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Controls on algal abundance in a eutrophic river with varying degrees of impoundment (Kalamazoo River, Michigan, USA)

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Abstract

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This study examined how nutrients and hydraulic flushing interact to regulate growth of phytoplankton in the Kalamazoo River (Michigan, USA), which has seven reservoirs with summer residence times ranging from <1 to 12 days. The largest reservoir, Lake Allegan, suffers from eutrophication and resultant impairments of beneficial uses, problems being addressed by a TMDL focused on control of phosphorus. Water residence time was the most important control on algal growth in the various impoundments, including Lake Allegan, where residence time remained <12 days through the summer. Based on longitudinal surveys, free-flowing river reaches appeared to remove phytoplankton, whereas a series of old decommissioned dams above Lake Allegan evidently contributed to algal biomass accumulation in the river. Nutrient concentrations were generally high throughout the river system; thus, algal growth may not be nutrient-limited at present. Phytoplankton in the two largest reservoirs was dominated by diatoms and green algae during late summer, despite nutrient concentrations that would tend to favor cyanobacteria in lakes. The relative availability of phosphorus (P), nitrogen (N), and silicon (Si) can indicate how algal growth may respond if nutrient concentrations were to decrease in the future. Nutrient ratios suggest that N and Si could be important in addition to P, depending on the reservoir and the season. In reservoirs with short water residence times, strategies to control eutrophication by reducing phosphorus loading may not yield results as readily as they do in lakes; hydraulic flushing, other nutrients, and upstream impoundments must also be considered.

Key Words: rivers, reservoirs, TMDL, phosphorus, nitrogen, algae, phytoplankton, eutrophication

Impoundments are ubiquitous in rivers of the industrialized world. Impoundment changes the characteristics of a river from a fluvial environment to a more lacustrine one, increasing water residence time and enhancing sediment accumulation, nutrient transformation, and autochthonous primary production (Friedl and Wüest 2002). Water quality problems associated with excess nutrient loading to rivers often are manifested as phytoplankton blooms in reservoirs along the river's course. Impoundments can be viewed as lying along a river-lake continuum from slowly flowing rivers to waterbodies more akin to lakes, with water residence times of several weeks or longer (Straskraba 1999). In addition to traditional dams for hydropower and reservoir creation, many kinds of structural modifications to rivers produce some degree of impoundment, including low-head navigation dams, road crossings, pipelines, and diversion dams, and thus the range of impoundment scenarios is quite wide.

Phytoplankton often flourish in impounded reaches with sufficiently long residence times due to constant riverine inputs of nutrients, increased light penetration as suspended solids settle, and warming water temperatures (Pridmore and McBride 1984, Soballe and Kimmel 1987, Heiskary and Walker 1995, van Nieuwenhuyse and Jones 1996, Straskraba 1999). As river water is slowed in a reservoir and phytoplankton growth proceeds, nutrients are drawn down and may eventually become limiting. Potentially limiting nutrients include phosphorus (P), nitrogen (N), and, in the case of diatoms, silicon (Si). The availability of these nutrients relative to the elemental composition of algal biomass provides an indication of which one will eventually become the limiting factor for algal growth (Sterner and Elser 2002). Understanding the

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transition between control of algal growth by water residence time versus by nutrient availability or light is critical for management of eutrophication in impounded rivers.

This study examined algal abundance in the lower Kalamazoo River of southwestern Michigan, USA, where there are several impoundments producing reservoirs with a range of water residence times (Fig. 1). The largest one (Lake Allegan) suffers from eutrophication and resultant impairments of beneficial uses, problems being addressed by a phosphorus Total Maximum Daily Load (TMDL) under Section 303(d) of the Clean Water Act, under the direction of the Michigan Department of Environmental Quality (MDEQ). Water quality impairments in Lake Allegan include low transparency, low dissolved oxygen, and an undesirable fish community (thought to be related to low oxygen). The cause of these problems has been ascribed to excessive phytoplankton growth and the consequent high oxygen demand, presumably at night and upon decomposition of the algal biomass (Heaton 2001). An upstream reservoir of similar dimensions called Morrow Lake, which reportedly has better water quality and a more desirable fish community, has been used by the MDEQ as a reference to set the target phosphorus load for the Lake Allegan TMDL. Several smaller impoundments as well as free-flowing reaches lie between these two larger reservoirs.

This study evaluated the relative importance of control of algal abundance by water residence time vs. nutrients in Lake Allegan and other impounded reaches of the river system, with the ultimate objective of understanding whether reductions in phosphorus and other nutrients in the river are likely to improve water quality in these kinds of reservoirs. We hypothesized that the relatively short water residence time relative to algal growth rates limits phytoplankton growth within all of these reservoirs including Lake Allegan, making nutrient availability secondary in importance.

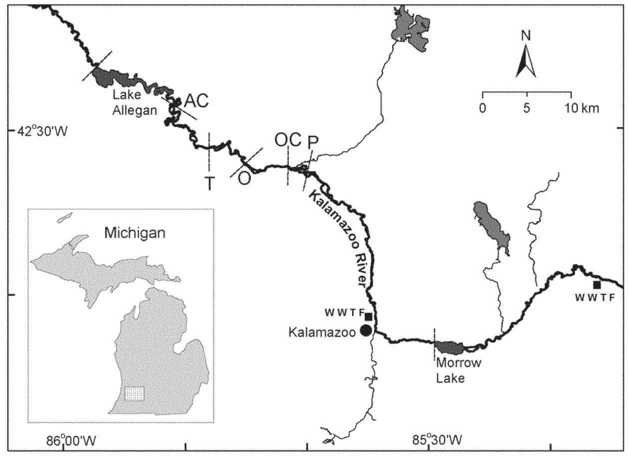

Figure 1.-The lower Kalamazoo River, showing the functioning hydroelectric impoundments producing the two largest reservoirs (Lake Allegan and Morrow Lake) as well as the smaller impoundments (from upstream to downstream, P = Plainwell dam, OC = Otsego City Dam, O = Otsego Dam, T = Trowbridge Dam, AC = Allegan City Dam) and the two major waste water treatment facilities (WWTFs) serving the cities of Battle Creek (just east of the map) and Kalamazoo.

