

## Downstream variations of phytoplankton in the St. Lawrence River (Québec, Canada)

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### Abstract

Longitudinal variations of phytoplankton biomass and composition were assessed in a 250 km-long section of the St. Lawrence River, which alternately runs through narrow (< 2 km) river cross sections and wide (up to 10 km) fluvial lakes. In the main river stem, concentrations of suspended matter and total phosphorus increased with distance downstream, whereas light penetration decreased. Seasonal changes in plankton composition and biomass were more important than those resulting from differences in water mass (tributary) of origin. Sampling at three cross river sections and in two fluvial lakes showed a progressive downstream decrease in phytoplankton biomass and changes in size structure and taxonomic composition. River plankton was primarily composed of small (< 10  $\mu\text{m}$  equivalent spherical diameter), truly planktonic cells belonging to Cryptophyceae and diatoms, with Chlorophyceae in summer. Plankton sampled in summer among rooted macrophytes in fluvial lakes exhibited a higher biomass of resuspended periphytic algae than in the main river stem, which contributed slightly to downstream phytoplankton biomass.

Successive river cross sections always shared about 50% of their taxa, indicating a rapid downstream transport of algae within the main water mass. However, the proportion of species common to all cross sections was highest during the spring freshet, and lowest during summer low discharge, likely resulting from the development of a distinct flora in fluvial lakes during summer. Conversely, about 30% of the identified taxa were exclusive to a cross section and were replaced by others occurring downstream. Overall, phytoplankton composition along the St. Lawrence River is primarily controlled by advective forces, which result in a homogeneous flora in the main river stem, with a local contribution of resuspended periphyton from fluvial lakes.

### Introduction

Advection of lake phytoplankton into a large river subjects it to major changes in growth conditions: turbulence due to advection homogenizes the water column, exposing algae to periods of high subsurface light intensity down to (sometimes) complete darkness in the deepest river segments (Reynolds, 1994). In contrast with the conditions prevailing in the main river channel, shallow, slow-flowing nearshore and meandering areas favor retention of locally produced plankton

(Lewis, 1988; Moss & Ball, 1989), which is exposed to overall higher light intensities. Submerged macrophytes often growing in those areas support abundant periphytic algae, which potentially contribute to river plankton biomass when resuspended into the water column (Whitton, 1975; Wetzel, 1983). Depending on their particular characteristics, incoming tributaries provide an additional input (or dilution) of dissolved and particulate (living and non living) material (Hynes, 1970), thus changing phytoplankton diversity and biomass. Domestic and industrial effluents discharged into

the river represent a particular class of tributaries (del Giorgio et al., 1991; Stevenson & White, 1995), since they potentially contribute toxic contaminants and/or nutrient enrichment (Allan, 1986). Because river phytoplankton diversity and biomass cumulate elements from advected as well as locally produced flora, composition at a given point is expected to diverge from the seeding lake flora with distance downstream.

The phytoplankton of the Laurentian Great Lakes, which discharge into the St. Lawrence River, has been extensively studied (Prescott, 1951; see the reviews by Vollenweider et al., 1974; Munawar & Munawar, 1986). Although studies carried out in the St. Lawrence River are less comprehensive, they can supply data to reconstruct the common features of phytoplankton assemblages over the 600 km-long fluvial portion, between Lake Ontario and the saltwater transition zone, near Quebec. Species composition in the first 100 km closely resemble that of Lake Ontario (Mills et al., 1981), although chlorophyll *a* (Glooschenko et al., 1972; Bertrand & Vincent, 1994), biomass and productivity (Mills & Forney, 1982) decrease. Species composition is less variable at stations located in the main river channel as compared to those located nearshore (Mills et al., 1981).

Surveys conducted over distances of 200–500 km within the main St. Lawrence river channel highlight the spatial continuity of species composition, diversity index ( $H'$ ), total cell volume (Provencher, 1976) and chlorophyll *a* (Painchaud et al., 1993; Bertrand & Vincent, 1994) in the rapidly circulating, central water mass of the river. In contrast, nearshore stations located over the same distance exhibited a high level of spatial variability, associated to areas of slow current, sheltered bays and downstream of specific tributaries (Provencher, 1977; Contant & Lacoursière, 1978; Roche & Ass., 1982). Incoming tributaries support a wide range of chlorophyll *a* concentration (1.6–58.6  $\mu\text{g l}^{-1}$ ), cell biomass (0.7–5.9  $\text{mg l}^{-1}$ ), diversity and species composition (Provencher, 1977).

Although the above studies provide regional descriptions of an apparently complex situation, they bring little evidence for the underlying mechanisms controlling spatio-temporal variability of river phytoplankton. However, when taken together, these studies all point to the effect of hydrodynamic conditions (i.e. discharge and residence time) on river phytoplankton distribution and abundance (Moss & Balls, 1989). Evidence from other river systems further reveals a dilution effect of high water discharge on phytoplankton

biomass (Lack, 1971; Moore, 1976; Baker & Baker, 1979).

Phytoplankton from the main river channel would remain homogeneous owing to its rapid flow rate through the fluvial system. This assemblage would differ from phytoplankton growing in adjacent, yet hydrodynamically isolated, slow flowing fluvial lakes. We hypothesize that high discharge through the main river channel would maintain a strong spatial continuity within the St. Lawrence River, whereas riparian areas, human impacts and tributaries would increase the heterogeneity of river flora. This study characterizes the downstream changes in phytoplankton in the St. Lawrence, and contrasts phytoplankton rapidly advected in the main river channel with that growing in the extensive riparian areas provided by fluvial lakes. Since residence time is a function of seasonal variations of discharge and of riparian vegetation growth, we carried out sampling over spring, summer and fall.

### Study area and sampling design

The study was carried out in a 250 km-long section of the St. Lawrence River, which alternately runs through narrow (< 2 km) cross sections and wide (up to 10 km) fluvial lakes (Figure 1). River cross sections are deep (10–15 m) and fast flowing (1  $\text{m s}^{-1}$ ) river segments, whereas fluvial lakes are shallow (< 3 m), slow flowing (< 0.3  $\text{m s}^{-1}$ ) widenings of the river. Fluvial lakes are extensively colonized by submerged macrophyte beds (*Myriophyllum* spp., *Elodea canadensis* Michx., *Vallisneria americana* Michx., *Potamogeton* spp.). Sampling was carried out at Cornwall (160 km downstream of Lake Ontario), Lake Saint-Louis (250 km), Les Grèves (335 km), Lake Saint-Pierre (380 km) and Port Saint-François (410 km) (Figure 1).

The St. Lawrence River originates from the Laurentian Great Lakes (mean annual discharge: 7,300  $\text{m}^3 \text{s}^{-1}$ ); waters from this basin are very clear ("green") and are characterized by their high conductivity (> 250  $\mu\text{S cm}^{-1}$ ) and low concentrations of total organic carbon (< 3.6  $\text{mg l}^{-1}$ ) (Désilets & Langlois, 1989; Rondeau, 1993). The confluence of des Outaouais River (mean annual discharge: 1980  $\text{m}^3 \text{s}^{-1}$ ) in Lake Saint-Louis introduces a distinct fluvial water mass, which flows along the north shore of the St. Lawrence. Tributaries discharging on the north shore of the St. Lawrence drain the Canadian Precambrian Shield; they have a characteristic brown colour, low conductivity (< 160

