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Potamoplankton size structure and taxonomic composition: Influence of river size and nutrient concentrations

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Abstract

We measured the size structure and taxonomic composition of phytoplankton in temperate rivers during base flows of summer to investigate the influence of river size, ambient nutrient concentration, and light availability on potamoplankton community structure. Algal biomass was measured in three size classes (2–20, 20–64, and >64 μm) by microscope enumeration of water samples collected in 31 rivers and by chlorophyll *a* in water samples collected in 46 rivers in another year across Ontario and western Quebec. Nanoplankton dominated the potamoplankton biomass across the range of river nutrient concentrations (total phosphorus 5–280 μg P L^{-1}), water residence times (1–39 d), and light regimes (euphotic zone to mixing depth ratio 0.1–33). Both nanoplankton (2–20 μm) and total potamoplankton biomass were significantly correlated with water column total phosphorus concentrations and were not related to water residence time or light availability. On average, diatoms contributed the largest percentage of the total biomass, followed by cryptophytes and an equal percentage of chlorophytes and chrysophytes. The contribution of any one division to total biomass was not significantly correlated with nutrients, water residence time, or light regime. In contrast to temperate lake systems, both the proportion of biomass in larger size classes and the contribution of cyanobacteria did not change significantly as a function of nutrient concentrations. However, community size structure varied in relation to river size: netplankton (>64 μm) contributed slightly more to total biomass at sites with both shorter (<2 d) and longer (>10 d) water residence times. These results point to differences between the phytoplankton of lakes and rivers in response to eutrophication.

Taxonomic descriptions of phytoplankton communities in rivers have been reported for decades (e.g., Talling and Rzóska 1967; Holmes and Whitton 1981). However, the ecological determinants of community structure have been less explored (Reynolds and Descy 1996), despite the importance of river phytoplankton as a source of autochthonous organic carbon (Vannote et al. 1980; Thorp and Delong 1994). Few size structure analyses of river phytoplankton exist (Rojo et al. 1994). Size structure analysis is a simple and informative approach to investigating community structure and function (Peters 1983; Kalff 2002). This is because physiological processes (e.g., growth, nutrient uptake) and ecological processes affecting growth and loss rates (e.g., sedimentation, grazing) are related to cell size (Malone 1980; Reynolds 1984). Phytoplankton size structure is sensitive to ecosystem perturbations such as nutrient enrichment and food web manipulation (Sprules and Munawar 1986; Vanni 1987; Cottingham 1999).

In temperate lakes, phytoplankton size structure varies predictably with lake trophic status. Small algae (<20–35 μm) typically dominate in oligotrophic waters, and the relative contribution of large algae tends to increase with nutrient concentrations (Watson and Kalff 1981; Kalff 2002). The large algae that commonly proliferate in eutrophic lakes are typically filamentous or colonial forms of cyanobacteria (Pick and Lean 1987; Watson et al. 1997; Smith 2003). Shifts in size structure associated with nutrient enrichment could be the result of differences in resource requirements and uptake rates of taxa of various sizes (e.g., Malone 1980), increased grazing pressure, or both (Vanni 1987; Cottingham 1999).

Current theories explaining phytoplankton community structure in lakes might not apply to rivers because of obvious differences in the physical environment. It is generally believed that hydrological and hydrodynamic factors, such as discharge or water residence time, are of greater importance to planktonic development in rivers compared with lakes (Soballe and Kimmel 1987; Reynolds and Descy 1996). In contrast to lake phytoplankton, algae suspended in river waters or potamoplankton are constrained by advective losses associated with downstream flow. Water residence time, which is related to discharge and upstream drainage area (Soballe and Kimmel 1987), could therefore influence the community structure of river phytoplankton. Because the growth rate of algae is inversely related to cell size (Malone

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Table 1. Means, medians, and ranges for physical variables, nutrient concentrations, phytoplankton biomass, and Chl *a* measured in rivers in Ontario and Quebec. Means and medians are based on two sites per river in 1994 and one site per river in 1998.

Variable	1994 (n=31 rivers)			1998 (n=46 rivers)		
	Mean	Median	Range	Mean	Median	Range
Discharge ($m^3 s^{-1}$)	34	20	0.9–250	100	9	0.1–1,197
Drainage area (km^2)	3,953	2,500	548–23,620	8,732	2,395	45–90,900
Depth (m)	3.4	3.1	1.0–15.7	3.5	2.1	0.2–23.0
Water residence time (d)	7	6	3–19	9	7	1–39
Light attenuation (m^{-1})	1.8	1.1	0.7–4.9	1.9	1.45	0.6–6.1
$Z_{eu}:Z_{tot}$	1.4	1.4	0.5–2.8	2.8	1.4	0.1–32.9
TP ($\mu g L^{-1}$)	32	15	7–200	32	18	5–280
TN ($\mu g L^{-1}$)	1,130	470	272–5,330	805	541	203–6,633
TN:TP	40	34	22–146	37	29	3–257
Chl *a* ($\mu g L^{-1}$)	6.8	3.8	2.1–28.0	6.5	2.5	0.8–136.7
Algal biomass ($\mu g L^{-1}$)	1,295	765	182–5,727	—	—	—

1980; Reynolds 1984), small-sized algae with faster growth rates should theoretically dominate in systems with short water residence times, and large cells should contribute a greater proportion to total biomass with increasing residence times. Yang et al. (1997) observed longitudinal changes in phytoplankton size structure in the Rideau River, Ontario, Canada, in which large size classes (>20- and >64-μm fractions) increased downstream relative to smaller size classes. However, in their study, the size structure of the potamoplankton might have reflected longitudinal increases in both water residence time and ambient nutrient concentrations.

