Long-term seasonal effects of dreissenid mussels on phytoplankton in Lake Simcoe, Ontario, Canada

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Abstract

The invasion of dreissenid mussels to Lake Simcoe coincided with notable changes in the ecosystem, including a period of lower phytoplankton biovolume, particularly at shallower sites. Dreissenid grazing effects are typically most prominent during the summer season in the nearshore areas of lakes. Grazing effects in the winter are small because dreissenid filtration rates, especially those of zebra mussels (\textit{Dreissena polymorpha}), decrease in cold temperatures. Phytoplankton dynamics in the winter season are poorly characterized, particularly in lakes that experience ice cover. The purpose of this study was to examine the effects of dreissenids on the seasonality of phytoplankton dynamics in the nearshore waters of the lake using long-term monitoring data from unchlorinated water treatment plant (WTP) intake pipes. The long-term dataset from the WTPs showed significant and sustained declines in phytoplankton biovolumes and chlorophyll \textit{a} (Chl-\textit{a}) concentrations in the 12-year period following the invasion of dreissenid mussels to Lake Simcoe. The decline was smallest during the ice-covered winter months (Jan–Mar). The fall phytoplankton peak observed in the pre-dreissenid years shifted to a smaller peak during the winter in post-dreissenid years. We hypothesized that reduced dreissenid grazing pressure during the winter, and possible improved under-ice light conditions that we attribute to climate change, may be contributing to this shift. Phytoplankton biovolume data collection continues to be important in Lake Simcoe as a measure of phytoplankton biomass. Our results also indicate that winter phytoplankton biovolumes should be considered when managing lakes experiencing both climate change and dreissenid mussel effects.

Key words: chlorophyll \textit{a}, dreissenid mussels, grazing, phytoplankton, seasonality, under-ice, water treatment plant intake pipes, winter

Introduction

Decline in phytoplankton populations through grazing is one of the most notable effects of dreissenid establishment in freshwater ecosystems (Higgins and Vander Zanden 2010). The presence of these invasive mussels has also altered the typical seasonal patterns of phytoplankton found in temperate dimictic lakes. Specifically, the recent declines in the late winter (Kerfoot et al. 2010) and spring (Barbiero et al. 2006) phytoplankton blooms in the Laurentian Great Lakes have been attributed to the cold-water adapted quagga mussel (\textit{Dreissena rostriformis bugensis}). Few studies report on winter phytoplankton dynamics (Jewson et al. 2009, Kerfoot et al. 2010, Twiss et al. 2012) because year-round sampling of temperate lakes is often inhibited by weather and ice conditions.

When accessing the lake is prohibitive due to logistical and financial constraints, water samples taken from water treatment plant (WTP) intake pipes can be used to sample the nearshore area of lakes. Untreated water collected...
from the intake pipes is assumed to represent the lake near the inflow of the intake pipe. Makarewicz (1991) confirmed that water collected from the Brockport WTP on the south shore of Lake Ontario during calm meteorological conditions is representative of the nearshore area of the lake at the inflow of the intake pipe for a number of chemical and biological parameters including chlorophyll a (Chl-a) concentrations and phytoplankton biovolume; however, this study was conducted prior to dreissenid establishment. Several studies have also employed this method of sample collection, including studies looking at the effects of dreissenids on phytoplankton in the Laurentian Great Lakes (Nicholls and Hopkins 1993, Nicholls et al. 1999, Winter et al. 2012). The use of intake pipes is appealing as a safe, inexpensive, and non-labour intensive means to collect year-round samples to detect seasonal shifts in phytoplankton populations. They allow us to test if declines in winter–early spring phytoplankton blooms, as measured in Lake Michigan using satellite imagery (Kerfoot et al. 2010), are also occurring in ice-covered lakes where satellite images are unable to capture changes in Chl-a concentrations through the ice. The use of WTPs to evaluate seasonal patterns in phytoplankton populations may not be appropriate in lakes where dreissenids are established because mussel grazing within the intake pipe could lower phytoplankton measurements unless the pipes are treated to prevent colonization, or if flow rates are high enough to prevent grazing. The optimal water velocity for dreissenid grazing is 9 cm s\(^{-1}\), with a velocity twice as high significantly reducing the filtration rate of the mussels (Ackerman 1999). Ideally, studies using intake pipes to collect phytoplankton data in lakes with dreissenid mussels should use intakes with high water velocities and/or low mussel densities within the pipe.