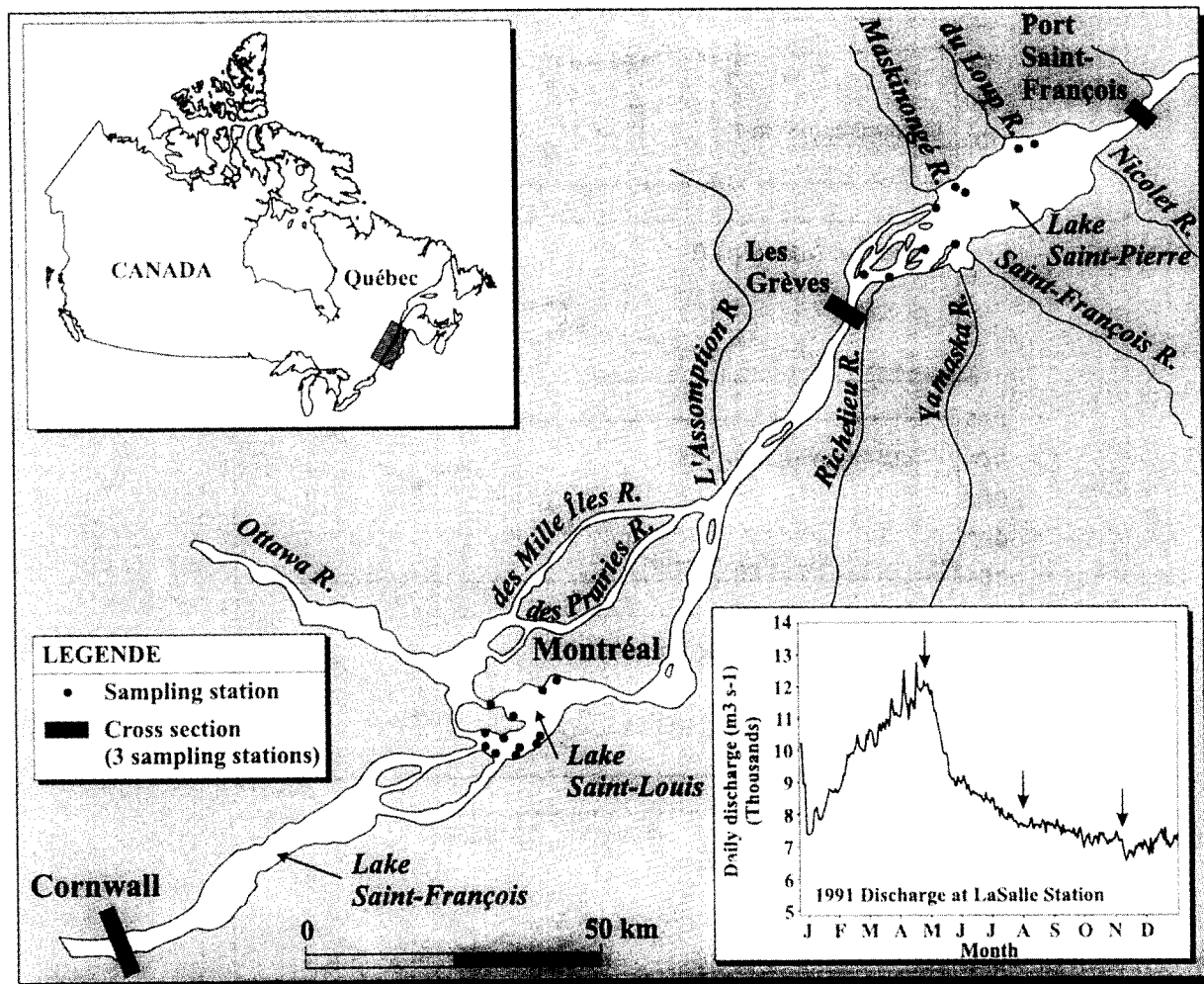


Figure 1. Location of the study area (upper left inset) and of sampling sites in the St. Lawrence River. Example of the 1991 yearly discharge ( $\text{m}^3 \text{s}^{-1}$ ) of the St. Lawrence at LaSalle, downstream of Lake Saint-Louis; vertical arrows indicate sampling dates (lower right inset, Environment Canada 1994).

$\mu\text{S cm}^{-1}$ ) and high total organic carbon concentrations ( $> 6 \text{ mg l}^{-1}$ ) (Cluis et al., 1990).

Median values obtained from multiple-years surveys (Sylvestre et al., 1987; Rondeau, 1993) plainly demonstrate the downstream gradients in physical and chemical conditions in the main St. Lawrence River channel (Figure 2). Median conductivity values (Figure 2a) show the progressive dilution of the heavily mineralized Great Lakes waters by the soft waters flowing from des Outaouais River (dotted horizontal line) and other tributaries draining the Precambrian Shield. Suspended solids (Figure 2b), total organic carbon (Figure 2c) and total phosphorus (Figure 2d) concentrations increase whereas light availability ( $Z_e/Z_t$ , Figure 2e) decreases downstream. These changes can be attribut-

ed to the inflow of a number of tributaries draining agricultural areas and to domestic effluents from the greater Montreal urban area (3 millions inhabitants), 290 km downstream of Lake Ontario.

In order to collect representative phytoplankton samples, 3 transversal stations (north, center and south) were sampled at each cross section, and whereas 10–12 stations were sampled in each fluvial lake. Lake stations were widely distributed over areas colonized by submerged macrophytes, to contrast their flora with plankton from rapidly flowing cross sections. Sampling was carried out according to a Lagrangian scheme: sampling started at Cornwall and proceeded to Les Grèves and Port Saint-François on subsequent days. To account for seasonal variability, this exercise

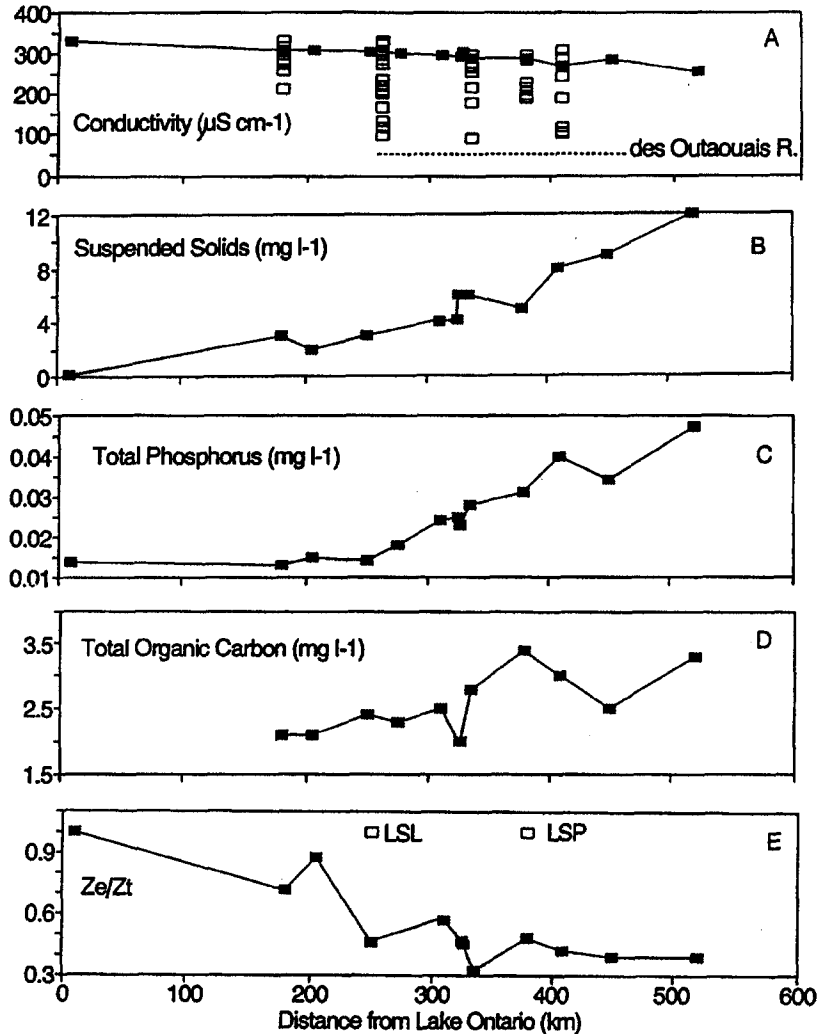


Figure 2. Median values of multi-year surveys (dark squares) of conductivity, suspended solids, nutrients, dissolved organic carbon and light penetration in the main river channel of the St. Lawrence River between the outlet of Lake Ontario (Sylvestre et al. 1987) and the saltwater transition zone (Rondeau 1993). Top panel: Conductivity values measured at each sampling station (open squares) are compared with median values reported for the channel (dark squares) and des Outaouais River (horizontal dotted line). Bottom panel: Light penetration values for the main river channel (full squares) are compared to values for fluvial lakes (open squares).

