Phytoplankton growth in the Ohio, Cumberland and Tennessee Rivers, USA: inter-site differences in light and nutrient limitation

Richard W. Koch[1,*], Debbie L. Guelda[1] and Paul A. Bukaveckas[2]
[1]*Department of Biology, Bemidji State University, Bemidji, MN 56601, USA*
[2]*Department of Biology and Center for Watershed Research University of Louisville, Louisville, KY 40292, USA*
*Author for correspondence (Fax: 218.755.4107; e-mail: rkoch@bemidjistate.edu)

Abstract

Seasonal patterns in resource limitation of phytoplankton growth were assessed monthly within three large rivers with differing extents of water regulation. The Ohio River is regulated by low dams that do not substantially modify discharge, while the Cumberland and Tennessee Rivers are impounded by a series of high dams to enhance water storage for downstream flood control. Laboratory dilution assays with light and nutrient manipulations indicated that light was the main factor limiting phytoplankton growth at irradiances below 7 E m^{-2} d^{-1}. Light limited growth was frequent in the turbid, higher discharge of the Ohio River, but was rare in the heavily regulated Tennessee and Cumberland Rivers. When irradiance exceeded 7 E m^{-2} d^{-1}, phytoplankton were either P-limited (Cumberland River), co-limited by P and N (Tennessee River), or Si limited (Ohio River). Site-specific differences in nutrient limitation were consistent with differences in ambient nutrient levels, with the Tennessee and Cumberland Rivers characterized by lower N and P concentrations, and the Ohio River by lower Si. Downstream nutrient depletion was evident in the Ohio River through comparison of an upstream and a downstream site, with nutrient limitation (Si) occurring more frequently downstream. Phytoplankton growth rates at ambient light and nutrient levels ranged from 0.1 to 1.5 d^{-1} in the Ohio River and 0.2 to 0.6 d^{-1} in the Tennessee and Cumberland Rivers. Growth rates were greatest at the onset of the summer base pool, as light intensities increased and nutrient levels were maximal. Our findings indicate that multiple factors regulate phytoplankton growth in regulated rivers and that spatial complexity may arise from differences in discharge and water aging.

Introduction

Light and nutrients are generally regarded as the main factors regulating phytoplankton growth, and have been used to model phytoplankton production and community succession (Hamilton and Schladow 1997; Huisman et al. 1999). The leading paradigm of ecological succession contends that as light intensity becomes optimal, nutrients become limiting and phytoplankton communities shift from rapidly growing (r-selected) to slower growing (k-selected) species (Kilham and Kilham 1990). Stable populations, however, are rarely attained in aquatic systems due to the dynamic nature of resources (Huisman et al. 1999). Current theory suggests that phytoplankton growth rates are chronically suppressed by low nutrient concentrations (Sommer 1991).

Resource limitation is common in freshwater phytoplankton, although the identity of limiting resources can vary spatially and seasonally. Lakes are generally regarded as phosphorus limited due to high N:P loading, rates of N-fixation by cyanobacteria and sediment retention of phosphorus (Schindler 1977; Levine et al. 1992). Nitrogen, however, has been recognized as a factor limiting phytoplankton growth in systems where nitrogen inputs are low (Elser et al. 1990; Saunders et al. 2000) or when anthropogenic phosphorous loading is high (McCauley et al. 1989). Similarly, high combined loading rates of nitrogen and phosphorus have been shown to allow limitation

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by other nutrients, such as silica (Rahm et al. 1996; Conley et al. 1993).

Interactions between light and nutrient limitation are common in systems where spatial and seasonal variations in discharge, turbidity and nutrient availability are especially dynamic (Oliver and Ganf 1988; Carignan and Planas 1994; Knowlton and Jones 2000). Sterner (1994), for instance, found that although phytoplankton growth rates in a Southwestern U.S. reservoir were suppressed by low nutrient concentrations throughout much of the year, the severity of nutrient limitation varied in response to sporadic storm-induced increases in turbidity. Nutrient availability is also thought to decrease with distance downstream in advective systems due to biotic uptake, particularly during low discharge (Elser and Kimmel 1985; Kennedy and Walker 1990). Nutrient limitation is less common in unimpounded rivers where high discharge and elevated turbidity maintain low light conditions. Evaluation of some shallow European rivers, however, suggest that nutrients can become limiting during low flow, low turbidity periods (Lack 1971; Reynolds and Descy 1996; Garban et al. 1999).

Large rivers have traditionally been regarded as turbid, nutrient-rich environments where phytoplankton is strongly light limited (Vannote et al., 1980; Descy and Gosselain 1994; Reynolds and Descy 1996). Fluctuations in light and nutrient availability, however, are common with variations in discharge, and are therefore temporally dynamic and sensitive to human activities that modify riverine flow. Dynesius and Nilsson (1994) reported that nearly three quarters of the largest northern rivers have been impacted by water regulation structures, a condition which is likely to worsen as global water usage increases (Postel et al. 1996). Regulation of riverine flow varies considerably from low dams designed to maintain a minimal water depth for navigational purposes, to high dams that create large impounds for hydroelectric, recreation or flood control (Kennedy 2001). High dams have a greater impact on riverine hydrodynamics than low-head navigational dams, due to their larger water storage capacity, greater reduction of water velocity and enhanced water ageing (Vorosmarty et al. 1997). Reductions in water velocity decrease turbidity and advective (downstream) losses, factors predicted by the River Continuum Concept to limit phytoplankton production in large rivers (Vannote et al. 1980). Despite global concerns over water regulation practices (Postel et al. 1996; Vorosmarty et al. 1997), few stud-

ies have considered the implications of water storage on ecological processes in riverine ecosystems.

