetraedron* spp, *Pediastrum* spp, *Ankistrodesmus* spp, *Spirogyra* spp, *Staurastrum* spp, *Aulacoseira* spp, *Synedra* spp, *Cyclotella* spp, *Fragilaria* spp, *Pseudanabaena limnetica*, *C. erosa sensu lato*, *Peridiniopsis* spp, *C. hirundinella* and *D. divergens* in mid-depth and bottom waters were

equivalent in proportions, but lower than surface waters. (Fig. 4 b,c).

Light intensity and *P. limnetica* distribution

The vertical distribution of *P. limnetica* and light were examined over two independent days, 8th July 2012 and 8th September 2012. In combination, light, temperature and nutrients showed that Zeu/Zmix was <1.0 which highlights the importance of light and temperature for phytoplankton growth (except to *P. limnetica*) (Figs. 4, 5, 6, 10). Light levels from 0.5-12 m depths varied greatly, ranging from 0 to 265.6 μmol m⁻²s⁻¹ over the two study dates (Fig. 10). The highest maximum illumination was at mid-day (Fig. 10 a,b). In July, light penetration extended down to 3.5 m, whereas in September light penetration was down to 4 m. At 6 m depth, light was low at all times representing <1.3 μmol m⁻²s⁻¹. At 12 m light availability was less than 0.1% (0.02 μmol m⁻² s⁻¹) of ambient surface levels. Stratified sampling for *P.*