was carried out in May 1991, August 1991, November 1991 and April 1992. These sampling periods reflected seasonal variations in discharge, which corresponded to cumulative discharge values of 11900, 8100, 8200 and 10500  $\text{m}^3 \text{s}^{-1}$ , respectively, downstream of the confluence of des Outaouais with the St. Lawrence River (Figure 1, Environment Canada, 1994).

In fluvial lakes, the constraints imposed by growth and decay of submerged macrophytes restricted the sampling period to mid- to late summer. Therefore, water quality and phytoplankton were sampled in

August 1991 in Lake Saint-Louis (12 stations), and in August 1990 in Lake Saint-Pierre (10 stations).

## Material and methods

### *Water physical and chemical characteristics*

Downstream gradients of physical and chemical water characteristics were obtained from literature data (Sylvestre et al., 1987; Rondeau, 1993) and from mea-

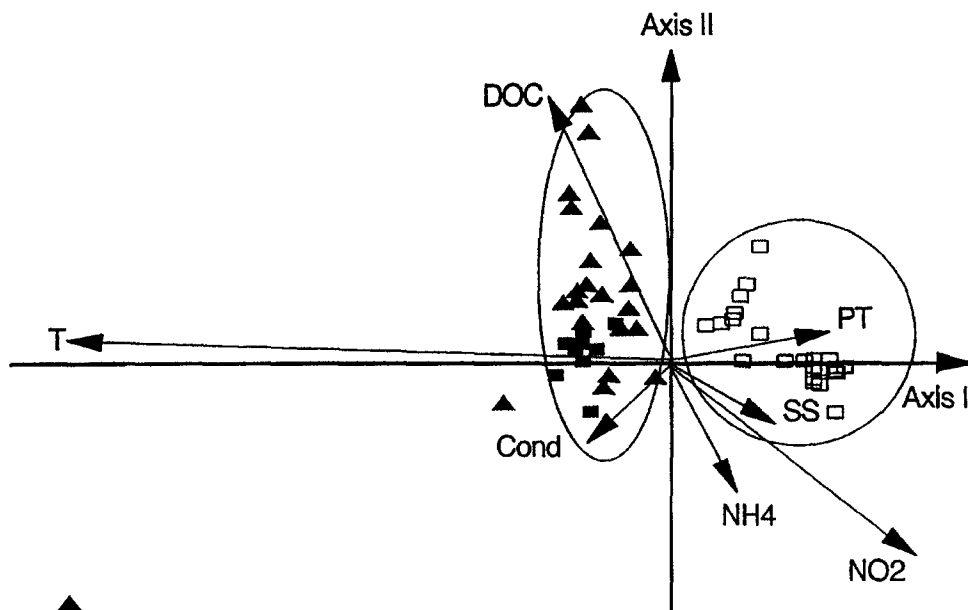


Figure 3. Results of detrended canonical correspondence analysis of the abundance of 311 species with six physical and chemical variables for all sampling points ( $n = 54$ ) in the St. Lawrence River. Location of sampling points was based on their species composition and abundance, superimposed to explanatory physical and chemical variables (arrows). Summer (full symbols), spring and fall (open symbols) are identified for river channel (squares) and fluvial lakes (triangles). Groups of samples corresponding to homogeneous species composition and abundance, characteristic of summer (enclosed in an oval) and spring and fall seasons (circled). Outliers in lower left corner correspond to two August samples from Lake Saint-Pierre, in which unusually large amounts of *Cladophora* and *Hydrodictyon* were found. These samples were excluded from Figure 4.

measurements at each station. Water temperature ( $^{\circ}\text{C}$ ), conductivity ( $\mu\text{S cm}^{-1}$ ) and dissolved oxygen ( $\text{mg l}^{-1}$ ) were measured 0.5 m below the surface with a Hydro-lab (<sup>TM</sup>) multiprobe. Water samples were pumped (March Meg, Model LC-3CP-MD) from the same depth and partitioned for various chemical and biological analyses. Suspended solids were filtered (Whatman GF/C) from a 0.5 l water sample (Environment Canada, 1993). Dissolved organic carbon (DOC) was measured after filtration ( $0.45 \mu\text{m}$  Nuclepore), using an infra-red carbon analyzer (Ionics 555, TC-TOC Analyzer). Nutrients (total P,  $\text{NH}_4$  and  $\text{NO}_2\text{-NO}_3$ ) concentrations ( $\text{mg l}^{-1}$ ) were determined colorimetrically (Technicon (<sup>TM</sup>) auto-analyzer) (Environment Canada, 1993). Light extinction coefficient ( $K$ ,  $\text{m}^{-1}$ ) values corresponding to given suspended solids concentrations (SS,  $\text{mg l}^{-1}$ ) were calculated from independent measurements in the St. Lawrence River (Hudon, unpubl. data), using the equation:

$$K = 0.436 + 0.064 \text{ SS} \quad r^2 = 0.37 \quad n = 68 \quad (1)$$

This value was used to estimate the depth of the euphotic zone (i.e. 1% of incident light =  $Z_e$ ) and

provided information on the light conditions in relation with total depth ( $Z_t$ ) obtained from navigation charts (Canadian Hydrographic Service, 1993).

#### *Phytoplankton composition and abundance*

Taxonomical composition, species richness, and numerical dominance were used as markers for water mass and to identify contributions from tributaries and fluvial lakes. Phytoplankton cells present in a 50-ml sample preserved in acid Lugol were identified and enumerated on about 30 random microscopic fields at  $800\times$  and two cross-shaped transects at  $200\times$ , using the Utermohl method (Lund et al., 1958). Diatom identification was verified on peroxyde-cleaned frustules permanently mounted in Hyrax (<sup>TM</sup>). Species richness ( $N$  = total number of species) and Shannon-Weaver (Shannon & Weaver, 1949) diversity ( $H'$ ,  $\text{bits ind}^{-1}$ ) were calculated for each sample.

Plankton abundance measurements included pigment and cell concentrations and total cellular biomass. Chlorophyll *a* and phaeopigments were extracted with 90% acetone and measured spectrophotometri-

cally before and after acidification, following the procedures of Lorenzen (1967). Fifteen specimens of each taxon were measured microscopically to assess mean cell volume, equivalent spherical diameter (ESD) and cell counts were converted into biomass values (Wetzel & Likens, 1991). Each species was allocated to a functional group (planktonic or periphytic), using monographs by Bourrelly (1972, 1981, 1985, 1988), Findlay and Kling (1979), Germain (1981), Irénée-Marie (1938), and Prescott (1951). Species reported to occur indifferently either in the plankton or the periphyton were treated as a separate group. Spatial changes in phytoplankton occurring during its downstream advection could then be characterized by total biomass as well as by changes in the representation of taxonomical groups, functional groups and size classes.

