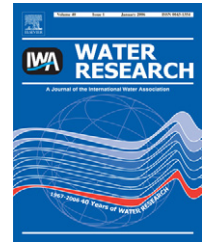


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# Interannual variation in diatom bloom dynamics: Roles of hydrology, nutrient limitation, sinking, and whole lake manipulation

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## ABSTRACT

Spring development of diatoms in Ford Lake, Michigan, USA was markedly different in 2004 from 2005 and 2006. In 2004, diatom biovolume surpassed  $15 \text{ mm}^3 \text{ l}^{-1}$  but in 2005 and 2006 maximum biovolume was less than  $5 \text{ mm}^3 \text{ l}^{-1}$ . Soluble reactive silica (SRSi) in 2004 fell below  $5 \mu\text{M}$  whereas in 2005 and 2006, SRSi remained above  $30 \mu\text{M}$ . Taxonomic composition was similar among years and consisted mainly of *Asterionella*, *Cyclotella*, *Fragilaria*, *Aulacoseira*, and *Synedra*. Bioassay experiments in 2005 demonstrated that P rather than Si was the element most limiting biomass development. However, P supply rate did not account for the differences among years. Model simulations of Si uptake, washout rates, and sinking implicated hydrologic differences among years as the cause of differential success by diatom populations in April of each year. Bioassay experiments performed after overturn demonstrated that diatoms could grow well in unamended lake water, but they did not flourish in the lake; model simulations implicated sinking losses as the reason. In summer 2006, we performed a selective withdrawal of hypolimnetic water from the outlet dam and weakened density stratification. An *Aulacoseira* bloom resulted in early to mid-August, depleting SRSi to less than  $30 \mu\text{M}$ . The lake, which had been acting as a P source, changed to a P sink during the bloom, and cyanobacteria did not develop as they had in all previous years. Stoichiometric calculations indicate that the net SRSi uptake and the net DP uptake during the induced bloom were consistent with diatom production.

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## 1. Introduction

Seasonal succession from spring diatom communities to summer communities of cyanobacteria or dinoflagellates is a well-known pattern long recognized worldwide (Sommer et al. 1986). The succession has been ascribed to depletion of Si, P, or both. Succession by heterocystous bluegreens has been linked to N depletion and particularly to low N:P ratios (Smith 1983, Hyenstrand et al. 1998). Taxon specific analyses have revealed virtually opposite growth responses of diatoms and cyanobacteria to environmental factors (Lehman et al. 2004). In this paper, we report a case study of diatom–cyanobacteria

succession, but with the application of a whole-lake experimental manipulation that reversed the pattern.

The Huron River watershed in southeastern Michigan, USA occupies  $2324 \text{ km}^2$ . The main stem extends 218 km from source to its mouth at Lake Erie, with 24 major tributaries adding about 590 km of additional stream length. Seven man-made impoundments occupy the heart of the watershed, including Ford Lake, constructed by Henry Ford in 1932 to supply electric power to his Motor Company.

Diatoms have been a consistent feature of Ford Lake since the lake's construction. Examination of sediment cores taken in 1991 (Donar et al., 1996) revealed the presence of both

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planktonic and benthic diatoms extending down to approximately 31 cm below the mud–water interface. The authors estimated an average sedimentation rate of  $0.5 \text{ cm yr}^{-1}$ , implying at that time 30–32 cm of sediment accumulation since the reservoir's creation.

Diatom populations usually achieve maximum abundance in late April or early May. Diatoms are then replaced by cyanobacteria, mainly *Aphanizomenon* and *Microcystis*. The bluegreens develop high biomass, carpet most of the lake's  $4 \text{ km}^2$  surface area, release microcystin toxins (Lehman, 2007), and are regarded as a major nuisance problem. Ford Lake nonetheless supports one of the most productive warm water sport fisheries in the State of Michigan and is used intensely for recreation, so there is an interest in practices that might extend the period of diatom abundance and contract the period of cyanobacterial dominance.

The purpose of this research project was first, to examine and numerically model causal factors in the population dynamics of diatoms in Ford Lake. Second, we tested our ability to transform the mid-summer phytoplankton community through whole lake manipulation and to test theory that a mid-summer diatom bloom could be artificially induced. The rise and fall of diatom abundance is presumed to represent a balance between in situ growth and loss processes, which may include sinking, grazing, parasitism, or washout. Growth rates are potentially affected by nutrient limitation.

## 2. Materials and methods

### 2.1. Study site

Our field site was the middle reach of the Huron River catchment in southeastern Michigan (United States Geological Service Cataloging Unit 04090005). The impoundments within the site are operated as “run of the river,” meaning that stage heights are regulated so that outflow matches inflow. In the case of Ford Lake, the hydroelectric turbines draw water from the topmost 5 m of lake depth, but they have constrained capacity. When river discharge exceeds the capacity of the turbines, an array of hydraulic gates can be opened at the base of the dam, at 11 m maximum water depth, to expel the excess inflow and maintain constant lake stage height.

### 2.2. Field sampling

Water was collected on a weekly to biweekly basis at both inlet and outlet of Ford Lake ( $42.21^\circ \text{N}$ ,  $83.56^\circ \text{W}$ ) as well as from the lake surface near the outlet dam. Raw water gathered in the field was filtered on site for nutrient analysis using Millipore™ disposable filter capsules of nominal  $0.45 \mu\text{m}$  pore size. From May to September, quantitative samples for phytoplankton counts and pigment analyses were collected from 0 to 5 m at Ford Lake using an integrative tube sampler.

A subsurface instrument mooring site was established in Ford Lake at 10.7 m water depth. During periods of field experiments up to 5 TR-1050 recording thermistors (Richard Brancker Research, Ltd.) and 2 Stevens-Greenspan CS304

data-loggers for temperature, dissolved oxygen, pH, and conductivity were deployed in situ and were programmed to log data at 5 min intervals.

Weather data were obtained from the National Climate Data Center for station 209218, 2.7 km from the lake.

### 2.3. Soluble reactive silica

SRSi was measured from filtrate according to Stainton et al. (1977). Silicate was reduced to silicomolybdate blue and read spectrophotometrically in a 1-cm cell at both 660 and 815 nm.

### 2.4. Particulate silica

Particulate Si (Part-Si) was measured by slight modification of the method of Paasche (1973). Raw water was dispensed as 15-ml samples into polystyrene centrifuge tubes with a two-drop addition of Lugol's iodine. The samples were sedimented by clinical centrifuge for 10 min at 3000 rpm, producing 1250g acceleration. The supernatant was decanted and 4-ml of 0.2 N NaOH was added. The tubes were placed in a water bath at  $85^\circ \text{C}$  for 1 h. After cooling, the samples were neutralized with 1-ml 0.8 N HCl. Blanks consisted of 4-ml of 0.2 N NaOH and 1-ml of 0.8 N HCl. A  $24 \mu\text{M}$  Si standard consisted of 4-ml of  $30 \mu\text{M}$  Si in 0.2 N NaOH and 1-ml of 0.8 N HCl. The samples, standards, and blanks were then processed according to SRSi protocol.

### 2.5. SRP, DP, and TP

Soluble reactive P (SRP) was measured from filtrate according to Strickland and Parsons (1972). Dissolved phosphorus (DP) and total phosphorus (TP) were measured from filtrate and raw water, respectively, by treating 40-ml samples with 0.4 g potassium persulfate, and heating to  $105^\circ \text{C}$  for 2 h. After cooling to room temperature, samples were processed as SRP. Sample absorbance was measured at 885 nm, using a 10-cm path-length cylindrical cell.