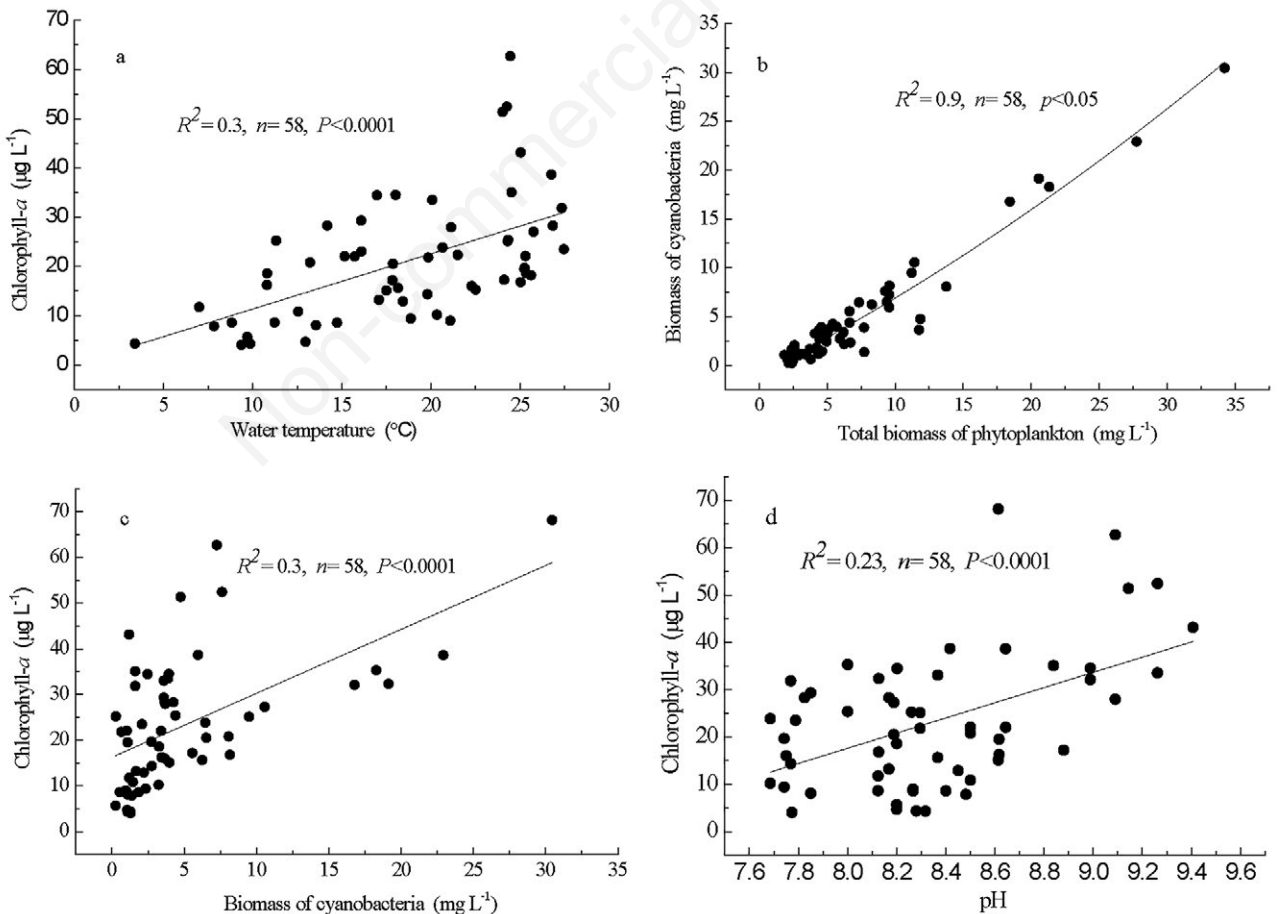


Fig. 8. Correlations between chlorophyll-*a* and water temperature (a), biomass of cyanobacteria and phytoplankton (b), chlorophyll-*a* and cyanobacteria (c), chlorophyll and pH (d).

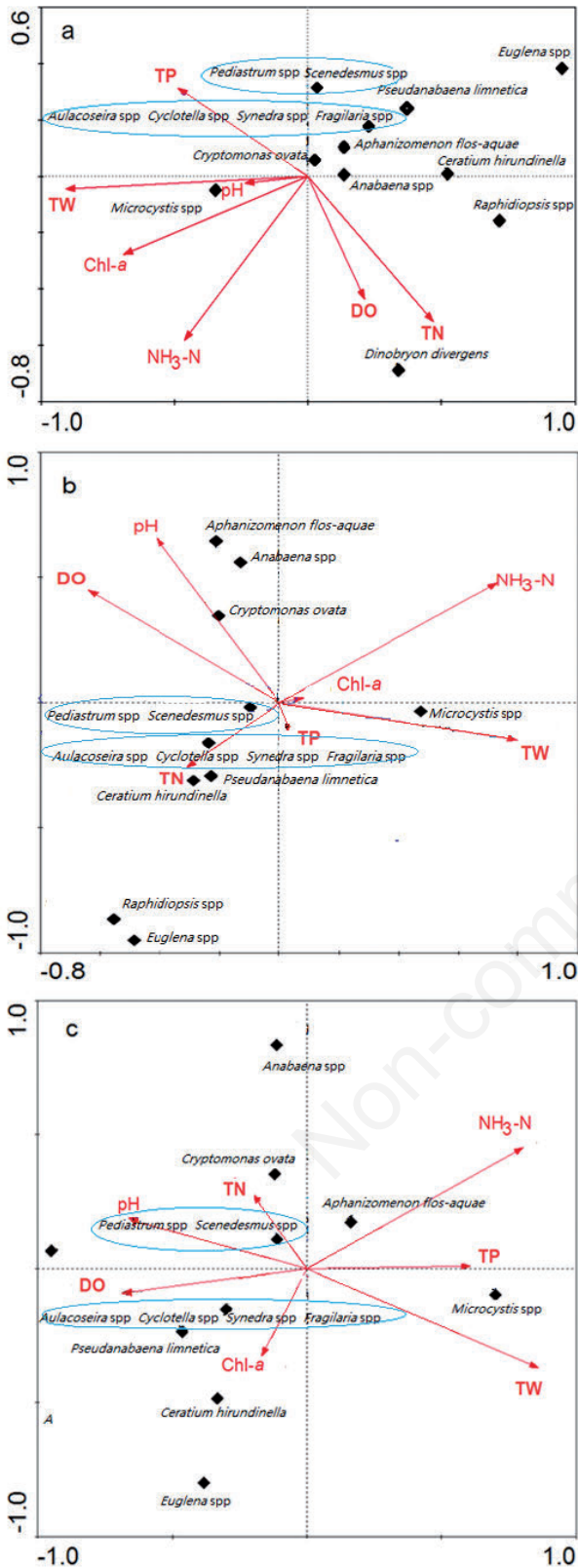


Fig. 9. CCA biplot representation of the impact of environmental factors and biomass on species from 2008 to 2014 using detrended canonical correspondence analysis (a: surface, b: middle, c: bottom).

