

# Effects of navigation dams, tributaries, and littoral zones on phytoplankton communities in the Ohio River<sup>1</sup>

John D. Wehr and James H. Thorp

**Abstract:** Phytoplankton and water chemistry variables were sampled monthly along a 361-km stretch of the Ohio River. We compared (i) regions from Ohio through Kentucky, (ii) sites above, below, and within tributaries, (iii) nearshore and channel habitats, and (iv) sites away from and near navigation dams. Densities of suspended cells were lowest during colder, high-flow periods (31 000 cells/mL) and greatest during warmer, low-flow summer (104 000 cells/mL). Of 134 taxa identified, >60% were diatoms, comprising 6% of cell numbers and 28% of total biovolume. Summer assemblages were dominated by colonial *Aphanothece saxicola*, *Merismopedia punctata*, *Microcystis aeruginosa*, and unicellular *Synechococcus* species. Diatoms *Melosira jurgensii* and *Melosira distans* were abundant in summer and *Cyclotella* spp. in spring. Concentrations of dissolved inorganic phosphorus ( $\approx 40 \mu\text{g/L}$ ) and dissolved inorganic nitrogen ( $\approx 1100 \mu\text{g/L}$ ) were high; neither was positively correlated with any phytoplankton variable. Interpool declines in picoplankton correlated with greater copepod nauplii densities. Navigation dams significantly reduced current velocity and densities of benthic forms; dissolved inorganic phosphorus levels were significantly greater. Near-dam sites had increased biomass of larger phytoplankton ( $>2 \mu\text{m}$ ) in winter, but lower densities during summer. Multiple regression identified temperature (+) and current velocity (–) as the main factors affecting phytoplankton densities in this large river.

**Résumé :** Le phytoplancton a été échantillonné et les caractéristiques chimiques de l'eau analysées tous les mois le long d'un segment de 361 km de la rivière Ohio. Nous avons comparé (i) les régions de l'Ohio au Kentucky, (ii) des sites en amont, en aval et à l'intérieur des tributaires, (iii) les habitats près des rives et dans les chenaux et (iv) les sites éloignés et proches des barrages pour la navigation. La densité des cellules en suspension était plus faible durant les périodes plus froides et de hautes eaux (31 000 cellules/mL) et plus élevée durant les périodes plus chaudes à basses eaux de l'été (104 000 cellules/mL). Des 134 taxons identifiés, >60% étaient des diatomées, constituant 6% du nombre de cellules et 28% du biovolume total. Les assemblages d'été étaient dominés par *Aphanothece saxicola*, *Merismopedia punctata* et *Microcystis aeruginosa*, organismes vivant en colonies, et par les espèces de *Synechococcus*, organismes unicellulaires. Les diatomées *Melosira jurgensii* et *Melosira distans* étaient abondantes durant l'été, et les espèces *Cyclotella* au printemps. Les concentrations de phosphore inorganique dissous ( $\approx 40 \mu\text{g/L}$ ) et d'azote inorganique dissous ( $\approx 1100 \mu\text{g/L}$ ) étaient élevées; ni l'une ni l'autre n'était corrélée positivement avec une quelconque variable liée au phytoplancton. Les diminutions interfosses du picoplankton étaient en corrélation avec les densités élevées de nauplii de copépodes. Les barrages de navigation ont réduit substantiellement la vitesse du courant et la densité des organismes benthiques; les concentrations de phosphore inorganique dissous étaient nettement plus élevées. Les sites près des barrages présentaient une biomasse accrue de phytoplancton de plus grande taille ( $>2 \mu\text{m}$ ) en hiver, mais des densités plus faibles en été. La régression multiple a révélé que la température (+) et la vitesse du courant (–) étaient les principaux facteurs influant sur la densité du phytoplancton dans cette grande rivière.

[Traduit par la Rédaction]

## Introduction

The large majority of ecological studies on autotrophic organisms of flowing waters has concentrated on streams and small rivers (Hynes 1989; Thorp et al. 1994). Of the studies that con-

cern larger rivers, many have focused on attached (periphyton) algal communities, such as in the Columbia and the Mississippi rivers (Cushing 1967; Luttenton et al. 1986). Such studies are needed because large rivers can support substantial benthic primary production (Wetzel 1975). Unfortunately, there is a persistent misunderstanding that the phytoplankton of large rivers is sparse and consists primarily of detached benthic forms suspended in the water column (Whitton 1975; Vannote et al. 1980). This misinformation is particularly surprising given the long history of floristic accounts of phytoplankton in rivers of Europe and North America. One of the earliest detailed studies of river algae was by Zacharias (1898), who characterized the phytoplankton in several large rivers in Germany and suggested that densities were inversely related to flow conditions. In North America, Kofoid (1903) reported on the planktonic organisms of the Illinois River between 1894 and 1899, observing blooms of cyanobacteria

Received March 13, 1996. Accepted July 15, 1996.  
J13352

J.D. Wehr,<sup>2</sup> Louis Calder Center and Department of Biology, Fordham University, P.O. Box K, Armonk, NY 10504, U.S.A.

J.H. Thorp, Large Rivers Program, Biology Department, University of Louisville, Louisville, KY 40292, U.S.A.

<sup>1</sup> Contribution No. 142 to the Louis Calder Center.

<sup>2</sup> Author to whom all correspondence should be addressed.  
e-mail: wehr@murray.fordham.edu

during the summer and diatom maxima in autumn and winter. In the intervening years, many studies described the potamoplankton of large rivers, but there continued to be a debate concerning whether a true phytoplankton community exists in rivers, or whether the assemblage consists primarily of resuspended cells from tributaries and lakes within the associated floodplain (see reviews by Hynes 1970; Whitton 1975).

More recent research on flowing waters has centered around the concepts proposed in the River Continuum Concept (RCC; Vannote et al. 1980). Among many ideas, the RCC predicts that in large-order (greater than sixth) rivers, phytoplankton production is light limited and that self-sustaining algal populations are unimportant to ecosystem metabolism because most large rivers are deep and turbid. This view has recently been challenged by authors who contend that floodplain inputs, littoral zone communities, and in situ production may be considerable in large rivers (Junk et al. 1989; Thorp and DeLong 1994). Another reason for a change of view is that most large rivers of the world are regulated to varying degrees by channelization (bank stabilization) and high or low (navigation) dams. The effects of these water-control measures are many, but a common feature is the creation of small impoundments or pools in which current velocity is reduced (see discussions by Lack 1971; Søballe and Kimmel 1987; Thorp and DeLong 1994; Thorp et al. 1994). These modifications also reduce effects of turbidity and downstream loss, factors that are predicted by the RCC to limit phytoplankton production in large unregulated rivers (Vannote et al. 1980).

To understand the role of resident phytoplankton communities in large regulated rivers, studies first need to identify the primary sources of these algae, as well as how communities respond to factors that characterize most large rivers of today. In connection with broader studies on the Ohio River ecosystem, we describe the first step in characterizing these influences on the phytoplankton communities over an annual cycle. Specifically, we examine the impacts of littoral communities, tributary rivers, and navigation dams on the development of phytoplankton assemblages. We also measured a series of physical and chemical variables that also may be affected by hydrological and anthropogenic features that are common to many large rivers worldwide.

## Methods

### Study sites and sampling

This study was conducted in parallel with a previously published account on the zooplankton of the Ohio River (Thorp et al. 1994) that provides details of the hydrology and other physical features of the Ohio and a full description of the size and location of study sites. Overall, our study spans a 361 km long stretch of the river beginning downstream of Cincinnati, Ohio, to about 60 km upstream of Evansville, Ind. The study was based on 12 monthly samples from February 1991 through January 1992 from three large reaches of the Ohio River (termed pools locally): (i) Markland pool (Ma; 155 km long), an upper constricted channel; (ii) McAlpine pool (Mc; 119 km), a midriver constricted section; and (iii) Cannelton pool (Ca; 185 km), which lies in a broader floodplain region downstream of Louisville, Ky. By design, each study pool was selected to include one major tributary (the Miami, Kentucky, and Salt rivers, respectively) in order to examine the influence of floodplain inputs and tributaries on the plankton and nutrient pools of the main river (see Thorp et al. 1994 for further details). Within each 100+ km pool, a 2 × 4 sampling

design included two habitats, pelagic (Channel) and littoral (Bank), and four sites, above tributary (ATR), in tributary (ITR), below tributary (BTR), and just above the navigation dam (LOW). All samples were spatially replicated five times. This resulted in a total of 3 pools × 4 sites × 2 habitats × 5 replicates = 120 samples collected each month.

On each sample date, five replicate phytoplankton samples were collected at a depth of 0.5–1.0 m using 20-L plastic buckets at each pool-site from a boat. Unconcentrated subsamples were placed in 20-mL plastic scintillation vials and preserved with Lugol's iodine until laboratory analysis. Physical measurements were made in situ as follows. Current velocity in the pelagic and littoral areas was measured with a Marsh McBirney velocity meter (model 201-D), and water temperatures were recorded with a YSI temperature probe. Water samples were retrieved for turbidity analysis from the main river sites and measured in NTU units with a Hach turbidimeter. Water samples for chemical analysis were filtered in line (Whatman GF/F) and frozen (–15°C) for later processing.

### Laboratory analyses

Subsamples (1–5 mL) of phytoplankton samples from all seasons and sites were observed to identify most taxa and establish a species list for later counting. This list represented >80% of all taxa encountered during the entire study. For enumeration, 10-mL aliquots of Lugol's preserved samples were placed in sedimentation chambers and allowed to settle for a minimum of 12 h. Identification and counting procedures followed the standard inverted microscope method (Utermöhl 1958), using a Nikon Diaphot microscope. A minimum of 10 grids and 1000 cells were enumerated from each sample.

Water chemistry samples were analyzed for concentrations of dissolved inorganic (=soluble-reactive) P (DIP) using antimony-ascorbate-molybdate (American Public Health Association 1985; Bran+Luebbe Analyzing Technologies 1986a),  $\text{NH}_4^+$ -N using phenol-hypochlorite, and  $\text{NO}_3^-$  (after reduction to  $\text{NO}_2^-$  in a Cd–Cu column) via reaction with sulfanilamide–NED (American Public Health Association 1985; Bran+Luebbe Analyzing Technologies 1986b, 1987a). Soluble-reactive Si (as  $\text{SiO}_2$ ) was measured via the molybdosilicate method (American Public Health Association 1985; Bran+Luebbe Analyzing Technologies 1987b), and  $\text{SO}_4$ -S was analyzed using the  $\text{BaCl}_2$  method (American Public Health Association 1985; Bran+Luebbe Analyzing Technologies 1989). The above procedures were modified for automated analysis and run on a Traacs 800 automated analyzer (Bran+Luebbe Inc., Buffalo Grove, Ill.). Ca and Mg concentrations were measured using flame atomic absorption spectroscopy (Perkin-Elmer model 1100B).

### Data analysis and statistics

The primary aim of our analysis was to test whether "structural" features of the Ohio River (regional pools, dams, tributaries, and littoral-pelagic habitats) significantly affected phytoplankton densities and water chemistry in the river. The questions posed in our objectives were addressed in each of four separate river seasons that we identified previously, based on temperature and flow conditions (Thorp et al. 1994). Data analysis was preceded by classifying the 134 algal and cyanobacterial taxa into six ecological (total: total >2  $\mu\text{m}$ ; planktonic forms: plankton >2  $\mu\text{m}$ ; benthic forms: picoplankton) and six taxonomic (cyanobacteria, cyanobacteria >2  $\mu\text{m}$ , Chlorophyta, Chrysophyta, Cryptophyta + Dinophyta, Bacillariophyta) categories. Species assigned to the benthic category were based on designations of Lowe (1974) and Whitton (1975). These 12 groups served as the dependent variables for all hypothesis tests.

