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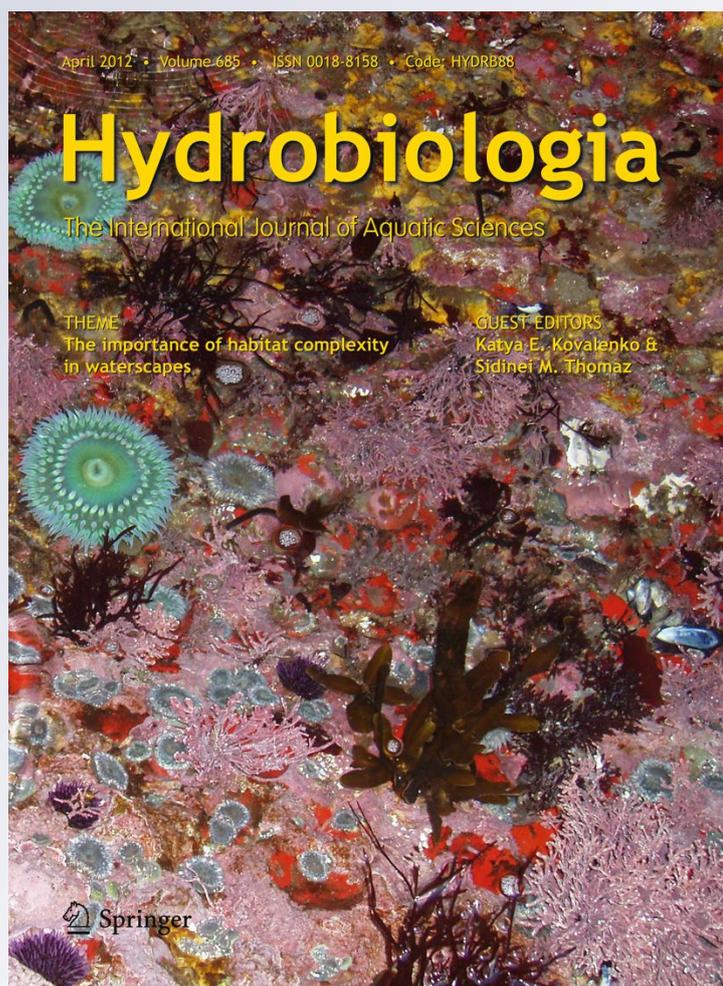
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Diatom response to the whole lake manipulation of a eutrophic urban impoundment

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Abstract Diatoms typically dominate during April and May in Ford Lake, a eutrophic urban impoundment in southeastern Michigan, USA, whereas cyanobacteria dominate during summer. To alter this, whole lake experiments were conducted during 2006 and 2008 in alternation with control years 2005 and 2007. In experimental years, water was withdrawn from the hypolimnion during summer to destabilize the stratified water column, promote deeper mixing, and reduce anoxia. In 2006, withdrawals occurred over a 6-week period with three discrete intervals, releasing $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ for the first and third intervals, and $1.5 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ for the second. In 2008, withdrawal occurred continuously for 6 weeks at a rate of $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$. In control years, water was released only from the epilimnion. Nuisance cyanobacteria replaced diatoms in control years when the lake became thermally stratified. Diatom response to experimentally induced mixing was examined with focus on 2008 as a model for future management. Selective withdrawal of hypolimnetic water destabilized the water column and promoted diatom summer blooms. Diatom success was greatest in 2008, with abundance reaching $10 \text{ mm}^3 \text{ L}^{-1}$ and persisting through spring and summer. Dominance

peaks of diatoms were punctuated when *Daphnia* populations approached or exceeded 3×10^5 individuals m^{-2} .

Keywords Community succession · Diatoms · Eutrophication · Hypolimnetic withdrawal · Nutrient limitation

Abbreviations

AOV	Analysis of variance
BV	Biovolume
DO	Dissolved oxygen
MANOVA	Multivariate analysis of variance
PC	Phycocyanin
SRP	Soluble reactive phosphorus
SRSi	Soluble reactive silicon

Introduction

River impoundments constructed for the purpose of generating hydroelectricity are common features of the industrialized North American upper Mid-West. Once constructed in urbanizing landscapes, they can become sites of intense recreational activity and accelerated lakeshore residential development. Cultural eutrophication of these basins detracts from their non-power-generating human uses, and so there is considerable interest in applying effective remedies to the offending ecological conditions in these constructed and managed ecosystems. One scientifically compelling feature

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of these environments is that the ecosystems are uniquely suited for testing ecological theory by direct whole lake manipulation. Depending on the individual situation, a number of potential master variables may be subject to manipulation including flushing rates and patterns, lake depth and depth variation, thermal stratification, and mixing patterns.

