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Extreme variability of cyanobacterial blooms in an urban drinking water supply

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Harmful cyanobacterial blooms are of increasing global concern and their prediction and management requires an improved understanding of the controlling factors for cyanobacterial growth and dominance. In Lake St Charles, the drinking water supply for Quebec City, Canada, harmful cyanobacterial blooms were first recorded in autumn 2006. Our aims were to define the temporal and spatial variations in the cyanobacterial community structure of this reservoir and to address the hypothesis that interannual variability in cyanobacterial biomass and species composition is mainly controlled by nutrients, temperature and water column stratification. Over five consecutive summers (2007–2011), the north basin had consistently higher concentrations of bloom-forming cyanobacteria than the south basin, and there were striking variations within and among years in total biomass and species composition. Correlation analysis underscored the contrasting environmental controls on different taxa of colonial cyanobacteria. *Anabaena flos-aquae* biovolume was correlated with surface temperature, water column stability (Schmidt index) and water residence time whereas *Microcystis aeruginosa* was highly correlated with total phosphorus and to a lesser extent with total nitrogen (TN), heat accumulation (degree-days above 20°C) and precipitation. *Aphanocapsa/Aphanothece* correlated significantly only with TN. These results also imply the sensitivity of high through-flow reservoir ecosystems to interannual variations in environmental forcing.

KEYWORDS: *Anabaena*; blooms; cyanobacteria; eutrophication; *Microcystis*; phytoplankton; reservoir

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INTRODUCTION

Cyanobacterial blooms have a wide range of impacts on aquatic ecosystems including shading of macrophyte communities, inhibition of zooplankton grazing, altered competitive interactions among phytoplankton and lethal impacts on fish and invertebrates caused by hypoxia (Havens, 2008; Vincent, 2009; Oliver *et al.*, 2012). The development of cyanobacterial blooms in drinking water supplies is of special concern given the ability of many cyanobacterial species to produce toxic compounds that are hazardous to animal and human health (Carmichael, 1992; Codd, 2000), to produce taste and odor compounds (Watson, 2003; Izaguirre and Taylor, 2004) and to cause filter clogging as a result of the high concentrations of biomass (Falconer, 1999). The occurrence of cyanobacterial blooms may therefore greatly increase the running costs for water treatment plants, as well as affect the confidence that residents place in their drinking water supplies.

One of the challenges for the water quality management of drinking water supplies is predicting the occurrence of blooms given the temporal variability in cyanobacteria and other phytoplankton. There is consensus that the typical phytoplankton succession often shows a pattern of greatest cyanobacterial abundance toward the summer when temperatures and water column stratification are maximal (e.g. Dokulil and Teubner, 2000; Latour *et al.*, 2004; de Figueiredo *et al.*, 2006; Paerl and Huisman, 2008). Although this pattern is often observed in dimictic lakes, it can be substantially modified by eutrophication, climate change and other factors. Predictive models for cyanobacteria abundance usually focus on total phosphorus (TP) and total nitrogen (TN) (Håkanson *et al.*, 2007), although nitrogen to phosphorus ratios (N/P) have also been identified in some studies as a potential factor affecting cyanobacterial dominance (Bulgakov and Levich, 1999; Smith and Bennet, 1999; Oliver *et al.*, 2012 and references therein).

An additional challenge for cyanobacterial monitoring in lakes and reservoirs is their potentially large spatial variability, both through the water column and over horizontal space, due to diverse ecological strategies (Carey *et al.*, 2012). Physiological variations among taxa may result in differences in response to spatial variations in environmental conditions. Furthermore, sampling protocols for bloom monitoring assume that the vertical distribution of cyanobacteria, like other groups of phytoplankton, is uniform throughout the mixed layer. However, some genera of cyanobacteria such as *Microcystis aeruginosa* and *Anabaena flos-aquae* are able to regulate their buoyancy during thermal stratification (reviewed in Oliver *et al.*, 2012). Cyanobacteria can be distributed horizontally in a patchy way due to the wind-driven accumulation of these surface blooms or by spatial variations in growth and loss processes (e.g. Ishikawa *et al.*, 2002).

Despite these potential spatial and temporal variations, many temperate lakes show an interannual regularity in the species composition and abundance of their phytoplankton communities (Talling, 1993; Kalff, 2002). This appears often to be the case for cyanobacteria, where the same genus or even species dominates each summer; for example, *Microcystis* in Lake Taihu, China (Chen *et al.*, 2003), and Lake Grangent, France (Latour *et al.*, 2004), and *Anabaena* in Fort Whytes Lakes, Canada (Dupuis and Hann, 2009), and Lake Rotongaio, New Zealand (Vincent, 1989). However, reservoir systems may deviate from this lake pattern given their short hydraulic residence times and more fluvial character. For example, in the Murray Darling River ecosystem, cyanobacterial proliferations have been linked to low discharge periods (Bormans *et al.*, 1997).

In Southern Quebec, Canada, cyanobacterial bloom events have been of increasing concern over the last decade. More than150 lakes were observed to contain substantial bloom-forming cyanobacteria in 2007, with implications for the sustained provision of ecosystem services from these waterbodies (Boissonneault *et al.*, 2007; Laurion *et al.*, 2009). One of these lakes, Lake St Charles, is the drinking water supply for 285 000 residents in Québec City, where cyanobacterial blooms were first reported in autumn 2006 (APEL, 2009). Since that time, the proliferation of harmful cyanobacteria such as *M. aeruginosa* and *A. flos-aquae* has become more pronounced in this lake, appearing earlier in the summer and persisting for a longer period (Bourget, 2011; Warren, 2011). A surface scum that had accumulated near the shoreline of Echo Bay in August 2007 had *M. aeruginosa* concentrations reaching 2 million cells mL^{-1} and 6.2 $\mu g\ L^{-1}$ of microcystin-LR, more than four times higher than Health Canada criteria for drinking water quality (analysis by Centre d'expertise et d'analyses environnementales du Québec, cited in Bourget, 2011).

Our aims in the present study were (i) to define the spatial and temporal variations in bloom-forming cyanobacteria in Lake St Charles as a case study of changing phytoplankton community structure in a north temperate reservoir and (ii) to address the hypothesis that cyanobacterial biomass and species composition are controlled by temperature, stratification conditions and N/P ratios. We undertook a 5-year study of the lake, measuring phytoplankton as well as physical and chemical variables. This provided a detailed multiyear data set for assessing the extent and causes of interannual and spatial variability in cyanobacterial communities.