Materials and methods

Study site

The Kalamazoo River watershed is located in southwestern Michigan. Land cover in the 5,230-km^2 watershed is primarily agriculture (58%) and forest (25%), and the two largest urban centers along the river are Battle Creek (54,000 inhabitants) and Kalamazoo/Portage (122,000). The mean annual discharge of the river above Lake Allegan is 38 m^3/s (Wesley 2005). Seven run-of-the-river impoundments (five small decommissioned ones and two larger ones producing hydropower) are located on the lower river (Fig. 1).

The largest reservoirs, Morrow Lake and Lake Allegan, are shallow (Table 1) and do not show persistent thermal

Table 1.-Morphometry, mean transparency, and the range of water residence time during sampling in the impoundments on the lower Kalamazoo River. Morphometric data are from the MDEQ and the U.S. Geological Survey. Secchi depth data are means for April-September from MDEQ (S. Heaton, MDEQ, unpublished data; n/a = not available). Residence times are based on the range of discharge observed during the study period. Data were not available for the impounded reach behind the Otsego City Dam; its dimensions are similar to the other smaller impoundments on the river.

	Morrow Lake	Plainwell Dam	Otsego Dam	Trowbridge Dam	Allegan City Dam	Lake Allegan
Area (10^3 m^2)	4,451	407	130	431	546	6,422
Volume (10^3 m^3)	7,400	529	114	322	986	21,200
Mean Depth (m)	1.66	1.30	0.88	0.75	1.80	3.3
Secchi Depth (m)	0.97	n/a	n/a	n/a	n/a	0.68
Residence Time (days)	2-7	0.05-0.73	0.01-0.15	0.02-0.21	0.08-0.65	3-11

stratification during the summer. No significant tributaries other than the Kalamazoo River flow directly into these two reservoirs. Water discharged at the dams is essentially drawn from the entire water column, and thus samples of the outflow represent the entire range of depth. Water levels are kept nearly constant behind the impoundments. Morrow Lake is located 69 km upstream of Lake Allegan.

The largest reservoir, Lake Allegan, clearly is hypereutrophic, with previous monitoring showing high summer chlorophyll *a* concentrations (67 µg/L), low transparency (Secchi depth 0.6 m), and high total phosphorus concentrations (96 µg/L; data are means for April-September 1998-2000; Heaton 2001). Morrow Lake has a morphometry similar to Lake Allegan, but with better water quality: no reports of nuisance algal blooms, lower chlorophyll *a* (23 µg/L), higher transparency (Secchi depth 1.0 m), and lower total phosphorus (58 µg/L; Heaton 2001). Morrow Lake's water quality and fish community were considered by MDEQ to be a realistic and desirable target for Lake Allegan. The premise of the TMDL is that a reduction of total phosphorus concentrations in Lake Allegan from 96 to 60 µg/L should produce a concomitant reduction in phytoplankton growth, thereby improving water quality conditions. Phosphorus limitation of phytoplankton has not been assayed in either reservoir but was presumed to occur because that is the most common situation in Michigan lakes.

Two substantial wastewater treatment facilities (WWTFs) influence the sampling reach (Fig. 1). The Battle Creek WWTF is 23 km upstream of the Morrow Lake inflow sampling location, and the Kalamazoo WWTF is 10 km downstream of the Morrow Lake outflow sampling location and 63 km above Lake Allegan. These effluents, together with some industrial effluents that are discharged into the main channel, likely account for about a third of the total P load reaching Lake Allegan (Heaton 2001).

The smaller impoundments are remnants of century-old hydroelectric dams where the turbines, gates, and spillways have been removed. The only remaining structures are the concrete walls and the foundations forming the sills. Backwaters produced behind these impoundments range in mean residence times from 0.01-0.73 day (Table 1). Flow is generally visible in the thalweg of these backwaters, and thus we refer to these reaches as semi-impounded.

Sample collection

In 2003, samples of inflow and outflow waters at Lake Allegan and Morrow Lake were collected in early spring (March 13, 2003) when the reservoirs were ice-covered, and weekly during summer (May 14-August 19, 2003), when nuisance algal blooms tend to occur. In 2004, inflow and outflow waters were sampled once during ice cover in early spring (Feb 10, 2004) and monthly during summer (May 26-September 20, 2004). Lake Allegan inflow and outflow and Morrow Lake inflow waters were sampled with a Van Dorn sampler, and Morrow Lake outflow waters by an extendable hand-held dipper. Temperature, pH, conductivity, and dissolved oxygen were measured at each sampling with a Hydrolab Sonde. Phytoplankton samples were collected once in July 2005 (reservoir outflows) and again in September 2005 (reservoir outflows plus Lake Allegan inflow). Dominant phytoplankton genera were identified but not enumerated.

Unexpectedly high chlorophyll concentrations in the Lake Allegan inflow led us to investigate whether this chlorophyll originated as algae exported from Morrow Lake or from new algal growth behind the smaller impoundments. Three longitudinal surveys of the river between Morrow Lake and Lake Allegan were conducted at varying discharges over a two-year period (2003-2004). Sampling dates followed periods of stable discharge for at least one week. The surveys began at the Morrow Lake inflow and concluded at the Lake Allegan outflow.

Laboratory analyses

Water samples were filtered on the day of collection through 0.45-µm membrane filters and refrigerated. Nutrients were measured by colorimetric analyses using long-pathlength spectrophotometry: ammonium by the phenylhypochlorite method (Aminot *et al.* 1997), soluble reactive phosphorus (SRP) by the acid molybdate method, and dissolved silicon by the ammonium molybdate method (Wetzel and Likens 2000). Total soluble phosphorus (in filtered water) and total phosphorus (unfiltered water) were determined by colorimetric analysis after persulfate digestion (Valderrama 1981, Langner and Hendrix 1982); standards included adenosine triphosphate to ensure efficient oxidation of organic matter. We calculated soluble organic P as the difference between total soluble P and soluble reactive phosphorus (SRP), and particulate P as the difference between total P and total soluble P. Nitrate was measured by membrane-suppression ion chromatography. Particulate matter was filtered onto Pall A/E glass fiber filters and immediately frozen. Material on the filters was later extracted overnight in the refrigerator with 95% ethanol, and chlorophyll *a* was measured by narrow-band fluorometry (Welschmeyer 1994).

