**Forecasting the magnitude and composition of
phytoplankton blooms in a eutrophic lowland river (Rivière
Yamaska, Que., Canada)**

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1 **Forecasting the magnitude and composition of phytoplankton**
2 **blooms in a eutrophic lowland river (Rivière Yamaska, Que.,**
3 **Canada)**

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Abstract

The mechanisms controlling phytoplankton biomass and composition in the lower reach of the eutrophic ($TP > 100 \mu\text{g P L}^{-1}$) Rivière Yamaska were studied over six consecutive summers characterized by high (2008–2009) and low (2012–2013) discharge conditions. In the lower river reach, periods of low river discharge favoured planktonic blooms ($> 20 \mu\text{g Chl-a L}^{-1}$) dominated by centric diatoms, in sharp contrast with numerous public reports of simultaneous occurrence of cyanobacterial proliferation in the upstream lakes and reservoirs. Daily cycles of hourly dissolved oxygen production were disrupted by floods but resumed in the days following flow abatement and persisted under low discharge conditions, suggesting that booms in the lower river reach resulted from local production, rather than advection from upstream reservoirs. Motile, flagellate chlorophytes and cryptophytes were more important under extreme high and low discharge conditions whereas cyanobacteria co-occurred with centric diatoms under intermediate discharge and highly illuminated conditions. Although the Rivière Yamaska's flow remained sufficient to avoid cyanobacterial proliferation even under lowest discharge conditions, our results suggest that increasing water residence time, either through severe drought or river damming, will amplify the risk of toxic algal blooms in the free flowing reaches of the lower Rivière Yamaska.

46 **Résumé**

47 Les mécanismes contrôlant la biomasse et la composition du phytoplancton dans le cours
48 inférieur eutrophisé ($TP > 100 \mu\text{g P L}^{-1}$) de la rivière Yamaska, furent étudiés lors de six
49 étés consécutifs, caractérisés par des débits élevés (2008–2009) et faibles (2012–2013).
50 Dans le cours inférieur de la rivière, les périodes de faible débit favorisaient la
51 prolifération du plancton ($> 20 \mu\text{g Chl-a L}^{-1}$) dominé par des diatomées centrales,
52 contrastant fortement avec les nombreux épisodes de prolifération de cyanobactéries
53 rapportés simultanément par le public dans les lacs et les réservoirs situés en amont. Les
54 cycles journaliers de production horaire d'oxygène dissous étaient interrompus lors des
55 crues, mais se rétablissaient dans les jours suivant la diminution du débit et persistaient
56 durant les périodes de faible débit, suggérant que les floraisons dans le cours inférieur de
57 la rivière résultaient de la production locale plutôt que de l'advection provenant des
58 réservoirs en amont. Les chlorophytes et cryptophytes flagellés mobiles étaient plus
59 importants sous les conditions de crue et d'étiage extrêmes tandis que les cyanobactéries
60 accompagnaient les diatomées centrales en conditions de débit intermédiaire et de forte
61 intensité lumineuse. Même si le débit de la rivière Yamaska est resté suffisamment élevé
62 pour éviter la prolifération de cyanobactéries même lors des débits les plus faibles, nos
63 résultats suggèrent que l'accroissement du temps de résidence, soit lors de sécheresses
64 sévères ou via la construction de barrages amplifiera le risque de floraisons de
65 cyanobactéries toxiques dans le cours principal de la basse Yamaska.

Introduction

Anthropogenic activities use a great quantity of water, which is returned to water bodies in a polluted state after agricultural, industrial or domestic use. Such contamination has disrupted nutrient dynamics and increased the occurrence of planktonic algal blooms in water bodies throughout the world (Conley et al. 2009; Hoekstra et al. 2011; Pick 2016). Although the development and spread of algal blooms are related to nutrient availability in most lakes (Hecky and Kilham 1988), plankton development in large, nutrient-rich rivers is often controlled by physical factors such as light intensity (i.e., precipitations and sunshine), water transparency (i.e., turbidity) and residence time (i.e., discharge) (Søballe and Kimmel 1987). Water discharge and turbidity were shown to control phytoplankton abundance in numerous temperate lowland rivers in North America (Baker and Baker 1979; Hudon 2000; Phlips et al. 2007; Hamilton et al. 2012), Europe (Descy et al. 1987; Kiss et al. 1994; Salmaso and Braioni 2008; Istvánovics and Honti 2011; Tavernini et al. 2011) and Australia (Hötzel and Croome 1996). Light availability was also occasionally limiting phytoplankton abundance in blackwater lowland rivers (Hammer 1965; Phlips et al. 2000; Hamilton et al. 2012).

River plankton composition is commonly dominated by centric diatoms (e.g., *Skeletonema potamos*, *Cyclotella* spp., *Discotella* spp., *Stephanodiscus* spp.), small flagellated Chlorophyta (*Chlamydomonas* spp., *Monoraphidium* spp.) and Cryptophyta (*Rhodomonas minuta* [= *Plagioselmis minuta*], *Cryptomonas erosa*) tolerant to turbulence and intermittent light (Kiss et al. 1994; Rojo et al. 1994; Hudon 2000). During drought conditions, however, diatom-dominated blooms typical of median discharge conditions

(Hötzel and Croome 1996) have been replaced by cyanobacterial blooms in the Murray River (Australia) (Al-Tebrineh et al. 2012). In the hypereutrophic Nakdong River (Korea), blooms are dominated by diatoms during wet periods and by toxic cyanobacteria during dry seasons (Jeong et al. 2007). In both the Murray and the Nakdong rivers, the severity of cyanobacterial blooms has been linked to the increase in water retention time in reservoirs designed to sustain irrigation and human consumption during drought periods (Mitrovic et al. 2011; Bowling et al. 2013). Increasing water temperature and the frequency of extreme drought episodes coincident with climate change have also been identified as drivers of the rising incidence of toxic cyanobacterial blooms (Paerl et al. 2011; Pick 2016).

A tributary of the St. Lawrence River that passes through farmland, the Rivière Yamaska (Quebec) is notorious for its high nutrient content (Hudon and Carignan 2008). Toxic cyanobacterial blooms are commonly reported in the upper lakes and reservoirs (MDDEFP 2014), with resulting impairment to drinking-water sources basin-wide (Rolland et al. 2005). Climate-change scenarios forecast increasing summer temperatures coupled with higher incidence of drought periods for rivers draining the St. Lawrence lowlands (CEHQ 2015), which could increase the frequency and severity of cyanobacterial blooms. This study aimed at developing a model for forecasting plankton blooms and species composition from environmental conditions in the lower reaches of the Rivière Yamaska. The response of planktonic biomass and species composition to discharge and water quality (SPM, TN, NO₂-NO₃, NH₄, TP, TDP, DOC) were examined over six consecutive summers, coinciding with years of high (2008, 2009) and extremely low (2012, 2013) discharge.

We hypothesized that high nutrient concentration, periods of low river discharge and high illumination would favour planktonic blooms ($> 20 \mu\text{g Chl-}a \text{ L}^{-1}$). In addition, a shift in plankton-species composition from diatoms to toxic cyanobacteria was expected to occur under drought conditions, as a result of increased residence time and water transparency. We also examined whether blooms in the lower reaches of the river were produced locally or coincided with cyanobacterial occurrence reported in upstream reservoirs, indicative of advection. Local plankton-production patterns under contrasting discharge conditions were assessed using high-frequency (hourly) measurements of dissolved O_2 from automated probes. Advection of cyanobacteria from upstream reservoirs to the lower river reaches was examined using reports of cyanobacterial occurrence made by citizens to the MDDELCC (2008–2012) along the north branch of the Rivière Yamaska (MDDELCC 2016, Fig. 1). This information allowed us to forecast planktonic blooms under a range of discharge conditions and gain insights on the future occurrence of potentially toxic cyanobacteria in the lower reaches of this heavily farmed watershed.