METHOD

Site description

Lake St Charles is located 21 km north of Québec City at latitude 46°54′N, longitude 71°22′W and it covers a total area of 3.6 km^2 with a total volume of 14.8×10^6 m^3. The lake is composed of two sub-basins that differ in morphometry: the north basin is conical and reaches a maximum depth of 17.5 m, and the south basin has a maximum depth of 6 m (Fig. 1). The watershed of Lake St Charles extends over an area of 169 km^2. The mountains around the lake are composed of granite and gneiss covered by boreal forest, whereas the valley is overlaid by fine glacial sediments (Gérardin and Lachance, 1997). The watershed of Lake St Charles is subject to a temperate sub-humid climate, with an annual rainfall around 1300 mm. The principal inflow to Lake St Charles is the Hurons River, which drains 80% of the watershed and the single outflow is the St Charles River. The mean annual discharge measured at the gauging station of the St Charles River, 9 km downstream of the lake is 8.5 m^3 s^{-1} (Gaborit *et al.*, 2010). The trophic status of Lake St Charles is considered to be oligo-mesotrophic to mesotrophic depending on trophic indicators (D.C. Rolland *et al.*, unpublished data). Eight principal sampling stations were selected, covering several bays as well as the open waters of the lake (Fig. 1). In 2009, triplicate samples were taken at each station to assess the within-station variability. The sampling was undertaken once or twice per month throughout summer, between May and October.

Physical, hydrological and meteorological variables

A thermistor chain (Onset Tidbit TBI32, resolution 0.2°C) was installed in the deepest part of the lake (17.5 m) to obtain continuous measurements of temperature down the water column over the entire sampling periods. These data were then used to calculate two indices. First, the temperature values were converted to density and water-column stability was estimated by the Schmidt stability index (S, g cm^{-1}), calculated as:

$$S = A_0^{-1} \sum (z - z*)(\rho_z - \rho*)A_z\Delta_z$$
$$\rho* = V^{-1} \sum (V_z\rho_z)$$

where A_z is the lake area (m^2), ρ_z the density (g cm^{-3}) at depth z (m), z* the depth where the mean density ρ* is found, and V the volume of water (m^3). Depth intervals (Δ_z) of 1 m were used for the calculations. Second, as a measure of favorable conditions for cyanobacterial production, cumulative degree-days (°C day) were calculated by summing the recorded degrees (C°) each day above 20°C, a value that has been considered a threshold for cyanobacterial growth (Dupuis and Hann, 2009; Neuheimer and Taggart 2007).

Meteorological data were obtained from the weather station at Québec City Airport, located 14 km west of the lake (Environment Canada, 2012). The water level (WL, m) of Lake St Charles was measured near the dam at the outflow of the lake. The average water residence time (WRT, days) for each summer was obtained from the lake volume (V_L, m^3) and the average summer water outflow (Q, m^3 s^{-1}) as V_L/Q. The lake volume was calculated for each day from the WL and the hypsographic curve of the lake (D.C. Rolland *et al.*, unpublished data). The average summer water outflow was estimated by using the outflow measured each day at the gauging station of the River St Charles (CEHQ, 2012). This station is 9 km below the outlet of the lake, and the values were corrected for other watersheds discharging into the river between the lake outlet and the gauging station, as well as for the drinking water intake, also located upstream of the station.

Biological variables

Integrated water samples were collected with a 30-mm diameter plastic tube that extended from the surface to 2 m depth, and these were immediately transferred in the field into brown plastic bottles. The sampling was always done in the morning (8:00–10:00) in the north basin and at the same time the next day in the south basin. A volume of 250 mL was filtered under low light onto Whatman GF/F filters (nominal pore size of 0.7 μm), immediately after sampling to minimize the degradation of pigments. The filters were stored at −80°C until extraction of pigments in boiling ethanol (65°C), and the chlorophyll *a* (Chl-*a*) concentration was determined by fluorometry (Varian Cary Eclipse spectrofluorometer, Varian Inc., Canada) before and after acidification (Nusch, 1980). Another 250 mL was transferred into polyethylene bottles, fixed with Lugol's iodine (5% final concentration) and stored in the dark at 4°C. These samples were then used for the enumeration of cyanobacteria. The sedimentation method (Utermöhl, 1958) was used to concentrate samples before enumeration using an inverted microscope (Zeiss Axiovert 200), and biovolume (BV, mm^3 L^{-1}) was calculated from the cell counts and size measurements. The enumeration was done for two sites in 2007 and 2008 (N3 and N4), eight sites in 2009 and four sites in 2010 and 2011 (N3, N4, S2 and S4).

Chemical variables

For chemical analysis, unfiltered water samples were collected in polyethylene bottles previously washed with

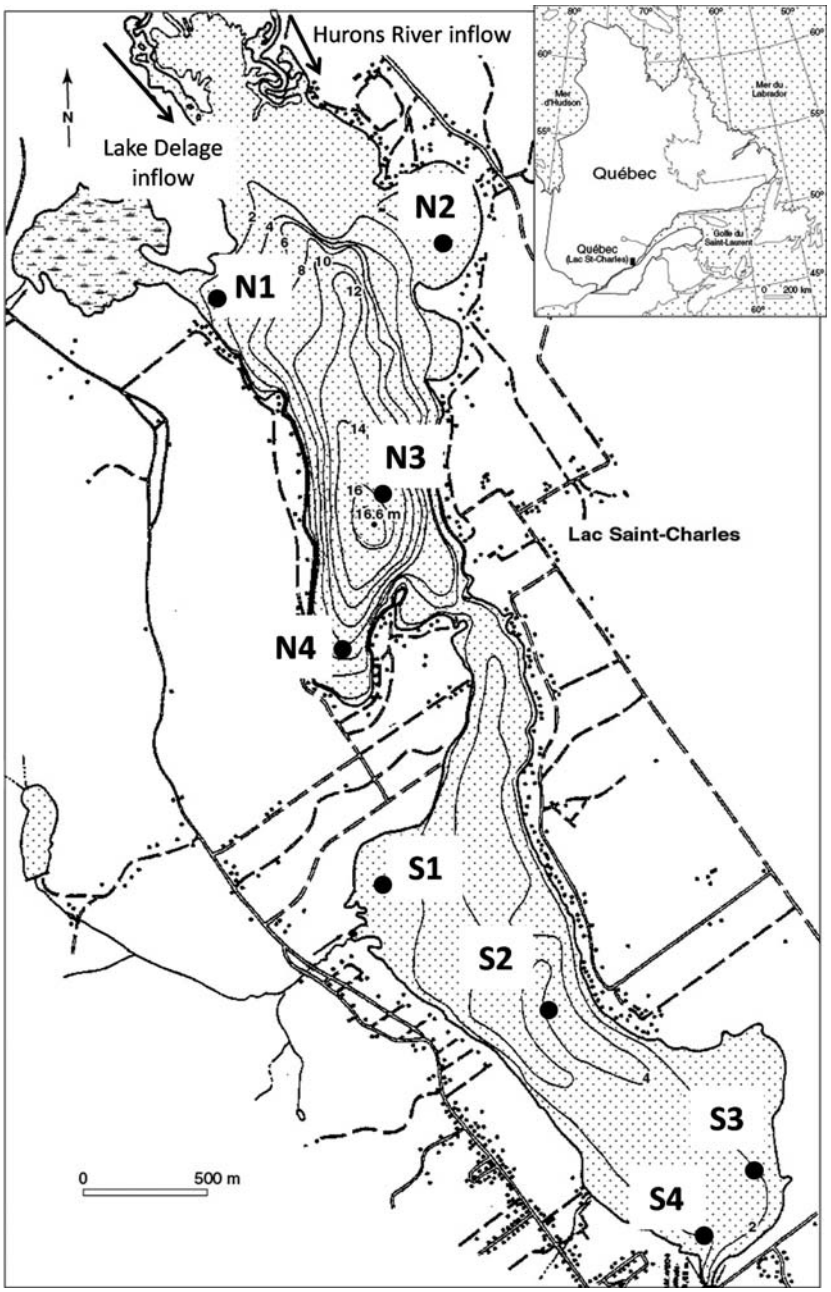

Fig. 1. Map of the Lake St Charles and location of the sampling sites. Northern basin: Talbot Bay (N1), Des Aigles Pêcheurs Bay (N2), deepest point of the lake (N3), Echo Bay (N4). Southern basin: Des Milans Bay (S1), middle of the southern basin (S2), beach (S3), dam (S4).