Ford Lake, southeast Michigan, USA, was impounded from the Huron River in 1932 by Henry Ford to generate hydroelectric power for the Ford Motor Company factory in Ypsilanti, Michigan. The turbines are designed to draw water from the top 5 m (Ferris & Lehman, 2007), and sluice gates are present at the base of the dam to manage high flow or flood conditions. The impoundment is operated as “run of the river,” ensuring that outflow matches inflow and that surface height does not change. The dam has powered various industries, including the Willow Run B-24 Liberator bomber plant during World War II, the largest factory in the world at that time, and still produces power commercially today. The Ypsilanti Wastewater Treatment Plant was in operation from 1935 to 1982 on the north shore of Ford Lake, and its discharge was significant to the ecological history of the lake (Donar et al., 1996). The land surrounding Ford Lake supports a variety of uses, including industry, agriculture, and residential areas (Donar et al., 1996), and the lake itself is used for recreation. Diatoms have been a permanent feature of Ford Lake since its construction in 1932, though their dominance fluctuates over years and seasons. Typically, diatoms achieve their maximum abundance in late April or early May and are dominated by *Asterionella formosa* Hassall (Ferris & Lehman, 2007).

Although the Ypsilanti Wastewater Treatment Plant was dismantled, the Ann Arbor Wastewater Treatment Plant, 9.5 km upstream of the lake, currently releases tertiary-treated effluent into the Huron River (Lehman et al., 2009a, b). Intense nuisance blooms of *Aphanizomenon flos-aquae* (Linnaeus) Ralfs ex Bornet & Flahault and *Microcystis aeruginosa* (Kützing) Kützing have consistently followed the spring diatom bloom, including toxic strains of *Microcystis* (Lehman et al., 2009a). Phosphorus from agricultural and urban runoff as well as wastewater discharge likely contribute to the success of cyanobacteria in Ford Lake, but internal P loading resulting from anoxia is a significant contributor during thermal stratification (Lehman, 2011). Hypolimnetic anoxia is a recurring feature of

the lake during summer. This in turn causes a change in oxidation state of the iron in the lake sediments and releases phosphate through the classic mechanism articulated by Mortimer (1941). The result is a supply of phosphorus into the lake water, or internal P loading, when iron is reduced to ferrous (FeII) form under anoxia (Boström & Pettersson, 1982; Nürnberg et al., 1986; Sommer et al., 1986; Lehman, 2011).

New river impoundments are often eutrophic because flooded soils release nutrients (Dokulil & Teubner, 2003; Straškraba, 2005). Ford Lake conformed to this pattern and was considered eutrophic from its start (Donar et al., 1996), sustaining both cyanobacteria and diatom species indicative of mesotrophic to eutrophic conditions (e.g., *A. formosa*, *Fragilaria crotonensis* Kitton, *Melosira varians* Ag and *Aulacoseira granulata* (Ehrenberg) Simonsen) (Van Dam et al., 1994; Blinn & Herbst, 2003; Potapova & Charles, 2007).

Whole lake experiments were conducted in the summers of 2006 and 2008 in an effort to alter the normal succession of the spring diatom bloom by summer cyanobacterial nuisance blooms. Water was discharged from the hypolimnion through the lower floodgates of the dam in order to destabilize the water column and allow deeper mixing. We predicted that this physical manipulation would alter the lake both chemically and biologically: (1) it would prevent anoxia in the hypolimnion, keeping P in an iron trap in the sediments thereby reducing internal P loading and, moreover, preventing denitrification and nitrate ammonification, thus slowing the loss of nitrate that typically preceded the rise of N-fixing cyanobacteria and (2) it would promote turbulence that would allow sinking diatom assemblages to be restored to the photic zone. Diatom growth could then sequester dissolved nutrients from the water, making them unavailable for a cyanobacterial succession.

It is well known that diatoms require physical mixing to minimize sedimentation losses. Reynolds et al. (1984) reported that *A. formosa* and *F. crotonensis* populations require at least 2 m of mixed layer depth for positive net growth. As *r*-selected species, diatoms grow quickly compared to other algal groups like dinoflagellates and cyanobacteria (Reynolds et al., 1984; Sommer et al., 1986), and so environments conducive to diatom growth can lead to considerable and rapid change in a lake. Artificial destratification and consequent deeper mixing of Ford Lake in 2006

resulted in a promising summer diatom bloom as compared to previous years (Ferris & Lehman, 2007). This study examined the diatom response to a whole lake manipulation performed in 2008 compared with three previous years. After calibration experiments in 2006, we believed that we understood how to transform the phytoplankton community at will and we tested this knowledge in 2008.