Material and methods

Study area

The Rivière Yamaska (watershed area 4784 km^2 , average annual discharge $87 \text{ m}^3 \text{ s}^{-1}$) is located in southern Quebec and flows northwest over 160 km from its headwaters at Lac Brome to its mouth at Lac Saint-Pierre (St. Lawrence River), draining 268 000 ha (56% of watershed area) of farmland, including corn, soy and hog production (Fig. 1). Both the main branch (Lac Brome) and the north branch (Lac Waterloo) of the Rivière Yamaska alternate between fast-flowing and impounded lacustrine segments, the

latter of which serve as sources of drinking water and recreational areas for local communities. The population of the Yamaska watershed (257 500 inhabitants, Statistics Canada 2011) is dispersed across 90 municipalities within the Montérégie administrative region.

Between 2008 and 2012, cyanobacterial occurrences were signalled by the public in 20 water bodies in the Montérégie administrative region, sampled analyzed and blooms were confirmed ($\geq 20\,000$ cells mL^{-1}) by the Quebec Ministry of the Environment (MDDEFP 2014; MDDELCC 2016). Recurrent blooms (i.e. reported over four, five or six years) were sampled in 15 of those water bodies. Taxonomical analysis of water samples revealed the occurrence of several potentially toxic genera, among which the most common were *Aphanizomenon*, *Dolichospermum*, *Microcystis* and *Woronichinia*. Toxin concentrations exceeding the standard for drinking water (≤ 1.5 μg toxin L^{-1} microcystin LR equivalent toxicity, INSPQ 2005, Gouvernement du Québec 2016) were measured in 17 Montérégie water bodies and 12 of those exhibited concentrations above the threshold for recreational activities (≤ 16 μg toxin L^{-1} Microcystin LR equivalent toxicity, INSPQ 2005, MDDEFP 2014). Microcystin LR was also measured in the liver of exploited fish species (*Perca flavescens*; $0.72 - 17.81$ ng g tissue^{-1}) in four lakes of the Yamaska watershed (Deblois et al. 2008).

Sampling and analyses

Water chemistry

Water quality data during summer (generally June to August or September in 2008–2013) were obtained from grab samples taken under the bridge of Route 132 at the community of Yamaska ($46.0051^{\circ}\text{N} - 72.9101^{\circ}\text{W}$) (Fig. 1, No. 1). Weekly water

samples were collected just below the surface for analysis. Bulk (raw) water samples were analyzed for total phosphorus (TP) and total nitrogen (TN). Suspended particulate matter (SPM; APHA 1995) and planktonic chlorophyll-*a* (Environment Canada 2005) were collected from filters (Whatman GF/F). Filtered water was analyzed for total dissolved phosphorus (TDP), nitrites-nitrates (NO₂-NO₃), ammonia nitrogen (NH₄) and dissolved organic carbon (DOC) (Environment Canada 2005). TP and TDP concentrations were measured by acid digestion followed by colorimetry with ammonium molybdate. TN concentrations were determined using persulfate digestion with a LACHAT Continuous Flow Quick-Chem 8000. NO₂-NO₃ was analyzed by nitrate-to-nitrite reduction in a cadmium column prior to colorimetry. NH₄ concentrations were determined by colorimetry after the addition of sodium nitroprusside and phenate sodium. DOC was oxidized to carbon dioxide by the addition of persulfate prior to infrared detection (Shimadzu TOC-5000; Environment Canada 2005). Chlorophyll-*a* was determined spectrophotometrically using cold 95% ethanol extraction following the procedures of Wetzel and Likens (1991), a modified version of Lorenzen (1967) (Environment Canada 2005).

Short-term variability (hourly average derived from a 15-minute or 30-minute interval, June –September) of turbidity, conductivity and dissolved O₂ as a response to discharge variations was assessed. Measurements were made at 15-minute (2008 only) or 30-minute intervals by an automated YSI multi-probe (Model 6600 V2) moored 200 m downstream from the Route 132 bridge, where water-quality samples were taken. The multi-probe was equipped with temperature, conductivity, turbidity, dissolved O₂ and pH sensors; sensors were calibrated before mooring. Every two weeks, the multi-probe was

retrieved, cleaned and verified, and data were downloaded. Calibration was verified again in the laboratory after the final retrieval. Moorings were made during the summers of 2008 (June 25 – Sept. 24), 2009 (June 29 – Sept. 4), 2011 (June 23 – Sept. 7) and 2012 (June 19 – July 28), covering a wide range of discharge conditions.

Hydrological and meteorological data

Daily discharge values for Rivière Yamaska were obtained (2008–2013) from the Centre d'Expertise Hydrique du Québec (CEHQ 2014, Rivière Yamaska at Saint-Hyacinthe, station no. 030345; watershed area: 3334 km²) (Fig. 1, No. 2). Additional hydrometric information (mean depth, river width, wetted area, current speed) was obtained at high- and low-river stages from gauging stations located downstream of major impoundments (personal communication: Luc Gauthier, Direction de l'expertise hydrique, MDDELCC, 675, René Lévesque est, Québec, Que.). Reports of cyanobacterial occurrence in the upper part of the watershed were examined more closely for the north branch of the Rivière Yamaska, which comprises five major lakes and dammed impoundments: Lac Waterloo, Shefford-Vale, Granby, Farnham and Saint-Hyacinthe (Table 1, Fig. 1, No. 2–6). Reservoir information (surface area, maximum volume, watershed area) was obtained from CEHQ (2016). Land use data (Fig. 1) for 2010 was obtained from the North American Land Change Monitoring System (NALCMS) (available at <https://landcover.usgs.gov/nalcms.php>). Distribution of cropland in the St. Lawrence River valley and distance (km) between gauging stations and our sampling site (Fig. 1, No. 1) were assessed using ArcGIS.

The above information was used to calculate reach length (the distance between successive sites), transit time to the next reach and the cumulative advection time to the

sampling site. The predominance of turbulent vs. laminar flow under low- and high-river discharge conditions was roughly assessed by estimating Reynolds number (Re , dimensionless), using the equation

$$Re = \rho v L / \mu$$

where ρ is the density of water (1000 kg m^{-3}), v is the average current speed (m s^{-1}), L is the hydraulic diameter of the river ($L \text{ (m)} = 4 * \text{wetted section (m}^2) / \text{river width (m)}$) and μ is the dynamic viscosity of water at 20°C (0.001 Pa s).

Daily meteorological conditions (air temperature and precipitation) were obtained from Environment Canada (Meteorological Service of Canada, <http://climat.meteo.gc.ca/>) for Saint-Hyacinthe Meteorological Station no. 7027361 (Fig. 1, No. 2). The effect of precipitation on physical and chemical water quality was examined using the cumulative precipitations at Saint-Hyacinthe over the three days prior to sampling.

Hourly values of photosynthetically active radiation (PAR, Li-Cor LI1400 and Li-Cor LI1000 Data logger) were measured at the Station de Biologie des Laurentides (Université de Montréal) located at Saint-Hippolyte ($45.98854 - 74.00583$) (Fig. 1, No. 8). Light intensity measurements (mean hourly PAR values, $\mu\text{mol m}^{-2} \text{ s}^{-1}$) averaged for the three days prior to sampling (14 hours of daylight) were deemed to be an adequate proxy for illumination in the lower Yamaska watershed, given that summer weather patterns travel along the St. Lawrence River valley in a north-easterly direction.

Underwater light penetration in the Rivière Yamaska was estimated from previous relationships, linking the coefficient of diffuse light attenuation (k , m^{-1}) to DOC (mg C L^{-1})

225 ¹) and SPM (mg L⁻¹) concentrations ($k = 0.28 * (SPM^{0.44}) * (DOC^{0.63})$; Hudon, unpubl.
226 data).