In this study we used laboratory bioassays with light and nutrient amendments to assess resource limitation of phytoplankton in three Midwestern U.S. rivers, each characterized with different water regulation regimes. We quantified growth limitation of phytoplankton in the Ohio, Tennessee and Cumberland Rivers under variable flow conditions to test the hypothesis that enhanced water residence time in the reservoirs of the Cumberland and Tennessee Rivers favors nutrient limitation, while shorter water residence time within navigational pools of the Ohio River favors light limitation. The Ohio River is expected to have higher flow velocities, which will maintain turbid, light-limited conditions. Lower discharge and increased water aging in reservoirs of the Cumberland and Tennessee Rivers are expected to increase light levels and induce nutrient limitation.

Materials and methods

Study sites

The Ohio River flows 1570 km from Pittsburgh, PA, to the Mississippi River in Cairo, IL. The river is subdivided into 20 navigational pools by a series of low dams, which act to maintain a minimum depth of 2.74 m during the summer base pool. In order to assess the spatial variation in resource limitation that might arise from longitudinal gradients in nutrient availability, we sampled two sites in the Ohio River. The upstream site (OR-UP) was located in the McAlpine pool, near Westport, KY, at Ohio River Kilometer (ORK) 928, and the downstream site (OR-DOWN) was in the Smithland pool, near Smithland, KY at ORK 1460. Long-term (1970 to 2000) average annual discharge is 3470 m^3 s^{-1} at the McAlpine dam and 4500 m^3 s^{-1} at the Smithland dam (data from United States Geological Survey). The downstream increase in discharge is predominantly due to tributary inputs from the Green and Wabash rivers at ORK 1255 and 1357, respectively. The average depth (channel cross-section) at the two sites is similar (7 m at base pool). Historical estimates of water transit times (calculated as pool volume/discharge) vary seasonally, ranging from <1 to 130 d in the McAlpine pool and <1 to 110 d in the Smithland pool.

Lake Barkley and Kentucky Lake are the last in a series of impounds along the Cumberland and

Tennessee Rivers, respectively. These rivers drain into the Ohio River at 18 and 50 km below our downstream sampling site (OR-DOWN). Lake Barkley was impounded in 1966 and has a length of 190 km and surface area of 380 km^2. Kentucky Lake was impounded in 1964, extends for 297 km and has a surface area of 800 km^2. Long-term (1976 to 2000) average annual discharge is 1090 m^3 s^{-1} from Lake Barkley and 1860 m^3 s^{-1} from Kentucky Lake (data from Tennessee Valley Authority, TVA). Water residence times range from 4 to 110 d for Kentucky Lake and 2 to 70 d for Lake Barkley (data from TVA). Our sample sites were located 50 km and 30 km upstream of the Barkley and Kentucky dams, respectively, at which locations the average cross-sectional depths were at 5 m during summer base pool.

Sampling

Water samples were collected monthly from March to November 1999. Temperature and dissolved oxygen profiles indicated that the water column was unstratified and well mixed at all sites and dates; therefore, all samples were collected at a depth of 1 m. Photosynthetically active radiation (PAR) was measured at 0.5 m depth increments at one reservoir (Kentucky Lake) and one Ohio River site (upstream) using a LiCor photometer with integrated up-welling, down-welling and deck sensors. The attenuation coefficient, k_d, was highly correlated ($r^2 = 0.99$, $n = 28$) with particulate organic matter (POC). The slopes and y-intercepts for the regressions between k_d and POC were similar for Kentucky Lake and OR-UP (data not shown). This regression was therefore used to estimate k_d from measured POC concentrations at Lake Barkley and OR-DOWN. Mean water column irradiance [$E_{(zmean)}$] for each site was calculated from k_d, average daily solar irradiance penetrating the water surface [$E_{(0)}$] and average cross-sectional depth (z_{mean}), using the following equation:

$$E_{z\,mean} = E_{(0)}e^{-k_d z_{mean}}.$$

Water samples for chlorophyll and dissolved inorganic nutrients were transported on ice and stored in the dark at 4 °C until further processing. Samples were analyzed within 48 hrs after collection. Dissolved silica (SiO$_2$) was analyzed on whole water using an automated method for molybdate-reactive silica (Clesceri et al. 1998). Nitrate and soluble reactive phosphorus (SRP) were analyzed on 0.5 μm filtrate using automated cadmium reduction and ascorbic acid

methods, respectively (Clesceri et al. 1998). A subsample of 0.5 μm filtrate was acidified with 2N HCl and analyzed for dissolved organic carbon (DOC) on a Shimadzu TOC analyzer. A 20 L carboy of whole water from each site was placed on ice and transported to the lab for the bioassay experiments outlined below.