We proposed the following hypotheses:

- (1) Hypolimnetic discharge of $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ or 1.7% of lake volume daily is sufficient to destabilize the lake during summer and to prevent hypolimnetic anoxia and denitrification.
- (2) Diatom abundance increases in response to experimental manipulation as the water column destabilizes and nitrate persists.
- (3) Diatom success in the summer precludes the growth of the cyanobacteria otherwise characteristic of this period.
- (4) Diatom community dominants shift with differing grazing, nutrient, and mixing conditions.

Materials and methods

Study site

Ford Lake (42.221°N, 83.581°W) lies within the Huron River catchment in Washtenaw County of southeastern Michigan. The lake has a surface area of about 4 km², a mean depth of 4.3 m, and a maximum depth of 10.8 m (Lehman et al., 2007). Ford Lake is one of seven impoundments within this 2,300 km² watershed that is tributary to Lake Erie (Ferris & Lehman, 2007). Other limnological features of the lake are described by Lehman (2011).

Field sampling

From April to September of 2005–2008, water was collected weekly at three stations (denoted F1, F2, and F3; Fig. 1) located, respectively, near the western inlet (5 m depth), the center (7 m depth), and near the eastern outlet dam (10 m depth). In 2008, samples were collected through October. Temperature and dissolved oxygen (DO) were measured at meter intervals in situ using a Hach model HQ30 meter with LDO luminescent sensor. Water transparency was measured to

0.1 m resolution using a 20-cm diameter plain white Secchi disk. Raw water was filtered on site for nutrient analysis using Millipore™ disposable filter capsules of nominal 0.45 μm pore size. Water was collected from 2, 6, 8, and 10 m depth at F3 by submersible pump and was filtered without prior exposure to the atmosphere. Quantitative samples for phytoplankton counts, pigment analyses, and nutrients were collected from 0 to 5 m at each site using an integrative tube sampler. Phytoplankton samples were preserved with acid Lugol's iodine. Zooplankton were collected at station F3 while at anchor by vertical tows of a conical net with 30-cm mouth diameter, 1:5 aspect ratio, and 64-μm mesh aperture (Lehman et al., 2007). Quantitative subsamples were enumerated to the species level for Cladocera and to genus level for Copepoda.

Water chemistry and pigment analysis

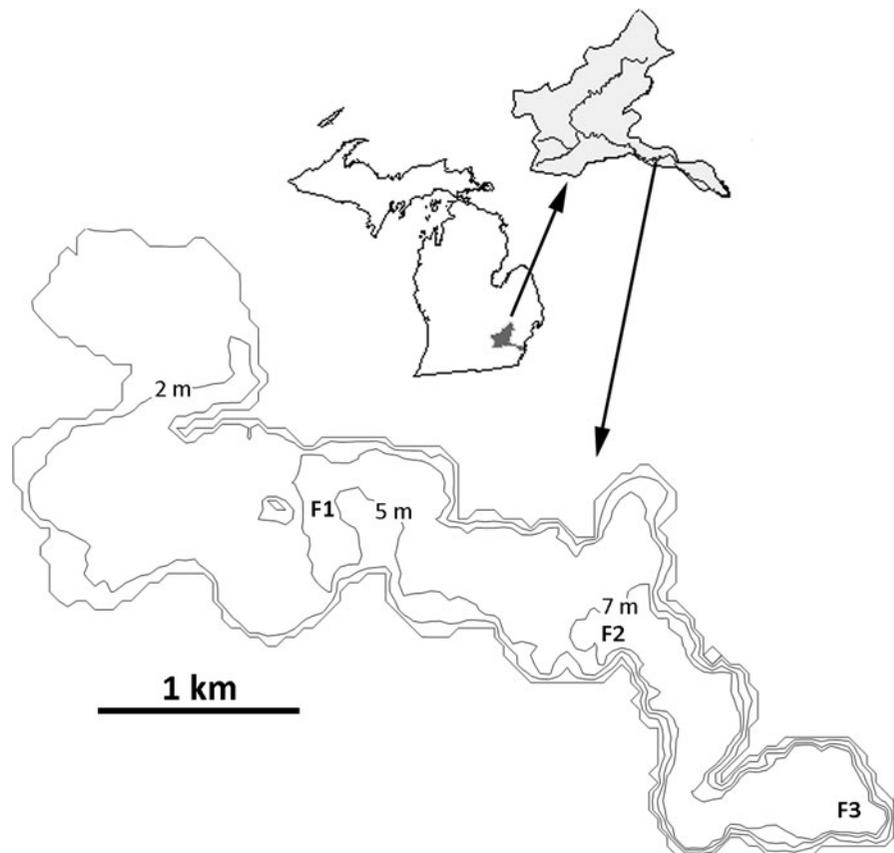
Filtrate samples were measured for nitrate and soluble reactive silicon (SRSi) (Lehman et al., 2009a, b) within 24 h of field collection. Chl *a* and phycocyanin (PC) were measured as extracted fluorescence (Lehman et al., 2009a) from particulates retained on Whatman™ GF/C filters.