227 **Phytoplankton composition and abundance**

228 Phytoplankton biomass and species composition of samples from the lower
229 reaches of the Rivière Yamaska (Fig. 1, No. 1) collected simultaneously with water
230 chemistry were preserved with acidified Lugol's solution prior to their analysis at the
231 Canadian Museum of Nature (Ottawa, Ontario). Phytoplankton was identified to the
232 lowest possible taxonomic level and enumerated using modified sedimentation chambers
233 (Hamilton et al. 2002). Aliquots of 0.5 to 4 mL were settled and examined with a Leica
234 DMR compound microscope using phase-contrast and bright-field optics; enumerations
235 were carried out on random transects scanned across the settling chamber at 200× or
236 400×, and 800×. The larger and often rarer taxa were enumerated by examining either
237 half or the complete chamber. Diatom identifications were verified from acid-cleaned
238 frustules on permanently mounted slides with Naphrax for light microscope examination.
239 In addition, specimens were dried on aluminum foil and mounted with double-sided
240 carbon tape on aluminum stubs for scanning electron microscopy examination. Taxa were
241 identified using the monographs of Hüber-Pestalozzi (1938, 1961, 1968), Prescott (1951),
242 Findlay and Kling (1979), Germain (1981), Krammer and Lange-Bertalot (1986–1991),
243 Anagnostidis and Komarek (1988), Ettl and Gärtner (1988) and Compère (1989), among
244 others (for a complete list, see Hamilton et al. 1997). All taxa enumerated are catalogued
245 in a photomicrograph collection associated with this study held at the Canadian Museum
246 of Nature. A voucher sample collection from this study (2008–2011) is archived in the
247 Canadian Museum of Nature (CANA 85711–85732, 85822–85848). Plankton abundance

measurements included cell density and biomass. The total volume of each taxon was calculated from the average dimensions measured on numerous specimens if the taxon was common, or one specimen if rare using one of seven geometrical shapes (sphere, ellipsoid, cylinder, cone, double cone, rectangular box, prism on parallelogram-base) (Hillebrand et al. 1999; Gosselain and Hamilton 2000). The total biovolume of phytoplankton was converted to wet weight assuming a density of 1.

Episodes of cyanobacterial occurrence reported by the public throughout the Yamaska watershed (2008–2012) were sampled, identified and compiled into a database (MDDELCC 2016). The database comprised for each date, the location (Lat, Long) and abundance (no. of cells L^{-1}) of each cyanobacterial genus occurring at each site. Episodes reported in the upper reaches (Fig. 1, No. 2 and 3) and along the north branch of the Rivière Yamaska (Fig. 1, No. 4–6) in August and September 2009 were used to compare the timing and composition of cyanobacterial occurrence between successive river reaches down to our study site (Fig. 1, No. 1), indicative of downstream advection.

Statistical analyses

Relationships between plankton biomass and environmental variables were explored using Spearman correlations. The delay between changes in discharge and the ensuing plankton blooms was estimated from the correlation (Pearson r) between chlorophyll- a and mean Q over previous days, with increasing lag periods between two and seven days. Groups of taxa showing a high relative abundance at the same time were identified from a cluster analysis of the relative abundance of major taxa through time, using the Lance and Williams nonmetric coefficient as a dissimilarity measure for flexible-beta clustering (SAS/STAT 13.1, Cluster procedure). This dissimilarity measure

was selected because the resulting clusters represented groups of taxa dominating plankton assemblages (i.e., representing a high proportion of total biomass) in the same samples at the same time.

The relationships between plankton biomass (Chl-*a*) and water-quality variables (SPM, NO₂-NO₃, NH₄, DOC, TP, TDP) were assessed using principal components analysis (PCA) on log-transformed variables. The influence of environmental variables on water chemistry was then evaluated by plotting and calculating the correlation (Pearson *r*) between PCA axes and log₁₀-transformed mean river discharge, cumulative precipitation and mean PAR (all, three days prior to sampling). Time-series data were smoothed by calculating a three-hour moving average.

The critical discharge and light conditions yielding different planktonic chlorophyll-*a* concentrations were modelled using a regression tree analysis (De'ath and Fabricius 2000) implemented with procedure HPSPLIT from SAS/STAT, version 13.1 (SAS Institute).

Results

Hydrological and environmental characteristics of the Rivière Yamaska

Hydrometric measurements taken downstream of five north branch impoundments 50.5–164 km upstream of our study site revealed the high range in current speed and residence time experienced in each river section under high- and low-river stages (Table 1). For example, at the station located downstream of Saint-Hyacinthe's dam (Fig. 1, No. 2), mean current speed varied from 0.08 to 1.6 m s⁻¹ over the range of river discharge (2.57–755 m³ s⁻¹), resulting in transit times between 7.4 and 0.4 days

(Table 1) to our sampling site in the lower Rivière Yamaska (Fig. 1, No. 1). Even under the lowest discharge conditions, river-flow dynamics at all sites were dominated by turbulent forces, as shown by the very high Reynolds number values ($\geq 0.09 \times 10^6$, Table 1).

Daily hydrological conditions in the Rivière Yamaska at Saint-Hyacinthe (Fig. 1, No. 2) during the summers (June 1 – Sept. 30) of 2008–2013 exhibited a large degree of short-term (day-to-day) variability and also differed markedly between years (Fig. 2). Summer discharge at Saint-Hyacinthe ranged from a minimum daily base flow of $2.5 \text{ m}^3 \text{ s}^{-1}$ (Sept. 1, 2012) to a maximum value of $730 \text{ m}^3 \text{ s}^{-1}$ (Aug. 29, 2011). Discharge showed significant differences among years, with exceptional drought conditions in 2012 and 2013 ($Q < 15 \text{ m}^3 \text{ s}^{-1}$) and comparatively wet summers in 2008 and 2009 ($Q > 47 \text{ m}^3 \text{ s}^{-1}$) (Table 2). Light intensity showed an inverse pattern, with significantly higher illumination in 2011–2013 ($\text{PAR} > 750 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) than in 2008–2010 ($\leq 600 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) (Table 2). Daily precipitation also tended to be lower in 2011–2013 ($< 2.5 \text{ mm}$) than in 2008–2010 ($> 3 \text{ mm}$), albeit without significant difference among years. Not surprisingly, mean daily discharge was positively correlated with mean daily precipitation ($r = 0.86$, $N = 6$, p (one-tailed) = 0.01) and negatively correlated with mean hourly PAR ($r = 0.77$, $N = 6$, p (one-tailed) = 0.04).

Physical and chemical water characteristics exhibited inter-annual differences related to discharge and climatic conditions (Table 3). As anticipated, TP ($106\text{--}142 \text{ } \mu\text{g P L}^{-1}$) and TDP ($35\text{--}57 \text{ } \mu\text{g P L}^{-1}$) concentrations were high at all times (Table 3). The wet summer of 2008 showed the lowest water temperature, SPM concentration and turbidity, but the highest DOC concentrations of all years. Conversely, summers of low discharge

coincided with higher average water temperature ($> 24^{\circ}\text{C}$) compared to years of high discharge ($< 22.5^{\circ}\text{C}$). In addition, the dry, sunny summer of 2012 coincided with minimum concentrations of TN, $\text{NO}_2\text{-NO}_3$, NH_4 , and DOC, and the highest temperature, turbidity and SPM concentrations of all years. Light-extinction coefficient always remained high ($4.6\text{--}6.6\text{ m}^{-1}$) (Table 3), yielding a euphotic depth (Z_{eu} , $\geq 1\%$ of incident light intensity) of about 1 m. Given an estimated drop in mean river depth (Z_t) from 3 to 1 m over the range of discharge that we sampled, Z_{eu}/Z_t ratio would rise from ≈ 0.3 (high discharge in 2008) to ≈ 0.9 (low discharge in 2012). Dropping discharge thus exposes phytoplankton to slower current, longer residence time, shallower depth and higher light intensity, yielding longer advection time from upstream reservoirs, yet more favourable growth conditions (high light, low turbulence) for local phytoplankton.

Phytoplankton biomass and species composition

In contrast with environmental variables, which exhibited notable differences between years of contrasting discharge, neither phytoplankton cell biomass nor chlorophyll-*a* concentration in the lower Rivière Yamaska showed any significant difference between years, owing to the large short-term (within-year) variability (Table 4, Fig. 2). Plankton biomass showed a "boom and bust" pattern over wet summers (2008, 2009) and tended towards higher, more-stable values during dry summers (Table 4, Fig. 2). Bloom concentrations ($> 20\text{ }\mu\text{g Chl-}a\text{ L}^{-1}$) were observed for 35 of the 60 samples taken over the six summers of our study.

