Nutrient and light limitation of reservoir phytoplankton in relation to storm-mediated pulses in stream discharge

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With 6 figures and 1 table

Abstract: We investigated the dynamics of nutrient and light limitation of phytoplankton in a reservoir ecosystem in relation to storm-mediated variation in stream discharge, and how dynamics differed at a shallow site near stream inflows versus one in deep water near the lake outflow. Storm-mediated discharge events reduced the severity of nutrient limitation and increased the severity of light limitation, as predicted by a model of reservoir resource limitation developed by KIMMEL et al. (1990). The severity of nutrient limitation was negatively correlated with discharge to the lake; the correlation was strongest with discharge over the preceding 10–14 day period and weaker at shorter and longer time scales. However, discharge events also flushed phytoplankton from the lake and enhanced light limitation, so it is not clear by which mechanism(s) discharge events mediate phytoplankton resource limitation. Phytoplankton near stream inflows were less nutrient limited than phytoplankton at the lake outflow, consistent with predictions of the KIMMEL et al. (1990) model. However, this was true even when streamflow was negligible, suggesting alternative mechanisms for reduced nutrient limitation near stream inflows. In contrast to predictions of the model, phytoplankton were not more light limited near stream inflows than at the outflow; shallower depth near inflows compensated for higher turbidity, in terms of the light climate experienced by phytoplankton. Our results show that the mechanisms by which discharge events mediate phytoplankton resource limitation are complex and require further study in reservoirs as well as other aquatic systems subject to a high degree of temporal variation in discharge.

Key words: Phytoplankton, reservoirs, nutrients, irradiance, sediments.

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Introduction

Organisms are often constrained by the relative balance of energy vs. materials needed for growth and reproduction, relative to the availability of these resources in the environment (LAMPERT 1977, MÜLLER-NAVARRA & LAMPERT 1996, STERNER & ELSER 2002). Nutrients and light often limit the growth of primary producers, and the relative availability of these two resources varies temporally and spatially in most ecosystems (STERNER & ELSER 2002). Thus, the severity by which primary producers are limited by these factors also may vary (CHAPIN et al. 1982, ROSEMOND 1993, KNOWLTON & JONES 1996).

In aquatic ecosystems, the severity and relative importance of nutrient and light limitation can vary seasonally in response to environmental drivers such as allochthonous nutrient inputs, incident solar radiation, thermal stratification and internal nutrient cycling (e. g., SOMMER et al. 1986, KIMMEL et al. 1990). Aquatic ecosystems subject to large and variable inputs of light-attenuating sediment may show particularly variable patterns of nutrient and light limitation; this includes ecosystems as diverse as estuaries (ALPINE & CLOERN 1992, FISHER et al. 1999), floodplain lakes (CARIGNAN & PLANAS 1994, SQUIRES & LESACK 2002, 2003) and elongate glacial lakes (PETERS 1979). Reservoirs may exhibit particularly variable nutrient and light availability, both temporally and spatially (e. g., ELSER & KIMMEL 1985, SOBALLE & THRELKELD 1985, KIMMEL et al. 1990, KNOWLTON & JONES 1996, BUKAVECKAS & CRAIN 2002).

KIMMEL et al. (1990) developed a conceptual model of nutrient and light limitation of reservoir phytoplankton. Because reservoirs have large watersheds (scaled to lake size and compared to natural lakes), they can receive considerable inputs of nutrients, as well as suspended sediments that can reduce light intensity (KIMMEL et al. 1990, KNOWLTON & JONES 1995). According to the KIMMEL et al. (1990) model, inputs of water, nutrients and sediments from these relatively large watersheds mediate the relative importance and timing of nutrient vs. light limitation of reservoir phytoplankton.

Nutrients and sediments are often delivered to reservoirs in pulses associated with storms that induce high-discharge runoff events (KIMMEL et al. 1990, KNOWLTON & JONES 1996, VANNI et al. 2001), and these pulses can affect resource limitation of phytoplankton in at least three ways. Runoff events may supply nutrients in excess, which may directly alleviate nutrient limitation, and may also increase concentrations of suspended sediments, which may increase the severity of light limitation. Light-limited phytoplankton may be unable to allocate excess nutrients to growth and hence may exhibit little or no nutrient limitation. Finally, storms can flush phytoplankton from the lake, reducing phytoplankton biomass. If phytoplankton exhibit density-dependent growth, they should be less nutrient-limited when their biomass is low. Thus,

storm-induced pulses can lead to marked temporal variation in the relative severity of limitation by nutrients and light.

Spatial variation in resource limitation may be pronounced in reservoirs. According to the KIMMEL et al. model, phytoplankton growing in shallow areas near stream inflows may be more exposed to stream-derived sediment and nutrient pulses than phytoplankton growing in deeper, thermally stratified areas near dam outflows. Therefore, phytoplankton near inflows should be more light-limited (because of higher concentrations of suspended sediment) and less nutrient-limited than phytoplankton "downlake" (KIMMEL et al. 1990).

Thus, there exists a general model for reservoirs that predicts how nutrient and light limitation of phytoplankton vary spatially and temporally (KIMMEL et al. 1990). Some aspects of this model have been tested several times, particularly the spatial aspect of nutrient limitation. Thus, several studies show that phytoplankton "downlake" are more nutrient limited than phytoplankton "uplake" near stream inflows (e. g., ELSER & KIMMEL 1985, GROEGER & KIMMEL 1988, BUKAVECKAS & CRAIN 2002, but see STERNER 1994). Light limitation has been investigated less frequently, but evidence exists for frequent light limitation of reservoir phytoplankton (KNOWLTON & JONES 1996, KNOLL et al. 2003).

The temporal aspects of the KIMMEL et al. (1990) model have also been investigated infrequently, especially in relation to individual runoff events and at temporal scales relevant to phytoplankton generation times. Several studies show that reservoir phytoplankton are less nutrient limited during periods of high discharge (e. g., SØBALLE & THRELKELD 1985, SØBALLE & KIMMEL 1987, BUKAVECKAS & CRAIN 2002), but these trends have mainly been shown at seasonal scales. Individual storm-induced runoff events may mediate nutrient and light limitation over short temporal scales (a few days), because phytoplankton have short generation times. However, phytoplankton can also store nutrients, so it is possible that they are less responsive to nutrient pulses than would be indicated by their generation times. Little is known about the temporal scale over which phytoplankton nutrient and light limitation respond to variations in nutrients and light in nature (STERNER 1994). We are unaware of any studies that have explicitly examined how temporal variation in nutrient and light limitation relate to individual storm-induced pulses of nutrients and sediments in a reservoir ecosystem, or that have explicitly evaluated the temporal scale over which phytoplankton respond to variation in nutrients and light. Our study attempted to fill this void.

We examined temporal and spatial variation in phytoplankton nutrient and light limitation in a reservoir that receives significant nutrient and sediment pulses from its watershed. Our general hypothesis is that pulses of nutrients and sediments will reduce nutrient limitation and exacerbate light limitation.

We also explicitly examined the temporal scale over which these pulses mediate nutrient limitation. We hypothesized that nutrient limitation status is most closely related to pulse magnitude (i. e., stream discharge) over time scales similar to phytoplankton generation times (i. e., on the scale of a few days to a week), and less related to discharge over shorter or longer periods of time. To address these questions we employed an approach that combines frequent experimental bioassays with high-resolution monitoring of nutrient and sediment inputs and concentrations.

