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Phytoplankton production in a large, regulated river: A modeling and mass balance assessment

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Abstract

Phytoplankton production in riverine systems is regulated by hydrologic processes and coupled optical dynamics, which determine the light dosages experienced by phytoplankton during transit within a defined reach. We used data on river stage, discharge, and channel geomorphometry to model changes in light availability experienced by phytoplankton during transit within a 122-km navigational pool of the Ohio River. Whole-pool estimates of phytoplankton production were derived from photosynthesis–irradiance relationships and modeled values of light availability. Derived estimates of primary production showed good agreement with whole-pool mass balances for algal carbon. The sum of upriver inputs and autochthonous production agreed to within 10% of downriver export. During a summer with above normal discharge (1998), phytoplankton production within the pool corresponded to <10% of phytoplankton inputs from upstream and tributary sources. During lower flows in 1999, phytoplankton production in the pool exceeded external inputs of algal carbon. Modeled estimates of primary production were used to predict seasonal and longitudinal variation in algal abundance assuming a constant C : chlorophyll ratio. Model results showed good agreement with measured chlorophyll values and supported the hypothesis that biomass development was constrained by light availability and transit time within the pool. The model overestimated chlorophyll in late summer when grazing might limit biomass accumulation. The cumulative irradiance experienced by phytoplankton during transit within the pool was found to be a good predictor of autotrophic potential and for interpreting complex interactions arising from seasonal hydrologic cycles and the influence of water regulation structures.

Limnologists have debated the importance of phytoplankton production in rivers. Deep and turbid conditions characteristic of many large rivers have led some to argue that phytoplankton are of little importance to riverine food webs, particularly in light of large allochthonous inputs from floodplain and upstream sources (Vannote et al. 1980; Junk et al. 1989; Devol and Hedges 2001). More recent studies have shown that algal abundance in some rivers is comparable to moderately productive lentic systems with well-established plankton-based food webs (Wehr and Thorp 1997). Algal carbon in rivers derives from in situ production, tributary inputs, and floodplain sources. Algal carbon can comprise a significant portion of riverine particulate organic carbon (POC), with estimates of 38% reported for the tidal-influenced Hudson River (Findlay et al. 1996) and 15–65% for European rivers (Admiraal et al. 1992; Gosselain et al. 1994; Köhler 1995). Moreover, algal carbon is thought to have a greater nutritive value for grazers and decomposers; therefore, its importance to secondary production might be disproportionate to its mass (Thorp and Delong 1994).

Despite recent interest, riverine phytoplankton are less well known than their lentic and marine counterparts, and basic questions about sources and fate of algal carbon in large rivers remain unresolved (Wehr and Descy 1998). Potential factors regulating phytoplankton production include water transit time, light availability, nutrient limitation, sedimentation, and grazing. Upstream sources of algal carbon and top-down controls (benthic or pelagic grazers) have been shown to be important in some systems (Caraco et al. 1997; Gosselain et al. 1998*a*,*b*), whereas others have concluded that phytoplankton abundance is largely determined by light limitation of autochthonous production (Cole et al. 1992; Basu and Pick 1997; Wehr and Descy 1998). Because phytoplankton are continually advected downriver, net production within a defined reach can occur only when growth rates exceed downstream losses. Growth rates are suppressed by low light availability due to attenuation from suspended particulate matter and, in some rivers, because of deep mixing depths. Thus, photosynthetic gains are often closely balanced against respiration losses. Biomass accrual is restricted to shallow reaches of the river during periods of low discharge and turbidity where phytoplankton experience prolonged exposure to favorable light climates (Reynolds and Descy 1996). Correlating temporal or spatial variation in phytoplankton production with concurrent measures of optical properties is difficult because light dosages experienced by cells traveling downriver integrate changes in river depth and transparency over spatial and temporal scales that are determined by water transit time. An understanding of riverine algal dynamics that yields predictive capability therefore requires an integrative assessment of hydrologic–optical conditions and their effects on phytoplankton production.

Complex interactions arising from spatial variation in channel geomorphometry and seasonal variation in river

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depth, discharge, and transparency are well-suited to analyses with models. Models simulating river hydrodynamics have been used by hydrologists to predict the timing and location of flood events, the removal of materials from banks and riverbeds, and the effects arising from water control structures (Wurbs and James 2002). Limnologists have incorporated various aspects of these models in their attempts to simulate riverine phytoplankton dynamics and identify specific hydrologic variables regulating algal abundance. For example, Billen et al. (1994) modeled phytoplankton in the River Seine and concluded that community shifts and biomass fluctuations were related to the intensity, timing, and phosphorus content of high-water pulses associated with spring runoff. Caraco et al. (1997) modeled spatial and temporal variation in phytoplankton abundance in the Hudson River and demonstrated both light-limited growth during pre–zebra mussel invasion years and grazer-controlled growth after zebra mussel establishment. Phlips et al. (2000) accurately depicted longitudinal gradients in phytoplankton biomass for a black-water river by modeling spatial and temporal variation in light availability as a function of water color and channel morphometry.

The development of riverine phytoplankton models is dependent on an accurate depiction of hydrologic processes at temporal and spatial scales relevant to algal growth rates. River stage and channel geomorphometry are key variables because these determine the average (cross-channel) depth and, when combined with light attenuation, the average light level experienced by phytoplankton. Cross-channel area coupled with measurements of discharge can be used to estimate average water velocity and thereby determine phytoplankton transit times for a specified reach. Fortunately, requisite hydrologic and geomorphic data are available for many rivers in the north temperate zone making these systems amenable to modeling approaches. If algal growth rates are strongly regulated by hydrologic and optical conditions, then hydrodynamic-based models should accurately depict spatial and temporal patterns in phytoplankton abundance. If other factors such as grazing and nutrient limitation are important, then models that exclude these will perform poorly. In this way, the success of hydrodynamic-based models provides a test of the hypothesis that physical processes regulate phytoplankton growth in rivers.

Incorporating the variety of factors that influence transit time and light availability is of central importance to modeling phytoplankton in rivers. This task is complicated by the modification of the flow regime of the majority of the world's large rivers by human activities (Dynesius and Nilsson 1994; Vorosmarty et al. 1997). Water regulation practices vary according to management needs but often include dams constructed to make rivers navigable for commercial shipping (Sparks 1995). Navigation dams are typically short (low head) structures designed to maintain a minimum depth during low flow conditions (Sparks and Spink 1998). Low-head dams regulate but do not eliminate flowing conditions and, unlike flood control (high head) dams, do not inundate large areas. Navigation dams locally reduce current velocity and thereby promote sedimentation and increase water clarity. However, navigation dams also raise surface water elevation, thereby increasing average depth. The net effect of these processes on light availability will vary depending on discharge and proximity to the dam. Despite recent controversy surrounding the construction and removal of dams, few studies have explicitly considered their effects on water column processes in rivers including phytoplankton production.

In this study, we investigate phytoplankton production in a large, regulated river of the midwestern United States (Ohio River) to assess the potential importance of autotrophy in this system. We present a hydrodynamic-based model that quantitatively simulates light availability, primary production, and river chlorophyll using input data on channel morphometry, water transit time, and photosynthesis–irradiance relationships. We describe seasonal and longitudinal variation in phytoplankton production and biomass (as chlorophyll) in relation to hydrologic and optical conditions for a 122-km-long pool defined by upriver and downriver navigation dams. Finally, we construct a mass balance to assess the importance of phytoplankton production within the pool relative to algal carbon inputs from upriver and tributary sources.