Phytoplankton cell biomass was positively correlated with chlorophyll-*a* concentrations ($r = 0.75$, $p < 0.001$, $N = 54$). Both cell biomass and chlorophyll-*a* were negatively correlated with discharge ($r = -0.50$, $p < 0.001$ and $r = -0.70$, $p < 0.001$,

respectively, $N = 54$) and less strongly with precipitations ($r = -0.44$, $p < 0.001$ and $r = -0.40$, $p < 0.05$, respectively, $N = 57$), likely resulting from the indirect relationship between precipitation and discharge. In contrast, neither indicator of plankton abundance showed any significant correlation with water chemistry (TP, NH_4 , $\text{NO}_2\text{-NO}_3$, DOC and SPM concentrations).

Phytoplankton species composition over the 2008–2013 period was generally dominated by diatoms (47–84% of total biomass) (Table 4, Fig. 3), with a smaller proportion of chlorophytes (9–22%) and other algae. Chrysophytes (0.7–10%), cryptophytes (3–20%) and pyrrhophytes (1–14%) represented variable proportions of the total biomass among years (Fig. 3). Diatoms represented the bulk ($\geq 60\%$) of biomass in 2008–2011, but were equalled by other taxonomical groups ($\approx 50\%$ of total biomass) during the dry summers of 2012 and 2013 (Fig. 3). The highest abundance of cyanobacteria was observed in 2010, during which seven out of the 11 samples comprised > 1 million colonies L^{-1} . No monthly or temporal trend indicative of a seasonal succession in phytoplankton composition could be detected.

Five taxa of centric diatoms (*Aulacoseira granulata*, *Skeletonema potamos*, *Stephanodiscus parvus*, *Cyclotella meneghiniana* and *Discotella stelligera* (= *Cyclotella stelligera*)) constituted the bulk of cell biomass over most years (Table 4). Other diatoms primarily comprised benthic pennate forms (*Fragilaria* spp., *Navicula* spp., *Nitzschia* spp., *Ulnaria* spp.), which represented $> 5\%$ of total biomass during wet years. The balance of biomass was associated with sporadically occurring taxa over the years, such as *Carteria* spp. and other chlorophytes (2008, 2011), various cyanobacteria (2009–2011), *Cryptomonas erosa* (2010, 2011, 2013) and *Peridinium* (2010, 2013)

(Table 4). The planktonic flora of the summer of 2013 showed an unusually high biomass of other small flagellate taxa such as *Chlamydomonas* spp. and *Pteromonas aculeata*—taxa seldom observed over previous years.

The co-occurrence of most common taxa was determined from a cluster analysis carried out on their relative abundance, highlighting four major clusters (Fig. 4). The first cluster was formed by the dominant group of centric (all but *Ulnaria* spp.) diatoms (*Stephanodiscus parvus*, *Skeletonema potamos*, *Cyclotella meneghiniana*, *Discotella stelligera*) representing the bulk of biomass in most samples. Cluster II included taxa that commonly occurred, but were less abundant than those from the previous group. Cluster II was characterized by diatoms (*Aulacoseira granulata*, *Nitzschia* spp. and *Navicula* spp.) and flagellated Chlorophyta (*Pediastrum* spp., *Scenedesmus* spp., *Chlamydomonas* spp.), Euglenophyta (*Phacus* spp.), Cryptophyta (*Cryptomonas erosa*) and Pyrrophyta (*Peridinium* spp.). Cyanobacteria (*Aphanizomenon* spp., *Dolichospermum* spp. and other cyanobacteria) exclusively formed Cluster III, a commonly occurring group, but with generally low biomass. Finally, Cluster IV included sporadically occurring yet occasionally abundant taxa, such as various Chlorophyta (*Actinastrum* spp., *Carteria* spp., *Closterium* spp., *Cosmarium* spp., *Monoraphidium* spp., *Pteromonas aculeata*), Pyrrophyceae (*Gymnodinium* spp.), Chrysophyta and assorted diatoms (*Fragilaria* spp., *Melosira varians*).

Relationships between plankton biomass and environmental conditions

The relationships between planktonic chlorophyll-*a*, SPM and chemical water characteristics measured over the six sampling seasons were examined using Principal Component Analysis (Fig. 5A). The first principal component (40.1% of total variance)

was positively correlated with DOC ($r = 0.72$) and all dissolved nutrients, including TDP ($r = 0.83$), NH_4 ($r = 0.70$) and $\text{NO}_2\text{-NO}_3$ ($r = 0.65$) and negatively correlated with chlorophyll-*a* ($r = -0.75$). This is indicative of agricultural surface runoff. In contrast, the second principal component (25.0% of total variance) exhibited strong positive correlations with SPM ($r = 0.91$) and TP ($r = 0.83$). These correlations are indicative of the effects of entrainment of phosphorus-rich particles eroded from the watershed and/or resuspended from the river bed.

The first principal component was positively correlated with discharge, ($r = 0.72$, $p < 0.001$, $N = 50$) (Fig. 5B), suggesting that increasing runoff induced both the rise in dissolved nutrients and the coincident drop in chlorophyll-*a*. Planktonic chlorophyll-*a* at our sampling site (Fig. 1, No. 1) showed a strong negative correlation with mean daily discharge at Saint-Hyacinthe (Fig. 1, No.2); discharge chlorophyll-*a* correlations calculated with a lag-time between two ($r = -0.65$) and seven days ($r = -0.70$) were all significant, but was highest with a three-day lag ($r = -0.74$, $p < 0.001$, $N = 54$). The lesser correlation values recorded between the first principal component and PAR ($r = -0.57$, $p < 0.001$, $N = 50$) and with precipitations ($r = 0.49$, $p < 0.001$, $N = 47$) (not shown) could result from the indirect relationships between sunny weather, precipitation and discharge. On three dates (July 15, 2009, August 6 and 13, 2008) that coincided with samples taken during high discharge conditions ($>120 \text{ m}^3 \text{ s}^{-1}$) (Fig. 5B), plankton biomass was low ($< 3 \mu\text{g Chl-}a \text{ L}^{-1}$) and stood out as maximum values of Component I (i.e., high TDP, DOC, $\text{NO}_2\text{-NO}_3$ and NH_4). In contrast, sampling on several dates in June and July 2012 (June 26, July 3, 10 and 23) occurred during low discharge ($<15 \text{ m}^3 \text{ s}^{-1}$) conditions and yielded high plankton biomass ($15\text{--}35 \mu\text{g Chl-}a \text{ L}^{-1}$), corresponding to low Component I (i.e.,

low TDP, DOC, NO₂-NO₃ and NH₄) values (Fig. 5B). In summary, variations in planktonic chlorophyll-*a* were better explained by changes in discharge conditions than by nutrient concentrations, which were in excess at all times. The short-term sequence of events that illustrate the effects of discharge variations on O₂ production by local plankton, chlorophyll-*a* and water quality will be examined below in more detail.

Effects of short-term variability in discharge on planktonic O₂ production

The short-term response of local phytoplankton to changes in discharge and turbidity was examined through the daily variations of dissolved O₂ concentration. High and variable discharge in August 2008 (Fig. 6A) contrasted with low but stable discharge in June 2012 (Fig. 6B).

In 2008, three peaks in discharge were observed on August 4, 8 and 10, after which discharge dropped and rose again slightly on August 20 (Fig. 6A). Turbidity followed a similar pattern. During the flood event, dissolved O₂ concentrations showed no daily cycles and remained at around 80% saturation. After discharge receded (August 15), planktonic O₂ production started rising and exhibited daily cycles in phase with daylight. Over the same period, chlorophyll-*a* concentration rose from < 2 µg Chl-*a* L⁻¹ during the flood to 19 µg Chl-*a* L⁻¹ (August 20) and 25 µg Chl-*a* L⁻¹ (August 27). Cell biomass followed the same pattern as chlorophyll-*a* concentration, rising from 167 to 1000 (August 20) and 3000 (August 27) µg L⁻¹. Interestingly, the lesser rise in discharge observed on August 20 introduced some irregularity, but it did not interrupt the daily cycles of O₂ production, thereby maintaining the rise in planktonic biomass.