Prior to analyses, all data were checked for assumptions of normality and homogeneity of variances. Of 24 variables tested, 20 were strongly skewed, but a  $\log_{10}$  transformation enabled the use of parametric statistical tests. Downstream effects of regional pools were analyzed using analysis of variance (ANOVA), with post hoc analyses using Tukey's honestly significant difference (HSD) among

**Table 1.** Physical conditions in the main channel of the Ohio River during February 1991 to January 1992.

Variable	Markland pool			McAlpine pool			Cannelton pool		
	ATR	BTR	LOW	ATR	BTR	LOW	ATR	BTR	LOW
Temperature (°C)									
Min.	5.5	5.5	4.5	4.0	4.0	3.0	4.0	4.0	5.9
Mean	15.8	15.8	14.2	15.2	15.0	13.8	14.5	14.7	15.2
Max.	29.0	28.0	26.0	27.0	26.0	25.0	26.5	27.0	27.0
Current (m/s)									
Min.	0.05	0.08	0.09	0.10	0.17	0.14	0.21	0.22	0.17
Mean.	0.53	0.46	0.44	0.77	0.70	0.32	0.60	0.68	0.46
Max.	1.21	1.42	1.30	1.68	1.61	0.68	1.10	1.18	0.85
Turbidity (NTU)									
Min.	4.0	5.5	3.0	2.0	2.5	2.0	2.0	2.5	2.0
Mean	17.9	14.8	17.5	18.8	16.4	12.6	17.2	17.4	12.3
Max.	39.5	41.0	46.0	50.0	40.0	33.0	34.0	35.5	25.5

Note:  $n = 12$  for each pool-site grouping; ATR, above tributary; BTR, below tributary; LOW, at navigation dam.

individual groups (Sokol and Rohlf 1995). Effects of hypothesized factors (navigation dams, tributaries, pelagic versus littoral) were analyzed using a stratified (monthly) Student *t* test. Relationships between measured physical and chemical factors and phytoplankton abundances were first examined using (Pearson's) linear correlation. For all hypothesis tests, effects were judged to be significant if the probability of an event having occurred owing to chance (*P*) was  $< 0.05$ . A more complete set of analyses examined the combined influences of physical and chemical variables on the phytoplankton community, using stepwise multiple linear regression (MLR). In these, 12 independent variables were tested for their effects on phytoplankton:  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , DIP,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , total dissolved inorganic N (DIN), Si,  $\text{SO}_4\text{-S}$ , the inorganic N:P ratio, current velocity, temperature, and turbidity. Because regression relationships between putative positive factors and phytoplankton abundance may be either positive (=stimulation) or negative (=consumption), we are applying these empirical models mainly as a guide to examining broad patterns in the river. The maximum criterion for inclusion of independent variables into each model was  $\alpha = 0.05$ , and the minimum for exclusion was  $\alpha = 0.10$ . Data were compiled and analyzed using SYSTAT 5.1 (Wilkinson 1992).

## Results

### Physical and chemical conditions

Seasonal patterns of physical and chemical conditions described in Thorp et al. (1994) are summarized here to emphasize differences as they affect the phytoplankton communities among pools, sites, and specific months under study (Table 1). Average current velocities varied among sites, but overall were not significantly less near the navigation dams (LOW sites). However, specific patterns within each regional pool did occur. On average, current velocity was reduced near the McAlpine dam (*t* test:  $P < 0.05$ ), but was not significantly different at either the Markland or Cannelton dam over the year (*t* tests:  $P = 0.78$  and  $P = 0.13$ , respectively). This decline in current in the lower McAlpine pool did not coincide with

lower (nonalgal) turbidity levels here or at any LOW site ( $P > 0.05$ ). Tributary inputs and navigation dams had apparently no significant effects on either variable in the main river. Average, minimum, and maximum temperatures exhibited no consistent or significant pattern along the downriver gradient or with respect to the presence of dams or tributaries.

Chemical conditions varied considerably along the course of the river (Table 2; Fig. 1). DIP concentrations averaged 43  $\mu\text{g P/L}$  riverwide and differed among sites during April, July, and January (ANOVA:  $P < 0.05$ ), but not during October ( $P = 0.068$ ). Tributaries had no significant overall effect on DIP concentrations in the main river, regardless of time of year (*t* test:  $P > 0.05$ ). DIP concentrations were, however, lower in sites near navigation dams during April and October (*t* tests:  $P = 0.001$  and  $P = 0.018$ , respectively). Regional (downstream) patterns (Fig. 1) suggest that DIP was relatively constant along the entire river in April and during all months within the upper Markland region of the Ohio (ANOVA:  $P > 0.05$ ). Further downstream, DIP concentrations varied more widely. The most pronounced changes in DIP along the river gradient were observed in the McAlpine region, particularly above and below the McAlpine dam (Mc LOW). DIP concentrations more than doubled in Mc LOW during July and January and decreased by roughly 50% at the same site during October.

DIN concentrations in the Ohio were typically high, with an annual average of 1120  $\mu\text{g N/L}$ , most of which was  $\text{NO}_3\text{-N}$  (Table 2; Fig. 2). DIN levels were similar along the main regions of the river, with the exception of one highly significant site effect during January (ANOVA:  $P < 0.001$ ). Tributaries and navigation dams apparently did not affect DIN levels ( $P > 0.05$ ), with the exception of greater concentrations at the McAlpine Dam during July and January and lower levels of DIN during October (*t* test:  $P < 0.05$ ). Dissolved Si levels were low (annual average  $< 5 \text{ mg/L}$  at all pools and sites) and varied by only a factor of roughly 5 over the annual cycle. None of

**Table 2.** Chemical variables measured in the main channel of the Ohio River during February 1991 to January 1992.

Variable	Markland pool			McAlpine pool			Cannelton pool		
	ATR	BTR	LOW	ATR	BTR	LOW	ATR	BTR	LOW
<b>DIP (<math>\mu\text{g P/L}</math>)</b>									
Min.	21.3	15.3	22.2	3.8	4.5	15.7	13.0	21.9	21.9
Mean	39.8	39.9	39.6	34.9	43.0	52.1	55.6	48.7	36.8
Max.	71.4	79.8	58.3	81.0	78.3	102.4	100.9	80.1	69.0
<b>NH<sub>4</sub>-N (<math>\mu\text{g N/L}</math>)</b>									
Min.	68	23	78	4	12	17	66	3	32
Mean	227	225	163	157	184	153	262	231	199
Max.	737	864	442	433	513	600	643	727	482
<b>NO<sub>3</sub>-N (<math>\mu\text{g N/L}</math>)</b>									
Min.	189	214	202	165	167	158	191	263	200
Mean	819	799	886	727	788	919	894	735	716
Max.	1473	1619	1543	1655	1602	2151	1818	1583	1553
<b>DIN (<math>\mu\text{g/L}</math>)</b>									
Min.	286	314	333	303	312	232	634	362	294
Mean	1124	1106	1143	941	1004	1148	1236	1043	985
Max.	1779	1854	1828	1840	1831	2410	2470	1722	1666
<b>N:P ratio</b>									
Min.	11.6	12.6	12.0	11.5	6.6	3.8	9.6	7.1	12.6
Mean	30.4	33.0	30.0	37.1	29.0	28.2	27.0	24.0	28.2
Max.	49.6	63.5	48.5	178.9	129.9	65.9	76.1	57.6	45.5
<b>Si (mg/L)</b>									
Min.	1.9	2.0	2.1	0.7	2.2	1.0	1.9	<0.1	1.1
Mean	4.4	4.6	4.8	3.5	4.1	3.7	4.4	4.1	3.3
Max.	6.3	9.0	10.9	8.1	6.0	6.6	9.5	14.1	6.9
<b>SO<sub>4</sub>-S (mg S/L)</b>									
Min.	23.4	11.8	14.1	9.2	3.4	10.0	20.0	5.8	8.0
Mean	69.2	61.1	62.2	54.4	55.3	55.2	55.1	50.6	51.7
Max.	111.8	115.1	116.0	137.2	128.2	127.2	108.8	115.6	114.4
<b>Ca (mg/L)</b>									
Min.	14.4	6.0	13.3	10.0	9.2	8.8	10.2	11.5	6.5
Mean	31.6	29.5	32.4	22.0	30.1	23.1	35.7	33.5	33.2
Max.	44.9	46.4	43.5	38.1	80.4	46.5	53.6	50.8	48.9
<b>Mg (mg/L)</b>									
Min.	5.5	1.6	2.0	1.9	1.4	1.5	3.0	1.7	1.5
Mean	9.0	10.3	8.9	7.9	8.2	8.7	9.4	9.5	8.8
Max.	13.8	25.2	14.5	16.8	15.2	15.9	14.8	16.1	16.1

Note:  $n = 60$  for each; ATR = above tributary, BTR = below tributary, LOW = at navigation dam.

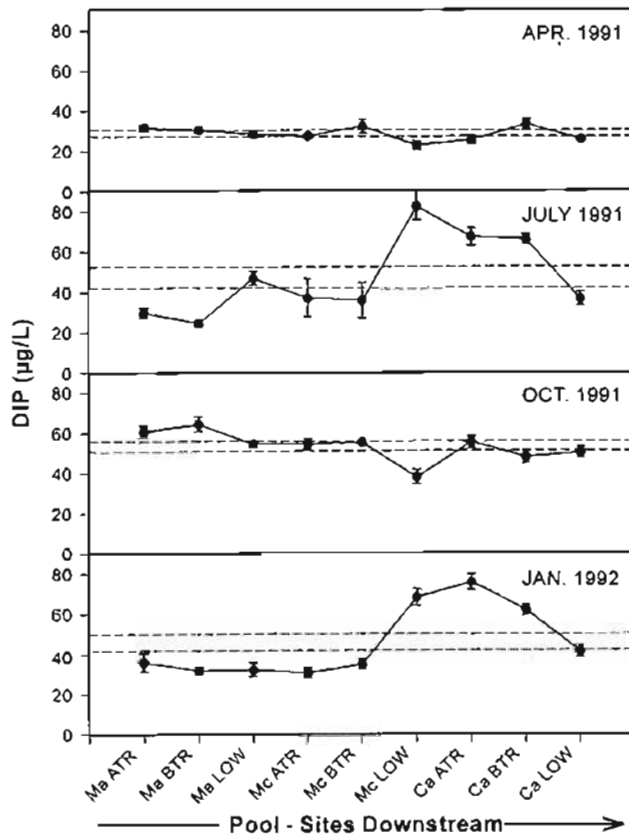
the above data exhibited temporally or spatially consistent downstream patterns, such as increasing eutrophy along the river gradient.