### Statistical analyses

The relationships between phytoplankton community composition and environmental factors were summarized by canonical correspondence analysis (CCA, Ter Braak, 1986). This analysis relates samples to positions along ordination axes according to the similarity in species composition among samples. This part of the procedure allows to identify groups of samples bearing similar composition (311 species  $\times$  54 samples). Environmental factors (temperature, conductivity, suspended solids, dissolved organic carbon, total phosphorus, nitrates-nitrites and ammonium) are then related to ordination axes using superimposed vectors drawn from corresponding measurements of physical and chemical water characteristics. Correlation coefficients (Pearson  $r$ ) can then be calculated between the axes of the CCA, phytoplankton species and physical-chemical variables. This analysis allows to identify groups of planktonic species characteristic of given environmental conditions and thus, to assess whether species composition varies more markedly with season or with water mass. Sites were compared using non parametric statistics, while taking into account the seasonal distribution of samples. All comparisons of means were made using non parametric ANOVA (SAS, PROC NPAR1WAY); groups characterized by significantly different mean values were identified using Wilcoxon ranked scores. First, all August samples ( $n = 31$ ) were used for an overall analysis of downstream gradients, while taking into account the alternance of cross sections and fluvial lakes. Second, downstream gradients from all cross section data were identified.

Number of samples for this analysis equalled 32 instead of 36 samples (3 sites  $\times$  3 stations  $\times$  4 periods) due to incomplete data in November (only one station sampled in Les Grèves and Port Saint-François).

## Results

Three hundred and eleven taxa belonging to 7 classes were enumerated in the samples. Chlorophyceae were most diverse taxonomic group with 129 taxa, followed by diatoms (i.e. Bacillariophyceae, 84 taxa), Cyanobacteria (42 taxa) and Chrysophyceae (29 taxa). A detailed list of taxa, mean individual cell volume and functional groups can be found in Paquet et al. (1995).

### Seasonal variation

Most variation in species composition was associated with seasonal changes, as shown by the distribution of points along the first (horizontal) axis of the CCA (Figure 3). This axis (35% of the total variance) was negatively correlated with water temperature ( $r = -0.98$ ,  $p < 0.001$ ), and positively correlated with nitrates ( $r = 0.83$ ,  $p < 0.001$ ), suspended solids ( $r = 0.33$ ,  $p < 0.05$ ) and total phosphorus ( $r = 0.33$ ,  $p < 0.05$ ). Regardless of collection site, points located on the left side of the first axis (full symbols enclosed in the oval) corresponded to samples taken in summer (August), whereas samples from spring (April–May) and fall (November) were located on the right side (circled open symbols, Figure 3). Summer plankton biomass was generally low ( $0.80 \text{ mg l}^{-1}$ ) and comprised a high proportion of Chlorophyceae (54%) and Cryptophyceae (29%). *Eudorina elegans* Ehr. (found in 51% of the 31 summer samples), *Sphaerocystis Schroeteri* Chodat (56%) and *Spirogyra* sp. Link (15%) were the most common species of green algae, accompanied by *Chroomonas acuta* Uter. (76%), *Rhodomonas minuta* Sk. (90%), *Cocconeis placentula* Ehr. (90%), *Aulacoseira granulata* (Ehr.) Simonsen (22%). Two samples from Lake Saint-Pierre were identified as outliers (Figure 3, full triangles in lower left quadrant) in the summer group, owing to their high biomass of filamentous green algae (*Cladophora* Kuetz. and *Spirogyra* sp.).

Total plankton biomass in spring ( $1.66 \text{ mg l}^{-1}$ ) and fall ( $1.04 \text{ mg l}^{-1}$ ) was somewhat higher than in summer, and was dominated by diatoms (57 and 29% of total biomass, respectively) and Cryptophyceae (15 and 32%). Colonial diatoms such as *Asterionella formosa* Hassall (found in 78% of the 23 samples), *Aula-*

*coseira islandica* (O. Muller) Simonsen (morphotype *helvetica*) (74%), *Tabellaria flocculosa* var. *linearis* Koppen (70%), *Fragilaria crotonensis* Kitton (70%), *Stephanodiscus binderanus* (Kuetz.) Kr. (65%), *S. parvus* Stoermer & Hakansson (57%), *S. niagare* Ehr. (30%) were most common, together with *Gymnodinium fuscum* (Ehr.) Stein (52%), *Cryptomonas erosa* Ehr. (76%) and *Dinobryon sociale* var. *americanum* Back. (70%).

The occurrence of such marked seasonal changes in plankton abundance and composition prompted the use of seasonally-balanced designs or single season data for spatial comparisons.

#### Water mass of origin

The water mass from which each sample originated was revealed by its position along the second axis (vertical) of the CCA (Figure 3). This axis (18% of the total variance) was positively correlated with dissolved organic carbon ( $r = 0.40$ ,  $p < 0.05$ ), and negatively correlated with nitrates ( $r = -0.41$ ,  $p < 0.05$ ) concentrations. In contrast with the ordination of points along the first axis, which formed two distinct seasonal groups, points were uniformly distributed along the second axis, indicating that samples were drawn from water mixtures ranging from predominantly brown (upper half of Figure 3) to green (lower half) waters. This observation is supported by conductivity measurements at each sampling site, which lay between low values for des Outaouais River and the high values in the main navigation channel (Figure 2a). The same pattern was visible for all sampling sites, with the exception of Cornwall, which was located upstream of the confluence of des Outaouais River and thus comprised green waters only (Figure 2a).

In addition, bi-variate correlations between DOC concentration and total cell biomass ( $r = 0.074$ , n.s.) or with chlorophyll *a* concentration ( $r = 0.16$ , n.s.) were not significant, further indicating that the origin of water mass had no clear bearing on total phytoplankton biomass. The occurrence of variably mixed waters and the lack of relation between phytoplankton biomass and water mass thus suggested that an average value derived from all samples collected at each site would be representative of downstream changes of phytoplankton composition.

#### Downriver changes across fluvial lakes and cross sections in August

A general decrease in total phytoplankton biomass was observed between Cornwall and Port Saint-François (Table 1). Lake Saint-Pierre exhibited a break in this trend, with biomass values twice ( $2.54 \pm 5.15 \text{ mg l}^{-1}$ ) as high as observed in Cornwall ( $1.24 \pm 0.21 \text{ mg l}^{-1}$ ). However, the high standard deviation associated to Lake Saint-Pierre stemmed from the presence of two samples characterized by unusually high amount of resuspended filamentous periphytic green algae, previously identified in the CCA (Figure 3). Exclusion of these two samples from the calculations yielded an average phytoplankton biomass ( $0.58 \pm 0.29 \text{ mg l}^{-1}$ ) more consistent with those observed upstream in Les Grèves and downstream in Port Saint-François, and was therefore used in Figure 4. The significance of these outliers will be discussed separately.

In general, the St. Lawrence River phytoplankton summer biomass is characterized by the predominance of small (equivalent spherical diameter ESD  $< 20 \mu\text{m}$ ) (Figure 4a), truly planktonic (Figure 4b) Chlorophyceae and Cryptophyceae (Figure 4c). The two-fold decrease in plankton biomass observed between Cornwall and Port Saint-François resulted primarily from the decline of the smallest phytoplankton size class (ESD  $< 10 \mu\text{m}$ ) (Figure 4a), somewhat compensated by an increase in resuspended periphytic and indifferent species (Figure 4b). Detailed description of the phytoplankton at each site and of the downstream changes in phytoplankton composition are outlined below.