Cell counts and measurements

Cell counts were typically conducted for the deepest sampling site, F3, where diatom diversity was greatest (Donar et al., 1996), supplemented rarely by counts from F2 when F3 samples were unavailable.

Lugol's preserved samples were placed by pipette into a 2.3-cm diameter cylindrical settling chamber 1.6 cm high. Samples were allowed to settle for at least 1 h before using an Olympus IMT-2 inverted light microscope to count diatoms. Sixty random fields were searched at 375× for each sample date. This procedure duplicated the counting methods employed by Ferris & Lehman (2007). Frustule dimensions were measured at 600×. Counts were converted to biovolume (BV) (mm³ L⁻¹) using geometric formulae for shapes most closely approximating each species (e.g., rectangular solids for *Asterionella*, *Diatoma*, *Fragilaria*, *Tabellaria*; cylinders for *Aulacoseira*, *Cyclotella*, *Stephanodiscus*). The number of cells measured in each sample was dependent on the abundance and size variation of each genus, with more measurements taken for the more abundant or

Fig. 1 Ford Lake sampling sites *F1*, *F2*, and *F3*



more size-variant genera. Only one cell measurement was taken from any given colony to ensure independent measurements.

Diatom cleaning and reference slide preparation

Identities of the dominant diatom taxa were verified by optical microscopy after preparing permanent mounts of cleaned frustules in high-refractive index media. A few drops of acid Lugol's preserved lake samples were placed by pipette onto glass cover slips and heated until all water had evaporated. Where lake samples contained few diatoms, samples were concentrated by allowing the diatoms to sink in a settling chamber for at least an hour. A few drops containing sedimented cells from the bottom of the settling chamber were then transferred to cover slips and heated to dryness. Cover slips were enclosed in borosilicate Petri dishes and were placed in a muffle furnace heated to 560°C for 20 min in order to incinerate organic matter (Zoto et al., 1973). Ashed cover slips were mounted to glass

microscope slides with synthetic resin diatom mountant ZraxTM dissolved in xylene as described by W.P. Dailey (personal communication). Mounted slides were heated at 100°C for 4–6 h to remove the xylene. Cleaned slide mounts were checked with taxonomic references (Patrick & Reimer, 1966) and communication with a diatom expert (N. Andresen, Ypsilanti Township) to verify species identification.

Statistical methods

All statistical analyses were performed using SPSS PASW Statistics 18 Release 18.0.3 (2 Sep 2010). Statistical tests were considered significant at $\alpha = 0.05$. To test for differences among the experimental years (2006, 2008) and the control years (2005, 2007), we applied multivariate analysis of variance (MANOVA) to a set of response variables including epilimnetic and hypolimnetic temperatures, hypolimnetic DO, transparency, epilimnetic pigments, algal BV, nitrate, and SRSi. We compared the 10 weeks each year from the end of

June to the end of August. The first date included each year coincided with the date preceding the first experiment in 2006 or 2008. We compared years only to the end of August because selective withdrawal experiments concluded in both years in August.

Water temperatures and Secchi depths were suitable for parametric analyses without transformation. The other variables exhibited lognormal skew and were subjected to logarithmic transformation before analyses. Variables that contained occasional values of zero (i.e., PC and cyanobacteria or diatom BV) were first transformed by addition of a constant approximately equal to the limits of detection: $0.1 \mu\text{g L}^{-1}$ for PC and $0.1 \text{mm}^3 \text{L}^{-1}$ for BV. If MANOVA detected significant interannual variation, Bonferroni-adjusted post-hoc contrasts were examined for all pairwise interannual comparisons.

Results

Hydrology, experimental destratification, and diatom abundance

Three selective withdrawal experiments were performed in 2006: 22–30 June, 14–21 July, and 26th July to 4th August. In the first experiment, $3 \times 10^5 \text{m}^3 \text{d}^{-1}$ were withdrawn from the hypolimnion. In the second experiment, $1.5 \times 10^5 \text{m}^3 \text{d}^{-1}$ were withdrawn, and in the third experiment, $3 \times 10^5 \text{m}^3 \text{d}^{-1}$ were again withdrawn. The larger withdrawal volumes were successful in destabilizing lake thermal stratification, and summer blooms of cyanobacteria did not develop in 2006 during the experimental period (Ferris & Lehman, 2007). The whole lake manipulation of 2008 involved continuous floodgate withdrawal of hypolimnetic water from 27th June to 6th August at the rate of $3 \times 10^5 \text{m}^3 \text{d}^{-1}$, with successively smaller volumes withdrawn each day until 13 August, which successfully destabilized the water column during that time. The duration of the 2008 experiment was limited by low levels of precipitation and runoff, which curtailed river flow below the amount sufficient for the experiment to continue past mid-August. *Aphanizomenon* bloomed in September of that year, much later than in control years, and only after our experiment was concluded. The experimental year 2008 was more successful at stimulating diatom production than had been experimental year 2006. Concentrations of DO at

6 m were significantly greater in 2006 and 2008 than in 2005 and 2007 during July and August (AOV, $P < 0.05$), indicating that vertical mixing was more effective in the experimental years.