Lake Simcoe, Ontario, Canada, is a large lake that experienced eutrophication in the 1970s and 1980s due to total phosphorus (TP) loading from the watershed. Excess TP loading has been linked to cold-water fish declines and associated impacts to the multimillion Canadian dollar recreational fishing industry on the lake (Palmer et al. 2011). As a result, the Lake Simcoe Protection Act was passed in 2008, making Lake Simcoe the only lake in Canada with its own legislation to manage its water quality (Government of Ontario 2008). Reductions in TP loading (Young et al. 2011), combined with the establishment of dreissenid mussels in 1996 (Evans et al. 2011), were temporally consistent with declines in open-water Chl-a concentrations at shallow lake stations (Young et al. 2011); however, the long-term trends in phytoplankton biovolumes reveal recent (~2004) increases in phytoplankton biovolumes at some stations in the lake (Winter et al. 2011).

To date, the only seasonally explicit phytoplankton study conducted on Lake Simcoe was prior to dreissenid establishment, and it reported a fall peak in biovolume during the open-water season (Nicholls 1995). Since the introduction of the dreissenids, zebra mussels (Dreissena polymorpha) have remained the dominant dreissenid species within the lake (Ozersky et al. 2011a). As of 2008, zebra mussels make up 19.1% of the total macroinvertebrate abundance in Lake Simcoe, while quagga mussels amount to only 0.6% (Ozersky et al. 2011b). Unlike quagga mussels, zebra mussels are not well adapted to colder water temperatures (Stanczykowska et al. 1975, Kerfoot et al. 2010); thus, mussel grazing pressure should be reduced in the winter.

An additional ecosystem stressor, climate change, has been suggested to cause increased duration of thermal stratification in the lake (Stainsby et al. 2011) and decreased ice-cover duration, which has been linked to changes in phytoplankton species composition in Lake Simcoe (Hawryshyn et al. 2012). The effects of climate change on winter phytoplankton dynamics in Lake Simcoe remain unknown.

The objectives of this study were to use data collected from WTP intakes to analyze the seasonal dynamics in phytoplankton biovolume and Chl-a concentrations before and after the invasion of dreissenids in Lake Simcoe. We hypothesized that dreissenid effects on phytoplankton would be maximized during the summer season when mussel filtration rates are assumed to be highest; however, climate associated changes in winter conditions may also influence variations in phytoplankton seasonal patterns.

**Study site**

Lake Simcoe is the largest (excluding the Laurentian Great Lakes) hard-water lake in southern Ontario, Canada. It has a surface area of ~722 km\(^2\), a volume of \(11 \times 10^8\) m\(^3\), and a mean depth of 14.2 m (Nicholls 1995, Palmer et al. 2011). The lake completely freezes over most winters from late December to early April (Hawryshyn et al. 2012).

As part of the long-term water quality monitoring program on Lake Simcoe conducted by the Ontario Ministry of the Environment (OMOE), biweekly samples were collected from 2 WTPs (Beaverton and Sutton) located on the southeastern shore of the lake (Fig. 1). The Beaverton WTP has an unchlorinated intake pipe with a diameter of 500 mm that extends approximately 986 m into the lake from the shore. The intake of the pipe is located near the lake bottom at a site where the water column is roughly 5 m deep. Water flows through the pipe at an average rate of 2.2 million L day\(^{-1}\) at a velocity of 13.0 cm s\(^{-1}\) (C. Anderson, Regional Municipality of...
Durham, Feb 2011, pers. comm.). The pipe did not receive any special treatment against mussel build up, the mussels did not inhibit flow within the pipe, and annual inspections of the pipe by divers confirmed that mussel build up was minor (C. Anderson, Regional Municipality of Durham, Oct 2012, pers. comm.). Residual chlorination from a nearby chlorinated intake pipe in Beaverton may have contributed to the minimal mussel build up in the untreated pipe; however, the chlorination in the nearby pipe was stopped at least 2 hours before sample collection so as to not affect the samples.

The Sutton WTP was located on the southeastern shore of the lake in the Town of Georgina, Ontario. The Sutton intake had significant mussel build up, to the point that inflow was inhibited, and mussels were removed annually by flushing the pipe with high velocity water in the late spring–early summer (S. Kelsey, Regional Municipality of York, Oct 2012, pers. comm.). The pipe had a diameter of 254 mm and extended 180 m into the lake. Water flowed through the pipe at an average velocity of 55.3 cm s$^{-1}$ (S. Kelsey, Regional Municipality of York, Dec 2012, pers. comm.). The intake was 4 m below the lake surface at a site where the lake was ~5–6 m deep. The plant was in commission until late November 2003 when the nearby Georgina WTP replaced it (S. Kelsey, Regional Municipality of York, Jan 2012, pers. comm.). Data from the Georgina WTP were not included in this analysis because the intake pipe is chlorinated, which could affect phytoplankton biovolumes and Chl-$a$ concentrations. Moreover, as illustrated in nearby Lake Ontario, the nearshore zone of large lakes is highly variable (Howell et al. 2012), and there could be spatial differences in water quality parameters between the old Sutton intake and the new Georgina intake.