Methods

Site description—The Ohio River is the largest tributary of the Mississippi River and the second largest river (by discharge) in the United States. The watershed is predominantly (48%) agricultural and encompasses an area of 528,360 km^2. The river is 1,578 km in length beginning at the confluence of the Allegheny and Monongahela Rivers and ending where it joins the Mississippi. The Ohio River is subdivided along its length into a series of pools by 20 low-head dams, which provide a minimum 3 m depth for navigation. A historical perspective on river management and water quality is provided by Pearson (1992). Our study site was the McAlpine pool, a 122-km reach defined by the upstream Markland Dam at Ohio River kilometer (ORK) 855 and the downstream McAlpine Dam at ORK 977. The principal water sources of the McAlpine Pool are the upper Ohio River and the Kentucky River, accounting for 92 and 7% of pool output, respectively. Nutrient and phytoplankton dynamics are described in Wehr and Thorp (1997) and Bukaveckas et al. (2001) and will be briefly summarized. Dissolved inorganic fractions of N (dissolved inorganic nitrogen) and P (PO_4) are generally high with typical ranges of 1,000–2,000 μg N L^{-1} and 20–80 μg P L^{-1}. Silica depletion is observed in late summer with September–October concentrations <0.5 mg L^{-1} and Si : P below the Redfield ratio. Summer phytoplankton communities are dominated by cyanobacteria and diatoms.

Sampling and analytical methods—Data were collected at four sites within the main channel of the Ohio River and one in the Kentucky River. The four mainstem sites were located 8.0 km below the upper dam (ORK 863), 3.5 km below the confluence of the Kentucky River (ORK 882), midpool (ORK 933), and 10.0 km above the lower dam (ORK 967). The Kentucky River was sampled 1 km above its confluence with the Ohio River. Chlorophyll *a* (Chl *a*), particulate organic carbon, temperature, turbidity, and water-

Table 1. Abbreviations, descriptions, and units for input and output terms used in the Ohio River Algal Chlorophyll model.

Term	Definitions	Units
Inputs		
Chl_{IN}	Starting Chl *a* concentration in box *n*	mg m^{-3}
E_{max}	Irradiance at solar noon	μmol photons m^{-3} s^{-1}
K_d	Total light attenuation coefficient (K_{chla} + K_{part})	m^{-1}
K_{chla}	Light attenuation coefficient of Chl *a*	m^{-1}
K_{part}	Light attenuation coefficient of suspended sediments	m^{-1}
Resp	Phytoplankton respiration coefficient	percent P_{max}
DayHours	Number of hours of light in day	h
C : Chl	Ratio of algal carbon to Chl *a* (w/w)	dimensionless
P_{max}	Light saturated rate of photosynthesis	mg C (mg Chl *a*)$^{-1}$ m^{-3} h^{-1})
alpha (α)	Light-limited rate of photosynthesis per photon	mg C (mg Chl *a*)$^{-1}$ m^{-3} h^{-1} (μmol m^{-2} s^{-1})$^{-1}$
E_k	Irradiance at light saturation (P_{max}/α)	μmol photons m^{-2} s^{-1}
Albedo	Fraction of irradiance reflected from surface	percent of E_{max}
Depth (*z*)	Hydraulic depth of each box	m
ResTime	Residence time of water/chlorophyll in each box	h
Volume	Volume of box	m^3
Outputs		
r	24-h box-specific chlorophyll growth rate	mg Chl *a* m^{-3} d^{-1}
Chl_{OUT}	Chlorophyll concentration after box-specific growth	mg Chl *a* m^{-3}
BoxIrr	24-h box-specific cumulative available irradiance	mol photons m^{-2}
CI	Whole-pool cumulative box irradiance	mol photons m^{-2}

column light attenuation were measured at all sites through two growing seasons (May–October 1998 and 1999). A Lagrangian approach was used to sample the same parcel of water moving downstream based on estimated transit times within the McAlpine pool (*see model below*). Sampling events were timed at approximately every two river flushings. Because of interannual differences in discharge (*see Results*), there were eight sample periods in 1998 and five sample periods in 1999. Water samples were collected in the main channel within 1 m of the surface. Periodic comparisons of near-shore versus main channel and surface versus bottom samples confirmed that the system was well mixed; temperature and Chl *a* exhibited little lateral or vertical variation at a given site. Samples were transported to the lab for processing within 4 h of collection.

Subsurface irradiance (E_z) was measured at 0.5-m depth intervals from surface to bottom (starting at 0.1 m) using Li-Cor 192SA cosine-corrected upwelling and downwelling sensors. Surface irradiance (E_0) measurements were recorded using a Li-Cor 190SA flat-plate quantum sensor. Simultaneous measurements were recorded from all three sensors using a Li-Cor 1000 data logger, and four replicate profiles were obtained at each sampling location. Water column irradiance was corrected for changing cloud cover using surface values. The downwelling light attenuation coefficient (K_d) was calculated by least-squares linear regression of natural log–transformed irradiances values against depth where K_d is the negative slope of the equation (Kirk 1994). Turbidity was measured using a Hach turbidimeter (model 2100A).

Primary production was measured at the midpool site by incubating triplicate 60-ml water samples injected with 1.0 μCi $NaH^{14}CO_3$. Samples were incubated at each of three depths for 2 h in situ (between 1200 and 1500 h). Samples were immediately filtered through 0.45-μm Gelman Metrical membrane filters, dried overnight, and stored until analysis. Filters were dissolved in 6.5 ml of Aqua-sol, and radioactivity was measured using a Tri-Carb 1900 TR liquid scintillation counter. Quenching was corrected using an external unquenched ^{14}C standard with known activity. Irradiance-specific carbon uptake rates were calculated as in Wetzel and Likens (1991).

Depending on suspended sediment concentrations, between 200 and 1,000 ml of river water were filtered through a 0.5-μm glass fiber filter (Gelman A/E), and the filters were frozen until analysis. Chl *a* was extracted in 90% buffered acetone, and concentrations were determined by fluorometry using a Turner Designs 10-AU fluorometer with acid correction following U.S. EPA standard method 445.0, revision 1.2 (Arar and Collins 1997). Dissolved inorganic carbon (DIC) samples were collected in 50-ml acid-washed plastic syringes and analyzed on a Shimadzu carbon analyzer (model TOC-5050A) using the combustion/nondispersive infrared gas analysis method (APHA 1992). Particulate organic carbon (POC) concentrations were determined from material collected on precombusted, 0.5-μm glass fiber filters. Filters were dried overnight at 70°C, weighed, combusted at 450°C for 4 h, and massed again. POC was estimated to be 41% of the ash-free dry mass (determined from subsamples run on a Perkin-Elmer CHN analyzer).

