Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions

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In 2011, Lake Erie experienced the largest harmful algal bloom in its recorded history, with a peak intensity over three times greater than any previously observed bloom. Here we show that long-term trends in agricultural practices are consistent with increasing phosphorus loading to the western basin of the lake, and that these trends, coupled with meteorological conditions in spring 2011, produced record-breaking nutrient loads. An extended period of weak lake circulation then led to abnormally long residence times that incubated the bloom, and warm and quiescent conditions after bloom onset allowed algae to remain near the top of the water column and prevented flushing of nutrients from the system. We further find that all of these factors are consistent with expected future conditions. If a scientifically guided management plan to mitigate these impacts is not implemented, we can therefore expect this bloom to be a harbinger of future blooms in Lake Erie.

extreme precipitation events | climate change | aquatic ecology | *Microcystis* sp. | *Anabaena* sp.

Eutrophication of freshwater and coastal marine ecosystems resulting from increased anthropogenic nutrient loading to receiving waters has become a global problem (1). Examples of eutrophic lakes with severe toxic cyanobacterial blooms include Lake Taihu in China (2), Lake Winnipeg in Canada (3), and Lake Nieuwe Meer in The Netherlands (4). Lake Erie, the shallowest, most productive, and most southern of the Laurentian Great Lakes, has experienced substantial eutrophication over the past half century. In the 1960s and 1970s, excess phosphorus from point and nonpoint sources produced nuisance algal blooms, poor water clarity, and extensive hypoxic areas (5). In response, the United States and Canada implemented phosphorus loading reduction strategies through the Great Lakes Water Quality Agreement (6, 7). These load reductions resulted in a rapid and profound ecological response as predicted by a range of models (8–10). Despite early success from these management actions, however, hypolimnetic oxygen depletion rates, hypoxia extent (11, 12), and algal biomass (13–15) have increased systematically since the mid-1990s. Of greatest concern is the increase in toxin-forming strains of the cyanobacteria *Microcystis* sp. and *Anabaena* sp. that produce the hepatotoxin microcystin and the neurotoxin anatoxin, respectively. Even nontoxic forms of these blooms, however, severely stress the ecological structure and functioning, as well as the aesthetics, of the Lake Erie ecosystem. Possible causes for these more recent increases include increases in agricultural nonpoint sources of bioavailable phosphorus (16), the presence of invasive mussel species, specifically *Dreissena rostriformis bugensis* (quagga mussels) and *Dreissenid polymorpha* (zebra mussels) (17–20), and internal phosphorus loading to Lake Erie's central basin that increases in response to hypoxic conditions (21).

In 2011, Lake Erie experienced an algal bloom of record-setting magnitude (Fig. 1). Land use, agricultural practices, and meteorological conditions may all have contributed to stimulating and exacerbating the bloom. We hypothesize that severe spring precipitation events, coupled with long-term trends in agricultural land use and practices, produced a pulse of remarkably high loading of highly bioavailable dissolved reactive phosphorus (DRP) to the western basin of Lake Erie. Uncommonly warm and quiescent conditions in late spring and summer, and an unusually strong resuspension event immediately preceding bloom onset, are further hypothesized to have provided ideal incubation, seeding, and growth conditions for bloom development. *Dreissenid* populations (22, 23), and phosphorus levels in lake sediments (24, 25) have been stable in recent years, and neither of these factors is therefore hypothesized to be a significant additional contributing factor. Here we test these causal hypotheses and their correspondence with long-

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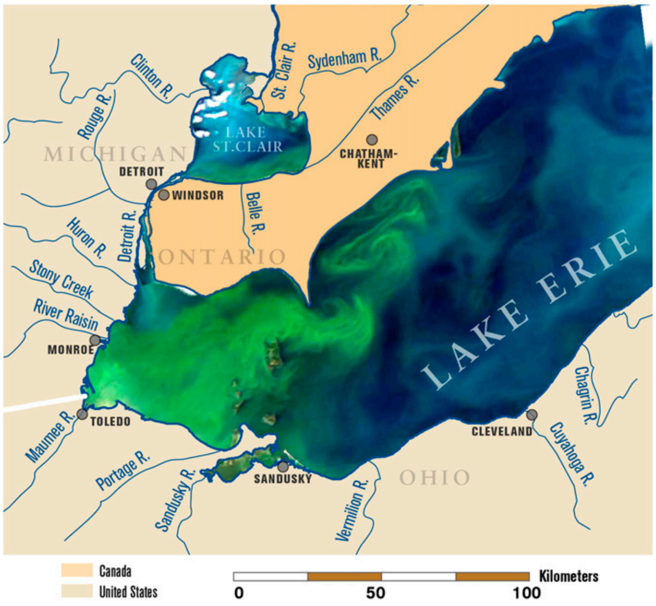