#### Phytoplankton community

During 1991–1992, we observed a total of 134 algal and cyanobacterial taxa, most of which were recognized to species level (Appendix). Most of the phytoplankton species diversity was contributed by diatoms (Bacillariophyta; 82 taxa, about

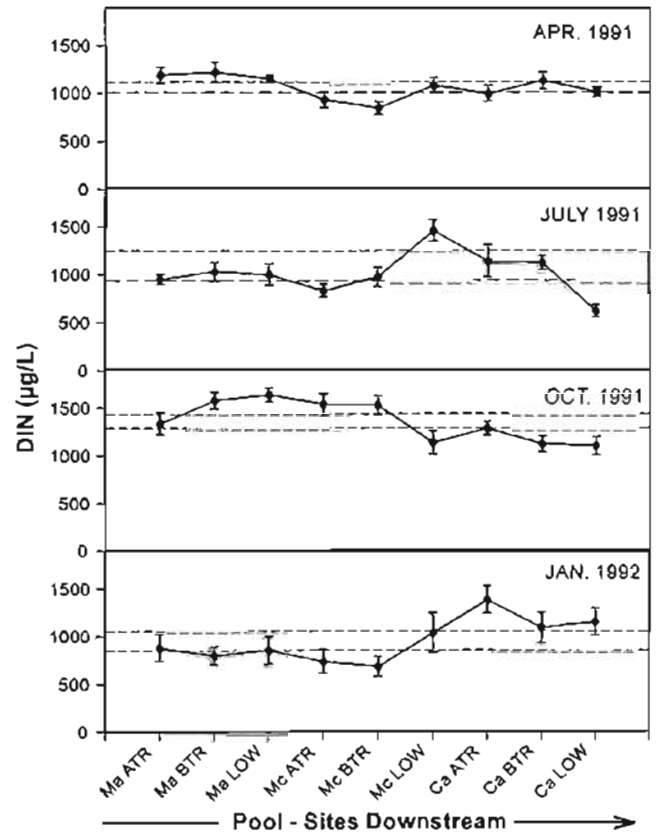
60%), although a majority of these taxa were rarely observed or occurred in low densities. The importance of members of the cyanobacteria and Chlorophyta was greatest in warmer months. For example, 14 cyanobacterial and 22 green algal taxa were identified from these two groups in July, but only 11 and 9 were recognized in January. Few representatives of the dinoflagellates, cryptophytes, and chrysophytes were seen during any time of the year. In contrast, diatom species number was lowest in July (30 taxa) and greatest in April (59 taxa).

Fig. 1. Concentrations of DIP (mean  $\pm$  1 SE) in the nine stations of the Ohio River measured during four seasons during 1991–1992.  $n = 10$  for each point; broken lines indicate the 95% confidence intervals of the mean concentration on that date.



Abundances of the 10 most important individual taxa (most to species level) also varied according to time of year (Fig. 3). A number of species were encountered in nearly all samples and on most dates. By far the most ubiquitous and abundant taxon was *Synechococcus* sp., a collection of small cyanobacteria  $< 2 \mu\text{m}$  in size (annual average 62% of cells, 9.9% of total biovolume). Its maximum density was observed in April and May (riverwide average  $\approx 65\,000/\text{mL}$ ) and minimum in late autumn (October–November average  $\approx 22\,000/\text{mL}$ ). Whether this category represents one or several species is unknown. The colonial cyanobacteria *Aphanothece saxicola*, *Merismopedia tenuissima*, *Microcystis aeruginosa*, and *Pseudanabaena catanata* were abundant only during warmer months (June–October). The most important diatom species, *Melosira jurgensii* and *Melosira distans*, also were more abundant during the warmer months (June–October). Other important species, including the diatoms *Cyclotella comia*, *Cyclotella meneghiniana*, *Asterionella formosa*, and *Fragilaria crotonensis* (last two not shown), were more abundant during the cooler months of November–January. Other ubiquitous nondiatom taxa, including *Scenedesmus quadricauda*, coccoid cells 2–4  $\mu\text{m}$ , and a small unidentified flagellated chrysophyte, tended to be more abundant in spring–summer. A few taxa were sporadically abundant but rare during other times of the year, such as *Gonium pectorale*, *Pseudanabaena catanata*, and *Chroococcus limneticus* during the summer and *Melosira*

Fig. 2. Concentrations of DIN ( $=\Sigma \text{NO}_3 + \text{NO}_2 + \text{NH}_4$ ) (mean  $\pm$  1 SE) in the nine stations of the Ohio River measured during four seasons during 1991–1992.  $n = 10$  for each point; broken lines indicate the 95% confidence intervals of the mean concentration on that date.



*granulata* in the spring. Many species identified in phytoplankton samples were probably benthic or periphyton forms that had become resuspended into the water column. Ubiquitous but nonabundant taxa include the diatoms *Achnanthes minutissima*, *Navicula radiosa*, *Rhizosolenia curvata*, and *Surirella ovata*. The most common diatoms, however, were true planktonic forms.

#### Effects of river structure on the phytoplankton community

The abundance and composition of the phytoplankton community differed according to their locations along the Ohio River (Fig. 4). The annual averages of total cell numbers in the Ohio differed along the river course, with the McAlpine pool having the lowest overall densities (pairwise  $t$  test:  $P < 0.05$ ). Cannelton pool near Louisville had consistently more resuspended benthic forms in the water column than the upper two regions. Patterns in densities also differed according to taxonomic group. Cyanobacterial numbers reflected the general trend of total cell density, but densities of greens and chrysophytes tended to increase further downstream. Considered during four separate temperature–flow periods (see Methods), certain patterns emerge (Table 3). The abundances of phytoplankton within most ecological and taxonomic groups changed significantly on progressing downstream and during most periods of the annual cycle. Perhaps the most

Fig. 3. Densities of the 10 most common algal and cyanobacterial species observed in the Ohio River during four seasons during 1991–1992. Bars represent means + 1 SE ( $n = 72$  for each).

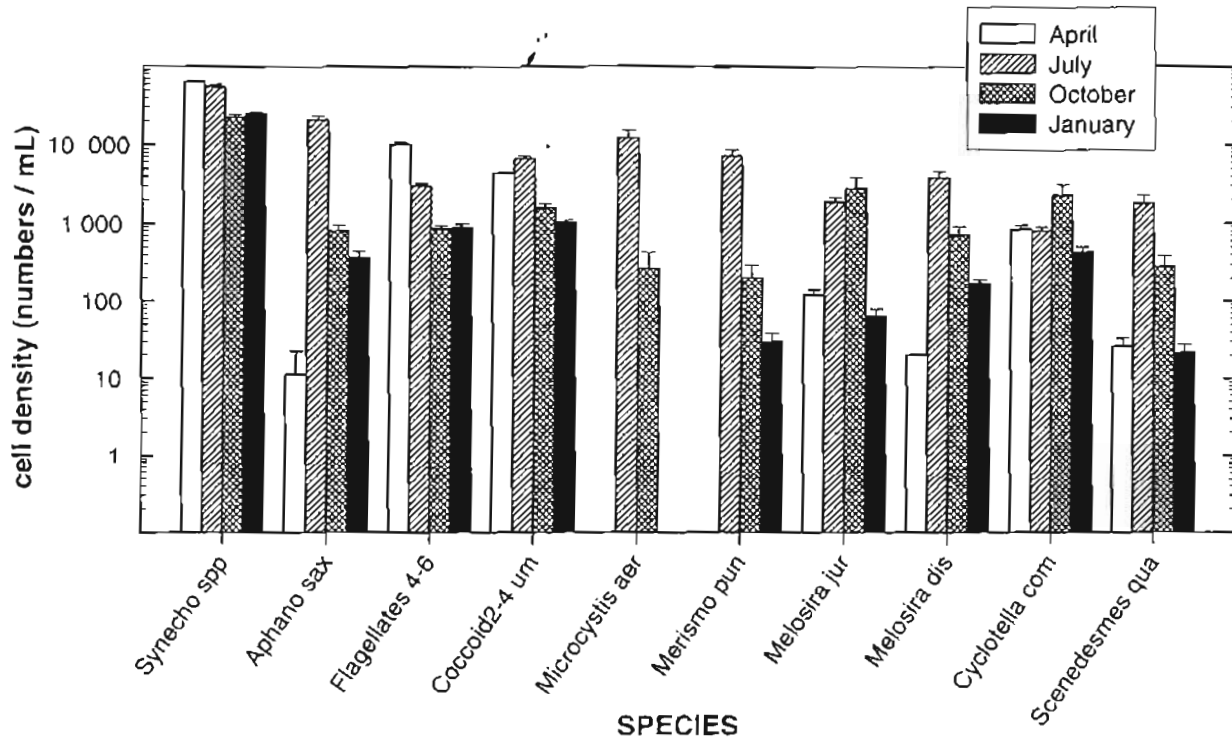
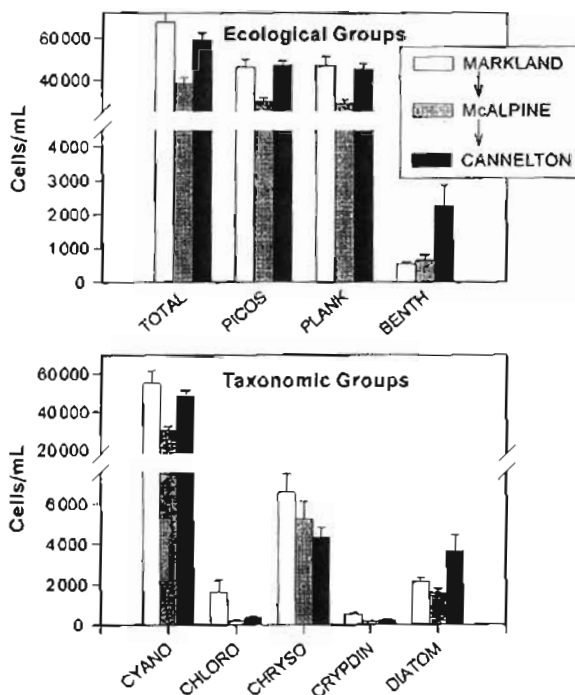


Fig. 4. Differences in the densities of phytoplankton in the Ohio River according to regional river pool. Data are classified into four ecological and five taxonomic groups (see Methods). Bars represent means + 1 SE ( $n = 72$  for each).



pronounced difference was that during each period examined, total densities in the Ohio were consistently greatest in the upper Markland region and consistently lowest in midriver samples within the McAlpine pool (also lowest variation among sites).

Specific patterns suggest that during high-flow conditions in January, phytoplankton communities were most similar among river regions. In July, interpool differences were most pronounced. Markland pool had the highest numbers of total cells ( $P < 0.001$ ), but the lowest numbers of resuspended benthic forms and diatoms ( $P < 0.05$  and  $P < 0.01$ , respectively). Abundances of a few planktonic taxa were significantly lower in Markland, including *Melosira distans* and several *Navicula* species. In none of the general ecological or taxonomic categories were densities greatest in the downstream Cannelton pool. However, a bloom of *Microcystis aeruginosa* and *Melosira jurgensii* in Cannelton exceeded densities observed elsewhere in the Ohio ( $P < 0.01$  for each).

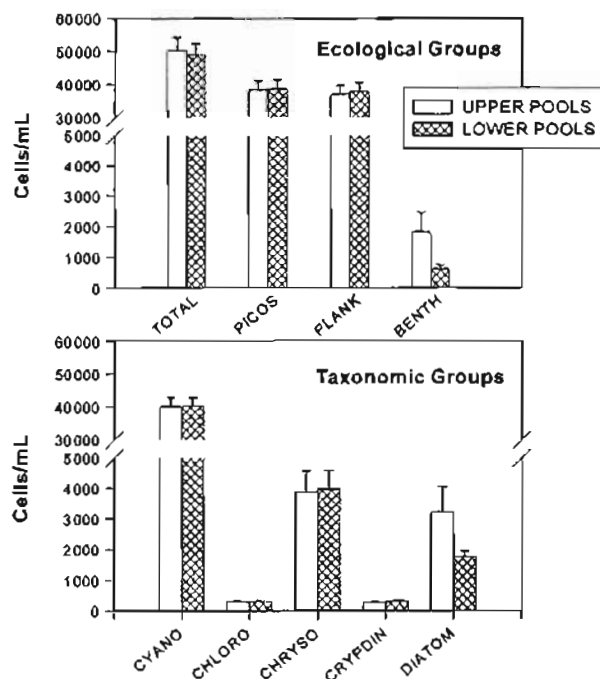
Although navigation dams exerted some significant effects on water chemistry conditions in the Ohio, they had fewer significant effects on phytoplankton community structure (Fig. 5). The greatest general effect was a threefold decrease in the abundances of resuspended benthic forms in pools near the dams (ANOVA:  $P < 0.001$ ). This pattern was also reflected in a reduction in the average diatom density at these sites. The effects of navigation dams were most pronounced during the summer, when temperatures were greatest and flow conditions were at a minimum (Table 4). July was the only month during which total cell densities (and most other categories) declined in the low pools near the navigation dams. In a few instances,

**Table 3.** Contrasts among three regions of the Ohio River (pools: Markland, McAlpine, and Cannelton) on phytoplankton abundance (see Methods for details).

