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From River to Lake: Phosphorus partitioning and algal community compositional changes in Western Lake Erie

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ABSTRACT

The Maumee River is an important source of phosphorus (P) loading to western Lake Erie and potentially a source of *Microcystis* seed colonies contributing to the development of harmful algal blooms in the lake. Herein, we quantified P forms and size fractions, and phytoplankton community composition in the river–lake coupled ecosystem before (June), during (August), and after (September) a large *Microcystis* bloom in 2009. Additionally, we determined the distribution and density of a newly emergent cyanobacterium, *Lyngbya wollei*, near Maumee Bay to estimate potential P sequestration. In June, dissolved organic phosphorus (DOP) was the most abundant P form whereas particulate P (partP) was most abundant in August and September. Green algae dominated in June (44% and 60% of total chlorophyll in river and lake, respectively) with substantial *Microcystis* (17%) present only in the river. Conversely, in August, *Microcystis* declined in the river (3%) but dominated (32%) the lake. Lake phytoplankton sequestered <6% of water column P even during peak *Microcystis* blooms; in all lake samples <112 μm non-algal particles dominated partP. *Lyngbya* density averaged 19.4 g dry wt/m^2, with average *Lyngbya* P content of 15% (to 75% maximum) of water column P. The presence of *Microcystis* in the river before appearing in the lake indicates that the river is a potential source of *Microcystis* seed colonies for later lake blooms, that DOP is an important component of early summer total P, and that *L. wollei* blooms have the potential to increase P retention in nearshore areas.

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Introduction

Summer blooms of the planktonic toxic cyanobacterium *Microcystis aeruginosa* have become more frequent in western Lake Erie since the mid-1990s (Conroy et al., 2005). In high-bloom years, surface scums of *Microcystis* may stretch for hundreds of square kilometers and produce concentrations of microcystin toxin that exceed World Health Organization guidelines for human consumption (Rinta-Kanto et al., 2005). Rapid growth of *Microcystis* in the water column begins in early summer as water temperatures increase above 15 °C (Reynolds, 1973) and blooms typically end in early fall as water temperatures decline and *Microcystis* colonies sink and settle on the lake floor (Thomas and Walsby, 1986).

During the growing season, the development of *Microcystis* blooms is closely linked with available nutrient concentrations, especially nitrogen (N) and phosphorus (P). In nutrient-poor waters, *Microcystis* is generally out-competed for P due to the higher P uptake kinetics of green algae and diatoms (Baldia et al., 2007; Tilman et al., 1986). Cyanobacteria have a total phosphorus (TP) threshold of 0.010 mg/L (Steinberg and Hartmann, 1988) and the probability that cyanobacteria will become dominant over other phytoplankton species increases with increasing TP to a maximum probability of about 80% when lake TP reaches or exceeds 0.100 mg/L (Downing et al., 2001). In laboratory studies, *Microcystis* growth increased linearly with TP and reached a plateau at 0.220 mg/L TP (Baldia et al., 2007). In addition to increasing overall *Microcystis* growth rates, increasing P concentration also promotes the growth of toxic versus non-toxic strains of *Microcystis* (Davis et al., 2009), thereby increasing the toxicity of the population. Toxicity may also be increased by factors such as iron deficiency and the formation of surface scums that increase the synthesis of toxin (Sevilla et al., 2008; Wood, et al., 2011).

A second major harmful algal bloom (HAB) species, the filamentous benthic mat-forming cyanobacterium, *Lyngbya wollei*, became established

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in Maumee Bay in 2006. It is unknown whether *Lyngbya* in Lake Erie is native or a recently introduced strain. However, the large blooms of this species that have occurred annually since 2006 are believed to be unprecedented, producing mats that often wash ashore, depositing up to 2 t of algal biomass per meter of shoreline (Bridgeman and Penamon, 2010). Although the Lake Erie strain of *Lyngbya* has not been found to produce toxins, it has become a serious nuisance for marinas, public beaches, and lakefront property owners. Most studies of *Lyngbya* have been conducted in the southeastern USA where it has become a nuisance in recent years (Joyner et al., 2008) and is known to produce paralytic shellfish toxins (Carmichael et al., 1997). Although increasing *Lyngbya* is thought to be linked to increasing nutrient concentrations of the waters of the Southeast over the last few decades, no strong linkages between *Lyngbya* presence/growth rates and water column nutrient concentrations have been observed (Cowell and Botts, 1994; Stevenson et al., 2007). In western Lake Erie, *Lyngbya* was found to grow mainly in the Maumee Bay area with the most frequent occurrence and the greatest biomass at bottom depths between 1.5 and 3.5 m (Bridgeman and Penamon, 2010). Combined, *Microcystis* and *Lyngbya* present a potential hazard to human and wildlife health and a detriment to recreational and other beneficial uses of the near-shore and shoreline areas.

The proximity of *Microcystis* and *Lyngbya* blooms to the inflow of the Maumee River and Maumee Bay suggests that nutrients loaded from the river may influence the development of algal blooms in western Lake Erie. Measurements during the bloom of 2008 indicated that *Microcystis* growth rates were greater in the vicinity of Maumee Bay than in offshore waters and that *Microcystis* was most frequently phosphorus limited (Chaffin et al., 2011). Excluding contributions from the upper Great Lakes and Michigan via the Detroit River, the Maumee River watershed is the single greatest external source of phosphorus to Lake Erie, contributing about 35% of the total TP load in 1994 (Schwab et al., 2009). From 1975 through the mid-1990s, annual phosphorus loadings from the Maumee River declined (Richards and Baker, 2002), but from about 1995 to 2008, annual phosphorus loads increased with dissolved reactive P (DRP) loadings in 2007 and 2008 higher than in any year since 1975 (OEPA, 2010). Research into the causes of the trend towards increasing annual DRP loadings are ongoing with investigations of agricultural practices within the watershed and potential changes in the timing of annual precipitation.