hydrochloric acid (10%) and rinsed seven times with deionized water. These samples were preserved in sulfuric acid (0.2% final concentration), and later digested with persulfate to determine TN and TP, respectively, with a Lachat flow injection analyzer and Genesys 10UV spectrophotometer (Thermo Spectronic) using standard techniques. Filtered water samples (0.2 μm filter) were analyzed for nitrate (NO_3^-) using a Dionex ICS 2000 ionic chromatograph, and for soluble reactive phosphorus (SRP) by a colorimetric method using the above spectrophotometer.

Statistical analysis

Analysis was performed using SIGMASTAT (version 11.0). Initial Shapiro–Wilk tests indicated that the data for most variables were not normally distributed, and Mann–Whitney non-parametric rank sum tests were

therefore performed to test differences between two independent observations. Kruskal–Wallis ANOVA on rank tests was used to compare more than two independent observations, and then all pairwise multiple comparisons were made using Dunn's method to identify significant differences ($P < 0.05$) between groups. The Spearman rank-order correlation analysis was conducted on the entire data set. Given the spatial correlation among environmental variables and certain gaps in the data set, it was considered inappropriate to apply multivariate analysis (Legendre and Legendre, 2012).

RESULTS

Meteorological conditions

Summer temperatures for the period from May to October during the 5 years of study (Table 3.1) were within the climate range for the period 1971–2000, which was 13.9 ($\pm$ 1.2)°C (Environment Canada, 2012). However, 2010 was characterized by more frequent periods of high warm temperatures, particularly in July, August and September. Rainfall between May and October was significantly higher in 2007, 2008 and 2011 and significantly lower in 2010 than the average conditions from 1971 to 2000 (689 mm of total precipitation, with 85 rainy days, Environment Canada, 2012). The total amount of precipitation between May and October was higher by 14% in 2007, 21% in 2008 and 11% in 2011 compared with this average. The variation in the WL was moderate during the 2007 and 2009 summers (respectively, 30 and 70 cm of variation between min and max; Table I). The WL was high throughout the 2008 summer, with a maximum value that exceeded the dam threshold. The Quebec Province experienced severe flooding at the beginning of summer 2011, including in the Lake St Charles watershed, and the WL of the lake rose to the full height of the dam on 4 May. This was also the year of shortest hydraulic residence time during the study period [19% below the 5-year mean value of 72 ($\pm$ 13) days]. In contrast, summer 2010 was a much drier season: the volume of precipitation was 15% less than the average from 1971 to 2000, the WL fell to a minimum of 1.95 m on 6 September, and the residence time that year was 28% longer than the 5-year mean value. There was a close inverse correlation between the WL and the lake WRT ($r = -0.92$, $P < 0.001$).

Water temperature and stratification

A maximum of 210°C-days was recorded in early September 2010 (Fig. 2). In 2008, the heat accumulation in the lake was much smaller, with a maximum of only 50°C-days by early September. The accumulation of heat was intermediate in 2007, 2009 and 2011 (respectively, 100, 92 and 113°C-days), with the maximum cumulative value reached by the middle of August.

The Schmidt stability index (S; Fig. 3) did not vary significantly between 2007 and 2009 but was significantly different in 2008, 2010 and 2011 ($P = 0.021$). The variability of S, as indicated by the standard deviation of average seasonal values, was intermediate in 2007 (190 g cm^{-1}), lower in 2008 and 2009 (respectively, 153 and 160 g cm^{-1}) and higher in 2010 and 2011 (respectively, 233 and 239 g cm^{-1}). Years 2007, 2008 and 2009 showed two periods of maximal stability: during the first part of summer (mid-June 2007, mid-July 2008 and end of June 2009) and during the second part of summer (early August 2007, early September 2008 and mid-August 2009). These periods of maximal stability varied in amplitude and duration. In 2010, there were two periods of maximal stability restricted to the first part of the summer (early June and mid-July), whereas in 2011 there were three brief periods of maximal stability during the first part of the summer (mid-June, mid-July and early August).

Nutrient concentrations

The average TP concentrations in the surface waters of Lake St Charles (Table II) were significantly higher in 2011 (by 29%) and lower in 2009 (by 30%) by comparison with the 5-year mean (9.5 μg L^{-1}). The average TN concentrations were significantly lower in 2009, 2010 and 2011(respectively, by 40.7, 23.8, and 9.6%) relative to the mean for the 5 years (0.35 mg L^{-1}). As a result, there was a wide range in TN:TP from 26 to 39. These values place Lake St Charles in an oligotrophic to near mesotrophic state (Kalff, 2002). Concentrations of surface SRP were near or below the detection limit (0.5 μg L^{-1}) each year. Surface NO_3^-–N concentrations were generally in the range 50–150 μg L^{-1}, with values in 2008 and 2011 that were higher than the overall mean (by 10 and 28%, respectively).

Spatial variation of the cyanobacterial communities

There was a significant ($P < 0.05$) but not close correlation ($r = 0.47$) between the total BV of cyanobacteria and Chl-*a* concentration. The former varied to a much greater extent among stations and among years: the overall coefficient of variation for cyanobacterial BV was 173%, while that for Chl-*a* was 44%. This greater variability was also apparent from the analysis of triplicate

Table I: Meteorological data for the 184 day period of sampling (1 May to 31 October) from the Québec City Airport weather station (Environment Canada)

Variables	Year				
	2007	2008	2009	2010	2011
Mean temperature ± SD (°C)	14.8 ± 4.8	14.3 ± 5.2	13.7 ± 5.7	15.2 ± 6.1	15.2 ± 5.2
Maximum extreme temperature (°C)	31.8 (2 August)	30.3 (2 September)	30.5 (17 August)	33.4 (7 July)	31.2 (22 July)
Days of daily mean temperature > 20°C	22/184	17/184	25/184	45/184	35/184
Days of daily mean temperature > 25°C	0/184	0/184	1/184	7/184	0/184
Total rainfall (mm)	783	831	696	585	764
Maximum daily rainfall (mm)	60.8 (20 July)	52.6 (14 September)	45.4 (29 July)	32.6 (8 September)	52.0 (28 August)
Total number of rainy days (mm)	82	96	88	90	96
Minimum WL (m)	2.49	2.53	2.10	1.95	2.19
Maximum WL (m)	2.78	3.39 (threshold)	2.81	2.99	3.39 (threshold)
Average residence time (days)	66 ± 18	65 ± 21	77 ± 16	91 ± 14	58 ± 15

Also given are the WLs relative to a reference datum at the dam across the lake outflow and estimates of hydraulic residence time in the lake (mean ± SD).

