Environmental factors influencing phytoplankton communities in Lake Diefenbaker, Saskatchewan, Canada

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Introduction

Planktonic algae are useful indicators of water quality (Padisák et al., 2006) because their spatial and temporal patterns reflect both short- and long-term environmental changes in lakes and reservoirs (Salmaso, 2010). For instance, the bacillariophytes have been used in paleolimnological studies to track water quality changes attributed to climate change (Rühland et al., 2008) and nutrient enrichment (Hall & Smol, 2010). Other studies have used the presence of cyanobacteria to indicate nutrient enrichment from anthropogenic activities at low nitrogen to phosphorus ratios (Rejmánková et al., 2011). Moreover, cyanobacterial blooms in freshwater lakes and reservoirs are of concern because certain species have been reported to produce compounds (e.g., geosmin and cyanotoxins) that affect water quality and use (Izaguirre & Taylor, 2004; Landsberg, 2002).

Several environmental factors, including nutrients, light availability, temperature, and grazing pressure, have been reported to affect the growth, distribution, and composition of phytoplankton communities in lakes and reservoirs (Torremorell et al., 2009). River-connected reservoirs often have pronounced spatial gradients in these environmental factors, resulting in reservoirs being characterized into three zones: riverine, transitional, and lacustrine (Kimmel et al., 1990). Changes in phytoplankton abundance and composition along nutrient gradients (especially phosphorus [P] and nitrogen [N]) have been reported (Reynolds, 2006). For instance, P limitation or N limitation, particularly in the lacustrine zones, may favor non N-fixing or N-fixing cyanobacterial growth, respectively (Paerl et al., 2011; Schindler et al., 2008). Other secondary nutrients are also important for the growth and distribution of phytoplankton. For example, silica is essential for the growth of bacillariophytes (Lampert & Sommer, 1997).

In addition to nutrients, hydrological variables such as inflow rates and water residence time play an important role in regulating the growth, biomass, and composition of phytoplankton (Borges et al., 2008). River inflow often carries suspended sediments into reservoirs that increase turbidity and in turn affect the light available for phytoplankton growth and photosynthesis (Straskraba, 1999; Yip et al., 2015; Zohary et al., 2010). This may shift the phytoplankton composition in favor of planktonic algae that can tolerate low light conditions (Obertegger et al., 2007). For instance, cryptophytes have been reported to grow and reproduce under low light conditions due to their unique
photosynthetic and accessory pigments (Tardio et al., 2003). In addition, the cryptophytes possess flagella that enable them to regulate their position in the water column for optimum light conditions (Reynolds, 2006). High inflow may wash out phytoplankton (Roelke et al., 2010) and reduce their reproductive capacity (Reynolds, 1990). Furthermore, inflow also affects water residence time in reservoirs and nutrient loading (Schindler, 2006). Several studies have reported that lakes and reservoirs with low flushing rates are often dominated by cyanobacteria (Huszar & Reynolds, 1997).

Scientists have detected a significant increase in the temperature of lakes around the world, which they attribute to climate warming (Schindler & Smol, 2006). Climate warming will affect the intensity and duration of thermal stratification in lakes and reservoirs (Adrian et al., 2009) with implications for phytoplankton community composition (Peeters et al., 2007; Winder & Schindler, 2004). Buoyant cyanobacteria and phytoflagellates (e.g., cryptophytes) are favored over non-buoyant planktonic algae (e.g., bacillariophytes) during periods of thermal stratification because they are able to regulate their position in the water column for optimum nutrient and light conditions (Jöhnk et al., 2008). Conversely, bacillariophytes often thrive during periods of complete mixing of the water column because their heavy siliceous cell wall causes them to sink during thermal stratification (Winder & Sommer, 2012). Water temperature affects the growth and replication rates of most planktonic algae (Paerl et al., 2011). Maximum growth rates are achieved by most phytoplankton at a water temperature of about 20 °C (Knapp et al., 2004). For instance, the cryptophytes have been shown to achieve maximum growth at 23.5 °C (Morgan & Kalff, 1979). But as water temperatures increase above 25 °C, the cyanobacteria achieve maximum growth rates and may outcompete other phytoplankton groups such as cryptophytes, diinoflagellates, and chlorophytes (Paerl et al., 2011). Conversely, bacillariophytes prefer colder water and are abundant in temperate lakes and reservoirs in fall and spring when water temperatures are cooler (Winder & Sommer, 2012).