Data collected in recent years indicates the frequent presence of a steep gradient of TP and DRP from high concentrations at the Maumee River mouth to 10-fold lower concentrations in the open waters of the western basin (Moorhead et al., 2008). The main processes that account for the gradient are likely to be the mixing of river water with lake water, the settling of P-rich suspended sediments in the river plume, and the uptake of available P by phytoplankton and benthic algae. It is unknown, however, how the partitioning of P changes as water moves from the Maumee River into the open lake and what effects summer *Microcystis* and *Lyngyba* blooms may have on available water column P. In addition to supplying nutrients, recent observations in another Lake Erie watershed (Sandusky River) suggest that some tributaries may also supply quantities of HAB species (Conroy et al., 2008) that may act as inocula that accelerate and exacerbate HAB development in the lake.

In this research we attempted to increase the understanding of the linkages between one major tributary, the Maumee River and western Lake Erie by taking seasonal "snapshots" of the river–lake system. We analyzed nutrient data and algal communities at locations ranging from 125 km upstream from the river mouth to the open waters of the lake 31 km from the river mouth on three occasions that were intended to capture conditions before, during, and after the development of algal blooms in the lake. Based on previous years' observations of low *Microcystis* density near the mouth of the Maumee River during blooms (Chaffin et al., 2011), we hypothesized that the river would contain only low densities of *Microcystis*, and therefore would not be a major potential source of *Microcystis* seed colonies to the lake. Because available phosphorus is often a limiting nutrient to algal production, we tracked several forms of phosphorus in the river and lake. Finally, because large nearshore biomasses of phytoplankton and benthic algae may have the potential to affect the export of phosphorus to offshore waters, we measured the phosphorus content of two major bloom species and compared their P content to the water column. We hypothesized that during blooms, a significant fraction of water column P would be contained within *Microcystis* and *Lyngbya* cells which—especially in the case of *Lyngbya*—could affect the export of available P to offshore waters.

Methods

In order to determine the concentration and forms of phosphorus and phytoplankton present in the Maumee River (MR) relative to Lake Erie and how these varied during algal blooms, coordinated sampling of the river and lake was conducted on three occasions in 2009: pre-bloom (June), mid-bloom (August), and late-bloom (September). Eleven sites were selected, including five MR sites at locations 125 km, 104 km, 99 km, 54 km, and 38 km upstream from the mouth of the river, and six Lake Erie sites 2 km, 7 km, 14 km, 15 km, 27 km, and 31 km into the open lake (Fig. 1). River sites were selected based on shoreline access and to potentially differentiate between the influence of various sub-tributaries on the MR. River sites were sampled at mid-channel at 1/4 the distance to both banks. Samples were collected by wading at shallow sites and by boat at deeper sites. Lake sites were chosen to represent waters ranging from the MR mouth to the open waters of the western basin that are normally outside of the direct influence of the MR. To avoid the influence of storm events, sampling was conducted only after at least 1 week of dry weather. Although it was not possible to sample both river and lake on the same date, lake samples were collected within a few days of the river sampling and no precipitation or storm events occurred between the river and lake sampling. River sampling dates were June 9, August 4, and September 9. Lake sampling dates were June 15, August 6, and September 11.

At all site-dates, data included vertical profiles of temperature, conductivity, dissolved oxygen, turbidity, pH, chlorophyll *a* fluorescence (using a YSI 6600 multi-probe), and secchi depth. Tube samplers were used to collect a vertically integrated water sample through at least 3/4 of the water column for phytoplankton, extracted chlorophyll *a* and nutrient analyses. A FluoroProbe (bbe Moldaenke, Series 3) was used to determine the contribution of four different algal groups [a) green algae + euglenoids (hereafter termed "greens"), b) phycocyanin-rich cyanobacteria including *Microcystis* (hereafter termed "cyanobacteria"), c) bacillariophyceae + pyrrophyta (hereafter "diatoms"), and d) cryptophytes + phycoerythrin-rich cyanobacteria (hereafter "cryptophytes)] to total chlorophyll *a* concentration based on the fluorescence of characteristic algal pigments. The FluoroProbe was slowly lowered and raised through the entire water column and data was collected at intervals of 5 s. Results are presented as an average of water column readings for each site. It is known that FluoroProbes tend to underestimate chlorophyll concentration when algal densities and turbidity are high (Gregor and Marsálek, 2004), therefore raw FluoroProbe data was corrected for the river and lake on each date using total extracted chlorophyll *a* data for each water sample. The FluoroProbe was calibrated in the laboratory for chromophoric dissolved organic matter (CDOM) for each sample with water filtered through 0.22 μm membrane filters (Twiss, 2011). Total extracted chlorophyll *a* was determined by extracting chlorophyll from a GFF filter containing algae from 50 mL of water samples in dimethyl formamide (Speziale et al., 1984) and reading on a fluorometer (Turner 10-AU) previously calibrated with chorophyll *a* standards.