Bioassays

Dilution bioassays (Sommer 1989; Sterner 1990) were used to quantify phytoplankton growth rates under variable light and nutrient conditions. Cultures were diluted using a ratio of 9:1 (filtered:whole) with 0.5 μm filtrate. Incubation times were short (72 hrs) to reduce density-dependent and grazing-induced effects on growth rates. A 2 × 3 factorial design with replication (n = 2 replicates × 2 light levels × 3 nutrient treatments) was used to quantify light, nutrient and their combined effects on algal growth rates.

Ambient light treatments ranged from 2 to 10 E·m^{-2}· d^{-1} (36 to 160 μE m^{-2} sec^{-1}), and approximated the average water column irradiance. A high light treatment (20 E · m^{-2} d^{-1} as 350 μE m^{-2} sec^{-1}) was used to measure light-saturated growth rates. We used 2 nutrient amended treatments (+NP and +NPSi), which received 15 μg SRP L^{-1} (as NaH$_2$PO$_4$ · H$_2$O), 350 μg N-NO$_3$ L^{-1} (as NaNO$_3$) and 3 mg SiO$_2$ L^{-1} (as Na$_2$SiO$_3$ · 5H$_2$O). Ambient nutrient treatments received no additional nutrients. Cultures (700 ml total volume) were incubated in 1 L Erlenmeyer flasks for 3 d with constant shaking at ambient (field) water temperature and 16:8 (L:D) photoperiod.

Phytoplankton growth rates were calculated from linear regressions of the natural logarithms of chlorophyll as a function of time. Other studies have suggested using particulate carbon or particulate nitrogen (Sterner 1994; Sterner and Grover 1998); however, the presence of much non-algal PC and PN at the outset of our incubations (>70% of PC and PN, personal data) would likely result in under estimation of algal growth. In light of this observation, our analyses are based on growth rates calculated from changes in chlorophyll ($r_{chlorophyll}$) between the start and end of each experiment. Chlorophyll was collected on precombusted 0.45 μm glass fiber filters, cold extracted in 90% buffered acetone (Clesceri et al. 1998) and quantified using a Turner-100 fluorometer. Extracts were re-analyzed following acidification with 0.2 N HCl to separate phaeopigments from chlor *a*.
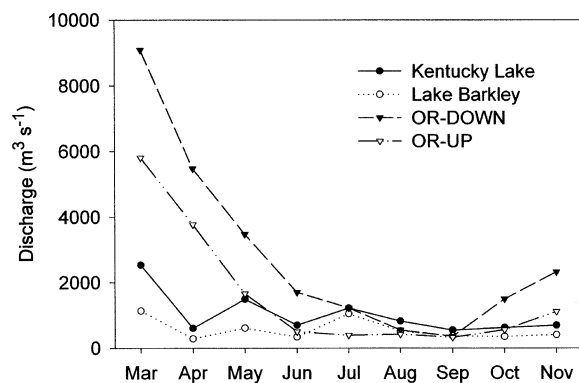
Figure 1. Average monthly discharge for Kentucky Lake, Lake Barkley and the McAlpine (OR-UP) and Smithland (OR-DOWN) navigational pools of the Ohio River from March to November 1999. Data from Tennessee Valley Authority and Army Corp of Engineers.
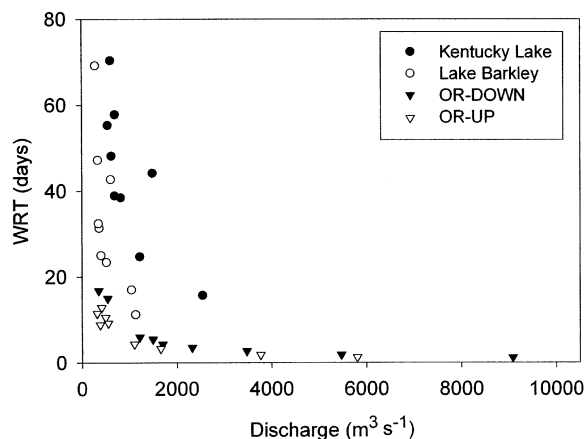

Figure 2. Water residence time as a function of discharge for Kentucky Lake, Lake Barkley and two sites in the Ohio River (OR-DOWN and OR-UP) from March to November 1999.

Statistical analyses

Two-factor ANOVA using light and nutrient treatments as categorical variables were performed for each experiment to assess resource limitation by light or nutrients. Phytoplankton limitation solely by P or N could not be resolved from ANOVA using this design since all nutrients were added in combination. Inferences of P or N limitation were made from regressions of phytoplankton growth rates and initial nutrient concentrations. Silica limitation was evaluated by comparing growth rates from the +NP and +NPSi treatments. All statistical analyses were performed using SigmaStat 2.03.

Results

Site Characteristics

Discharge showed strong seasonal patterns at all sites, with March and April values $3\times$ (KY Lake and Lake Barkley) to $15\times$ (OR-UP and OR-DOWN) greater than those occurring in June through Oct (Figure 1). Average discharges during 1999 were 2300 m^3 s^{-1} for OR-UP, 4000 m^3 s^{-1} for OR-DOWN, 700 m^3 s^{-1} for Lake Barkley and 1400 m^3 s^{-1} for Kentucky Lake. Discharge during summer base pool (June-Sept) was similar among all four sites (c. 500 m^3 s^{-1}). Discharge was generally less than the long-term average at each site due to low precipitation in 1999. Water residence times from March to November 1999 were consistently higher in Kentucky Lake (mean 44 d), followed by Lake Barkley (mean 32 d) and the two Ohio River pools (mean 6 d). Water residence time decreased exponentially with increase in discharge (Figure 2).