Model development—The Ohio River Algal-Chlorophyll (ORACHL) model links hydrologic, geomorphic, and optical data with photosynthesis–irradiance (P-E) curves to predict spatial and temporal variation in algal abundance (*see Table 1* for terms and definitions). P-E relationships are widely used to extrapolate from discrete measurements of production to depth-integrated, annualized (or growing season) estimates

(Morel and Antoine 2002). For this application, we used seasonally adjusted P-E curves and model-derived estimates of water column light availability to estimate depth-integrated, net primary production for the McAlpine Pool. Production estimates, water transit times, and a fixed carbon to Chl *a* ratio (C : Chl) were used to model seasonal and longitudinal variation in river chlorophyll concentrations. Cumulative light dosages experienced by phytoplankton during transport within the McAlpine Pool were used to characterize seasonal and spatial variation in autotrophic potential.

A one-dimensional hydrologic model (HEC-RAS; U.S. Army Corps of Engineers 1998, version 2.2) was used to depict river hydraulics. The model contains geomorphic data consisting of cross-channel depth profiles obtained at 1-km intervals along the length of the McAlpine Pool. At each transect location, the model estimates surface water elevation based on river stage and discharge recorded continuously at the downriver (McAlpine Dam) U.S. Geological Survey gauging station. Surface water elevation and channel morphometry are used to estimate cross-sectional area and average (cross-sectional) depth. Average water velocity is estimated from cross-sectional area and discharge. These data allow derivation of the volume and transit time for each 1-km reach delineated by an upstream and downstream transect location.

To characterize the light climate of the river, we calculated light dosages experienced by phytoplankton within each 1-km reach and during transport through the entire pool. Reach-specific light dosages were derived as a function of transit time, average depth, daily solar radiation, and light attenuation. Surface irradiance ($E_{0(t)}$) was modeled at hourly (t) intervals (Kirk 1994) using the calculated daily maximum solar irradiance (E_{max}; Iqbal 1983) and the photoperiod (D).

$$E_{0(t)} = E_{max}\sin^3\left(\frac{\pi t}{D}\right) \quad (1)$$

Light attenuation coefficients for each reach were modeled using the measured value from the upstream sampling location (ORK 863) corrected for downstream changes in chlorophyll. Because light attenuation was primarily caused by nonalgal suspended particulate matter, K_d values for the upstream station accurately depicted conditions throughout the pool. Measured K_d values obtained at three downstream sampling sites showed that longitudinal variation was rare, except on one occasion (July 1999) when downstream chlorophyll increases resulted in higher attenuation at the midpool site (*see Results*). The daily average irradiance within each 1-km reach was calculated assuming complete lateral and vertical mixing,

$$\text{Irr} = \int_{t=1}^{24} \frac{E_{0(t)} - [E_{0(t)}e^{(-K_d z)}]}{K_d z}\,dt \quad (2)$$

where z is the average (cross-sectional) depth. Daily irradiance and water residence time (ResTime) were used to estimate the cumulative irradiance experienced by an algal cell traveling the length of each 1-km reach. These values were summed for all reaches to derive the cumulative irradiance (CI) experienced by an algal cell traveling the length of the McAlpine Pool.

$$\text{CI} = \sum_{\text{Box}=1}^{112} (\text{Irr})\left(\frac{\text{ResTime}}{24}\right) \quad (3)$$

Primary production was modeled as a function of light levels using P-E relationships described in Jassby and Platt (1976).

$$P = P_{max}\tanh\left(\frac{\alpha E}{P_{max}}\right) \quad (4)$$

P is the biomass-specific rate of production (expressed per unit chlorophyll) at irradiance E. Alpha is the slope of the light-limited production curve, and P_{max} is the maximum light-saturated rate of photosynthesis. Six P-E models were derived by aggregating data according to year (1998, 1999) and season (spring, summer, fall). Model fit values (R^2) ranged from 0.87 to 0.96 ($p < 0.001$ for all models). Net primary production (NPP) was calculated assuming respiration to be a constant fraction (0.10) of P_{max}. Respiration losses were subtracted after each hour of growth over a 24-h cycle.

Each reach had a chlorophyll input value (Chl_{IN}) from upriver and a reach-specific chlorophyll growth rate (r), which together were used to calculate the outgoing chlorophyll concentration (Chl_{OUT}).

$$Chl_{OUT} = Chl_{IN}\left[\exp\left(r \times \frac{\text{ResTime}}{24}\right)\right] \quad (5)$$

Chlorophyll growth rates were derived from NPP assuming a C : Chl ratio of 20 (w/w). This ratio was determined empirically through growth experiments conducted in 2,000-liter outdoor mesocosms using natural phytoplankton communities at our midpool sampling location. Variable shade levels were used to mimic the range of light intensities occurring in the deepest and shallowest reaches of the McAlpine Pool. The range of light dosages resulted in varying yields of POC and chlorophyll during the 72-h experiment. POC was regressed against chlorophyll ($R^2 = 0.90$; $p < 0.001$) and the slope of this line was used to estimate the C : Chl ratio. Our ratio was similar to that derived using Ohio River light and nutrient data and previously published regression models (C : Chl = 17–22; Cloern et al. 1995). For each model run, the initial K_d and Chl_{IN} for the most upstream reach were specified based on values measured at the uppermost sampling location. The resultant change in chlorophyll concentration (Chl_{OUT}) for Reach 1 then became Chl_{IN} for Reach 2, and this process was repeated sequentially downriver to depict longitudinal patterns in chlorophyll. Kentucky River contributions of chlorophyll and water were included as inputs for the reach located at the confluence of the Ohio and Kentucky Rivers. Chl_{OUT} values at locations corresponding to the four sampling sites were used to compare model-derived and measured chlorophyll concentrations. A total of 13 model runs were performed to depict the range of hydrologic and optical conditions occurring in the river at the time that field measurements were obtained.

Mass balances—Water and material budgets were derived for the length of the growing season (May–October) in both

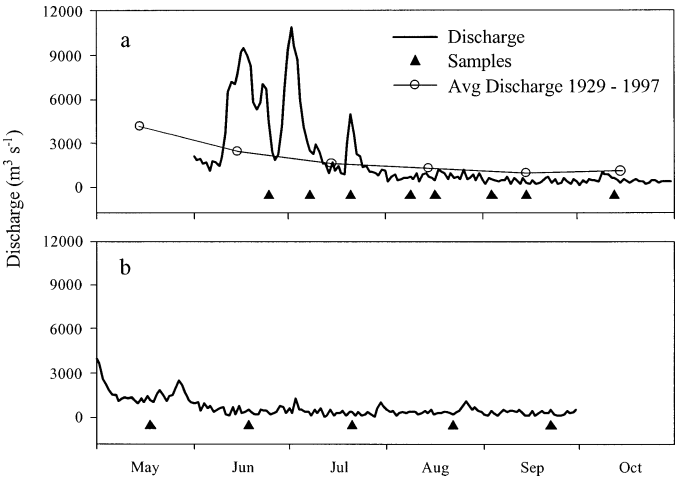

Fig. 1. Sample times and daily discharge of the Ohio River at Louisville, Kentucky, during May–October 1998 and 1999. Sampling intervals were timed to occur at approximately every two river flushings based on water transit times for the McAlpine Pool. Long-term averages of monthly discharge are plotted for comparison.

years and for each of the 13 sampling periods. Input and output fluxes of algal carbon and POC were estimated from measurements of concentration and discharge at the Kentucky River and the upper and lower Ohio River dams. Discharge was measured continuously, whereas concentrations were linearly interpolated between sample periods (Jossette et al. 1999). Algal carbon concentrations were estimated from Chl *a* assuming a C : Chl ratio of 20 (*see Phytoplankton model above*). Budgets were constructed for the whole pool and separately for upper and lower portions of the pool delineated by the midpool sampling site (ORK 933). Because there were no major tributaries downstream of the Kentucky River, discharge at the midpool site was assumed to be equivalent to discharge at the downriver dam.