Lake Diefenbaker (LD) is a large river-connected reservoir in the Canadian Prairies (Fig. 1). It receives about 98% of its water from the South Saskatchewan River (SSR) and serves as an important source of water for domestic consumption, irrigation, recreation, aquaculture, and power generation in southern Saskatchewan (Saskatchewan Water Security Agency, 2012). Despite its importance, extensive studies on the phytoplankton community composition in LD are limited. The bacillariophytes dominated the phytoplankton from June to August in LD from 1967 to 1969 (Royer, 1972). Cyanobacteria dominated during the open-water season from July to October 1984 and in June 1985 (SEPS & EC, 1988). McGowan et al. (2005) reported that siliceous algae (mainly bacillariophytes and chrysophytes) and cryptophytes dominated the phytoplankton in the Qu'Appelle arm (Fig. 1) of the reservoir from May to August from 1995 to 2003. Unfortunately, a comprehensive analysis relating the water column phytoplankton community composition to environmental factors has been absent in LD.

Moreover, residents living along LD have complained about the occurrence of episodic algal blooms. Blooms have been reported, especially in the arms (Hecker et al., 2012; Fig. 1). Therefore, the specific objectives of this study were (1) to characterize the trophic status of the reservoir, (2) to examine the spatial and temporal distribution of the major phytoplankton groups, and (3) to relate the phytoplankton distribution to environmental factors during the 2 years of our study (2011 and 2012). Such information is essential for the management of Lake Diefenbaker.

Materials and methods

Sampling sites

Lake Diefenbaker (51° 1'53"N, 106° 50'9"W) was created from the construction of dams in the Gardiner and Qu'Appelle arms in 1967 (Saskatchewan Water Security Agency, 2012) (Fig. 1). The reservoir has a length of approximately 182 km and a width of 2–3 km. The volume and the surface area of reservoir are approximately 9 km³ and 394 km², respectively (Sadeghian et al., 2015). The mean depth of the reservoir is 22 m, and the maximum depth is 59 m near the Gardiner Dam. In the open-water seasons of 2011 and 2012, water samples were collected within the epilimnion from a 2-m depth at 9 sites located down the length of the reservoir (Fig. 1). Each site was sampled once every month from June to October. We avoided sampling in the month of May because of the presence of ice cover. All water samples were collected with a Van Dorn sampler (6.4 L), poured into 20-L poly-bags, and kept in the dark in coolers. Water samples were returned to the laboratory at the University of Saskatchewan and stored at ambient condition (light and temperature) until processed for water chemistry the following
day. Water samples that were collected for phytoplankton analysis were fixed immediately in 1% Lugol’s solution.

Physical variables

Water temperature (WT), pH, conductivity (SpCon), and dissolved oxygen concentrations (DO) were measured using a YSI 6600 v2 multi-parameter sonde. These variables were reported at 2-m depth only. The mixing depth ($z_{mix}$) was defined as the depth from the water surface to a point where the temperature change was greater than 0.5 °C/m.

Water samples collected at 2-m depth were analyzed for the following chemical variables. We used the method of Parsons et al. (1984) to determine total phosphorus (TP), total dissolved phosphorus (TDP), and dissolved reactive phosphorus (DRP). We measured total nitrogen (TN), total soluble reactive phosphorus (TSR-P), and total dissolved nitrogen (TDN). We used the method of Bachmann & Canfield (1996) for the determination of total phosphorus (TP) as described in Sereda et al. (2012). We measured particulate phosphorus (PN) using an ANCA-GSL sample preparation unit coupled to a Tracer 20 mass spectrometer as reported in Vandergrucht et al. (2013). The particulate phosphorus (PP) used in the calculation of particulate nitrogen to particulate phosphorus molar ratios (PN:PP) was derived by difference (TP − TDP = PP) (Vandergrucht et al., 2013).

Chlorophyll a (chl a) samples were collected on 47 mm GF/F filters with vacuum filtration (10 psi) under low light conditions. Pigments were extracted and analyzed according to Bergmann and Peters (1980) and the absorbance read at 665 nm as described in Vandergrucht et al. (2013).