Material and methods

Study site

We examined the temporal dynamics of nutrient and light limitation in Acton Lake, a hypereutrophic reservoir located in southwestern Ohio, USA (WINNER et al. 1962, NOWLIN et al. 2005, VANNI et al. 2005). The lake has a surface area of 232 ha and mean depth of 3.9 m, and a large watershed relative to lake surface area (watershed area:lake area = 111); the majority of the watershed (89 %) is agricultural land (KNOLL et al. 2003), mostly row crops (corn and soybeans). Hence the lake receives considerable quantities of nutrients and suspended sediments, particularly during storm events (VANNI et al. 2001). Summer phytoplankton biomass is high (summer chlorophyll is typically $\sim 60\,\mu g\,L^{-1}$; VANNI et al. 2006) and transparency is low (Secchi depth is generally 0.5–0.7 m). Phytoplankton biomass is composed of a diverse group of flagellates and diatoms in spring and is dominated by cyanobacteria in summer (HORGAN 2005). When nutrients are limiting, phytoplankton are typically limited by phosphorus and not nitrogen (VANNI et al. 2006). Water exits the lake only over the spillway (i. e., there is no release of water from the hypolimnion), which tends to moderate lake-level fluctuations.

Inputs of water, nutrients and sediments

This study was conducted between April and September 2002. During this time, we quantified inputs of water, nutrients and suspended sediments via inflow streams using a high-frequency sampling program as part of a long-term project (VANNI et al. 2001). The volume of water entering Acton Lake (discharge) via three of its inflow streams was monitored every 10 min using pressure transducers that recorded stream stage, and rating curves that relate stage to discharge (VANNI et al. 2001). The catchments drained by these three streams are nearly identical in land use and they collectively drain 85 % of the lake's watershed (VANNI et al. 2001). Therefore, to obtain the total volume of water entering the lake, we summed discharge from the three streams, then divided by 0.85 to account for the small portion of the watershed that was not monitored.

Nutrient and sediment concentrations were quantified on water samples collected every 6 hours using automated ISCO water samplers (VANNI et al. 2001). During storm-induced runoff events, nutrient and sediment concentrations change rapidly in

these streams (VANNI et al. 2001). Therefore, we quantified nutrients and sediments on all samples (i.e. 6-hour intervals) during periods of high discharge. However, during low-flow periods, concentrations are more stable, so we quantified nutrients and sediments on a subset of samples (at least once per week per stream).

Samples were processed for concentrations of soluble nutrients and suspended sediment. Soluble nutrients were assayed on filtrates of samples passed through Pall A/E filters. Soluble reactive phosphorus (SRP) concentrations were assayed using the molybdate method, ammonium (NH_4) concentrations with the phenol-hypochlorite method and nitrate & nitrite with the cadmium reduction method. We assume that most "nitrate & nitrite" is nitrate (NO_3) and hence refer to this fraction hereafter as "nitrate". All soluble nutrient fractions were quantified using a Lachat FIA QC 8000 FIA auto-analyzer. Total suspended sediments (TSS) were quantified by filtering a known volume of water onto Pall A/E filters pre-weighed on a Mettler UMT ultra-balance to the nearest µg; filters were then dried at 60 ˚C for > 24 h and reweighed.

Nutrient loading rates for each of the three streams were obtained by multiplying mean hourly stream discharge for that stream by nutrient concentration during that hour. If a sample was collected from a stream within a particular hour, the concentration from that sample was multiplied by discharge for that hour. For all other hours, nutrient concentrations were linearly interpolated from the two concentrations before and after that sample and then multiplied by discharge for that hour. Within a stream, hourly loading rates were summed for each day to yield daily rates (kg d^{-1}). To obtain daily total loading to the lake from the entire watershed, daily loading rates from the three streams were added, and this sum was then divided by 0.85 to correct for the 15 % of the watershed that was not monitored. Finally, the daily loading rates (kg/d) were converted to loading rates per volume of lake water (µg or mg $L^{-1} d^{-1}$), using the entire lake volume.

To relate discharge and nutrient loading to storm events, we obtained hourly precipitation data from the meteorological station at the Miami University Ecology Research Center. This station is part of the US Environmental Protection Agency's Clean Air Status and Trends Network (CASTNET) and data are available at www.epa.gov/castnet. This site is located outside of Acton Lake's watershed, but is only about 5 km south of the lake.

Lake sampling

Acton Lake was sampled at two sites, an "Inflow site" located in shallow (~ 1 m) unstratified water near stream inflows, and an "Outflow site" located near the deepest part of the lake (~ 8 m) near the dam outflow. The Outflow site is thermally stratified during summer (NOWLIN et al. 2005). We sampled the lake (both sites each trip) on 68 days between 18 April and 30 September 2002. Sampling was more intense during April–mid August (on average, every 2 days) and less intense thereafter (weekly). Samples for nutrients, suspended sediments and phytoplankton biomass (chlorophyll) were collected with an integrated tube sampler that collected water from the surface to the bottom of the euphotic zone (defined as the depth at which irradiance equals 1 % of surface irradiance), which was always shallower than the mixed layer. At the Inflow site the euphotic zone generally encompassed the entire water column.

Lake samples were processed and analyzed for nutrients and suspended sediments in the same manner as stream samples. In addition, we quantified the concentration of non-volatile suspended solids (NVSS) in lake samples. NVSS represents the concentration of inorganic particles such as clay and silt (KNOWLTON & JONES 1995, 1996). After passing a known volume of water through Pall A/E filters and weighing filters for TSS (as described above for stream samples), filters were ashed in a muffle furnace at 550 °C for 4 hours to burn off organic matter and then re-weighed. The remaining ash (non-organic matter) is considered NVSS. Chlorophyll-*a* concentration was quantified by filtration onto Pall A/E filters, extraction with cold acetone, and analysis of fluorescence with a Turner TD-500 fluorometer. For each lake parameter (nutrient fractions, NVSS and chlorophyll), replicate integrated tube samples were collected at each site, processed separately, and then averaged.

Phytoplankton nutrient and light limitation

We conducted 17 standard bioassay experiments at each lake site to quantify the severity of phytoplankton nutrient limitation; 15 of these were conducted during May, June and July. For each experiment, water (with phytoplankton) was collected from the euphotic zone with repeated casts of an integrated tube sampler and transferred to translucent containers. Water was transported to the lab and held at lake temperature before initiating experiments later that same day or the following morning. Water was then passed through a 63 μm mesh to remove macrozooplankton and 350 mL dispensed into 500 mL flasks. Replicate flasks (2 per treatment) were randomly assigned to one of four treatments: Control (no nutrients added); + N (50 μmol/L N added as NH_4NO_3); + P (2.5 μmol/L P added as $NaH_2PO_4 * H_2O$); and + N & P. Phytoplankton were incubated at an irradiance of 200 μmol PAR m^{-2} sec^{-1} for 48 h, at which time samples from each flask were filtered and analyzed for chlorophyll. During the incubations (at ~24 h), flasks were swirled to suspend phytoplankton and other particles. We quantified the severity of nutrient limitation ($\Delta r_{treatment}$, DOWNING et al. 1999) as:

$$\Delta r_{treatment} = \ln(chl_{treatment}/chl_{control})/t$$

where the treatments are + N, + P or + N & P, $chl_{treatment}$ and $chl_{control}$ are final mean chlorophyll concentrations in the treatment and control flasks, and t is the duration of the experiments in days (t = 2 in all cases). Although we present Δr as our measure of nutrient limitation, we conducted statistical analyses on actual chlorophyll concentrations. Specifically, for each nutrient limitation experiment, we analyzed chlorophyll concentration (log-transformed) with 1-way ANOVA followed by Tukey HSD tests (JMP software, SAS Institute) to compare treatment means. We considered phytoplankton to be limited by nutrients if final log(chlorophyll) concentration was significantly higher in one or more of the nutrient treatments than in the Control.