We compared inputs (upper Ohio River and Kentucky River), pool outputs (at McAlpine Dam), and within-pool production to assess sources and fate of algal carbon within the McAlpine Pool. Daily whole-pool net primary production (DNPP, tonnes C d^{-1}) was estimated as the product of NPP and volume for each reach summed for all reaches. NPP for the entire growing season was estimated by linear interpolation of Chl *a* concentrations between sampling periods. Daily values for light attenuation were derived by regression using river turbidity measurements recorded daily at the McAlpine Dam by the Louisville Water Company (unpubl. data). Paired K_d and turbidity measurements obtained during this study were related using least-squares regression ($n = 54$, $R^2 = 0.97$).

Results

Average daily discharge varied between 200 and 11,000 $m^3\ s^{-1}$ and resulted in pool transit times ranging from <1 d to 25 d during May–October 1998 and 1999 (Fig. 1). Discharge patterns during the 2 yr differed markedly. In 1998, three high-discharge events (4,000–10,000 $m^3\ s^{-1}$) occurred in early summer, and base flows were not reached until August. In 1999, discharge exceeded 3,000 $m^3\ s^{-1}$ on only one occasion (May), and river flow was consistently below the long-term average throughout the summer. As a consequence, almost three times as much water passed through the McAlpine pool during the 1998 growing season (25.7 km^3) compared to 1999 (8.7 km^3). Average transit times for the McAlpine Pool were shorter in 1998 (8.4 d) compared to 1999 (15.4 d).

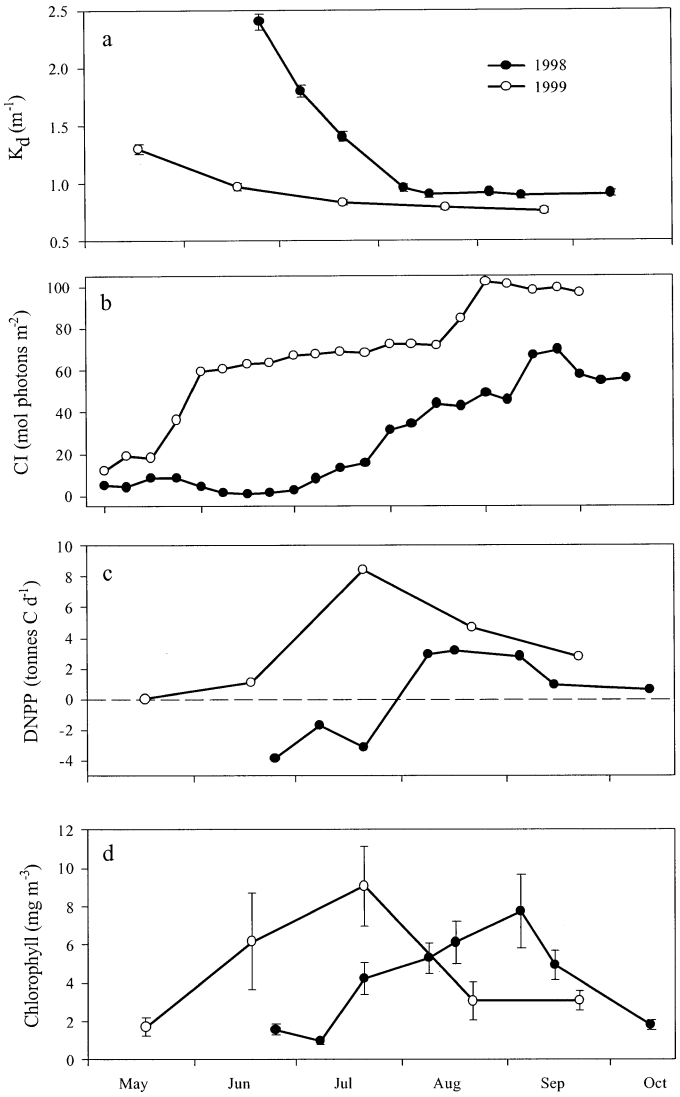

Fig. 2. Temporal variation in light attenuation (K_d), cumulative irradiance (CI), daily net primary production (DNPP), and chlorophyll during May–October 1998 and 1999. (a, d) Light attenuation and chlorophyll values are averages (with SE) for four sample locations within the McAlpine Pool. (b) Cumulative irradiance (CI) data are weekly values derived from daily solar radiation, mixing depths, K_d, and water transit times. (c) DNPP data were estimated from measured algal biomass (as Chl *a*) and modeled production (P-E curves).

Interannual differences in discharge had a marked effect on seasonal patterns in light attenuation (Fig. 2). Attenuation coefficients were greater throughout 1998 compared to 1999. In 1998, K_d exceeded 1.5 m^{-1} ($z_{1\%} < 2.0$ m) during the

period when discharge was elevated and did not decline below 1.0 m^{-1} ($z_{1\%}$ = 3 m) until August. In 1999, K_d was below 1.5 m^{-1} throughout the growing season, and 1% light levels typically ranged from 4 to 7 m. Measured K_d values exhibited little longitudinal variation as indicated by low coefficients of variation among the four sampling locations. Model-derived estimates of the cumulative irradiance experienced by phytoplankton during transit through the McAlpine Pool reflected interannual differences in light attenuation and discharge (Fig. 2). During the high-flow year (1998), cumulative irradiance was low (<20 mol photons m^{-2}) throughout much of the growing season (May–August), and peak values (60 mol photons m^{-2}) were not observed until September. During the low-flow year, cumulative irradiance reached 60 mol photons m^{-2} by June and remained high through the end of the growing season. Primary production and chlorophyll followed seasonal and interannual patterns in cumulative irradiance. In 1998, whole-pool daily net primary production (DNPP) was negative until late in the growing season (August) when peak productivity was 3 t C d^{-1}. Positive DNPP during August–September was largely offset by negative DNPP in preceding months and resulted in a low estimate of total production during the growing season (8 t C). In 1999, DNPP was positive throughout most of the growing season, and peak rates in July were 8 t C d^{-1}. As a result, total production during the growing season was substantially higher (362 t C) than the previous year. In both years, primary production declined in September–October despite continued increases in cumulative irradiance. Average (whole-pool) chlorophyll concentrations increased from 2 to 8 mg m^{-3} during the growing season and coincided with increases in cumulative irradiance. Peak values were similar in both years, although the timing of the chlorophyll peak was delayed during the high-flow year (September 1998) compared to the low-flow year (July 1999). Chlorophyll concentrations decreased in late summer, matching declines in DNPP.