In contrast, low discharge conditions were observed in 2012, with very slight rises on June 28 and 29, and July 6 (Fig. 6B). Turbidity values remained stable and relatively low, albeit higher than under comparable discharge in 2008. Clear diurnal cycles in dissolved O₂ were visible during the entire 20-day period. Between June 26 and July 3, however, dropping O₂ saturation (from 140 to 60%) and chlorophyll-*a* concentration (from 35 to 15 µg Chl-*a* L⁻¹) were observed, coincident with overcast and intermittent rain conditions, bringing a slight rise in discharge (from 5.2 to 33 m³ s⁻¹) on June 29 (Fig. 6B). Over the same period, plankton biomass dropped from 2600 (June 26) to ≈ 800 mg m⁻³ (July 3 and 10). Sunny conditions returned between July 3 and 10, with stable discharge and chlorophyll-*a* concentrations (18 µg Chl-*a* L⁻¹) and O₂ cycles showing an upward trend towards saturation. Overall, periods of low and stable discharge coincided with relatively high plankton biomass and sustained daily O₂ production cycles, which were modulated by variations of incident light intensity.

Is there a correspondence between cyanobacterial occurrence in upstream reservoirs and lower river reaches?

In the north branch of the Rivière Yamaska, cyanobacterial occurrence was reported by citizens or organisms to MDELCC at numerous sites and dates over the 2008–2012 period (Table 1). Cyanobacteria were reported in variable abundance over 26 days in Lac Waterloo, 14 days in the Réservoir Choinière, 39 days in Lac Boivin, 6 days in Farnham and 3 days in Saint-Hyacinthe (Fig. 1 No. 2–6, Table 1). Lac Waterloo episodes were dominated by *Microcystis*, whereas those occurring in downstream impoundments were characterized by *Woronichinia* and a co-occurrence of either *Aphanizomenon* (in Réservoir Choinière) or *Microcystis* further downstream (Table 1). In

contrast, blooms at our sampling site in the lower reach of the river (Fig. 1, No. 1) were generally dominated by diatoms and other algae, with a small cyanobacterial biomass (Fig. 3, Table 4).

The timing of cyanobacterial occurrence was examined more closely for the months of August and September 2009, during which period they were reported at several locations in all the impoundments of the north branch of the Rivière Yamaska. Cyanobacterial occurrence (listed here in order according to their location downstream) was reported in Lac Waterloo (August 11, 2009), Réservoir Choinière (August 27), Lac Boivin (August 5, 13, 20 and 26, September 2, 8, 16, 24 and 29), Farnham (August 24 and 28, September 10) and Saint-Hyacinthe (August 21, 24 and 28, September 10). No pattern could be detected between the timing or magnitude of cyanobacterial episodes among sites, or with respect to hydrological conditions. Since advection time between these reaches is generally less than one day (Table 1), the general lack of pattern suggested that cyanobacterial episodes in different reservoirs/lakes did not stem from advection between reaches but were stimulated by favourable environmental conditions in different parts of the watershed.

There was no correspondence between the dominant species or total biomass of cyanobacteria reported near Saint-Hyacinthe (August 21, 24 and 28, September 10, 2009) and those measured at our study site 50 km downstream (Table 1). In terms of composition, however, it is worthy of notice that, out of the 56 samples collected in 2008–2013 at our sampling site, *Woronichinia* was recorded in only two samples taken in August 2009 (12 and 26), and in very small numbers. Given the low discharge at Saint-Hyacinthe in August and September 2009 (median $11.5 \text{ m}^3 \text{ s}^{-1}$, range $3.7\text{--}117.2 \text{ m}^3 \text{ s}^{-1}$),

travel time from the Saint-Hyacinthe dam to our study site could take up to 7 days (Table 1).

Forecasting biomass and composition from discharge and light conditions

A combination of discharge and light conditions yielded four groups of chlorophyll-*a* concentrations in a binary model that explained 59% of the total variance in our data set (Fig. 7). Mean chlorophyll-*a* concentration was lowest ($6.4 \mu\text{g Chl-}a \text{ L}^{-1}$) at high discharge ($\geq 44 \text{ m}^3 \text{ s}^{-1}$). Lowest discharge conditions ($< 15 \text{ m}^3 \text{ s}^{-1}$) yielded intermediate chlorophyll-*a* concentrations ($23.3 \mu\text{g Chl-}a \text{ L}^{-1}$). Maximal chlorophyll-*a* concentration (mean = $51.6 \mu\text{g Chl-}a \text{ L}^{-1}$) were reached under intermediate discharge ($15\text{--}43 \text{ m}^3 \text{ s}^{-1}$) and high ($\geq 783 \mu\text{mol m}^{-2} \text{ s}^{-1}$) illumination (Fig. 7); incident light $< 783 \mu\text{mol m}^{-2} \text{ s}^{-1}$ yielded a lower ($27.6 \mu\text{g Chl-}a \text{ L}^{-1}$) mean chlorophyll-*a* concentration. Plankton biomass thus appeared primarily controlled by discharge, with a small influence of light intensity at intermediate discharge values.

The correspondence between the four classes of chlorophyll-*a* identified above (Fig. 7) and taxonomic composition of each cluster (Fig. 4) were determined by allocating samples to the combination of discharge and light conditions under which they were collected (Table 5). Total biomass increased five-fold, whereas chlorophyll-*a* rose eight-fold between the lowest and highest groups of plankton abundance. Centric diatoms (Cluster I) always represented a high proportion of total biomass ($\geq 40\%$), but accounted for the highest fraction (65%) of total biomass at intermediate discharges ($15\text{--}43 \text{ m}^3 \text{ s}^{-1}$). Under both extreme high and extreme low discharge conditions, a mixed group of benthic diatoms, chlorophytes, chrysophytes and pyrrhophytes (Clusters II and IV) dominated the

biomass of plankton assemblages, and were complemented by truly planktonic centric diatoms (Cluster I). Under the highest ($\geq 44 \text{ m}^3 \text{ s}^{-1}$) and lowest (< 15) discharge conditions, mixed algae representing five phyla (Cluster II) were dominant (42–45% of total biomass). Cyanobacteria (Cluster III) always represented a minor fraction of total biomass ($< 3\%$), but they reached their highest biomass at intermediate discharge and high illumination. Finally, sporadically occurring flagellates (Cluster IV) were most common (15%) under extreme high and extreme low discharge (Table 5).

Discussion

Magnitude of phytoplankton blooms

Results from the present study supported our first hypothesis that discharge and meteorological conditions determined the onset and magnitude of phytoplanktonic blooms in the nutrient-rich Rivière Yamaska. Over the 2008–2013 period, plankton biomass was strongly correlated to discharge (–) and indirectly linked to PAR (+) and precipitation (–), but showed little relationship to nutrient and DOC concentrations. These results indicate that under conditions of excess nutrient concentrations, physical conditions such as discharge and light availability control planktonic-bloom formation at short (weekly), intermediate (seasonal) and long (inter-annual) time scales.

Linearization of the drainage network in heavily farmed watershed increases river flashiness (ratio of maximum to minimum daily flow), which was reported to be high in the Yamaska (842-fold), and the neighbouring Saint-François (181-fold) and L'Assomption (134-fold) rivers (Hudon and Carignan 2008). Weather conditions and discharge were primary drivers of phytoplankton community in temperate Rideau River (Ontario) (Hamilton et al. 2012) as well as in tropical St. Johns River (Florida, U.S.A.)

(Phlips et al. 2007). Light availability limited phytoplankton abundance in blackwater lowland rivers such as the Rio Negro (Brazil) (Hammer 1965), the Rideau (Canada) (Hamilton et al. 2012) and the St. Johns (U.S.A.) (Phlips et al. 2000).