**Methods**

**Sample collection and analysis**

Water from the Beaverton WTP intake pipe was collected year-round at biweekly intervals from 1982 to 2008. Similarly, the Sutton WTP plant was sampled from 1983 to 2003. The water samples were analyzed by standard OMOE protocols for Chl-$a$ concentrations (Young et al. 2011) and phytoplankton biovolume estimates (Winter et al. 2011). Phytoplankton biovolume data from the Beaverton WTP were determined from single samples before 1991 and pooled monthly samples after 1991. Sutton WTP phytoplankton biovolume monitoring was not initiated until 1991; therefore, we chose not to include it in our analyses due to the uneven distribution of data between pre- (1991–1993) and post- (1996–2003) dreissenid years.

**Data analysis**

Dreissenid mussels were introduced into Lake Simcoe in 1994 and became established by 1996 (Evans et al. 2011). Data from 1982 to 1993 were selected to represent the lake before dreissenid invasion (pre-dreissenids), while data from 1996 to 2008 were selected to represent the lake after dreissenid establishment (post-dreissenids) in the Beaverton WTP. In the Sutton WTP, pre-dreissenid years are represented by data from 1983 to 1993, while post-dreissenid years are represented by data from 1996 to 2003 only. We chose not to include data from 1994 and 1995 in our analyses because these years represent the initial years after invasion when dreissenid populations were in flux and their distribution within the lake was poorly characterized (Evans et al. 2011).

The pre- and post-dreissenid differences in phytoplankton biovolumes and Chl-$a$ concentrations in the WTPs were analyzed using open-water (May–Oct) means to test for dreissenid mussel effects; this also allowed us to compare our results with previously published monitoring data on the lake. The Chl-$a$ data were first averaged by month, and the monthly means were then used to calculate the open-water averages. Prior to calculating monthly averages, outliers from each year were identified as Chl-$a$ values that did not fall within 3 standard deviations of the mean for that particular year. Data points identified as outliers were removed unless there were low or high values (i.e., values that were below or above, respectively, 3 standard deviations of the mean) on dates immediately before or after the outlier, based on the null hypothesis that values follow a normal distribution.
before or after the sampling date. Beaverton phytoplankton data were not screened for outliers because the post-1991 data were composed of monthly pooled samples. To be consistent with the post-1991 data, the single phytoplankton counts from 1982 to 1991 were also not tested for outliers. The single samples were averaged by month. The monthly samples (single samples averaged by month or pooled monthly samples) were then averaged by open-water season (May–Oct) for all the analyses except the 2-way ANOVA and Tukey HSD tests used to analyze changes in the monthly phytoplankton and open-water Chl-α values pre- and post-dreissenids.

One-way ANOVAs on log₁₀-transformed data were used to test the differences pre- (1982–1993) and post- (1996–2008) dreissenids for both open-water phytoplankton biovolumes and Chl-α concentrations in the Beaverton WTP. A one-way ANOVA on log₁₀-transformed data was also conducted on the Sutton WTP open-water Chl-α means to test the difference between pre- (1983–1993) and post- (1996–2003) dreissenid years. Visual inspection of the quantile-quantile (Q-Q) plots of the residuals from the one-way ANOVAs confirmed that the data in each of the 3 analyses (Beaverton phytoplankton biovolume, Beaverton Chl-α, and Sutton Chl-α) were normally distributed. A Bartlett test was used to determine that the data for each of the tests also met the assumption of heteroskedasticity. A nonparametric Spearman’s correlation was used to examine the relationship between the 2 WTPs for Chl-α concentrations. Spearman’s correlations were also applied to examine the relationships between Chl-α concentrations and phytoplankton biovolumes using open-water means of each year for the Beaverton WTP.