MANOVA (Table 1) detected significant differences among years with respect to epilimnetic temperature, hypolimnetic oxygen, PC (but not Chl *a*), nitrate, SRSi, and BV of both cyanobacteria and diatoms. The temperature effect traced to the fact that the lake epilimnion in 2008 was on average 1.6°C cooler than 2005; the effects on other variables were generally related to differences between control and experimental years (Fig. 2). Maximum concentrations of cyanobacteria BV and PC were elevated in control years, and experimental years were characterized by elevated diatom BV and reduced SRSi. The changes in diatom and cyanobacteria community composition were largely compensatory, thus accounting for the lack of statistically significant change in Chl *a* levels or transparency (Table 1), but biomass data revealed substantial interannual changes (Figs. 2, 3). As predicted, experimental years exhibited elevated median levels of nitrate and hypolimnetic oxygen.

Table 1 Statistical significance of interannual differences in physical, chemical, and biological response variables assessed by MANOVA

Variable	<i>P</i>	2005	2006	2007	2008
<i>T</i> at 2 m	0.04	a	a, b	a, b	b
<i>T</i> at 8 m	NS				
DO at 8 m	0.008	a	a, b	a	b
Secchi depth	NS				
Chl <i>a</i>	NS				
PC	<0.0005	a	b	a	a
Cyano-BV	0.004	a	a, b	a, c	a, b, c
Diatom BV	0.002	a	a	a	b
NO ₃	0.001	a	b	a, c	a, b, c
SRSi	<0.0005	a	a, b	a	b

Epilimnetic temperature was measured at 2 m; hypolimnetic temperature and DO were measured at 8 m. 2005 and 2007 are control years; 2006 and 2008 are experimental years. Years that are not significantly different in Bonferroni post-hoc contrasts are denoted by common letters in the rightmost four columns

NS not significant

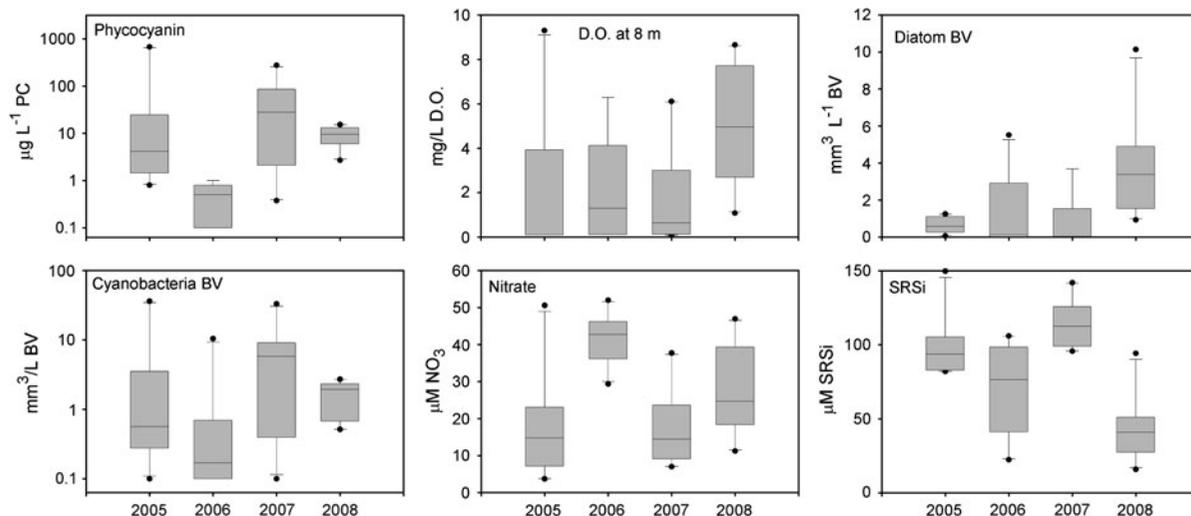
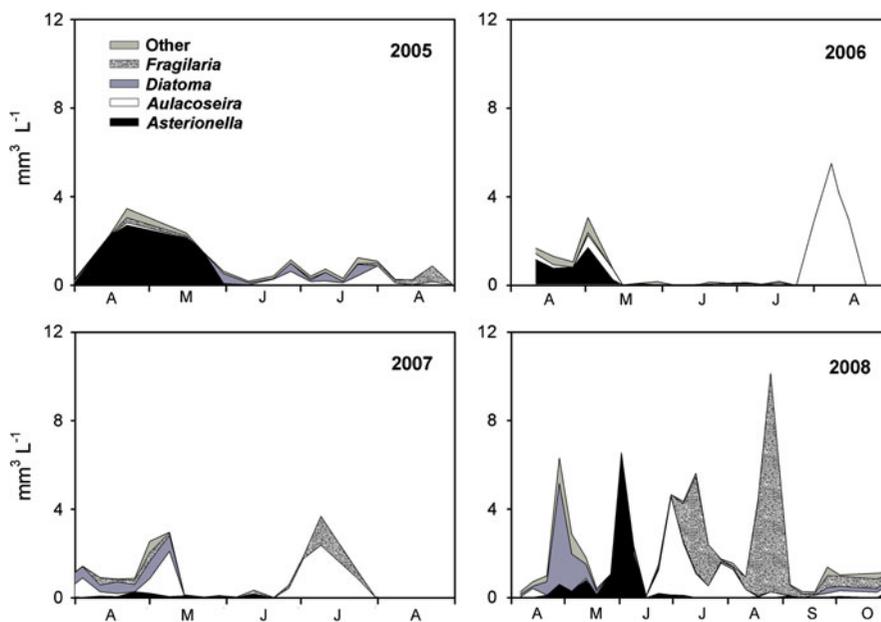