In addition to the effects of water residence time, phytoplankton might be more susceptible to light limitation in rivers than in lakes because of higher turbidity from suspended material and the lack of vertical stratification. Cole et al. (1992) found that in deep sections of the Hudson River, the depth of mixing was greater than the depth of the euphotic zone. This resulted in phytoplankton cells remaining below the 1% light level for a period long enough to make net algal growth impossible. Light conditions might also affect the size distribution of river phytoplankton. The low light regime of deep or turbid rivers could contribute to the observed dominance of large diatoms (Reynolds 1994; Rojo et al. 1994).

In this study, we tested the general hypothesis that potamoplankton community structure varies as a function of three main factors in rivers: nutrient concentration, water residence time, and light availability. Other factors, such as grazing by zooplankton or benthic organisms, which might also control community structure, were not considered. On the basis of theories of phytoplankton community structure for temperate lakes, we predicted that the proportion of large-sized algae would increase with higher ambient nutrient concentrations in rivers and that cyanobacteria would contribute to this increase. We anticipated that longer residence times and inadequate light conditions would also promote large-sized algae. These hypotheses were tested with two independent data sets consisting of measurements and samples obtained during different years in rivers located in Ontario and western Quebec, Canada.

For a broad-scale comparison of rivers, we chose to sample a large number of rivers during summer low flows over a short time frame. Although seasonal variability can be high in north temperate rivers (e.g., Basu and Pick 1995, 1997), variability within rivers is generally smaller than the variability that can be observed among rivers (Basu and Pick 1996).

Materials and methods

River sampling and analyses in 1994—Water samples were collected once from 31 rivers across Ontario and western Quebec, Canada, during July 1994 at two sites per river (5–10 km apart and with no tributaries in between). The rivers are the same as those described in Basu and Pick (1996). The rivers encompass a range of sizes (as determined by either catchment area, discharge, or water residence time at the sampling site) and trophic status (as determined by total phosphorus or total nitrogen concentrations; Table 1). The rivers drain watersheds on either Canadian Shield granitic bedrock or sedimentary bedrock of the Great Lakes and St. Lawrence Lowlands, and land use varied from undisturbed forest to agricultural and residential development. The rivers were of medium size, with mean annual discharge ranging from 0.9 to 250 $m^3 s^{-1}$ (Water Survey of Canada 1990). Sampling sites were close to discharge gauging stations of the Water Survey of Canada and were not close to major tributaries, lake outflows, or major point sources such as urban centers. Samples were not collected following rain events.

Estimates of mean daily discharge ($m^3 s^{-1}$) for each river were obtained from government agencies and private industries operating gauging stations close to sampling sites. The theoretical water residence time (WRT) for the section upstream of the gauging station was calculated as a function of drainage area (A_d, km^2) and discharge (Q, $m^3 s^{-1}$) with the equation $WRT = 0.08A_d^{0.6}Q^{-0.1}$ (Soballe and Kimmel 1987, after Leopold et al. 1964). For this data set, WRT is a direct function of river size. The WRT was considered the same at both sites because of their relative proximity. Drainage areas were obtained from the Water Survey of Canada (1990) and were determined for the area upstream of the gauging station. WRT was calculated with the 7-d average

of mean daily discharge prior to and including the sampling date (Pace et al. 1992; Basu and Pick 1996).

At each river site, integrated water samples (surface to within 0.5 m of the river bottom) or surface grab samples (at shallow sites <1 m deep) were collected from one-third, midchannel, and two-thirds distances along a transect perpendicular to the shoreline. Three nutrient samples were collected, one from each of the three distances along the transect. Nutrient samples were analyzed for total phosphorus (TP) and total nitrogen (TN) concentrations following standard methods (Basu and Pick 1995). Five chlorophyll *a* (Chl *a*) samples were collected, one from each of the one-third and two-thirds distances, and three from midchannel. Overall, the cross-channel variability in total Chl *a* averaged about 15%. Water samples were filtered through Whatman GF/F filters, and the Chl *a* was extracted with DMSO and acetone (Burnison 1980). One taxonomic sample of 100–200 ml was collected midchannel at each of the two sites per river and preserved in acidified Lugol's solution. Light attenuation in the water column was calculated by measuring irradiance (μmol photons m^{-2} s^{-1}) midchannel at various depths with a LiCor 185B 4π underwater photometer. The light attenuation coefficient was used to estimate the euphotic zone depth (1% of incident light). The ratio of the euphotic zone (Z_{eu}) to the mixing depth (Z_{tot}, the mean depth of the river at the sampling site) was used as a measure of light availability and is reported as $Z_{eu}:Z_{tot}$ (Table 1).