	April		July		October		January	
	F	P	F	P	F	P	F	P
<b>Community</b>								
Total cells	12.74	<0.001	15.84	<0.001	17.26	<0.001	7.24	0.001
Total >2 $\mu\text{m}$	35.44	<0.001	25.35	<0.001	18.17	<0.001	3.06	ns
Planktonic species	17.13	<0.001	10.96	<0.001	16.36	<0.001	8.98	<0.001
Planktonics >2 $\mu\text{m}$	2.24	ns	14.32	<0.001	12.44	<0.001	7.17	0.001
Benthic species	48.24	<0.001	11.02	<0.001	19.21	<0.001	18.34	<0.001
Picoplankton	17.54	<0.001	9.87	<0.001	17.66	<0.001	10.05	<0.001
<b>Taxonomic</b>								
Cyanobacteria	17.66	<0.001	16.07	<0.001	18.96	<0.001	8.84	<0.001
Cyanobacteria >2 $\mu\text{m}$	3.15	0.049	22.56	<0.001	19.28	<0.001	0.72	ns
Chlorophyta	3.10	ns	30.29	<0.001	10.60	<0.001	2.13	ns
Chrysophyta	30.95	<0.001	5.17	0.008	None		12.46	<0.001
Crypto-Dinophyta	7.53	0.002	14.05	<0.001	24.38	<0.001	10.48	<0.001
Bacillariophyta	8.02	0.001	13.71	<0.001	16.80	<0.001	15.53	<0.001

**Note:** Phytoplankton responses are grouped into major categories on the basis of ecological and taxonomic properties (defined in Methods); differences are based on ANOVA; none, no cells of this category observed; F, calculated F ratio; P, probability; ns, nonsignificant,  $P > 0.05$ ; data were log transformed to correct for normality.

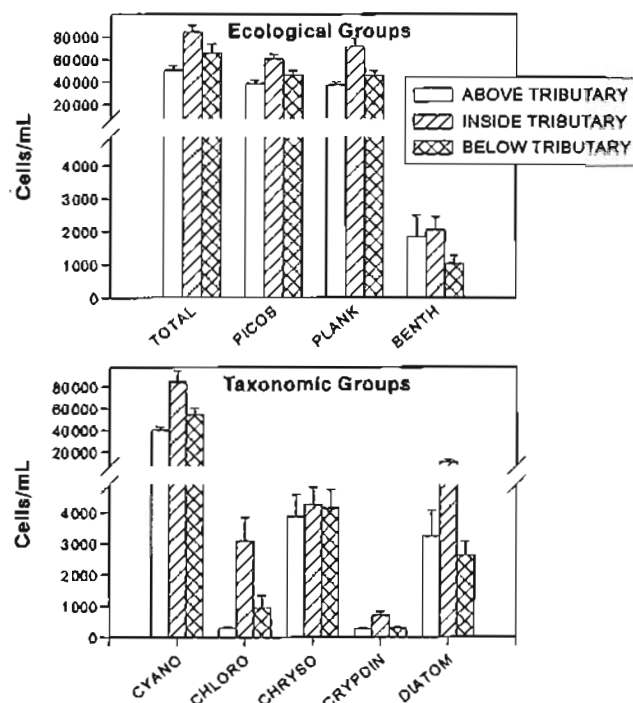
**Fig. 5.** Effects of navigation dams on densities of phytoplankton in the Ohio River. Upper pools are main river sites (BTR) above the influence of the dams; lower pools are main river sites (LOW) at the dams (see Fig. 4 for additional details).



cell abundances significantly increased in these sites. During January, the density of larger cells and colonies (all those >2  $\mu\text{m}$ ) and the density of chrysophytes increased near navigation dams.

In nearly all cases examined, tributaries (ITR) had signifi-

**Fig. 6.** Effects of major tributary rivers on densities of phytoplankton in the Ohio River. Sites are main river locations above, within, and downstream of tributaries at each regional pool (see Fig. 4 for additional details).



cantly greater densities of most phytoplankton species and groups than were observed in the main river (Fig. 6). This was especially true of diatoms and green algae; on average, tributaries contained 10-fold and 15-fold greater numbers of cells

**Table 4.** Comparisons of phytoplankton communities from above (designated main river below tributary, BTR) and below low-head navigation dams (designated main river, LOW) at each of three dam locations on the Ohio River.

Community	April		July		October		January	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Total cells	-0.46	ns	-3.47	0.001	0.50	ns	1.55	ns
Total >2 $\mu\text{m}$	0.44	ns	-3.45	0.002	0.41	ns	2.13	0.040
Planktonic species	-0.33	ns	-2.73	0.010	0.70	ns	1.58	ns
Planktonics >2 $\mu\text{m}$	0.44	ns	-1.14	ns	1.36	ns	0.39	ns
Benthic species	-3.17	0.003	-3.32	0.002	-3.36	0.002	-3.96	<0.001
Picoplankton	-0.39	ns	-2.88	0.007	0.33	ns	1.55	ns
<b>Taxonomic</b>								
Cyanobacteria	-0.39	ns	-3.30	0.002	0.07	ns	1.60	ns
Cyanobacteria >2 $\mu\text{m}$	0.37	ns	-3.42	0.002	0.90	ns	1.30	ns
Chlorophyta	0.08	ns	-1.65	ns	0.83	ns	-2.90	0.012
Chrysophyta	0.51	ns	-3.16	0.003	None		2.02	0.051
Crypto/Dinophyta	-0.50	ns	0.66	ns	1.47	ns	0.20	ns
Bacillariophyta	0.52	ns	-1.80	ns	0.87	ns	-0.22	ns

Note: Phytoplankton responses are grouped into major categories on the basis of ecological and taxonomic properties (defined in Methods); differences are based on independent Student *t* tests with pooled variances; none, no cells of this category observed; *t*, calculated *t* value comparing upstream (BTR) versus at the dam (LOW); a positive *t* score indicates that densities increased at the dam sites of the main river; a negative score indicates a significant reduction; *P*, probability; ns, nonsignificant,  $P > 0.05$ .

**Table 5.** Comparisons of phytoplankton communities from above (designated ATR) and below (designated BTR) three major tributaries entering three regions of the Ohio river.

Community	April		July		October		January	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Total cells	-0.55	ns	2.46	0.019	1.34	ns	-0.68	ns
Total >2 $\mu\text{m}$	1.52	ns	2.01	0.043	2.18	0.036	0.14	ns
Planktonic species	0.34	ns	2.27	0.029	1.26	ns	-0.84	ns
Planktonics >2 $\mu\text{m}$	0.91	ns	1.29	ns	2.02	ns	0.24	ns
Benthic species	-0.42	ns	-0.63	ns	0.34	ns	0.80	ns
Picoplankton	0.32	ns	2.25	0.031	1.20	ns	-0.85	ns
<b>Taxonomic</b>								
Cyanobacteria	0.33	ns	2.74	0.010	1.22	ns	-0.73	ns
Cyanobacteria >2 $\mu\text{m}$	0.48	ns	3.21	0.003	0.25	ns	2.46	0.020
Chlorophyta	0.97	ns	1.54	ns	0.98	ns	-1.57	ns
Chrysophyta	1.80	ns	1.55	ns	None		-0.79	ns
Crypto/Dinophyta	-1.43	ns	0.16	ns	1.22	ns	-0.49	ns
Bacillariophyta	0.08	ns	0.39	ns	1.65	ns	-0.15	ns

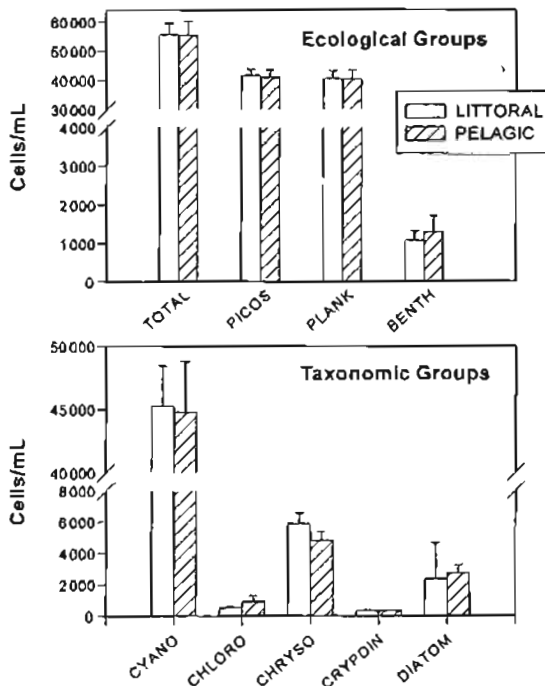
Note: Phytoplankton responses are grouped into major categories on the basis of ecological and taxonomic properties (defined in Methods); differences are based on independent Student *t* tests with pooled variances; none, no cells of this category observed; *t*, calculated *t* value comparing above versus below sites; a positive *t* score indicates that densities increased in the main river below the tributaries; a negative score indicates a significant reduction; *P*, probability; ns, nonsignificant,  $P > 0.05$ .

than the main channel of the Ohio. The annual averages indicate, however, only small effects on downstream (BTR) sites. For example, despite consistently large differences in absolute densities of diatoms in ATR versus ITR sites, sites down-

stream of tributaries (BTR) experienced no significant increases during any of the four seasons considered (Table 5). Green algae, chrysophytes, and cryptomonads-dinoflagellates were also unaffected by inputs from tributaries. This was true



Fig. 7. Differences in the densities of phytoplankton in the Ohio River in nearshore littoral habitats and open river pelagic habitats (see Methods for details of sampling locations; see Fig. 4 for additional details).



also of total cell densities in three of four seasons as well. Of the few significant effects of tributaries on downstream phytoplankton communities, most occurred during the summer. Planktonic forms, picoplankton, and cyanobacteria increased significantly below tributaries only during July. Most of this change was associated with increases in densities of the picoplankter *Synechococcus* sp. ( $t$  test:  $P = 0.031$ ) and two large colonial forms, *Aphanothece saxicola* ( $t$  test:  $P = 0.002$ ) and *Chroococcus limneticus* ( $t$  test:  $P = 0.030$ ). Among 30 species of diatoms observed during the summer period, densities of only the small centric *Cyclotella meneghiniana* were greater below tributaries ( $t$  test:  $P = 0.026$ ). In January, only the larger celled and colonial cyanobacteria increased in sites downstream of tributaries.