Results

River discharge tended to be highest February-May and lowest June-September in both 2003 and 2004 (Fig. 2). Discharge in the 2003 sampling period was 78% of the long-term mean discharge for March-September, and in the 2004 sampling period it was 113% of the long-term mean. This study focused on the latter part of the 2003 sampling period, when the lower discharge produced longer residence times in the reservoirs, thereby enhancing the potential for algal growth and, presumably, the resultant water quality impairments in Lake Allegan.

Water residence times in the reservoirs vary inversely and linearly with discharge because the reservoir volumes are approximately constant. Water residence times were calculated from USGS discharge records and reservoir volumes (Table 1), assuming complete mixing of through-flowing river water with the entire reservoir volume. Lake Allegan had a longer residence time than Morrow Lake, but on sampling dates it remained <12 days (Fig. 3).

Field measurements indicated no persistent thermal stratification or oxygen depletion in the two reservoirs (Reid 2005). Thermal profiles in the deepest part of each reservoir were measured from a boat during August, when thermal stratification of local lakes was maximal, and even at the deepest water near the dams we found no evidence for persistent stratification. Deployment of a dissolved oxygen sensor that made continuous measurements over a diel cycle in late summer did not reveal nocturnal depletion of dissolved oxygen in the near-surface waters of either Lake Allegan or Morrow Lake. Thus, we found no evidence that the water column became anoxic during the summer in either reservoir, although the possibility remains that an anoxic stratum developed at night along the bottom.

Water temperatures increased over the sampling periods, with the reservoir outflow temperatures generally warmer than inflows (data not shown). The maximum summer outflow temperatures were 30°C and 27°C in 2003 in Lake Allegan and Morrow Lake, respectively, and 26°C in both reservoirs in 2004 (Reid 2005).

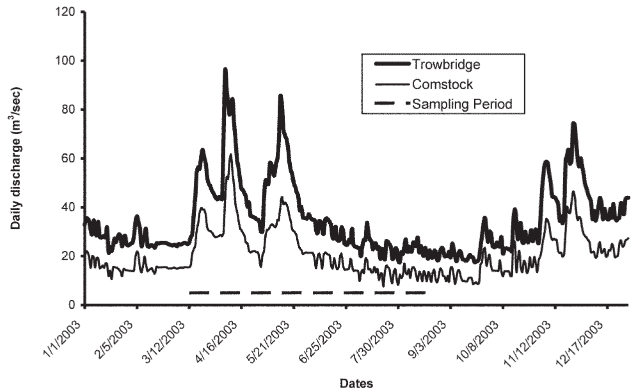

Figure 2.-Mean daily discharge below Morrow Lake (Comstock gauge) and above Lake Allegan (Trowbridge gauge) during 2003. Data from the U.S. Geological Survey.

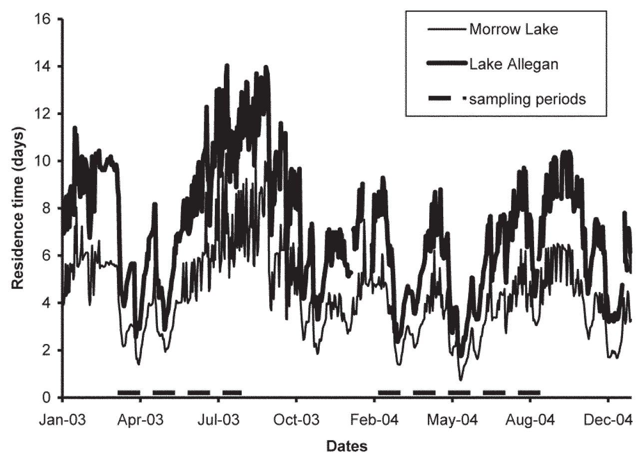

Figure 3.-Residence times during 2003 and 2004 for Lake Allegan and Morrow Lake, calculated from the U.S. Geological Survey's daily discharges.

Inflow and outflow comparisons for the largest reservoirs

Phytoplankton abundance, as indicated by chlorophyll *a* concentrations, generally increased as water passed through both Morrow Lake and Lake Allegan, with the largest increases during periods of longer residence times in 2003 (Fig. 4A, 4B, 5A, and 5B). The Morrow Lake outflow attained chlorophyll *a* concentrations comparable to those in Lake Allegan despite a shorter water residence time. The Lake Allegan inflow carried elevated chlorophyll *a* compared with the inflow to Morrow Lake, particularly at lower discharges.

Transparency was not measured in this study. Secchi depth over the period of April-September was measured by the MDEQ from 1998-2003 and averaged 0.68 m in Lake Allegan. The compensation depth above which net algal photosynthesis could occur was thus approximately twice this (Wetzel 2001), or 1.4 m. The mean depth of Lake Allegan is 3.3 m; therefore, sufficient light to support algal growth could penetrate about 40% of the water column. In Morrow Lake, Secchi depth measured by the MDEQ averaged 0.97 m (1998-2003), and the compensation depth was thus approximately 1.9 m. The mean depth of Morrow Lake is 1.66 m; therefore sufficient light to support algal growth could penetrate throughout the entire water column. Visual inspection of the outflow waters of both reservoirs indicated particulate material was largely composed of algae and organic detritus.

Total phosphorus concentrations were high in both reservoirs compared to most inland lakes of the region (Fig. 4C, 4D, 5C, and 5D). Lake Allegan often showed a reduction in concentration from inflow to outflow, indicating that the reservoir retained some of the phosphorus inputs, whereas Morrow Lake appeared to be a source of phosphorus to through-flowing river water at longer residence times in