The two algal samples from each river were enumerated following the Utermöhl method on a Wild M40 inverted microscope at ×125, ×250, and ×500 magnifications (Lund et al. 1958). Taxonomic references used are listed in Yang et al. (1997). Cell dimensions were measured in each sample, and cell volumes were estimated by approximation to geometric shapes of known volume with the counting program of Hamilton (1990). Algal biomass (μg L^{-1}) was determined by converting calculated cell volumes to biomass assuming a specific density of 1 g cm^{-3}. The biomass of each taxon was assigned to one of three size classes on the basis of its average greatest axial linear dimension (Reynolds 1984): nanoplankton (2–20 μm), microplankton (20–64 μm), and netplankton (>64 μm). Picoplankton cells (0.2–2 μm) were not enumerated because they tend to be underestimated by inverted light microscopy compared with more appropriate epifluorescence techniques (Pick and Caron 1987). Autotrophic picoplankton cells are generally not a significant component of river plankton (Reynolds et al. 1994).

The means for physical and chemical variables, as well as for the algal biomass, are based on the average of the two sites sampled per river in 1994 (Table 1).

River sampling and Chl a size fractionation in 1998—Water samples were collected once from 46 rivers from Ontario and western Quebec in June and July 1998 at one site per river. We sampled only one site because, for the 1994 data set, differences in nutrient concentrations and phytoplankton biomass between upstream and downstream sites were small relative to differences among rivers. In 1998, more rivers were sampled over a wider range in discharge (0.1–1,197 m^3 s^{-1}) following the same methods. On average, river flows were lower during July 1998 compared with July 1994. Gauging stations on eight small rivers (discharge < 5 m^3 s^{-1}) were not operational, so an estimate of discharge was obtained on the day of sampling by employing the velocity–area method (Herschy 1985). Discharge was computed by dividing a stream cross-section into a minimum of 12 cells of equivalent width and then measuring the average depth and average current velocity (with a hand-held Gurley current meter) in each cell. WRT was calculated as described for the 1994 sampling year, with the exception of WRT on the eight small rivers, which was limited to using the discharge data from the day of sampling only. Chlorophyll and nutrient concentrations were sampled along a cross-sectional transect as in 1994 except four Chl *a* samples were collected rather than five, one from each of the one-third and two-thirds distances and two from midchannel. Suspended Chl *a* was measured in three size classes by filtration, corresponding to nanoplankton (2–20 μm), microplankton (20–64 μm), and netplankton (>64 μm). Water was filtered in parallel through Poretics polycarbonate membranes (2 and 20 μm) and 64-μm Nitex mesh. Chl *a* in each size class was determined by the difference in Chl *a* on filters of successively larger pore size. Total Chl *a* was measured from water samples filtered through 2-μm membranes. Estimates of Chl *a* for each size class were averaged over the four samples per site. Chlorophyll and nutrient analyses were conducted as described earlier for the 1994 sampling.

Pearson correlation coefficients were calculated to determine the strength of relationships between phytoplankton community characteristics (biomass, size structure, general taxonomic composition) and river conditions (WRT, light availability, water column nutrient concentrations). The data required logarithmic or arcsine transformation to satisfy the assumptions of the parametric test. Probability values for correlation analyses were Bonferroni corrected to limit the experiment-wise error rate. Simple linear regressions were calculated for significant relationships identified in the correlation analysis.

Results

Size distribution of potamoplankton—Small algae <20 μm dominated the phytoplankton biomass of the rivers during summer base flows (Fig. 1). On average, approximately two-thirds of total Chl *a* was in the nanoplankton (2–20 μm) size class. Measurements of volume-converted biomass from the taxonomic enumerations also indicated that the majority of biomass was in the nanoplankton fraction. The largest size fraction, netplankton (>64 μm), contained the least amount of biomass. Relative to volume-converted biomass, Chl *a*–based measurements showed a higher proportion of biomass in the nanoplankton fraction and a lower proportion in the larger fractions of the microplankton (20–64 μm) and netplankton. Although the two data sets are not directly comparable, the use of Chl *a* as a measure of standing crop could introduce some bias because smaller cells tend to have higher chlorophyll per unit biomass (Malone 1980).

Both total Chl *a* and total algal biomass from enumerations were positively correlated with ambient TP or TN concentrations (Table 2). Chl *a* and algal biomass in the nano-

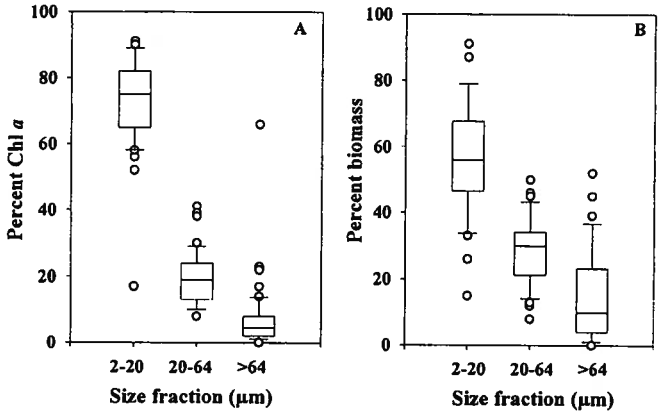

Fig. 1. Proportion of potamoplankton Chl *a* and biomass in three size fractions (2–20, 20–64, and >64 μm). Box plots represent (A) the distribution of percent Chl *a* (n = 46) and (B) percent biomass (n = 31) among rivers for each fraction. The central line of each box is the median, the outer edges of each box are the 25th and 75th percentiles, and the limits of error bars are at the 10th and 90th percentiles.