Bursts of high discharge yielded the lowest Chl-*a* concentrations. Maximum chlorophyll-*a* concentrations were forecasted to occur after three consecutive days of intermediate ($15\text{--}43\text{ m}^3\text{ s}^{-1}$) discharge conditions and high light intensity. Surprisingly, prolonged episodes of extreme drought ($< 15\text{ m}^3\text{ s}^{-1}$) did not lead to major bloom events, but rather to sustained high values of chlorophyll-*a* and cell biomass. High phytoplankton biomass ($120\text{ }\mu\text{g Chl-}a\text{ L}^{-1}$) was reported under low discharge ($< 30\text{ m}^3\text{ s}^{-1}$) in large eutrophic rivers such as the Danube (Europe) (Kiss et al. 1994). Water discharge and turbidity were shown to control phytoplankton abundance in numerous lowland rivers such as the Someş (Romania/Hungary) (Istvánovics et al. 2014), the Po (Italy) (Tavernini et al. 2011), the Adige (Italy) (Salmaso and Braioni 2008), the Ebro (Spain) (Sabater et al. 2008), the Meuse (Belgium) (Descy et al. 1987), the Mississippi (U.S.A.) (Baker and Baker 1979) and the Murray (Australia) (Hötzels and Croome 1996). Although discharge is the most commonly used variables to describe residence time, water velocity (a function of channel cross-section) is a more useful variable to compare the potential for thermal stratification favourable to cyanobacterial development (Mitrovic et al. 2003). In the free-flowing lower Rivière Yamaska, minimal current velocity (0.08 m s^{-1}) under drought conditions were still above values impeding cyanobacterial blooms ($0.03\text{--}0.05\text{ m s}^{-1}$, Mitrovic et al. 2011).

542 **Composition of phytoplankton blooms**

543 The phytoplankton species in the lower Rivière Yamaska were typical of
544 assemblages occurring in many temperate, nutrient-rich riverine systems around the
545 world. Centric diatom assemblages found in our study are similar to the flora of the Loire
546 (France) (Abonyi et al. 2012), the Tisza (Europe) (Istvánovics et al. 2010) and the
547 Danube (Várbíró et al. 2007), which were characterized by *Scenedesmus* spp., *Cyclotella*
548 *meneghiniana*, *Nitzschia acicularis*, *Skeletonema potamos* and *Stephanodiscus hantzschii*.
549 In the Rivière Yamaska, centric diatoms dominated over most summers, except for the
550 dry summer of 2013, which had higher abundances of chlorophytes (e.g., *Pteromonas*
551 *aculeata*, *Chlamydomonas* spp.) and cryptophytes (e.g., *Cryptomonas erosa*). The
552 tolerance of centric diatoms and mixotrophic cryptomonads to low light availability is
553 well documented (Reynolds and Descy 1996) and explains their year-round dominance in
554 large rivers (Rojo et al. 1994; Hudon 2000; Hamilton et al. 2011; Abonyi et al. 2012). It
555 is noteworthy that summers of lowest discharge in the Yamaska (2012, 2013) coincided
556 with a reduction in diatom abundance. Diatoms were replaced by small, motile, flagellate
557 taxa better suited to withstand low turbulence and maintain themselves in the water
558 column (Kruk et al. 2010; Istvánovics et al. 2010).

559 Although riverine plankton assemblages tend to be dominated by truly planktonic
560 species, benthic and tychoplanktonic taxa (e.g., *Ulnaria* spp., *Fragilaria* spp.) detached
561 from their substrate or brought in by tributaries and from slow-flowing littoral areas also
562 contribute to seston diversity (Hudon et al. 1996). The group of taxa defined by our
563 Cluster II included many tychoplanktonic taxa (euglenoids, pennate diatoms,
564 pyrrhophytes, cryptophytes, various chlorophytes), which together represented 25–45%

of total plankton biomass, depending on the combination of discharge and incident light intensity.

Local production vs. advection of plankton from upstream reservoirs

Our short-term measurements of O₂ production under rising and falling discharge (2008) revealed that plankton production was temporarily interrupted during episodes of rising discharge, but resumed when discharge returned to low values. In contrast, during the dry summer of 2012, planktonic O₂ production and biomass remained generally high, but were modulated by climatic events (sunshine, precipitation).

In upstream lakes and reservoirs, eutrophic conditions and longer residence times favoured toxic cyanobacterial blooms. Public reports of cyanobacterial occurrence likely underestimate the frequency and duration of cyanobacterial blooms. Public reports to MDDELCC suggested that such episodes occurred independently within each impoundment and did not show evidence of spreading downstream. Indeed, in the 1000 km-long Loire (Abonyi et al. 2012) and the Murray River (Al-Tebrineh et al. 2012), markedly different planktonic assemblages were shown to occur simultaneously in spatially distant reaches representing different riverine habitats. During the summer 2010 drought event in Australia, however, a bloom of *Dolichospermum* (*Anabaena*) *circinalis* confined to a small package of water was followed over a distance of 650 km in the mid- and lower Murray River (Bowling et al. 2013). Targeted surveys should be carried out in the future to determine the fate of blooms in Yamaska reservoirs once they are released downstream.

Persistent turbulence, dilution by incoming tributaries and short residence time could limit cyanobacterial abundance in the free-flowing downstream reach of the Rivière Yamaska, even under the lowest discharge conditions observed in this study. Lake Ontario plankton showed a clear shift in composition and biomass after entrainment into turbulent St. Lawrence River (Hudon et al. 1996). Cyanobacterial assemblages growing in the upper reaches of the Rivière Yamaska do not persist after being flushed out of stratified reservoirs into the free-flowing, turbid river stem, regardless of discharge condition. Under high discharge conditions, transit time is short, but underwater light is restricted by deep waters whereas under low discharge conditions, transit time is long, but underwater light conditions are more favourable. As shown by our measurements of short-term O₂ production, bloom formation in the lower reaches of the river were rather controlled by enhanced local plankton production under intermediate discharge and sunny conditions.

Why aren't lower Rivière Yamaska blooms dominated by cyanobacteria?

Contrary to our second hypothesis, the lowest discharge did not lead to the dominance of cyanobacteria blooms in the lower Rivière Yamaska, as previously reported for eutrophic rivers experiencing drought conditions (e.g., Nakdong River (South Korea), Jeong et al. 2007; Murray River (Australia), Bowling et al. 2013). Under low discharge conditions in the Rivière Yamaska (2012), water temperature was warmer (by about 3°C), the river was shallower (by about 2 m) and the water column was better illuminated ($Z_{eu}/Z_t \approx 0.9$ instead of ≈ 0.3) than under high discharge (2008) conditions. Although current speed was markedly reduced ($< 0.1 \text{ m s}^{-1}$) under low discharge conditions, river flow remained turbulent, as shown by high values of Reynolds number. Under high turbulence and

nutrient availability, slow-growing cyanobacteria cannot compete with fast-growing diatoms and chlorophytes (Reynolds and Descy 1996). The presence of slow-flowing reaches, fluvial lakes and impoundments along the course of the river likely plays a major role in cyanobacterial proliferation. In the temperate Spree (Europe) (Köhler 1993) as well as in tropical Darling River (Hötzel and Croome 1994; Mitrovic et al. 2003) and St. Johns River (Phlips et al. 2007), prolonged retention time of water in fluvial lakes/impoundments were shown to allow the development of stable cyanobacteria populations. Under calm conditions, planktonic diatoms are replaced by flagellated taxa, which are eventually outcompeted by cyanobacteria that can control their depth in stratified systems.

Management implications

Given the forecasted changes in climate for southern Quebec (CEHQ 2015), prolonged drought periods followed by episodes of heavy rainfall and warmer temperatures are likely to occur more frequently during summer. Such conditions will exacerbate the problem of eutrophication, particularly the proliferation of potentially toxic cyanobacteria (Paerl et al. 2011). Chronically low discharge could intensify the pressure to construct additional dams and water retention structures along the course of the Rivière Yamaska, thus increasing residence time and particle sedimentation, and favouring vertical stratification in the river. In turn, the development of a stable epilimnetic layer with high light availability will likely enhance the development of blooms of potentially toxic, diazotrophic cyanobacteria. For example, in nutrient-rich, heavily impounded river systems such as the Murray and Nakdong rivers, cyanobacterial blooms were mitigated through discharge management (Jeong et al. 2007; Mitrovic et al.

2003, 2011). Cyanobacterial blooms are a common occurrence in the upper Rivière Yamaska and our study highlighted the strong interaction between river discharge and bloom magnitude and species composition. Although the flow in the lower reaches of Rivière Yamaska has so far remained sufficient to avoid cyanobacterial proliferation, our results suggest that further increasing water residence time, either through severe drought or river damming, will amplify the risk of toxic algal blooms.