To illustrate longitudinal gradients in phytoplankton production, we selected three dates representative of high discharge (June 1998: 6,684 m^3 s^{-1}), moderate discharge (August 1998: 690 m^3 s^{-1}), and low discharge (July 1999: 480 m^3 s^{-1}). Increases in river stage and light attenuation during periods of elevated discharge resulted in relatively deep conditions (8–12 m) and low average daily irradiance (Irr < 2 mol photons d^{-1}) throughout the pool (Fig. 3a). Decreases in discharge were accompanied by decreases in river depth of up to 5.5 m in the upper pool, whereas in the lower pool, the dam maintained a constant surface water elevation (Fig. 3b). Depth differences between the upper and lower portions of the pool were associated with pronounced longitudinal gradients in light availability. During periods of moderate discharge, average irradiance in the upper pool exceeded 8 mol photons m^{-2} d^{-1} and was twofold higher compared to the lower pool. At low discharge, average irradiance in the upper pool increased further to 11 mol photons m^{-2} d^{-1} (Fig. 3c). Because K_d was similar throughout the pool, downstream gradients in light availability were attributable solely to changes in depth. Changes in river stage were coupled with changes in water transit time, and their combined effects resulted in large (30-fold) differences in cumulative

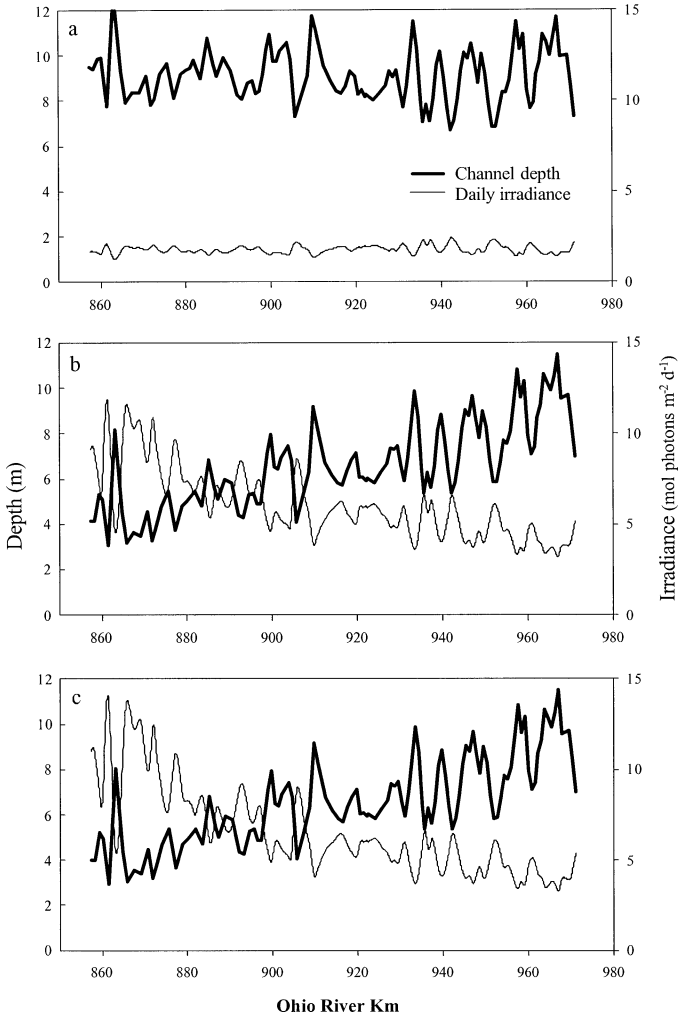

Fig. 3. Longitudinal variation in average (cross-sectional) channel depth and daily irradiance within the McAlpine Pool of the Ohio River for three dates representative of (a) high (June 1998), (b) moderate (August 1998), and (c) low (July 1999) flow conditions.

irradiance. When discharge exceeded 6,000 m^3 s^{-1}, transit times were ~1 d, and cumulative irradiance was low (2 mol photons m^{-2}). At low discharge (~500 m^3 s^{-1}), transit time increased to 11 d and cumulative irradiance was 66 mol photons m^{-2}.

Model-derived estimates of chlorophyll and primary production followed longitudinal gradients in light availability. During high discharge, the model predicted near-zero (or negative) DNPP and low chlorophyll concentrations throughout the pool (Fig. 4a). Measured chlorophyll concentrations were uniformly low (1 mg m^{-3}) at this time. At moderate discharge, the model predicted positive DNPP in the upper pool (up to 100 mg m^{-3} d^{-1}) and near-zero production in the lower pool. Chlorophyll was predicted to increase slightly in the upper pool before declining in the lower pool (Fig. 4b). Measured chlorophyll concentrations increased from 2 mg m^{-3} at the most upstream station to 7 mg m^{-3} at the midpool site. At low discharge, the model predicted high rates of DNPP in the upper pool (up to 300 mg m^{-3} d^{-1}) and low or negative DNPP in the lower pool

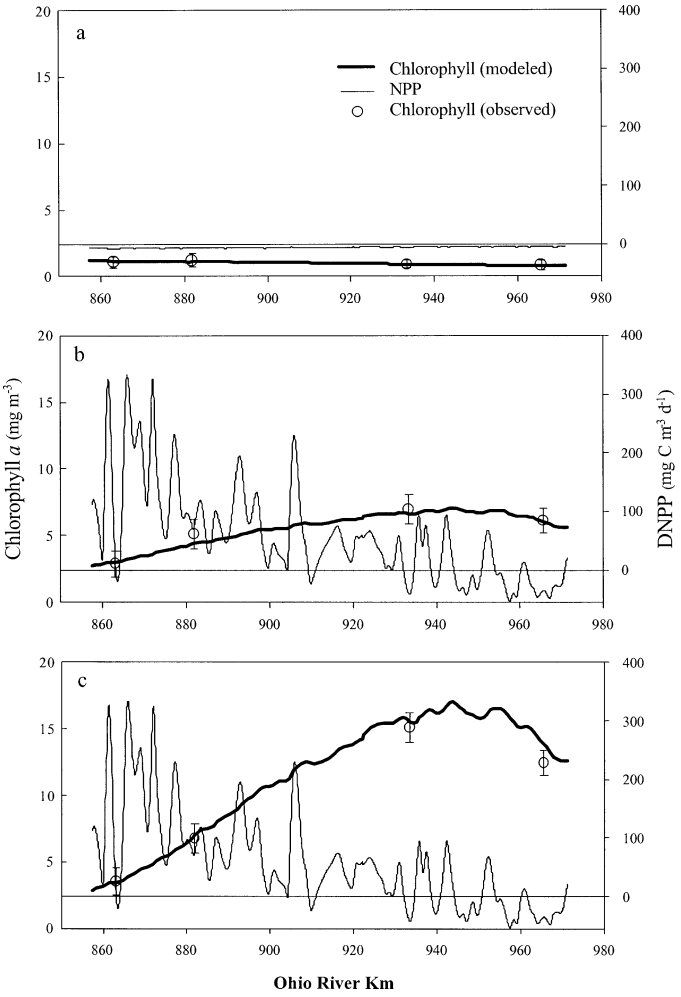

Fig. 4. Longitudinal variation in observed chlorophyll concentrations (circles ± SE), model-predicted chlorophyll concentrations, and daily net primary production for three dates representative of (a) high (June 1998), (b) moderate (August 1998), and (c) low (July 1999) flow conditions.