Finally, we collected samples from midriver (pelagic) and nearshore (littoral) habitats to determine if the shallower, slower flowing conditions were perhaps more amenable to plankton development in the river. When viewed over the entire year, there were no significant differences in the densities of any ecological or taxonomic group between these two habitats (Fig. 7). The averages for pelagic and littoral densities within each category varied within  $\pm 20\%$  of each other riverwide. With one exception, subsequent analyses of differences (via  $t$  tests) also indicated no differences among these two habitats ( $P > 0.05$ ) for all individual seasons. During April, chrysophyte densities were significantly greater in littoral habitats than in the midriver pelagic zone. This difference was associated solely with 2.4-fold greater numbers of an unidentified tiny golden flagellate ( $4 \mu\text{m}$  wide  $\times$   $6 \mu\text{m}$  long) in littoral habitats ( $t$  test:  $P < 0.034$ ). Densities of all other taxa were insignificantly different between these two habitats.

### Effects of physicochemical factors on Ohio River phytoplankton

Many of the temporal and spatial patterns observed for the phytoplankton community may be in part the result of changes in physical and chemical variables described earlier (Tables 1 and 2). To consider whether specific factors may be responsible for regulating densities in the Ohio River, a two-step analysis was used. First, correlations between chemical and biological variables were used to identify the primary factors probably influencing numbers of phytoplankton in certain ecological and taxonomic categories. Second, multiple regressions were used to determine the best quantitative model for predicting phytoplankton numbers.

Variations in many of the major physical and chemical variables measured correlated significantly with differences in densities of several phytoplankton groups in the Ohio River (Table 6). The most consistent pattern we observed with pairs of variables was with temperature; cell densities in all 12 phytoplankton groups correlated positively with greater temperatures (all  $P < 0.001$ ). Among the algal nutrients, DIP concentrations correlated negatively with 10 phytoplankton variables, and inorganic N:P ratios correlated positively with nine phytoplankton variables. Larger colonial cyanobacteria were not significantly correlated with either total DIN or N:P ratio. Certain ecological and taxonomic groups exhibited different patterns in their responses to the suite of variables considered. Perhaps owing to the very large proportion of cells  $< 2 \mu\text{m}$ , total cells, total cyanobacteria, and picoplankton densities responded similarly, with strong positive temperature, N:P, and turbidity correlations and negative correlations with DIP. Other groups were more distinct. In particular, benthic forms correlated negatively with current velocity, but with none of the common nutrient measures. Chrysophytes also were somewhat unlike other groups, having a positive correlation with current velocity, turbidity, and DIN but not with  $\text{NO}_3\text{-N}$ . Even though some of the chrysophyte taxa possess Si scales, neither members of this group nor diatoms correlated with dissolved Si. Variations in diatom densities correlated with a few variables only weakly; the strongest were significant positive correlations with temperature and dissolved Mg.

These relationships were considered for three major groups using MLR. The most important predictor of total phytoplankton density in the Ohio was found by MLR to be temperature (Table 7). Greater water temperatures were associated with significantly greater total cell density. The relationship explained only about 15% of the total variation (Fig. 8). The complete MLR model predicted that greater DIP and  $\text{SO}_4\text{-S}$  concentrations and greater current velocities would have negative impacts on total cells. On the basis of microscopic examinations, most of the river turbidity was not caused by phytoplankton cells, but MLR nonetheless predicted greater numbers during periods of higher turbidity. The six-variable model explained about 60% of the total variation in total cell densities.

Densities of planktonic forms were apparently affected by factors similar to those affecting total cells: turbidity was the best single predictor, which explained about 20% of the variation in planktonic densities (Table 7; Fig. 8). The complete predictive model contained the same independent variables (predictors) as for total cells, but their order of importance differed slightly.

**Table 6.** Correlations between 12 physical and chemical variables and phytoplankton abundances represented in 12 taxonomic and ecological categories (see Methods) measured for the Ohio River.

Ecological categories												
	Total cells		Total >2 $\mu\text{m}$		Planktonic		Planktonic >2 $\mu\text{m}$		Benthic		Picoplankton	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Temperature	0.386	***	0.509	***	0.282	***	0.363	***	0.295	***	0.247	***
Current	ns		ns		ns		ns		-0.192	**	ns	
Turbidity	0.329	***	ns		0.443	***	ns		ns		0.497	***
DIP	-0.377	***	-0.368	***	-0.395	***	-0.425	***	ns		-0.362	***
NH <sub>4</sub> -N	0.258	***	0.127	*	0.286	***	ns		ns		0.339	***
NO <sub>3</sub> -N	-0.253	***	-0.207	***	-0.241	***	-0.194	**	ns		-0.226	***
DIN	ns		ns		ns		ns		ns		ns	
N:P ratio	0.311	***	0.302	***	0.311	***	0.334	***	ns		0.294	***
Si	ns		ns		ns		-0.133	*	ns		ns	
SO <sub>4</sub> -S	-0.129	*	ns		-0.175	**	ns		ns		-0.198	**
Ca	0.188	**	0.185	**	0.195	**	0.206	***	ns		0.164	**
Mg	0.264	***	0.275	***	0.257	***	0.199	**	0.173	**	0.241	***

Taxonomic categories												
	Cyano		Cyano >2 $\mu\text{m}$		Chloro		Chryso		Crypto-Dino		Bacillario	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Temperature	0.361	***	0.408	***	0.519	***	0.520	***	0.499	***	0.286	***
Current	ns		-0.390	***	-0.342	***	0.155	*	-0.381	***	-0.122	*
Turbidity	0.339	***	-0.476	***	-0.249	***	0.303	***	-0.333	***	ns	
DIP	-0.408	***	-0.122	*	-0.274	***	-0.236	***	ns		-0.182	**
NH <sub>4</sub> -N	0.262	***	-0.258	***	-0.132	*	0.516	***	ns		ns	
NO <sub>3</sub> -N	-0.294	***	-0.136	*	ns		ns		0.148	*	ns	
DIN	ns		ns		ns		0.201	**	0.159	*	ns	
N:P ratio	0.292	***	ns		0.240	***	0.339	***	ns		0.222	***
Si	ns		-0.292	***	-0.222	**	ns		-0.204	*	ns	
SO <sub>4</sub> -S	-0.156	**	ns		0.141	*	0.149	*	0.465	***	ns	
Ca	0.179	**	ns		0.261	***	0.215	**	0.129	*	0.251	***
Mg	0.226	***	ns		0.156	*	0.572	***	0.317	***	0.291	***

Note: *r*, Spearman's product-moment correlation coefficient; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

Densities of benthic taxa suspended in the water column could not be precisely estimated. Temperature was again the most important factor affecting cell densities, but only described about 9% of the total variation in their numbers (Fig. 8). The MLR approach was also less effective at producing a model that reliably estimates densities of benthic taxa in the water column ( $P < 0.001$ , but  $r^2 = 0.18$ ). A further difference in these results was that greater levels of DIN were predicted to cause a reduction in cell densities and DIP concentrations were unimportant. Current velocity was not selected in this model.

## Discussion

Our data show that the Ohio River supports a diverse and substantial phytoplankton community throughout its length. Phytoplankton densities  $\geq 10^4$  cells/mL are comparable with many other large rivers in North America (Søballe and Kimmel 1987), including the Arkansas (Williams 1964),

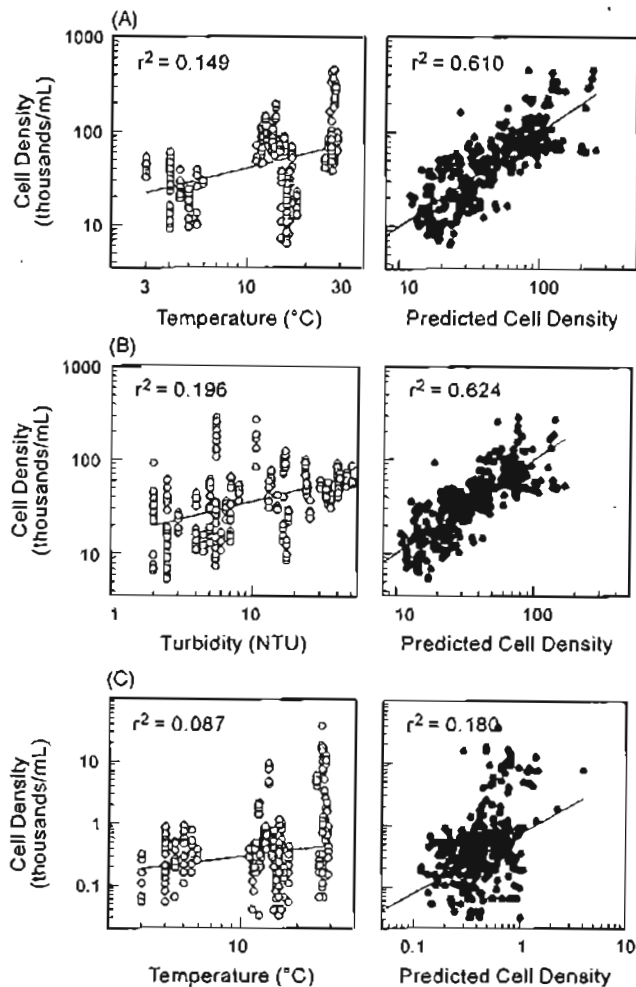
Hudson (Marshall 1988), Mississippi (Lange and Rada 1993), and Ohio (Peterson and Stevenson 1989), and many European rivers such as the Rhine (Admiraal et al. 1994), Meuse (Descy et al. 1987), Severn (Swale 1969), Thames (Lack 1971), and Wye (Jones 1984). Surface (1–5 m) phytoplankton densities in the Rio Tapajós, a large clearwater river in the Amazon basin, are also within the range observed in the Ohio; densities are perhaps an order of magnitude less in blackwater sections of the Amazon proper (Sioli 1975). Typical cell concentrations observed in large rivers are comparable with moderately productive lentic ecosystems with well-established plankton-based food webs. The numerical predominance of picoplankton-sized cells in the Ohio is typical of many freshwater systems (Stockner 1988), although there are few reports from rivers. Marshall (1988) found that autotrophic picoplankton were also numerically dominant in the Hudson River, but constitute  $< 5\%$  of the total biovolume. Our estimates suggest that even during maximum picoplankton numbers, picoplankton

Table 7. Summary of MLR analyses used to determine the major factors affecting key phytoplankton densities in the Ohio River.

MLR analyses			Total cells/mL ( $r^2 = 0.610$ )			Planktonic cells/mL ( $r^2 = 0.624$ )			Benthic cells/mL ( $r^2 = 0.18$ )						
Step	Independent variable	Slope	t	P	Independent variable	Slope	t	P	Independent variable	Slope	t	P			
1	Temperature	0.96 ± 0.06	15.8	***	Turbidity	0.61 ± 0.04	14.4	***	Temperature	1.09 ± 0.15	7.23	***			
2	DIP	-0.24 ± 0.06	-3.6	***	Temperature	0.79 ± 0.05	14.7	***	NH <sub>4</sub> <sup>+</sup> -N	-0.58 ± 0.11	-5.29	***			
3	Turbidity	0.59 ± 0.05	12.5	***	Current	-0.13 ± 0.02	-5.07	***	Turbidity	0.29 ± 0.10	2.79	**			
4	Current	-0.14 ± 0.03	-5.1	***	Ca <sup>2+</sup>	0.24 ± 0.05	5.11	***	DIN	-0.58 ± 0.19	3.04	**			
5	SO <sub>4</sub> -S	-0.26 ± 0.05	-4.7	***	SO <sub>4</sub> -S	-0.21 ± 0.05	-4.46	***	SO <sub>4</sub> -S	-0.28 ± 0.13	-2.18	*			
6	Ca <sup>2+</sup>	0.26 ± 0.05	4.9	***	DIP	-0.19 ± 0.06	-3.23	**	y intercept	2.54 ± 1.20					
	y intercept	7.61 ± 0.45			y intercept	7.48 ± 0.41									
ANOVA															
			Total cells/mL			Planktonic cells/mL			Benthic cells/mL						
Source	SS	df	MS	F ratio	P	SS	df	MS	F ratio	P	SS	df	MS	F ratio	P
Model	147.8	6	24.63	76.79	***	123.9	6	20.64	81.26	***	94.25	5	18.85	12.06	***
Residual	94.3	294	0.32			74.7	294	0.25			439.0	281	1.56		

Note: The independent variables tested were the 12 physical and chemical variables listed in Table 6. Significance of individual variables tested via Student's *t* test;  $r^2$ , coefficient of determination of the complete model; *P*, probability of a significant effect; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

Fig. 8. Bivariate and multiple regressions predicting the density of (A) total, (B) planktonic, and (C) benthic cells in the Ohio River during 1991–1992. Independent variables in each bivariate regression are the factors selected by MLR as the primary factor affecting cell densities in each category; predicted density is the multivariable model established by MLR (see Table 7 for details).



cells represent only about 10% of the total summer phytoplankton biovolume in the Ohio.