Trophic state indices and phytoplankton identification and counting

We estimated the trophic status of LD using Carlson’s (1977) trophic state indices (TSI) for chlorophyll a (TSI$_{chl}$ a), Secchi depth (TSI$_{SD}$), and total phosphorus (TSI$_{TP}$) (TSI values <40 = oligotrophy, 40–50 = mesotrophy, 50–70 = eutrophy, and 70–80 = hypereutrophy).

Preserved samples collected at 2-m depth were settled in a settling chamber. Settled samples were identified and counted on an Olympus inverted (IX51) microscope using the technique of Utermöhl (1958). Each taxon was identified to genus level with the use of several keys (Bellinger & Sigee, 2010; Brook et al., 2002; Wehr & Sheath, 2003). Fields of view in transects (each transect represents a diameter of the counting chamber) were counted until a minimum of 400 cells were enumerated for each sample. We used image-Pro Analysery 7.0 computer software to estimate the size of the phytoplankton and used a computerized phytoplankton counting program “Algalica (Version 4.0)” developed by Gosselain and Hamilton (2000) to calculate final biomass for each taxon.

Data analyses

We only analyzed phytoplankton groups that contributed >10% to the total phytoplankton biomass, which were the bacillariophytes and cryptophytes. Hence, we investigated the relationship between environmental factors and the biomass of bacillariophytes and cryptophytes using multiple linear regression (MLR) analyses. To reduce the number of predictor variables in our MLR: First, we selected variables that were correlated to the biomass of the bacillariophytes or the biomass of the cryptophytes at $p < 0.1$. Second, in situations where we have two or more covariates, we considered only the strongest covariate. The environmental predictors considered in our model for the bacillariophytes were hydrological (inflow), physical (WT, $Z_{mix}$), and chemical (pH, TP, NH$_4^+$, DOC, and PN:PP). The environmental predictors considered in our model for the cryptophytes were hydrological (inflow), physical (WT, $k_d$), and chemical (pH, TN, NO$_3^-$, DOC and PN:PP). We removed rows with missing values from our data set. Only the dependent variables, bacillariophyceae biomass and cryptophyte biomass were transformed (i.e., log10) to homogenize their variance. Statistical significance was set at an alpha level of 0.05. We used second-order Akaike’s information criterion (AICc) from the package MuMIn (Barton, 2011) to select our best MLR models. Here we used cor2pcor to calculate partial correlations (Opgen-Rhein & Strimmer, 2007) and vif to estimate the variance inflation factor (VIF), a method to check for collinearity between predictor variables used in the model (Heiberger & Holland, 2004). VIF values greater than 5 are evidence of collinearity. However, large VIF values can be tolerated if all of the model coefficients were significantly different from zero (Heiberger & Holland, 2004). We used Spearman’s rank correlation for other bivariate relationships between environmental variables when parametric statistics were not appropriate. All statistics were performed in R version 2.15.2 (R Development Core Team, 2012).

Results

Physical variables

Mean monthly WT was consistently above 15 °C from upstream sections to downstream sections in both years during the open-water season (Table 1). Mean WT increased from June to July and then decreased in September and October (Fig. 2A). The maximum WT occurred in July and August while the minimum WT occurred in October in both years. Mean DO concentrations were consistently observed above 7.0 mg/L throughout the reservoir in both years at the 2-m depth (Table 1). Conductivity was similar throughout the reservoir. Mean $Z_{mix}$ was similar from June to August and deepened from September to October in both years (Fig. 2B). Mean $Z_{mix}$ increased from the upstream sections to the downstream sections of the reservoir in both years (Table 1). Mixing and thermal stratification events were not uniform across sites in both years; the water column was stratified from July to September (Hudson & Vandergrucht, 2015). Mean $Z_{em}$ increased from June to October in both years (Fig. 2C). Mean $Z_{em}$ and mean SD were lowest at both M3 and M5 (upstream sites) but increased further downstream. Mean $k_d$ decreased from June to October in both years (Fig. 2D) and was greatest at M3 and M5 decreasing downstream (Table 1). We observed peak flows into the reservoir from the South Saskatchewan River (SSR) in June of both years, (Fig. 2E).