Algal nutrient limitation is sometimes a function of light intensity (e. g. KNOWLTON & JONES 1996), because light-limited phytoplankton may not be able to take advantage of available nutrients. To evaluate this possibility, we also conducted four nutrient limitation experiments in which we incubated phytoplankton at a variety of light intensities (hereafter, "nutrient × light experiments"). Our goal was to determine the extent to which nutrient limitation is expressed at different light intensities. Thus, in

addition to our standard irradiance (200 µmol m^{-2} sec^{-1}), we also used treatments of 25 µmol m^{-2} sec^{-1} (both sites) as well as 50 µmol m^{-2} sec^{-1} and 100 µmol m^{-2} sec^{-1} (Outflow site only) on four dates: 1 July, 8 July, 22 July and 29 July. These experiments were conducted using the same methods as the standard nutrient bioassays. In the nutrient × light experiments, we were mainly interested in whether nutrient limitation generally interacts with light limitation, and not necessarily in the identity of the limiting nutrient. Therefore we analyzed each of these experiments with 2-way ANOVA using only the + N & P treatments (this is further justified because phytoplankton were P limited during this time, and growth was similar in the + P and + N & P treatments; see Results). Thus, for Outflow experiments we used a 2 × 4 ANOVA with 2 nutrient levels (Control vs. + N & P) and 4 light levels; for Inflow experiments, we used a 2 × 2 ANOVA because we incubated Inflow phytoplankton only at 25 and 200 µmol m^{-2} sec^{-1}.

To assess the potential severity of light limitation in Acton Lake, we quantified the light intensity to which phytoplankton were exposed (light in the mixed layer, I$_{mix}$) and estimated photosynthetic rates of Acton phytoplankton growing at these irradiances. To estimate irradiance at the lake surface we obtained hourly solar radiation data (W/m^2 total solar radiation) from the Miami University Ecology Research Center CASTNET site (see website link above), which we converted to PAR (µmol m^{-2} sec^{-1}) using a relationship between the two irradiance measures (r^2 = 0.979, using hourly values) that we developed by continuously monitoring PAR (Li-Cor LI–189 spherical quantum photometer) placed adjacent to the CASTNET sensor for several days in May and June 2003. To estimate I$_{mix}$, we used the surface PAR data along with the in-lake light attenuation coefficient and depth of the mixed layer. The light attenuation coefficient (k, m^{-1}) was obtained by measuring irradiance at 0.5 m intervals (using a Li-Cor 189 sensor) from just below the lake surface to the bottom of the mixed layer, at both lake sites. We measured light profiles on 67 of the 68 lake sampling dates. A single site-specific k value for the mixed layer was obtained for each sampling trip, as the slope of the regression between ln(I$_z$) vs. z, where I$_z$ is irradiance at depth z (m), using all depths throughout the mixed layer. We estimated the depth of the mixed layer using temperature and oxygen profiles, and obtained

$$I_{mix} = (1 - \exp(-k * z_{mix}))/(k * z_{mix}),$$

where z$_{mix}$ is the depth of the mixed layer (STERNER 1990). To obtain light in the mixed layer on dates on which we did not sample, we linearly interpolated k and z$_{mix}$ between sampling dates.

To quantify light limitation, we estimated photosynthetic rates in Acton Lake as a function of I$_{mix}$, and related these to light-saturated photosynthetic rates. To do this, we used photosynthesis-irradiance (PI) curves generated from ^{14}C uptake rate (primary productivity) experiments (KNOLL et al. 2003) generated on 7 dates during the study period, at both sites. Details of the ^{14}C uptake experiments are given in KNOLL et al. (2003) and VANNI et al. (2006). Briefly, we incubated Acton phytoplankton (from both sites) at a range of irradiances and quantified photosynthetic ^{14}C uptake. We used the PSPARMS program (FEE 1990) to generate PI curves and the associated photosynthetic parameters α (the slope of the photosynthesis vs. irradiance curve at low, light-limiting irradiances) and P$_m^B$ (light-saturated, chlorophyll-specific photosynthetic

rate). α and P_m^B were linearly interpolated for all dates in between the 7 dates on which they were measured. Actual chlorophyll-specific photosynthetic rate (P_{lake}) in the mixed layer was estimated as (FEE 1990):

$$P_{lake} = 0 \qquad \qquad \text{if } I_{mix} < I_k/20$$
$$P_{lake} = \alpha I'(1-(I'/(4I_k))) \quad \text{if } I_k/20 < I_{mix} < 2I_k$$
$$P_{lake} = P_m^B \qquad \qquad \text{if } I_{mix} > 2I_k$$

where $I_k = P_m^B/\alpha$ and $I' = I_{mix} - (I_k/20)$. Observed photosynthetic rates were then divided by P_m^B to obtain photosynthetic rate as a percentage of the light-saturated rate.

We also calculated a light limitation index,

$$\Delta r_{light} = \ln(P_m^B/P_{lake})/2.$$

Δr_{light} scales similarly to the Δr values used to express nutrient limitation. We then compared the relative strength of nutrient limitation and light limitation using the ratio $\Delta r_{N\&P}/\Delta r_{light}$. $\Delta r_{N\&P}$ was used in this index because growth should be (and in fact was) highest when N and P are both added.

Correlations between environmental variables and nutrient limitation

We hypothesized that runoff events (periods of high discharge) can alleviate nutrient limitation of phytoplankton by at least three mechanisms: provision of excess nutrients, induction of light limitation, and advective loss of biomass. We examined the relationship between nutrient limitation and indicators of these three mechanisms using linear regression. Specifically, for each lake site we regressed nutrient limitation status ($\Delta r_{N\&P}$, dependent variable) against SRP and DIN concentrations (nutrient-related independent variables), NVSS concentration and I_{mix} (light-related independent variables), and chlorophyll concentration (biomass-related independent variable) on the day phytoplankton were collected for the nutrient limitation experiment ($n = 17$ experiments at each site). For I_{mix}, we also tried regressions using irradiance over the 3 day interval before the experiment, as phytoplankton may acclimate to light over several days, but results were nearly identical so we present here only results using I_{mix} on the day of the experiment. For all regressions, the independent variables were log-transformed prior to analyses.