Fig. 1. MODIS satellite Image of Lake Erie on September 3, 2011, overlaid over map of Lake Erie tributaries. This image shows the bloom about 6 wk after its initiation in the western basin. On this date, it covers the entire western basin and is beginning to expand into the central basin, where it will continue to grow until October (Fig. S1).

term trends to assess whether the 2011 bloom was driven by a unique and unfortunate combination of circumstances or whether it is a harbinger of future eutrophication conditions expected under evolving land management practices and climate change in the region.

Results and Discussion

Lake Erie's 2011 algal bloom began in its western basin in mid-July, and estimates from remotely sensed data (26) indicate that it covered an area of ~600 km^2 during the initial phase (Fig. S1). In situ sampling of algal biovolume, areal coverage, and duration indicate that by early September the bloom was at least 2.4 times greater than the previous largest bloom (2008), and four times greater than the average of blooms between 2002 and 2010 (14). As *Microcystis* declined in the western basin in the latter part of the summer, the bloom spread into the central basin, eventually extending 150 km eastward and persisting until mid-October. At its peak in early October, the extent of the bloom was estimated to be more than 5,000 km^2 (26) (Fig. S1). The peak bloom intensity, calculated from remote sensing, was 7.3 times greater than the average for the previous 9 years and 3.3 times greater than the previous peak observed in 2008. Cyanobacteria, which were undetectable in June, represented 60–98% of in situ fluorescence measured from surface water throughout the western basin during the bloom.

Taxonomic analysis of the phytoplankton community confirmed that composition was almost entirely *Microcystis*. Microcystin toxin was detected at most western basin sampling sites with water-column integrated concentrations ranging from 0.1 μg/L to 8.7 μg/L. Surface toxin concentrations could have reached over 4,500 μg/L in early August assuming all *Microcystis* and microcystin formed a surface scum 10 cm in thickness. The World Health Organization guideline for microcystin in recreational waters is 20 μg/L (27), pointing to potential for adverse health effects in 2011. DNA analysis of *Microcystis* from various locations indicated similar strains in the western and central basins, suggesting that the central basin bloom arose from the eastward migration of *Microcystis* colonies from the original bloom. As the abundance of the nonnitrogen fixing *Microcystis* began to decline significantly in the western basin in late August, it was replaced by a secondary bloom of nitrogen-fixing *Anabaena* sp., suggesting that the *Microcystis* bloom had largely depleted bioavailable nitrogen in the lake. This was confirmed by in situ sampling of algal nutrient concentrations (*SI Materials and Methods* and *SI Results and Discussion*).

Microcystis sp. and *Anabaena* sp. are both potentially toxic cyanobacteria. *Microcystis* thrives in Lake Erie, where its growth is stimulated by high concentrations of DRP and combined inorganic nitrogen (i.e., ammonia and nitrate) (28). Concentrations of bioavailable phosphorus appear to govern the ultimate biomass of *Microcystis*, but Lake Erie's low bioavailable nitrogen-to-phosphorus ratio in late summer also provides cyanobacteria, including those that are nonnitrogen fixing, an additional competitive advantage over other phytoplankton classes (29–31). Temperature and mixing conditions are also important in determining growth, because cyanobacteria have a higher temperature optimum (on the order of 25 °C) than eukaryotic phytoplankton (17, 32), and temperature-dependent gas vacuoles increase *Microcystis* buoyancy, allowing them to rise to more favorable light and temperature conditions under quiescent conditions (33).