Water chemistry variables

Mean epilimnetic pH was consistently observed above 8.0 throughout the reservoir in both years (Table 1). In general, mean concentrations of TP, TDP, TN, and NH$_4^+$ concentrations were greater in 2011 compared to 2012. Mean concentrations of TP, TDP, TN, and NH$_4^+$ decreased from June to August and were similar from September to October in both years (Fig. 2F–I). Mean TP concentrations decreased from
upstream sections to downstream sections, whereas mean TN, TDN, and NO₃ concentrations followed a reverse pattern in both years (Table 1). Mean TDP, DRP, and NH₄⁺ concentrations varied from upstream sections to downstream sections of the reservoir in both years (Table 1). Generally, DOC concentrations were greater in 2012 compared to 2011. Mean DOC concentrations remained similar from June to October, and throughout the reservoir in 2011, whereas concentrations increased from June to August and decreased from August to October (Fig. 2J) and varied throughout the reservoir in 2012 (Table 1). Mean PN:PP ratios varied from the upstream sections to the downstream sections of the reservoir in both years, with the largest ratios occurring at site U3-M (downstream in the Gardiner arm) in both years (Table 1).

Chlorophyll a concentrations varied along the length of the reservoir (Fig. 3). We observed a seasonal bimodal distribution of chl a concentration in both years with a peak from June to July, followed by a secondary peak from September to October. The lowest chl a concentrations was observed in August in both years. The greatest concentration of chl a occurred at the midstream sites (C1-M, C2-M, U2-M and F4-M) of the reservoir in both years except at site M3 (upstream sites close to Highwood) in October. Chlorophyll a concentration was positively correlated with total phytoplankton biomass (r = 0.30, p = 0.004).

### Trophic state indices and phytoplankton composition and distribution

The mean TSIchl a = mean TSISSD and mean TSIpp decreased down the length of the reservoir with the greatest values observed at the most upstream site (M3) in both years. At midstream and downstream sites (i.e., U1-M, C1-M, C2-M, U2-M, F4-M, C3-M, and U3-M) TSIchl a = TSISSD and TSIpp were similar to each other (Fig. 4).

In both years, we identified 72 phytoplankton genera comprising 33 chlorophytes, 17 bacillariophytes, 12 cyanophytes, 3 euglenophytes, 3 pyrrophytes, 2 chrysophytes, and 2 cryptophytes (Table 2). The bacillariophytes and the cryptophytes dominated the phytoplankton seasonally and spatially in both years (Fig. 5A–D). The bacillariophytes contributed about 39% and 46% of total phytoplankton biomass in 2011 and 2012, respectively, while the cryptophytes contributed 43% and 38% of total phytoplankton biomass in 2011 and 2012, respectively. The cyanophytes and chlorophytes were always represented during the sampling periods but contributed very little to the total biomass (<5% in both 2011 and 2012; Fig. 5). The other phytoplankton groups were not consistently observed during the 5 months of sampling.

The bacillariophytes consisted of small centric (Cyclotella, Stephanodiscus) to large centric (Aulacoseira) and pennate forms (Asterionella, Tabellaria). The cryptophytes consisted of members from the genera Cryptomonas and Rhodomonas. The cryptophytes dominated in June and July with peak contributions in June 2011 and in July 2012. Conversely, the bacillariophytes contributed more in the spring in both years (Fig. 5A–D). The other phytoplankton groups were not consistently observed during the 5 months of sampling.

### Table 1

<table>
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<tr>
<th>Sites</th>
<th>Variables</th>
<th>M3</th>
<th>M5</th>
<th>U1-M</th>
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<th>C2-M</th>
<th>U2-M</th>
<th>F4-M</th>
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<td>DO (mg/L)</td>
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<td>281. ± 4.0</td>
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<td>NH₄⁺ (μg/L)</td>
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<td>TN (μg/L)</td>
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<td>137.3 ± 1.2</td>
<td>166.8 ± 2.2</td>
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Fig. 2. Monthly average and standard errors of chemical and physical variables measured in Lake Diefenbaker from June to October in 2011 (squares) and 2012 (triangles): water temperature (°C) (A), mixing depth (m) (B), euphotic depth (m) (C), extinction coefficient (m) (D), inflow from the SSR (m³/s) (Peak in June) (E), total phosphorus concentration (µmol/L) (F), total dissolved phosphorus concentration (µmol/L) (G), total nitrogen concentration (µmol/L) (H), ammonium concentration (µmol/L) (I), and dissolved organic carbon concentration (mg/L) (J).