A misunderstanding in aquatic ecology is the idea that large rivers lack a substantial phytoplankton community (Wetzel 1975; Junk et al. 1989). The view that self-sustaining algal populations are unimportant in large-order rivers may have been derived from the idea that most large rivers are deep and turbid; thus, phytoplankton production would be light limited most of the year (e.g., Vannote et al. 1980). Early reports suggested that much of the presumed phytoplankton community was either resuspended benthic species or cells washed in from pools or tributaries connected to lakes. Our data indicate that few ( $\approx 10\%$  by species, 5% by numbers) of the Ohio River taxa were resuspended benthic forms (such as biraphid pennate diatoms) or tychoplanktonic species from littoral areas (e.g., *Mougeotia* sp.). The literature also suggests that lower reaches of rivers may have considerable in situ primary production, with associated planktonic and microbial food webs (Sedell et al. 1989; Cole et al. 1991; DeRuyter VanSteveninck et al. 1992). This production is supported in many large rivers

by floodplain and anthropogenic inputs of nutrients (Friedrich and Müller 1984; Junk et al. 1989). Lack (1971) regarded the River Thames essentially as a series of nutrient-enriched impoundments with short retention times. Regions of the upper Mississippi where navigation dams have been constructed also support considerable phytoplankton communities, similar to levels observed in stratified lakes (Lange and Rada 1993). A detailed production budget for the River Lot (France) indicates that despite considerable abiotic (mineral particles) and allochthonous (detrital) light attenuation, navigation dams and water flow regulation favor the development of large phytoplankton populations during many months of the year (Decamps et al. 1984). We contend that these features are typical of many large rivers worldwide.

We found the species composition of the Ohio River phytoplankton to consist predominantly of diatoms, representing more than 60% of the species total. This general result is commonly reported in many large rivers (e.g., Williams 1964; Peterson and Stevenson 1989; Admiraal et al. 1994) but may obscure important temporal patterns in the community. Periods of maximum phytoplankton concentrations in the Ohio, as with most large rivers, occur during the summer, when temperatures are warmer and discharge is reduced. Midsummer assemblages in the Ohio were dominated in numbers (and biovolume) by colonial cyanobacteria, especially *Aphanothece saxicola*, *Merismopedia punctata*, and *Microcystis aeruginosa*, along with unicellular *Synechococcus* spp. Chlorophytes (*Scenedesmus* spp. and other members of the chlorococcales) also peaked at this time. A few diatom species (*Melosira* spp.) were also abundant in the summer, but at the summer phytoplankton peak, they contributed on average only about 5.6% by number and 28% by volume. Diatoms were numerically more important in the community during the late autumn and early spring, when densities of cyanobacteria averaged between half and a third of their midsummer levels.

These results parallel findings from some large rivers, such as the Wye (Jones 1984), Severn (Swale 1969), Mississippi (Baker and Baker 1981; Huff 1986), and Hudson (Marshall 1988). The nearby Mississippi, which later joins the Ohio, is of particular interest to our work. During most years, the river typically experiences a distinct low-flow period in the summer, which appears to support large blooms of cyanobacteria (especially *Aphanizomenon flos-aquae*). During other periods the river is dominated by centric diatoms (e.g., *Melosira granulata*, *Melosira italica*, and *Cyclotella meneghiniana*). However, during 1986, the summer phytoplankton community of the upper Mississippi ( $\approx 1110$  km) continued to be dominated numerically and in biovolume by the diatoms *Melosira granulata*, *Stephanodiscus astrea*, and *Cyclotella* spp. (Lange and Rada 1993). The authors suggested that a higher summer discharge in 1986 may have enabled diatoms to remain suspended in the water column and reduced stratification, which favors gas-vacuolate cyanobacteria. In our study on the Ohio, *Aphanothece* and *Microcystis* were the predominant bloom-forming species during the summer of 1991. Earlier data (1960–1964) from the Ohio River near Louisville indicated a distinct bimodality in phytoplankton communities, with greens (chlorococcales dominant 26% of all dates) and cyanobacterial forms (*Microcystis* and other cyanobacteria 5% of all dates) dominant in the

summer (Nall 1965; Riley 1969). Diatom maxima were observed during the spring and late fall (*Melosira* spp. 46% of dates; *Cyclotella* + *Stephanodiscus* 9% of dates). The River Rhine also is dominated by centric diatoms, such as *Stephanodiscus* in spring, but this dominance continues through the summer with multiple peaks of more than one species from this genus (Admiraal et al. 1994). All other reports from the Ohio suggest that *Stephanodiscus* is common, but we did not find it abundant. One possible reason for its low numbers may be that larger sized diatoms (with rapid sinking rates) may require extended periods of low discharge to maintain populations within the euphotic zone. More recently (1979–1981), abundances of several cyanobacterial (*Anacystis* and *Oscillatoria*) and green algal (*Scenedesmus*) genera were shown to be strongly correlated with higher temperatures (Peterson and Stevenson 1989). The abundances of other taxa (e.g., *Chlamydomonas* and *Navicula* spp.) were inversely related to temperature during those years.

#### Differences in the community among river pools

The three large river segments we studied were compared to examine longitudinal differences in phytoplankton communities on a broader landscape level. Assemblages differed significantly among these pools during all times of the year. One of the most consistent results was that abundances of most planktonic forms were greatest in the upper (Markland) region of the Ohio, while densities of resuspended benthic forms were consistently greatest (but still <10% of the total) in the lowest study region (Cannelton). At first consideration, this pattern may seem counterintuitive. The RCC (Vannote et al. 1980) and riverine productivity model (Thorpe and Delong 1994) each predict a greater (if limited) importance of phytoplankton to food webs in lower (larger order) reaches of rivers. However, average discharge increased along this stretch of the Ohio by only 19% (Ma = 2726 m<sup>3</sup>/s, Mc = 3032 m<sup>3</sup>/s, and Ca = 3240 m<sup>3</sup>/s), and most of it flows through a geologically constricted valley; river order does not change. Despite its 360-km length, the present study was not sufficient to evaluate continuum effects on plankton abundances. There are also important physical changes in the Cannelton reach, with the "falls of the Ohio" creating increased turbulence, while the lower portion of the Cannelton pool flows through a broader floodplain. Densities of chrysophytes (mainly flagellates 4–6 µm) and green algae (mainly *Scenedesmus*, *Chlorella*, and *Actinastrum*) declined in this section. Overall, however, the lowest cell densities of most phytoplankton groups, as well as total densities (about 30% less on average), were observed in the middle McAlpine pool. We observed no significant differences in major algal nutrients or physical factors within this section of the Ohio (Tables 1 and 2). However, during this same period, total zooplankton densities were significantly greater in the McAlpine pool than in both upriver and downriver sections, primarily the result of much greater numbers of copepod nauplii (Thorpe et al. 1994). The largest decline (40%) in phytoplankton numbers (36 500 to 21 800 cells/mL) between the Markland and McAlpine pools (from Ma LOW to Mc ATR) was observed in the picoplankton. Copepod nauplii feed primarily on algae, especially smaller forms (Williamson 1991); hence, grazing pressure seems a plausible cause for the dramatic declines in phytoplankton in the McAlpine pool.

#### Effects of navigation dams

A prominent feature of the Ohio, like many large rivers worldwide, is the presence of low-head navigation dams, which may influence the biomass and community structure of plankton communities. While large (high head) dams used for reservoir construction and power generation have profound effects on current velocities, residence time, and other conditions (Thornton et al. 1990), impacts of low-head navigation dams are more subtle. Average current velocity at the McAlpine dam was significantly reduced, but low sites in the other two pools were apparently unaffected. Certain nutrients were significantly different near navigation dams. DIP levels were at times significantly greater (January–July) while at other times significantly less (October), particularly in the McAlpine pool. With reduced current velocity, nutrient (especially P) spiraling lengths are expected to be shortened, and biotic processes (e.g., bacterial remineralization) may enhance availability (Newbold et al. 1981). However, our data for DIN and dissolved Si indicate no clear patterns with respect to navigation dams. In contrast, phytoplankton strongly influence levels of dissolved N, P, and Si in the River Rhine (Admiraal et al. 1994).

Navigation dams had significant, but fairly subtle effects on selected parts of the phytoplankton community (Fig. 5; Table 4). No general pattern for the effect of dams was observed on total phytoplankton densities in the river, although numbers of all cells >2 µm were significantly greater in low pools near navigation dams in January. In contrast, during July, abundances of many phytoplankton groups were significantly reduced at these sites. Only one group was consistently affected by this factor in the Ohio. Densities of benthic species were significantly lower just above low-head dams on all dates and among all sites. This suggests that small (and sometimes statistically nonsignificant) reductions in current velocity may allow bottom-dwelling species to settle out of the water column, even though this may have negligible effects on the total community. Also, sites just above navigation dams tend to be much deeper than other locations on the Ohio. This result is similar to results presented for the upper Mississippi and the River Wye in which heavy-walled diatoms are kept suspended in the water column during periods of high discharge (Jones 1984; Lange and Rada 1993). It also indicates that the current velocities in most parts of the Ohio usually are great enough to maintain a small assemblage of dislodged cells from solid substrates and river sediments. Thus, changes in discharge and navigation dams may have complex effects on river phytoplankton. Resuspension may increase total cell (especially benthic) densities, but can also dilute planktonic numbers. Descy et al. (1987) developed a model that predicts that seasonal variations in growth rates of river phytoplankton may affect their ability to compensate for the dilution effects of increased discharge. Further studies on the effects of navigation dams in large rivers must also take into account different growth rates of various phytoplankton species, which in general are known to vary inversely with cell size (Raven 1987).