The phytoplankton assemblage from Cornwall in August was distinct from that of all other downstream stations, in that it was the most representative of a species-rich (45 species) truly planktonic small-cell assemblage (Table 1). Taxa  $< 20 \mu\text{m}$  ESD represented 92% of total biomass (Figure 4a). This station comprised the highest biomass of truly planktonic algae ( $1.21 \text{ mg l}^{-1}$ ) and the lowest biomass of resuspended periphyton ( $0.007 \text{ mg l}^{-1}$ ) (Figure 4b). This assemblage comprised the highest cell concentration ( $18.05 \times 10^6 \text{ cells l}^{-1}$ ) (Table 1), primarily composed of small greens (*Sphaerocystis Schroeteri*, 43% of total cell number), blue-greens (*Aphanocapsa delicatissima* W., 16%) and Cryptophyceae (*Chroomonas acuta*, 9%) (Table 2). Chrysophyceae (especially *Chrysococcus minutus* Nyg., *Mallomonas* spp. and *Ochromonas* cf. *globosa* Sk.) also exhibited a significantly ( $p < 0.05$ ) higher biomass ( $0.04 \text{ mg l}^{-1}$ ) than at any other downstream site ( $0.01 \text{ mg l}^{-1}$ ).

Table 1. Comparison of phytoplankton characteristics at the five sites in August.

Variable / Site Mean (s.d.)	Cornwall <i>n</i> = 3	Lake Saint-Louis <i>n</i> = 12	Les Grèves <i>n</i> = 3	Lac Saint-Pierre <i>n</i> = 10	Port Saint-François <i>n</i> = 3
Total biomass (mg l <sup>-1</sup> )	1.24 (0.21)	0.85 (0.38)	0.56 (0.16)	2.54 (5.15)	0.61 (0.20)
Cell concentration (× 10 <sup>6</sup> ind l <sup>-1</sup> )	18.05 (4.83)	11.90 (7.33)	5.51 (0.43)	5.37 (4.14)	6.60 (1.25)
Species richness ( <i>N</i> )	45 (2)	35 (5)	41 (3)	30 (5)	42 (9)
Diversity <i>H'</i> (bits ind <sup>-1</sup> )	2.73 (0.11)	2.82 (0.44)	3.08 (0.20)	2.68 (0.66)	3.57 (0.64)
Chlorophyll <i>a</i> (μg l <sup>-1</sup> )	3.50 (0.75)	3.61 (1.93)	1.94 (0.15)	5.66 (8.13)	2.37 (0.97)
Phaeopigments (μg l <sup>-1</sup> )	0.17 (0.03)	0.27 (0.19)	0.54 (0.08)	0.10 (0.04)	0.23 (0.07)
Phaeopigments/Chl <i>a</i>	0.05 (0.02)	0.11 (0.09)	0.28 (0.04)	0.04 (0.02)	0.10 (0.02)

Downstream of Cornwall, the results were examined to determine whether phytoplankton properties corresponded either to site characteristics (i.e. fluvial lake or cross section) or to site position in the downstream gradient. The flora from Lake Saint-Louis shared many characteristics with Cornwall, but also exhibited the characteristics of a transition area with the flora found further downstream. The contribution of cells < 10 μm ESD to total biomass decreased by 50% in comparison with Cornwall (Figure 4a) and phaeopigment to chlorophyll *a* ratio doubled (Table 1). Cell concentration in Lake Saint-Louis (11.90 × 10<sup>6</sup> cells l<sup>-1</sup>) was lower than in Cornwall, but still significantly higher than at downstream sites (Table 1). Two of the numerically dominant species (*S. schroeteri* and *C. acuta*) found in Cornwall remained the same in Lake Saint-Louis, whereas the previously dominant Cyanobacteria was replaced by two others (*Merismopedia tenuissima* Lemm. and *Synechocystis* sp. Sauvageau). These results suggest that phytoplankton from Lake Saint-Louis represented a somewhat degraded version of the planktonic assemblage from Cornwall.

In some respects, Lake Saint-Louis shared characteristics with Lake Saint-Pierre rather than with

the cross sections, thus showing spatial discontinuity. Average number of species enumerated in samples from both lakes was significantly lower (30–35) than at the cross sections (41–45) (Table 1). Chlorophyll *a* concentration in each fluvial lake was higher than at their respective upstream cross section (Table 1). Truly planktonic species accounted for a smaller proportion of the biomass in fluvial lakes than at the cross sections, representing 80% of the total biomass in Lake Saint-Louis and 69% of that of Lake Saint-Pierre (after exclusion of the two samples unusually rich in periphyton) (Figure 4b).

Phytoplankton species assemblages in lakes Saint-Louis and Saint-Pierre were dominated by different species of Cryptophyceae (*Chroomonas acuta* and *Rhodomonas minuta*, respectively) and of Chlorophyceae (*Sphaerocystis schroeteri* and *Coccomyxa minor* sensu Findlay & Kling). Filamentous periphytic chlorophytes belonging to the genera *Oedogonium* Link., *Spirogyra* and *Ulothrix* were found in both lakes, whereas they were absent from cross sections. Both lakes supported the same three common species of cyanobacteria (*Merismopedia tenuissima*, *Oscillatoria utermoehlii* De Toni and *Synechocystis* spp.), which represented 20–40% of total cell numbers. These char-



Table 2. Dominant species composition (% in numbers) at the river cross sections

Group	Taxa	Percentage of cell number		
		Cornwall	Les Grèves	P. St-François
<b>May 1991</b>				
Cyano	<i>Merismopedia tenuissima</i>	53	7	10
Bacillario	<i>Aulacoseira islandica v. helvetica</i>	9	4	2
Cyano	<i>Limnothrix planktonica</i>	7	2	0
Bacillario	<i>Asterionella formosa</i>	2	4	4
Crypto	<i>Rhodomonas minuta</i>	2	9	9
Cyano	<i>Chloroglea</i> sp.	0	28	0
Chloro	<i>Monoraphidium contortum</i>	1	26	21
Chloro	<i>Micractinium pusillum</i>	0	0	23
<b>Mean cell number (<math>10^6 \text{ l}^{-1}</math>)</b>		<b>10.4</b>	<b>7.97</b>	<b>7.23</b>
(s.d., $n = 3$ )		(1.89)	(7.40)	(3.90)
<b>Aug. 1991</b>				
Chloro	<i>Sphaerocystis schroeteri</i>	43	29	24
Cyano	<i>Aphanocapsa delicatissima</i>	16	8	7
Crypto	<i>Chroomonas acuta</i>	9	15	13
Cyano	<i>Aphanocapsa elachista</i>	8	0	0
Cyano	<i>Merismopedia tenuissima</i>	4	< 1	3
Crypto	<i>Rhodomonas minuta</i>	3	4	4
Chloro	<i>Pediastrum boryanum</i>	< 1	< 1	7
<b>Mean cell number (<math>10^6 \text{ l}^{-1}</math>)</b>		<b>18.05</b>	<b>5.51</b>	<b>6.60</b>
(s.d., $n = 3$ )		(4.83)	(0.43)	(1.25)
<b>April 1992</b>				
Cyano	<i>Merismopedia tenuissima</i>	12	3	0
Bacillario	<i>Aulacoseira islandica v. helvetica</i>	11	6	10
Crypto	<i>Rhodomonas minuta</i>	9	5	14
Cyano	<i>Synechocystis</i> sp.	8	4	0
Dino	<i>Dinobryon sociale</i>	8	7	4
Cyano	<i>Limnothrix planktonica</i>	0	8	1
Chloro	<i>Westellopsis linearis</i>	0	14	12
Bacillario	<i>Stephanodiscus parvus</i>	< 1	3	5
<b>Mean cell number (<math>10^6 \text{ l}^{-1}</math>)</b>		<b>4.16</b>	<b>4.57</b>	<b>3.18</b>
(s.d., $n = 3$ )		(0.16)	(1.74)	(1.27)

acteristics indicate that phytoplankton growing in fluvial lakes, and particularly in Lake Saint-Pierre, represented a periphyton-enriched version of that found in the main river channel.