Light attenuation coefficients (k_d) showed seasonal variations, but were generally similar (0.7 to 1.1 m^{-1}) among the four sites (data not shown). Lowest attenuation coefficients (< 1 m^{-1}) corresponded with summer low-flow conditions. Average water column irradiance (PAR; Figure 3) followed seasonal patterns and inter-site difference in water depth and k_d. Ambient light levels were highest in Lake Barkley (mean $\pm$ SE, 8.3 $\pm$ 0.7 E m^{-2} d^{-1}) and lowest at the upstream Ohio River site (5.0 $\pm$ 0.8 E $\cdot$ m^{-2} d^{-1}). Differences were most apparent in early summer (April–June) when light availability was substantially greater in Kentucky Lake and Lake Barkley than in OR-UP and OR-DOWN. At all sites, highest water column irradiance was associated with low discharge and high daily solar irradiance (July). Water temperatures ranged from 8 °C (March) to 29 °C (July), and showed no consistent differences among sites (Figure 3). Chlor a was seasonally variable but generally low, ranging from 1 to 26 μg L^{-1} (Figure 3). Chlorophyll was highest in Lake Barkley (15 $\pm$ 2 μg L^{-1}) and lowest at OR-UP (4 $\pm$ 1 μg L^{-1}).

Ambient nutrient concentrations varied among sites, with N-NO_3 generally lower in Kentucky Lake and Lake Barkley, and SiO_2 lower in the Ohio River. Average N-NO_3 in Kentucky Lake and Lake Barkley (300 μg L^{-1}) were $4\times$ lower than the Ohio River (1100 μg L^{-1}). Summer minima in Kentucky Lake and Lake Barkley were 17 and 180 μg N-NO_3 L^{-1}, respectively; whereas, riverine concentrations were never below 600 μg N-NO_3 L^{-1} (Figure 4). SiO_2
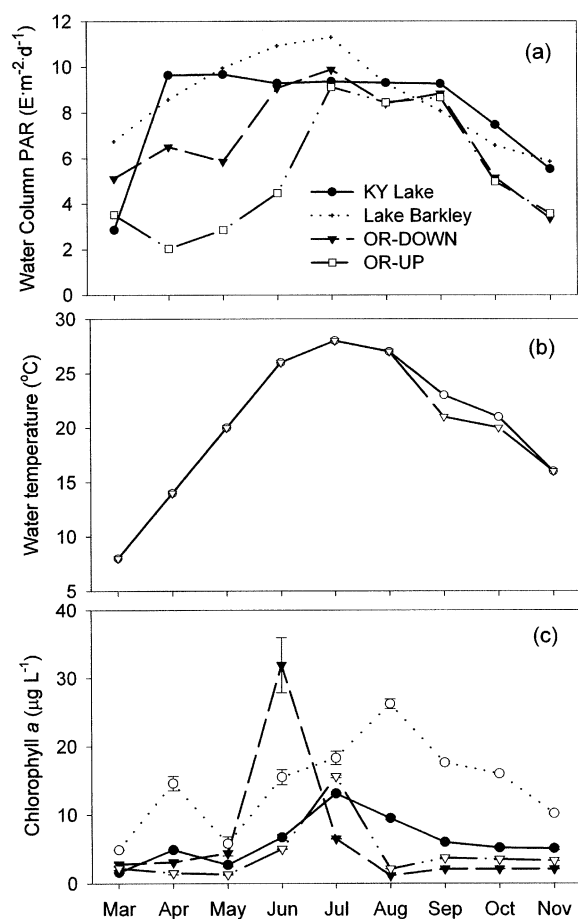
Figure 3. Monthly patterns in (a) average water column irradiance; (b) water temperature; and (c) chlorophyll concentration for Kentucky Lake, Lake Barkley and two sites in the Ohio River (OR-DOWN and OR-UP) from March to November 1999.

Figure 4. Ambient field concentrations of (a) N-NO$_3$; (b) SiO$_2$; and (c) SRP for Kentucky Lake, Lake Barkley, OR-DOWN and OR-UP from March to November 1999.

showed little seasonal variation in Kentucky Lake and Lake Barkley (2 to 5 mg L^{-1}), but decreased rapidly in the Ohio River, from 5 mg L^{-1} in April to less than 1 mg L^{-1} by June (Figure 4). SRP was generally similar among the four sites with highest average values occurring at Lake Barkley (24 μg L^{-1}) and lowest at Kentucky Lake (14 μg L^{-1}; Figure 4). Similar seasonal patterns were observed at all 4 sites with low concentrations during March-July ($<$20 μg SRP L^{-1}) that gradually increased to 20–30 μg SRP L^{-1} by Nov.