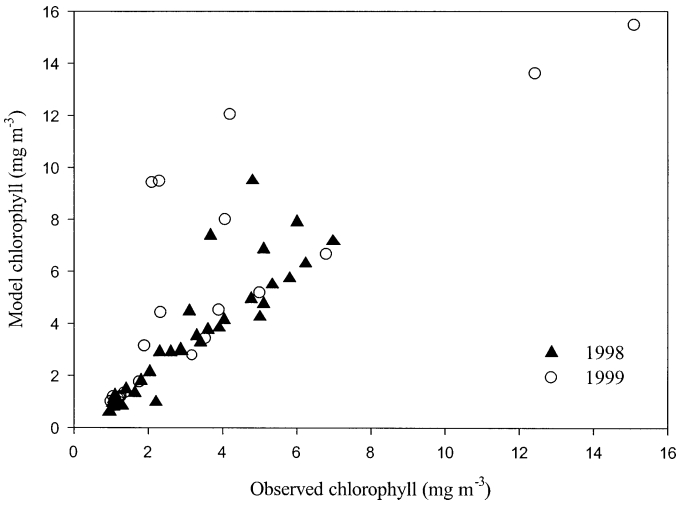

Fig. 5. Observed versus model predicted chlorophyll concentrations for four sampling locations within the McAlpine Pool sampled during 1998 and 1999.

(Fig. 4c). Chlorophyll was predicted to rise threefold before declining slightly in the lower third of the pool. Measured chlorophyll values increased from 3 to 15 mg m^{-3} between the upper and midpool sampling locations and then decreased to 12 mg m^{-3} at the most downstream site.

Patterns depicted for low and moderate flow conditions were generally indicative of longitudinal gradients in chlorophyll observed within the McAlpine Pool. Midpool chlorophyll concentrations exceeded upstream and downstream values during 12 of 13 sampling periods. Chlorophyll concentrations increased by an average of 2.4 mg m^{-3} during transit from the upstream to the midpool site, and concentrations at the downstream site were on average 1.0 mg m^{-3} lower compared to the midpool peak. A comparison of model-derived and measured chlorophyll values for all dates and sites showed good agreement between observed and expected values for most sample periods (Fig. 5; $R^2 = 0.81$ and 0.62; 1998 and 1999, respectively). Slopes of the regression lines were near unity (1.18 ± 0.01 and 0.97 ± 0.17), and intercepts were near zero (−0.24 ± 0.38 and 1.68 ± 0.90; 1998 and 1999, respectively). Model simulations for August and September of both years were exceptional in that the model overestimated downriver chlorophyll increases. During this period, long transit times and high light dosages were predicted to increase chlorophyll concentrations to 5–12 mg m^{-3} at the mid- and downriver sampling locations. Observed chlorophyll concentrations were lower, ranging from 2 to 6 mg m^{-3}. Excluding these data yielded a strong fit for modeled and observed chlorophyll concentrations for remaining dates (9 of 13) across both years ($R^2 = 0.96$).

Discharge data and chlorophyll concentrations for the primary inflow (Kentucky River) and the upper and lower Ohio River sampling sites were used to estimate water and algal C fluxes into and out of the McAlpine Pool during each of the 13 sampling periods (Fig. 6). Discharge data showed good agreement, with upper Ohio and Kentucky River inputs balancing outputs at the McAlpine Dam to within an average of 3% (range, 1–7%). These data suggest that the sampling events occurred during periods when changes in river storage were small in comparison to input–output fluxes and that ungauged sources (small tributaries, groundwater) did not contribute appreciably to the water balance of the McAlpine Pool. By comparison, differences between input and output fluxes of algal C exceeded 10% on 9 of 13 sampling dates. In 1998, flux rates were high and there was no consistent pattern with respect to differences between inputs and outputs. In 1999, the McAlpine Pool was a net source of algal C, with outputs exceeding inputs by an average difference of 46% (range, 12–70%). Separate budgets for the upper and lower sections of the McAlpine Pool (delineated by our midpool sampling location) showed that the upper pool was a net source of algal C during both years (12 of 13 sampling periods), whereas the lower pool was a net sink (11 of 13 periods). Outputs of algal C from the upper pool exceeded inputs by 20% in 1998 and by 51% in 1999, whereas outputs from the lower pool were smaller than inputs by an average of 26% (1998) and 14% (1999).

Model-derived estimates of NPP and measured input–out-

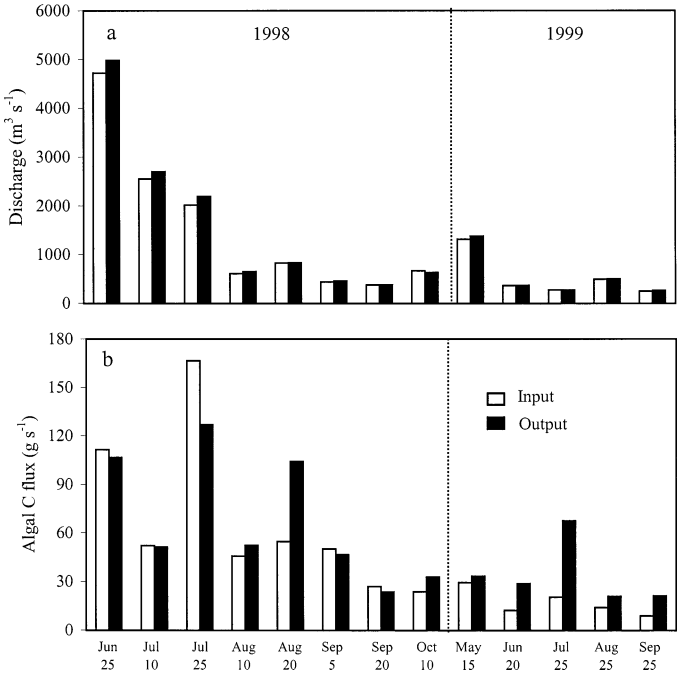

Fig. 6. Input and output fluxes of (a) water and (b) algal C to/from the McAlpine Pool of the Ohio River. Inputs include tributary and upstream sources; outputs represent losses at the downstream dam. Data are for 13 sampling dates in 1998 and 1999 with multiple collections occurring in July, August, and September 1998.

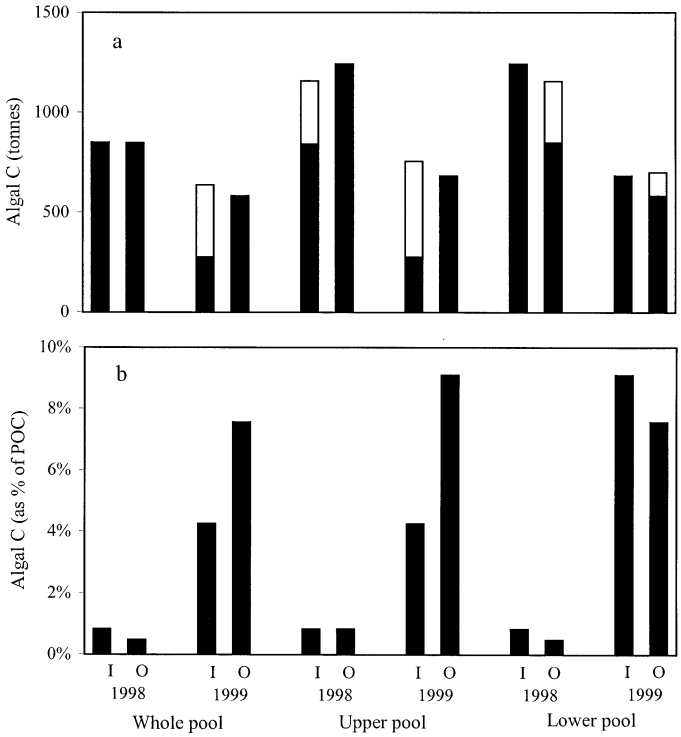

Fig. 7. (a) Mass balance of algal C for the McAlpine Pool (Whole Pool) and for upper and lower portions of the pool (delineated by the midpool sampling location) for the period May–October 1998 and 1999. Inputs (I) represent contributions from upstream and tributary sources (dark bar) and primary production (open bar) where NPP > 0. Outputs (O) include downstream export (dark bar) and algal respiration (where NPP < 0). (b) The proportion of algal C relative to POC for inputs (from upstream and tributary sources) and outputs to and from the McAlpine Pool.

