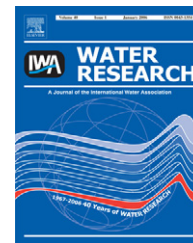


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Interannual variation in diatom bloom dynamics: Roles of hydrology, nutrient limitation, sinking, and whole lake manipulation

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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 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 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 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°N , 83.56°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°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°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°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°C , and both initial and time series fluorescence were measured with a Turner Designs Model 10 fluorometer using the long wavelength UV

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