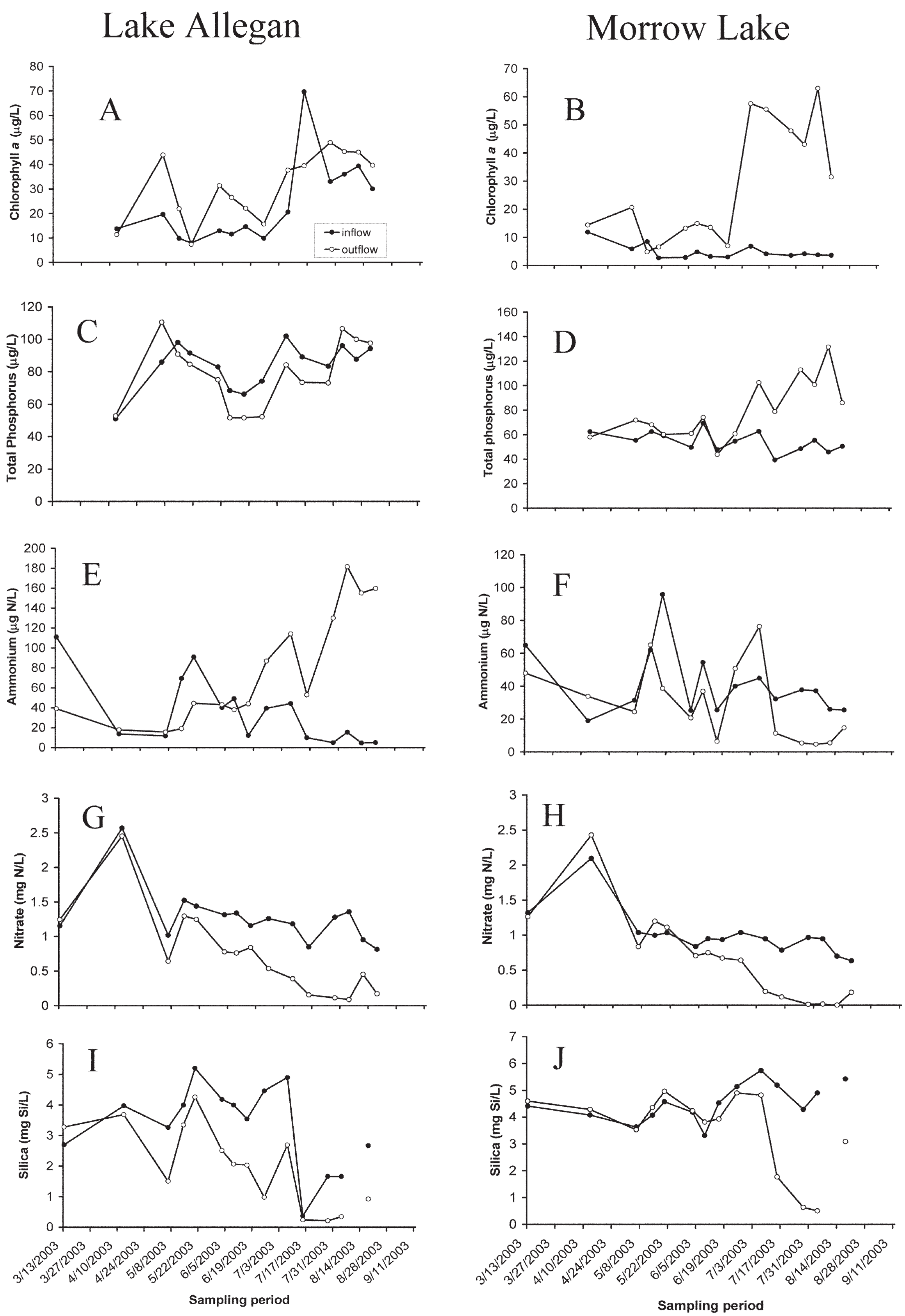

Figure 4.-Chlorophyll *a*, total phosphorus, ammonium, nitrate, and silicon concentrations in the inflow and outflow waters at Lake Allegan (left) and Morrow Lake (right) during the 2003 sampling period.