put fluxes were used to construct algal C mass balances for May–October of both years (Fig. 7). During the high-flow year (1998), algal C inputs from the upper Ohio and Kentucky Rivers were large (843 t) and closely matched export from the McAlpine Pool (849 t). Algal C production estimated as the difference between input and output fluxes was low (6 t) and comparable to model-derived estimates of NPP (8 t). In 1999, algal C inputs from upstream and tributary sources were 276 t, while export from the McAlpine Pool was 583 t, suggesting that internal algal C production exceeded external inputs. Algal C production estimated from the difference between input and output fluxes was 307 t and comparable to the model-derived estimate of NPP (362 t). Using measured algal C fluxes at our midpool sampling location, we developed separate mass balances for upper and lower portions of the pool. In the upper pool, the model predicted that in-pool production contributed 315 t (1998) and 480 t (1999) of algal C, and flux comparisons showed that the upper pool was a net source of algal C in both years (400 and 407 t, respectively). NPP represented 27% (1998) and 63% (1999) of total algal C inputs to the upper pool. In the lower pool, the model predicted net losses of algal C (NPP < 0) in both 1998 (307 t) and 1999 (118 t), and flux comparisons showed that the lower pool was a net sink for algal C (394 and 100 t, respectively). Algal C losses within the lower pool corresponded to 27% (1998) and 17% (1999) of algal C export from the pool. With the inclusion of model-derived estimates of NPP, algal C budgets for the upper and lower pools balanced to within 10% in both years.

We evaluated algal C dynamics in the broader context of particulate organic carbon fluxes. During the high-flow year, algal C constituted a small fraction ($<2\%$) of POC inputs and outputs from the McAlpine Pool. During lower flows in 1999, algal C accounted for 4% of inputs and 8% of outputs from the pool. Enrichment of POC with algal C was a result of gains in algal C occurring in the upper pool. The proportion of algal C in water leaving the upper pool increased despite the upper pool being a net source of POC in both years (10 of 12 budgets, mean difference = 19%). Although algal C represented only a small fraction of POC, autochthonous production accounted for 30% of the POC gain in the whole-pool budget and 47% in the upper-pool budget during the low-flow year.

Discussion

We developed a hydrodynamic-based model to predict variation in primary production and chlorophyll arising from seasonal hydrologic cycles and the effects of water regulation structures. We first consider the utility of the model for depicting seasonal and longitudinal patterns in the Ohio River and then consider its potential applicability to other riverine systems. Last, we consider the importance of algal C production relative to upstream and tributary sources in this and other riverine systems.

Model predictions were tested using two approaches: first, by comparing predicted and measured chlorophyll concentrations and, second, by using model-derived estimates of NPP to balance input–output budgets for algal C. Predicted chlorophyll concentrations typically agreed to within 1 mg m^{-3} of measured values, and model-derived estimates of NPP balanced algal C budgets to within 10%. The model accurately predicted seasonal variation during years which differed in the timing, frequency, and severity of high-discharge events. The model also depicted longitudinal gradients arising from water regulation effects over a wide range of discharge conditions. Because our model considered only hydrologic and optical constraints on phytoplankton growth, good agreement between observational data and model predictions supports our hypothesis that these factors regulate primary production and chlorophyll development within the Ohio River. Discrepancies occurred in late summer of both years (4 of 13 dates) during periods of extended low discharge (<500 m^3 s^{-1}) when transit times and cumulative irradiance were maximal. The model predicted larger downstream increases in chlorophyll than were observed. NPP and chlorophyll concentrations declined throughout the pool at this time despite continued increases in cumulative irradiance. These findings suggest that factors other than light limitation might constrain phytoplankton production in late summer.

Late summer declines in algal biomass have been reported in other river studies, and in some cases, these have coincided with the onset of nutrient depletion (Moss et al. 1989; Basu and Pick 1996). Nitrogen and phosphorus concentrations in the Ohio River are typically high and ranged from 1,000 to 1,500 μg NO_3-N L^{-1} and 10 to 30 μg P-PO_4 L^{-1} at our midpool site during the period of this study (Koch and Bukaveckas unpubl. data). Neither N nor P exhibited a late-summer decline, but silica concentrations decreased during the growing season in both 1998 (from 6.1 to 0.8 mg L^{-1}) and 1999 (from 3.1 to 0.6 mg L^{-1}). Wehr and Thorp (1997) observed a similar decline, although silica concentrations were not found to be a significant predictor of phytoplankton cell densities in multiple regression models. Dilution bioassay experiments using phytoplankton collected from our midpool sampling location showed that the frequency of light limitation decreased and the frequency of nutrient limitation increased in late summer (Koch and Bukaveckas unpubl. data). These data suggest that declines in production during the period when cumulative irradiance was increasing could be due in part to silica limitation.

Reynolds and Descy (1996) noted that the warm temperatures, high light, and low flow conditions typical of summer do not always coincide with peaks in algal biomass since these conditions favor zooplankton grazing and phytoplankton sedimentation. Grazing by zooplankton was the putative cause of summer phytoplankton declines in the Meuse, Moselle, and Rhine rivers (de Ruyter van Steveninck et al. 1992; Gosselain et al. 1998*a*,*b*). Zooplankton densities were measured monthly at our midpool site during 1998 and 1999 as part of a related study on the role of algal C in zooplankton nutrition (Guelda and Bukaveckas unpubl. data). In 1998, zooplankton densities peaked in September (53 individuals L^{-1}), coinciding with the observed phytoplankton decline. However, zooplankton densities in 1999 were lower ($\sim$10 individuals L^{-1}) and did not exhibit a late-summer peak. Thus, our data do not provide compelling evidence that pelagic grazing alone could account for late-summer algal declines in the Ohio River. An earlier study of *Dreissena* and *Corbicula* production in the McAlpine pool showed that mussel densities peaked during late summer with estimated filtration rates of 30% d^{-1} in the upper pool and 10% d^{-1} in the lower pool (Sellers 1995). High filtration rates combined with long transit times during this period (>10 d) might allow benthic grazers to substantially reduce phytoplankton densities. We incorporated a grazing component into the ORACHL model and found that filtration rates of 40% d^{-1} were required to simulate the observed decline. The combined effects of pelagic and benthic grazing could account for the observed declines in NPP and chlorophyll during late summer.