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861

862 **Table 1.** Hydrological characteristics of Rivière Yamaska (north branch) at five gauging stations located downstream of an
863 impoundment, derived from point measurements obtained at individual river cross-sections under low and high discharge conditions.
864 Reservoir information from CEHQ (2016). Hydrometric information at gauging stations from Luc Gauthier, MDDELCC (personal
865 communication). Information on reported cyanobacterial occurrences (MDDELCC 2016).

Site	Lac Waterloo	Shefford-Vale	Granby	Farnham	Saint-Hyacinthe
Hydrometric station no.	30343	030309	030340	30302	030345
Fig. 1 location	(6)	(5)	(4)	(3)	(2)
Watershed area (km ²)	31.2	131	235	1231	3334
Lake/impoundment name	Lac Waterloo	Réservoir Choinière	Lac Boivin	R. Yamaska (Farnham dam)	R. Yamaska (Saint-Hyacinthe dam)
Impounded area (ha)	159	456.4	197	8.2	200.9
Distance to sampling site (km)	164.0	145.4	124.9	98.5	50.5
Low/high river stage					
River discharge (m ³ s ⁻¹)	0.04 / 4.94	0.11 / 17.10	0.87 / 25.20	3.22 / 260	2.57 / 755
Mean river depth (m)	0.12 / 0.85	0.15 / 0.99	0.23 / 1.26	0.30 / 1.87	0.38 / 4.16
River width (m)	1.8 / 10.0	2.3 / 13.4	9.9 / 26.0	75.0 / 80.3	84.0 / 113.2
River wetted section (m ²)	0.22 / 8.50	0.34 / 13.30	2.27 / 32.80	22.50 / 150.10	32.10 / 471.00
Mean current speed (m s ⁻¹)	0.19 / 0.59	0.32 / 1.29	0.38 / 0.77	0.14 / 1.73	0.08 / 1.60
Re *10 ⁶ (dimensionless)	0.09 / 2.01	0.19 / 5.12	0.35 / 3.89	0.17 / 12.94	0.12 / 26.63
Length of downstream reach (km)	18.6	20.5	26.4	48.0	50.5
Transit time to next reach (h)	27.2 / 8.8	17.8 / 4.4	19.3 / 9.5	9.5 / 7.7	175.0 / 8.8
Time (d) to sampling site (No. 1)	10.4 / 1.7	9.3 / 1.3	8.6 / 1.1	7.8 / 0.7	7.4 / 0.4
Cyanobacterial episodes (2008–2012)	26				
Number of dates reported		14	39	6	3
Dominant genera	<i>Microcystis</i>	<i>Woronichinia</i> <i>Aphanizomenon</i>	<i>Woronichinia</i> <i>Microcystis</i>	<i>Woronichinia</i> <i>Microcystis</i>	<i>Woronichinia</i> <i>Microcystis</i>

Table 2. Mean (s.d., N) Rivière Yamaska discharge (at Saint-Hyacinthe, CEHQ station 030345), photosynthetically active radiation and precipitation recorded over the period of water quality and phytoplankton sampling of each year (N = number of days). Differences among years were tested using one-way ANOVA (of Log-transformed values); letters indicate years that are significantly different (n.s.: not significant; $p < 0.001$: highly significant difference ***; n.a.: not available).

	2008	2009	2010	2011	2012	2013	ANOVA (signif)
Sampling period	Jun. 25 – Sept. 24	Jun. 29 – Sept. 9	July 13 – Sept. 29	May 31 – Aug. 24	June 26 – Sept. 17	July 2 – Aug. 27	Years
Discharge (Q, m ³ s ⁻¹)	63.6 <i>a</i> (96.0, 91)	47.7 <i>ab</i> (50.9, 67)	24.9 <i>bc</i> (26.0, 72)	22.4 <i>c</i> (20.5, 86)	8.0 <i>c</i> (6.3, 83)	14.2 <i>c</i> (8.5, 50)	***
Photosynthetically active radiation (μmol m ⁻² s ⁻¹)	601.2 <i>b</i> (222.1, 83)	583.8 <i>b</i> (223.4, 73)	586.4 <i>b</i> (250.2, 79)	753.9 <i>a</i> (255.4, 86)	772.3 <i>a</i> (242.1, 84)	801.2 <i>a</i> (227.4, 54)	***
Precipitation (mm)	4.4 <i>a</i> (10.4, 91)	3.0 <i>a</i> (8.2, 67)	3.3 <i>a</i> (6.6, 72)	2.3 <i>a</i> (5.1, 58)	2.4 <i>a</i> (5.8, 83)	2.4 <i>a</i> (5.4, 50)	n.s.

Table 3. Mean (s.d., N) daily values of water temperature and turbidity and concentrations of chemicals measured at the time of phytoplankton sample collection at our sampling site (Fig. 1, No. 1) in the Rivière Yamaska (2008–2013). Water temperature and turbidity data were obtained from the high frequency YSI multi-probe mooring for the entire sampling period. Because the YSI mooring covered a shorter period in 2012 (June 26 – July 28) than in 2008, 2009 and 2011, it was excluded from the inter-annual comparisons of temperature and turbidity. Results presented are for a one-way ANOVA (Log-transformed values) between years; letters indicate years that are significantly different (n.s.: not significant; $p < 0.001$: highly significant difference ***; n.a.: not available).

	2008	2009	2010	2011	2012	2013	ANOVA (signif)
Water temperature (°C)	21.8 <i>a</i> (2.5, 92)	22.2 <i>ab</i> (2.1, 73)	n.a.	23.3 <i>b</i> (2.4, 77)	25.0 (1.7, 44)	n.a.	***
Turbidity (NTU)	45.8 <i>a</i> (45.5, 92)	108.1 <i>b</i> (76.8, 70)	n.a.	94.7 <i>b</i> (29.6, 72)	268.2 (278.0, 37)	n.a.	***
k (m ⁻¹)	4.55 <i>a</i> (0.70, 13)	5.20 <i>ab</i> (1.81, 7)	6.61 <i>b</i> (0.35, 8)	5.14 <i>ab</i> (1.72, 11)	5.39 <i>ab</i> (1.12, 7)	5.25 <i>ab</i> (0.86, 9)	***
Suspended particulate matter (mg L ⁻¹)	27.5 <i>b</i> (7.9, 14)	44.4 <i>ab</i> (25.5, 7)	78.6 <i>a</i> (11.0, 10)	61.7 <i>ab</i> (37.6, 11)	78.1 <i>a</i> (33.8, 7)	56.1 <i>ab</i> (20.6, 9)	***
DOC (mg C L ⁻¹)	8.3 <i>a</i> (1.3, 13)	8.0 <i>a</i> (0.4, 7)	7.5 <i>ab</i> (0.6, 8)	6.2 <i>cd</i> (0.7, 11)	5.4 <i>d</i> (0.3, 7)	6.6 <i>bc</i> (0.8, 9)	***
TN (mg N L ⁻¹)	n.a.	3.0 <i>a</i> (1.4, 7)	1.9 <i>a</i> (0.6, 8)	2.6 <i>a</i> (1.5, 11)	1.0 <i>b</i> (0.3, 7)	2.1 <i>a</i> (0.9, 9)	***

NO ₂ -NO ₃ (mg N L ⁻¹)	1.2 <i>ab</i> (0.5, 14)	2.2 <i>ab</i> (1.5, 7)	1.1 <i>ab</i> (0.7, 9)	1.7 <i>a</i> (1.6, 11)	0.4 <i>b</i> (0.2, 4)	1.5 <i>ab</i> (1.1, 9)	n.s.
NH ₄ (µg N L ⁻¹)	21.0 <i>ab</i> (12.2, 12)	29.1 <i>ab</i> (24.1, 7)	15.1 <i>ab</i> (4.3, 8)	36.0 <i>a</i> (39.4, 11)	9.0 <i>b</i> (3.9, 7)	15.8 <i>ab</i> (7.2, 9)	n.s.
TP (µg P L ⁻¹)	106.5 <i>a</i> (29.1, 13)	140.1 <i>a</i> (33.3, 7)	140.9 <i>a</i> (22.8, 9)	130.2 <i>a</i> (37.1, 11)	141.9 <i>a</i> (37.2, 7)	119.7 <i>a</i> (25.5, 9)	n.s.
TDP (µg P L ⁻¹)	50.7 <i>a</i> (25.6, 13)	57.0 <i>a</i> (34.1, 7)	45.1 <i>a</i> (20.2, 8)	41.0 <i>a</i> (22.2, 11)	35.9 <i>a</i> (10.1, 7)	35.3 <i>a</i> (17.4, 9)	n.s.