We took a more detailed approach to quantifying the relationship between nutrient limitation status and indicators of water and nutrient inputs. Because we are uncertain over what time period phytoplankton respond to nutrient and water inputs, we examined correlations over several different discharge intervals. Phytoplankton typically have generation times on the order of days, so one may hypothesize that nutrient limitation status should be determined by discharge over the previous several days (e. g., 1 day to 1 week). However, phytoplankton biomass is sometimes highly correlated with nutrient loading over the previous several weeks or months, or even on an annual basis (WETZEL 2001). Therefore, we examined correlations between discharge and nutrient limitation status over a variety of time periods. Specifically, we examined the correlations between $\Delta r_{N\&P}$ and Q_t, where Q_t is discharge occurring in the preceding time period t. Q_t was obtained by taking the mean of all hourly discharge measurements in the period preceding collection of phytoplankton for a given experiment. We explored 8
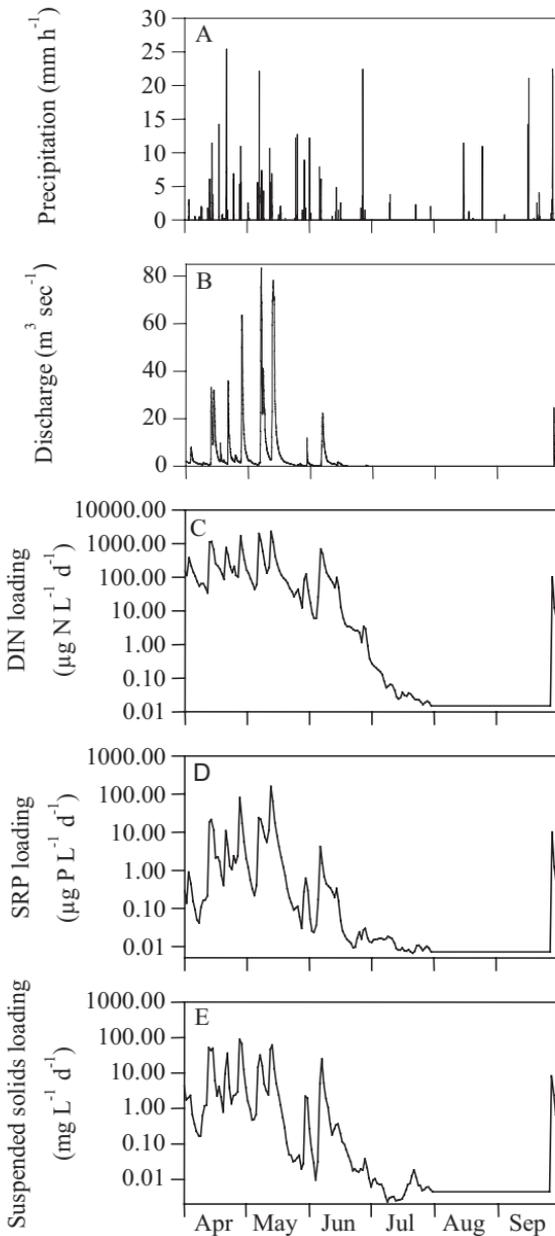
Fig. 1. (A) Precipitation, **(B)** discharge (hourly means), **(C)** loading of dissolved inorganic nitrogen (DIN), **(D)** soluble reactive phosphorus (SRP), and **(E)** total suspended solids to Acton Lake during the study period. Nutrient and sediment loading rates are expressed as mass delivered per liter of lake water.

different discharge-averaging time periods (1, 2, 4, 7, 10, 14, 21 and 30 d), and log-transformed discharge prior to conducting these analyses.

Results

Inputs of water, sediment and nutrients to Acton Lake

Discharge of water from streams to Acton Lake exhibited typical seasonal patterns. In spring (April–mid-June), discharge was high, and peaks in discharge were associated with precipitation events (Fig. 1 A, B). Discharge remained low in summer despite the occurrence of several storms, and showed a small peak in late September after a few relatively heavy rains. The closer association between storm events and discharge in spring (and fall) compared to summer reflects the balance of precipitation and evapotranspiration in the watershed; in summer terrestrial vegetation utilizes much of the precipitation, leaving relatively little for runoff.

Inputs of soluble nutrients and suspended solids to Acton Lake were correlated with discharge (Fig. 1 C–E). Peaks and declines in loading of soluble reactive phosphorus (SRP) and suspended solids (TSS) were more tightly associated with discharge than were inputs of dissolved inorganic nitrogen (DIN, i. e., $NH_4 + NO_3$); this is because SRP and TSS concentrations increase and decline rapidly during runoff events while concentrations of nitrate (which comprises the bulk of DIN loading) decline much more gradually as storms subside (VANNI et al. 2001).

Dynamics of nutrients, sediments and phytoplankton in Acton Lake

Concentrations of soluble nutrients and suspended sediments in Acton Lake were generally associated with discharge (Fig. 2). SRP concentrations increased from mid-April to mid-May and then declined rapidly as discharge decreased (Fig. 2 A, B), presumably due to uptake by phytoplankton. SRP concentrations remained low throughout the duration of the study, except for a one-day peak on June 6 at the Inflow site that corresponds to a storm event on that day. Nitrate concentrations declined during the period of high discharge, increased in early June, and then gradually declined throughout summer (Fig. 2 C). The gradual decline in NO_3 concentration reflects both the slow decline in NO_3 inputs as well as uptake by phytoplankton (HORGAN 2005).

Ammonium (NH_4) concentrations tended to be high during the period of high discharge, declined in late May and were generally low from early June throughout summer (Fig. 2 D). However, we observed several discrete NH_4 peaks during summer, especially at the Inflow site. High NO_3 concentrations and occasional peaks in NH_4, rendered dissolved N relatively more available than dissolved P to phytoplankton during much of summer.

Concentrations of non-volatile suspended solids (NVSS) in Acton Lake generally corresponded to discharge, especially at the Outflow site (Fig. 2 E). Thus, NVSS concentrations were high in April and May at the Outflow site
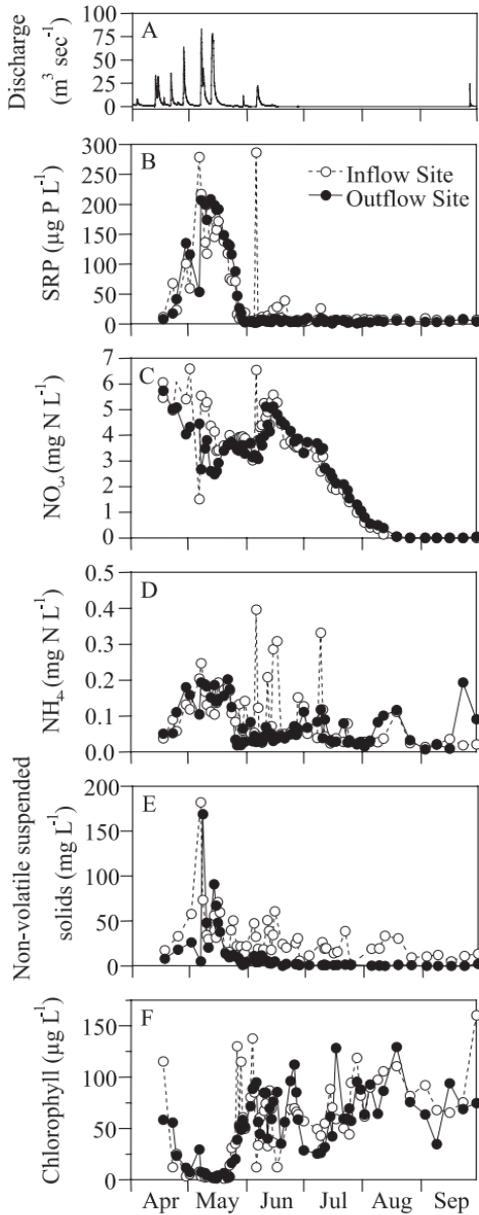
Fig. 2. Concentrations of nutrients, sediments and phytoplankton at Inflow and Out-flow sites in Acton Lake. **A.** Discharge, reproduced from Fig. 1 to show its association with concentrations. **B.** SRP. **C.** Nitrate. **D.** Ammonium. **E.** NVSS. **F.** Chlorophyll.

and low during summer. Patterns were generally similar at the Inflow site, except that NVSS concentrations were almost always higher than at the Outflow site, probably because of sediment resuspension in shallow areas.

Phytoplankton biomass (chlorophyll) was low during the high-discharge period of late April through late May, increased rapidly in late May–early June, and remained high through most of summer (Fig. 2 F). Low chlorophyll during high discharge probably resulted from flushing of phytoplankton from the lake, and perhaps from light limitation induced by high NVSS concentrations. The increase in phytoplankton in late May–early June coincides with declining SRP concentration; once SRP was depleted, phytoplankton biomass oscillated but showed no consistent increase or decrease (Fig. 2 B, F).