limnetica was conducted from 7:00-19:00 hrs on July 8th and Sept. 8th 2012. Throughout the day, *P. limnetica* numbers were consistent throughout the water column with densities >10⁷ L⁻¹ (Fig. 11). Vertical distributions of *P. limnetica* did not differ significantly from 0.5-10 m depths. Below 11 m, which also coincides with light extinction, a significant decline in filament density was observed.

DISCUSSION

Changes in the phytoplankton community were studied to document cHABs and the recovery of Hongfeng Lake reservoir, after the introduction of fish farming and reservoir eutrophication. Nine years after the termination of fish farming there was a shift in community structure away from cHABs to a more diverse algal community dominated by *P. limnetica*. *Pseudanabaena* spp do not dramatically affect water quality (Acinas *et al.*, 2009), although the production of microcystin was

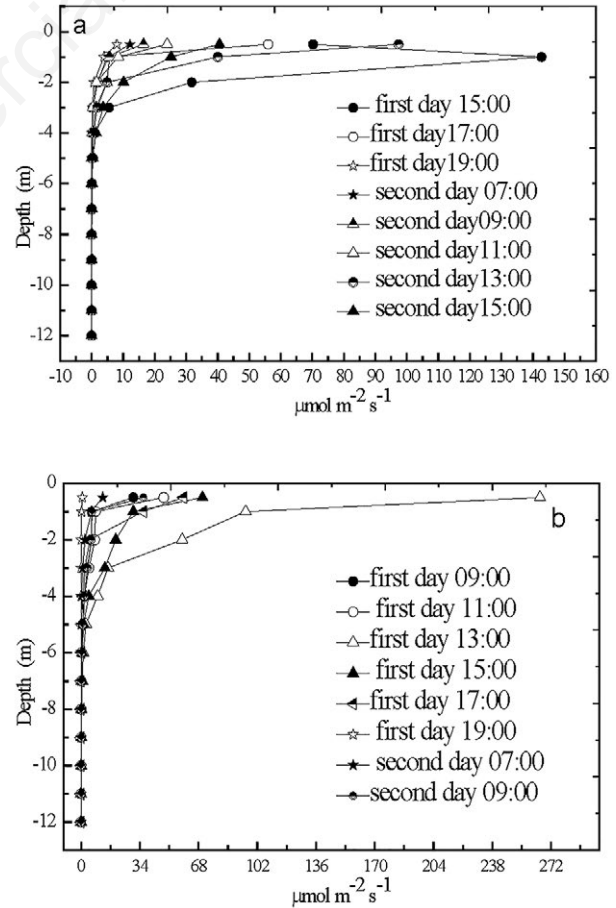


Fig. 10. Depth-time distribution of light at Site 6 in Lake Hongfeng in July (a) and September (b) 2012.

reported at least once in natural populations (Maršálek *et al.*, 2003). This community shift illustrates that when excess nutrients are eliminated from lake systems, natural species competition under varied environmental factors will favor a more diverse and healthier ecosystem.

Hongfeng Lake reservoir is an important water source for the City of Guiyang. Since 1996, this reservoir has been protected from excessive anthropogenic activities, although some industrial development and signs of disturbance impacts are evident. After 2008, there were 28 species of fish in Hongfeng Lake reservoir belonging to 4 orders and 6 families (Mou *et al.*, 2012). One of the species (*C. carpio*), was cultured by in framing cages, and indirectly had a significant effect (nitrification) on the reservoir during fish farming (Long *et al.*, 2013). Prior to 1994 (before fish farming), there was no evident top-down impact by the fish community on water quality (Shi, 1982). Since 2008 (after fish farming), the fish community has maintained populations around 51.6×10^{-3} (SD ± 36.5) ind m^{-3} (Mou *et al.*, 2012) and there was no

significant difference in the fish communities of 1981 and 2010 with the main species represented by *C. carpio* (He *et al.*, 2010). At present, the fish standing stock is not high enough to have a significant top-down effect on the phytoplankton of a eutrophic/mesotrophic system.