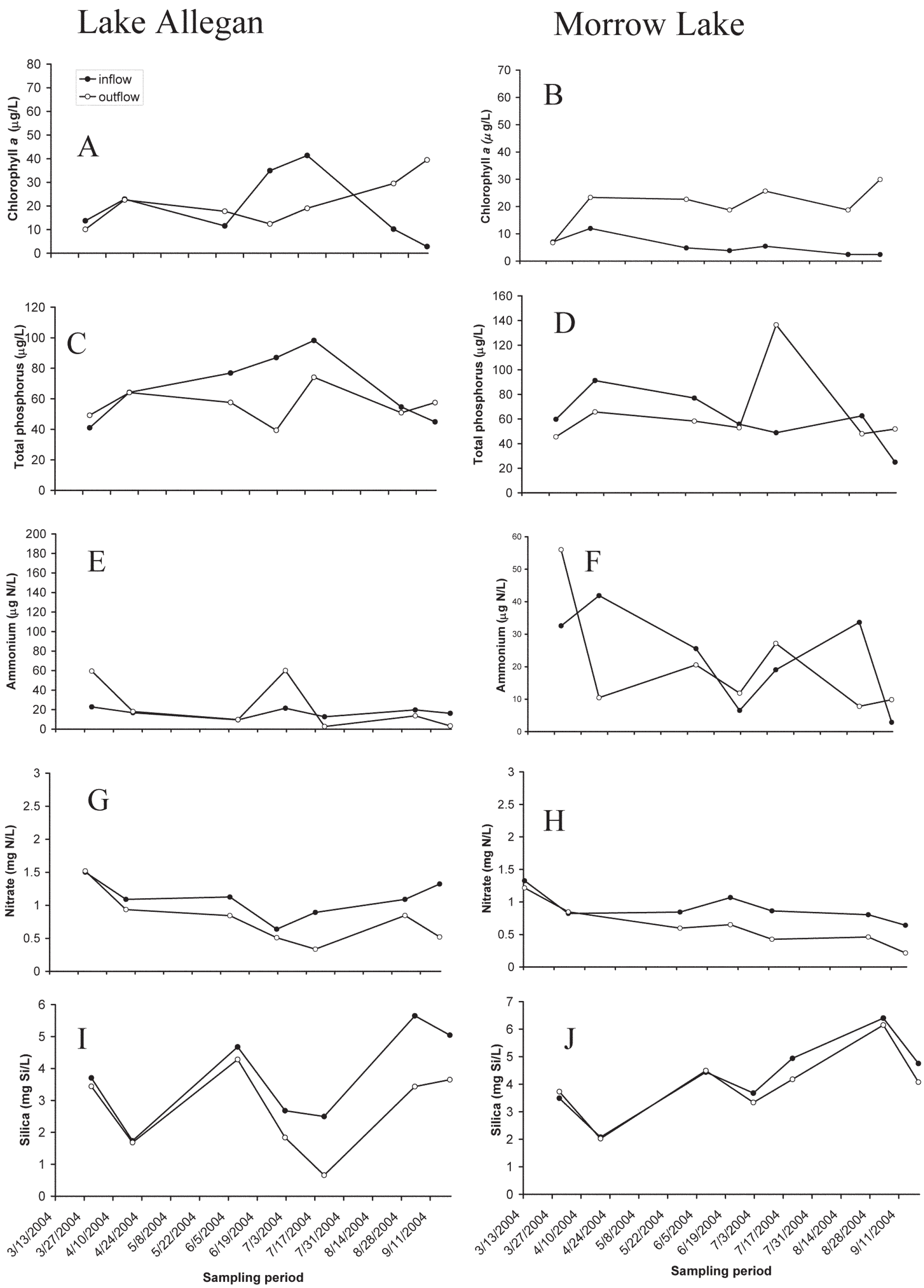

Figure 5.-Chlorophyll *a*, total phosphorus, ammonium, nitrate, and silicon concentrations in the inflow and outflow waters at Lake Allegan (left) and Morrow Lake (right) during the 2004 sampling period.

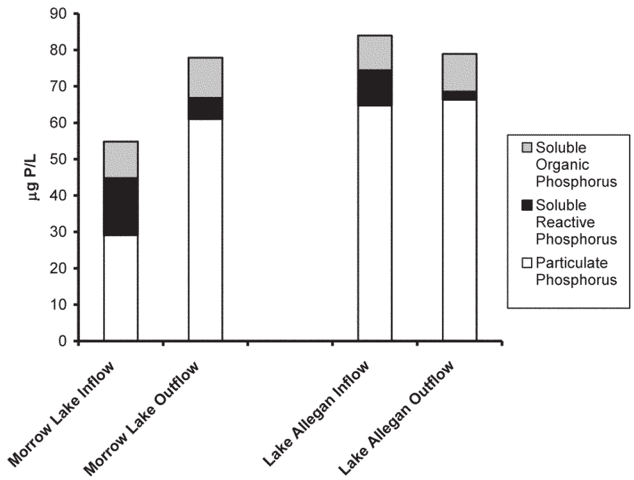

Figure 6.-Mean phosphorus concentrations for Morrow Lake and Lake Allegan during the 2003 samplings (14 dates).

July and August 2003. Comparison of mean patterns in P forms for the 2003 sampling period indicated that soluble reactive phosphorus decreased and soluble organic phosphorus showed little change from the inflow to outflow in both reservoirs (Fig. 6).

Ammonium concentrations were variable and showed no consistent change in the reservoirs at higher discharges (Figs. 4E, 4F, 5E, and 5F). Comparing the outflow to the inflow at lower discharges in 2003, Morrow Lake showed a consistent decline in ammonium concentrations starting in mid-July, in contrast to a marked increase in ammonium observed in Lake Allegan during the same time. There was a consistent decline in nitrate concentrations from the inflow to the outflow waters in both reservoirs except during the early spring sampling dates (Figs. 4G, 4H, 5G, and 5H).

Dissolved silicon concentrations decreased from inflow to outflow in Lake Allegan on most sampling dates, suggesting substantial diatom production, and outflow waters showed near depletion of silicon in late summer (Figs. 4I, 4J, and 5I). Inflow waters to Lake Allegan also showed decreased concentrations of silicon at lower discharges in 2003. In Morrow Lake, substantial silicon removal did not occur until the lower discharges in 2003, and there was much less change at higher discharges in 2004 (Fig. 5J).

Factors controlling algal growth

Diatoms and green algae dominated the phytoplankton of both Lake Allegan and Morrow Lake in the late summer samplings (Table 2). Green algae dominated in the Lake Allegan outflow and were also the most common algae in the inflow, with diatoms also moderately abundant. In the Morrow Lake outflow, the most common phytoplankton were diatoms, with green algae moderately abundant.

Ratios of available nutrient forms can indicate the nutrient most likely to limit phytoplankton growth (Wetzel 2001). Algal growth in these nutrient-rich waters may not be nutrient-limited at present, but the ratios can provide insight into the likely result of future reductions in nutrient concentrations, such as the total phosphorus reduction prescribed by the Lake Allegan TMDL. The N:P molar ratio for phytoplankton biomass in lakes and oceans tends to be between 10:1 and 20:1 (Wetzel 2001, Sterner and Elser 2002). Available forms are here considered to include dissolved inorganic N (DIN = nitrate + ammonium) and total P. Molar ratios of available N:P (DIN:TP) in outflow waters of Lake Allegan and Morrow Lake during the 2003 sampling period indicated a shift from potential P limitation in April-June to potential N limitation in late July-August, while inflow waters remained potentially P-limited during that time (Fig. 7). Thus, there appear to be changes in potential nutrient limitation between the inflows and outflows of these reservoirs, with a greater difference across Morrow Lake.

The concept of elemental ratios in algal biomass in relation to ratios of available nutrients can be extended to the case of diatoms, which require silicon as well as N and P and

Table 2.-Dominant algal genera observed in samples collected during the period of maximum phytoplankton biomass in July and September 2005.

Site	Very common	Moderately common
Morrow Lake Outflow	*Fragilaria, Cyclotella, Nitzschia, Cryptomonas, Synedra*, ciliates, small chrysophytes	*Oocystis, Pediastrum, Scenedesmus, Sphaerocystis*
Lake Allegan Inflow	*Scenedesmus, Sphaerocystis, Pediastrum*	*Cyclotella, Melosira*
Lake Allegan Outflow	*Cryptomonas,Sphaerocystis, Scenedesmus, Pediastrum, Oocystis, Cyclotella, Synedra*, small greens	*Melosira*