### 2.6. Dissolved nitrogen (DN) and particulate nitrogen (PN)

DN was measured using 10-ml filtrate. For PN, 100-ml of raw water was filtered through 25-mm Whatman™ GF/C filters and placed in 10-ml deionized water. DN and PN samples were treated with alkaline persulfate oxidant, heated to  $105^\circ \text{C}$  for 6 h, and later neutralizing with HCl according to D'Elia et al. (1977). Nitrate in the resulting digests was measured by second derivative UV spectroscopy (Crumpton et al., 1992) by scanning from 260 to 200 nm at 0.5 nm intervals using a 1-cm quartz cuvette. Filtrate was used for nitrate determination without previous digestion.

### 2.7. Alkaline phosphatase (AP)

AP was measured using a modification of Turner Designs™ application method 998-2679. One milliliter aliquots of  $36 \mu\text{M}$  4-methylumbelliferyl phosphate (MUP) in 50 mM pH 8.0 TRIS buffer were added to 4-ml raw water at  $22^\circ \text{C}$ , and both initial and time series fluorescence were measured with a Turner Designs Model 10 fluorometer using the long wavelength UV

filter kit (P/N 10-302R) with 310–390 nm excitation filter and 410–600 nm emission filter. Fluorescence changes were converted to rate of substrate hydrolysis using reference standards of 2  $\mu\text{M}$  4-methylumbelliferone as sodium salt. Enzyme activity was normalized to Chl *a* concentration and was expressed as nmol MUP hydrolyzed ( $\mu\text{g Chl } a$ )<sup>-1</sup> h<sup>-1</sup>.

## 2.8. Chlorophyll and phycocyanin

For spectrophotometric analysis of chlorophyll, 250-ml of raw water was filtered through Whatman™ AH filters and filters were frozen over silica gel desiccant until extraction. Fluorometric assays for chlorophyll used 100-ml samples. Pigments were extracted by macerating filters in ice-cold 90% v/v acetone by tissue grinder, then filtering the slurry through a Whatman GF/D filter. Chlorophyll *a* was measured fluorometrically using a Turner Designs TD700 fluorometer with 436 nm excitation filter and 680 nm emission filter; spectrophotometric determination used the trichromatic method and 5-cm optical path length (Arar, 1997).

Phycocyanin was measured fluorometrically after extraction in 0.05 M phosphate buffer at pH 7 (Lehman, 2007).

## 2.9. Diatom counts

Water samples were preserved from sampling dates and experiments with Lugol's iodine. For counts of springtime populations, fixed samples were placed in a cylindrical settling chamber 1.6 cm high and 2.3 cm in diameter for at least 1 h prior to counting with an Olympus IMT-2 inverted light microscope. Time series tests demonstrated that longer settling times did not yield more diatom cell counts. Diatoms were measured using an ocular eyepiece calibrated with a stage micrometer. For each sample, 60 fields were counted at 375X, representing a total searched volume of 0.174-ml. Dimensions of 30 cells from each abundant taxon were measured at 600X and average cell biovolumes were estimated using standard geometric solids. During August 2006, 2.5-ml aliquots of the preserved samples were filtered onto 25-mm diameter Gelman™ 0.45  $\mu\text{m}$  Metrical membrane filters. Filters were dried and cleared with immersion oil, then diatoms were counted and measured using an Olympus BHA compound microscope with interference contrast optics.

Prevalence ( $P_r$ ) and intensity of infection ( $\hat{I}$ ) of the dominant spring species, *Asterionella formosa* Hass., by chytrids were measured according to Ibelings et al. (2004). At least 100 cells were examined in each sample, and the number of chytrids attached to each was recorded.

## 2.10. Laboratory experiments

### 2.10.1. Nutrient bioassays

Potential nutrient limitation was investigated through nutrient bioassay experiments involving additions of P as phosphate or Si as silicate to raw water samples (Table 1). Treatments were conducted using 1-L polycarbonate bottles, incubated at 22 °C under continuous light at 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR (400–700 nm) from General Electric “Bright Stik Gro & Sho” 33W fluorescent tubes. Initial and final measurements were made for Chl *a*, DP, NO<sub>3</sub>, and SRSi concentrations, and

**Table 1 – Bioassay experiments conducted from February to May 2005**

Experiment	Duration	Procedure and treatment
B1	4–10 February 2005	Four controls; four replicate additions of ca. 0.5 $\mu\text{M}$ P.
B2	1–7 April 2005	(Identical to B1)
B3	8–14 April 2005	Four controls; four replicate additions of ca. 0.3 $\mu\text{M}$ P.
B4	15–21 April 2005	Four controls; four replicate additions of ca. 50 $\mu\text{M}$ Si.
B5	22–28 April 2005	(Identical to B4)
B6	4–7 May 2005	Four controls; four replicate additions of ca. 0.5 $\mu\text{M}$ P; four replicate additions of ca. 50 $\mu\text{M}$ Si; four replicate additions of both P and Si.
B7	11–14 May 2005	(Identical to B6)

Additions of P and Si were made to water from Ford Lake. SRSi, Part-Si, SRP, DP, TP, DN, PN, NO<sub>3</sub>, Chl *a*, *b*, and *c* were measured in all experiments; AP was not measured in experiment B4.

for AP activity, as well. Statistical comparisons among treatments were conducted using t-tests when only two treatments were present (Control Versus Addition); one-way analysis of variance (AOV) was used when multiple treatments were present. In the latter cases, pair-wise contrasts were performed post-hoc using Bonferroni-adjusted probabilities (SYSTAT 10). T-tests were one-tailed using the a priori assumption that nutrient addition should increase growth with respect to Control if the cells are nutrient limited.

Additional experiments were performed to assess diatom growth potential in unamended lake water after the spring diatom bloom had subsided (Table 2). All growth experiments used water from near or at the inlet of Ford Lake. Four replicate 1-L polycarbonate bottles were incubated without amendment. Measurements were made for Part-Si, Chl *a*, Chl *b*, and Chl *c* at both initial and final times.

### 2.10.2. SRSi remineralization and biogenic Si in lake sediments

Rates at which SRSi redissolves from mud into lake water were measured using sediment cores obtained from Ford Lake during June 2005. Eight cores were collected with a Kajak–Brinkhurst (K–B) gravity corer (Brinkhurst et al., 1969); three cores were taken at a 5.2 m site, three at an 8 m site, and two from a 10 m site. Initial SRSi concentrations were measured in the headspace water, and final concentrations were measured after 24 h incubation. The experiment was repeated 3 times. Subsequently, all cores were extruded at 1-cm intervals to a depth of 8 cm. Fresh mass of each section was recorded, and the samples were dried to constant mass at 55 °C and pulverized in a grinding mill. Subsamples from 35 samples representing all stations and all depths were

**Table 2 – Growth experiments conducted weekly from May to August 2005**

Experiment	Duration
G1	25 May–1 June
G2	2–6 June
G3	9–13 June
G4	16–20 June
G5	23–27 June
G6	27 June–1 July
G7	7–11 July
G8	11–14 July
G9	14–18 July
G10	18–21 July
G11	21–25 July
G12	25–28 July
G13	1–3 August

subjected to X-ray fluorescence spectroscopy for elemental determination of Total Si (GeoAnalytical Laboratory, Washington State University, Pullman, WA, USA). In addition, 5-mg subsamples from 19 core sections representing all sites and the full range of depths were added to 1% Na<sub>2</sub>CO<sub>3</sub> and heated at 85 °C for 6 h, a time period determined by preliminary time-series digestions. The digests were cooled, neutralized with 1N HCl, filtered to remove particulates, and the filtrate was analyzed for SRSi. The solubilized Si was regarded as biogenic Si.

### 2.10.3. Sinking rates

In August 2006, we collected lake water and used the SETCOL method (Bienfang, 1981) to quantify sinking rate of the diatom assemblage.