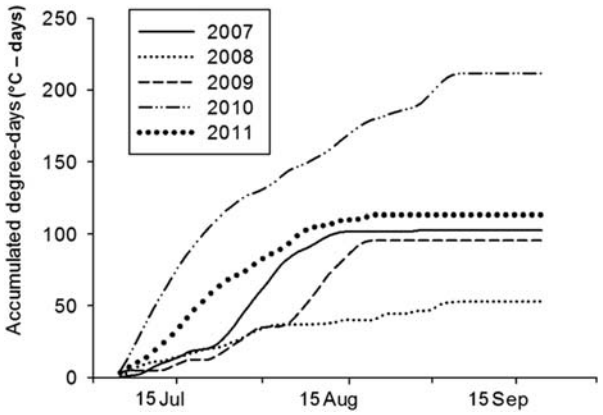

Fig. 2. Cumulative degree-days during five consecutive summers (2007–2011) at site N3 (station codes given in Fig. 1 legend).

samples at each station in 2009 (Fig. 4). The coefficient of variation in total cyanobacterial concentrations among triplicates ranged from 3.2 to 74%, with most coefficients below 15%. The maximum within-site variation was recorded in June (CV for triplicates of 26% at N3, 36% at N4, 74% at S1 and 64% at S2) but occurred at low cell concentrations (respectively, 5393, 5336, 2728 and 2712 cells mL^{-1}).

The spatial heterogeneity of cyanobacterial communities in Lake St Charles was closely examined in 2009 (Fig. 5). The otal cyanobacterial BV showed no significant difference among the eight sampling stations (mean ± SD of $0.251 \pm 0.018\ mm^3\ L^{-1}$; $P = 0.900$). However, the community structure was clearly different between the north and south basins. *Anabaena flos-aquae* accounted for 5.6% (N3) to 13.0% (N1) of the total BV of cyanobacteria in the north basin, but appeared only sporadically in the south basin (less than 0.5%). In contrast, *Aphanothece* sp. accounted for less than 0.5% of total BV in the north basin, but up to 33.6% (S4) to 40.1% (S2) of total BV in the south basin. *Aphanocapsa* sp. appeared in similar concentrations among all sampling sites, but accounted for a consistently less proportion of the total BV (2.4–4.1%). *Aphanothece* and *Aphanocapsa* cells were very small compared with other taxa (around 1% of the *A. flos-aquae* cell volume) resulting in a low BV contribution despite relatively high cell concentrations. *Microcystis aeruginosa* appeared only sporadically at all stations (<0.5%), except in S4 where there was a slightly higher accumulation (3.1%). *Woronichinia* sp. was always dominant in the north basin (78.9–86.9%) whereas *Snowella* sp. was dominant in the south basin (39.7–44.1%). These latter two taxa have large cells (twice the volume of *A. flos-aquae* cells) and were therefore disproportionately important in cell BV relative to their total cell concentrations.

In 2010, the horizontal distribution pattern of cyanobacteria (Fig. 5) was strikingly different when compared with 2009. Maximum concentrations were observed in the middle of north basin (N3; $0.360 \pm 0.011\ mm^3\ L^{-1}$), whereas the minimum was observed at the outflow near the dam (S4; $0.140 \pm 0.010\ mm^3\ L^{-1}$), but the overall statistical analysis showed no significant differences among sites ($P > 0.5$). Community structure was less variable across the lake than in 2009, with *A. flos-aquae* comprising the greater part of total BV at all sites (60.9% in S4 to 89.7% in S2). For *M. aeruginosa*, there was a south/north difference with an order of magnitude greater BV in the north basin (around $0.04\ mm^3\ L^{-1}$ at N3 and N4) relative to the south basin (0.004 and $0.009\ mm^3\ L^{-1}$ for S3 and S4, respectively). *Aphanizomenon* sp. was in higher concentration at S4 ($0.020\ mm^3\ L^{-1}$) than in other stations. There was no significant difference among all stations for the other taxa, which appeared sporadically and contributed globally less than $0.030\ mm^3\ L^{-1}$.

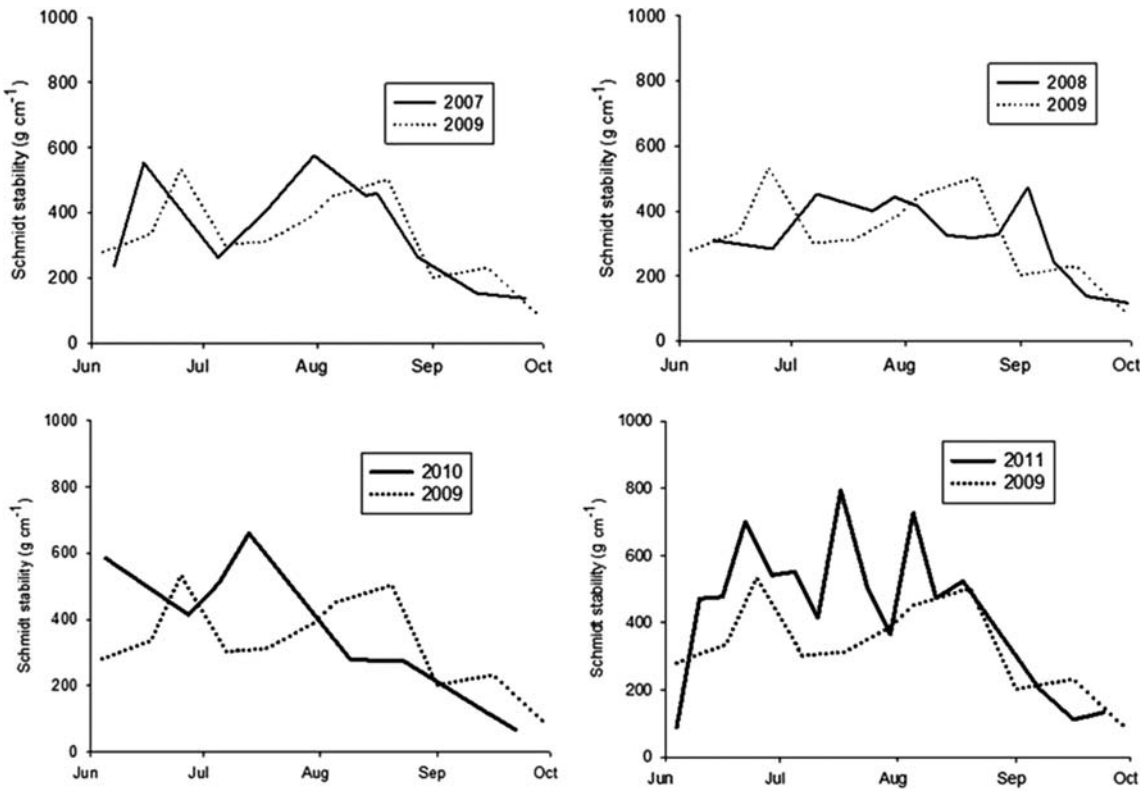

Fig. 3. Pairwise comparisons of the Schmidt stability index of the water column during five consecutive summers (2007–2011) at site N3 (station codes given in Fig. 1 legend). Year 2009 is used as a comparison because it was less subject to cyanobacterial blooms.