We hypothesize that trends in agricultural land use contributed to the 2011 bloom. Corn cropland increased 11% nationally and land in the federal Conservation Reserve Program (CRP) decreased 14% between 2008 and 2011 (Fig. S2). Similar trends in the western Lake Erie watershed could lead to increased phosphate fertilizer use, because phosphate is applied to corn at a 36% higher rate than to soybeans in Ohio (*SI Materials and Methods* and *SI Results and Discussion*), and because the conversion of CRP land to agriculture would also substantially increase phosphate use. Together, these could result in greater phosphorus runoff and higher loadings in western Lake Erie. However, trends in the Lake Erie watershed deviate sharply from those national trends. Both corn cropland and CRP land changed only slightly from 2008 to 2011 (*SI Materials and Methods*, *SI Results and Discussion*, and Fig. S2). It is therefore unlikely that recent agricultural land use trends are important drivers of the 2011 bloom.

Long-term trends in agricultural nutrient management practices, on the other hand, are consistent with a potential for higher nutrient loading (Table S1). Three management practices—autumn fertilizer application, fertilizer being broadcast on the surface rather than injected in the soil, and conservation tillage—can create conditions for enhanced DRP runoff. These practices have increased in the region over the last 10 y, although in some cases evidence is only anecdotal. Consistent with these trends is the observed 218% increase in DRP loadings between 1995 and 2011 ($P = 0.0004$) from the Maumee River, the main tributary to the western basin, whereas runoff increased by only 42% ($P = 0.12$) over the same period (*SI Materials and Methods*, *SI Results and Discussion* and Table S2).

Autumn weather conditions in 2010 were ideal for completing harvest and preparing fields for the following year, increasing autumn application of fertilizer. The spring of 2011 then experienced a series of large storm runoff events between February 17 and June 8, including a major event with peak daily mean discharge exceeding 2,200 m^3/s on May 25–27 (*SI Materials and Methods* and *SI Results and Discussion* and Fig. 2*A*). This storm represents the 99.8th percentile for Maumee daily discharge since 1975, when intensive monitoring of this tributary began. During this peak event, convective cells originated from a low-pressure system centered over the southern Great Plains and propagated to the north and east over a 2-d period (Fig. S3). The peak 24-h accumulated precipitation exceeded 50 mm over the Maumee River basin on May 26, contributing to a total of over 170 mm of rain in May 2011. This is over 75% above the prior 20-y average for May (97 mm averaged over 1986–2005). Total discharge and phosphorus loads for the 111-d (February 17 to

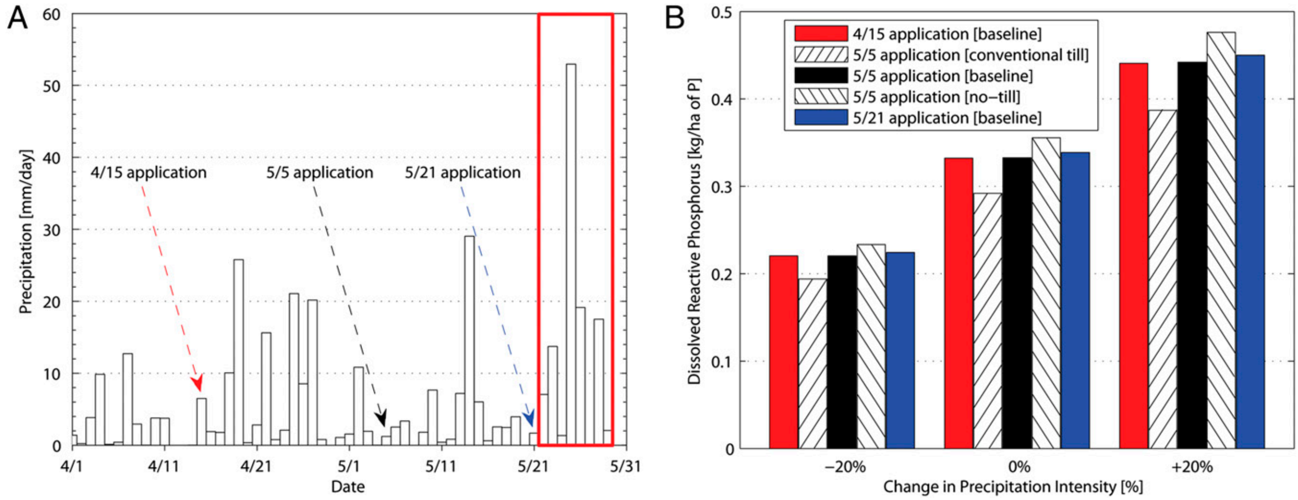

Fig. 2. (*A*) Time series of precipitation over the Maumee watershed, with the three different fertilizer application scenarios (arrows) used in the SWAT simulations. (*B*) Dissolved reactive phosphorus (DRP) yield (kilograms of P per hectares) response to different precipitation intensities, fertilizer application timing, and tillage practices. All DRP yields are summed over May 21–30, 2011 (red box in *A*). Baseline tillage practices include a realistic combination of conventional and no-till practices. Alternate tillage practice scenarios include either all conventional or all no-till practices with fertilizer application on May 5.