In order to quantify *Microcystis* biovolume and determine the partitioning of phosphorus into *Microcystis* and size fractions, multiple vertical plankton tows were collected at lake sites only using a weighted112-um mesh net equipped with a flow meter towed from within 1 m of the lake bottom to the surface. Trials indicated that

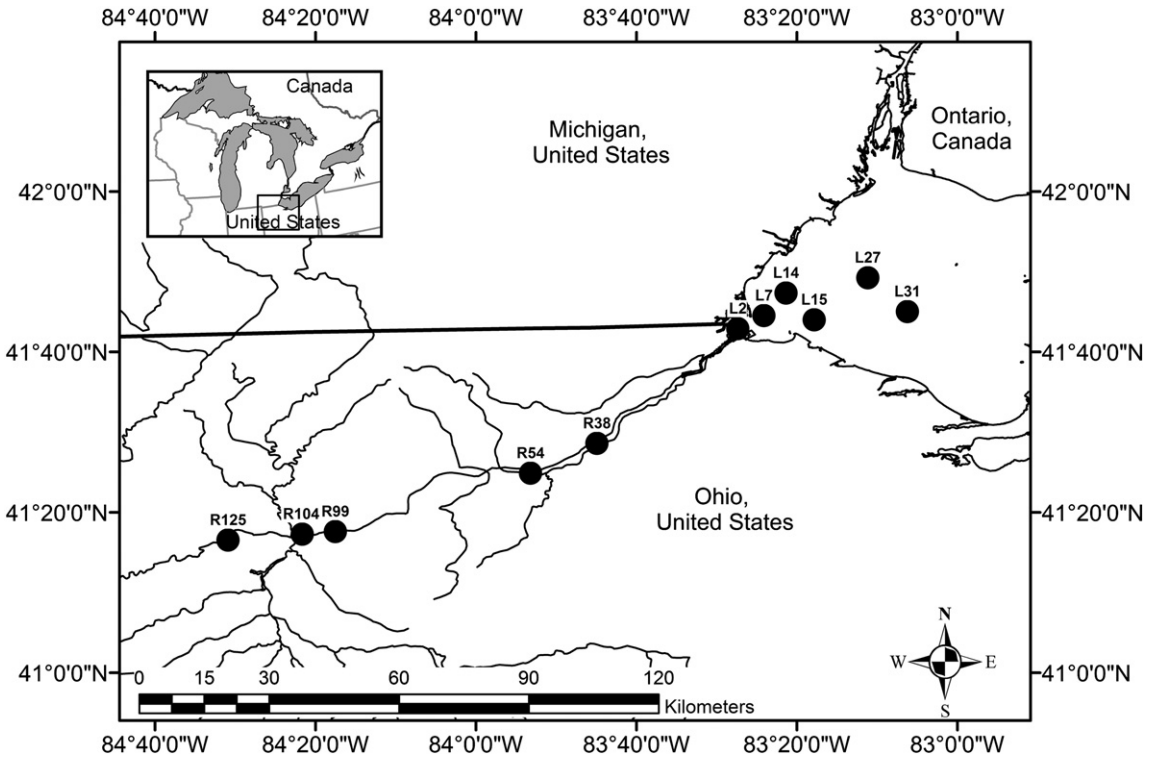

Fig. 1. Sampling locations on Maumee River and western Lake Erie in 2009. Site labels refer to distance from the mouth of the river in kilometers.

the net effectively collected crustacean zooplankton, most rotifers, large diatom and green algal colonies and 93% of the total *Microcystis* cells in the water column (Chaffin et al., 2011). The contents of two tows were preserved in 4% buffered formalin for analysis of *Microcystis* biovolume. Additional tows were processed beginning within 1 h of returning to the laboratory for subsequent P analyses.

Phosphorus analyses methods were based on USEPA method 365.1 (1993) and Standard Methods (Eaton and Franson, 2005). For all date-sites, whole and filtered (0.45 μm) water samples were collected for analyses of total phosphorus (TP), dissolved reactive phosphorus (DRP), and dissolved organic phosphorus (DOP). In order to determine the concentration of DOP, a second portion of the filtered sample was digested in 13 N sulfuric acid to convert all hydrolyzable dissolved P present to orthophosphate (total dissolved P, TDP). DOP was calculated as DOP = TDP − DRP. We recognize that acid digestion may not extract all organic P, therefore our DOP data may underestimate the actual total dissolved organic P. Total particulate P (TPP) was calculated as TPP = TP − TDP. Tow samples were processed to determine the partitioning of lake water column TPP into *Microcystis* and different size categories. Tow samples representing a known volume of lake water were diluted with filtered lake water and placed in Imhoff cones for separation of negatively and positively buoyant plankton (Chaffin et al., 2011). Both buoyant (>99% *Microcystis* colonies) and non-buoyant (zooplankton, colonial phytoplankton >112 μm) plankton portions were dried at 70 °C to constant weight, weighed, and analyzed for P content by adding weighed subsamples to 50 mL of DI water and measuring TP as for water samples above. Because of very low *Microcystis* density in June, samples from all 6 lake sites were combined in order to produce enough material for analysis.