Changes in the monthly Chl-α concentrations and phytoplankton biovolumes pre- and post-dreissenids were analyzed using log₁₀-transformed monthly data from the Beaverton WTP. A 2-way ANOVA and a Tukey HSD test were used to compare the changes in Chl-α concentrations and phytoplankton biovolumes pre- and post-dreissenids for each individual month. Within-year monthly changes in Chl-α concentrations were also tested using a similar approach for data from the Sutton WTP intake pipe. A visual inspection of the Q-Q plots of the residuals revealed that the Chl-α data were normally distributed in both Beaverton and Sutton; however, the Beaverton phytoplankton biovolume data showed deviations from normality. Two outliers from the log₁₀-transformed biovolume data were identified; their removal caused the Q-Q plot to be nearly linear and did not change the results of the 2-way ANOVA, suggesting that our analysis was robust to these minor deviations from normality. The results presented here include the 2 outliers in the 2-way ANOVA. The data for all 3 tests met the assumption of heteroskedasticity, as determined by a Bartlett test. All statistical analyses and figures were done using R, a statistical programming language (R Development Core Team 2011).

### Results

#### Changes in phytoplankton biovolumes and Chl-α concentrations in the WTPs

During the open-water season, the Beaverton WTP had significantly lower phytoplankton biovolumes (reported as settled algal volume, mm³ m⁻³ of lake water sampled) and Chl-α concentrations (mg Chl-α L⁻¹ of lake water sampled) after dreissenid establishment (Table 1; Fig. 2). Similarly, open-water Chl-α concentrations in the Sutton WTP were significantly lower post-dreissenids (Table 1; Fig. 2). There were 3 notable dates when phytoplankton biovolumes in the Beaverton WTP were extremely high (>10 000 mm³ m⁻³) that occurred in October and November 1985 as well as October 1988. These were included in the analysis. The differences in open-water

<table>
<thead>
<tr>
<th></th>
<th>Pre-dreissenids</th>
<th>Post-dreissenids</th>
<th>ANOVA result testing differences pre- and post-dreissenids</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Beaverton</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>phytoplankton biovolume (mm³ m⁻³)</td>
<td>887.87 ± 204.58</td>
<td>64.81 ± 16.12</td>
<td><em>p &lt; 0.001</em> (F₁,123 = 87.87)</td>
</tr>
<tr>
<td>Chl-α (µg L⁻¹)</td>
<td>1.85 ± 0.30</td>
<td>0.78 ± 0.06</td>
<td><em>p &lt; 0.001</em> (F₁,123 = 22.46)</td>
</tr>
<tr>
<td><strong>Sutton</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl-α (µg L⁻¹)</td>
<td>2.48 ± 0.22</td>
<td>0.74 ± 0.10</td>
<td><em>p &lt; 0.001</em> (F₁,17 = 58.59)</td>
</tr>
</tbody>
</table>

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phytoplankton biovolume before and after dreissenids were significant, even when these extreme values were removed ($F_{1,23} = 99.51$, $p < 0.001$). The removal of the 3 outliers also had no effect on the year-round phytoplankton data, which still showed a significant interaction between the effects of month and dreissenid presence ($F_{11,270} = 11.17$, $p < 0.001$). Tukey HSD results showed that phytoplankton in October and November, the months affected by the outliers, remained significantly ($p < 0.001$) lower post-dreissenids, even when the outliers were removed.

Sutton and Beaverton Chl-a concentrations were significantly and positively correlated across all years studied ($\rho_{20} = 0.72$, $p < 0.001$). In pre-dreissenid years, the Chl-a concentrations at the WTPs were significantly positively correlated ($\rho_{19} = 0.69$, $p = 0.02$), but there was no relationship among post-dreissenid years ($\rho_{7} = -0.38$, $p = 0.36$). In 1996, like the pre-dreissenid years, Chl-a in the Sutton intake was higher than in Beaverton. This was followed by a period of similar Chl-a values in both intake pipes until 2001 and 2002 when the Chl-a concentrations in the Sutton pipe were lower than Beaverton. In 2003, the last year the Sutton intake was in operation, Chl-a values became similar again at both intakes (Fig. 2).

Open-water phytoplankton biovolumes and Chl-a concentrations in the Beaverton WTP were strongly correlated ($\rho_{26} = 0.82$, $p < 0.001$) for all years. In the pre-dreissenid years, Chl-a concentrations and phytoplankton biovolumes had a significant positive relationship ($\rho_{11} = 0.76$, $p = 0.007$), but there was no relationship in the post-dreissenid years ($\rho_{12} = 0.39$, $p = 0.19$). Chl-a concentrations were more variable in the post-dreissenid years than phytoplankton biovolumes, which remained consistently low (Fig. 2).