Table 2. Pearson correlation coefficients relating total biomass and the biomass of size classes to ambient total phosphorus (TP) and total nitrogen (TN) concentrations, water residence time (WRT), and the ratio of the euphotic zone to the mixing depth (Z_{eu} : Z_{tot}). Phytoplankton biomass was measured as volume-converted biomass (n=31 rivers) and Chl *a* (n=46 rivers). All variables were log transformed. Probability values were Bonferonni corrected.

	TP (μg L^{-1})	TN (μg L^{-1})	WRT (d)	Z_{eu} : Z_{tot}
Biomass (μg L^{-1})				
Total	0.756***	0.694***	−0.044	−0.090
2–20 μm	0.793***	0.763***	−0.210	−0.085
20–64 μm	0.595**	0.541*	0.011	−0.170
>64 μm	0.222	0.196	0.443	−0.074
Chl *a* (μg L^{-1})				
Total	0.668***	0.690***	−0.170	0.058
2–20 μm	0.590***	0.617***	−0.140	0.000
20–64 μm	0.695***	0.757***	−0.283	0.155
>64 μm	0.400	0.374	−0.284	0.291

* p<0.05, ** p<0.01, *** p<0.001.

plankton and microplankton (20–64 μm) size classes were also positively correlated with ambient TP and TN concentrations. In contrast, Chl *a* and algal biomass in the largest size class of netplankton (>64 μm) were not related to TP concentration, suggesting that this fraction does not respond to nutrient enrichment (Table 2).

The positive relationship between total phytoplankton biomass and ambient TP concentration was primarily from increasing biomass in the nanoplankton fraction. Figure 2 provides the linear regression model relating nanoplankton and total potamoplankton biomass to TP. Contrary to our initial predictions, large algae did not contribute a greater proportion to community biomass in rivers of higher trophic status (Table 3). The proportion of algal biomass and Chl *a* in the 20–64- and >64-μm size classes generally did not change with trophic status, as measured by total algal biomass or TP and TN concentrations, with the exception of the percentage of >64-μm Chl *a* that was slightly negatively correlated with total biomass (Table 3).

Phytoplankton biomass did not vary in relation to WRT, which for this data set is related to river size. Total Chl *a* and total algal biomass were not significantly correlated with WRT, and likewise, WRT did not influence the biomass in each size class (Table 2). There was no correlation between TP concentration and WRT for the volume-converted biomass data set collected in 1994 (r = −0.22, p = 0.235, n = 31) and a negative correlation for the Chl *a* data set collected in 1998 (r = −0.38, p = 0.010, n = 46).

The size structure of phytoplankton communities was not strongly influenced by WRT, although there was a marginal increase in the proportion of large-sized algae in rivers with long WRT (i.e., larger rivers; Table 3). The proportion of volume-converted biomass of netplankton tended to increase with WRT (r = 0.50, Bonferroni-corrected p = 0.063, n = 31) for midsized rivers (discharge range = 0.9–250 m^3 s^{-1}; Table 3; Fig. 3). Furthermore, a nonlinear pattern in the proportion of >64-μm Chl *a* was observed over the wider range of river sizes sampled in 1998 (Fig. 3). The relative contribution of Chl *a* of netplankton was greatest in the smallest and largest rivers. This trend was assessed graphically with a locally weighted sequential smoothing technique (LOWESS) and then approximated with a quadratic function (Fig. 3). The proportion of netplankton biomass was only slightly higher in large rivers (<25% for volume-converted biomass, <10% for Chl *a*).

The light environment encountered by phytoplankton changed in relation to river size. The ratio of the euphotic depth to the total depth (Z_{eu} : Z_t) decreased in relation to WRT (r = 0.66, p < 0.001, n = 73), and the largest rivers (i.e.,

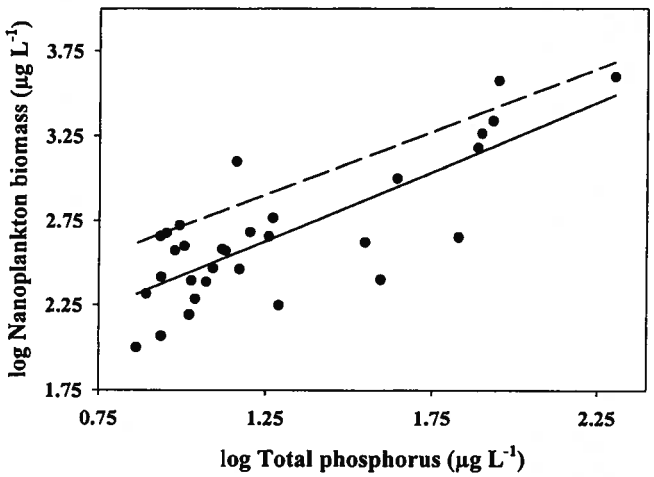

Fig. 2. Relationship between ambient total phosphorus concentrations and volume-converted nanoplankton (2–20-μm size class) biomass in 31 rivers of Ontario and western Quebec (log[nanoplankton biomass] = 0.82 log TP + 1.61; r^2 = 0.63, p < 0.001, $F_{1,29}$ = 49.3). The dotted line corresponds to the regression model relating total potamoplankton biomass to TP concentration (log[potamoplankton biomass] = 0.74 log TP + 1.97; r^2 = 0.57, p < 0.001, $F_{1,29}$ = 38.7).