Phytoplankton nutrient limitation

Phytoplankton were limited often by P, while N limitation was observed only in September (Fig. 3). When P was limiting, there was little evidence of co-limitation (i.e., Δr_P and $\Delta r_{N\&P}$ were similar; Fig. 3 B, C). However, during periods of N limitation in September, we observed evidence of co-limitation at the Outflow site, i.e., chlorophyll was significantly higher in the $+N\&P$ treatment than in the $+N$ treatment (Fig. 3 B, C).

Nutrient limitation (Δr) was much more severe during summer than spring at the Outflow site; patterns were qualitatively similar but less pronounced at the Inflow site (Fig. 3 A–C). Phytoplankton were not significantly nutrient limited during the first 5 experiments at either site ($P > 0.07$ in all cases). Thereafter, phytoplankton were consistently nutrient limited in all experiments ($P < 0.027$ in all cases) at the Outflow site, and in all experiments ($P < 0.045$ in all cases) except 6 June ($P = 0.887$) at the Inflow site. Δr_P and $\Delta r_{N\&P}$ increased more or less steadily from late May through early July at the Outflow (Fig. 3 B). On most dates (14 of 17 experiments), and on all dates from 3 June onwards (11 experiments), phytoplankton were more nutrient limited at the Outflow site than at the Inflow site.

Responses to storms are also apparent at shorter time scales, and responses seemed to be site-dependent. For example, after the two large May storms, Δr_P and $\Delta r_{N\&P}$ began to increase at both sites, and continued to increase at the Outflow site more or less consistently through early July. However, Δr_P and $\Delta r_{N\&P}$ declined at the Inflow site on 3 June and 6 June, in association with two small discharge peaks preceding these dates (Fig. 3 B, C). Phytoplankton at the Inflow site were still significantly nutrient limited on 3 June, but not on 6 June. Both of these storms produced noticeable peaks in SRP inputs (Fig. 1 D), and the latter storm yielded a pronounced peak in SRP concentration at the Inflow site but not at the Outflow site (Fig. 2 B). Overall, these dynamics suggest that large storms such as those in April and early May reached the Outflow site but that small storms such as those in late May early June affected only the Inflow site.
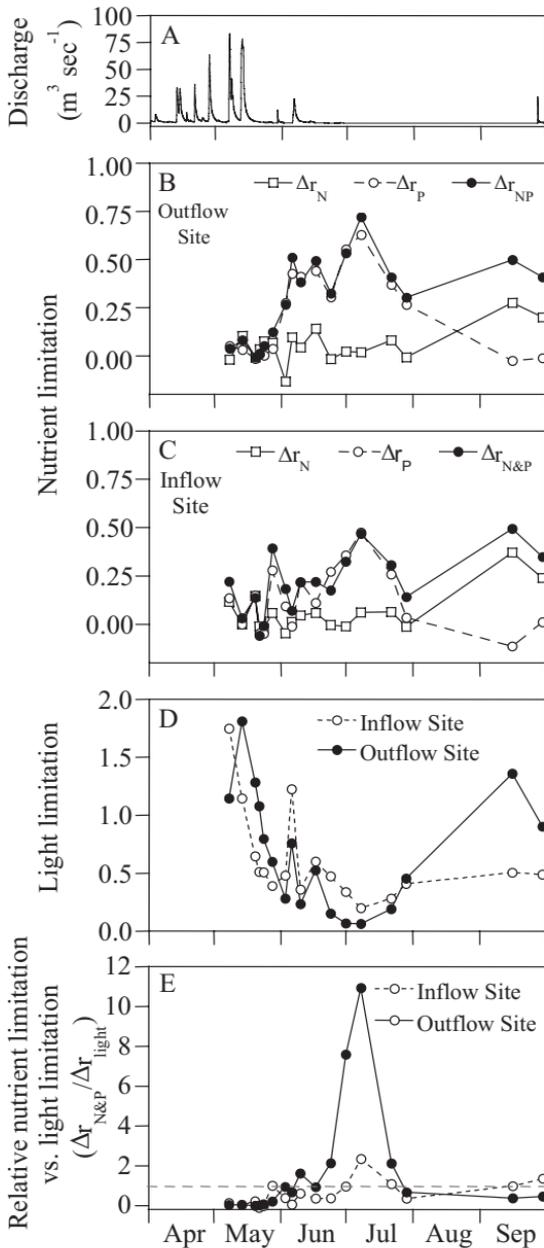
Fig. 3. Indices of nutrient and light limitation of Acton Lake phytoplankton. **A.** Discharge, reproduced from Fig. 1 to show its association with limitation indicators. **B, C.** Nutrient limitation status at the Outflow and Inflow sites, respectively. **D.** Light limitation at the Inflow and Outflow sites. **E.** Relative severity of nutrient vs. light limitation. The dashed line (= 1.0) represents equal severity of nutrient and light limitation.

Nutrient vs. light limitation

The nutrient × light experiments showed that phytoplankton nutrient limitation was expressed more at high light than at low light (Fig. 4). During these experiments (July), phytoplankton were limited only by P and not N, and grew similarly in the + P and + N & P treatments at all light levels. Therefore, we consider here only results from the Control and + N & P treatments (Fig. 4). In 3 of the 4 Inflow experiments (all but 22 July), there was a significant light × nutrient interaction (Fig. 4 A). At the Outflow (Fig. 4 B), there was a significant light × nutrient interaction in the first 2 experiments, a marginally significant interaction in the 22 July experiment ($P = 0.0544$) and no interaction in the 29 July experiment ($P = 0.1054$). Patterns were similar across experiments; Outflow phytoplankton showed no evidence of nutrient limitation (i. e., Δr was near zero) at the lowest light intensity ($25 \, \mu mol \, m^{-2} \, sec^{-1}$), and Δr was highest at the highest light intensity ($200 \, \mu mol \, m^{-2} \, sec^{-1}$; Fig. 4 A). Phytoplankton at the Inflow site also showed this pattern in three experiments (Fig. 4 B).

Light intensity in the mixed layer of Acton Lake (I_{mix}) varied greatly over the course of the study (Fig. 5). I_{mix} was low during the period of high discharge and showed a general increase from late May through June (Fig. 5 A,
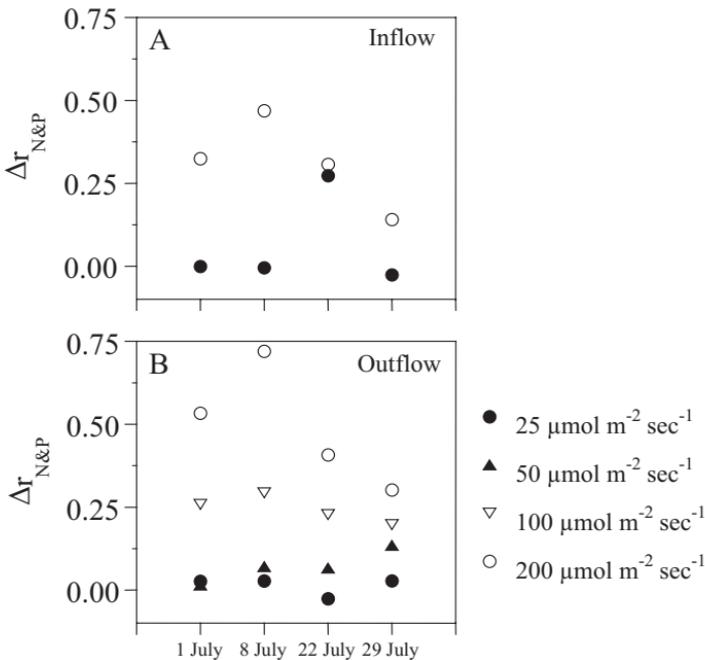

Fig. 4. Nutrient limitation ($\Delta r_{N \& P}$) at different irradiance levels in the nutrient × light experiments. **A.** Inflow site. Phytoplankton were incubated at 2 irradiance levels. **B.** Outflow site. Phytoplankton were incubated at 4 irradiance levels.