In order to estimate the P content of benthic *Lyngbya* relative to the water column, surveys of *Lyngbya* distribution and biomass in Maumee Bay and vicinity were conducted in June (N = 50), July (N = 90), and August 2009 (N = 77). Sites were arranged in transects perpendicular from the shoreline and were selected to survey a range of bottom types and depths. Sampling at each site consisted of 5 replicate grabs using an Ekman grab sampler. *Lyngbya* was separated from the samples, dried at 70 °C to a constant weight, and then averaged over the 5 samples and recorded as g/m^2. Subsamples of *Lyngbya* were used for analyses of P content using inductively coupled plasma optical emission spectroscopy on 150 mg of dried tissue (N = 15) collected from various lake sites in June, July, and August 2009.

Results

Results of P analyses of river and Lake Erie water samples in June 2009 indicated high concentrations of TP (avg. = 0.235 mg/L), DRP (avg. = 0.096 mg/L), and DOP (avg. = 0.137 mg/L) in the Maumee River at that time (Fig. 2A). There was no apparent difference between river sites, but all forms of P decreased markedly from near the river mouth to the open waters of the lake (June avg. lake TP = 0.044 mg/L). Most (avg. 62%) of the P present in the river and lake in June was in the form of dissolved organic P (Fig. 2B). A substantial percentage (41%) of P in the river was in the form of DRP, but this proportion was lower in the lake (18%). Phosphorus concentrations of river and lake samples during the lake *Microcystis* bloom in August were similar to June (Fig. 2C), except for very high TP concentrations at the two most downriver sites. As in June, August TP concentration was greater in the river than in the lake and decreased further in the lake with increasing distance from the river mouth. In August however, the forms of P were very different. Relatively little DOP (avg. = 0.017 mg/L) or DRP (avg. = 0.004 mg/L) was measured at all river sites except one and particulate P accounted for 80% of TP (Fig. 2D). Samples collected in September showed the least difference between river and lake waters, with TP concentrations lower in the river (avg. = 0.122 mg/L) than in previous months and lake concentrations slightly greater (avg. = 0.070 mg/L; Fig. 2C). As in August, particulate P was the most abundant P fraction (river and lake average = 73%); however there was more available DRP (avg = 0.014 mg/L) in the lake in September than in the previous 2 months (Fig. 2E).

Particulate P was a major percentage of total P in August and September (Fig. 3). Although the most conspicuous particles in the water column in these months were dense colonies of *Microcystis*,

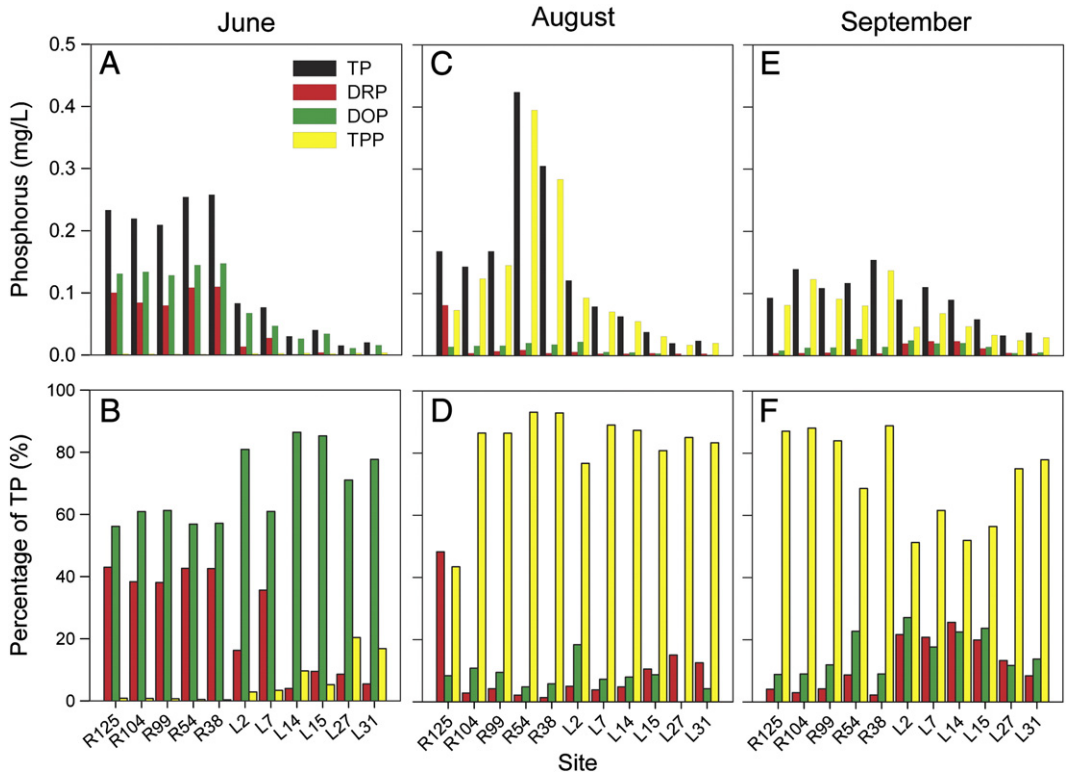

Fig. 2. Phosphorus (P) concentrations and percentages at Maumee River and western Lake Erie sites in June (A, B), August (C, D), and September 2009 (E, F). P is given in mg/L in the forms of Total P (TP), Dissolved Reactive P (DRP), Dissolved Organic P (DOP), and Total Particulate P (TPP). Sites are arranged from farthest upstream (R125 = 125 km upriver) from the river mouth to farthest offshore in Lake Erie (L31).