Cyanobacteria blooms (cHABs) appeared during and after the fish farming from 1995 - 2007. The yearly blooms in 2008 - 2009 followed a dominant succession of species starting with *Microcystis* spp and *P. limnetica* (summer) followed by *A. flos-aquae* (winter/spring). Cyanobacteria densities reached $>10^8 L^{-1}$ for both *Microcystis* spp and *A. flos-aquae* which was significantly higher than total phytoplankton densities of $>10^6 L^{-1}$ observed prior to the blooms (1980-1994) (Chen *et al.*, 1998; Zhong and Shi, 1992). Biomass trends in 2008 - 2009 followed cell densities with *Microcystis* blooms in the summer (July-September) and *A. flos-aquae* blooms in February-April. High TN (mean $4.9 mg L^{-1}$) and TP (mean $0.07 mg L^{-1}$) concentrations during and after fish farming, attributed to undigested and wasted feedstock, were the primary factors for the cHABs after 1994 (Liang *et al.*, 1998; 1999; 2003). There was no significant relationship between TN:TP ratios and cyanobacterial blooms, although some importance in the combined effect of these nutrients could be seen for *Microcystis* spp. This has also been reported by other authors (Pick, 2016 and references within). With lower nutrient loads (TP $<0.04 mg L^{-1}$; TN $<1.8 mg L^{-1}$) after 2010, competitive species shifts to *P. limnetica* occurred along with other taxa from the diatom, chlorophyte, chrysophyte and cryptophyte communities. This shift was linked to a number of factors including light, temperature and nutrients.

Water temperature, light and pH

There is clearly a temporal discontinuity between different cyanobacteria species and cHABs. In this study water temperatures up to $28^\circ C$ were important for *Microcystis* spp growth. Other studies have also shown that water temperature had an impact on cHABs (Ma *et al.*, 2015). Nalewajko and Murphy (2001) noted that harmful cyanobacteria tolerate higher temperatures relative to other algae, while Okino (1973) commented that in several Japanese lakes *Microcystis* spp did not appear (germinate and develop) until the water temperature was $>20^\circ C$. Thomas and Walsby (1986) suggested that declining temperature might in some way be affecting the buoyancy of colonies, which could affect the growth rate of *Microcystis* spp. Further Kruger and Eloff (1978) found a sharp decline in the growth rate of *Microcystis* spp below $15^\circ C$, while Robarts and Zohary (1987) reported that water temperature for the optimum growth of *Microcystis* spp was between $25-30.5^\circ C$. In this study, we found that the biomass of *Microcystis* spp was positively associated with water temperature up to $28^\circ C$

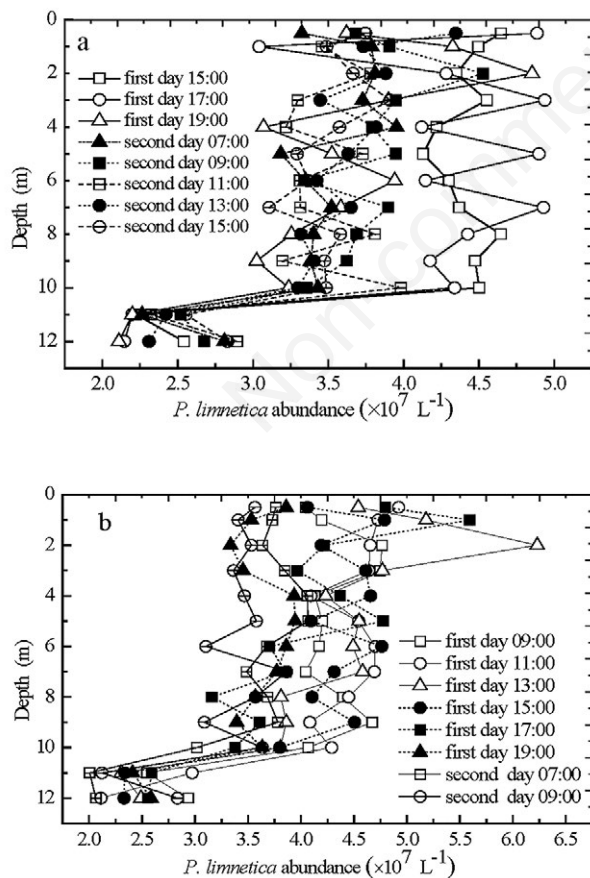


Fig. 11. Vertical profiles of *P. limnetica* in Lake Hongfeng Site 6 in July (a) and September (b) 2012.