#### Effects of tributaries

We also consider whether planktonic communities in the Ohio consist of resident populations or are washed in from lakes and rivers fed by three major tributaries (Miami,

Kentucky, and Salt rivers). If tributaries do not significantly alter the biomass or composition of river plankton, we may assume that the phytoplankton community is sustained by reproducing populations from the main channel and backwaters, rather than by renewal from other sources. The communities inside these tributaries differed significantly from the main river in several aspects. Tributary rivers tended to have greater total densities of phytoplankton ( $\approx 60\%$  greater); with a greater proportion consisting of colonial cyanobacteria (50% greater), green algae (threefold greater), and diatoms (fivefold greater). Picoplankton-sized cells were less important in these smaller rivers. Despite large differences in densities of certain forms, effects of these tributaries on the main river were not large. Total densities of suspended cells in the Ohio above and below these tributaries were insignificantly different year-round. However, during the summer and fall, certain larger forms such as colonial cyanobacteria (e.g., *Aphanocapsa saxicola*) and some diatom species (e.g., *Cyclotella meneghiniana*) were found in significantly greater densities downstream of tributaries. Tributaries also had few important effects on zooplankton communities in the Ohio (Thorp et al. 1994), with the exception of greater densities of rotifers ( $\approx 40\%$  increase) and cladocerans (twofold increase). We suspect that the lack of strong tributary effects on Ohio plankton assemblages is the result of considerably larger total flow in the main river than in the smaller tributaries. For example, the average discharge of the Kentucky River (enters at McAlpine Pool) is  $\approx 240 \text{ m}^3/\text{s}$  ( $\approx 8\%$  of total), compared with  $3032 \text{ m}^3/\text{s}$  in the Ohio. The Salt River (enters at Cannelton Pool) contributes only an additional  $\approx 50 \text{ m}^3/\text{s}$ . The communities in the main river would appear to consist of resident populations. In other large rivers, rapid doubling rates during the spring and summer (0.5–1.1/day) are able to sustain populations despite considerable downstream drift (Descy et al. 1987; DeRuyter VanSteveninck et al. 1992). Studies on the balance between dilution rates and growth rates of dominant species are necessary to further establish the importance of autotrophy in the lower sections of the Ohio.

#### Pelagic and littoral communities in the Ohio River

The flood-pulse concept introduced the idea that large rivers can maintain substantial in situ production in part by receiving nutrient and particulate inputs from flooded littoral and terrestrial (riparian) areas (collectively the aquatic-terrestrial transition zone, or ATTZ) adjacent to the river channel (Junk et al. 1989); these authors predicted that primary production in littoral and ATTZ areas should be greater than in the main channel. In contrast with zooplankton, whose average total densities were roughly 60% greater in littoral versus pelagic sites of the Ohio (Thorp et al. 1994), phytoplankton densities showed almost no difference with respect to these habitats. Because sampling was entirely restricted to suspended ( $\approx$  planktonic) forms, probable differences in periphytic and benthic species were not seen. Another factor in this portion of the Ohio is that nearly all the river is located within a geologically constricted valley, with small floodplains above Louisville, Ky. Changes in flow conditions over the year brought about considerable dilution effects with probably little import of ATTZ-resident materials or populations in the Ohio. We suspect that the

pattern in periphyton production in these two habitat types may be quite different.

#### Effects of physical and chemical factors

MLR analysis revealed that temperature and current velocity were important regulators of total density and the density of major phytoplankton groups in the Ohio. These are common factors affecting phytoplankton communities in other large rivers, such as the Mississippi (Lange and Rada 1993), Meuse (Descy et al. 1987), and Rhine (Admiraal et al. 1994). Water residence time (inversely related to discharge) was of critical importance in a cross-system analysis of rivers, impoundments, and lakes (Søballe and Kimmel 1987). For example, algal cell densities per unit P were least in rivers, an effect that was thought to be caused by the short residence time in flowing waters. The lack of any positive dependence of phytoplankton standing crop on  $\text{PO}_4\text{-P}$  concentrations in the Ohio River, while also seen in the upper Mississippi (Lange and Rada 1993), is still somewhat surprising. Concentrations of DIP in the Ohio remained fairly high throughout the year (40–50  $\mu\text{g P/L}$ ; Table 2) and exhibited no obvious seasonal patterns (Thorp et al. 1994). It is possible that primary production in the Ohio was simply not nutrient limited and was affected primarily by the dilution effects of river discharge. The effect of interannual variations in flow conditions is also important, as shown in the Mississippi by Lange and Rada (1993). They found that extended high-flow periods may cause shifts in community composition and can reduce interpool differences within the river. An obvious summer decline in dissolved Si in our study suggests biotic depletion, as has been observed by others (Admiraal et al. 1994; Descy et al. 1987; DeRuyter VanSteveninck et al. 1992), but not universally (Lange and Rada 1993). However, diatoms did not feature strongly in the Ohio phytoplankton community during 1991–1992, and both MLR and correlation analysis did not identify Si concentrations as a significant variable related to algal, or even diatom, densities. Other chemical factors, such as  $\text{SO}_4\text{-S}$  (– effect) and  $\text{Ca}^{2+}$  (+ effect), were also included in these empirical models, although their quantitative importance in explaining variation in phytoplankton densities was minor. We know of no studies that document the influence of  $\text{SO}_4\text{-S}$  on river phytoplankton, although Brasfield (1972), also using multiple regression, found that elevated  $\text{SO}_4\text{-S}$  in the Gallinas River (New Mexico) is strongly associated with greater levels of coliform bacteria. The Ca content of major rivers varies widely, and algal species requirements also differ markedly, but an earlier study of major phytoplankton genera in the Ohio (Peterson and Stevenson 1989) did find positive correlations between certain major taxa and greater total alkalinity, which typically corresponds to higher  $\text{Ca}^{2+}$  levels. Moss (1988) also commented that certain algal groups, such as desmids (rare in the Ohio River), are strong calciphobes.

While physical factors (temperature and flow) appear to have had the greatest impact on phytoplankton communities, our data suggest that biotic regulation by grazing zooplankton may also play an important role. Experimental studies are needed that can tease apart the influences of herbivory, nutrient supply, and flow regime on the growth rates of primary producers in large rivers. Further studies are also needed to examine the coupling between the resuspension of benthic and periphytic forms on the total biomass of cells suspended in the

water column. These connections may enable the river to maintain a positive autotrophic balance during winter and spring when discharge is high and temperatures are reduced.

## Acknowledgments

We gratefully acknowledge the efforts and assistance of Wei Fang, Kim Greenwood, and Dr. Kim H. Haag in collecting plankton and water chemistry samples during this study. We also thank Lori Campbell for assistance with water chemistry analyses. J.H.T. was supported by a grant from the National Science Foundation (NSF) (DEB-9307225) and J.D.W. by the Routh Endowment Fund and the NSF (DIR-9002145).

## References

- Admiraal, W., Breebaart, L., Tubbing, G.M.J., VanZanten, B., DeRuitjer VanSteveninck, E.D., and Bijkerk, B. 1994. Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwater Biol.* **32**: 519–531.
- American Public Health Association. 1985. Standard methods for the analysis of water and wastewater. 16th ed. American Public Health Association, Washington, D.C.
- Baker, A.L., and Baker, K.K. 1981. Seasonal succession of the phytoplankton in the upper Mississippi River. *Hydrobiologia*, **83**: 295–301.
- Bran+Luebbe Analyzing Technologies. 1986a. Ortho phosphate in water and seawater. Industrial method No. 812-86T. Bran+Luebbe Inc., Buffalo Grove, Ill.
- Bran+Luebbe Analyzing Technologies. 1986b. Ammonia in water and seawater. Industrial method No. 804-86T. Bran+Luebbe Inc., Buffalo Grove, Ill.
- Bran+Luebbe Analyzing Technologies. 1987a. Nitrate/nitrite in water and seawater. Industrial method No. 818-87T. Bran+Luebbe Inc., Buffalo Grove, Ill.
- Bran+Luebbe Analyzing Technologies. 1987b. Silicates in water and wastewater. Industrial method No. 785-86T. Bran+Luebbe Inc., Buffalo Grove, Ill.
- Bran+Luebbe Analyzing Technologies. 1989. Sulfate in water and wastewater. Industrial method No. 847-87T. Bran+Luebbe Inc., Buffalo Grove, Ill.
- Brasfield, H. 1972. Environmental factors correlated with size of bacterial populations in a small polluted stream. *Appl. Microbiol.* **24**: 349–352.
- Cole, J.J., Caraco, N.F., and Peierls, B. 1991. Phytoplankton primary production in the tidal, freshwater Hudson River, New York (USA). *Verh. Int. Ver. Theor. Angew. Limnol.* **24**: 1715–1719.
- Cushing, C.E. 1967. Periphyton productivity and radionuclide accumulation in the Columbia River, Washington, USA. *Hydrobiologia*, **29**: 125–139.
- Decamps, H., Capblancq, J., and Tourenq, J.N. 1984. Lot. In *Ecology of European rivers*. Edited by B.A. Whitton. Blackwell, Oxford. pp. 207–235.
- DeRuyter VanSteveninck, E.D., Admiraal, W., Breebaart, L., Tubbing, G.M.J., and van Zanten, B. 1992. Plankton in the River Rhine: structural and functional changes observed during downstream transport. *J. Plankton Res.* **14**: 1351–1368.
- Descy, J.-P., Servais, P., Smits, J.S., Billen, G., and Everbecq, E. 1987. Phytoplankton biomass and production in the River Meuse (Belgium). *Water Res.* **21**: 1557–1566.
- Friedrich, G., and Müller, D. 1984. Rhine. In *Ecology of European rivers*. Edited by B.A. Whitton. Blackwell, Oxford. pp. 265–315.
- Huff, D.R. 1986. Phytoplankton communities in navigation pool No. 7 of the upper Mississippi River. *Hydrobiologia*, **136**: 47–56.
- Hynes, H.B.N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ont.
- Hynes, H.B.N. 1989. Keynote address. In *Proceedings of the International Large River Symposium (LARS)*. Edited by D.P. Dodge. Can. Spec. Publ. Fish. Aquat. Sci. No. 106. pp. 5–10.
- Jones, F.H. 1984. The dynamics of suspended algal populations in the lower Wye catchment. *Water Res.* **18**: 25–35.
- Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood-pulse concept in the river–floodplain systems. In *Proceedings of the International Large River Symposium (LARS)*. Edited by D.P. Dodge. Can. Spec. Publ. Fish. Aquat. Sci. No. 106. pp. 110–127.
- Kofoid, C.A. 1903. The plankton of the Illinois River, 1894–1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part 1. Quantitative investigations and general results. *Bull. Ill. State Lab. Nat. Hist.* **6**: 95–629.
- Lack, T.J. 1971. Quantitative studies on the phytoplankton of the Rivers Thames and Kennet at Reading. *Freshwater Biol.* **1**: 213–224.
- Lange, T.R., and Rada, R.G. 1993. Community dynamics of phytoplankton in a typical navigation pool in the upper Mississippi River. *J. Iowa Acad. Sci.* **100**: 21–27.
- Lowe, R.L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. U.S. E.P.A. Environ. Mon. Ser. No. EPA-670/4-74-005.
- Luttenton, M.L., Vansteenburgh, J.B., and Rada, R.G. 1986. Phycoplankton in selected reaches of the Upper Mississippi River: community composition, architecture, and productivity. *Hydrobiologia*, **136**: 31–46.
- Marshall, H.G. 1988. Seasonal phytoplankton composition and concentration patterns within the Hudson River. Final report. Hudson River Foundation, New York.
- Moss, B. 1988. Ecology of fresh waters. 2nd ed. Blackwell, Oxford.
- Nall, R.W. 1965. Some factors affecting phytoplankton pulses in the Ohio River at Louisville, Kentucky. Ph.D. dissertation, University of Louisville, Louisville, Ky.
- Newbold, J.D., Elwood, J.W., O'Neill, R.V., and VanWinkle, W. 1981. Measuring nutrient spiralling length in streams. *Can. J. Fish. Aquat. Sci.* **38**: 860–863.
- Peterson, C.G., and Stevenson, R.J. 1989. Seasonality in river phytoplankton: multivariate analyses of data from the Ohio River and six Kentucky tributaries. *Hydrobiologia*, **183**: 99–114.
- Raven, J.A. 1987. Physiological consequences of extremely small size for autotrophic organisms in the sea. In *Photosynthetic picoplankton*. Edited by T. Platt and W.K.W. Li. Can. Bull. Fish. Aquat. Sci. No. 214. pp. 1–70.
- Riley, M.B. 1969. Some observations of the phytoplankton of the McAlpine pool of the Ohio River. M.S. dissertation, University of Louisville, Louisville, Ky.
- Sedell, J.R., Richey, J.E., and Swanson, F.J. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? In *Proceedings of the International Large River Symposium (LARS)*. Edited by D.P. Dodge. Can. Spec. Publ. Fish. Aquat. Sci. No. 106. pp. 49–55.
- Sioli, H. 1975. Tropical river: the Amazon. In *River ecology*. Edited by B.A. Whitton. Blackwell, Oxford. pp. 461–488.
- Søballe, D.M., and Kimmel, B.L. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. *Ecology*, **68**: 1943–1954.
- Sokol, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. W.H. Freeman & Co., New York.
- Stockner, J.G. 1988. Phototrophic picoplankton: an overview from marine and freshwater ecosystems. *Limnol. Oceanogr.* **33**: 765–775.
- Swale, E.M.F. 1969. Phytoplankton in two English rivers. *J. Ecol.* **57**: 1–23.
- Thornton, K.W., Kimmel, B.L., and Payne, F.E. (Editors). 1990. Reservoir limnology: ecological perspectives. Wiley, New York.