Algal growth rates

Algal growth rates ($r_{chlorophyll}$) in non-amended assays (ambient light and nutrients) ranged from 0.3 to 1.5 d^{-1}, corresponding to algal doubling times of 60 and 12 h, respectiv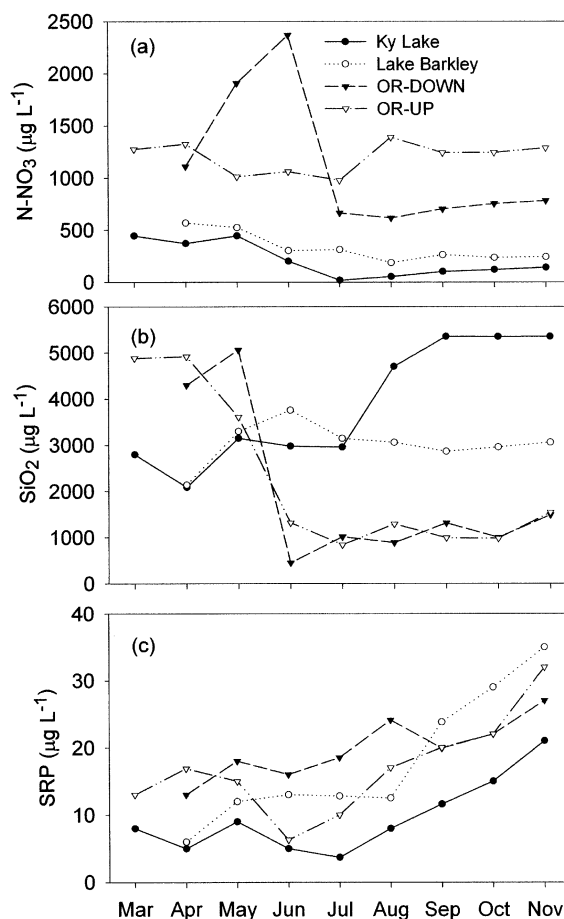ely. No consistent seasonal patterns were observed. Average growth rates (Figure 5) were higher among the Ohio River sites (OR-DOWN: 0.9 d^{-1} and OR-UP: 0.7 d^{-1}) compared to Kentucky Lake and Lake Barkley (0.4 d^{-1}) (P $<$ 0.001, n $=$ 38). To quantify the severity of growth limitation, we calculated the Relative Growth Rate (RGR; Sterner, 1994) as a ratio of the growth rate at ambient light and nutrients to the maximum observed growth rate (light and/or nutrient amended treatments). RGR values, ranged from 0.3 to 0.9 among all sites, indicating that realized (non-amended) phytoplankton growth rates were 30–90% of resource-saturate growth rates. Mean RGR values were lowest in Kentucky Lake (0.5 RGR) and greatest in Ohio River downstream (0.8 RGR). Distinct, but contrasting seasonal patterns were apparent in Lake Barkley and OR-UP, with more severe limitation occurring during April through June in Lake Barkley and July through Nov in OR-UP. RGR val-
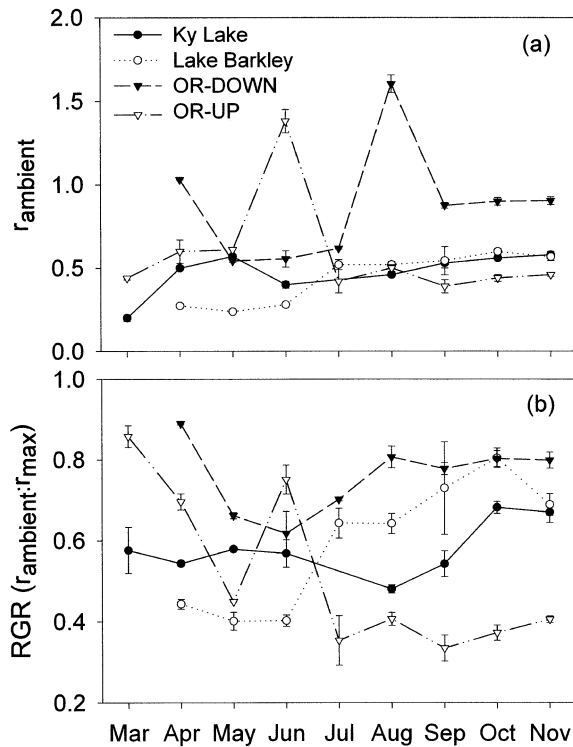
Figure 5. (a) Phytoplankton growth rates at ambient light and nutrient conditions for two sites in the Ohio River (OR-DOWN and OR-UP) and two reservoirs (Kentucky Lake and Lake Barkley). (b) Relative Growth Rate expressed as the ratios of growth rates at ambient and saturating nutrient and light conditions. Error bars denote $\pm$ 1 SE for two replicates.

Figure 6. Effects of daily light dosage on phytoplankton growth rates ($r_{chlorophyll}$) and light/nutrient limitation. (a) Chlorophyll growth rates of ambient nutrient and nutrient amended (+NPSi) assays as function of daily light dosage. Error bars indicate $\pm$ 1 SE for each temperature group. (b) Percent of assays indicating light (solid bars) or nutrient (open bars) limitation as a function of daily light dosage.

ues for OR-DOWN and Kentucky Lake exhibited little seasonal variability.