(Fig. 9). When the surface water temperature of Hongfeng Lake reservoir was $>20^{\circ}\text{C}$ the biomass of *Microcystis* spp was $>3.0\text{ mg L}^{-1}$, and Chlorophyll-*a* exceeded 20 g L^{-1} , which shows the significant of surface water temperature on growth, when nutrient conditions are optimized. In contrast, the biomass of *A. flos-aquae* was optimized with water temperatures $<20^{\circ}\text{C}$. Other studies suggest that persistent blooms of *A. flos-aquae* and *Anabaena* spp can occur between $15\text{--}20^{\circ}\text{C}$, while *Microcystis* spp cannot grow well at water temperatures $<15^{\circ}\text{C}$ (Robarts and Zohary, 1987). Water temperature was a controlling factor in the succession of *A. flos-aquae* and *Microcystis* spp blooms in Lake Hongfeng during the spring and summer season of 2008-2009 (Fig. 8).

Light is a limiting factor ($Z_{eu}/Z_{mix} < 10.0$) in Hongfeng lake reservoir. Phytoplankton biomass in Hongfeng lake reservoir decreases with declining light levels and water depth. However, after 2010, in day experiments the vertical distribution of *P. limnetica* was not significantly difference from 0.5-10 m, with consistent densities $>10^7\text{ L}^{-1}$ and biomass ($>0.198\text{ mg L}^{-1}$). In addition, the biomass of *P. limnetica* was also not significantly different in surface, and mid-depth waters from 2010 - 2014 with no correlation between light intensity and vertical distributions. *Pseudanabaena* spp have higher levels of phycocyanin which can absorb light for growth at deeper water depths (Acinas *et al.*, 2009). Light throughout the water column had little impact on the growth of *P. limnetica* and this in part explains the prominence of *P. limnetica* when optimal bloom conditions were not present for *Microcystis* spp and *A. flos-aquae*. *Pseudanabaena limnetica* had a competitive advantage with a wider tolerance of light changes when nutrients were lower.

Phytoplankton photosynthesis removes CO_2 from the aquatic environment which can result in a rise of pH (Qui and Gao, 2002). Several studies have reported higher pH conditions caused by cyanobacteria growth (Oliver and Ganf, 2000; O'Neil *et al.*, 2012; Qui and Gao, 2002). To support this, Laamanen *et al.* (2002) and Hu (2011) reported that *A. flos-aquae* and *Microcystis* spp bloom were significantly correlated with high pH 9-11. The present study found higher pH values in surface waters were positively correlated with higher productivity (biomass and chlorophyll-*a*), although the relationship was not linear (Fig. 8d). This was evident with cyanobacteria blooms of *Microcystis* spp in July 2008-2009, growing at pH >8.5 . However, there was no correlation between pH and biomass of cyanobacteria in mid-depth and bottom waters suggesting that cyanobacterial blooms in the surface waters of the reservoir were not affecting pH levels in lower waters of the reservoir. Other algae, specifically chlorophytes and cryptophytes were not linked to pH.

Nutrients impacts on phytoplankton biomass

Relationships of cyanobacteria growth with nitrogen and phosphorus are still a hotspot of uncertainty in the scientific literature (Anderson *et al.*, 2002; Pick, 2016), because N and P are essential elements for phytoplankton growth (Conley *et al.*, 2009). Some studies have shown TP concentration below 0.01 mg L^{-1} , will limit the size of phytoplankton to $<35\text{--}50\text{ }\mu\text{m}$, while TP concentrations $>0.05\text{ mg L}^{-1}$, will encourage the dominance of larger phytoplankton species (Watson *et al.*, 1992). In our study, TP concentrations averaged 0.055 mg L^{-1} from 2007-2009, with large taxa becoming smaller after 2009 under lower TP concentrations. TN was also significantly reduced after 2010 and correlated well with the community shift.