June 8) and 15-d (May 25 to June 8) periods covering the springtime precipitation events (Fig. S4) are among the largest observed since 1975, for periods of those lengths. Similarly, total discharge and DRP loads during the March-to-June timeframe, which is the critical period for setting up algal blooms (26), were the largest since intensive monitoring began in 1975. This is in stark contrast to these months in 2012, when discharge from the Maumee was only 20% and DRP loading was 15% of 2011 values.

We use the Soil and Water Assessment Tool (SWAT) model (34, 35) to test the impact of precipitation intensity and agricultural nutrient management practices on expected nutrient loading, to determine whether these factors are likely to be responsible for the loading observed in 2011. SWAT simulations indicate that DRP yields are sensitive to precipitation intensity (higher intensity increasing yields, Fig. 2*B*), fertilizer application timing (proximity to storm events increasing DRP yields, Fig. 2 *A* and *B*), and tillage practices (no-till increasing DRP yields, Fig. 2*B*), with precipitation having the strongest influence and fertilizer timing having the least influence (*SI Materials and Methods* and *SI Results and Discussion*). This supports the hypothesis that the confluence of long-term trends in agricultural nutrient management practices and extreme precipitation events was a strong contributor to the DRP yields that triggered the 2011 bloom.

We also hypothesize that temperature and wind conditions over the lake both before and during the bloom encouraged bloom growth, because warm and quiescent conditions before bloom onset led to minimal flushing of the system and reduced vertical lake mixing that allows *Microcystis* to take advantage of its buoyancy regulation. However, wind and surface water temperature data from the lake buoy indicate a lower frequency of warm and quiescent conditions during the 2011 prebloom period (defined as daily average wind stress $\tau < 0.05$ Pa and temperature $T > 15$ °C) (36) relative to other bloom years (*SI Materials and Methods* and *SI Results and Discussion*). In addition, although a particularly strong wind-driven resuspension event before the bloom onset could encourage fast initial bloom growth, wind conditions that led to the resuspension event immediately preceding bloom onset were not unusual relative to other years. After bloom initiation, on the other hand, conditions were indeed more conducive to bloom growth relative to other years, as quantified by the percent of time under warm and quiescent conditions after bloom onset (62% relative to 35–56% in other years, $P = 0.015$). These buoy-based observations are consistent with satellite-derived lake temperatures that were 3 °C warmer than the 1992–2011 summer climatology and 1 °C warmer than 2010 temperatures (*SI Materials and Methods*, *SI Results and Discussion*, and Fig. S5).

To investigate the role of lake circulation in encouraging the bloom, we apply 3D hydrodynamic and particle transport models (*SI Materials and Methods* and *SI Results and Discussion*). Simulations show that western basin monthly circulation is characterized by a broad west–east flow that exits the basin via three channels (North, Middle, and South), with low current magnitudes correlated with increased residence times (Fig. 3). All simulated years exhibit relatively low-magnitude currents during summer months (May–August), but 2011 had an extended period with weak currents (consistent with weaker winds) from late winter through summer (February–July) (Fig. S6). The residence times in the western basin during this period were 46% and 36% longer than in the previous years (2009 and 2010, respectively). Furthermore, residence times of Maumee River water in June 2011 were 53% longer than in the previous years and 77% longer (>90 d) than the estimated mean hydraulic residence time of the western basin (Fig. S7). Simulations also show that the long residence times were accompanied by a "short circuiting" of Detroit River waters, leading to minimal mixing between the Detroit and Maumee River waters along the western and southern shores of the basin, thus diminishing dilution of nutrient-rich Maumee River waters. Although some mixing occurs near the islands between the western and central basins during April–August, Detroit and Maumee waters primarily leave the western basin through the North and Middle/South Channels, respectively (Fig. S8). Location and timing of bloom initiation is consistent with simulated advection of the elevated late spring Maumee runoff, suggesting that the water mass present at the first stages of the bloom initiation likely originated from the Maumee River close to June 1.