The Les Grèves cross section supported a low plankton biomass ( $0.56 \text{ mg l}^{-1}$ , Table 1), comprising mostly (96%) phytoplanktonic taxa (Figure 4b). Dominant species composition (Table 2) and high (96%) proportion of biomass comprised by small ( $< 20 \mu\text{m}$  ESD) cells made this assemblage qualitatively similar to that found in Cornwall (Figure 4). Average species rich-

ness per sample (40), total cell concentration ( $5.51 \times 10^6 \text{ cells l}^{-1}$ ) (Table 1) and biomass of Cryptophyceae ( $0.19 \text{ mg l}^{-1}$ , Figure 4c) were lower than previously observed in Cornwall. These observations, in conjunction with a sharp rise in the phaeopigments/ chlorophyll *a* ratio (Table 1) indicated a further degradation of phytoplankton condition downstream of Montreal.

Although Lake Saint-Pierre phytoplankton exhibited some common traits with Les Grèves, other characteristics of its flora differed markedly from that of the upstream cross sections. Small ( $< 20 \mu\text{m}$  ESD)

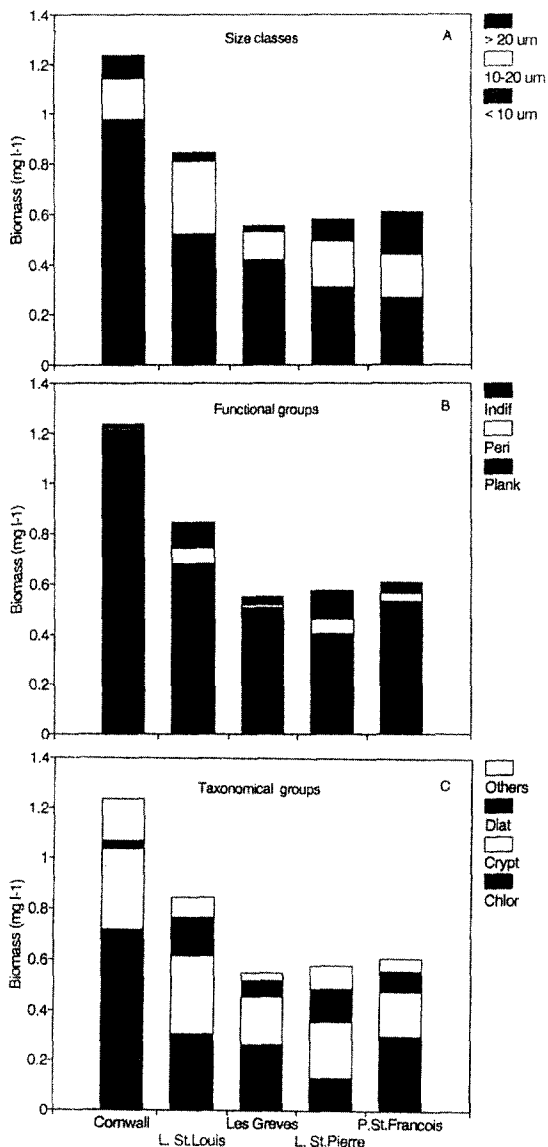


Figure 4. Downstream changes in phytoplankton biomass ( $\text{mg l}^{-1}$ ) in August, showing the allocation of biomass with respect to size classes (top panel), functional groups (middle panel) and taxonomical groups (bottom panel). The two outliers samples identified in Figure 4 are excluded from Lake Saint-Pierre biomass.

phytoplankters represented only 84% of total biomass in lake Saint-Pierre, in contrast with the three upstream sites ( $> 92\%$ ) (Figure 4). Species richness (30), cell concentrations ( $5.37 \times 10^6 \text{ cells l}^{-1}$ ) and cryptophyte biomass ( $0.23 \text{ mg l}^{-1}$ ) were low in Lake Saint-Pierre. Numerical dominance was achieved by a small ( $< 5 \mu\text{m ESD}$ ), truly planktonic coccoid green alga (*Coc-*

*comyxa minor*), whereas large periphytic green algae represented a large (but highly variable) proportion of the biomass (Table 1). Floating algal mats belonging to filamentous periphytic *Cladophora* were exclusively found in Lake Saint-Pierre. Samples characterized as outliers in the CCA and excluded from Figure 4 were rich in *Cladophora*, together with colonies of *Hydrodictyon reticulatum* Lag., *Spirogyra* and *Ulothrix* sp. The added component of more suspended periphytic green algae in larger numbers accounts for the high concentration of chlorophyll *a*, low phaeopigment to chlorophyll *a* ratio and low species diversity in Lake Saint-Pierre (Table 1).

In Port Saint-François, small phytoplankton size fractions ( $< 20 \mu\text{m ESD}$ ) represented an even lower (72%) proportion of biomass than was previously observed in Lake Saint-Pierre (Figure 4a). Truly planktonic species represented only 87% of the biomass at Port Saint-François, in contrast with 98% in Cornwall and 93% at Les Grèves (Figure 4b). Of all the cross sections, Port Saint-François reached the highest biomass of resuspended periphyton ( $0.04 \text{ mg l}^{-1}$ ), thus showing a small influence from Lake Saint-Pierre. Port Saint-François was similar to Les Grèves with respect to species richness (42), cell concentration ( $6.60 \times 10^6 \text{ cells l}^{-1}$ ) (Table 1) and biomass of Cryptophyceae ( $0.18 \text{ mg l}^{-1}$ ) (Figure 4c). Dominant species composition and biomass still resembled closely that of upstream cross sections, with a predominance of planktonic *S. schroeteri*, *C. acuta* and *A. delicatissima* W. (Table 2). Phaeopigment to chlorophyll *a* ratio was lower than in Les Grèves, but higher than in Lake Saint-Pierre (Table 1). Port Saint-François phytoplankton thus resembled that of upstream cross sections, but also showed to some degree the influence of Lake Saint-Pierre.

#### Effects of seasonal water discharge on phytoplankton downstream variations

The intensity of downstream changes in plankton composition over different seasons was assessed using presence-absence of individual taxa as markers of water mass (Figure 5). For example, in August 1991, 32% (11 out of 34) of the taxa recorded in Cornwall were exclusive to that cross section, whereas it shared 50% (17 out of 34) of its taxa with the other two downstream sites. Such calculation indicated that about half of the species encountered were found at the three cross sections, with a higher (55%) proportion under conditions of high discharge (April–May), than under low

seasonal flow conditions (42%) (August–November) (Figure 5). Conversely, the percentage of species exclusive to a single cross section was low (24%) under high discharge and high (33%) under low discharge. This suggested that physical entrainment by water flow had a strong uniformizing effect on river phytoplankton, maintaining longitudinal continuity within the main channel of the St. Lawrence.

Relative abundance of dominant species (% in number) at each cross section shifted downstream (Table 2). For example, in May, two Cyanobacteria (*Merismopedia tenuissima*, 53% and *Limnothrix planktonica* (Wolosz.) Meffert, 7%) and two diatoms (*Aulacoseira islandica* var. *helvetica* 9%, and *Asterionella formosa* 2%) comprised the bulk (71%) of cell numbers in Cornwall. The same four species were still present in Les Grèves and Port Saint-François, but dropped to 17 and 16% of total cell numbers at each site, respectively. Dominance shifted to another Cyanobacteria (*Chloroglea* sp., 28%) and a Chlorophyceae (*Monoraphidium contortum* (Corda) Kom.-Legn., 26%) in Les Grèves, and was restricted to Chlorophyceae (*Monoraphidium contortum*, 21% and *Micractinium pusillum*, 23%) in Port Saint-François. The same phenomenon could be observed for the other sampling periods (Table 2); November data was excluded from Table 2 since only one sample was taken in Les Grèves and in Port Saint-François. Such changes in dominant species abundance likely reflected the combined effects of low survival of upstream algae carried downstream and the emergence of new dominant species via local growth and the inflow from tributaries.