Under fish farming, the dominant phytoplankton were colonial *Microcystis* spp, *A. flos-aquae* and *Anabaena* spp. After 2009, when TP levels were significantly lower ($<0.04\text{ mg L}^{-1}$), phytoplankton species with smaller filament sizes and biovolumes (like *P. limnetica*) dominated. Likewise, diatoms with smaller sizes and biovolumes were prominent species from January 2010-2014. In this study, CCA results support the observation that eutrophication processes favored larger cyanobacteria taxa. Under lower nutrient conditions, small taxa with lower nutrient requirements and taxa with broader niches (population reserves) were better able to compete. Higher densities and biomass of *P. limnetica*, and diatoms in Hongfeng Lake reservoir further sequestered TP from the soluble phosphorus fraction, which reduced the availability of soluble P for the reintroduction and bloom formation of larger taxa. Xu *et al.* (2010) also reported that *Microcystis* spp blooms were limited by lower phosphorus concentration in Lake Taihu. We also found that a lower TP concentration (0.02 mg L^{-1}) in Apr. 2014, enhanced the growth and biomass of *Dinobryon divergens* (24.3 mg L^{-1}). The development of competitive succession over the last seven years from cyanobacterial blooms to mixed cyanobacteria with diatoms and chrysophytes (*D. divergens*) suggests that recovery to pre-fisheries water quality is developing. However, a steady state is not present and the very recent re-occurrence of *Microcystis* spp (0.011 mg L^{-1}) in higher numbers illustrates the biological instability of the reservoir. Inorganic nitrogen was another key factor for phytoplankton development. Previous studies suggest that moderate levels ($0.3\text{--}0.8\text{ mg L}^{-1}$) of inorganic nitrogen are required for the growth and reproduction of *Microcystis* spp (Ma *et al.*, 2015). In this study $\text{NH}_3\text{-N}$ was positively associated with *Microcystis* growth throughout the water column.

The reduced periodicity of TN may have been the factor that triggered the transform of phytoplankton composition during June to September 2009 (Fig. 5a). In

contrast, the increase in TN after 2009 with seasonal fluctuations may have induced the growth of *P. limnetica* (a poor nitrogen fixer). In the later scenario, higher TN (1.0–2.3 mg L⁻¹) and low TP conditions (ca. 0.03 mg L⁻¹) will in part determine the phytoplankton community structure after cHAB events.

Other studies have attributed different factors to the collapse of cHABs. *A. flos-aquae* blooms were affected by photo-oxidation, O₂ toxicity, and viruses (Coulombe and Robinson, 2011). In this study, nutrients, light, temperature, and other algae were studied. It could be that other parameters not studied could have more of an effect on biological process and biota. Viruses and O₂ toxicity are interesting factors but to date they have not been routinely observed in cHAB cultures and/or culture experiments. In the future, eDNA studies might help resolve the potential impacts of other less obvious biological factors. Enhanced nutrients induced the development of cHABs in Hongfeng lake reservoir. Once introduced, other factors (e.g., light, temperature) played a role after nutrient reductions, in the alterations of blooms through species community shifts under changing optimum conditions.

Global implications

Anthropogenic and natural trophic factors are important in the stability of the pelagic community. It is well documented that anthropogenic impacts from reservoir development cause cHABs (Pick and references within, 2016). Higher temperatures, nutrients (TN, TP) and reasonable light will favor the development of cHABs like *Microcystis* spp. With the control of nutrient loads a community shift away from cHABs can occur. In this study a decline in nutrients, with a drop in TP relative to TN, favored a shift from *Microcystis* summer blooms to *P. limnetica* and other algae like *Aulacoseira* spp, *Synedra* spp, *Cyctotella* spp (*sensu lato*) and *Fragilaria* spp (*sensu lato*). In Hongfeng reservoir *P. limnetica* can out-compete *Microcystis* spp when temperatures are <20°C and TP is <0.03 mg L⁻¹. Although only a selected number of environmental variables were examined, the CCA analysis over 7 years supports observations that temperature and nutrients were associated with the species shifts. Therefore, the replacement of cHABs with less toxic cyanobacteria creates a potentially interesting scenario (new community condition) for reservoir water quality management and the removal of harmful cyanobacteria. *Pseudanabaena limnetica* is a filamentous, nonheterocystous freshwater cyanobacterium (Alvensleben *et al.*, 2013) with only one tentative report of toxin production (Maršálek *et al.*, 2003). Thus, the new community condition with *P. limnetica* is less problematic compared to cHABs with *Microcystis* and *Aphanizomenon* blooms.