Fig. 2 Box plots of response variables measured weekly from late June to late August for control years (2005, 2007) and experimental years (2006, 2008)

Fig. 3 Diatom community succession in experimental (2006, 2008) and control (2005, 2007) years ($\text{mm}^3 \text{L}^{-1}$)



The most successful year for diatoms of those examined was 2008, with a maximum BV of $10.1 \text{ mm}^3 \text{L}^{-1}$ and four distinct BV peaks. BV maxima were $3.5 \text{ mm}^3 \text{L}^{-1}$ in 2005, $5.6 \text{ mm}^3 \text{L}^{-1}$ in 2006, and $3.7 \text{ mm}^3 \text{L}^{-1}$ in 2007. All four 2008 peaks exceeded $4 \text{ mm}^3 \text{L}^{-1}$, each composed of different species dominants (Fig. 3). The April communities of both 2005 and 2006 were dominated by *A. formosa*, consistent with observations from previous years

(Ferris & Lehman, 2007). The two largest BV maxima across years occurred during and shortly following experimental periods ($5.6 \text{ mm}^3 \text{L}^{-1}$ on 8 August 2006 and $10.1 \text{ mm}^3 \text{L}^{-1}$ on 25 August 2008) and were dominated by *Aulacoseira* spp. and *Fragilaria* spp., respectively. There was also a summer diatom bloom during July of control year 2007. The lake mixed following rainstorms associated with a cold front, which circulated the nutrients that had accumulated in

the hypolimnion. This stimulated a temporary diatom bloom, but cyanobacteria eventually dominated the phytoplankton as the lake once again stratified (Lehman et al., 2009a, b).

Seasonal succession

In both experimental and control years, Ford Lake experienced a diatom bloom in April–May (Fig. 3). *Diatoma tenue* C. Agardh and *Asterionella formosa* were the dominant groups representing this spring community, though there was a significant presence of *Aulacoseira granulata* in 2007. June was a period of low-diatom abundance in all years except 2008. Summer blooms of *Aulacoseira* were present in all years except 2005. Continuous diatom presence with successive BV peaks from April through August occurred only in 2008, and BV maxima that year ranged from 5.6 to 10.1 $\text{mm}^3 \text{L}^{-1}$. The first peak occurred the week of 28 April and consisted primarily of *Diatoma*. *Synedra nana* F. Meister was prevalent during this time but did not contribute substantially to BV. *Asterionella* dominated the second peak during early June. The third diatom peak coincided with the start of artificially induced destratification of the water column and spanned the end of June through mid-July. *Aulacoseira* and *Fragilaria* became dominant at that time, marking a community shift away from *Asterionella*, *Diatoma*, and *Synedra*. The final and largest BV peak of 2008 was at the end of August and was due almost exclusively to *F. crotonensis* (97%) with lower abundance of *Aulacoseira* spp. *F. crotonensis* dominance was a unique feature of the 2008 diatom assemblage. Indeed, the species had accounted for less than 10% of diatom BV in previous years (Ferris & Lehman, 2007). There were low incidences of *Cyclotella kützingiana* Thwaites and *Navicula* spp. throughout the season, but these taxa did not contribute significantly to BV (<3.5% of total diatom BV) and did not display differential success with time. Diatoms persisted through October at low biomass (<2 $\text{mm}^3 \text{L}^{-1}$) as *Aphanizomenon flos-aquae* took over the phytoplankton community.