### 2.11. Experimentally induced diatom bloom

From 26 July to 4 August 2006, discharge of epilimnetic water through the hydroelectric turbines at Ford Lake dam was decreased so that water could be selectively withdrawn from the hypolimnion by opening gates at the base of the dam (11 m depth). Then on 12 August, epilimnetic discharge was curtailed to its minimum possible and all available flow was discharged from the base until 19 August. The objective was to destabilize the water column by weakening the thermal gradient and to deepen the mixed layer. Measurements of SRSi in inlet and outlet, as well as diatom biovolume measurements were used to document the resulting bloom of *Aulacoseira*.

### 2.12. Hydrology and diatom growth model

Daily discharge records for Ford Lake dam were supplied by Ypsilanti Charter Township officials (J. Brinker and M. Saranen, pers. commun.). Calculated flow rate (Q) is reported in m<sup>3</sup> d<sup>-1</sup>.

Flushing time ( $T_f$ ) was calculated using Q and lake volume ( $V = 17,370,000 \text{ m}^3$ ). During the time period of model calcula-

tions, the lake was either isothermal and well mixed or water was being discharged from both epilimnion and hypolimnion. For any given arbitrary starting day, designated  $t = 0$ ,  $T_f$  was calculated from the implicit function given in Eq. (1).

$$V = \int_0^{T_f} Q dt. \quad (1)$$

Discharge of the Huron River into Ford Lake was estimated from hydrologic data. Daily discharge records for the Huron River at Ann Arbor were obtained from USGS on-line archives for station 04174500. Daily volumetric discharge from the Ann Arbor Wastewater Treatment Facility upstream from Ford Lake was provided by city officials (E. Kenzie, pers. commun.). Daily water income to Ford Lake was calculated from the USGS records at Ann Arbor, with correction for incremental catchment area downstream. The catchment area is 9.2% greater at the Ford Lake inlet than at the gage site in Ann Arbor. Flow rates were consequently adjusted by the factor 1.092, plus the treated wastewater volume. We performed an independent check on this calculation using recent historical data. The USGS maintained an active stream gage in the Huron River at Forest Street just above Ford Lake (USGS 04174800) from October 1989 to September 1994. Quets (1991) reported malfunctions in gage operation in 1989 and in 1990 prior to June. Consequently, the records from that suspect period were disregarded and linear regression was conducted with the daily discharge data from 1 June 1990 to 30 September 1994.

Local drainage and net runoff in excess of evaporation to Ford Lake were calculated as the difference between measured dam discharge, measured daily changes in lake stage height multiplied by lake surface area, and estimated Huron River inflow. The resulting calculation produced a small numerical difference between large numbers, specifically river inflow and dam discharge. In an attempt to isolate the small hydrologic signal from propagated random error, the resultant difference was smoothed by 5-point moving mean. The nutrient chemistry of this local drainage was assumed to be the same as that of the Huron River inflow.

A box model was constructed for April and May of 2004, 2005, and 2006 to test the hypothesis that only two factors are sufficient to account for differences in spring diatom dynamics among years: (1) flow rate differences and (2) onset of thermal stratification and sinking losses. SRSi at the Ford Lake inlet was measured at weekly intervals. Inlet SRSi concentrations were linearly interpolated between sample dates. Concentration changes owing to fluxes of SRSi into and out of Ford Lake ( $Si_{in}$  and  $Si_{out}$ , respectively,  $\mu\text{M d}^{-1}$ ) were defined by Eqs. (2) and (3), where  $[SRSi]_{in}$  is the measured concentration of the inlet water and  $[SRSi]_{lake}$  is the calculated concentration within the lake.

$$Si_{in} = [SRSi]_{in} Q/V, \quad (2)$$

$$Si_{out} = [SRSi]_{lake} Q/V. \quad (3)$$

Rate of SRSi uptake ( $U_{Si}$ ,  $\mu\text{M Si d}^{-1}$ ) within the lake was calculated according to Eq. (4), where  $[Diatom Si]_{lake}$  is the calculated concentration of diatom Si (for comparison with observed values),  $Si_0$  is the threshold concentration for silica uptake,  $K_{Si}$  is the half-saturation constant, and  $\mu$  is maximum

intrinsic growth rate ( $d^{-1}$ ).

$$U_{Si} = \{([SRSi]_{lake} - Si_0)/(K_{Si} + [SRSi]_{lake} - Si_0)\} \mu [Diatom Si]_{lake} \quad (4)$$

For modeling purposes, the rates of change of  $[SRSi]_{lake}$  and  $[Diatom Si]_{lake}$  were calculated according to Eqs. (5) and (6), where  $Si_{remin}$  ( $\mu M Si d^{-1}$ ) is the rate at which Si is remineralized from sediment into lake water.

$$d[SRSi]_{lake}/dt = Si_{in} - Si_{out} - U_{Si} + Si_{remin}, \quad (5)$$

$$d[Diatom Si]_{lake}/dt = U_{Si} - [Diatom Si]_{lake} Q/V. \quad (6)$$

The only loss rates considered were washout owing to flushing rate and sinking loss. For parsimony of model parameters, we assumed that sinking loss was zero during isothermal mixing, but became non-zero and constant at stratification.

Maximum intrinsic growth rate ( $\mu$ ,  $d^{-1}$ ) of the diatom population was assumed identical across years. Growth rate and onset dates of thermal stratification for each year, four variables in all, were calculated using the “Solver” function of Microsoft Excel™. The criterion was to minimize the sum of squared deviations between model SRSi and observed lake SRSi for all years by varying only  $\mu$  and the date of onset of thermal stratification each year. Upon identification of a unique optimal solution, sensitivity analysis was performed by increasing and decreasing each of the four model variables by 3–4% in order to assess the first derivatives of their contributions to model success.

### 3. Results

#### 3.1. Field observations

Fig. 1 shows the seasonal pattern of SRSi concentration entering and leaving Ford Lake from January 2004 to September 2005. Silica concentrations exhibit seasonal depression during spring even at the inlet, indicating silica uptake in upstream lakes. Ford Lake was a major sink for SRSi during April–May of 2004, but not in 2005. Fig. 2 focuses on the inlet and outlet concentrations of SRSi during April–May of 2004, 2005, and 2006. In 2006, as in 2005, SRSi was not nearly as strongly depleted as it was in 2004. Fig. 2 also shows daily discharge ( $Q$ ) from Ford Lake (Fig. 2d). Flows in April of 2005 and 2006 were greater than in 2004. Fig. 2e shows flushing time  $T_f$ , Eq. (1), for Ford Lake, demonstrating that flushing time exceeded 20 d for most of April 2004 when SRSi losses

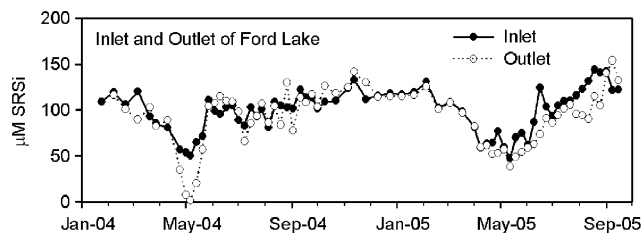


Fig. 1 – SRSi concentration at inlet and outlet of Ford Lake from January 2004 to September 2005.