Table II: Nutrient and Chl-a concentrations in the surface waters of Lake St Charles

	Year				
Variables	2007	2008	2009	2010	2011
TP (μg L^{-1})	9.6 ± 2.3 (79)	9.4 ± 2.9 (77)	6.7 ± 1.3[a] (7)	7.8 ± 1.4[a] (7)	12.3 ± 2.9 (12)
TN (μg L^{-1})	341 ± 71 (46)	375 ± 117 (77)	211 ± 51[a] (7)	270 ± 82[a] (7)	320 ± 121 (18)
TN/TP	36 ± 14 (46)	39 ± 11 (77)	31 ± 15 (7)	35 ± 11 (7)	26 ± 19 (12)
SRP (μg L^{-1})	0.33 ± 0.21 (43)	0.82 ± 0.83 (66)	—	—	0.93 ± 0.56 (11)
NO_3^-–N (μg L^{-1})	94 ± 27 (48)	129 ± 33 (48)	85 ± 57[a] (7)	110 ± 80[a] (7)	150 ± 103 (7)
Chl-*a* (μg L^{-1})	6.5 ± 2.8 (71)	7.5 ± 3.1 (77)	4.0 ± 1.1 (65)	3.2 ± 1.0 (86)	3.7 ± 1.8 (12)

Values are summer means ± SD, with the number of samples given in parentheses.
[a]Provided by MDDEP (2011).

Temporal variation in the cyanobacterial communities

Cyanobacteria were present on all sampling dates and all sites, but their abundance ranged over more than 2 orders of magnitude, from a minimum of 0.01 mm^3 L^{-1} on 27 September 2011 to a maximum of 3.90 mm^3 L^{-1} on 17 August 2007. There were large differences in the median value of cyanobacterial BV in the north basin among the five summers of sampling (Fig. 6; $P = 0.031$). BV was highly variable both over the summer season and interannually. Furthermore, the timing of peak cyanobacterial biomass differed among years: August 2007, September 2008, September 2009, July 2010 and August 2011.

Microcystis aeruginosa was the dominant phytoplankton in August 2007, both in terms of BV and density (maximum concentration of 10^5 cells mL^{-1}), but this dominance did not occur throughout the entire summer (Fig. 6). July communities were dominated by *Aphanocapsa* sp., whereas in September *Aphanothece* sp. and *M. aeruginosa* co-dominated. In summer 2008, there was a slight increase in the cyanobacteria BV at the end of the summer, with a co-dominance of *M. aeruginosa* (maximum concentration of 10^4 cells mL^{-1}) and *Aphanocapsa* sp. in

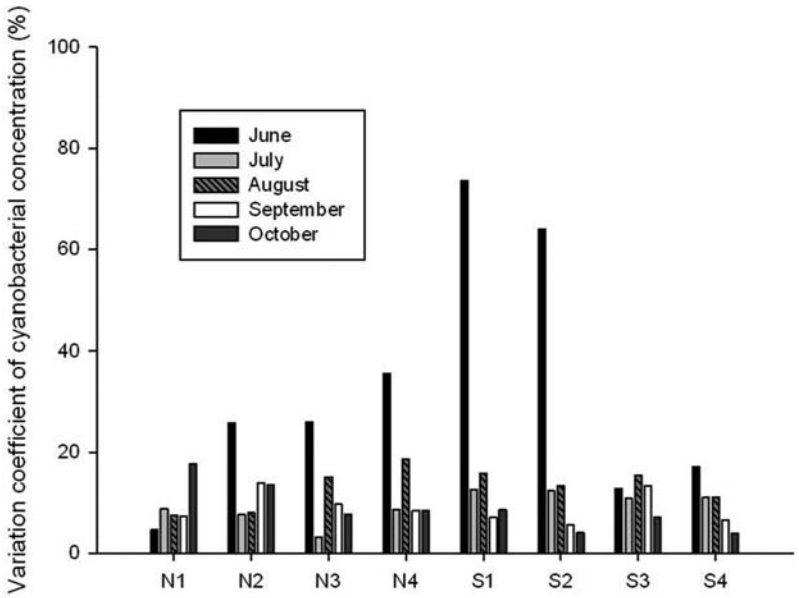

Fig. 4. Coefficient of variation (%) of cyanobacterial concentrations among each triplicate sampled in summer 2009.

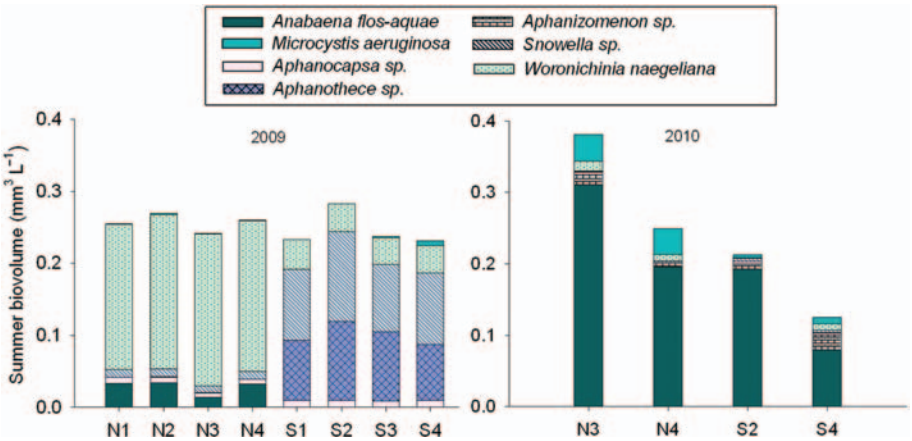

Fig. 5. Total BV and specific composition of cyanobacteria during summers 2009 and 2010. The values are averages for 10 (2009) and 13 (2010) sampling dates.

September. Bloom-forming cyanobacteria (*A. flos-aquae* and *M. aeruginosa*) were scarce in 2009 with a maximum density of $<10^3$ cells mL^{-1}. Throughout the summer, the water column was dominated by *Woronichinia* sp. but its concentration remained low. *Aphanothece* sp. BV was negligible in 2009, but this taxon was often dominant in terms of cell concentration, with averages of 22 416 cells mL^{-1} in July, 14 303 cells mL^{-1} in August and 11 898 cells mL^{-1} in September. In 2010, *A. flos-aquae* dominated from June to September in term of BV and density (2×10^4 cells mL^{-1}). *Aphanizomenon* sp. appeared in August 2010 in low concentrations, but was absent during the other summers. In 2011, the total BV of cyanobacteria remained low throughout the summer, with dominance of the assemblage by *A. flos-aquae*, but at low density (less than 10^3 cells mL^{-1}).