B), corresponding to a decline in NVSS concentration, increasing incident so-lar radiation, and increasing stability of stratification (i. e., shallower mixing depth). I_{mix} increased during this period despite increasing phytoplankton bio-mass (Fig. 2 F). From early July onwards, we observed a general decline in light in the mixed layer (Fig. 5 B), coinciding with declining incident solar ra-diation, a deepening of the thermocline (at the Outflow site) and an increase in phytoplankton (Fig. 2 F). The irregular increases and decreases in light inten-sity on a daily basis reflect daily variation in solar radiation (cloud cover). Even though the Inflow site is more turbid than the Outflow site (higher NVSS
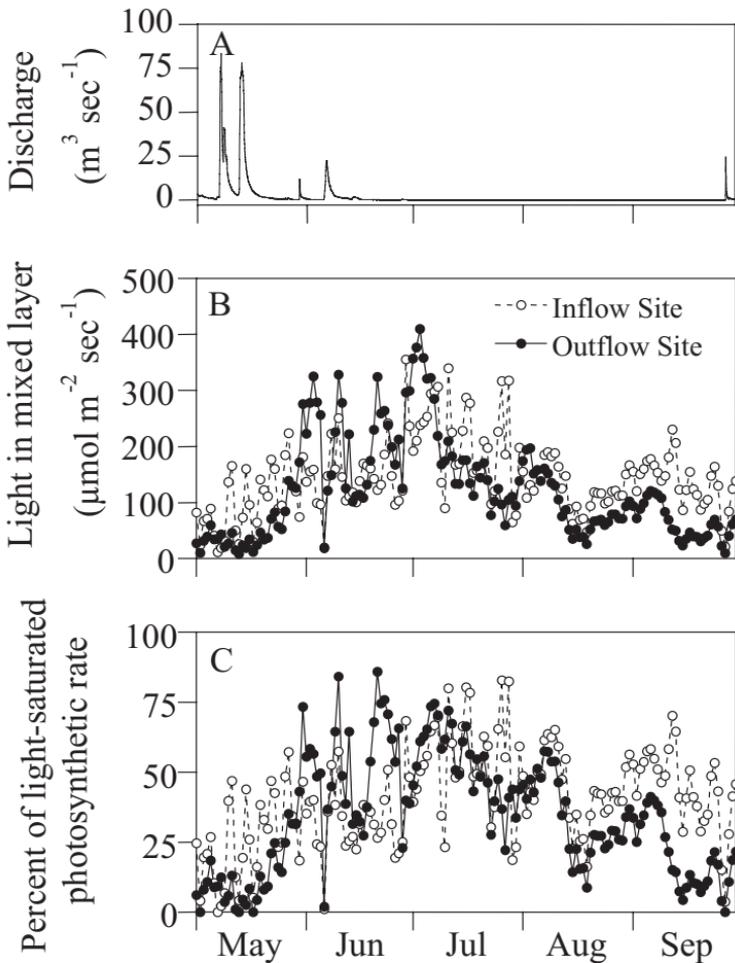

Fig. 5. Photosynthetic radiation and light limitation at Inflow and Outflow sites. **A.** Discharge, reproduced from Fig. 1 to show its association with irradiance and light limitation. **B.** Light in the mixed layer over 24 hours. **C.** Phytoplankton photosynthe-sis, expressed as percent of light-saturated photosynthetic rates.

and k), I_{mix} tended to be similar at the two sites or higher at the Inflow site, owing to shallower mixing depth at the Inflow site. As a consequence of variable light intensity, phytoplankton photosynthetic capacity (expressed as percent of light-saturated photosynthesis) was also highly variable and corresponded to I_{mix} (Fig. 5 C). During much of the study, phytoplankton were photosynthesizing at considerably less than light-saturated rates.

The relative severity of nutrient limitation vs. light limitation also varied greatly seasonally (Fig. 3). During the period of high discharge, phytoplankton were strongly light-limited at both sites, but the severity of light limitation declined markedly through early June as discharge and NVSS concentration declined, and as nutrient limitation increased (Fig. 3 D). Light limitation increased at both sites during September, and this trend was stronger at the Outflow; nutrient limitation also increased somewhat at this time. At the Outflow site, nutrient limitation ($\Delta r_{N \& P}$) and light limitation (Δr_{light}) were negatively correlated ($r^2 = 0.329$, P = 0.0171, n = 17 dates), and this correlation was stronger when the two September experiments were omitted from the regression, i. e. after the thermocline began to seasonally deepen ($r^2 = 0.545$, P = 0.0017). Δr_{light} and $\Delta r_{N \& P}$ were not significantly correlated at the Inflow site, either with ($r^2 = 0.106$, P = 0.2029) or without ($r^2 = 0.126$, P = 0.1932) inclusion of September data. The nutrient/light limitation ratio ($\Delta r_{N \& P}/\Delta r_{light}$) increased steadily from late May through mid July, especially at the Outflow site, reflecting both increased nutrient limitation and decreased light limitation (Fig. 3 B–E). The nutrient/light limitation ratio declined in late July and remained near 1 after this, corresponding to decreasing light intensity (Fig. 3 E).

Correlations between environmental variables and nutrient limitation

Correlations between (log-transformed) mean discharge and $\Delta r_{N \& P}$ were negative (i. e., higher discharge resulted in less nutrient limitation) and significant (P < 0.025 in all cases) for all discharge-averaging periods at both sites (Fig. 6 A). At the Inflow site, the strongest correlation between discharge and $\Delta r_{N \& P}$ was observed when discharge was averaged over the preceding 10 days (r = -0.662, $r^2 = 0.438$, P = 0.0038), whereas at the Outflow site the strongest correlation was observed when discharge was averaged over the preceding 14 days (r = -0.743, $r^2 = 0.552$, P = 0.0006; Fig. 6 A). For all discharge-averaging periods except 30 d, correlations between discharge and $\Delta r_{N \& P}$ were stronger at the Outflow site than at the Inflow site (Fig. 6 A).