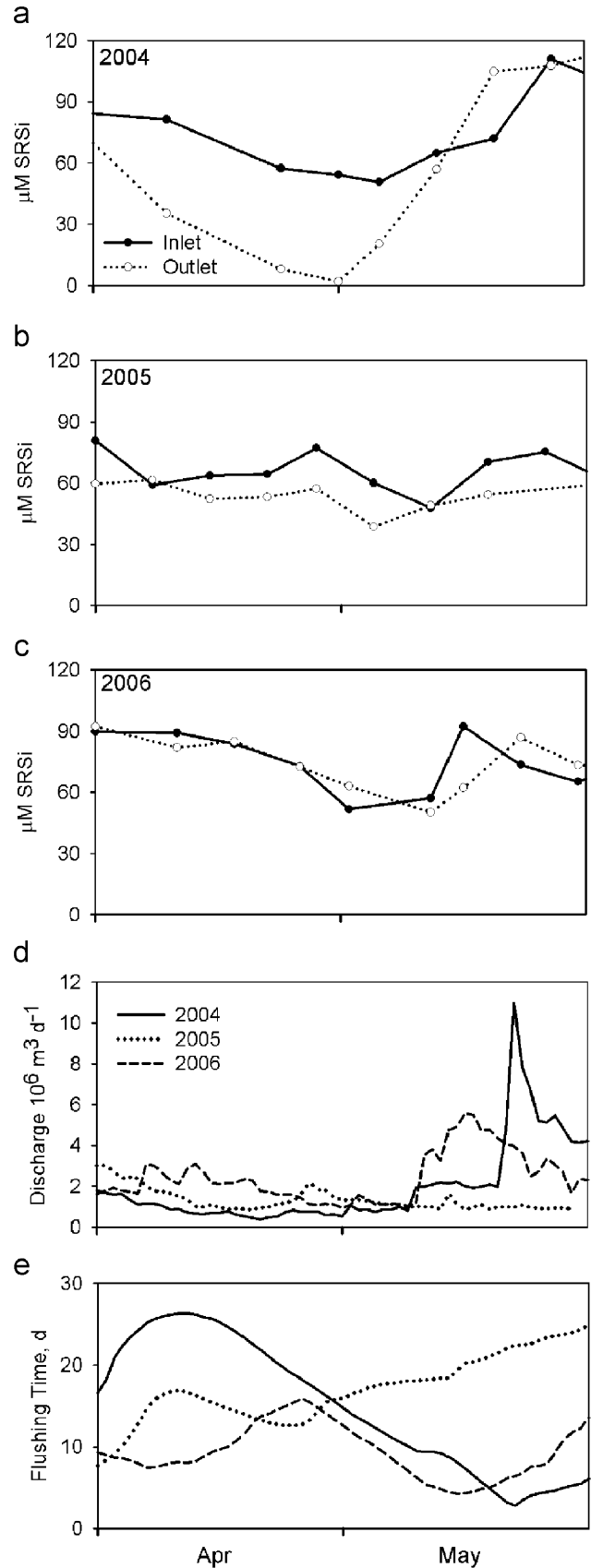


Fig. 2 – SRSi concentrations entering and leaving Ford Lake during April and May of 2004 to 2006 (a–c); daily discharge ( $Q$ ) of the Huron River from Ford Lake (d), and flushing time  $T_f$  (e).

were greatest, but was less than 20 d during April of the other years.

In April and May of each year, the phytoplankton of Ford Lake was dominated by *Asterionella formosa* Hass. The species represented on average 82% of the total vernal diatom biovolume in 2004, 81% in 2005, and 54% in 2006. *Aulacoseira* accounted for 9–24% and *Cyclotella* accounted for 2–14% of diatom biovolume on average. *Synedra* species and *Fragilaria* accounted for less than 10% of diatom biovolume. In 2004 and 2005, the spring diatom flora was succeeded during summer by cyanobacteria, mainly *Aphanizomenon* and *Microcystis*. Ford Lake has been plagued by dense blooms of these species since its construction. Fig. 3 reports the mean concentrations of Chl *a* and phycocyanin in the 0–5 m stratum. Dense populations of cyanobacteria did not develop in early to mid August of 2006 as in previous years, leading to much lower phycocyanin levels in 2006; instead the lake became dominated by *Aulacoseira*.

Prevalence of chytrid infection of *Asterionella* in both 2004 and 2005 remained below 10% (Table 3) in the lake as well as in experiments. In 2006, a maximum of 22.1% of *Asterionella* cells became infected. One-way AOV, however, could detect no significant differences among years ( $P = 0.13$ ) or between lake and final experimental controls ( $P = 0.54$ ).

Daily air temperatures were compared among years by AOV during the period from 15 April to May, when diatoms routinely reach maximum abundance. The year 2005 was significantly cooler during this period by 4 C compared with both 2004 and 2006. The years 2004 and 2006 were indistinguishable, however ( $P = 0.20$ ).

### 3.2. Laboratory experiments

#### 3.2.1. Comparison of trichromatic and fluorometric determination of Chl *a*

Simultaneous determination of Chl *a* by spectrophotometric and fluorometric methods yielded a linear regression ( $x$ -axis = fluorometric Chl *a*) with slope 0.9225 (SE = 0.0174,  $n = 71$ ,  $r^2 = 0.976$ ), slightly less than 1:1 at the 95% confidence level. The trichromatic equations used to estimate Chl *a*, *b*, and *c* thus produced a consistent underestimate of Chl *a* by about 8% with respect to the fluorometric method. In recognition of this fact, Chl *a* determinations by the two methods were never used interchangeably in statistical tests.

#### 3.2.2. Nutrient bioassays

Statistical significance of treatment effects in bioassay experiments are reported in Table 4. Addition of P consistently resulted in positive growth effects. Silica addition produced evidence of positive growth enhancement only once, B5. Initial SRSi on 22 April 2005 (start of B5) was 35.6  $\mu\text{M}$  in Ford Lake. After 6 d of experimental incubation, SRSi in Control bottles had fallen to 1.8  $\mu\text{M}$  (SD = 1.3,  $n = 4$ ). The results apply to experimentally enclosed water samples in the laboratory; at the same time in the field SRSi concentrations leaving Ford Lake never dropped below ca. 30  $\mu\text{M}$  (Figs. 1 and 2). In experiments B6 and B7, involving factorial addition of P and Si, there was little to no evidence that addition of Si enhanced production beyond the significant effect of adding P alone.

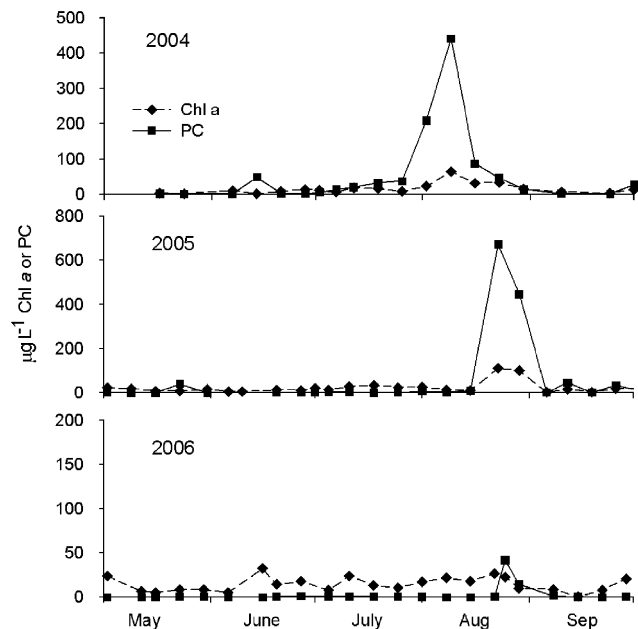


Fig. 3 – Mean concentrations of Chl *a* and phycocyanin (PC) from 0 to 5 m in Ford Lake. Note differences in vertical scale among years.