**Fig. 2.** Long-term trends in (A) open-water (May–Oct) phytoplankton biovolume (reported as settled algal volume, mm$^3$ m$^{-3}$ of lake water sampled); and (B) Chl-a (reported as mg Chl-a L$^{-1}$ lake water sampled) means for the Beaverton WTP (circles). Open-water (May–Oct) Chl-a means are also shown for the Sutton WTP (triangles). The error bars signify the SE around the open-water means. The dotted line indicates the year dreissenids became established in Lake Simcoe (1996; Evans et al. 2011).
Seasonal trends in phytoplankton biovolumes and Chl-a concentrations

There was a post-dreissenid seasonal shift in the Chl-a peak from fall (Oct–Dec) to winter-early spring (Dec–Apr) at the Sutton WTP (Fig. 3). Similarly, there was also a post-dreissenid seasonal shift in the Chl-a peak from fall (Oct–Dec) to winter (Jan–Mar) in the Beaverton WTP (Fig. 4). This shift was not as obvious in the phytoplankton biovolume data as it was in the Chl-a concentrations at the Beaverton WTP (Fig. 3). Phytoplankton biovolume data showed that the late spring–early summer (Apr–Jun) and fall (Sep–Dec) phytoplankton peaks disappeared after the dreissenid introduction and were replaced with a single, smaller peak in the winter and early spring encompassing the ice covered period (Dec–Apr).

Year-round phytoplankton biovolume data from the Beaverton WTP revealed a significant interaction between the effects of month and dreissenid presence (F_{11,270} = 11.31, p < 0.001). A Tukey HSD showed significant decreases post-dreissenids for all months, with the exception of the ice-covered winter months (Jan–Mar), which showed no significant differences (Table 2). Year-round Beaverton Chl-a concentrations also showed a significant interaction between the effects of month and dreissenid presence (F_{11,268} = 5.41, p < 0.001). Chl-a concentrations in Beaverton WTP samples decreased significantly from pre- to post-dreissenids in May and again in the late fall (Oct–Dec; Table 2). Similarly, Chl-a concentrations in the Sutton WTP also showed a significant interaction between the effects of month and dreissenid presence (F_{11,197} = 7.96, p < 0.001). A Tukey HSD showed the Sutton Chl-a concentrations decreased significantly post-dreissenids in May and June then again in October and November (Table 2), while the rest of the months of the year showed no significant differences. Chl-a concentrations in both WTPs, along with the phytoplankton biovolumes in Beaverton WTP samples, increased in January and February post-dreissenids, although none of these increases were significant (Table 2).

Discussion

Phytoplankton biovolumes and Chl-a concentrations declined significantly after the establishment of dreissenids in the nearshore of the main basin of Lake Simcoe; however, the interpretation of these results is complicated by phosphorous load reductions in the 1980s and early 1990s, which also contributed to declines in pelagic phytoplankton biovolumes (Winter et al. 2011). The post-dreissenid declines in phytoplankton were most evident in the early summer and fall. On a monthly basis, January and February phytoplankton biovolumes and Chl-a concentrations in the nearshore tended to be higher post-dreissenids, although these changes were not significant. Overall, the traditional bimodal pattern of phytoplankton biovolume in the nearshore (i.e., peaks in May and Oct–Dec) disappeared after the establishment of dreissenids in Lake Simcoe and was replaced in recent years by a relatively smaller-magnitude phytoplankton peak under-ice in the winter.

Fig. 3. The monthly mean Chl-a concentrations from the Sutton WTP. Pre-dreissenid years (1983–1993) are indicated by open shapes and post-dreissenid years (1996–2003) are indicated by filled shapes.
 Spatial and temporal dreissenid effects in Lake Simcoe

This study shows that Chl-a concentrations and phytoplankton biovolumes in the eastern nearshore zone of Lake Simcoe decreased significantly after the invasion of dreissenids; however, the analyses of long-term changes in phytoplankton biovolumes from a station (E51) sampled roughly 10 km away from the Beaverton intake showed no significant long-term declines (Winter et al. 2011). Similarly, phytoplankton sampled from a deepwater station (S15) near the Sutton WTP also did not show significant declines in phytoplankton biovolume (Winter et al. 2011). We hypothesized that the lack of observable dreissenid effects in the offshore areas of the lake may be due to a nearshore–offshore gradient in mussel filtering effects as predicted by the nearshore shunt hypothesis (Hecky et al. 2004), similar to that reported in Lake Erie (Depew et al. 2006, North et al. 2012).