Correlations between biotic and abiotic variables

For the entire 5 years of seasonal and spatial data, there were significant correlations between the abundance of specific cyanobacterial taxa and certain environmental variables (Table III). The BV of *A. flos-aquae* (BV_{Anab}) was positively correlated with the surface water temperature, Schmidt stability index, average WRT over the previous 15 days and total precipitation over the previous 3 days, whereas it was negatively correlated with the average WL

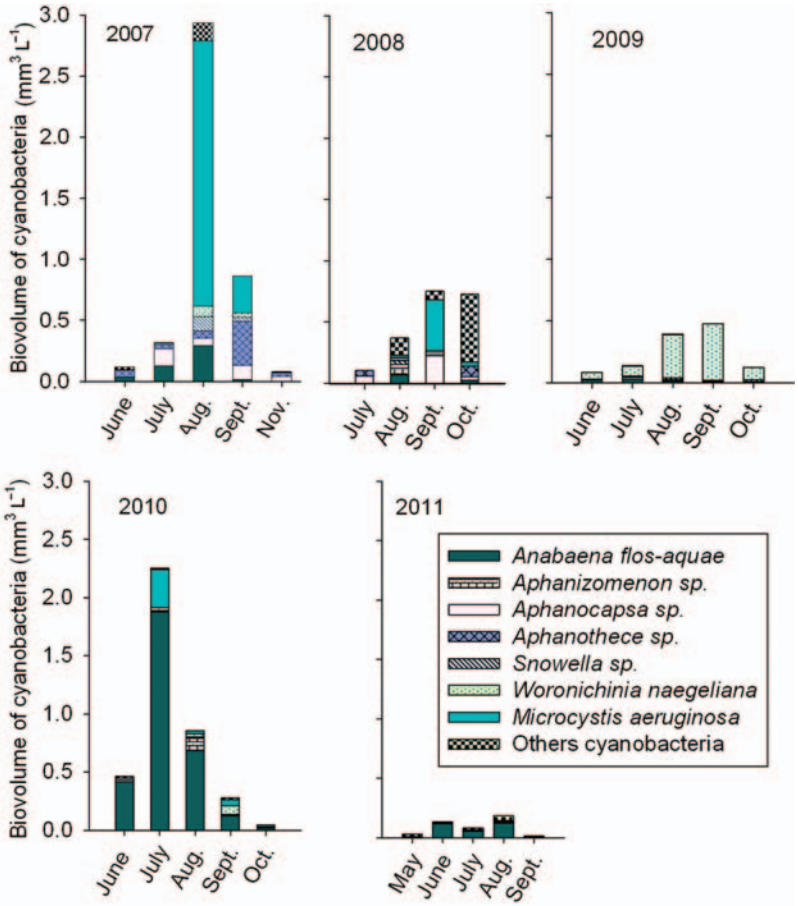

Fig. 6. Seasonal and interannual variations in total BV and specific composition of cyanobacteria in the north basin of Lake St Charles.

Table III: Spearman's rank correlations between biotic and abiotic variables of surface water

	Abiotic variables								
Biotic variables	$T°^a$	DD[a]	S^a	WRT^a_{15}	WL^a_{15}	PPT[a]	TP[b]	TN[b]	TN/TP[b]
BV_{TOT}	0.18	0.02	0.19	0.33**	−0.26*	0.20*	0.59*	0.64*	−0.68*
BV_{Anab}	0.48**	0.02	0.33**	0.30**	−0.26*	0.27*	0.44	0.30	−0.45
BV_{Micro}	0.16	0.25*	−0.09	0.12	−0.14	0.22*	0.70*	0.60*	−0.27
BV_{Aphano}	0.13	−0.10	0.09	0.05	0.01	0.13	0.19	0.58*	−0.32
BV_{others}	0.01	0.09	0.07	0.09	−0.08	0.19*	0.43	0.27	−0.54
Chl-*a*	−0.06	0.10	−0.25*	0.01	0.01	0.20*	0.48	0.61*	−0.40

Biotic variables: BV of total cyanobacteria (BV_{TOT}, $mm^3\ L^{-1}$), *A. flos-aquae* (BV_{Anab}, $mm^3\ l^{-1}$), *M. aeruginosa* (BV_{Micro}, $mm^3\ L^{-1}$), *Aphanocapsa/Aphanothece* sp. (BV_{Aphano}, $mm^3\ L^{-1}$) and of others groups of cyanobacteria (BV_{others}, $mm^3\ L^{-1}$), concentration of Chl-a ($\mu g\ L^{-1}$). Abiotic variables: water temperature ($T°$, °C), degree-days (DD, °C-days), Schmidt stability index (S, $g\ cm^{-1}$), average WRT for last 15 days (WRT_{15}, days), average WL for last 15 days (WL_{15}, m), total precipitation for the last 3 days (PPT, mm), TP concentration ($\mu g\ L^{-1}$), TN concentration ($mg\ L^{-1}$) and ratio of TN to TP (TN/TP).
[a]$N = 88$.
[b]$N = 21$.
*$P < 0.05$.
**$P < 0.001$.

over the previous 15 days. The BV of *M. aeruginosa* (BV_{Micro}) was positively correlated with the cumulative degree-days, TP, TN and total precipitation over the previous 3 days. The BV of *Aphanocapsa/Aphanothece* spp. (BV_{Aphano}) was positively correlated with only TN, whereas the BV of other non- dominant cyanobacteria (BV_{others}) was positively correlated with the total precipitation over the previous 3 days. Chl-*a* was positively correlated with precipitation and TN and negatively with the Schmidt stability index.

DISCUSSION

Spatial and temporal variability

The cyanobacterial communities in Lake St Charles were characterized by a pronounced heterogeneity across the lake in terms of both biomass and structure. We observed marked differences in species composition between the north and south basins in 2009 (Fig. 5). That summer, there were large concentrations of *A. flos-aquae* in the north basin whereas negligible concentrations occurred in the south basin. The population of the north basin was relatively homogeneous, with little variation among sites. This *A. flos-aquae* population would seem to have its origin within or upstream of the north basin and may be retained within this sector of the lake by recirculation processes.