Table 3 – Numbers of uninfected ( $N_u$ ) and infected ( $N_i$ ) *Asterionella* cells from Ford Lake and from experiments in 2005 during the critical period from 15 April to May 15

Date	$N_u$	$N_i$	$N_p$	$P_r$	$\hat{I}$
2004 Lake					
10 April 2004	110	1	1	0.9	1.0
23 April 2004	175	2	2	1.1	1.0
6 May 2004	175	2	2	1.1	1.0
13 May 2004	109	9	10	7.6	1.1
2005 Lake (Exp initial)					
22 April 2005 (B5)	126	1	1	0.8	1.0
4 May 2005 (B6)	102	9	17	8.1	1.9
11 May 2005 (B7)	107	11	24	9.3	2.2
2005 Lab (Exp final)					
28 April 2005 (B5)	123	10	27	7.5	2.7
7 May 2005 (B6)	181	6	9	3.2	1.5
14 May 2005 (B7)	125	1	1	0.8	1.0
2006 Lake					
18 April 2006	105	12	26	10.3	2.2
26 April 2006	109	31	83	22.1	2.7
2 May 2006	127	2	2	1.6	1.0
12 May 2006	101	20	54	16.5	2.7

$N_p$  is total number of attached parasites encountered.  $P_r = N_i \times 100 / (N_i + N_u)$ ;  $\hat{I} = N_p / N_i$ . Experiment initial and final samples in 2005 were from the control treatments.

#### 3.2.3. Alkaline phosphatase

Table 5 reports initial and final AP activity in bioassay experiments. In all cases, final AP activity became significantly elevated with respect to starting levels. Initial levels represent ambient lake conditions. By the end of the

experimental incubations, all added P had been removed by biological uptake, and AP activity in +P treatments was not consistently lower than Control levels. AP activities at the end point of each experiment were consistently higher than AP activities measured in the lake.

### 3.2.4. Stoichiometries of nutrient consumption

P additions produced large increases in biomass measured as Chl *a* in experiments B1–B7, by factors ranging from 1.8 to 21.7-fold over initial lake conditions (Table 6). These large increases made it possible to estimate stoichiometries of biomass production and nutrient uptake among Chl *a*, N, P, and Si. Differences between initial and final concentrations were compared across experiments. The ratios of Chl *a* production to consumption of SRSi, DP, and NO<sub>3</sub> are reported in Table 6; the relative consumption ratios of Si to N or P, and N to P are reported, as well. Mean values of these stoichiometries were calculated using all experiments from 2005

except B7. In B7, diatoms were not the dominant biomass component, resulting in anomalous ratios involving SRSi. In experiments that were dominated by diatoms (B1–B6), the mean ratio of N to P uptake was 56.0 mol:mol and the mean ratio of SRSi to P uptake was 155.3 mol:mol.

### 3.2.5. Growth experiments

Table 7 reports production of Part-Si and of Chl *a*, *b*, and *c* in growth experiments. Part-Si consistently increased in all experiments except G6. Chl *a* likewise increased in most cases, but results for Chl *b* and *c* were not consistent across dates.

### 3.2.6. Si regeneration

In three replicate experiments each using 8 sediment cores, mean release of SRSi from mud to water was 2.65 (SE = 0.26,  $n = 24$ ) mmol Si m<sup>-2</sup> d<sup>-1</sup>. Using the estimated mud surface area of 4,039,000 m<sup>2</sup>, and lake volume of 17,370,000 m<sup>3</sup>, these

**Table 4 – Effect of nutrient additions**

Treatment	Chl <i>a</i>	Chl <i>b</i>	Chl <i>c</i>	Part-Si	PN
B1 +P	<0.001	<0.001	<0.001	<0.001	<0.001
B2 +P	<0.001	NS	<0.001	0.011	0.002
B3 +P	0.001	NS	NS	<0.001	NS
B4 +Si	NS	NS	NS	NS	NS
B5 +Si	NS	NS	0.028	<0.001	0.033
B6 Overall	<0.001	<0.001	<0.001	0.001	<0.001
B6 +P	<0.001	<0.001	<0.001	NS	<0.001
B6 +Si	NS	NS	NS	NS	NS
B6 +Si+P	<0.001	<0.001	NS	NS	<0.001
B6 P vs. Si	<0.001	<0.001	<0.001	0.004	<0.001
B6 P vs. Si+P	NS	NS	NS	NS	0.004
B6 Si vs. Si+P	<0.001	<0.001	0.03	0.002	<0.001
B7 Overall	<0.001	<0.001	0.046	<0.001	<0.001
B7 +P	0.001	<.001	NS	<0.001	<0.001
B7 +Si	NS	NS	NS	NS	NS
B7 +Si+P	<0.001	<0.001	NS	<0.001	<0.001
B7 P vs. Si	0.008	<0.001	NS	<0.001	<0.001
B7 P vs. Si+P	NS	NS	NS	NS	NS
B7 Si vs. Si+P	<0.001	<0.001	NS	<0.001	<0.001

Experiments B1–B5 were subjected to one-tailed t-tests. Experiments B6 and B7 were subjected to one-way AOV followed by pairwise Bonferroni-adjusted contrasts among treatments. All contrasts are with respect to Control unless otherwise indicated. Values are statistical probabilities of significance; NS = not statistically significant.

**Table 5 – Initial and final AP activity in bioassay experiments**

	Initial	Final: CTL	Final: +P	Final: +Si	Final: +P+Si
B1	0	53.9–67.0	26.0–39.7	—	—
B2	34.5	66.1–77.4	48.8–54.2	—	—
B3	7.1	36.5–46.0	34.1–39.6	—	—
B5	18.3	49.2–52.5	—	54.4–66.9	—
B6	0.9	30.7–35.6	17.6–24.9	35.3–43.4	25.3–31.2
B7	22.4	40.1–45.6	24.8–40.8	35.4–48.0	28.3–38.3

Units are nmol MUP ( $\mu\text{g Chl } a$ )<sup>-1</sup>h<sup>-1</sup>. Final values are 95% CI among replicates. CTL = Control (no addition). AP was not measured in B4.

**Table 6 – Relative biomass increase, measured as Chl *a*, and stoichiometries computed from net changes in concentrations in experiments with +P addition**

	Chl <i>a</i> final/initial	Chl <i>a</i> /SRSi	Chl <i>a</i> /DP	Chl <i>a</i> /NO <sub>3</sub>	SRSi/NO <sub>3</sub>	SRSi/DP	NO <sub>3</sub> /DP
B1	21.7 (1.99)	0.23 (0.02)	41.6 (3.91)	0.99 (0.08)	0.24 (0.01)	177.3 (1.91)	41.8 (1.62)
B2	5.5 (0.20)	0.26 (0.01)	55.0 (3.23)	0.73 (0.08)	0.37 (0.04)	209.4 (8.68)	78.1 (7.69)
B3	2.2 (0.13)	0.24 (0.03)	27.3 (2.91)	0.51 (0.05)	0.48 (0.01)	113.0 (1.47)	53.8 (0.76)
B6+P	2.5 (0.19)	0.33 (0.05)	37.3 (4.27)	0.77 (0.10)	0.43 (0.01)	114.4 (3.10)	48.8 (0.49)
B6+P+Si	2.3 (0.12)	0.20 (0.02)	32.7 (2.97)	0.57 (0.05)	0.35 (0.01)	162.2 (2.81)	57.2 (0.41)
B7+P	1.8 (0.12)	0.36 (0.09)	20.2 (4.78)	0.46 (0.12)	0.78 (0.02)	56.9 (2.19)	44.2 (1.17)
B7+P+Si	2.0 (0.11)	0.35 (0.05)	27.4 (3.05)	0.54 (0.07)	0.64 (0.02)	79.2 (3.15)	50.9 (2.56)
Mean		0.25 (0.02)	38.8 (4.69)	0.71 (0.09)	0.37 (0.04)	155.3 (18.6)	56.0 (6.12)

Replication  $n = 4$  in all cases; values reported as mean (SE). For computing stoichiometries, Chl *a* is net production; SRSi, NO<sub>3</sub>, and DP are as net uptake. All units are  $\mu\text{M}$  except Chl *a* ( $\mu\text{g L}^{-1}$ ). B7 is not included in calculation of mean stoichiometries.