Fig. 3. Spatial (from upstream sections to downstream sections) and temporal (June to October) distribution of chlorophyll a concentrations in Lake Diefenbaker for 2011 and 2012.
the lowest contribution of the cryptophytes and the bacillariophytes, respectively, to the total phytoplankton biomass occurred at site M5 in both years (Fig. 5C and D).

We selected inflow, WT, $Z_{max}$, $k_d$, pH, TN, TP, NH$_4^+$, NO$_3^-$, DOC, and PN:PP as explanatory variables in our models to reduce collinearity. We reported only our most parsimonious models because the AICc difference with the second best next models was greater than 2 (Burnham & Anderson, 2004). Our most parsimonious model ($n = 50$) confirmed that inflow and water temperature (WT) successfully explained 41% of the variability of the biomass of the cryptophytes. Specifically, the biomass of cryptophytes showed an increasing relationship with inflow and WT. The partial correlation coefficient between the biomass of cryptophytes and inflow (when WT was partialled out) was 0.5, whereas the partial correlation coefficient between the biomass of cryptophytes and WT (when inflow was partialled out) was 0.45. In a separate bivariate relationship, we found cryptophyte biomass to be positively correlated with dissolved organic carbon concentrations ($r_s = 0.33$, $p = 0.018$). Our most parsimonious model ($n = 50$) successfully explained 38% of the variability of the biomass of the bacillariophytes. Mixing depth was positively related to the biomass of cryptophytes (partial correlation of 0.62 when PN:PP was partialled out), whereas PN:PP was negatively related to the biomass of the bacillariophytes (partial correlation coefficient of 0.35 when PN:PP was partialled out).

**Discussion**

Trophic status of Lake Diefenbaker

Our assessment of the trophic status of LD using Carlson’s trophic indices revealed a decreasing trend in all indices (TSI$_{chl}$, TSI$_{SD}$, and TSI$_{TP}$) along the length of the reservoir (Fig. 4), as observed in other river-connected reservoirs (Kimmel et al., 1990). For instance, Bolgrien et al. (2009) noticed a similar trend in the trophic status from the riverine to the lacustrine zones in three large reservoirs on the Missouri River (Lake Oahe, Lake Sakakawea, and Fort-Peck Lake). Haggard et al. (1999) reported that the upstream riverine zone was the most productive in Beaver Lake. However, the TSI values for all three indices were different at upstream sites in LD. Specifically, the TSI$_{chl}$ and the TSI$_{TP}$ were greater and indicated an eutrophic condition, especially at M3 (Fig. 4), compared to the TSI$_{chl}$ in both years. This is related to the high flow events in 2011 and 2012, when large nutrient loads and
tial bloom forming-and toxin-producing cyanobacterial genera to October in 2011 and 2012. In the Cyanobacteria * indicates potential phytoplankton communities (Dubourg et al., 2015). As a result, all three trophic states indices were similar at midstream and downstream sites but not at upstream sites. This suggests that midstream and downstream sites were P limited according to Carlson and Havens (2005). Dubourg et al. (2015) also reported that P was the major limiting nutrient of phytoplankton in LD in 2013. Because high flow events resulted in the overestimation of the TSI values from SD and TP, especially at upstream sites, we subsequently used only chl a to estimate the trophic status of LD (Carlson & Havens, 2005).

The TSI as determined from chl a is the most definitive trophic status index because chl a concentration is the only direct measure for algal biomass that is free from interference (Bolgrien et al., 2009; Carlson, 1977; Carlson & Simpson, 1996). The TSIchl a placed LD as mesotrophic system (i.e., moderately productive, see Fig. 4). We also observed a highly diverse phytoplankton community (72 phytoplankton genera comprised of the seven planktonic algal divisions; Table 1), which is consistent with the general phytoplankton diversity of temperate mesotrophic lakes (Watson et al., 1997). For instance, Leitão et al. (2003) observed 79 phytoplankton genera in the deep temperate mesotrophic Voglas reservoir in France, and Negro et al. (2008) observed 72 phytoplankton genera in the deep temperate mesotrophic Valparaíso reservoir in Spain.

### Table 2

List of phytoplankton genera identified in Lake Diefenbaker from June to October in 2011 and 2012. In the Cyanobacteria * indicates potential bloom forming-and toxin-producing cyanobacterial genera (Cronberg & Annadotter, 2006; Beaulieu et al., 2014).