Nutrient limitation status ($\Delta r_{N \& P}$) was also correlated with variables related to nutrients, irradiance and phytoplankton biomass, particularly at the Outflow site. Nutrient limitation ($\Delta r_{N \& P}$) was negatively correlated with SRP concentration at both sites, but the relationship was much stronger at the Outflow site ($r^2 = 0.676$, P < 0.0001) than at the Inflow site ($r^2 = 0.443$, P =
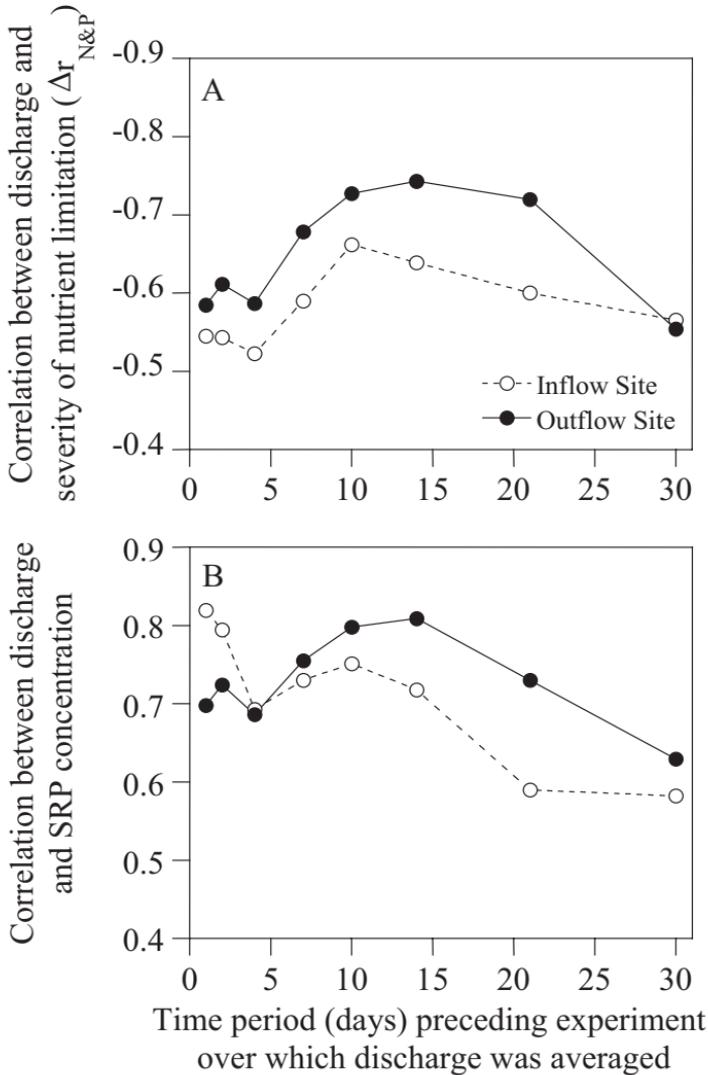
Fig. 6. Relationship between the period (days) over which discharge was averaged prior to a nutrient limitation experiment, and correlations between discharge and nutrient limitation **(A)**, and between discharge and SRP concentration **(B)**. For each nutrient limitation experiment, discharge in the specified time period was averaged. For each of the various time periods, nutrient limitation ($\Delta r_{N\&P}$) or SRP was then regressed against discharge over that period.

0.0035). $\Delta r_{N\&P}$ was not related to DIN concentrations at the Outflow site ($r^2 = 0.062$, P = 0.3366), although we observed a marginally significant negative correlation between $\Delta r_{N\&P}$ and DIN at the Inflow site ($r^2 = 0.243$, P = 0.0443). At the Outflow site, $\Delta r_{N\&P}$ was also significantly and positively correlated

with both chlorophyll ($r^2 = 0.433$, P = 0.0041) and I_{mix} ($r^2 = 0.358$, P = 0.0112), and negatively correlated with NVSS ($r^2 = 0.474$, P = 0.0022). At the Inflow site, $\Delta r_{N \& P}$ was positively correlated with chlorophyll ($r^2 = 0.273$, P = 0.0315) but was not correlated with NVSS (P = 0.4689) or I_{mix} (P = 0.1842).

Because nutrient limitation status ($\Delta r_{N \& P}$) was correlated with the concentration of SRP (which was usually the limiting nutrient) and because periods of high discharge were associated with large inputs of SRP, we explored further the relationship between discharge (at various time scales) and SRP concentration. Thus, we regressed SRP concentration (on the day of experiments) against log(discharge) over various time intervals, for both sites. At the Outflow site, the correlation between discharge and SRP concentration was greatest (most positive) when discharge was averaged over the preceding 10–14 days (Fig. 6 B). This patterns is very similar to that for discharge vs. $\Delta r_{N \& P}$ (Fig. 6A). In contrast, the correlation between discharge and SRP concentration at the Inflow site was greatest when discharge was averaged over the preceding 1 or 2 days (Fig. 6 B).

Discussion

Our results provide support for some, but not all, elements of the model developed by KIMMEL et al. (1990) to explain temporal and spatial variation in resource limitation of reservoir phytoplankton (Table 1). One of the unique aspects of our study is its fine-scale temporal resolution and its explicit relation to discharge at multiple temporal scales. In addition, we found differing levels of support for temporal vs. spatial aspects of the KIMMEL et al. (1990) model. Therefore, we consider temporal and spatial aspects of the model separately, beginning with the former.

Temporal patterns in nutrient and light limitation in relation to discharge

In agreement with the KIMMEL model, storm-induced discharge events alleviated nutrient limitation. Nutrient limitation ($\Delta r_{N \& P}$) was significantly negatively correlated with discharge at both sites and over all discharge-averaging periods. Interestingly, correlations were strongest when discharge was averaged over 10–14 days prior to an experiment, a period that is probably longer than phytoplankton generation times. This suggests that the nutrient limitation status of phytoplankton is a function of conditions experienced by phytoplankton over several cell divisions, which is consistent with the idea of luxury uptake. The correlations are consistent with the dynamics of SRP and chlorophyll in the lake; SRP concentrations declined over a ~ 2 week period in late

Table 1. Extent to which predictions of the KIMMEL et al. (1990) model were supported by the results of this study.

Prediction Related to temporal dynamics	Prediction supported?	Mechanism(s) consistent with model?
1) Storm-mediated discharge events decrease the severity of nutrient limitation	Yes	Mechanism not clear; storms increase nutrients, but also decrease light and phytoplankton biomass
2) Storm-mediated discharge events increase the severity of light limitation	Yes	As postulated by model, sediments delivered by storms decreased irradiance and enhanced severity of light limitation
Related to spatial patterns		
3) Nutrient limitation is more severe at outflow than near stream inflows	Yes	Model postulates that pattern is driven by streamflow, but pattern was also observed when streamflow was negligible
4) Light limitation is more severe near stream inflows than at the outflow	No	Although light attenuation was higher at Inflow Site, I_{mix} was not consistently lower because of shallower depth at Inflow Site

May, and this coincided with a sharp increase in phytoplankton over the same period. Alternatively, the correlations could reflect nutrient cycling processes within the lake. Although high discharge events clearly yield substantial inputs of available P (i. e., SRP; Fig. 1 B, D), most P delivered to Acton Lake via its inflow streams is in particulate form, especially during storms (VANNI et al. 2001). Most of this particulate P is probably unavailable to phytoplankton, but some of it probably becomes available later via remineralization by microbes (NOWLIN et al. 2005) and/or detritivorous fish (SCHAUS et al. 1997). Limnologists have long known that phytoplankton response to nutrient loading can be temporally uncoupled from nutrient delivery; for example, summer phytoplankton biomass is often correlated with spring total P loading (WETZEL 2001).

On the other hand, at the Outflow site nutrient limitation ($\Delta r_{N \& P}$) was strongly and negatively correlated with SRP concentration measured on the day of the experiment; the correlation was weaker but still significant at the Inflow site. These results, especially from the Outflow site, suggest that nutrient limitation status reflects instantaneous P availability.

Nutrient limitation status was also correlated with phytoplankton biomass (chlorophyll), NVSS concentration, and I_{mix}. This suggests that the severity of nutrient limitation may be mediated by any or all of the hypothesized mechanisms associated with discharge events (elevated nutrient inputs, reduced light, and reduced biomass due to flushing). It is difficult to ascertain the relative importance of these mechanisms, but it is clear that phytoplankton often are not nutrient limited following discharge events, even when they are grown at

an irradiance of $200\,\mu mol\ m^{-2}\ sec^{-1}$ (Fig. 3). However, flushing may play a role in mediating this pattern, because low biomass may render nutrients relatively more available, per cell.