Table 3. Pearson correlation coefficients relating the proportion of biomass in size classes to total biomass, ambient TP and TN concentrations, WRT, and $Z_{eu}:Z_{tot}$ (as defined in Table 2). Phytoplankton biomass was measured as volume-converted biomass (n=31 rivers) and Chl *a* (n=46 rivers). Percent biomass and percent Chl *a* were arcsine transformed, and all other variables were log transformed. Probability values were Bonferonni-corrected.

	Biomass (μg L^{-1})	TP (μg L^{-1})	TN (μg L^{-1})	WRT (d)	$Z_{eu}:Z_{tot}$
% biomass (μg L^{-1})					
2–20 μm	−0.003	0.240	0.296	−0.414	0.066
20–64 μm	0.122	−0.123	−0.122	0.087	−0.197
>64 μm	0.124	−0.232	−0.280	0.499	−0.020
% Chl *a* (μg L^{-1})					
2–20 μm	0.251	−0.103	−0.108	0.173	−0.273
20–64 μm	−0.073	0.163	0.287	−0.351	0.268
>64 μm	−0.435*	−0.085	−0.167	0.014	0.170

* $p<0.05$.

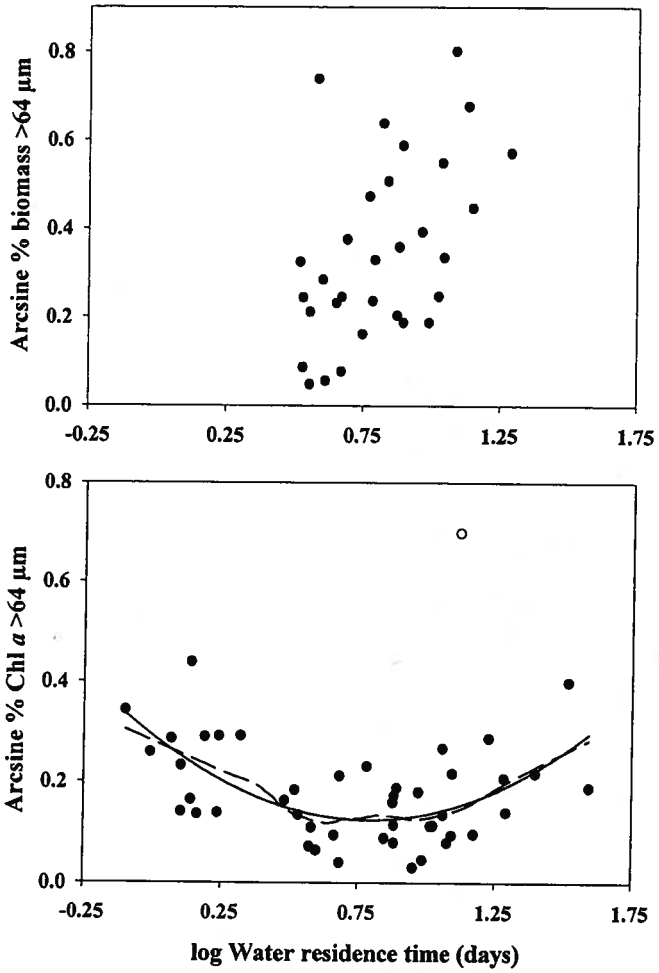

Fig. 3. Relationship between water residence time and the proportion of netplankton biomass (>64 μm) measured as (A) volume-converted biomass and (B) Chl *a*. For the Chl *a* data, a locally weighted sequential smoothing technique (LOWESS) provided a model-free assessment of the nonlinear trend (dotted line), which was subsequently approximated with a quadratic model (solid line: arcsin[%Chl *a* (>64 μm)] = 0.29 − 0.42 log WRT + 0.27(log WRT)^2; $r^2 = 0.37$, $p < 0.001$, $F_{2,42} = 12.4$, $n = 45$ rivers). One outlier (open circle) was removed from the Chl *a* model.

WRT > 10 d) tended to have ratios less than 1. This suggests that phytoplankton in larger systems were exposed to less light than in smaller rivers where, on average, the water column was completely illuminated (i.e., ratios > 1). However, neither phytoplankton biomass nor Chl *a* were correlated with the ratio of euphotic depth to total depth ($p > 0.05$; Table 2). Furthermore, the proportion of algal biomass and Chl *a* in size classes was not correlated with the ratio of euphotic depth to total depth ($p > 0.05$; Table 3).