## Discussion

### *Influence of seasons and of water mass*

The seasonal assemblages of plankton observed in our study exhibited the same general pattern as described in a wide range of temperate river systems: diatoms formed the spring bloom; summer biomass was low, characterized by Chlorophyceae and Cryptophyceae; fall biomass increased with the proportion of diatoms.

In the St. Lawrence (Cardinal, 1961) as in other studies (Peterson & Stevenson, 1989), seasonal variations were more important than differences among river sites in the determination of phytoplankton composition and abundance (Figure 3). Seasonal changes in plankton composition were related more strongly

to water temperature than to nutrients concentrations measured during sampling (Figure 3). The influence of water mass was visible through the high correlation of the second CCA axis with DOC concentrations but accounted for only 18% of the total variance. Since our samples originated from mixed green and brown waters in variable proportions, it was not possible to characterize the effect of water mass on phytoplankton composition. The confluence of des Outaouais River with the St. Lawrence was perceptible by an increase in concentrations of DOC and suspended solids (Figure 2) and corresponded with a decrease in phytoplankton biomass at Lake Saint-Louis (Figure 4). Previous studies of phytoplankton (Alaerts-Smeesters & Magnin, 1973) and periphyton (Ahmad et al., 1974; De Sève & Goldstein, 1981) in Lake Saint-Louis showed a low phytoplankton biomass ( $0.3 \text{ mg l}^{-1}$ ) in des Outaouais River. Plankton biomass reported for St. Lawrence tributaries were in the same order of magnitude as those observed in our study: l' Assomption ( $0.7 \text{ mg l}^{-1}$ ), Saint-François ( $1.9 \text{ mg l}^{-1}$ ), Yamaska:  $0.5 \text{ mg l}^{-1}$ ) and Nicolet ( $1.6 \text{ mg l}^{-1}$ ) rivers (Provencher, 1977). Since all these tributaries are located downstream of Montreal (Figure 1), and their detailed taxonomic composition is not available, it is not possible to differentiate their specific impact from that of the urban area itself. However, given that des Outaouais and other tributaries account for only about 20% of the St. Lawrence discharge at Québec, it is likely they exert little effect on the overall biomass and composition of the St. Lawrence River phytoplankton. The influence of individual tributaries should be measurable only in their immediate area of confluence, which would account for the high variability in biomass previously observed in the nearshore areas of the St. Lawrence River (Provencher, 1977). In contrast, phytoplankton biomass from the St. Lawrence are consistently lower than reported in smaller, slow-flowing rivers, in which maximum chlorophyll a concentrations are commonly  $> 10 \mu\text{g l}^{-1}$  (Baker & Baker, 1979; Descy, 1987).

### *Downstream changes in phytoplankton composition*

This study highlights the importance of the small ( $< 10 \mu\text{m}$  ESD) size fraction in the St. Lawrence flora, both numerically (Table 2) as well as in proportion of total biomass (Figure 4), in accordance with recent findings (Bertrand & Vincent, 1994; Frenette et al., 1995). Studies in Lake Ontario report that the  $< 20 \mu\text{m}$  size fraction commonly represented 40–60% of total phytoplankton biomass (in the order of  $1.0 \text{ mg}$

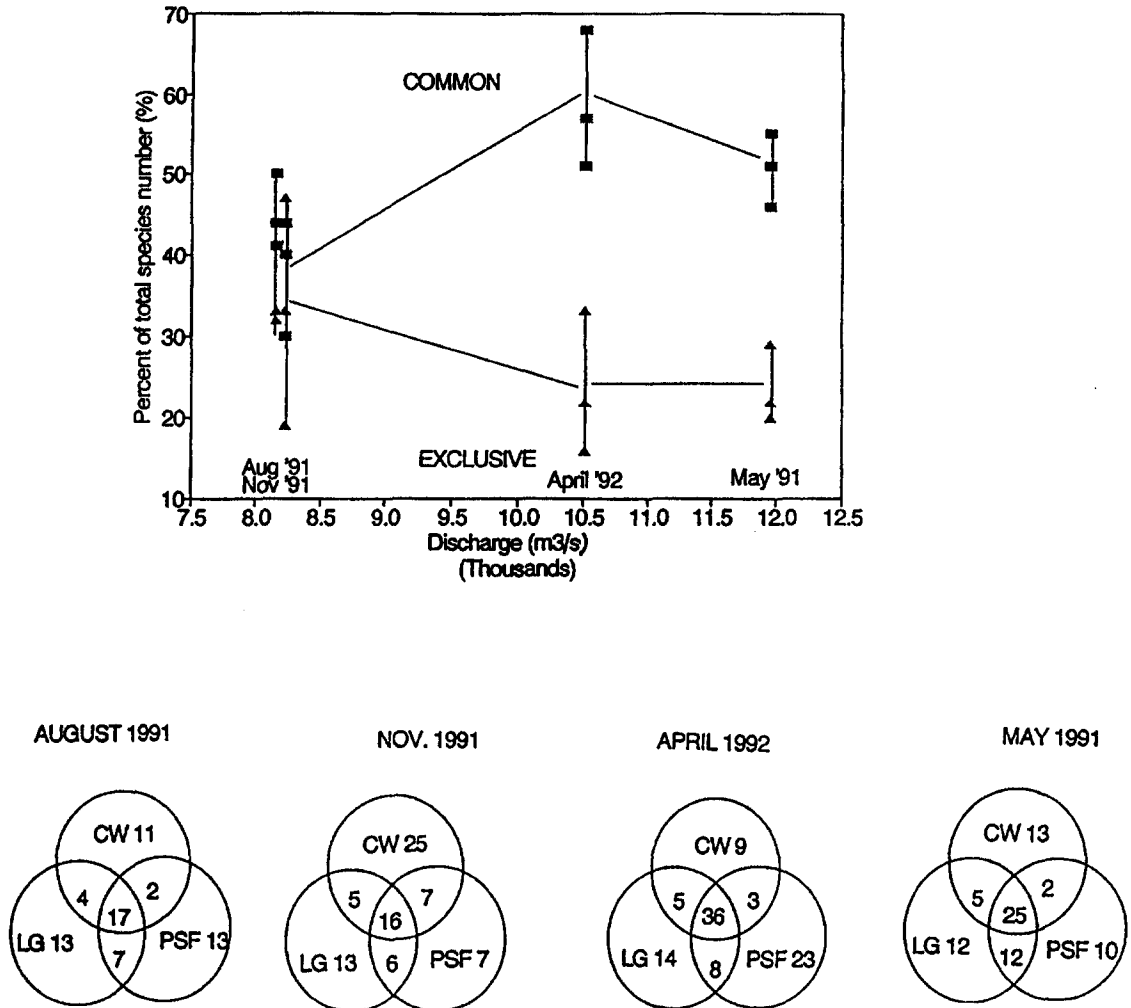


Figure 5. Relationship between St. Lawrence and Ottawa River discharge ( $\text{m}^3 \text{s}^{-1}$ ) and proportions of species common to all or exclusive to each river cross sections. Overlapping circles indicate, for each sampling period, the number of species common to all (inner triangle) or exclusive to (outer section) river cross sections. CW, Cornwall; LG, Les Grèves; PSF, Port Saint-François.

$l^{-1}$ ) in summers of 1980–83 (Munawar et al., 1987). Nanoplankton was also reported to comprise  $> 40\%$  in the upper St. Lawrence River (Mills et al., 1981). Winter observations in the first 200 km downstream of Lake Ontario (Mills et al., 1981) showed a decrease in biomass accompanied by a shift from large ( $> 70 \mu\text{m}$ ) to small ( $< 10 \mu\text{m}$ ) plankton size fractions. Our results support these observations, and further indicate that small size fractions remain a major component of total biomass throughout our study area. However, during summer, the passage through fluvial lakes increased the proportion of larger size fractions in total biomass, owing to the presence of resuspended periphytic and indifferent species.