<table>
<thead>
<tr>
<th>Phyla</th>
<th>Genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyanophytes</td>
<td>Anabaena*</td>
</tr>
<tr>
<td></td>
<td>Aphanothece</td>
</tr>
<tr>
<td></td>
<td>Chroococcus</td>
</tr>
<tr>
<td></td>
<td>Coelosphaerium*</td>
</tr>
<tr>
<td></td>
<td>Microcystis*</td>
</tr>
<tr>
<td></td>
<td>Planktothrix*</td>
</tr>
<tr>
<td></td>
<td>Pseudanabaena*</td>
</tr>
<tr>
<td></td>
<td>Woronichinia*</td>
</tr>
<tr>
<td>Euglenophytes</td>
<td>Euglena</td>
</tr>
<tr>
<td></td>
<td>Trachelomonas</td>
</tr>
<tr>
<td>Chrysophytes</td>
<td>Dinobryon</td>
</tr>
<tr>
<td></td>
<td>Mallomonas</td>
</tr>
<tr>
<td>Pyrrophytes</td>
<td>Ceratium</td>
</tr>
<tr>
<td></td>
<td>Peridinium</td>
</tr>
<tr>
<td>Cryptophytes</td>
<td>Cryptomonas</td>
</tr>
<tr>
<td></td>
<td>Rhodomonas</td>
</tr>
</tbody>
</table>

associated turbidity were carried into upstream LD from the SSR. This non-algal turbidity associated with the high flows reduced water transparency (Hudson & Vandergucht, 2015), resulting in light limitation of phytoplankton communities (Dubourg et al., 2015). Most of the nutrients associated with such high flows are typically characterized by loads of non-bioavailable P (Kimmel et al., 1990). Furthermore, the gradual settling of allochthonous organic matter from the water column along the length of the reservoir resulted in the loss of P and turbidity from the reservoir (Hudson & Vandergucht, 2015; Kimmel et al., 1990). Thus, all three trophic states indices were similar at midstream and downstream sites but not at upstream sites. This suggests that midstream and downstream sites were P limited according to Carlson and Havens (2005). Dubourg et al. (2015) also reported that P was the major limiting nutrient of phytoplankton in LD in 2013. Because high flow events resulted in the overestimation of the TSI values from SD and TP, especially at upstream sites, we subsequently used only chl a to estimate the trophic status of LD (Carlson & Havens, 2005).

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**Phytoplankton composition and major groups in relation to environmental variables**

The cryptophytes and bacillariophytes were the dominant groups in terms of biomass (both contributed ~89% of total phytoplankton biomass) during our study and in previous LD studies. For instance, McGowan et al. (2005) reported that siliceous algae (mainly bacillariophytes and chrysophytes) and cryptophytes were the dominant phytoplankton in the Qu’Appelle arm of Lake Diefenbaker from 1995 to 2003. Ote et al. (personal communication) reported that the bacillariophytes and cryptophytes dominated from August 2008 to November 2011 within 20 km of the aquaculture facility in LD (site F4-M; Fig. 1). The dominance of the bacillariophytes and cryptophytes has also been reported in lakes and reservoirs of similar trophic status elsewhere. For instance, Tolotti et al. (2010) reported that the bacillariophytes and cryptomonads were the prominent groups in deep temperate mesotrophic Lake Santa Croce reservoir in Italy. Simek et al. (2008) reported that the cryptophytes dominated in spring to early summer and the bacillariophytes dominated in summer to fall in deep temperate meso-eutrophic Rimov Reservoir in the Czech Republic.

Cryptophytes have been reported to have high nutrient affinities and growth rates (Dokulil, 1988; Tolotti et al., 2010). Therefore, their positive relationship with inflow may be related to their ability to take up flow-associated available nutrients for rapid growth. As such, they have the ability to compensate for washout during high flow events as observed in Lake Santa Croce, Italy (Tolotti et al., 2010). As phagotrophs, cryptophytes have the ability to engulf bacterial cells during low light conditions to compensate for low photosynthetic rates (Bellinger & Sigee, 2010), and to use organic matter as a source of carbon (osmotrophy) (Gillott, 1990). Interestingly, the greatest contribution of the cryptophytes to the total phytoplankton biomass occurred at M5 (Fig. 5C and D). This site was characterized by high turbidity due to large deposit of allochthonous organic matter during the high flow events (Hudson & Vandergucht, 2015).
Therefore, it is possible that our observed positive relationship between inflow and cryptophytes may be related to the increase in bacterial abundance linked to allochthonous organic matter or the allochthonous organic matter associated with the high flow events, both of which the cryptophytes can consume (Tranvik et al., 1989). For instance, Simek et al. (2008) reported that the summer abundance of cryptophytes in the mesotrophic Rimov reservoir may be related to the abundance of certain bacterioplankton and extracellular phytoplankton production. There are some indicators that osmotrophy was occurring in LD due to the positive relationship we found between cryptophytes and DOC ($r_s = 0.33$, $p = 0.018$).