Late-summer declines in phytoplankton production could also arise from increases in respiratory costs at higher temperatures, though we have no direct measurements to test this hypothesis. Our model uses seasonally adjusted P-E parameters, and because P_{max} was highest in late summer, respiration is assumed to be highest at this time. However, we cannot discount the possibility that respiration accounts for a larger fraction of P_{max} when water temperature is higher. Several studies have suggested that respiration varies as a fraction of P_{max}, with typical values ranging from 0.05 to 0.25 depending on species composition (Geider and Osborne 1989; Beardal and Raven 1990). The relatively low values used in our model (0.10) and a similar study of the Hudson River (0.07–0.12; Cole et al. 1992; Caraco et al. 1997) are typical of diatoms and chlorophytes that dominate phytoplankton communities in these rivers (Wehr and Thorp 1997; Smith et al. 1998). Our model was highly sensitive to assumed values of respiration during periods of long water transit time. At a transit time of 20 d, reducing respiration to 5% of P_{max} yielded 10-fold higher estimates of DNPP and poor correspondence for algal mass balances and measured versus modeled chlorophyll. Increasing respiration to 15% of P_{max} yielded DNPP values less than zero over the full range of observed transit times. By comparison, the model exhibited little sensitivity to C : Chl ratios, with values ranging from 10 to 30, yielding predictions within 10% of those derived from the assumed value (20).

Incorporating a standardized measure of algal–light relations (P-E curves) into an existing hydrodynamic model allowed us to accurately depict seasonal and spatial variation in river chlorophyll and to derive estimates of primary production that showed good agreement with algal C mass balances. Requisite data for modeling, including channel geomorphology, discharge, and water transparency, are available for many large rivers because of the activities of various governmental and private agencies. Thus, our general approach can be widely applicable for rivers in diverse hydrogeomorphic settings. We hypothesized that phytoplankton growth was regulated by light availability and therefore that quantification of light dosages experienced by phytoplankton traveling through the pool was central to understanding seasonal and spatial variability in biomass accrual. Consistent with our findings, other studies have shown that river depth

gradients and hydrology can affect the amount and duration of light energy available to riverine phytoplankton (Cole et al. 1991; Reynolds and Descy 1996; Knowlton and Jones 2000). We found that cumulative irradiance estimates were a useful means of characterizing the light environment of the river by integrating the effects of variable depth, transit time, and transparency. Derivation of this metric for other rivers would provide a basis to assess intersystem differences in autotrophic potential. Our analyses relied on a simple (one-dimensional) representation of river hydrodynamics, which proved to be sufficient for depicting seasonal and longitudinal patterns in phytoplankton production. The Ohio River is characterized by a constricted channel in its upper reaches (including the McAlpine Pool) with few side channels or backwater areas (Thorp et al. 1998). Two-dimensional flow models might be required in systems where channel morphometry or seasonal inundation creates lateral variation in flow velocity and gives rise to lateral variation in phytoplankton production (Reynolds 1996; Bukaveckas et al. 2002).

In free-flowing rivers, spatial variation in channel morphometry and temporal variation in surface water elevation determine the depth of the water column and, in conjunction with changes in transparency, the light environment experienced by phytoplankton (Cole et al. 1991; Reynolds and Descy 1996). Our study of the Ohio River suggests that the presence of water regulation structures substantially alters spatial and temporal patterns in light intensity and that these effects have important consequences for phytoplankton production. During low to moderate discharge conditions (representing the majority of sampling periods in this study), longitudinal gradients in depth arising from the downriver dam resulted in threefold differences in irradiance over the length of the McAlpine Pool. Light attenuation changed very little in parcels of water traveling downstream (typically $<7\%$) regardless of the initial (upstream) suspended particle load. Therefore, longitudinal gradients in light availability were attributed to changes in depth. The downstream decrease in light availability was associated with a unimodal-shaped pattern in chlorophyll concentrations. Higher rates of primary production in the upper, shallow reaches of the pool resulted in increasing chlorophyll concentrations, with peak levels occurring at the midpool site. Negative NPP brought modest declines in chlorophyll in the deeper, lower pool. Similar longitudinal patterns in phytoplankton abundance have been reported for other rivers (Cole et al. 1992; Descy and Gosselain 1994; Basu and Pick 1997) and attributed to downstream increases in depth, tributary dilution, grazing, and sedimentation. In our study, negative growth rates and slower water velocity in the lower pool were sufficient to account for downstream chlorophyll declines.

Algal carbon fluxes were driven by interannual variation in upstream inputs and autochthonous production. The McAlpine Pool was found to be a net sink or source of algal C in 9 of 13 sampling periods when the balance between inputs and outputs differed by more than 10%. Mass balance and modeling data suggest that the upper pool was typically a source of algal carbon because greater light availability allowed net production and biomass accrual. Deeper depths and decreased light availability in the lower pool caused new biomass to be partially consumed by metabolic demands. In 1998, losses in the lower pool were approximately equal to algal carbon gained in the upper pool, whereas during lower flows in 1999, upper pool gains exceeded downriver losses. Net gains from primary production exceeded algal C inputs from upstream and tributary sources during May–October of that year. Lewis (1988) and Cole et al. (1992) have argued that a positive C balance could not be achieved by phytoplankton in the main stem of the Orinoco and Hudson Rivers because respiration exceeded photosynthesis. Observed increases in biomass were attributed to influxes of algal C from floodplain lakes (Orinoco) and to longitudinal and lateral variation in depth (Hudson). Our findings show that the presence of water regulation structures (low-head dams) has fundamentally altered patterns of phytoplankton production in the Ohio River through the creation of longitudinal gradients in depth and light availability. The cumulative effect of these structures on production and fate of algal C is unknown and merits further attention.

Despite gains from autochthonous production, algal C represented a relatively small fraction (1–7%) of POC outputs from the McAlpine Pool. These values were lower than those typically reported for European rivers (Admiraal et al. 1992; Gosselain et al. 1994; Köhler 1995) and might reflect differences in autotrophic potential arising from faster transit times and deeper mixing depths in the Ohio River. For example, in the River Spree (Köhler 1995), the growing season discharge was 16–25 $m^3\ s^{-1}$, mixing depths averaged 2 m, and chlorophyll concentrations exceeding 50 mg m^{-3} were not uncommon. Mixing depths in the River Meuse ranged between 3 and 6 m, with chlorophyll concentrations typically 20–80 mg m^{-3} (maximum, 140 mg m^{-3}; Descy and Gosselain 1994). In the Ohio River, light and depth constraints on phytoplankton were especially apparent at high discharge ($>5{,}000\ m^3\ s^{-1}$) when mixing depths exceeded 8 m throughout the McAlpine Pool and daily average irradiance (<2 mol photons $m^{-2}\ d^{-1}$) was within the range of previously reported estimates of compensation irradiance (Siegel et al. 2002). Although phytoplankton account for a relatively small proportion of POC in our system, concurrent mesocosm studies have shown that population growth rates of dominant zooplankton taxa were correlated with algal C abundance (Guelda et al. unpubl. data). Therefore, our studies of the Ohio River support the contention that autochthonous sources of carbon are important in riverine food webs despite the quantitative prevalence of nonalgal C (Thorp et al. 1998; Dettmers et al. 2001; Thorp and DeLong 2002).

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