Planned increases in dam building around the world

over the next 50 years will have significant environmental consequences (Ansar *et al.*, 2014). Increased evaporation, sedimentation and nutrient loading in constructed reservoirs and impoundment lakes will change water quality and ecosystem stability across ecoregions (Maavara *et al.*, 2015). Further, many of the planned dams are located in regions which already have poor water quality or ecosystem resilience (Stone, 2011; Ziv *et al.*, 2012). The occurrences of cHABs, in reservoirs and impoundments, will increase into the next century with yet further unknown economic and environmental implications. In addition, the increased frequency of extreme events like droughts and flooding will also impact phytoplankton communities with potential temporal and spatial increases in cHABs. The management of harmful cyanobacterial will be an important component of our future water footprint.

CONCLUSIONS

Over the last 22 years significant phytoplankton changes in Hongfeng lake reservoir have been observed with multiple years of cHABs. Data collected over these years have helped unravel the transition of growth from a low productive lake/reservoir to one with repetitive bloom events. With the introduction of fish farming and other anthropogenic activities, the reservoir went into ultra-eutrophic primary production with repeated cHAB events. After the cessation of fish farming there has been a slow recovery of the reservoir in both algal productivity and nutrient loading. A conversion from problematic species (*Microcystis* spp, *A. flos-aquae*) to the less problematic species *P. limnetica* and other associated non-cyanobacteria taxa (e.g., *D. divergens*) was observed after 2010. *Pseudanabaena limnetica* is potential a nuisance taxon but with a lower cHABs concern. Based on current fish populations estimates, a top-down impact on the food web is not evident. Thus, trophic factors (bottom-up) were examined, and correlations between cHABs and selected environmental variables were observed. The paradox of the plankton blooms can be explained by varying chemical factors, physical factors (light, and temperature) and species competitive succession. Higher temperatures, nutrients (TN, TP) and reasonable light favored the development of *Microcystis* spp blooms, which occurred after anthropogenic manipulations of the reservoir. *Microcystis* blooms under these conditions have been reported globally (Pick and references within, 2016). With the control of nutrient loads, a decline in TP relative to TN favored a shift from *Microcystis* summer blooms to the growth of *P. limnetica* with other algae like *Aulacoseira* spp, *Synedra* spp, *Cyctotella* spp (*sensu lato*) and *Fragilaria* spp (*sensu lato*). In Hongfeng reservoir *P. limnetica*, a light tolerant species, can out-compete *Microcystis* spp when

temperatures are $<20^{\circ}\text{C}$ and TP is $<0.03\text{ mg L}^{-1}$. The apparent competitive advantage of *P. limnetica* and other algae (e.g., *Aulacoseira* spp, *Synedra* spp, *Cyctotella* spp, *Fragilaria* spp) are enhanced by their distribution throughout the epilimnion. *Pseudanabaena limnetica* is a filamentous, nonheterocystous freshwater cyanobacterium which is not as problematic as *Microcystis* and *Aphanizomenon* species. In Hongfeng lake reservoir, the initial introduction of nauseous *Microcystis* and *Aphanizomenon* blooms was directly related to nutrient loading, while the continued reoccurrence of these species appears to be associated with cyst availability, temperature, growing season and biotic competition. Although only a selected number of environmental variables were examined, the CCA analysis over seven years supports observations that temperature, and nutrients were associated with biological competition and species shifts. The replacement of cHABs with the growth of less toxic cyanobacteria like *P. limnetica*, and other algae creates a potentially interesting scenario (new community condition) for the removal of problematic taxa.

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