Water temperature affects the growth of most phytoplankton and is associated with thermal stratification (Adrian et al., 2009; Paerl et al., 2011). Cryptophytes have been shown to achieve maximum growth at 23.5 °C (Morgan & Kalff, 1979) and, unlike the bacillariophytes, are favored during periods of thermal stratification due to their ability to maintain an elevated position in the water column with their flagella (Reynolds, 2006). The greatest contribution of the cryptophytes to the total phytoplankton biomass coincided with the onset of thermal stratification, when the reservoir's water temperature was warmest (July, ~ 22 °C). Thus, the relationship with water temperature suggests the importance of warm conditions and thermal stratification on the abundance of cryptophytes in LD (Morgan & Kalff, 1979; Reynolds, 2006). Weyhenmeyer et al. (2004) also reported that the biomass of the cryptophytes remained high during summer stratification in Lake Mälaren, in Sweden.

Mixing depth and PN:PP successfully explained 38% of the variability in the biomass of the bacillariophytes. However, mixing depth explained a greater proportion of bacillariophytes biomass compared to the PN:PP ratio (partial correlation of 0.62 versus −0.35, respectively; Table 3). This suggests that the biomass of the bacillariophytes was more related to $Z_{mix}$ than nutrients. The genus Aulacoseira contributed to the majority of bacillariophyte biomass (80%). The genus Aulacoseira has previously been shown to be dependent on mixing to remain suspended in the water column (Reynolds, 2012). In addition, the greatest contribution of the bacillariophytes to the total phytoplankton biomass occurred during periods when the water temperature was lowest and isothermal. Bacillariophytes can grow rapidly and outcompete other phytoplankton groups under low water temperatures (Rothenberger et al., 2009). Thus, the relationship between the biomass of bacillariophytes and the mixing depth and PN:PP successfully explained 38% of the variability in the biomass of the bacillariophytes. However, mixing depth explained a greater proportion of bacillariophytes biomass compared to the PN:PP ratio (partial correlation of 0.62 versus −0.35, respectively; Table 3).

### Table 3

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Estimate</th>
<th>Partial correlation</th>
<th>$p$ value</th>
<th>VIF</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptophytes</td>
<td>Intercept</td>
<td>0.9181</td>
<td></td>
<td></td>
<td>65.4</td>
</tr>
<tr>
<td></td>
<td>Inflow (m$^3$/s)</td>
<td>0.0006</td>
<td>0.50</td>
<td>0.0022</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td>WT (°C)</td>
<td>0.0473</td>
<td>0.45</td>
<td>0.00124</td>
<td>1.05</td>
</tr>
<tr>
<td>Bacillariophytes</td>
<td>Intercept</td>
<td>1.5224</td>
<td></td>
<td></td>
<td>65.6</td>
</tr>
<tr>
<td></td>
<td>$Z_{mix}$(m)</td>
<td>0.0348</td>
<td>0.62</td>
<td>0.00001</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>PN:PP</td>
<td>−0.0239</td>
<td>−0.35</td>
<td>0.0149</td>
<td>1.04</td>
</tr>
</tbody>
</table>

Figure 5. Percentage of phytoplankton groups by total biomass from June to October 2011 (A) and 2012 (B) and from upstream sections to downstream sections in 2011 (C) and 2012 (D) in Lake Diefenbaker.
depth suggests the importance of cool, isothermal conditions for bacillariophyte abundance in LD. Gillett and Steinman (2011) reported that bacillariophytes were abundant in Muskegon Lake (a mesotrophic lake in the USA) when the lake was also cool (−13 °C) and isothermal. However, Aulacoseira contributed the least (50%) to the bacillariophytes biomass at upstream sites (especially at M5 where we observed the lowest proportion of the bacillariophytes to the total phytoplankton biomass) compared to midstream and downstream sites (89%) in both years. Because of the typical shallow, nutrient-rich, turbid and turbulent conditions at upstream sites (Table 1), small centric diatoms (Cyclotella and Stephanodiscus), penate diatoms (Asterionella, Diatom, Fragilaria, Navicula, Nitzschia and Syndra), Cymatosira and Melosira are better adapted to these conditions and constituted the remaining half of the bacillariophytes biomass (Lucas et al., 2015; Padišak et al., 2006; Padišak et al., 2009; Reynolds et al., 2002).