Of the original hypothesized causes of the monumental 2011 bloom, observations and simulations therefore confirm that long-term trends in agricultural practices are consistent with increasing DRP loads delivered to the western basin of Lake Erie, and that meteorological conditions in spring 2011 led to record-breaking nutrient loads to the lake during the late spring. This conclusion is further supported by substantially lower discharge in 2012 leading to lower DRP loading and a weaker bloom (37). Our results further show that weak circulation during summer 2011 led to

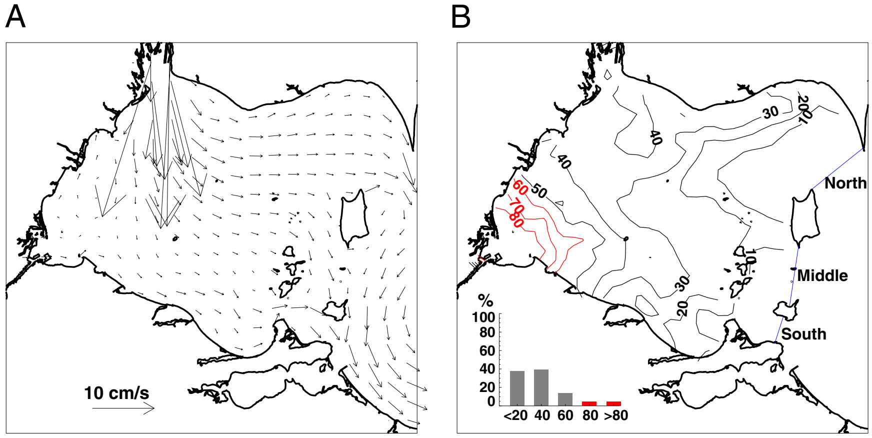

Fig. 3. Depth-averaged circulation (*A*) and residence times (*B*) in days of western basin of Lake Erie in June 2011. Red contours illustrate residence times that exceed the mean hydraulic residence time of the western basin. Histogram shows the percentage of water in the basin with residence times below 20 d, 20–40 d, 40–60 d, 60–80 d, and greater than 80 d.

longer residence times that incubated the bloom, and that warm and quiescent lake conditions after bloom onset allowed *Microcystis* to remain near the top of the water column and prevented flushing of nutrients out of the system. Conversely, data do not support the hypothesis that recent land use and crop choice trends in the watershed contributed to the observed significant increase in the 2011 nutrient loading. In addition, observations show that lake conditions were not unusually warm and quiescent before bloom onset, and the resuspension event immediately preceding the bloom was not of unusual magnitude. Overall, the magnitude of the 2011 bloom was thus caused by a confluence of long-term trends in agricultural nutrient management and extreme meteorological events conducive to bloom formation.

The degree to which the 2011 bloom is a harbinger of future conditions depends on the likelihood of these long-term agricultural trends continuing, and the likelihood of an increased frequency of meteorological conditions such as those observed in 2011.

Lacking policy intervention, many of the socioeconomic forces driving the trends in agriculture and nutrient management practices found to have exacerbated the 2011 bloom are likely to continue, increasing the likelihood of such massive blooms in the future. Factors such as increasing fertilizer costs, however, may provide some economic constraints. Furthermore, although crop choice was not found to have been a contributing factor in 2011, 2012 showed a marked increase in fertilizer-intensive corn acreage in the region (15% increase in Ohio; 4% increase in Michigan) (38). Nationally, planted corn acres were higher than a recent spike in 2007 and the highest since 1937, driven in large part by the high prices for corn resulting from biofuel policy (39). In addition, prospective changes to the CRP would lead to higher land use by agriculture overall (*SI Materials and Methods* and *SI Results and Discussion*). If the 2012 corn acreage is indicative of the future—and policies mandating higher biofuel production and lower CRP acres suggest that it is—then this trend will add to those trends found to have been significant in the 2011 loads.