Conspicuously few common genera were reported in case studies of river plankton (Rojo et al., 1994) which further attests to the downstream selection of taxa tolerant to the exacting growth conditions prevailing in rivers (see the review of Reynolds, 1994). Small-sized taxa, such as Cryptophyceae (*Rhodomonas*, *Cryptomonas*) and diatoms (*Asterionella*, *Stephanodiscus*, *Cyclotella*, *Fragilaria*) were reported to dominate the plankton flora in a large variety of north american (Williams & Scott, 1962) south american (Bonetto, 1986; Del Giorgio et al., 1991) and european (Swale, 1969; Lack, 1971; Jones & Barrington, 1985; Descy, 1987) rivers. The progressive replacement of species along the downstream axis, rather than a clear pattern

Table 3. Characteristics of St.Lawrence fluvial lakes

	Lake Saint-Louis	Lake Saint-Pierre
<b>Morphometric characteristics</b>		
Volume (km <sup>3</sup> ) <sup>1</sup>	1.8	3.5
Mean depth ( $Z_t$ , m)	3	2
Length (km)	23	40 <sup>2</sup>
<b>Light conditions</b>		
Suspended solids (mg l <sup>-1</sup> ) <sup>3</sup>	3	5
Extinction coefficient (K, m <sup>-1</sup> ) <sup>4</sup>	0.64	0.77
Euphotic depth ( $Z_e$ , m)	7.2	6.0
$Z_e / Z_t$	>1	>1
<b>Retention / advection rate</b>		
Main channel transit time (h) <sup>5</sup>	6.4	11.1
Average residence time (h) <sup>6</sup>	62.5	121.5

<sup>1</sup> From Allan (1986)

<sup>2</sup> Between Richelieu and Nicolet rivers (Figure 1)

<sup>3</sup> Median concentration from Rondeau (1993) and Figure 2b

<sup>4</sup> Calculated from equation (1) (see text)

<sup>5</sup> Time required to travel the length of lake at 1 m s<sup>-1</sup>

<sup>6</sup> Lake volume / average summer discharge (8000 m<sup>3</sup> s<sup>-1</sup>)

of loss or gain, would explain the stability of species richness and diversity (Table 2) throughout our study area.

#### *Phytoplankton growth conditions in channels and fluvial lakes*

The main channel of the St.Lawrence River is a deep (15 m), fast flowing (1 m s<sup>-1</sup>) section of the river, in sharp contrast with the shallow (2–3 m) fluvial lakes in which current speed drops to < 0.3 m s<sup>-1</sup> (Table 3). Turbulent mixing homogenizes phytoplankton throughout the water column in deep channels, whereas wind likely plays an important role in mixing waters of the wide, shallow fluvial lakes. Phytoplankton growth conditions in the main river channel thus differ markedly from those of fluvial lakes, particularly with respect to light regime and advection/retention rates.

Phytoplankton light regime in vertically mixed waters depends on mixing depth (equal total depth in the St.Lawrence; Simard, 1994) and on water clarity, which is a function of the concentration of suspended solids. The increase of concentration of suspended solids in the St.Lawrence main river channel (Figure 2b) therefore decreases light availability for advected phytoplankton (Figure 2e). At the Cornwall site, the ratio of the depth of the euphotic zone ( $Z_e$ ) on total

depth ( $Z_t$ ) was > 0.6, meaning that > 60% of the water column into which algae were advected downstream received sufficient light intensity for photosynthesis. Cloern (1987) suggested that light limitation should be expected when the ratio  $Z_e/Z_t$  was < 0.2. Ratio values of < 0.3 in Les Grèves and < 0.4 in Port Saint-François (Figure 3e) indicate the prevalence of low light levels for phytoplankton growth in the main channel. In contrast, both fluvial lakes are sufficiently shallow to allow for light penetration to the bottom ( $Z_e/Z_t > 1$ , Table 3), in spite of the increase in suspended solids concentrations. It is therefore likely that changes in phytoplankton composition and decrease in abundance observed in the main channel downstream of Cornwall resulted, at least in part, from low light availability to drifting algae.

Advection and retention rates in the main channel and the fluvial lakes also markedly differ, owing to different current speed and flow conditions. In the main river channel (at 1 m s<sup>-1</sup>) phytoplankton would travel the 250 km distance between Cornwall and Port Saint-François in about 70 h, including 6.4 h and 11.1 h to cross the length of Lakes Saint-Louis and Saint-Pierre, respectively (Table 3). However, this value only accounts for water travelling at top speed in the main channel crossing the length of fluvial lakes. Calculation of average lake flushing time (lake volume / average summer discharge) increases the residence time in each lake to 62 and 121 h, respectively (Table 3), but still likely underestimates residence time of water in the shallow, nearly stagnant riparian areas. Our results indicate that, in spite of longer retention time, increase in algal biomass in fluvial lakes result from periphyton growth and resuspension rather than from plankton biomass accumulation.

#### *Periphyton contribution to fluvial phytoplankton*

The predominance of truly planktonic algae in the St.Lawrence River flora and the stability of cell biomass are not surprising, given its origin in the Great Lakes. This situation differs markedly from smaller rivers (mean annual discharge < 500 m<sup>3</sup> s<sup>-1</sup>) in which benthic and periphytic algae represent a major source of algae (Moore, 1976; Swanson & Bachmann, 1976; Jones & Barrington, 1985), and in which plankton biomass is negatively related to discharge (Swale, 1969; Lack, 1971; Baker & Baker 1979). In the St.Lawrence, the passage of water through fluvial lakes slightly increased the resuspended periphyton component, modified the dominant species composition, but

had little effect on downstream biomass. The lack of biomass increase downstream of fluvial lakes suggests hydrodynamic isolation from the main channel, and a reduced contribution to river phytoplankton. This observation implies that, during summer, most local algal production is retained and processed within fluvial lakes, with little exportation to the adjacent main river channel. This situation is similar to the Orinoco (Lewis, 1988) and the Parana (Bonetto, 1986) floodplain under low discharge conditions, which exhibit high productivity yet remain isolated from the main river channel.

Within fluvial lakes, the presence of abundant macrophytes provided substrate for periphytic growth, which significantly enriched local plankton. True plankton was least abundant ( $p < 0.05$ ) and resuspended periphyton was most abundant ( $p < 0.05$ ) in Lake Saint-Pierre and Port Saint-François, whereas the opposite situation was found upstream at the Cornwall site.

Lakes Saint-Louis and Saint-Pierre supported an average periphyton biomass of 0.11 and 1.11  $\mu\text{g g}^{-1}$  macrophyte (dry weight), respectively (B. Pinel-Alloul, *Dép. des Sciences Biologiques, Université de Montréal, pers. comm.*). Although plankton (this study) and periphyton were sampled simultaneously at the same lake stations, no correlation was observed between phytoplankton and periphyton biomass (Hudon, unpubl. data). The 10-fold higher periphyton biomass recorded in Lake Saint-Pierre could stem from high nutrient inflow from tributaries draining agricultural land and from the Montreal urban area. Filamentous, periphytic green algae were shown to respond positively to phosphorus inputs in lakes (Cattaneo, 1987). In both lakes, their accidental resuspension in the plankton (albeit in comparatively small amounts) was sufficient to raise the biomass of periphytic taxa, shift species composition and raise size class distribution.

This observation strongly supports the hypothesis of advective control of phytoplanktonic flora in the St. Lawrence, and shows a higher degree of differentiation in the lateral (i.e. riparian vs main channel) than in the longitudinal (upstream vs downstream) axis.

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