Phytoplankton growth rates increased with light intensity, maximizing at irradiances from 7–9 E m^{-2} d^{-1} (Figure 6). Light limited growth became more frequent as irradiances decreased below 10 E m^{-2} d^{-1}, with 100% of assays exhibiting light limitation below 5 E m^{-2} d^{-1} (Figure 6). Light was limiting to phytoplankton growth in 11 of the 17 Ohio River experiments (OR-UP and OR-DOWN combined; March through May and Aug through Nov), but was rarely limiting in the Kentucky Lake and Lake Barkley (March and November only; Table 1).

At irradiances greater than 4 E m^{-2} d^{-1}, growth rates were significantly higher in nutrient amended (+NPSi) assays than those with ambient nutrient concentrations (t-test, P < 0.001). On average, nutrient additions increased growth rates by 60%. The incidence of nutrient limitation increased with irradiance (Figure 6), with greater than 80% of assays showing nutrient responses at light levels exceeding 6
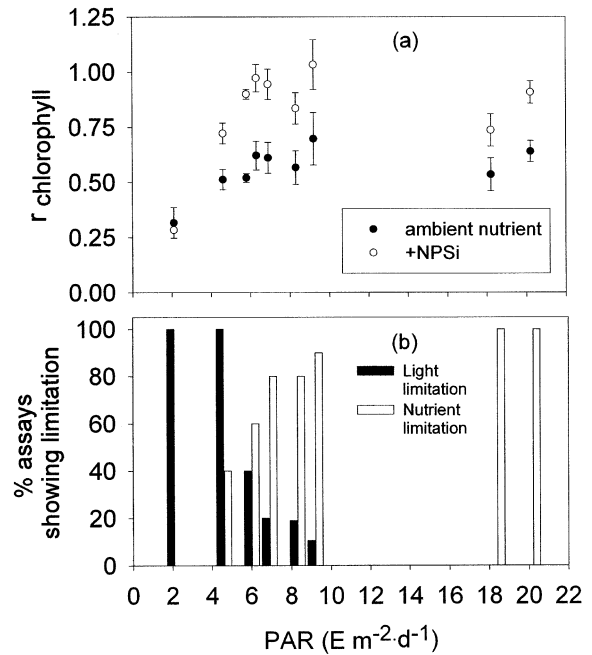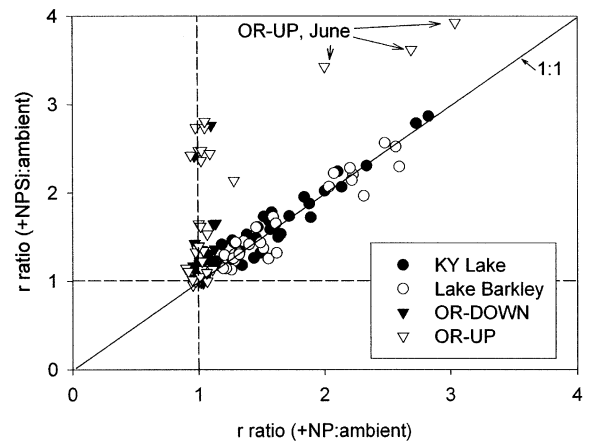

Figure 7. Comparison of the ratios of phytoplankton growth rates ($r_{chlorophyll}$) under ambient conditions (unamended) to nutrient amended assays receiving N and P (x-axis, +NP:ambient) and N, P and Si (y-axis, +NPSi:ambient). Ratios greater than 1.0 (dashed lines) indicate stimulation of phytoplankton growth rates by nutrient amendment. Points above 1:1 equivalence (solid line) indicate response to Si beyond that of N and P.

Table 1. Summary of 2-factor ANOVA of phytoplankton growth rates grouped by site and month with light and nutrient as categorical variables. Positive growth responses to light (L), nutrient (N) and their combined effects (L*N) at P < 0.05 are noted. "n.a." indicates that no data were available for analyses.

Site	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Kentucky Lake	L								L
		N	N	N	N	N	N	N	N
									L*N
Lake Barkley	n.a.								L
		N	N	N	N	N	N	N	N
OR-DOWN	n.a.	L						L	L
			N	N	N	N	N	N	N
OR-UP	L	L	L				L	L	L
				N	N	N	N	N	

E m^{-2} d^{-1}. Overall, nutrients stimulated phytoplankton growth in 20 out of 34 experiments (Table 1). Nutrients limited phytoplankton growth in Kentucky Lake and Lake Barkley from April through Nov (Table 1). Phytoplankton in the Ohio River exhibited growth responses to nutrient additions from May through Nov (OR-DOWN) and June through Oct (OR-UP) (Table 1).