The lake-wide abundances of dreissenids in Lake Simcoe show that waters 10 m deep in the eastern main basin have higher estimated dreissenid densities (2000–4000 individual mussels m⁻²) than the shallower region near the Beaverton intake pipe (<2000 individual mussels m⁻²; North et al. 2013); however, long-term monitoring stations in the eastern basin stratify for at least a few weeks during the summer (Young et al. 2010). Stratification can reduce filtering effects of dreissenids because it decreases the supply of phytoplankton to the mussels residing on the lake bottom (Hecky et al. 2004; Boegman et al. 2008). Climate-related increases in the length of the stratification period in Lake Simcoe (Stainsby et al. 2011) may therefore be reducing the influence of dreissenids on the open-water phytoplankton community.

The Beaverton and Sutton WTPs followed the same year-to-year patterns in open-water (May-Oct) Chl-a means across all years studied; however, this relationship was not significant when examined during post-dreissenid
years only. Chl-α in the Sutton WTP was higher than in Beaverton in the pre-dreissenid years and the first post-dreissenid year (1996) and then became equal to or lower than Beaverton during the rest of the post-dreissenid years. The larger post-dreissenid Chl-α declines in the Sutton intake relative to the Beaverton intake suggests that grazing effects are higher near the Sutton intake. There is a higher density of dreissenid mussels near the Sutton intake (2000–4000 individual mussels m⁻²) compared to the area surrounding the Beaverton intake (<2000 individual mussels m⁻²; North et al. 2013), despite being located at similar depths. Because both intakes are located in shallow epilimnetic waters, the higher density of dreissenids around the Sutton intake likely results in a larger grazing effect on the Chl-α values. The WTP operators did notice a high dreissenid infestation in the Sutton intake pipe, while the Beaverton intake pipe was reported to have minimal mussel build up.

The nearshore zone of Lake Simcoe has not been well represented in the OMOE’s long-term water quality monitoring program. Recently, Guildford et al. (2013) sampled 10 nearshore stations and found that relative to offshore stations, the Chl-α and particulate nutrients (indicators of phytoplankton biovolume) were significantly lower in the nearshore areas of the lake where the entire water column is in contact with the dreissenid beds. They attributed this difference in Chl-α to higher dreissenid filtering effects in the nearshore.

Table 2. Monthly mean ± SE phytoplankton biovolumes and Chl-α concentrations pre- (1982–1993) and post- (1996–2008) dreissenid for the Beaverton WTP. Monthly mean ± SE Chl-α concentrations for the Sutton WTP are also shown for the pre- (1983–1993) and post- (1996–2003) dreissenid periods. A bolded pair of values indicates that the difference is significant at that WTP between the pre- and post-dreissenid periods. Significance was determined using a 2-way ANOVA followed by a Tukey HSD on log₁₀-transformed data and an alpha level of 0.05.

<table>
<thead>
<tr>
<th>Month</th>
<th>Beaverton phytoplankton biovolume (mm³ m⁻³)</th>
<th>Beaverton Chl-α (µg L⁻¹)</th>
<th>Sutton Chl-α (µg L⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pre-dreissenids</td>
<td>Post-dreissenids</td>
<td>Pre-dreissenids</td>
</tr>
<tr>
<td>January</td>
<td>252 ± 58</td>
<td>297 ± 117</td>
<td>1.53 ± 0.26</td>
</tr>
<tr>
<td>February</td>
<td>98 ± 16</td>
<td>273 ± 81</td>
<td>1.19 ± 0.09</td>
</tr>
<tr>
<td>March</td>
<td>235 ± 44</td>
<td>140 ± 27</td>
<td>1.56 ± 0.23</td>
</tr>
<tr>
<td>April</td>
<td>536 ± 100</td>
<td>121 ± 23</td>
<td>1.83 ± 0.23</td>
</tr>
<tr>
<td>May</td>
<td>1216 ± 187</td>
<td>58 ± 10</td>
<td>2.41 ± 0.32</td>
</tr>
<tr>
<td>June</td>
<td>840 ± 214</td>
<td>66 ± 20</td>
<td>1.52 ± 0.26</td>
</tr>
<tr>
<td>July</td>
<td>349 ± 145</td>
<td>52 ± 14</td>
<td>1.03 ± 0.20</td>
</tr>
<tr>
<td>August</td>
<td>342 ± 92</td>
<td>23 ± 4</td>
<td>1.15 ± 0.17</td>
</tr>
<tr>
<td>September</td>
<td>530 ± 136</td>
<td>65 ± 23</td>
<td>1.51 ± 0.26</td>
</tr>
<tr>
<td>October</td>
<td>2050 ± 896</td>
<td>127 ± 76</td>
<td>3.75 ± 1.42</td>
</tr>
<tr>
<td>November</td>
<td>2207 ± 333</td>
<td>39 ± 10</td>
<td>4.08 ± 0.53</td>
</tr>
<tr>
<td>December</td>
<td>1368 ± 232</td>
<td>244 ± 102</td>
<td>3.49 ± 0.49</td>
</tr>
</tbody>
</table>