Taxonomic composition of potamoplankton—A total of 285 algal taxa were identified from the 31 rivers. The majority of taxa identified belonged to the division Chlorophyta (40%), followed by Bacillariophyta (24%) and Chrysophyta (10%). Eighteen taxa were present in more than half of the rivers, and eight taxa in three-quarters of the rivers. In order of percent occurrence, these taxa included *Chromulina* spp., *Chrysochromulina parva, Cryptomonas* cf. *pusilla, Ochromonas* spp., *Cryptomonas erosa, Chlamydomonas* spp., *Plagioselmis nannoplanctica,* and *Cyclotella* cf. *comta.*

In contrast, diatoms (Bacillariophyta) contributed on average the largest percentage of the total biomass (34%), followed by cryptophytes (Crytophyta, 24%), and an equal percentage (15%) of chlorophytes (Chlorophyta) and chrysophytes (Chrysophyta; Fig. 4). Cyanobacteria contributed on average only 3% of the total biomass.

The biomass of individual divisions was examined in relation to the physical and chemical variables. Significant relations were only detected with the nutrient variables (Table 4). In particular, the variation in diatom and chlorophyte biomass was best explained by variation in TP (Fig. 5). Chrysophytes showed weaker but still significant positive relationships with TN and TP. However, both cyanobacteria and cryptophyte biomass varied across the rivers, independent of any of the physical or chemical variables considered (Table 4). Overall, the percent contribution to biomass of any one division was not significantly ($p > 0.05$) correlated with nutrients, WRT, or light regime.

Discussion

The positive relationship between potamoplankton biomass from enumerations and TP (Fig. 2) is consistent with

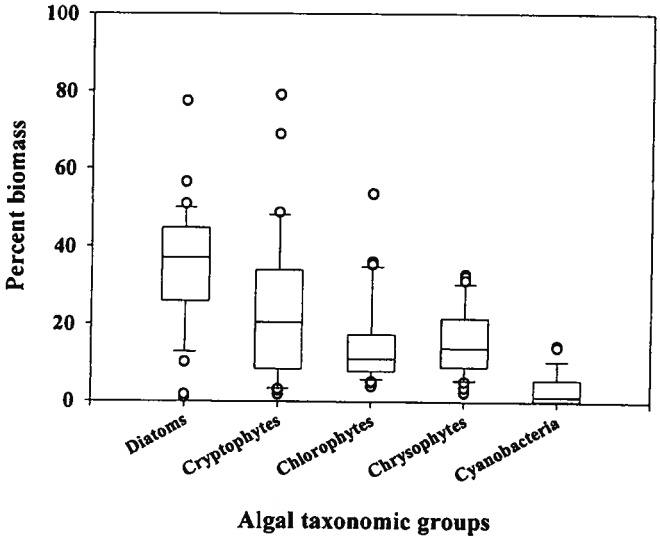

Fig. 4. Box plots of percent biomass in major algal divisions from 31 rivers in Ontario and western Quebec during summer base flows. The central line of each box is the median, the outer edges of each box are the 25th and 75th percentiles, and the limits of error bars are at the 10th and 90th percentiles.

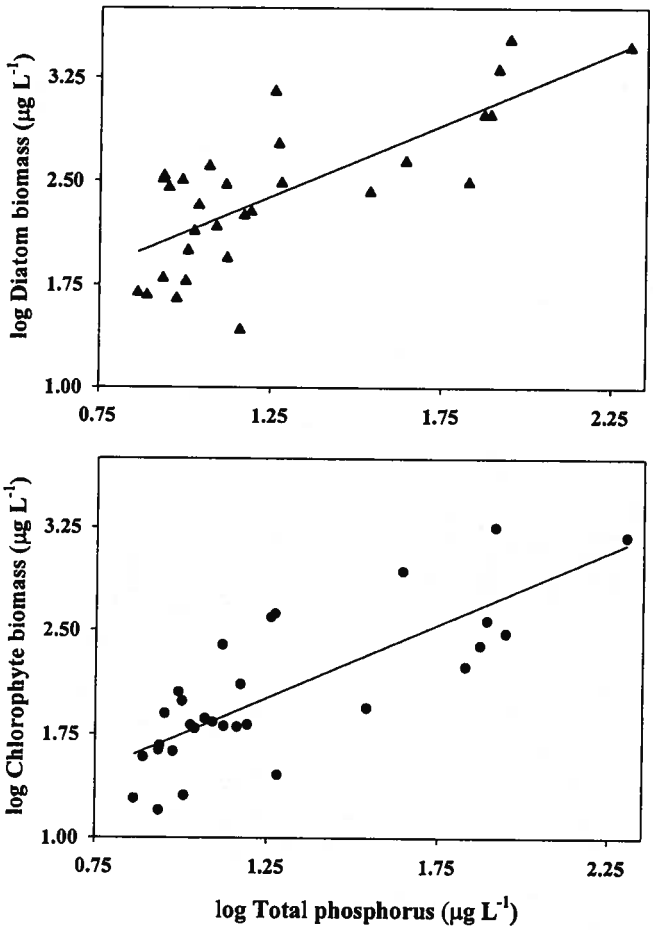

Fig. 5. (A) Relationship between ambient total phosphorus concentrations and diatom biomass (log[diatom biomass] = 1.09 log TP + 1.04; $r^2 = 0.57$, $p < 0.001$, $F_{1,28} = 36.7$). (B) Relationship between ambient total phosphorus concentrations and chlorophyte biomass (log[chlorophyte biomass] = 1.06 log TP + 0.69; $r^2 = 0.62$, $p < 0.001$, $F_{1,28} = 45.8$).