The spatial pattern of cyanobacteria differed markedly in 2010. We observed a significant difference in total BV between the north and south basins but the community structures were similar. *Anabaena flos-aquae* BV was higher in the north basin and particularly at N3, which is at the middle of this basin where depth is maximal (17.5 m). This was unexpected given that this sampling site should not be subject to wind accumulation effects. At N4, there was also a high BV of *A. flos-aquae* but less than at N3; this site was located in a steep-sided 8 m-deep bay (Echo bay), in which near shore cyanobacterial accumulations have been observed. Cyanobacterial populations may develop in the near shore N4 area, with subsequent transport to the center of the lake by surface water flow or a recirculation gyre. Such hydrodynamic effects have been observed in a much larger waterbody, Lake Biwa, Japan, where cyanobacterial blooms developed under low nutrient conditions in the center of the lake, after the advection of the source populations from near shore, nutrient replete environments (Ishikawa *et al.*, 2002). Rotational flow regimes have also been reported in smaller lakes (e.g. Forcat *et al.*, 2011)

We observed extreme interannual variations not only in cyanobacterial BV, but also in species composition (Fig. 6). The 2007 summer was characterized by high biomass of *M. aeruginosa* in August, whereas in 2008 there was lower biomass of *M. aeruginosa*, and in 2009 there was a high biomass of *Aphanothece sp.* In 2010, there was a high biomass of *A. flos-aquae*, but summer 2011 had low concentrations of this taxon. This variability in dominance suggests a similarly high variability in environmental conditions from one year to another and strong ecological sensitivity to these variations. This year-to-year variability with orders of magnitude differences in maximum population size as well as complete shifts in species dominance contrasts with the interannual variability usually observed in lakes subject to eutrophication and harmful cyanobacterial blooms. For example, in Lake Taihu in China (Chen *et al.*, 2003), Lake Kinneret in Israel (Zohary, 2004), Ben Chifley Reservoir in Australia (Rahman *et al.*, 2005) and Lake Erie in USA (Stumpf *et al.*, 2012), there was a tendency for the total cyanobacterial BV to increase each year after the onset of the first harmful bloom, and the same species continued to grow and dominate the community each year.

Factors controlling temporal variation

Water temperature

An increase in the abundance of cyanobacteria is often associated with high temperatures because of their warmer growth optimum relative to other groups of phytoplankton (Paerl and Huisman, 2008 and references therein). The maximum growth rates of most cyanobacteria are achieved at temperatures above 25°C (Robarts and Zohary, 1987), and even cold-tolerant cyanobacterial genotypes growing in polar and alpine environments often show warm temperature optima (Vincent and Quesada, 2012).

There was a positive relationship between the total BV of *A. flos-aquae* and water temperature (Table III), whereas *M. aeruginosa* was correlated with cumulative °C-days, a measure of thermal growth conditions. These and the other correlative relationships must be interpreted with caution given that the data cannot be considered spatially and temporally independent (Legendre and Legendre, 2012). The responsiveness of *Microcystis* to warm temperatures has been reported in several studies; for example, Johnston and Jacoby (2003) observed that *Microcystis* blooms in a mesotrophic lake were associated with temperatures above 22°C. The study of Wu *et al.* (2010) showed different responses of *M. aeruginosa* and *A. flos-aquae*, with the former growing faster than the latter at 20 and 25°C, but growing very slowly at 15°C. These observations imply that *A. flos-aquae* would occur in early spring when the water temperature is lower, and *M. aeruginosa* in mid to late summer when the epilimnion has sufficiently warmed. In Lake St Charles, the peak population of *M. aeruginosa* was indeed observed in mid-August 2007, corresponding to the time of cumulative warm growing conditions for that summer (~100°C-days; Fig. 2). Conversely, the peak population of *A. flos-aquae* was observed in early July 2010, which corresponded to a lower cumulative warmth (~50°C-days) but a higher water surface temperature compared with August. However, summer 2010 was a particularly warm summer (23.2 ± 2.7°C between 1 July and 30 August) with an elevated cumulative number of °C-days (210°C-days). *Anabaena flos-aquae* persisted throughout that summer, yet *M. aeruginosa* never rose to dominance,

implying the influence of other environmental conditions on its net growth and population size.

Water column structure

Another factor influencing the prevalence of cyanobacteria is water column stability (Paerl and Huisman, 2008; Taranu *et al.*, 2012). Gas vacuoles produced by some cyanobacteria such as *A. flos-aquae* and *M. aeruginosa* allow a competitive advantage for light over other non-buoyant phytoplankton under conditions of low mixing intensity (Reynolds and Walsby, 1975; Dokulil and Teubner, 2000; Visser *et al.*, 2005). For example, *Microcystis*, *Aphanizomenon* and *Anabaena* were observed to achieve their highest biomass when the duration of stratified conditions exceeded 3 weeks (Šejnohová and Maršálek, 2012).

The water column stability in Lake St Charles varied significantly among years (Fig. 3) but only *A. flos-aquae* correlated with the Schmidt stability index (Table III). Thermal stratification in the lake started earlier in 2010 than in the other summers and was well established by early June (Fig. 3). This situation appeared to favor *A. flos-aquae*, which dominated throughout the summer. N limitation can affect gas vesicle activation by restricting the production of essential proteins resulting in a loss of buoyancy (Chu *et al.*, 2007; Whitton, 2012 and references therein). During warm and dry summers such as 2010, the thermal stratification was strong and the epilimnion would have received only low inputs of N. The ability of *Anabaena sp.* to fix atmospheric N_2 would provide a competitive advantage against other species, whereas N limitation under such conditions would negatively impact the buoyancy capacity of non-N_2-fixing cyanobacteria such as *M. aeruginosa*. Under calm and turbid conditions, the flotation rate of *Anabaena circinalis* can be high due to trichome aggregation, whereas turbulent mixing may cause lower flotation rates by preventing trichome aggregation (McCausland *et al.*, 2005). Irradiance is strongly attenuated with depth in Lake St Charles (euphotic zone of 3.5 m; Watanabe, 2011), and *A. flos-aquae* may require a high degree of water column stability to dominate. Periods of short intermittent stability have been shown to result in a significant increase in the growth of this species (McCausland *et al.*, 2005), and a similar alternation of stratification and mixing may favor this taxon in Lake St Charles.

As described by Stoke's Law, colony size has a strong influence on the flotation rates of colonial cyanobacteria (Oliver *et al.*, 2012). *Microcystis aeruginosa* colonies smaller than 20 μm in diameter have a low migration capacity, whereas colonies around 1600 μm can migrate 10 m vertically over a period of hours (Cronberg and Annadotter, 2006). Large colonies tend to show little diurnal repositioning and are less affected by wind-induced mixing than small colonies and are thus mainly concentrated in the surface layer (Wu and Kong, 2009). *Microcystis aeruginosa* colonies in Lake St Charles were generally large and thus may have been less affected by intermittent decreases in water column stability. This would potentially explain the lack of correlation between *M. aeruginosa* BV and the Schmidt stability index.

Nitrogen and phosphorus

Phosphorus has been identified as a major factor controlling cyanobacterial population size (Zhang and Prepas, 1996; Downing *et al.*, 2001; Salmaso, 2002), and the increased enrichment of lakes by phosphorus leading to eutrophic conditions is often accompanied by the development of cyanobacterial dominance and blooms. N:P ratios have also been identified as a key factor for species composition in some studies (McQueen and Lean, 1987; Smith and Bennet, 1999; Havens *et al.*, 2003; Oliver *et al.*, 2012 and references therein), whereas many other studies have found little relationship with this variable (Pick and Lean, 1987; Downing *et al.*, 2001; Xie *et al.*, 2003; McCarthy *et al.*, 2009).