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881 **Table 4.** Mean (s.d.) total biomass, chlorophyll-*a* concentration and biomass of individual taxa representing at least 5% of total
882 plankton biomass for each year at our sampling site (Fig. 1, No. 1) in the Rivière Yamaska (2008–2013). For each year, the number of
883 samples (N) for taxonomical analysis is specified. Dominant taxa are indicated for each taxonomical group. The cluster to which each
884 taxon is associated from Fig. 4 is shown. (**Note:** —: not recorded; x: taxa representing <5% of average biomass).
885

	2008 (N = 10)	2009 (N = 10)	2010 (N = 11)	2011 (N = 12)	2012 (N = 8)	2013 (N = 9)	Cluster (Fig. 4)
Cell biomass (µg L ⁻¹)	1930.9 (2335.3)	2518.0 (2615.1)	1078.7 (653.0)	2876.9 (2626.5)	1355.2 (804.5)	4071.2 (4128.9)	
Chlorophyll- <i>a</i> (µg Chl- <i>a</i> L ⁻¹)	24.2 (23.0)	27.0 (25.0)	25.3 (9.7)	25.8 (18.6)	25.1 (7.7)	28.6 (18.3)	
Diatoms							
<i>Aulacoseira granulata</i> (Ehrenb.) Sim.	x	x	x	137.5	x	x	II
<i>Cyclotella/Discotella</i> spp.	218.7	227.5	490.0	317.2	138.3	1031.2	I
<i>Skeletonema potamos</i> (Weber) Hasle	437.7	1507.3	x	733.8	x	524.1	I
<i>Stephanodiscus parvus</i> Stoerm. & Hakansson	380.4	197.8	—	—	389.7	551.0	I
Other diatoms	147.6	x	64.6	151.6	x	x	II–IV
Chlorophyta							

<i>Carteria</i> spp.	444.2	x	—	866.5	—	—	IV
<i>Chlamydomonas</i> spp.	x	x	82.1	x	89.0	332.6	II
<i>Pteromonas aculeata</i> Lemmerm.	x	—	—	—	—	2420.8	IV
Other Chlorophyta	119.7	x	125.5	195.4	x	x	II–IV
Cryptophyta							IV
<i>Cryptomonas erosa</i> Skuja	x	x	54.9	228.9	x	520.6	II
Pyrrhophyta							IV
<i>Peridinium</i> spp.	x	x	64.7	x	172.5	x	II
Chrysophyta	x	x	—	x	132.5	x	IV
Cyanobacteria	x	317.7	98.9	160.7	x	x	III

Table 5. Biomass of planktonic algae (% of total biomass is shown in parentheses) belonging to each of the four clusters of algal taxa (Fig. 4) found in four classes ($\mu\text{g Chl-}a\text{ L}^{-1}$) of samples derived from regression tree analysis and defined by discharge (mean daily Q three days before sampling, $\text{m}^3\text{ s}^{-1}$) and light (mean hourly PAR three days before sampling, $\mu\text{mol m}^{-2}\text{ s}^{-1}$) (Fig. 7).

	Classes of samples ($\mu\text{g Chl-}a\text{ L}^{-1}$) defined by discharge (Q) and light (PAR) conditions			
	1 Q ≥ 44	2 Q < 15	3 Q 15–43 PAR < 783	4 Q 15–43 PAR ≥ 783
Mean ($\pm$ s.d.) Chlorophyll- <i>a</i> concentration in model ($\mu\text{g Chl-}a\text{ L}^{-1}$)	6.4 ± 7.8	23.3 ± 9.9	27.6 ± 14.9	51.6 ± 20.92
Mean biomass ($\mu\text{g L}^{-1}$) (%)				
Cluster I (Dominant centric diatoms)	350.1 (40)	779.7 (41)	1668.6 (65)	3235.3 (65)
Cluster II (Mixed algae from five taxonomical groups)	392.4 (45)	793.5 (42)	661.3 (26)	1393.5 (28)
Cluster III (Cyanobacteria)	5.7 (< 1)	33.2 (2)	33.7 (1)	128.6 (3)
Cluster IV (Mixed Chlorophyta, Chrysophyta and Pyrrhophyta)	130.9 (15)	282.9 (15)	205.9 (8)	203.1 (4)
Total plankton biomass ($\mu\text{g L}^{-1}$)	879.1	1889.3	2569.6	4960.5

Figure 1. Map of Rivière Yamaska watershed (bold outline) in the St. Lawrence River Valley (inset), Quebec. The Rivière Yamaska flows into Lac Saint-Pierre downstream of Sorel. Other major tributaries and flow direction (arrow) of St. Lawrence River are also shown. Sampling sites are indicated in the lower Yamaska (No. 1), the towns of Saint-Hyacinthe (No. 2) and Farnham (No. 3), and lakes and reservoirs along the north (No. 4–6) and main (No. 7) branches of the Rivière Yamaska where hydrological conditions were characterized (see Table 1). Locations of cyanobacterial episodes reported by the public (2008–2012, MDDELCC 2016) in the Rivière Yamaska watershed are shown (full circles). The distribution of farmlands (shaded area) for 2010 was obtained from the North American Land Change Monitoring System (NALCMS) (available at <https://landcover.usgs.gov/nalcms.php>). The location of Station de Biologie des Laurentides (No. 8) is also indicated.

187x183mm (300 x 300 DPI)

Figure 2. Temporal (2008–2013, Panels A to F) variations of plankton cell biomass (mg L^{-1} , inner left Y-axis, vertical bars) and chlorophyll-*a* ($\mu\text{g Chl-}a \text{ L}^{-1}$, outer left Y-axis, open circles) at our sampling site (Fig. 1, No. 1) in conjunction with discharge ($\text{m}^3 \text{ s}^{-1}$, right Y-axis, hairline) variations in the Rivière Yamaska downstream of Saint-Hyacinthe (Fig. 1 No. 2). Discharge data covers the same interval for each year; the name of each month is indicated at the beginning of each period.

Figure 3. Relative abundance (proportion of total biomass) of each taxonomic group for each sampling season at our sampling site (Fig. 1, No. 1) in the Rivière Yamaska.

129x83mm (120 x 120 DPI)

Figure 4. Cluster analysis of the relative abundance of major taxa in all Rivière Yamaska samples (Fig. 1, No. 1), using the Lance and Williams distance and flexible-beta clustering method. Four distinct groups (Clusters I–IV) were found to represent taxa dominating samples simultaneously, at a distance of 1.3 (vertical black line).

244x241mm (300 x 300 DPI)

Figure 5. A: Correlations of principal components with constituent chemical variables measured at our sampling site (Fig. 1, No. 1) in the Rivière Yamaska (May 2008 – Aug. 2013, N = 50).

Figure 5. B: Correlation between the first principal component and the mean river discharge for the three days prior to sampling; sampling dates are represented.

Figure 6. Hourly variations of water discharge (thin black line), turbidity (grey line) and dissolved O₂ (bold dotted line) at our sampling site (Fig. 1, No. 1) in the Rivière Yamaska. Point measurements of chlorophyll-*a* concentration (full circles) and total biomass (open squares) are also indicated. A: Flash discharge events August 2–28, 2008. B: Stable low discharge period June 22 – July 11, 2012.

215x279mm (150 x 150 DPI)

Figure 7. Hierarchical regression tree model predicting the concentration of planktonic chlorophyll-*a* ($\mu\text{g Chl-}a \text{ L}^{-1}$) at our sampling site (Fig. 1, No. 1) in the Rivire Yamaska (2008–2013) from the mean river discharge (*Q*) and illumination (*PAR*) over the three days prior to sampling. For each branch of the tree, the mean $\pm$ s.d. chlorophyll-*a* concentration ($\mu\text{g Chl-}a \text{ L}^{-1}$) and the number of samples (*N*) are specified; the model explains 59% of total variance in data.

143x103mm (144 x 144 DPI)