The negative relationship between the biomass of the bacillariophytes and the PN:PP is not fully understood. However, we speculated that the negative relationship between the biomass of the bacillariophytes and the PN:PP may be related to the more rapid loss of P from the water column, following the sedimentation of particles containing P, including the bacillariophytes during periods of thermal stratification (Kufel, 2001; Interlandi & Kilman, 1999; Tilman et al., 1986). Moreover, nutrients do not seem to play a major role in the dominance of the bacillariophytes; silica was not found to be at a concentration in LD that would limit their growth (Maavara et al., 2015; Gilpin et al., 2004) and P was weakly limiting in LD (Dubourg et al., 2015).

Nevertheless, the lowest contribution of both the bacillariophytes and cryptophytes to the total phytoplankton biomass and the lowest chl a concentrations occurred in August. This corresponds to period water clarity increases in LD (Yip et al., 2015). Although zooplankton abundance was not investigated during our study period, we speculated that the low relative biomass of bacillariophytes and the cryptophytes and the low chl a concentrations in August may be related to increase in zooplankton grazing (Vogt et al., 2015). Vogt et al. (2015) found a negative relationship between mean summer phytoplankton abundance (as chl a concentration) and total zooplankton abundance (explained 19% of the variation) in the Qu’Appelle arm of LD in their long-term study.

Cyanobacteria contributed <5% of the total phytoplankton biomass over the period of study. This may be attributed to washout from the high flow events (Roelke et al., 2010) and suppression of their growth from non-algal turbidity associated with the high flow (Paerl & Huisman, 2009; Reynolds, 1990). Godlewksa et al. (2003) reported that high water flow eliminated the usual cyanobacterial blooms that occur in autumn in Dobczce reservoir in Poland. However, it is well documented that high nutrient loads from high flow events followed by drought conditions (reduced water discharge and increased water residence time) can promote cyanobacterial blooms in lakes and reservoirs (Paerl & Huisman, 2009). For instance, in a previous study on LD, cyanobacteria dominated the phytoplankton biomass (79%) during a drought period with low flow from SSR (SEPS & EC, 1988). Hecker et al. (2012) commented on a cyanobacterial blooms that occurred in the southern and western parts of the reservoir in fall 2007, which also corresponded with low flow conditions (Hudson & Vandergucht, 2015).

Increased water residence time, extended and stable thermal stratification, and internal loading of nutrients from sediments have been reported to favor blooms of cyanobacteria (Nürnberg, 2009; Paerl et al., 2011; Paerl & Huisman, 2009). Despite the low cyanobacterial biomass in LD, we observed some potential toxin and bloom-forming genera (Table 2). Such genera of cyanobacteria may become an issue and threaten the water quality of LD, if early summer peak flow events are followed by any of the suitable environmental conditions mentioned above (Nürnberg, 2009; Paerl et al., 2011; Paerl & Huisman, 2009). For instance, North et al. (2015) found evidence to support internal P loading in LD.

Conclusion

Our results indicate that Lake Diefenbaker is a mesotrophic system overall, with a highly diverse phytoplankton community (72 phytoplankton genera). In both years of study, LD received high flows associated with high nutrient loads and non-algal turbidity from the South Saskatchewan River which may be responsible for the high biomass of cyanobacteria and bacillariophytes reported. There was no evidence to support an immediate threat to the water quality in LD because of the low cyanobacterial biomass observed during our study period. Therefore, we do not recommend any immediate management strategy for LD. However, we have provided useful information concerning the impending threat to the water quality of LD by some potential toxin and bloom-forming cyanobacterial genera under certain conditions. Most of the conditions highlighted are related to climate change. Therefore, future studies conducted in drought years may help elucidate the effect of climate change on phytoplankton community composition in LD.

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References