**Table 7 – Growth potential of inlet water to Ford Lake. Initial concentrations are compared with final concentrations reported as the 95% confidence interval among replicates**

	Part-Si			Chl <i>a</i>			Chl <i>b</i>			Chl <i>c</i>		
	Initial	95% CI		Initial	95% CI		Initial	95% CI		Initial	95% CI	
G1	13.6	55.0–59.6	+	6.1	12.9–15.7	+	0.64	0.7–0.9	+	2.4	1.9–2.8	0
G2	10.1	29.9–34.3	+	8.4	14.3–17.4	+	3.1	2.0–2.7	–	9.2	5.5–7.0	–
G3	11.9	31.1–38.5	+	9.4	21.3–24.9	+	0.7	4.2–4.9	+	0.96	1.4–1.6	+
G4	27.8	36.3–40.8	+	11.5	23.7–30.0	+	1.5	3.2–4.1	–	1.4	2.8–4.0	–
G5	14.2	48.7–55.7	+	6.9	20.0–27.2	+	1.3	3.8–4.0	+	2.1	4.3–5.8	+
G6	5.4	4.9–5.3	–	9.4	3.9–5.2	–	0.96	0.7–1.1	0	2.5	1.3–1.9	–
G7	17.8	47.0–49.8	+	11.5	42.9–50.0	+	2.1	7.4–8.8	+	2.5	5.3–12.4	+
G8	6.4	11.1–12.6	+	10.2	22.6–26.6	+	NA	NA		NA	NA	
G9	8.8	24.5–29.0	+	10.5	19.7–22.8	+	1.5	3.0–3.5	+	2.3	4.2–5.3	+
G10	11.9	24.6–26.4	+	46.5	15.2–24.1	–	5.9	2.0–5.5	–	7.5	0–4.2	–
G11	16.7	48.2–66.4	+	5.6	30.3–35.5	+	2.7	3.3–4.0	+	7.8	5.5–6.8	–
G12	13.5	32.8–36.2	+	43.4	22.9–31.9	–	5.1	3.9–7.1	0	3.4	1.3–7.2	0
G13	20.8	37.3–41.6	+	34.9	16.6–20.7	–	3.0	2.8–3.5	0	5.6	4.1–4.5	–

Symbols indicate increase (+), decrease (–), or no change (0) compared to initial value. Chl is reported by trichromatic spectrophotometric method except for G8, where only fluorometric measurements were made.

figures imply a daily addition of  $0.6\mu\text{M Si d}^{-1}$  to Ford Lake water from remineralization at the mud–water interface.

### 3.2.7. Sinking rate

Sinking rate of the diatom assemblage in August 2006 as determined by the SETCOL method was  $0.66\text{ m d}^{-1}$ . Sinking rate measurements were not performed previous to that time.

### 3.3. Hydrology

Our estimated river flow entering Ford Lake was on average 1.210 (SE = 0.003) times greater than the flow measured upstream at USGS 04174500. Linear regression of daily flows in the 1990s measured just above Ford Lake at USGS 04174800 versus those at USGS 04174500 yielded a straight line ( $r^2 = 0.98$ ) with slope 1.206 (SE = 0.005), not significantly different from our estimate. Linear regression of the estimated daily flows of the Huron River entering Ford Lake

versus daily discharge from the Ford Lake dam yielded a straight line ( $r^2 = 0.93$ ) with slope 1.086 (SE = 0.009).

### 3.4. Si and diatom growth model

We used empirical results from B6 and B7 to estimate the stoichiometry of diatom Si to diatom biovolume. Initial and final SRSi as well as diatom biovolumes were measured for Control, +P, and +P+Si treatments. For B6, the mean ratio of Si ( $\mu\text{mol}$ ) to biovolume ( $\text{mm}^3$ ) was 3.84 (SE = 0.37,  $n = 3$ ); in B7 the mean ratio was 2.22 (SE = 0.21,  $n = 3$ ). Biovolume in both experiments was dominated by *Asterionella*, and cell sizes were almost identical (2-tail t-test  $P = 0.4$  for mean cell size difference between experiments). We used the mean value of  $3\mu\text{mol Si mm}^{-3}$  in model calculations.

Si<sub>0</sub>, minimum SRSi concentration needed for uptake, Eq. (4), was set to  $0.6\mu\text{M}$ , which was the lowest SRSi value observed in any bioassay experiment with P addition alone. Based on



literature review, half-saturation constants for SRSi uptake by freshwater diatoms ranged from 1.3  $\mu\text{M}$  (Tilman et al., 1981) to 19.7  $\mu\text{M}$  (Tilman, 1977). We selected 15  $\mu\text{M}$  SRSi as a nominal half-saturation constant for model calculations ( $K_{\text{Si}}$ ).

Loss rate owing to sinking at establishment of thermal stratification was calculated from our measured sinking rate ( $0.66 \text{ m d}^{-1}$ ) divided by epilimnion thickness of 3 m:  $0.22 \text{ d}^{-1}$ .

Calculated  $\mu$  was  $0.263 \text{ d}^{-1}$  for all years; estimated dates of onset of thermal stratification and sinking losses were 2 May 2004, 1 May 2005, and 27 April 2006. Fig. 4 shows the fit of the model to data from April and May of each year (upper panel). The lower panel of Fig. 4 shows model-generated Diatom-Si as well as Diatom-Si calculated from measured diatom biovolume and Si stoichiometry. The Diatom-Si data were not used to fit the model.

Sensitivity analysis using 3–4% increments and decrements in parameter values (i.e.,  $0.01 \text{ d}^{-1}$  for  $\mu$ , 1 d for onset dates) revealed that growth rate  $\mu$  had the largest first-order influence on model goodness of fit; the relative effects of onset date of stratification were only 1% (2004), 16% (2005) and 6% (2006) as large as the effect of variation in  $\mu$ .

Given that predicted maximum growth rate of diatoms was identical in all 3 years, differences in flushing rates are sufficient to account for the differing degrees of silica depletion among years. Low concentrations of SRSi in late April of 2004, as well as elevated concentrations of Diatom-Si in late April correspond with lower flushing rate, which allowed the standing crop to increase. The predicted and

observed declines in Diatom-Si, and increases in SRSi during May result from sinking loss plus washout of the diatom crop as well as income of SRSi with river water.

### 3.5. Si mass balance and induced diatom bloom

Average hypolimnetic discharge from 26 July to 4 August was  $219,800 \text{ m}^3 \text{ d}^{-1}$  (Fig. 5). By midday of 28 July the lake became isothermal and fully oxygenated to at least 7 m (Fig. 6). Hypolimnetic discharge from 12 to 19 August was limited by the availability of water and unavoidable leakage at the turbines. SRSi began to decline in early August, then climbed again in late August. By 8 September, SRSi measured at the outlet of Ford Lake had risen to pre-bloom levels (Fig. 7). Numerical integration of input minus output SRSi from 28 July to 8 September revealed that  $1.67 \times 10^6 \text{ mol}$  SRSi were taken up in Ford Lake. During the same time period, the net uptake of DP was 9100 mol. Using our experimentally determined ratio of SRSi to DP (155.3: Table 6), the 95% confidence interval for expected DP uptake is 8700–14 100 mol,