these and other particles larger than >112 μm contained a relatively small amount of phosphorus (Figs. 3B, C). *Microcystis*-P (>112 μm and positively buoyant) averaged 2.7% of the particulate P, and 2.0% of the Total P during peak bloom months. Other large plankton (macrozooplankton, colonial green algae and diatoms; >112 μm and negatively buoyant), made up only 1.7% of particulate P and 1.0% of TP. Conversely, particles smaller than 112 μm constituted the major part of particulate P during the August and September bloom months. Fluorometric analysis of algal groups indicated that *Microcystis* dominated the phytoplankton community during August and September (see below), indicating that other algal groups likely would have been only minor contributors to particulate P <112 μm. Small-size particulate P, therefore, would have been made up of mostly non-algal particles (microzooplankton, bacteria, and suspended sediment) and averaged 95.6% of particulate P and 70.0% of TP.

In situ fluorometric analyses indicated differences in phytoplankton concentration (as indicated by total chlorophyll *a* (chl *a*) concentration per L) and algal groups between the Maumee River sites and Lake Erie sites. Green algae was the dominant group in both the river (12.2 μg chl *a*/L, 44% of phytoplankton community), and the lake (7.8 μg chl *a*/L, 60% of community) in June (Fig. 4A). The major difference between river and lake sites in June was in the concentration of cyanobacteria, which was relatively high in the river (4.2 μg chl *a*/L, 17% of total phytoplankton) and low in the lake (0.3 μg chl *a*/L, 2% of total phytoplankton). Observation of preserved samples using light microscopy indicated that greater than 90% of the cyanobacteria present in both the river and lake in June were comprised of *Microcystis* sp. During the lake *Microcystis* bloom in August, the cyanobacteria trends were reversed with much more cyanobacteria present in the lake (average 14.6 μg chl *a*/L, 32% of phytoplankton) than in the river (1.5 μg chl *a*/L, 3% of phytoplankton; Fig. 4B). Overall phytoplankton density remained greater in the river than in the lake due to increased densities of green algae (18.4 μg chl *a*/L) and diatoms (29.3 μg chl *a*/L). In September, average phytoplankton density increased in the river due to bloom conditions at the most downstream site (MR38). Green algae and cyanobacteria increased in the river in September (28.4 μg chl *a*/L, 11.7 μg/L respectively) while diatoms decreased (14.3 μg chl *a*/L; Fig. 4C). In Lake Erie, the algal bloom that had peaked in August was in decline in September with algal concentrations decreasing across all categories. However, cyanobacteria increased in dominance (47% of phytoplankton community).

Benthic surveys in June, July, and August of 2009 showed mats of *Lyngbya* tended to develop in shallow areas along the margins of Maumee Bay and adjacent areas where substrates consisted of sand, crushed dreissenid shells, and silt (Fig. 5). Although *Lyngbya* presence and biomass varied widely with water depth and substrate type, biomass tended to increase over the summer with the greatest overall biomass measured in August (average = 19.4 g dry wt/m^2, maximum = 314.8 g dry wt/m^2). The average P content of *Lyngbya* was 2.23 mg P/g dry weight, corresponding to an average P content of *Lyngbya* in western Lake Erie in August of 43.3 mg P/m^2. The maximum *Lyngbya* biomass observed in August was 314.8 g dry wt/m^2 with an associated P content of 702.0 mg P/m^2. In order to compare the P content of *Lyngbya* with P in the overlying water column, water column TP/m^2 was calculated as TP mg/L × depth (m) × 1000. The average of the six lake sites over the June, August, and September sampling dates (N = 18) was 240 mg TP/m^2. On average, therefore, the water column contained about 5.5 times more P per m^2 than did *Lyngbya*. In areas of dense *Lyngbya* growth however, *Lyngbya* contained about 3 times more P than in the overlying water column.

Discussion

General trends in Lake Erie nutrients and phytoplankton have been documented in recent decades (Conroy et al., 2008; Makarewicz et al., 1999; Rockwell et al., 2005) and the nutrient loading of several major Lake Erie tributaries have been tracked for over 30 years (Dolan and Richards, 2008; Richards and Baker, 1993). However, potential transformations of nutrient species and algal communities as