Our nutrient analyses indicate that nitrogen limitation is likely to be rare in Lake St Charles (Table II). However, significant correlations with TN suggest that nitrogen may be a controlling factor of *Aphanocapsa/Aphanothece* spp. and Chl-*a* and may also play a role in the dominance of *M. aeruginosa* (Table III), but to a lesser extent. Although nitrogen demands may be met by N_2-fixation by diazotrophic species, this process is more energetically costly than the assimilation of other forms of nitrogen such as ammonium or nitrate (Rabouille *et al.*, 2006). Thus, *A. flos-aquae* could be outcompeted by *M. aeruginosa* during periods of adequate nitrogen supply.

Our results suggest that in general P is limiting compared with N in Lake St Charles. The threshold of phosphorus generally mentioned in the literature to induce dominance of cyanobacteria is 20–30 $\mu g\ L^{-1}$ (Pick and Lean, 1987; Downing *et al.*, 2001; Jacquet *et al.*, 2005). Although the average TP measured in Lake St Charles never reached this threshold (Table II), there may be episodes of enhanced internal and external supply of bioavailable phosphorus that were not captured by our lake sampling location or frequency, and which may allow cyanobacteria to proliferate. An extreme value of 284 $\mu g\ L^{-1}$ of TP was recorded in the major inflow to Lake St Charles, the Hurons River, during flood conditions (Bourget, 2011). Furthermore, the modeling of phosphorus inputs by the Hurons River to the lake in 2008 revealed that the four most intense floods transported 46% of the summer inputs over short periods of time that totaled only 8 days (Bourget, 2011). In addition, hypolimnetic oxygen depletion in late summer at station

N3 was observed every year (D.C. Rolland *et al.*, unpublished data) and could potentially result in phosphorus release from sediments. These potential sources of phosphorus enrichment are mainly located in the north basin and could be an additional explanation for the greater success of cyanobacteria in this part of the lake.

The abundance of *M. aeruginosa* correlated with TP concentrations (Table III), consistent with previous observations in the literature (e.g. Reynolds *et al.*, 1981). *Microcystis* is able to increase its P uptake capacity in waters with a fluctuating P-supply (Šejnohová and Maršálek, 2012), as may be the case in Lake St Charles. There is evidence that increased temperature and P concentrations yield highest growth rates for toxic *Microcystis* cells, suggesting that ongoing eutrophication combined with climate warming could act synergistically to promote the growth of toxic populations of *Microcystis*, leading to blooms with higher microcystin content (Davis *et al.*, 2009).

Non-N_2-fixing species of cyanobacteria such as *M. aeruginosa* are often the dominant contributors to summer phytoplankton in lakes with TN:TP ratios much higher than the optimum ratio of 16:1 (Dokulil and Teubner, 2000). In Lake St Charles, the average TN:TP ratios were always higher than this threshold value (36 in 2007, 39 in 2008, 31 in 2009, 35 in 2010 and 26 in 2011), yet *M. aeruginosa* was only dominant in 2007 and 2008 and the potentially N_2-fixing *A. flos-aquae* dominated in 2010 and 2011 (Fig. 6). This is consistent with Dolman *et al.* (2012) who showed that the distribution of N_2-fixing taxa did not always differ from other cyanobacterial taxa in relatively N- or P-rich lakes. Furthermore, there was no statistical relationship between the BV of the two taxa and the TN:TP ratio in Lake St Charles. This absence of a relationship with TN:TP is consistent with the analyses by Downing *et al.* (2001) and Håkanson *et al.* (2007) of many data sets from throughout the world. Overall, our results imply that N and P supplies, but not the fluctuations in TN:TP, may affect the shift in dominance between *A. flos-aquae* and *M. aeruginosa* in Lake St Charles. There were striking differences among species in their correlations with limnological variables (Table III), indicating marked differences among taxa in their ecological preferences and in their responses to environmental changes.

Hydrology

The fluvial character of Lake St Charles and other reservoirs could potentially exert a wide range of effects on their phytoplankton biomass and species compositions and in contrasting ways. The inflow of high volumes of water during rain events can lead to a reduction in algal biomass due to high flushing rates and increased turbidity (Reichwaldt and Ghadouani, 2012). Nutrients are transported from the drainage basin to the lake during such events and less intense rainfall may increase cyanobacterial biomass through nutrient enrichment if the storm does not lead to rapid flushing or de-stratification (Reichwaldt and Ghadouani, 2012).

The BV of *M. aeruginosa* in Lake St Charles was positively correlated with the volume of precipitation (Table III) and may be linked to the input of nutrients such as N and P. However, this correlation was relatively weak and may operate only during less intense rainfall. *Anabaena flos-aquae* BV was positively correlated both with the volume of precipitation and the WRT (Table III). Such results suggest a sensitive equilibrium between conditions favoring its dominance: input of nutrients, water column stability and low flushing rate. Moreover, the positive correlation with rainfall but no correlation with N and P suggests that other components not measured during this study may influence the biomass of *A. flos-aquae*. For example, iron is an essential micronutrient for cyanobacterial growth because it is necessary for the synthesis and activities of key enzymes involved in photosynthesis, electron transport and energy transfer (Oliver *et al.*, 2012) and in some studies has been shown to stimulate N_2-fixing cyanobacteria (Wurtsbaugh and Horne, 1983; Wurtsbaugh, 1988).

Waterbodies with a WRT of less than 2 years experience the greatest interannual and seasonal variation in flushing rate caused by variations in runoff and their high catchment area to lake volume ratios (Kalff, 2002). Field observations in temperate reservoirs elsewhere have indicated that the effect of the flushing rate on the summer composition of phytoplankton communities becomes evident when the WRT declines below 60–100 days (Søballe and Threlkeld, 1985; Kimmel *et al.*, 1990). Similarly, the short residence time of Lake St Charles (30–100 days) may result in enhanced sensitivity to year-to-year fluctuations in hydrology, stratification and nutrient loading.

CONCLUSION

We defined the spatial and temporal variations of bloom-forming cyanobacteria in a north temperate reservoir that has a short WRT and low TP concentrations. Despite these limnological conditions, the noxious taxa *A. flos-aquae* and *M. aeruginosa* dominated the phytoplankton in some years, mostly in the north basin. Each year of sampling showed striking differences relative to other years in terms of the total biomass and structure of the cyanobacterial community, with dominance by a single species, which also varied among years. Our results suggest that temperature plays a key role in controlling

bloom-forming cyanobacteria and that the time of onset of warming, the maximum water temperature and the rate of accumulated heat affect the shift between *Anabaena* and *Microcystis*. Stratification of the water column favored bloom formers but *M. aeruginosa* appeared to be more competitive than *A. flos-aquae* under less stable conditions. Our results also imply that TN and TP supply, but not the fluctuations in TN:TP, may affect the shift in dominance between *A. flos-aquae* and *M. aeruginosa*. The extreme interannual variability in phytoplankton biomass and species composition observed here may prove to be a general feature of many high through-flow reservoirs, and it implies the need for vigilant environmental monitoring of such lakes to detect the onset of large fluctuations in drinking water quality each year.

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