Phytoplankton responses to nutrient additions indicate that growth rates in +NPSi assays were significantly greater than +NP assays for Ohio River sites (t-test, P < 0.001), but not in Kentucky Lake and Lake Barkley (t-test, P = 0.98). Comparison of the ratio of phytoplankton growth rates in assays with ambient nutrients to +NP ($r_{ambient}$: r_{NP}) and + NPSi ($r_{ambient}$: r_{NPSi}) indicated that silica addition in combination with N and P produced a greater growth response than only N and P for OR-UP and OR-DOWN, but not for Kentucky Lake and Lake Barkley (Figure 7). Phytoplankton in the Ohio River responded to addition of N and P alone only during June (OR-UP), when ambient SRP decreased to 6 μg L^{-1}. Low ambient growth rates and RGR values at OR-UP (Figure 5) corresponded with the period when silica concentrations were low (Figure 4). Initial silica concentrations were a weak, but significant predictor in variation of light-saturated growth rates in the Ohio River (OR-UP, $r^2 = 0.25$, P = 0.002). Seasonal variations in ambient growth rates and RGR values for Kentucky Lake and Lake Barkley followed seasonal changes in the availability of SRP. SRP accounted for $\sim$50% of the variation in light saturated growth rates in Kentucky Lake and

Table 2. Linear regression analysis of light-saturated phytoplankton growth rates of KY Lake and Lake Barkley as influenced by SRP and N-NO$_3$. β and m indicate y-intercept and slope of regression line, respectively. Non-significance is denoted by n.s.

Reservoir	Nutrient	R^2	P	β (SE)	m (SE)
KY Lake (n = 90)	SRP	0.36	<0.001	0.25 (0.005)	0.016 (0.002)
	NO$_3$-N	0.07	0.012	0.45 (0.04)	0.0003 (0.0001)
Lake Barkley (n = 84)	SRP	0.53	<0.001	0.33 (0.003)	0.008 (0.001)
	NO$_3$-N	0.001	0.712	n.s.	n.s.

Lake Barkley (Figure 8, Table 2). N–NO$_3$ was not found to be a useful predictor of growth rates.

Discussion

Our phytoplankton assay experiments demonstrated three major findings: 1) resource limitation is common in the Ohio River, Kentucky Lake and Lake Barkley, 2) the specificity of the limiting resource is both spatially and seasonally variable, and 3) shifts from light- to nutrient limitation occurred as water residence times increased. Phytoplankton growth rates under ambient conditions in these rivers, ranging from 0.4 to 0.9 d^{-1}, were comparable to values reported for other regulated rivers (Sterner 1990, 1994; Reynolds and
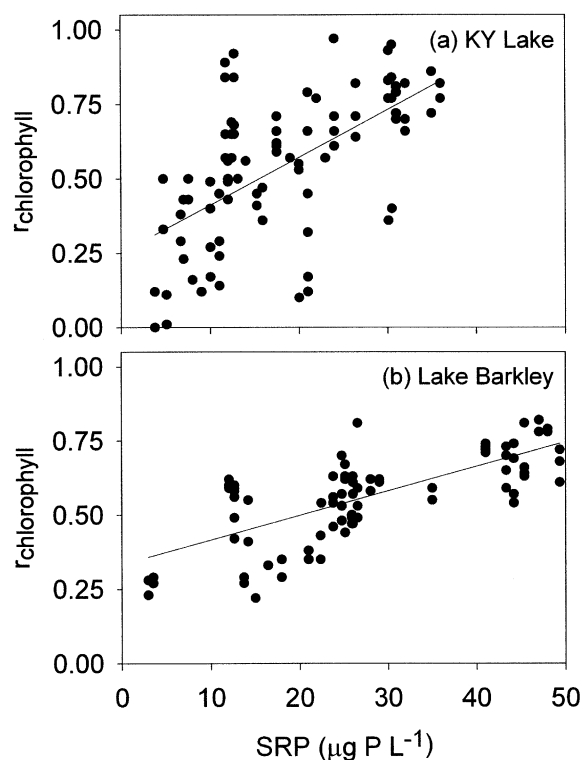
Figure 8. Light-saturated phytoplankton growth rates ($r_{chlorophyll}$) as influenced by SRP for (a) Kentucky Lake and (b) Lake Barkley.

Descy 1996; Sterner and Grover 1998). Using relative growth rates to estimate the severity of limitation, we found chronic growth suppression ranging from 10 to 70% of resource-saturated growth rates. Light was the primary factor limiting phytoplankton at irradiance below 7 E m^{-2} d^{-1}, generally occurring during elevated discharge and high turbidity in early spring. Reduced discharge during the summer pool increased water clarity, primary production, water retention and depletion of nutrients to levels that are limiting to phytoplankton. Our findings indicate that site-specific differences in discharge and water residence time can modify seasonal patterns in growth limitation. Lower than normal discharge during 1999, however, suggests that nutrient limitation may have been more prevalent during our study than during years with normal hydrological conditions.

Increased water retention and the sedimentation of particulate materials generally associated with reduced discharge, enhance light availability and reduce nutrient concentrations, both of which are expected to decrease the ratio of nutrient availability to biotic demand (Lind et al. 1992; Knowlton and Jones

2000). Light limitation will supersede nutrient limitation when irradiance is less than that needed to support photosynthetic production sufficient to balance respiratory losses. Our findings indicated that phytoplankton in the Ohio River, Kentucky Lake and Lake Barkley shifted from light- to nutrient limitation as irradiance increased above 5 to 7 E m^{-2} d^{-1}. This irradiance level, termed "column compensation point" (Talling 1971), is varies with algal taxonomy and physiological status (Huisman et al. 1999), with field studies from diverse aquatic systems reporting similar shifts from light to nutrient limitation at 4 to 8 E m^{-2} d^{-1} (Oliver and Ganf 1988; Carignan and Planas 1994; Knowlton and Jones 1996, 2000). In the current study, the timing and duration of light saturation varied seasonally with solar irradiance and spatially with water clarity and aging. Lower angle of incidence and shorter photic periods induced light limitation in March and Nov at all four sites. Greater solar irradiance, coupled with the longer water residence times in Kentucky Lake and Lake Barkley from April to Oct, and during low flow conditions (summer base-flow) in the Ohio River, allowed for enhanced light availability and induction of nutrient limitation in phytoplankton growth.