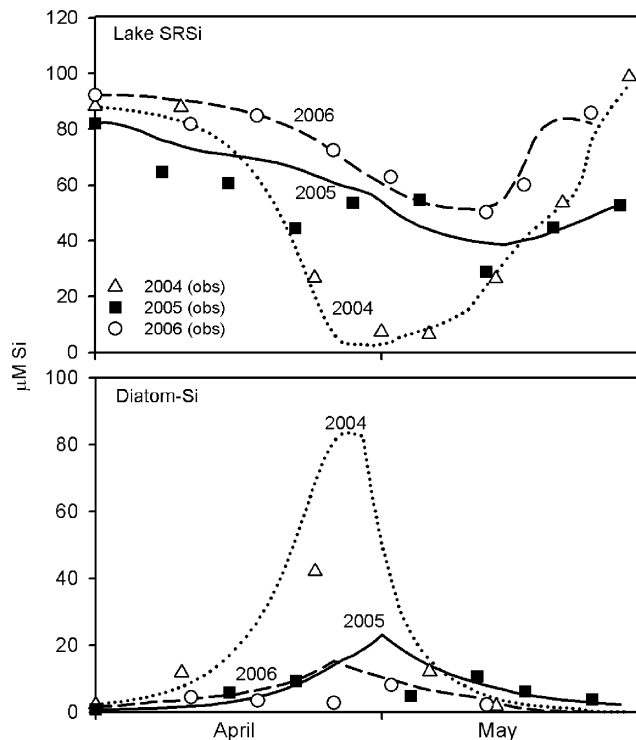


Fig. 4 – Model predictions (solid lines) and observed data (points) for SRSi and Diatom-Si in Ford Lake during April and May of 2004, 2005, and 2006.

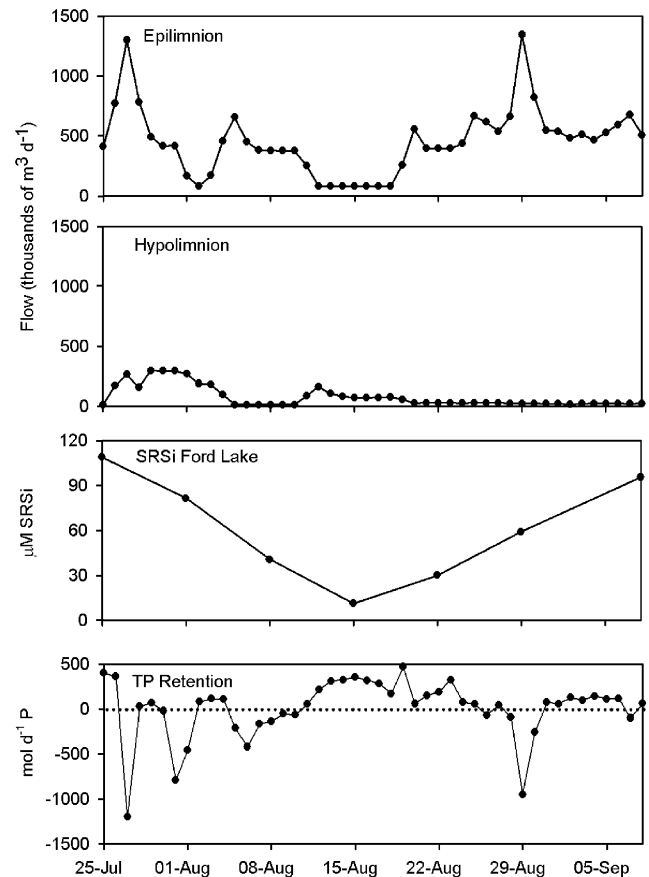
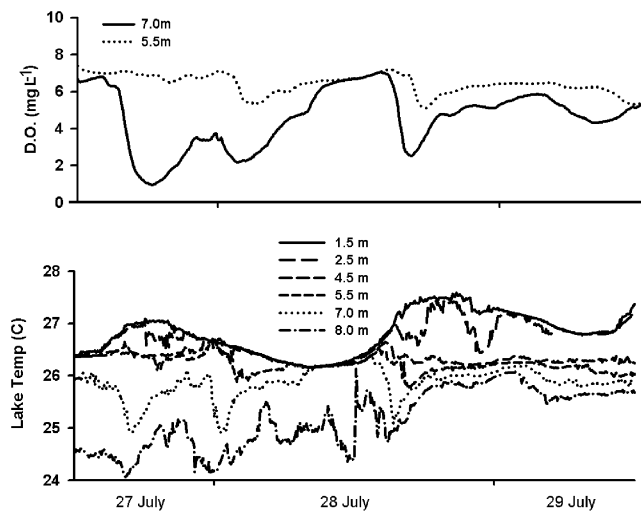
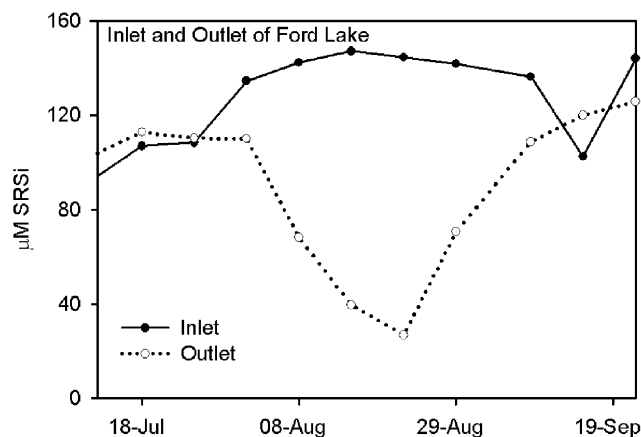


Fig. 5 – Experimental release of hypolimnetic water at the Ford Lake dam July–August 2006. Upper two panels show daily discharge from epilimnion (through hydroelectric turbines) and from gates at the base of the dam (hypolimnion). Depressed lake SRSi and daily TP retention (income minus outflow) are responses to the resulting diatom bloom.



**Fig. 6** – Temperature and dissolved oxygen measured at 5 min intervals at a series of depths in Ford Lake from noon 27 July 2006 to noon 29 July 2006.



**Fig. 7** – SRSi at inlet and outlet of Ford Lake from July to September 2006.

indicating that diatom production was sufficient to account for all of the DP uptake.

TP mass balance proved responsive to our experimental manipulation (Fig. 5). Both before and after the *Aulacoseira* bloom, Ford Lake often behaved as a source for TP, exhibited mainly in the form of exported algal particulates. During the diatom bloom, however, the lake behaved as a sink; 3300 mol of TP were retained from 11 to 25 August.

### 3.6. Biogenic Si accumulation

Total Si content of Ford Lake sediments determined by XRF spectroscopy was 15.2 (SD = 0.3,  $n = 35$ ) percent of dry mass. Biogenic Si was 1.7 (SD = 0.3,  $n = 19$ ) percent of dry mass, or 11% of Total Si. Donar et al. (1996) estimated sediment accumulation rate in Ford Lake as  $0.5 \text{ cm yr}^{-1}$ . Using this figure, the mean accumulation rate of biogenic Si from our 8 cores was  $0.908$  (SE = 0.017)  $\text{mol Si m}^{-2} \text{ yr}^{-1}$ . The surface area of Ford Lake is  $4.039 \times 10^6 \text{ m}^2$ . We independently calculated

the retention of SRSi in Ford Lake by mass balance over two annual periods, one of which included the April 2004 diatom bloom and one of which included the weaker 2005 bloom. From February 2004 to January 2005, areal retention of SRSi was  $1.09 \text{ mol Si m}^{-2} \text{ yr}^{-1}$ . From September 2004 to August 2005, areal retention of SRSi was  $0.94 \text{ mol Si m}^{-2} \text{ yr}^{-1}$ . In 2006, from 1 April to 27 July only  $0.22 \text{ mol SRSi m}^{-2}$  was retained, whereas SRSi retention from 28 July to 8 September was  $0.41 \text{ mol m}^{-2}$ .