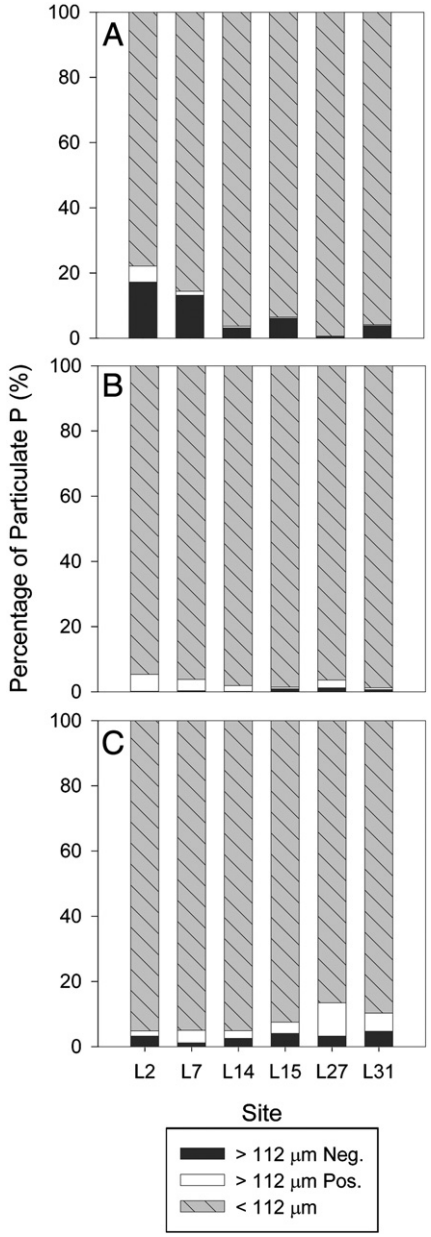

Fig. 3. Partitioning of water column P at six locations in western Lake Erie on June 15 (A), August 6 (B), and September 11, 2009 (C). Sites are arranged from closest to the Maumee River mouth (2 km) to farthest offshore (31 km). Bars represent percentage of water column P as Particulate P > 112 μm (negatively buoyant), Particulate P > 112 μm (positively buoyant = *Microcystis*), Particulate P < 112 μm, Dissolved Organic P, and Dissolved Reactive P.

they are transported downstream in tributaries and enter the lake are not well-documented. By collecting data from the river and the lake at nearly the same time, we hoped to better understand the changes in algal communities and phosphorus forms and size fractions between the river and lake and when and where they occur.

In the year of our study, concentrations of all forms of phosphorus were generally higher in the Maumee River than in the lake and there was relatively little difference between river sites. In June and especially in August however, there was a marked increase in TP concentration detected at R54 that was not accompanied by a corresponding increase in DRP, or DOP. This suggests that either smaller tributaries entering the Maumee River between the R99 and R54 sites contributed a substantial amount of P in particulate form to the river or that wind-driven resuspension of bottom sediments occurred. At all river and lake sites in June, the most abundant form of phosphorus was DOP. Given the high concentrations of DRP in the river at that time, high concentrations of DOP would be expected to have little additional influence on algal growth rates in the river. However in the offshore lake sites where DRP concentration was low, DOP may have been an important source of P for phytoplankton growth (Cotner and Wetzel, 1992).

In the August and September sampling dates, the prevalence of DOP declined and particulate P became the most abundant form of P. Analysis of filtered and size-fractionated samples indicated that most of the particulate P was in the form of particles smaller than 112 μm, suggesting that macrozooplankton and large algal colonies (the diatom *Aulacoseira* and cyanobacterium *Microcystis*) accounted for relatively little of the water column P in the lake. This was an unexpected result given that western Lake Erie experienced a dense bloom of *Microcystis* during those months. *Microcystis* colonies were the most conspicuous element in the water column with biovolumes averaging 53 mL in the plankton tows. The result of the phosphorus analysis did not support our hypothesis that during blooms a significant fraction of water column P would be found in *Microcystis* biomass.

Based on our observations during the previous 7 years that high biovolumes of *Microcystis* were usually not encountered at the mouth of the Maumee River, we hypothesized that the river would not be a seed source of *Microcystis* to the lake. Our observations in June, however, did not support our hypothesis. In situ analysis of algal pigment fluorescence at river sites indicated that cyanobacteria—identified as *Microcystis* via microscopy—were a large component of the phytoplankton assemblage at all river sites. In contrast, lake samples in June contained very little cyanobacteria. Contrary to our hypothesis, this result indicates that a significant population of *Microcystis* may develop in the Maumee River before the lake bloom develops and therefore the Maumee River may be a source of *Microcystis* inoculum for later blooms in the lake.

The presence of *Microcystis* in the river before it appears in the lake water column is suggestive, but not conclusive that the river is an important seed source of lake *Microcystis* and further studies will be needed to resolve this question. In particular, molecular and genetic data will be required to determine whether the strains of *Microcystis* that appear in the lake are also found in the river. There are known to be multiple genotypes or morphospecies of *Microcystis* in Lake Erie (Rinta-Kanto and Wilhelm, 2006), with a ratio of non-toxic:toxic genotypes of 3:1 (Dyble et al., 2008). A recent study found that Maumee River *Microcystis* were non-toxic, lacking the microcystin synthesis gene, mcyA (Kutovaya et al., in review), raising the possibility that the river contributes seed stock for non-toxic colonies while toxic colonies originate from a separate source, such as lake sediments. Sediments from Lake Erie collected 1 month before a bloom contained *mcyA* (one of the genes that regulate microcystin production) sequences found later in the water column during the bloom (Rinta-Kanto et al., 2009). Rinta-Kanto et al. (2009) were also successful in culturing sediment *Microcystis* in the laboratory, indicating *Microcystis* in lake sediments are viable. Lake sediments collected at our sampling sites in June were also found to contain significant numbers of *Microcystis* cells (C. Gruden, personal communication) that may have potentially contributed seed material for the late summer lake bloom in 2009.