Periods of high discharge were associated with high in-lake concentrations of NVSS and low I_{mix}, and as a consequence, pronounced light limitation. The nutrient × light experiments show that even when phytoplankton are potentially nutrient limited, they may not express nutrient limitation (i. e., $\Delta r_{N\&P}$ is ~0) if they are growing at low light intensity. These dynamics are consistent with the KIMMEL et al. (1990) model, in that the severity of nutrient- and light-limitation should be inversely correlated with, and mediated by, advective inputs of sediments. However, we also observed pronounced light limitation during late summer when stream inputs were negligible (Fig. 5). During this time, most light attenuation was due to phytoplankton rather than inorganic particles, and phytoplankton biomass was high at both sites (Fig. 2 F).

Although any or all of the proposed mechanisms may contribute to phytoplankton nutrient limitation status, all of them involve discharge as a major driver. Thus, we can view discharge as a "master variable" that can regulate phytoplankton nutrient limitation via several non-mutually exclusive mechanisms. This notion agrees with the KIMMEL et al. (1990) model in which discharge is viewed as a major force determining phytoplankton nutrient limitation, productivity, and community structure (Table 1).

Seasonal patterns of phytoplankton nutrient limitation in natural lakes are often somewhat similar to those we observed here (SOMMER et al. 1986), although mechanisms may differ. In relatively deep north-temperate lakes, nutrients are usually not limiting in early spring (just after ice-out) because nutrients derived from runoff of snowmelt are still available. In addition, the lake will not yet be thermally stratified, so phytoplankton may be light limited as they mix to deep waters. As thermal stratification proceeds, phytoplankton in these lakes become more nutrient limited and perhaps less light limited; they also may be limited by grazing (SOMMER et al. 1986, VANNI & TEMTE 1990). Thus, while discharge plays a role in mediating the seasonal dynamics of nutrient- and light-limitation in both systems (via spring snowmelt in north-temperate lakes), it is likely that short-term temporal variation in discharge is more important for phytoplankton in reservoirs than in natural lakes (KIMMEL et al. 1990, WETZEL 1990). In terms of temporal (and spatial) patterns of nutrient and light limitation, reservoirs are probably more similar to estuaries than to natural, thermally stratified lakes in the temperate zone. However, some natural lake types exhibit temporal variation that is probably similar to that of reservoirs, and because of similar mechanisms. For example, shallow floodplain lakes in areas as disparate as the arctic (SQUIRES & LESACK 2002, 2003) and the tropics (CARIGNAN & PLANAS 1994) are subject to pronounced seasonal and episodic variation in sediment inputs, which generates substantial

temporal variability in irradiance and phytoplankton light limitation. The temporal pattern in discharge that we observed in this study is typical of that for these streams (VANNI et al. 2001), so the temporal patterns of nutrient and light limitation that we observed are also probably typical for Acton and other reservoirs in the region.

Spatial patterns in nutrient and light limitation

The KIMMEL et al. (1990) model postulates that phytoplankton are less nutrient limited near stream inflows than near the dam, because streams deliver nutrients and these nutrients become less available towards the lake outflow. Conversely, the model predicts that phytoplankton near inflows should be more light limited than phytoplankton downlake because streams deliver light-attenuating sediment particles, most of which settle out before reaching the dam. In Acton Lake, phytoplankton were usually less nutrient limited at the Inflow site than at the Outflow site, as predicted by this model. However, this was true even during periods of low discharge, i. e. when streams were delivering essentially no nutrients (Table 1). Persistently lower nutrient limitation of Inflow phytoplankton (compared to Outflow phytoplankton) may result from several mechanisms. It may reflect delayed effects of nutrient loading (as suggested by correlations between discharge and Δr, discussed above). Alternatively, episodic sediment resuspension events may release nutrients from sediment porewaters (as suggested by periodic spikes in ammonium at the Inflow site; Fig. 2 D) and alleviate nutrient limitation. Finally, nutrient limitation may be less severe at the Inflow site because of nutrient excretion by detritivorous fish, which inhabit shallow oxygenated regions of the lake and provide substantial amounts of nutrients for phytoplankton (SCHAUS et al. 1997, VANNI et al. 2006). These mechanisms represent a potential departure from the KIMMEL et al. (1990) model, which asserts that within-lake nutrient cycling should be relatively unimportant near stream inflows in comparison to areas near the outflow.

Phytoplankton at the Outflow site were often more light limited than phytoplankton at the Inflow, based on photosynthetic rates (Figs 3, 5). This contrasts with predictions of the KIMMEL et al. (1990) model (Table 1), but agrees with results of KNOLL et al. (2003), who found that phytoplankton were equally light limited at Inflow and Outflow sites in 12 reservoirs (including Acton). Apparently, higher turbidity (higher k) at the Inflow site is offset by shallower mixing depth, compared to Outflow sites.

We also observed a spatial difference in the strength of the correlations between Q and $\Delta r_{N \& P}$; correlations were higher at the Outflow site than at the Inflow site for all but one discharge-averaging period (Fig. 6 A). At first glance

this may seem counterintuitive, because we would expect the Inflow site phytoplankton to be more highly correlated to discharge because of closer proximity to nutrient inputs. However, the internal cycling processes mentioned above (injection of porewater nutrients during sediment resuspension events and excretion by detritivorous fish) are likely more important at the Inflow site than at the Outflow site, and this could explain the differences between sites in correlation strength.

We also observed differences between sites in terms of the patterns of correlations between discharge and SPR concentrations (Fig. 6 B). At the Outflow site, correlations between discharge and SRP were greatest when discharge was averaged over intermediate time scales, a pattern very similar to the correlations between discharge and nutrient limitation. This, and the strong correlation between SRP and $\Delta r_{N\&P}$ at the Outflow site, suggests that SRP supply and concentration drive nutrient limitation at this site. In contrast, at the Inflow site the correlation between discharge and SRP was greatest when discharge was averaged over 1–2 days, yet at this site the correlation between discharge and nutrient limitation status was greatest at intermediate scales (~ 10 days). This suggests that phytoplankton at the Inflow site may react quickly to SRP delivered during storms but may react over longer scales to discharge. Again, perhaps this is due to large amounts of particulate P delivered in storms; these particles settle out quickly (hence more are deposited at the Inflow than at the Outflow) and nutrients from these particles may be mineralized over the next week or two by gizzard shad and microbes.

We should point out that the KIMMEL et al. (1990) model was developed mainly for larger reservoirs, where the potential for large differences between the Inflow and Outflow are likely. Acton Lake is relatively small (< 4 km from inflows to the dam) and hence spatial differences may be less pronounced than in reservoirs in which the dam is much farther from stream inflows. Thus, to a certain extent the apparent lack of support for some of the spatial aspects of the KIMMEL et al. (1990) model could be due to scale, i. e., the model may be more likely to find support in larger reservoirs. Future studies should explore the extent to which reservoirs of varying size conform to the predictions of the KIMMEL et al. (1990) model.

Conclusion

We found support for some of the predictions of the KIMMEL et al. (1990) model, but not others. In addition, some patterns of nutrient and/or light limitation agreed with predictions of the model, but apparently for mechanisms other than those proposed by KIMMEL et al. (1990). It is clear that storm-mediated discharge events can affect phytoplankton nutrient and light limita-

tion via several (potentially non-independent) mechanisms, and that these mechanisms may be difficult to disentangle even in a detailed study such as ours. Many aquatic ecosystems, such as reservoirs, floodplain lakes, estuaries and elongate drainage lakes receive temporally-variable pulses of water, sediments and nutrients that help generate and maintain spatial gradients. Thus, there is a need to better understand the mechanisms accounting for spatial and temporal variation in resource limitation in these systems.

Acknowledgements

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