Lehman et al. (2007) demonstrated that *Daphnia mendotae* abundances of ca. 3×10^5 individuals m^{-2} generate sufficient grazing pressure to cause declines in diatom populations in Ford Lake. During summer 2008, when *D. mendotae* populations achieved their highest abundances of 2.7×10^5 individuals m^{-2} on

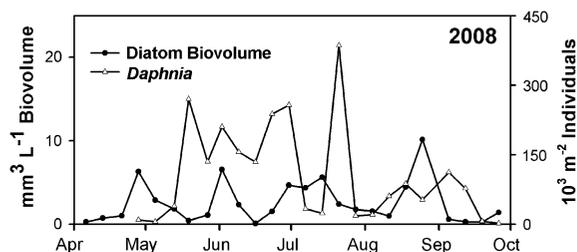


Fig. 4 Total diatom BV and abundance of *Daphnia mendotae* during 2008

19 May and 3.9×10^5 individuals m^{-2} on 21 July (Fig. 4), net intrinsic growth rates for diatom BV (r , d^{-1}) became negative (-0.21 and -0.12 , respectively), but otherwise there was no significant effect of *Daphnia* abundance on diatom r for all other dates of lower *Daphnia* abundance (linear regression $r^2 = 0.06$). In both May and July, the previous dominants were replaced by new species when diatoms recovered (Fig. 3).

In contrast to the continued presence of diatoms in 2008, diatoms largely disappeared from the phytoplankton assemblage from mid-May until the end of July in 2006, when an *Aulacoseira* spp. peak occurred following our third withdrawal experiment. Unlike 2008, however, *D. mendotae* never exceeded 1.2×10^5 individuals m^{-2} during that time and it is unlikely that grazing was a major factor in the lack of diatom success.

Diatom abundance corresponded to low-SRSi concentrations, and SRSi concentration increased with decreasing diatom BV (Fig. 5). The lowest SRSi recorded was $15.9 \mu\text{M}$ during the $10.1\text{-mm}^3 \text{L}^{-1}$ diatom BV peak at the end of August. SRSi climbed to $135.9 \mu\text{M}$ at the beginning of October with the onset of the cyanobacterial bloom and decline of diatom dominance.

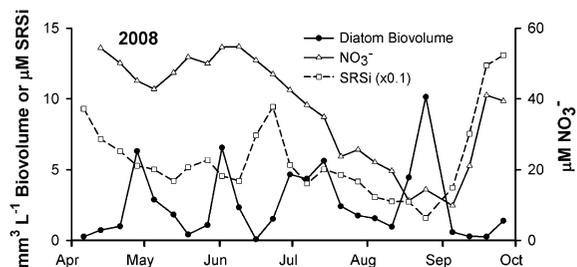


Fig. 5 Epilimnetic NO_3^- and SRSi in relation to diatom BV during 2008. Note that SRSi is plotted at 1/10th scale

Unlike SRSi, NO_3^- concentration in 2008 did not correlate with diatom oscillations throughout the season, but declined monotonically from a 54.8- μM maximum in June to 9.8 μM in early September (Fig. 5).

Discussion

Cool temperatures and lack of stratification are implicated as primary factors determining diatom success (Köster & Pienitz, 2006; Ferris & Lehman, 2007), as are abundant nutrients and water transparency (Lehman et al., 2004). The whole lake manipulations of 2006 and 2008 created unique circumstances for Ford Lake because typical transitional features like extended photoperiod and elevated water temperature occurred without the development of a persistent thermocline that otherwise might have accelerated diatom sinking losses. Overall, the experimental manipulation of 2008 prevented anoxia and rapid nitrate depletion during the summer. An important consequence of reduced anoxia and deeper mixing was diatom success despite elevated summer temperatures.