## 4. Discussion

### 4.1. Spring diatom dynamics

Hydrologic differences are sufficient to account for interannual differences in spring diatom crops in this riverine ecosystem. Wetter conditions and stronger river flow in April 2005 and 2006 compared to 2004 prevented diatoms from building large population densities in Ford Lake.

The most limiting nutrient for diatom growth in the Huron River during 2005 appeared to be P. Si limitation was induced in only one experiment. In experiment B5, commenced on 22 April 2005, enclosed diatoms were able to consume almost all the SRSi in Control treatments. Additional Si uptake and production of Part-Si occurred when SRSi was added. However, it must be emphasized that the bioassay experiments were conducted in 2005, when ambient lake SRSi remained at  $40 \mu\text{M}$  or greater. Judging from experimental results, in 2004 SRSi concentrations became depleted to such a degree that potential for Si limitation could have existed.

Alkaline phosphatase assays further support the contention that P was a limiting nutrient. In all experiments that were measured, AP increased during incubation compared with the levels originally present in lake water. This indicates that P uptake by enclosed populations depleted the resource enough to trigger a physiological indication of P limitation. The fact that the mean ratio of nitrate uptake to DP uptake in experiments was 56.0 (Table 6), well above the Redfield Ratio of 16 (Parsons et al., 1984), and well above the empirical threshold for P limitation (Hecky and Kilham, 1988) is further evidence of P limitation.

Growth experiments demonstrated that diatom populations could increase in Ford Lake water well after in situ populations had collapsed. One cause cited for diatom population decline is parasitism by chytrid fungi (Von Donk and Ringelberg, 1983; Holfeld, 1998; Happey, 1970), and chytrids were observed on Ford Lake diatoms. Prevalence of chytrid infection remained low, reaching at maximum only one quarter of the high prevalences encountered by Von Donk and Ringelberg (over 90% infected in their study), and prevalence did not vary systematically among years in Ford Lake. Von Donk and Ringelberg showed temperature to be influential in chytrid success. Although air temperatures were  $4^\circ$  cooler from mid-April to mid-May in 2005 compared with 2004, there was no difference between 2006 and 2004. In short, there is no consistent evidence that chytrid infection played a major role in diatom dynamics in Ford Lake. Additionally, chytrids did not prevent diatoms from increasing in the growth experiments.

The most obvious loss rate eliminated by the growth experiment design is sinking. During thermal stratification, Ford Lake typically mixes reliably to no more than 3 m over night. The ratio of measured sinking rate ( $0.66 \text{ m d}^{-1}$ ) to mixed layer depth (3 m) yields an imputed loss rate ( $0.22 \text{ d}^{-1}$ ) similar in magnitude to the estimated maximum in situ growth rate of the diatom populations. Sinking is thus the major reason that diatoms do not dominate during stratified summer conditions, although our whole lake experiment revealed that they have the potential to do so. In 2005, flushing time increased during May to values similar to those associated with the large diatom bloom of April 2004, but diatoms did not increase. Our model calculations point to sinking as the sole reason.

Jewson et al. (1981) examined the dynamics of a spring diatom bloom in the Lough Neagh in Northern Ireland. They measured a diatom crop increase of  $4\% \text{ d}^{-1}$  with the lake flushing rate ranging from  $0.23\%$  to  $0.57\% \text{ d}^{-1}$ . This flushing rate is far smaller than that of Ford Lake. They concluded that losses from washout were insignificant compared with the diatom growth rate, although it was noted that flushing may delay the onset of growth during slower growth periods. Rates of parasitism by chytrids were measured for *A. italica* and ranged from  $85 \text{ cells ml}^{-1}$  infected in early March to over  $400 \text{ cells ml}^{-1}$  in late March, corresponding to at most 5% of the population. Other diatom species were not adversely affected, and they believed chytrids did not play a role in diatom succession. Zooplankton had an estimated diatom consumption rate corresponding to only about 0.15% of the standing crop per day. Jewson et al. concluded that the availability of silica was the determining factor in limiting diatom growth. The lower flushing rate of Lough Neagh compared to Ford Lake enabled silica limitation to result. They noted that when silica was not limiting, sedimentation became the main determinant of diatom succession, as seems to be the case in Ford Lake when thermal stratification develops.

Model simulations for Diatom Si in Fig. 4 are in reasonably good agreement with the available biovolume data, even though there was no attempt to use the Diatom Si data when estimating model parameters. The entire data set from spring of 3 years can be largely explained by a single maximum growth rate, a single physiological uptake function for Si, a single sinking loss rate, and transition from well-mixed to stratified conditions during a critical 1 week period around 1 May each year. Although automated data loggers were not installed in the lake during the late April to early May periods, it is certainly consistent with periodic sampling observations that the onset of thermal stratification is about that time every year. Only 4 parameters had to be statistically estimated to fit SRSi data from the 3 years. Of these 4, maximum growth rate had the greatest relative effect on model performance, by far, and the onset dates for stratification were almost identical across years.

#### 4.2. Induction of diatom bloom in August

We were able to test the hypothesis that loss rates were dominated by sinking rather than by parasitism, herbivory, or warm water temperatures by purposefully destabilizing the

lake in August 2006. Total fluvial discharge during the first 2 weeks of August was less than half of that during April 2004 when diatoms nearly depleted the lake of SRSi. Losses from washout therefore seemed inconsequential. Growth experiments conducted during 2005 had already established that diatoms were capable of flourishing in Ford Lake water under summer environmental conditions provided that sinking was eliminated as a loss factor.

By selective withdrawal of hypolimnetic water we were able to reduce the thermal gradient between epilimnion and hypolimnion, and a series of partial to complete mixing events occurred during the experimental period. Drawdown of SRSi began soon after initial destratification, and continued until mid-August. Withdrawal of DP from the water into diatom biomass followed by sedimentation of some of the resulting crop sequestered the nutrients that otherwise could have been used by cyanobacteria populations, and large populations of the nuisance organisms did not develop in 2006.

#### 4.3. Sediment Si

Donar et al. (1996) measured biogenic Si from a single core drawn from a site in Ford Lake with slightly less than 5 m water depth, but near the 5.2 m site of 3 of our cores. We digitized the data ( $\text{mg SiO}_2 \text{ g}^{-1}$  dry mass) from their Fig. 2 from 0 to 25 cm sediment depth and calculated the mean biogenic Si to be 3.01 (SD = 0.76,  $n = 26$ ) percent of dry mass. This number is significantly higher than the 1.7% figure that we found. However, we note that the digestion method cited by Donar et al. (Davis and Simmons, 1979) involves 48 h digestion in a solution containing hydrofluoric acid. It seems possible that some of the abundant clay silicates in the mud may have been dissolved by this more aggressive digestion method.

Our estimates of biogenic Si accumulation in Ford Lake ( $0.9 \text{ mol Si m}^{-2} \text{ yr}^{-1}$ ) are close to the amount of SRSi retention estimated by mass balance ( $0.94\text{--}1.09 \text{ mol Si m}^{-2} \text{ yr}^{-1}$ ) during years with weak and strong planktonic diatom crops. We conclude that our two independent methods for estimating biogenic Si retention in Ford Lake are in reasonably good accord. This adds confidence to our estimation methods for mass balance and nutrient retention.

## 5. Conclusion

The nutrient factor-limiting diatom biomass in Ford Lake is usually phosphorus. The expression of growth potential during isothermal conditions is controlled by a physical factor: river flow and resulting washout rate. Sinking becomes the dominant loss factor when thermal stratification develops. Artificial destabilization of the water column can trigger diatom growth during the summer to levels usually seen only during the spring. Thus whole lake experimental manipulation can transform the biological community and suppress nuisance blooms of cyanobacteria.

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