While the Maumee River water developed a sizable *Microcystis* population before Lake Erie, the volume of water discharged from the river was too low for bulk transport of river *Microcystis* to solely account for the large *Microcystis* bloom that appeared in the lake several weeks later. The river discharge over the *Microcystis* growing season (June–Sept) is about 0.72 km^3 (USGS, 1930–2009 average), which would replace only about 2.9% of the water in the western basin (25 km^3, Bolsenga and Herdendorf, 1993). The bulk of the *Microcystis* biomass in western Lake Erie, therefore, is likely to be grown in the lake rather than transported from the river. As further evidence that lake *Microcystis* growth is important, a 2008 study indicated that *Microcystis* growth rates increased from the mouth of the Maumee River (site L2) to a maximum at locations 14–15 km from

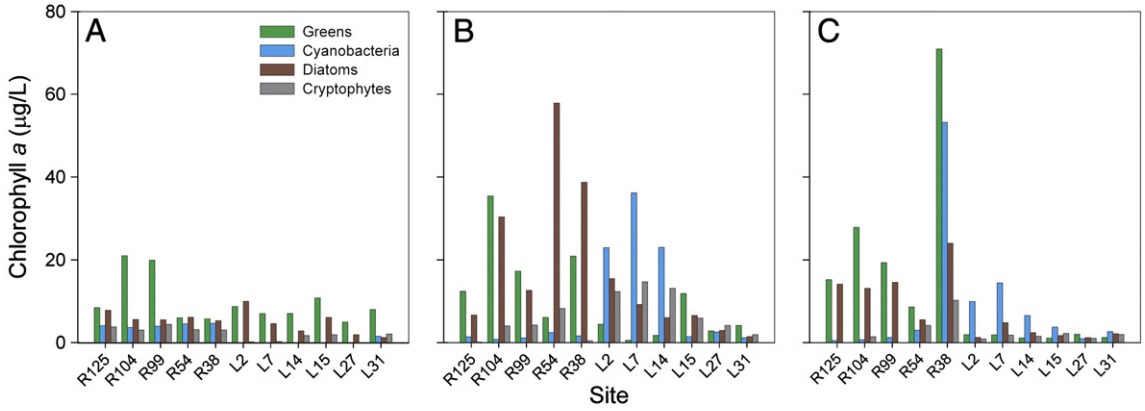

Fig. 4. Concentration of major river and lake phytoplankton groups for June 9–15 (A), August 4–6 (B), and September 8–11 (C), 2009. Sites are arranged from farthest upstream (R125) from the river mouth to farthest offshore in Lake Erie (L31).

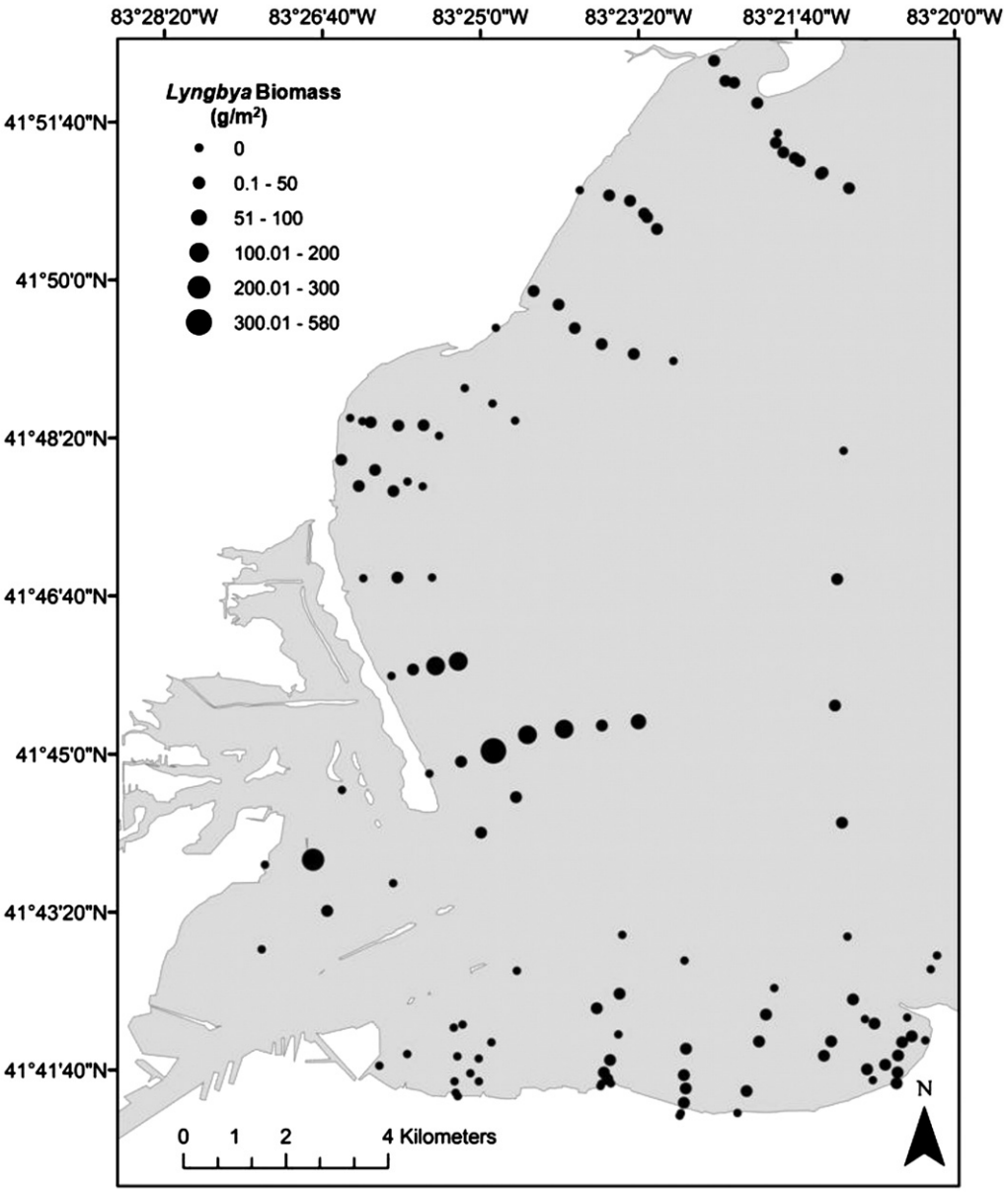

Fig. 5. Distribution and biomass (g/m^2 dry weight) of *Lyngbya wollei* in western Lake Erie in 2009.