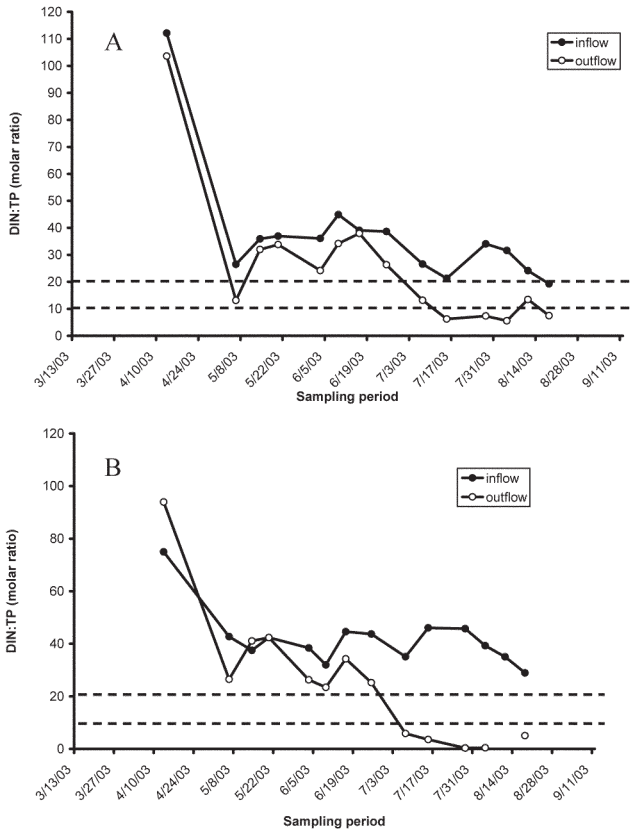

Figure 7.-Molar ratios of available N:P in the inflow and outflow waters at Lake Allegan (A) and Morrow Lake (B) during the 2003 sampling period. DIN = dissolved inorganic nitrogen (nitrate + ammonium) and TP = total phosphorus. Dashed lines show the thresholds of potential nitrogen limitation (DIN:TP <10) and phosphorus limitation (DIN:TP >20). In between these thresholds the two nutrients are potentially co-limiting.

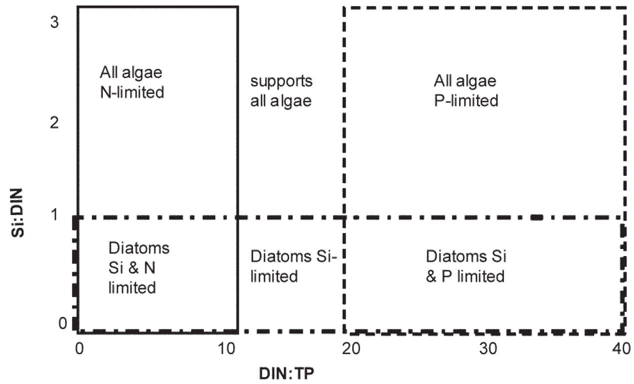

Figure 8.-Molar ratios of available nutrients serve as approximate indicators of potential nutrient limitation. The thresholds indicated by the boxes are based on the elemental ratios in algal biomass (N:P ~10-20 and, for diatoms, Si:N ~1).

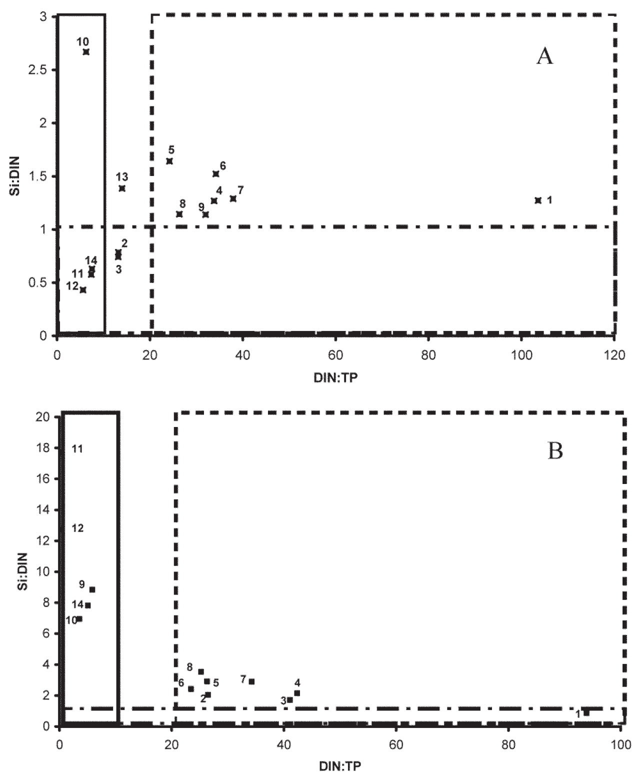

Figure 9.-Molar ratios of available nutrients in outflow waters of Lake Allegan (A) and Morrow Lake (B) during the 2003 sampling period. Potential nitrogen limitation is represented by solid box, phosphorus limitation by dashed box, and silicon limitation by Si: DIN ratios below the dotted-dashed line. The numbers correspond with the order of sampling dates beginning with April (1) through ending with August (14). Note different scales.

tend to have a molar Si:N of ~1:1 (Turner *et al.* 2003). A plot of Si:DIN versus DIN:TP indicates potential nutrient limitation for diatoms and for other algae (Fig. 8). When diatoms experience Si limitation, other forms of algae can become dominant.

Molar ratios of available nutrients in outflow waters of Lake Allegan and Morrow Lake indicate that all three nutrients are potentially important as limiting factors for algal growth in this river system (Fig. 9). Silicon limitation of diatom growth was potentially important in Lake Allegan, particularly late in the summer when N was more likely than P to limit all algae. In contrast, Si limitation would be less likely in Morrow Lake.

The relative importance of residence time and total P in predicting algal biomass in the reservoir outflows was investigated using linear regression analyses (Table 3). Residence time and total P, either separately or combined in a multiple