To determine if precipitation events such as those observed in spring 2011 are more likely to occur in the future, we evaluate spring (March–April–May) daily precipitation over the western Lake Erie basin from 12 Climate Model Intercomparison Project Phase 5 (CMIP5) climate models implementing the Representative Concentration Pathway 8.5 (RCP8.5) scenario (*SI Materials and Methods*, *SI Results and Discussion*, and Table S3) (40). The historical (1986–2005) CMIP5 simulations over the western basin overpredict the current frequency of events >10 mm (Fig. 4) and overestimate the current average springtime precipitation intensity by 30%. Despite this overprediction of the historical period, prior CMIP3 studies have shown that climate model simulations of large scale (>1,000 km) flow patterns can reliably reproduce observations, and multimodel predictions of increased future precipitation intensity are statistically significant (41). Under the future RCP8.5 scenario, the frequency of events of >20 mm, which have an approximately annual recurrence interval based on the observational record, increases by ∼50%, and the frequency of larger storms increases even more, with events >30 mm being twice as frequent. This suggests a potentially even greater increase in the frequency of occurrence of the largest storms, such as the one observed in 2011.

Weak lake circulation and quiescent conditions after bloom onset, as observed in 2011, are also consistent with observed trends of decreasing wind speeds over the continental United States (42) and elsewhere (43), suggesting that the long residence times and quiescent conditions observed in 2011 may not be uncommon in the future. A continuing trend toward lower wind speeds would contribute to the severity of blooms, both

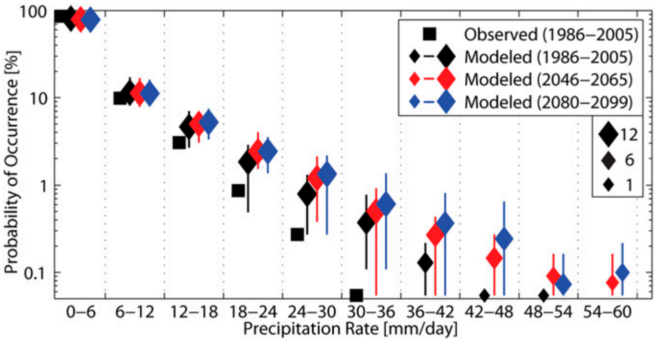

Fig. 4. Probability of daily precipitation intensities for spring (March–April–May) averaged over the western Lake Erie basin (40–43°N, 82–85.5°W) as observed by the Climate Prediction Center (CPC) gridded data (black squares) for the present-day time period (1986–2005), as modeled by a 12-model multimodel average for the same present-day time period (black diamonds) and for two future time periods of 2046–2065 (red diamonds) and 2080–2099 (blue diamonds). Vertical lines represent the range of individual model predictions for those models with a nonzero probability of a given event size. Diamond size represents the number of models included in each calculation (i.e., the number of models with nonzero probabilities for a given event size), ranging from 0 to 12. Individual model members are shown in Fig. S9.

through increasing residence times and decreased mixing in the water column.

In summary, we find that trends in agricultural practices, increased precipitation, weak lake circulation, and quiescent conditions conspired to yield the record-breaking 2011 Lake Erie algal bloom. We further find that all of these factors are consistent with expected future conditions. Lacking the implementation of a scientifically guided management plan designed to mitigate these impacts, we can therefore expect this bloom to indeed be a harbinger of future blooms in Lake Erie.

Materials and Methods

Microcystis biovolume and nutrient concentrations were determined at fixed locations in western Lake Erie, and molecular fingerprints were used to analyze *Microcystis* populations. Data on land use, county-level CRP land area, and crop-level phosphate fertilizer application were obtained from the US Department of Agriculture. Additional county-level nutrient use data were obtained from the Nutrient Use Geographic Information System. Meteorological analysis used data from the University Corporation for Atmospheric Research image archive and the College of DuPage. Daily precipitation observations were obtained from National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center. Analysis of discharge and phosphorus loading were based on data from the National Center for Water Quality Research at Heidelberg University and flow data from the US Geological Survey. The SWAT model was used to model nutrient loading. Lake Erie wind and temperature data were obtained from the NOAA National Data Buoy Center, and remote sensing lake surface temperature data were obtained from NOAA CoastWatch. Hydrodynamic modeling was conducted using the Beletsky and Schwab model and a particle tracking code was used for residence time calculations and river plume tracking. Present-day and future climate model analyses were based on the CMIP5 data archive. Detailed materials and methods, and references, are available in *SI Materials and Methods*. Information on data availability is provided in *SI Materials and Methods* and *SI Results and Discussion*.

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