P is regarded as the most common nutrient limiting autotrophs in freshwater systems (Schindler 1977), although N (Guilford and Hecky 2000) and Si (Rahm et al. 1996) can be potential factors under enhanced, but disproportionate, nutrient loadings. Minimal nutrient concentrations in the Ohio River of 600 μg NO$_3$-N L^{-1} and 10 μg SRP L^{-1} (with exception of the upstream site in July) suggested that these riverine phytoplankton were not N-limited and rarely P-limited during our study. Ohio River phytoplankton responded to N and P amendments only when silica was also added, suggesting that silica is at least a co-limiting nutrient under light saturated conditions in this system. Silica limitation has previously been inferred from seasonally low SiO$_2$ concentrations in the Ohio River (Wehr and Thorp 1996) and other riverine systems (Reynolds et al. 1994). Relatively high flow velocities in large rivers allow diatoms to remain in suspension and dominate plankton communities in many temperate rivers (Rojo et al. 1994), including that of the Ohio River (Wehr and Thorp 1996). Diatoms can greatly increase Si demand by removing 20 to 70% of SiO$_2$ in riverine systems (Garban et al. 1999; Knowlton and Jones 2000; Gibson et al. 2000). When N and P loading are high, biogenic removal of dissolved silica by diatoms could lead to silica limitation (Rahm et al. 1996). Silica depletion can be intensified in large regu-

lated rivers as sedimentation and limited re-suspension of diatoms during low flow velocities function as temporary sinks for dissolved silica (Gibson et al. 2000). Silica depletion was not evident in Lake Barkley and Kentucky Lake, where diatoms likely settle out of the water column under lower flow velocities and phytoplankton communities are dominated by Chlorophytes and Cyanobacteria (Williams 1999).

Our experiments indicated that P was the main nutrient limiting phytoplankton growth in Kentucky Lake and Lake Barkley, with N-deficiencies appearing in Kentucky Lake during late summer and autumn. Reynolds and Descy (1996) suggested that because of a high affinity for and rapid recycling of N and P, phytoplankton energetic requirements are met when ambient conditions exceed 3 μg P L^{-1} and 50 μg N L^{-1}. NO_3 and SRP in excess of these concentrations may imply the absence of nutrient limitation, however, under certain conditions half-saturation constants can be well above these thresholds (Sterner and Grover 1998). Of our assays, none showed initial SRP concentrations below 3 μg L^{-1} and only Kentucky Lake (May to Sept) exhibited N-NO_3 concentration below 50 μg L^{-1}. Using the Redfield ratio for N:P (16:1) as an estimate for inorganic nutrient requirements, our data suggests that P was the main limiting nutrient in Lake Barkley (N-NO_3:SRP ratios ranging from 200 to 20). In Kentucky Lake, however, there was evidence of a shift from P-limitation to N-limitation as N:P ratios decreased from approximately 125 (March to June) to less than 16 (July to Nov). Lower ambient concentrations of NO_3-N from July through Sept provide further evidence of N-deficient growth in Kentucky Lake that is not paralleled in Lake Barkley. Basin morphology may explain differences in nutrient variability between these two reservoir systems. Although these two systems have similar discharges, Kentucky Lake has nearly twice the surface area and therefore much higher water residence times than Lake Barkley. This result suggests that biotic uptake and depletion of nutrients are more severe in Kentucky Lake. In a survey of the Tennessee River system, Elser and Kimmel (1985) showed that nutrient availability tended to decrease downstream within individual reservoirs. Our sample sites were approximately 160 km from the head of Lake Barkley and 270 km from the head of Kentucky Lake. The extra distance would allow more time for biotic nutrient uptake in Kentucky Lake.

Nutrient depletion occurs downstream in riverine systems (Elser and Kimmer 1985; Kennedy and Walker 1990; Descy and Gosselain 1994). Comparis-

ons of our assays from the upstream and downstream sites of the Ohio River suggest that instream nutrient depletion does occur in the Ohio River, resulting in a higher frequency of nutrient limitation in downstream communities. Previous longitudinal surveys along the Ohio River also indicated downstream nutrient depletion (Bukaveckas et al. 2000), although our assays suggest that phytoplankton-induced depletion is likely to occur only during low flow, high light conditions.

Conclusions

The transformation from light to nutrient limitation in flowing waters and the specificity of the limiting nutrients, are dependent upon the interactions of nutrient loading, water residence time and flow velocity. A major effect of global dam construction is to transform free-flowing rivers from light limited, nutrient saturated environments to ones that are light saturated and nutrient limited. This favors increased nutrient retention and in the short term may partially mitigate the effects of anthropogenic nutrient loading on downstream and coastal areas. Additional research is necessary to investigate the interactive effects of nutrient depletion and community composition.

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