- Thorp, J.H., and DeLong, M.D. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, **70**: 305–308.
- Thorp, J.H., Black, A.R., Haag, K.H., and Wehr, J.D. 1994. Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. *Can. J. Fish. Aquat. Sci.* **51**: 1634–1643.
- Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Ver. Theor. Angew. Limnol.* **9**: 1–38.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The River Continuum Concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Wetzel, R.G. 1975. Primary production. *In River ecology. Edited by B.A. Whitton.* Blackwell, Oxford. pp. 230–247.
- Whitton, B.A. 1975. Algae. *In River ecology. Edited by B.A. Whitton.* Blackwell, Oxford. pp. 81–105.
- Wilkinson, L. 1992. SYSTAT for Windows: statistics, version 5 edition. SYSTAT, Inc., Evanston, Ill.
- Williams, L.G. 1964. Possible relationships between plankton–diatom species numbers and water quality estimates. *Ecology*, **45**: 809–823.
- Williamson, C.L. 1991. Copepoda. *In Ecology and classification of North American freshwater invertebrates. Edited by J.H. Thorp and A.P. Covitch.* Academic Press, New York. pp. 787–822.
- Zacharias, O. 1898. Das Potamoplankton. *Zool. Anz.* **21**: 41–48.

## Appendix

Phytoplankton species identified from the Ohio River during 1991–1992 (pools and sites are arranged in downstream order from left to right (+, presence at site; cf., approximate identification); see Methods for explanation of site names and locations).

	Markland pool				McAlpine pool				Cannelton pool			
	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW
<b>Cyanobacteria</b>												
<i>Anabaena</i> sp. A (3–4 µm)	+	+	+			+	+		+	+		
<i>Aphanizomenon flos-aquae</i>		+					+					
<i>Aphanizomenon cf. saxicola</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Chroococcus limneticus</i> (cf.)	+	+	+			+				+	+	+
<i>Chroococcus</i> sp. (≈5 µm)		+	+					+	+	+		
<i>Dactylococcopsis raphidioides</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lyngbya</i> sp. A (1.9–2.5 µm)			+				+			+		+
<i>Merismopedia punctata</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Merismopedia tenuissima</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Microcystis</i> cf. <i>aeruginosa</i>	+	+	+	+	+	+	+	+	+	+	+	
<i>Oscillatoria</i> sp. (5 µm)	+			+								
<i>Pseudanabaena catanata</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Rhabdoderma</i> cf. <i>minima</i>	+		+	+				+	+	+		
<i>Synechococcus</i> spp.	+	+	+	+	+	+	+	+	+	+	+	+
Cocoid cells (2–4 µm)	+	+	+	+	+	+	+	+	+	+	+	+
<b>Chlorophyta</b>												
<i>Actinastrum</i> cf. <i>gracilimum</i>	+	+	+	+	+	+	+		+	+	+	
<i>Ankistrodesmus falcatus</i>	+	+	+		+	+	+	+	+	+	+	+
<i>Characium</i> sp.		+	+									
<i>Chlamydomonas</i> sp. A (≈14 µm)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Chlorella</i> sp. (≈13 µm)		+										
<i>Coelastrum microporum</i> (cf.)	+	+		+						+		
<i>Dictyosphaerium ehrenbergianum</i>		+	+								+	
<i>Euastrum denticulatum</i> (cf.)	+	+										+
<i>Eudorina elegans</i>			+	+					+			
<i>Golenkinia radiata</i>	+							+	+	+	+	+
<i>Gonium pectorale</i>	+	+	+	+	+		+	+	+	+	+	+
<i>Haematococcus</i> sp. (7.5 µm)		+								+		
<i>Mougeotia</i> sp.		+										
<i>Oocystis</i> sp.	+	+		+	+	+		+			+	+
<i>Pandorina morum</i>							+			+		
<i>Pediastrum boryanum</i>	+	+									+	+
<i>Pediastrum duplex</i>	+	+		+	+		+			+		
<i>Scenedesmus quadricauda</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Scenedesmus dimorphus</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Selenastrum</i> cf. <i>westii</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sorastrum spinulosum</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Staurastrum gracile</i> (cf.)		+	+	+						+		
<i>Staurastrum not gracile</i>								+				
<b>Euglenophyta</b>												
<i>Euglena</i> cf. <i>tripteris</i>	+	+	+	+	+	+	+	+		+	+	+
<i>Phacus</i> sp. A												+



## Appendix (continued).

	Markland pool				McAlpine pool				Cannelton pool			
	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW
<b>Chrysophyta</b>												
<i>Dinobryon stipitatum</i> (cf.)	+	+	+	+	+	+	+	+		+	+	+
<i>Dinobryon divergens</i>						+						
<i>Mallomonas</i> sp. (small)								+				
<i>Ochromonas</i> sp. (6 × 4 µm)										+	+	
Resting cyst type A						+				+		
Small flagellates (8–15 µm)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Synura</i> sp. (11–15 µm/cell)						+				+		+
Tiny flagellates	+	+	+	+	+	+	+	+	+	+	+	+
<b>Pyrrophyta–Cryptophyta</b>												
<i>Ceratium hirundinella</i>		+	+	+								
<i>Ceratium</i> cysts		+	+	+	+	+		+		+		
<i>Cryptomonas</i> sp. A (25 µm)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Peridinium</i> sp.	+	+	+	+	+	+	+	+	+	+	+	
<b>Bacillariophyta</b>												
<i>Achnanthes lanceolata</i>		+	+	+	+	+	+	+	+	+	+	+
<i>Achnanthes minutissima</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Amphipecta pellucida</i>			+									
<i>Amphora ovalis</i>		+		+			+	+	+	+	+	+
<i>Amphora perpallida</i>		+				+	+				+	
<i>Asterionella formosa</i>	+	+	+	+	+	+	+	+	+		+	+
<i>Caloneis amphisbaena</i>	+	+									+	
<i>Caloneis venticosa</i> (cf.)						+						
<i>Cocconeis pediculus</i>						+	+		+	+		+
<i>Cocconeis placentula</i>	+	+	+			+	+	+	+	+	+	+
<i>Cyclotella comta</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cyclotella meneghiniana</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cyclotella ocellata</i> (cf.)		+							+			+
<i>Cymatopleura solea</i>	+							+				
<i>Cymbella amphicephala</i>	+		+	+			+	+	+			+
<i>Cymbella lunata</i>			+			+		+		+	+	+
<i>Cymbella minuta</i>	+	+	+	+	+	+	+		+	+	+	+
<i>Cymbella prostrata</i> (cf.)	+							+				
<i>Cymbella turgida</i>			+	+							+	
<i>Denticula tenuis</i> (cf.)				+								
<i>Diatoma anceps</i>							+					
<i>Diatoma vulgare</i>	+	+	+	+	+	+	+		+	+	+	+
<i>Diploneis elliptica</i> (cf.)				+						+		
<i>Eunotia exigua</i>	+				+							
<i>Eunotia pectinalis</i>	+								+		+	
<i>Eunotia perpallida</i>	+											+
<i>Fragilaria crotonensis</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Fragilaria virescens</i>	+	+		+	+			+	+	+	+	+
<i>Frustulia rhomboides</i>	+			+	+	+						
<i>Gomphoneis herculeana</i>	+						+		+			
<i>Gomphonema angustatum</i>	+	+	+	+	+	+	+		+	+	+	+
<i>Gomphonema subclavatum</i>	+	+		+	+			+				
<i>Gomphonema truncatum</i>	+		+				+	+			+	+
<i>Gyrosigma scalproides</i>	+	+	+	+		+	+		+	+	+	+
<i>Hantzschia amphioxys</i>						+	+			+	+	
<i>Melosira distans</i> (small var.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Melosira granulata</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Melosira gran.</i> v. <i>angustissima</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Melosira italica</i> (cf.)	+	+							+			+
<i>Melosira jurgensii</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Melosira varians</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Meridion circulare</i>	+	+	+	+	+				+	+	+	+
<i>Navicula confervacea</i>	+	+	+	+						+		+
<i>Navicula decussis</i> (cf.)	+	+	+	+	+	+	+			+	+	+
<i>Navicula exigua</i> (cf.)							+					

## Appendix (concluded).

	Markland pool				McAlpine pool				Cannelton pool			
	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW	ATR	ITR	BTR	LOW
<i>Navicula halophila</i> (cf.)		+		+	+						+	+
<i>Navicula integra</i>				+								
<i>Navicula menisculus</i>		+		+	+			+	+		+	
<i>Navicula muticoides</i>						+			+			
<i>Navicula pupula</i> v. <i>elliptica</i>	+		+	+	+							+
<i>Navicula radiosa</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Navicula reinhardtii</i> (cf.)				+				+	+	+		+
<i>Navicula</i> sp. L			+									+
<i>Navicula</i> sp. Q			+									
<i>Navicula</i> sp. R	+	+	+	+	+	+	+	+	+	+	+	+
<i>Neidium iridis</i> v. <i>amphigomphus</i>	+											
<i>Nitzschia acicularis</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia actinastroides</i> (cf.)	+	+				+				+		
<i>Nitzschia dissipata</i>	+		+			+			+	+		
<i>Nitzschia dubia</i>		+		+								
<i>Nitzschia fonticola</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia frustulum</i> (cf.)	+	+	+	+	+	+	+	+	+	+		+
<i>Nitzschia littoralis</i>	+	+					+		+			+
<i>Nitzschia palea</i> (cf.)	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia sigma</i> (cf.)	+		+	+	+		+		+		+	
<i>Pinnularia borealis</i>	+			+			+			+	+	
<i>Pinnularia braunii</i> (cf.)					+		+					
<i>Pinnularia maior</i>	+											
<i>Pinnularia rupestris</i> (cf.)	+											
<i>Plagiotropis lepidoptera</i>				+								
<i>Rhoicosphenia curvata</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Stauroneis anceps</i>								+				
<i>Stauroneis branderi</i>				+							+	+
<i>Stephanodiscus astraea</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Surirella linearis</i>		+	+	+			+	+	+	+	+	
<i>Surirella ovata</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Synedra delicatissima</i>	+	+	+	+	+	+	+		+	+	+	
<i>Synedra rumpens</i>	+	+	+	+	+			+	+	+	+	+
<i>Synedra ulna</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Synedra ulna</i> v. <i>amphirhynchus</i>	+									+	+	
<i>Synedra ulna</i> v. <i>contracta</i>	+		+	+			+	+				
<i>Tabellaria fenestrata</i>	+		+	+	+							