the river mouth (L14, L15) where the Maumee River plume typically mixes with open lake waters (Chaffin et al., 2011).

In August, the overall concentration of phytoplankton increased in both the river and lake, but in the river, the increase was due to the growth of green algae and diatoms as cyanobacteria became less prevalent. *Microcystis* was dominant at the near-shore sites in the lake in August reflecting "bloom" conditions but became relatively less abundant farther offshore. The phytoplankton community at river sites in September was similar to June except for site R38 that experienced high concentrations of green algae and cyanobacteria. The high densities at Site R38 may have been due to higher residency times at this location as the river widens, allowing dense phytoplankton to accumulate in the river. In the lake in September, overall phytoplankton concentrations declined but *Microcystis* became relatively more dominant at most sites, including the farthest from the river mouth. This observation reflects a tendency we have observed in recent years that blooms seem to appear first in the Maumee Bay region and then spread farther into the lake. MODIS satellite imagery in 2009 indicated that the bloom eventually spread throughout the western basin of Lake Erie (Space Science and Engineering Center, U. Wisconsin, Madison, WI, USA).

In scheduling each of our river sampling dates, we attempted to allow ample time for the river plankton community to develop by avoiding sampling during or within 1 week of high flow events that would tend to wash out the plankton community. Additional rationale for sampling at base flow were that the Maumee River was in the condition of base flow approximately 80% of the time (USGS, Maumee River Gauge) from June through September 2009, and that base flow sampling permitted comparisons throughout the growing season without the confounding effects of high flow events. However, this scheme had the disadvantage that three high flow events in June and one in August were not sampled. High flow events have the effect of delivering pulses of nutrients and suspended sediments to Lake Erie that may influence algal growth. Indeed, a recent study of western Lake Erie *Microcystis* biovolume and Maumee River nutrient loading from 2002 through 2009 indicated that summer pulses of DRP loading to the lake tended to be followed by increased lake *Microcystis* biovolume 4 to 8 weeks later (Bridgeman et al., in review).

Large *Lyngbya* blooms are a recent occurrence in Lake Erie and have been observed only since 2006. The distribution, biomass, and ecological impacts of this species in western Lake Erie are not yet well understood (Bridgeman and Penamon, 2010). In this study we attempted to track *Lyngbya* distribution and biomass throughout the growing season to determine peak biomass and phosphorus content and relate that, in turn, to P in the water column. In areas where *Lyngbya* was found to be growing throughout the summer, areal biomass increased to a maximum observed in our August survey. Estimates of maximum biomass in 2009 are conservative because *Lyngbya* biomass may have continued to increase for a few more weeks until September. Mid-September storms typically dislodge *Lyngbya* mats from the bottom whereupon they float to the surface and are deposited on the shoreline or carried out into the lake depending on prevailing winds and currents (Bridgeman and Penamon, 2010). In August, *Lyngbya* contained a significant amount of P per area, on average about 15% of total water column P and a maximum of 75% of total water column P. Although *L. wollei* coverage in Florida springs varies with sediment P content (Stevenson et al., 2007), it is not presently known whether and to what degree *Lyngbya* may obtain nutrients from the lake sediments, a potentially rich source of phosphorus. If *Lyngbya* obtains nutrients from the overlying water, then it is likely that more P is now being retained in near-shore waters (2–4 m depth) than before the appearance of *Lyngbya* blooms in 2006. If *Lyngbya* is capable of obtaining nutrients from the sediments, then those nutrients would become available as *Lyngbya* biomass decays. The fate of P and other nutrients contained in *Lyngbya* is not known and may depend on where mobile mats are ultimately deposited. *Lyngbya* trichomes are surrounded by a sheath that resists decay. Mats deposited on the shoreline in the fall have been observed to overwinter nearly intact and then decompose slowly in the spring. In this case, nutrients from the previous summer's bloom become available to the near-shore habitat the following spring. Floating mats have also been observed to drift over 100 km to the central basin of Lake Erie where they may then sink to the bottom and potentially contribute to the development of central basin hypoxia.

The Maumee River is a major source of phosphorus contributing to HABs in western Lake Erie. The results of our study show that the concentrations and forms of phosphorus present can vary considerably between the river and lake and over the course of the growing season. At times, the majority of the phosphorus can be present as dissolved organic P, a form that is not detected in standard analyses for dissolved reactive P but may also be available for growth of phytoplankton. Although relatively little water column P is contained in *Microcystis* cells during blooms, benthic *Lyngbya* mats contain considerable P that may be retained and recycled in near-shore areas, potentially increasing the gradient of productivity between near-shore and offshore waters of Lake Erie.

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