previous studies based on suspended Chl *a* measurements in rivers (Basu and Pick 1996; Van Nieuwenhuyse and Jones 1996; Heiskary and Markus 2001). Water residence time, which in this study is related to river size, had little effect on algal biomass over a wide range of biomass or suspended Chl *a* (Table 2). Van Nieuwenhuyse and Jones (1996) found that suspended Chl *a* in rivers was positively related to both TP concentration and river size (measured as catchment area) in a much larger data set, but catchment area only explained an additional 6% of the variation in the TP–Chl *a* model. Heiskary and Markus (2001) also found a significant relation between TP and suspended Chl *a* in Minnesota rivers, with no statistical effect of WRT, although year-to-year differences were observed in the relationship that they attributed to variations in discharge. In contrast to these broad-scale studies, discharge (and related physical variables) can be the main driving factor of potamoplankton dynamics at the scale of individual rivers and affects seasonal variation within rivers (e.g., Descy 1987).

Much of the variation in potamoplankton biomass along the nutrient gradient of the rivers in this study was due to increases in small nanoplankton algae (2–20 μm). Nanoplankton dominated the potamoplankton biomass during

Table 4. Pearson correlation coefficients relating division biomass to ambient TP and TN concentrations, WRT, and $Z_{eu}:Z_{tot}$ (as defined in Table 2). Phytoplankton biomass in each major division was measured as volume-converted biomass (n=31 rivers, each river the average of two sites). All variables were log transformed. Probability values were Bonferonni-corrected.

	Biomass (μg L⁻¹)	TP (μg L⁻¹)	TN (μg L⁻¹)	WRT (d)	$Z_{eu}:Z_{tot}$
Biomass (μg L⁻¹)					
Cyanobacteria	0.025	−0.206	−0.348	0.330	−0.086
Bacillariophyta	0.784***	0.727***	0.670**	−0.012	−0.202
Chlorophyta	0.827***	0.761***	0.775***	0.020	−0.162
Cryptophyta	0.426	0.131	−0.079	0.078	0.041
Chrysophyta	0.741***	0.627*	0.589*	−0.052	−0.476

* $p<0.05$, ** $p<0.01$, *** $p<0.001$.

base flows of both summers over a range of nutrient concentrations (Figs. 1, 2). In one of the few studies of size structure in rivers, Gosselain et al. (1998) found that algae <20 μm dominated community biomass throughout much of the summer in the eutrophic River Meuse, Belgium. This was also observed for the much larger and oligotrophic to mesotrophic St. Lawrence River, Canada (Hudon et al. 1996). These observations are in contrast to our current understanding of phytoplankton community structure across lakes: generally, large algae increase in importance with lake nutrient concentrations (Watson and Kalff 1981; Kalff 2002), and as a result, the size structure of phytoplankton communities changes in a predictable fashion. In this study, nanoplankton typically dominated in rivers that differed widely in depth, light availability, and WRT, as well as in nutrient concentrations. Overall, size structure of the potamoplankton along the nutrient gradient considered changed little (Table 3).

The difference between lakes and rivers in the size distribution of phytoplankton is likely related to the physical environment. Short WRTs, low light conditions, and shallow depths in rivers would tend to favor smaller cells with faster growth rates, greater photosynthetic efficiency, and lower sedimentation rates (Reynolds 1994; Reynolds and Descy 1996). The particular physical conditions encountered in rivers could prevent populations of large-sized algae (that grow too slowly to counter advective losses) from attaining dominance. Differences in food web structure between lakes and rivers might be an additional underlying mechanism. In eutrophic lakes, higher proportions of netplankton have been attributed to increased zooplankton grazing on small edible algae, which are largely within the nanoplankton (Vanni 1987; Cottingham 1999; Kalff 2002). Thus, the dominance of nanoplankton in eutrophic rivers and the lack of dominance by large algae could be due to comparatively low grazing pressure. Downstream flow limits zooplankton growth, and temperate rivers typically have lower zooplankton biomass than lakes (Pace et al. 1992; Basu and Pick 1996). Zooplankton grazing can occasionally have a significant effect on phytoplankton in large rivers, but only for short periods within the growing season (Garnier et al. 1995; Gosselain et al. 1998).