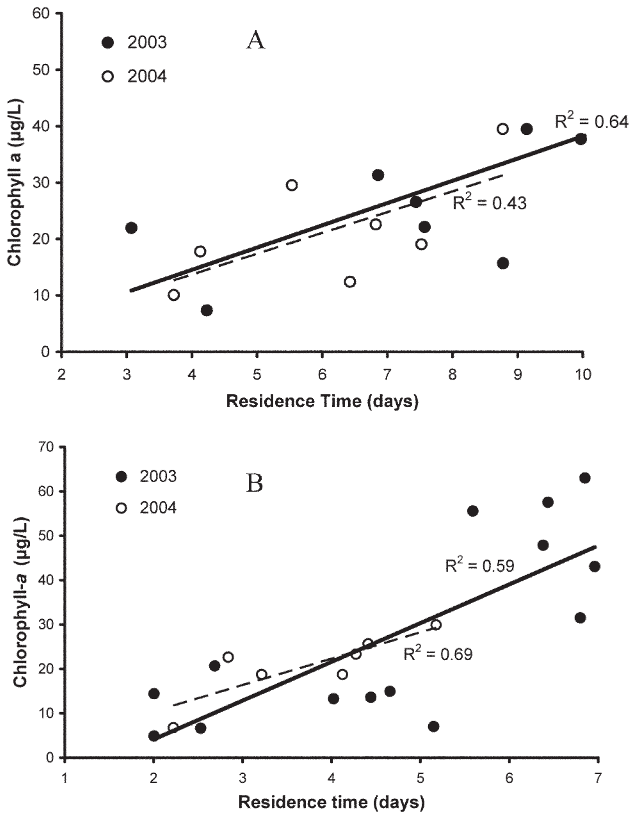

Figure 10.-Relationships between residence time and algal biomass (chlorophyll *a* concentrations) for Lake Allegan (A) and Morrow Lake (B). Linear regression models were fit separately for each of the two years; details are given in Table 3.

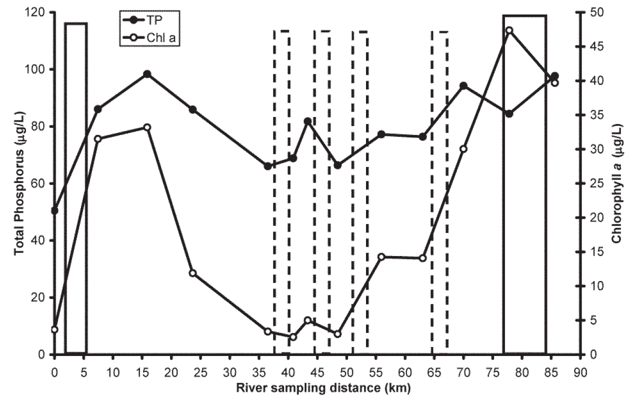

Figure 11.-Longitudinal river survey of total phosphorus and chlorophyll *a* concentrations at low discharge (August 18, 2003; 20 m^3/s at the Trowbridge gauge). The solid boxes represent the larger reservoirs (Morrow Lake and Lake Allegan) and dashed boxes represent the smaller impoundments (Plainwell + Otsego City, Otsego, Trowbridge, and Allegan City dams).

linear regression model, explained a substantial amount of variation in the algal biomass in Morrow Lake, whereas in Lake Allegan residence time and total P were equally good predictors of algal growth, but no improvement was obtained by considering them together. The relationship between residence time and chlorophyll *a* illustrates the differences between years; the slopes were similar between 2003 and 2004, although 2003 spanned a wider range of residence time (Fig. 10). The Morrow Lake data from 2003 suggest a residence-time threshold of around 5 days, above which algal growth increases more rapidly.

Longitudinal patterns in phosphorus and algal biomass

The longitudinal profiles of total phosphorus and chlorophyll *a* for the low-discharge sampling date showed that total phosphorus concentrations increased within Morrow Lake and in the vicinity of Kalamazoo, where the river receives wastewater effluent, then gradually declined downstream until the river reached the decommissioned impoundments (Fig. 11). Total phosphorus concentrations increased modestly through the reaches with the smaller impoundments above Lake Allegan. Chlorophyll *a* concentrations increased considerably in Morrow Lake, followed by a marked decline downstream,

Table 3.-Regression coefficients and p-values for residence time (RT) and/or outflow total phosphorus (TP) as predictors of outflow chlorophyll *a* for the spring and summer 2003 (15 samplings), 2004 (7 samplings) and combined 2003 and 2004 sampling periods.

	Morrow Lake chlorophyll *a*			Lake Allegan chlorophyll *a*		
	2003	2004	both years	2003	2004	both years
RT	R^2= 0.59 p<0.01	R^2=0.69 p=0.20	R^2=0.53 p<0.01	R^2=0.59 p<0.01	R^2=0.42 p=0.11	R^2= 0.60 p<0.01
Outflow TP	R^2= 0.71 p<0.01	R^2=0.15 p=0.38	R^2=0.65 p<0.01	R^2=0.26 p=0.061	R^2=0.064 p=0.056	R^2= 0.36 p<0.01
RT & TP	R^2= 0.77 p<0.01	R^2=0.70 p=0.08	R^2= 0.76 p< 0.01	R^2=0.75 P<0.01	R^2=0.42 p=0.32	R^2= 0.60 p<0.01

then gradually increased again as the river passed through the decommissioned impoundments. Chlorophyll *a* concentrations peaked above Lake Allegan, followed by a decline within the reservoir (Fig. 11). This longitudinal pattern was evident but less marked at higher discharges (Reid 2005).

Discussion

Reservoirs with short water residence times cannot be managed for eutrophication as if they were lakes because of the limitations on algal growth imposed by hydraulic flushing, and when they occur serially along a river course, the influence of algae exported from upstream reservoirs may need to be considered in management planning. This study has shown that water residence time is likely to be the most important control on algal growth in the various impoundments of the lower Kalamazoo River including Lake Allegan. Nutrient concentrations are generally high throughout the river system, and thus algal growth may not be nutrient-limited at present. Light limitation may be of greater importance in Lake Allegan than in Morrow Lake, although in both reservoirs algae cause much of the light attenuation. If nutrient concentrations were to decrease in the future, nutrient ratios provide an indication of how the algal growth may respond. The nutrient ratios suggest that N and Si could be important in addition to P, depending on the reservoir and the season.

Comparison between reservoirs

Lake Allegan's residence time ranged from 3 to 11 days and Morrow's Lake residence time ranged from 2 to 7 days, depending directly on discharge. Residence times of around 7 days or less limit phytoplankton production and species composition (Thornton 1990). Chlorophyll *a* and total P concentrations in these two reservoirs were highest when residence time was the longest (and ice cover was not present). Compared to Lake Allegan, phytoplankton in Morrow Lake must have been more limited by its shorter residence time.

Benthic algal growth is not dependent upon residence time but could be controlled by light and nutrients. In Morrow Lake, phytoplankton growth is more limited by flushing and the water column is shallower; thus, more light is able to reach the lake bottom, potentially allowing more benthic algal growth. In the larger and deeper Lake Allegan, phytoplankton may be the dominant form of algal production. Benthic algae can become dislodged and contribute to chlorophyll concentrations in the water column. We have observed floating mats of benthic microalgae in Morrow Lake, but the contribution of benthic algae to the chlorophyll measurements reported here for the outflow samples is not known.