The relationship between Chl-α concentrations and phytoplankton biovolume in the main basin nearshore of Lake Simcoe

There was a strong relationship between Chl-α concentrations and phytoplankton biovolumes in the Beaverton WTP (during the open-water season) across all years studied, but no significant correlation when only post-dreissenid years were investigated. The relationship between Chl-α concentrations and phytoplankton biovolumes has been found to vary substantially through the year and is affected mainly by light, temperature, and phytoplankton species composition (Felip and Catalan 2000). The increased water clarity in Lake Simcoe since the 1980s (North et al. 2013) could potentially result in a decrease in the amount of Chl-α, a light responsive pigment, per algal cell. Dreissenid grazing and photoacclimation have been linked to lower Chl-α concentrations in the nearshore of both lakes Simcoe (Guildford et al. 2013) and Erie (North et al. 2012). A weak relationship between Chl-α concentrations and phytoplankton biovolumes has also previously been reported for Lake Simcoe (Eimers et al. 2005). Our results emphasize the importance of measuring phytoplankton biovolumes as well as pigment concentrations when monitoring lakes subjected to stressors causing changes to the light regime.
Seasonal changes in phytoplankton dynamics

There were 2 distinct phytoplankton peaks in Lake Simcoe pre-dreissenids: one smaller peak in the spring and a second larger peak in the late fall, which had also been reported previously by Nicholls (1995). Nicholls (1995) attributed this fall phytoplankton peak to a period of low deep water dissolved oxygen (DO) concentrations, leading to P release from lake sediments, thus facilitating phytoplankton growth. Post-dreissenids, there were declines in Chl-α concentrations and phytoplankton biovolumes throughout the year, resulting in a single winter peak. In Lake Ontario, Nicholls (2001) found that dreissenid mussels in the first 3 years post-mussel establishment had the greatest effect on phytoplankton and Chl-α concentrations in the spring, fall, and winter. The present study, however, shows the smallest effect on phytoplankton during the winter months (Jan–Mar). In a recent study of Lake Ontario nearshore waters, Winter et al. (2012) also used WTP intake pipes to assess seasonal trends in the cell densities of diatoms in 2 time periods: one representing pre-dreissenids and higher TP concentrations (1987–1989), and the other representing post-dreissenids and lower TP concentrations (1999–2001). They report that in their 1999–2001 time period, diatom abundances were much lower during most months of the year, and the spring and fall peaks were absent, strikingly similar to what we report here for Lake Simcoe; however, a trend toward winter peaks replacing the historical bimodal patterns was not apparent in their analyses (Winter et al. 2012). In Lake Simcoe, we observed a Chl-α peak emerging under the ice in the winter since ~2000 at both WTPs. These results differed from previous work showing that the bimodal phytoplankton pattern (measured as Chl-α concentrations) did not generally change after the introduction of dreissenids in Lake Erie (Depew et al. 2006); however, this study had a limited seasonal extent and did not include under-ice samples.

Dreissenids have also been known to alter the seasonal succession of the relative phytoplankton communities, but not the seasonal pattern of overall phytoplankton biovolume (Naddafi et al. 2007). In Lake Erie, a decline in spring open-water phytoplankton blooms after the introduction of dreissenids has been reported (Barbiero et al. 2006). Work on southern Lake Michigan is also showing a disappearance of early spring (Vanderploeg et al. 2010) and late winter open-water (Kerfoot et al. 2010) phytoplankton blooms. The declines in Lake Michigan were attributed to the spread of the cold-adapted quagga mussels throughout the lake, especially into deeper depths. Moreover, quagga mussels in Lake Michigan have been found to be in better condition than zebra mussels (Nalepa et al. 2010).

Similar trends are seen in other Great Lakes where quagga mussels have been replacing zebra mussels as the dominant dreissenid species (Mills et al. 1999). Zebra mussels are still the dominant dreissenid species in Lake Simcoe (Ozersky et al. 2011b), so it is possible that there is a release from grazing pressure by zebra mussels at colder temperatures, which may be related to the winter phytoplankton peaks seen here. Most studies do not examine under-ice phytoplankton dynamics because low temperatures and light limitation are assumed to control the production of phytoplankton in the winter (Jewson et al. 2009); however, recent evidence from Lake Erie revealed a winter diatom bloom under-ice that was far greater than the subsequent springtime proliferation of phytoplankton (Twiss et al. 2012). Although the mechanisms driving the bloom in Lake Erie are different than in the seasonally ice-covered Lake Simcoe, high Chl-α concentrations have also been found under ice in Lake Simcoe (R.L. North, Trent University, 2012, unpubl. data).