Although nanoplankton largely dominated the biomass of this set of temperate rivers, the relative biomass of large-sized algae was slightly greater in both the very smallest and the largest rivers (Fig. 3). The nonlinear relationship between the proportion of Chl *a* in netplankton and WRT might reflect differences in the origin of the suspended algae. The smallest rivers (drainage area ≤ 203 km², WRT ≤ 2 d) had higher proportions of netplankton, primarily because of attached diatoms (*Cocconeis placentula, Navicula cryptocephala* sensu lato, and *Nitzschia* spp.), which would have dislodged from the riverbed. Suspended algae in low-order rivers are expected to originate primarily from the riverbed, whereas mid- to high-order systems support reproducing planktonic populations or true potamoplankton (Reynolds and Descy 1996). The increase in percent netplankton in medium to large rivers (WRT > 10 d) was largely due to greater biomass of colonial phytoplankton, primarily diatoms and chrysophytes (*Aulacoseira granulata, Aulacoseira islandica, Aulacoseira italica/subarctica, Dinobryon* spp., *Tabellaria fenestrata*). The filamentous centric diatom *Aulacoseira* was responsible for much of the observed netplankton increase in over half of the rivers. Colonial algae tend to have slower growth rates (Reynolds 1984), which might prevent these taxa from developing in rivers with short residence times. In previous studies of individual rivers, the observation that chlorococcalean green algae in upper reaches tend to be replaced by diatoms downstream has been attributed to changes in water depth: large, heavily silicified diatoms might overcome sedimentation losses in the turbulent deeper waters of large rivers and might also tolerate better, lower, light conditions (Reynolds and Descy 1996). Depth and WRT tend to be correlated among rivers, so their individual effect is difficult to separate.

In terms of the broad taxonomic composition of the potamoplankton, diatoms dominated the biomass of the study rivers. This is not a novel observation: Rojo et al. (1994) came to the same conclusion on examining the algal taxonomic literature from >60 rivers. Diatoms typically represent the majority of community biomass in temperate rivers, and blooming taxa are often small centric diatoms such as *Cyclotella* and *Stephanodiscus* (Gosselain et al. 1994; Rojo et al. 1994; Yang et al. 1997), that would be part of the nanoplankton fraction. Total phosphorus explained a significant amount of the variation in planktonic diatom biomass as well as that of chlorophyte biomass among the present rivers (Fig. 5). On the basis of seasonal studies and models for individual rivers, silica concentrations can be important in determining the relative abundance of diatoms and chlorophytes (Garnier et al. 1995). The role of silica in explaining the remaining between-river variation requires further study.

Along with diatoms, cryptomonads, which are generally small taxa (8–24 μm) and within the nanoplankton size range, also represented a significant fraction of the potamoplankton biomass in this set of rivers. However, their contribution was the most variable among the rivers, ranging from 1% to as high as 90%, and could not be related to any of the physical or chemical variables considered. Cryptomonads dominate the St. Lawrence River potamoplankton (Hudon et al. 1996), but seem to be less important in more eutrophic European rivers (e.g., Gosselain et al. 1994).

In this study, cyanobacteria contributed very little to the total potamoplankton biomass across the nutrient gradient. There was no significant correlation between cyanobacteria biomass (or percent contribution to biomass) and TP levels. In fact, cyanobacterial biomass was more closely related to WRT, although the relationship was not statistically significant. In temperate lakes, a similar gradient in TP would typically lead to significant increases in both biomass and percent contribution of cyanobacteria (Pick and Lean 1987; Watson et al. 1997; Downing et al. 2001). Previous researchers have also noted the generally low levels of cyanobacteria in temperate rivers (Rojo et al. 1994; Wehr and Descy 1998). In contrast, subtropical rivers in Australia can experience significant cyanobacterial blooms, particularly during low flows when the waters are almost stagnant (e.g., Sherman et al. 1998). More recently, Heiskary and Markus (2001) reported large biomass levels of cyanobacteria in Minnesota rivers, and using this data set, Smith (2003) provided a mod-

el showing increasing dominance of cyanobacteria as a function of TP. These Minnesota rivers had much higher levels of TP (32–350 μg P L^{-1}) than those of this study, which are mainly oligotrophic to mesotrophic following the temperate stream classification system of Dodds et al. (1998). Nevertheless, it would appear that increases in cyanobacteria in flowing waters occur at much higher nutrient levels than those triggering dominance in lakes. For cyanobacteria, which tend to be slow growing, WRT likely plays a role in modulating their response to eutrophication in rivers.

This study examined potamoplankton communities in relation to large-scale characteristics of rivers, but community structure is also determined by local physical conditions at a river site (e.g., Shermann et al. 1998). Even in rivers where potamoplankton predominates, a significant portion of the community can be benthic or epiphytic taxa (e.g., up to 30% of diatom biomass in the Rideau River; Yang et al. 1997). Sedimentation of main channel populations and local inputs of algae from dead zones, weed-beds, and benthos could represent important processes contributing to community structure (Reynolds 1994). These mechanisms and sources would contribute to the variation in taxonomic composition between rivers.

This study was limited to summer base flow conditions, and temporal variation of suspended algae, which can be significant in rivers, was not considered. Detailed seasonal studies of size structure over a range of rivers are required to determine whether the pattern of nanoplankton dominance holds on a yearly basis. Furthermore, this study was biased toward oligomesotrophic rivers, and a closer examination of more eutrophic rivers is warranted.

The potamoplankton of these temperate rivers was dominated during summer base flows by small algal taxa <20 μm. Algal biomass increased in relation to ambient TP concentration, but large algae did not contribute a greater proportion to total biomass in the more eutrophic rivers. Compared with temperate lakes, cyanobacterial biomass did not increase as a function of river nutrient concentrations. Overall, community structure based on broad taxonomic divisions or size distribution did not vary significantly with nutrient concentrations, but small shifts occurred with respect to WRT. The importance of nanoplankton over a wide range of river size and nutrient concentrations points to the advantages of small cell size in fluvial waters, regardless of taxonomic affiliation.

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