During summer when water residence time was relatively long and algal biomass was highest, nutrient concentrations changed from the inflow to the outflow in both reservoirs. Reservoirs with longer water residence times often function as sinks for total P (Soballe and Kimmel 1987, Straskraba 1999), but in this case changes were not great in water flowing through Lake Allegan, and Morrow Lake was a P source in late summer. Release of P from the sediments could explain the Morrow Lake source, and this might be enhanced at the warmest part of the year, but we are unsure why that would not occur in Lake Allegan as well. In Morrow Lake nitrate concentrations approached zero at the lowest discharges, while in Lake Allegan they did not fall as low (Fig. 4G and 4H). Morrow Lake's low summer nitrate concentrations may have resulted from benthic algal uptake as well as sediment denitrification, which can be a significant sink for nitrate even when the overlying water is oxic (Wall *et al.* 2005). Lake Allegan's apparent ammonium source may be from sediment mineralization of organic nitrogen or from dissimilatory nitrate reduction to ammonium, and its decrease in nitrate concentrations may have resulted from phytoplankton uptake as well as denitrification.

The greater degree of potential N limitation in Morrow Lake could have been caused by ammonium and nitrate uptake by benthic algae in shallower waters of the reservoir, due to the greater light availability compared to Lake Allegan. The Morrow Lake vertical profile showed that ammonium concentrations near the dam increased from 50 µg N/L near the surface to 90 near the bottom at 6-m depth (Reid 2005; data not shown). In Lake Allegan the potential for N limitation was not as great, perhaps due to greater ammonium production and/or less benthic algal uptake within the reservoir. Ammonium is generally preferred over nitrate as an N source for phytoplankton (Reynolds 1984). Based on N:P ratios, N was never potentially limiting in the inflow waters of either reservoir, although it was potentially limiting in the outflow waters during late summer (Fig. 7). High P and limited N availability normally favors N-fixing cyanobacteria in lakes (Wetzel 2001), but their relatively slow growth rates (Reynolds 1984) may have precluded their response in these reservoirs of short residence times.

The silicon depletion hypothesis (Conley *et al.* 1993) maintains that an increase in nutrient loading causes an increase in phytoplankton production, especially as diatoms. Diatom growth depends on the uptake of dissolved Si, and consequently Si concentrations can become limiting relative to N and P availability. In July 2003 in Lake Allegan, the Si:N ratio fell below 1:1 at the same time the chlorophyll *a* concentrations peaked. Other types of algae that do not require Si can then dominate the phytoplankton, including noxious bloom-forming species (Turner *et al.* 2003). Thus Si depletion could indirectly promote harmful algal blooms in Lake Allegan.

Algal growth in the river-reservoir system

Phytoplankton biomass increased in the larger reservoirs during the summer when residence times were above about 5 days, and diatoms and green algae dominated the phytoplankton on the two dates when samples were examined (Table 2). Given the short residence times of these reservoirs relative to algal growth rates, it makes sense that these waters would be dominated by faster-growing taxa, even in the presence of high nutrient concentrations that would favor dominance by colonial cyanobacteria in lakes without flushing.

Phytoplankton were abundant in the water exiting the reservoirs over the summer sampling periods, and this algal abundance should persist for some distance downstream. However, at least at low discharge, algae exiting Morrow Lake did not appear to be transported to Lake Allegan. Instead, that algal biomass largely disappeared and new algal growth appeared (Fig. 11). Possible loss processes that could account for the disappearance of algae in the free-flowing river below Morrow Lake include consumption by benthic filter feeders and sedimentation out of the water column. Benthic filter-feeding invertebrates were observed at high densities in this reach, including net-spinning hydropsychid caddisflies as well as an invasive clam, *Corbicula fluminea* (Strayer *et al.* 1999).

The smaller impoundments above Lake Allegan would not seem to encourage much additional phytoplankton growth considering their short water residence times of less than half a day (Table 1). Yet, chlorophyll *a* concentrations increased as the river passed through the smaller impoundments, until concentrations peaked above and within Lake Allegan (Fig. 11). Furthermore, algal biomass was often as high in the Lake Allegan inflow as in its outflow (Fig. 4A and 5A), possibly because significant off-channel waters occurring within the upstream semi-impounded reaches have much longer residence times and thus supply algae to the rivers, or because benthic algal growth becomes dislodged and contributes to suspended chlorophyll concentrations. Light conditions in these shallow semi-impounded reaches are ideal for benthic algal growth, and disturbance such as changing discharge as well as gas bubble buoyancy could dislodge these algae (van Nieuwenhuyse and Jones 1996). Further investigation would be required to test these hypotheses.

Implications for the TMDL

The Lake Allegan/Kalamazoo River TMDL is based on the assumption that reducing point and nonpoint sources of phosphorus would impact the phytoplankton growth in Lake Allegan and reduce harmful algal blooms. This study has shown that Lake Allegan has a residence time marginally long enough to permit much algal growth, and that Morrow Lake, the reference site for setting TMDL targets, has an even shorter residence time. Nutrient concentrations within both reservoirs are usually high enough to sustain high concentrations of phytoplankton, and phosphorus concentrations evidently are not the most important factor regulating phytoplankton growth. Residence time is paramount in limiting phytoplankton biomass in both Lake Allegan and Morrow Lake; nutrients are of secondary importance, and P, N, and Si are each potentially significant. Under these conditions, the availability of P may have to be greatly reduced before it would yield a noticeable decline in algal biomass and associated water quality problems.

The inflow to Lake Allegan displayed surprisingly high chlorophyll concentrations during the summer (Fig. 4A and 5A), and longitudinal patterns indicated that these did not simply reflect algal growth in Morrow Lake that was transported downstream (Fig. 11). If the net algal growth in the river above Lake Allegan is promoted by backwaters created by the smaller impoundments, removal of some or all of those impoundments to restore a free-flowing river channel may help diminish the problem of excessive algal growth in Lake Allegan, both by removing sources of algae and encouraging the development of populations of benthic invertebrates that consume algae.

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