In Lake Simcoe, long-term trends in open-water total phytoplankton biovolume and Chl-α concentrations showed no monotonic change in the deepest area of the lake, Kempenfelt Bay (Winter et al. 2011, Young et al. 2011). Total phytoplankton biovolume also displayed no significant trends in the main basin (Winter et al. 2011); however, there were significant declining trends in Chl-α concentrations at E51, a long-term monitoring station 10 km away from the Beaverton intake pipe (Young et al. 2011). In shallower Cook’s Bay, which has a high density of dreissenids (North et al. 2013), there were significant declines in both phytoplankton biovolumes and Chl-α concentrations over the last 3 decades (North et al. 2013). These declines were also temporally consistent with declines in TP loading from the tributaries to Cook’s Bay.

North et al. (2013) estimated that the dreissenid population was capable of filtering the entire volume of Lake Simcoe approximately 4 times each year. This estimate was based on dreissenid filtration only occurring 6 months of the year (during the summer months). Assuming the open-water phytoplankton are released from these grazing pressures during the winter months, the under-ice phytoplankton peaks may be related to bottom-up factors including nutrient supply, temperature, and light. The well-mixed winter water column may provide a sufficient supply of nutrients to the phytoplankton, releasing them from P limitation.

The increase in the length of stratification and air temperatures in Lake Simcoe during the open water season (Stainsby et al. 2011) provide evidence for climate change affecting the lake and is consistent with reports of increased temperatures and decreased snow depth on the ice in the nearby Laurentian Great Lakes area since the
1970s (Jensen et al. 2007, Hawryshyn et al. 2012). Under-ice Chl-a concentrations, unlike the open-water Chl-a, did not change over time. The lack of change in Chl-a during the winter could be caused by under-ice light limitation (Jewson et al. 2009), which would increase the Chl-a content in phytoplankton cells. This could explain why the winter peak is more evident with the Chl-a datasets, than phytoplankton biovolumes alone. Therefore, it is likely that the recent phytoplankton peaks in the winter were caused by possible regional increases in air temperatures and light availability through the ice, mediated by decreases in on-ice snow cover and a shorter ice-covered season.

Future monitoring efforts should be focused on the winter season to see if this novel trend continues in Lake Simcoe. With climate change, the WTPs could play an increasingly important role in winter monitoring since the warmer temperatures inhibit complete ice-cover of the lake. Unstable ice conditions could result in the cancellation of on-ice monitoring programs, as occurred in winter 2011–2012 (Joelle Young, OMOE, June 2012, pers. comm.).

Implications for management

This study was the first to look at year-round seasonal phytoplankton patterns in Lake Simcoe post-dreissenids. We found a shift in the phytoplankton peak from the late fall to winter. This phytoplankton peak in the winter occurred during a period when zooplankton are presumed to be in low abundance. The importance of this is 2-fold. First, a shift in the peak of primary production could potentially limit food availability to the zooplankters in the summer and result in reduced food resources for fish. This decline in zooplankton due to a shift in phytoplankton peaks has been observed in other large temperate lakes (Winder and Schindler 2004). Second, with a smaller abundance of zooplankton in the winter, phytoplankton may be less susceptible to grazing; decomposition of ungrazed cells may negatively influence hypolimnetic DO concentrations. Given that Chl-a concentrations seemed to be a poor indicator of phytoplankton biovolume post-dreissenids at our sites, the present study also illustrates the importance of including phytoplankton biovolumes when assessing changes in phytoplankton biomass, particularly in a system subject to changes in the light regime.

The intake pipes have the potential to be a useful tool to lake managers. The use of unchlorinated intake pipes allows year-round water sampling of nearshore areas of the lake safely and more cost effectively than lake sampling. Moreover, with evidence for the nearshore shunt occurring in Lake Simcoe (Guildford et al. 2013, North et al. 2013), the intake pipes could provide insight into the shallower nearshore area that is currently undersampled. This may become the only feasible option for winter sampling in the face of unstable ice cover due to climate change; however, results from intake pipes have not yet been directly validated against adjacent nearshore phytoplankton data in Lake Simcoe. Such a study is recommended to inform the use of the long-term phytoplankton monitoring data collected at the WTP intake pipes. Future work should also examine changes in winter concentrations of nutrients, light availability, temperatures, ice duration, and snow depth to determine the factors affecting the winter phytoplankton peaks.

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