Diatoms showed variation across control and experimental years in both abundance and dominance. Diatom BV reached a 10.1- $\text{mm}^3 \text{L}^{-1}$ maximum in 2008. This is not as high as the vernal peak exceeding 15 $\text{mm}^3 \text{L}^{-1}$ in 2004 (Ferris & Lehman, 2007), but is certainly higher than any BV maxima reached in 2005, 2006, and 2007. Furthermore, there was consistent diatom seasonal succession throughout the spring and summer of 2008, with minima following intense zooplankton grazing and preceding new BV peaks. Reynolds et al. (1984) reported similar results following artificial mixing. They found growth by *A. formosa* and *F. crotonensis* at atypical times as a result of destratification. Ford Lake experienced distinct diatom blooms in April and August of 2006, with little in between. This difference between experimental years may be attributable to the selective withdrawal regimes applied in the two different years. The 6-week withdrawal of $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ in 2008 was more conducive to diatom population growth and prevention of anoxia than were the episodic withdrawals of varying discharge in 2006 over a 6-week period. Selective withdrawal in 2006 was episodic and did not yield diatom growth until the end of July, when a

withdrawal of $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ was initiated. In contrast, initiation of hypolimnetic withdrawal in 2008 was immediately followed by diatom growth, which persisted throughout the spring and summer. Consistent with the results presented here, continuous withdrawal has been suggested elsewhere as a more effective means of water quality control than episodic withdrawal (Reynolds et al., 1984).

The Ford Lake diatom community experienced four BV peaks in 2008 representing a seasonal succession from *Diatoma tenue*, *Asterionella formosa*, and *Synechra nana* to *Aulacoseira granulata*, *Melosira varians*, *Fragilaria crotonensis*, and *Fragilaria capucina*. *Cyclotella kützingiana* and *Navicula* spp. were present at low frequencies from April through October but never experienced noticeable peaks. This succession from small easily edible to large, more inedible diatoms is consistent with the PEG model for phytoplankton succession (Sommer et al., 1986). *A. granulata*, *M. varians*, and *Fragilaria* spp. regularly form colonies of long helices or ribbons, generally unlike *A. formosa*, *D. tenue*, or *S. nana*. At the midsummer transition point when zooplankton are abundant, the most successful algal species are able to grow at a faster rate than the rate at which they are lost to grazing (e.g., Lehman, 1988; Agrawal, 1998 and references therein). In Ford Lake, these successful species were large: *A. granulata*, *M. varians*, and *Fragilaria* spp. Although Carotenuto & Lampert (2004) reported no significant differences in carbon incorporation by *Daphnia pulex* fed single cell diatoms compared to colonial diatoms including *Fragilaria*, they suggested that diatom colonies tend to be much larger in situ and may be excluded from the food groove.

Nutrient variation is also likely to have affected the observed succession. The 2008 mid-July rise in SRSi (94.2 μM), seemingly induced by artificial mixing, may have enabled the proliferation of *Aulacoseira granulata*. *A. granulata* is a heavily silicified species (Takano et al., 2004) and may rely upon high ambient-Si as a requisite for growth. Indeed, well-mixed columns are frequently cited as conducive to *Aulacoseira* blooms (e.g., Agbeti et al., 1997). Similarly, the mixing induced by the cold front in the summer of 2007 promoted *Aulacoseira* growth. The higher temperature optima of more heavily silicified taxa may also have facilitated this later community shift (Liukkonen et al., 1997). The population growth of *Fragilaria crotonensis* in the summer of 2008 must be

explained by other environmental factors apart from SRSi regeneration. This species has the same Si requirements for growth as *A. formosa* (Tilman, 1981), and so the rise in SRSi probably did not promote *F. crotonensis* success as it may have done for *A. granulata*. Some phytoplankton form large colonies when predation risk is high (Van Donk et al., 2011), which may have occurred in this *Fragilaria* population.

The abundance of *Aulacoseira* in the summers of 2006 and 2008 as well as that of *Fragilaria* in the late summer of 2008 attest to the successful induction of turbulence by artificial destratification. Both experimental years produced higher diatom BV peaks than did the control years, though the experimental regime of 2008 yielded a longer duration of diatom growth than that of 2006.

Conclusion

Whole lake manipulation of Ford Lake resulted in enhanced diatom community growth. Consistent selective deep withdrawal of $3 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ over a 6-week period yielded more consistent summer diatom production than in previous years. The phytoplankton succession observed in 2008 was unique, in that the shift from diatoms to cyanobacteria that is so commonly observed in temperate lakes, including Ford Lake, was delayed by at least 2 months. The positive response of diatoms to hypolimnetic withdrawal experiments documented in this study is relevant for lake management strategies aimed at reducing cyanobacterial blooms. This is especially important where cultural eutrophication threatens aquatic ecosystems by promoting cyanobacteria that release toxins and dominate phytoplankton communities. Experimentally induced summertime success of diatoms, moreover, suggests that the strong negative correlation often found between warm water temperatures, and diatom BV is not universal nor necessarily causal in all cases. The finding is more likely a consequence of the fact that the nonlinear relationship between temperature and water density makes it easier for strong density stratification to develop in warm water. In this study, the manipulation of the lake physical environment proved effective at stimulating diatom growth and thereby reducing cyanobacterial abundance.

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