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## Cold and wet: Diatoms dominate the phytoplankton community during a year of anomalous weather in a Great Lakes estuary



Jasmine L. Mancuso<sup>a,\*</sup>, Anthony D. Weinke<sup>a</sup>, Ian P. Stone<sup>a</sup>, Sarah E. Hamsher<sup>a,b</sup>, Manuel Villar-Argaiz<sup>c</sup>, Bopaiah A. Biddanda<sup>a</sup>

<sup>a</sup> Annis Water Resources Institute, Grand Valley State University, 740 Shoreline Drive, Muskegon, MI 49441, USA

<sup>b</sup> Biology Department, Grand Valley State University, 1 Campus Drive, Allendale, MI 49401, USA

<sup>c</sup> Instituto del Agua, Universidad de Granada, Granada, Spain

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### ABSTRACT

As sentinels of climate change and other anthropogenic forces, freshwater lakes are experiencing ecosystem disruptions at every level of the food web, beginning with the phytoplankton, a highly responsive group of organisms. Most studies regarding the effects of climate change on phytoplankton focus on a potential scenario in which temperatures continuously increase and droughts intersperse heavy precipitation events. Like much of the conterminous United States in 2019, the Muskegon River watershed (Michigan, USA) experienced record-breaking rainfall accompanied by unusually cool temperatures, affording an opportunity to explore how an alternate potential climate scenario may affect phytoplankton. We conducted biweekly sampling of environmental variables and phytoplankton in Muskegon Lake, a Great Lakes Area of Concern that connects to Lake Michigan. We compared environmental variables in 2019 to the previous eight years using long-term data from the Muskegon Lake Observatory buoy, and annual monitoring excursions provided historical phytoplankton data. Under cold and wet conditions, diatoms were the single dominant division throughout the entire growth season – an unprecedented scenario in Muskegon Lake. In 10 of the 13 biweekly sampling days in 2019, diatoms comprised over 75% of the phytoplankton community in the lake by count, indicating that the spring diatom bloom persisted through the fall. Additionally, phytoplankton seasonal succession and abundance patterns typically seen in this lake were absent. In a world experiencing reduced predictability, increased variability, and regional climate anomalies, studying periods of extreme weather events may offer insight into how natural systems will be affected and respond under future climate scenarios.

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### Introduction

As primary producers, phytoplankton form the base of the pelagic environment of freshwater ecosystems. A healthy, diverse phytoplankton community is necessary for proper ecosystem function and balance, playing a substantial role in important ecosystem processes, such as nutrient and organic matter cycling. Diversity is maintained through species interactions (e.g., competition for resources, epiphytic associations, antagonistic behavior), shifting environmental conditions, and periodic disturbances (Biddanda et al., 2021; Sigee, 2005). In temperate dimictic freshwater lakes, such as those in the Great Lakes region, a predictable seasonal

succession of phytoplankton community composition responds to temporal shifts in environmental variables. Briefly, phytoplankton growth is comparatively low in the winter; a diatom bloom occurs in the spring, as diatoms thrive in turbulent, low-light environments and variable nutrient concentrations; in late-spring, a clear-water phase occurs as resources deplete and zooplankton grow; small, fast-growing, inedible species (e.g., cryptomonads and chlorophytes) occur in low abundance near the end of this phase; a mixed bloom occurs in the summer and fall, including cyanobacteria, cryptophytes, chlorophytes, and dinoflagellates; and then diatoms often see a fall resurgence (Dodds and Whiles, 2019; Sommer, 1989).

While phytoplankton are cosmopolitan in nature, their diversity is found to vary across latitudinal, longitudinal, and altitudinal gradients (Stomp et al., 2011). Phytoplankton community diversity is largely controlled through bottom-up mechanisms, such as

\* Corresponding author at: Department of Biological Sciences, Oakland University, 318 Meadow Brook Road, Rochester, MI 48309, USA.

E-mail address: [mancusja@mail.gvsu.edu](mailto:mancusja@mail.gvsu.edu) (J.L. Mancuso).

nutrients, temperature, and light. Therefore, changes in land use and climate that impact local environmental variables threaten the biological integrity of the phytoplankton community (Stomp et al., 2011; Zhang et al., 2016). Furthermore, Ptacnik et al. (2008) and Ye et al. (2019) found that resource use efficiency positively correlated with phytoplankton diversity in freshwater, marine, and brackish ecosystems. Therefore, anthropogenically induced changes in community composition can lead to community imbalances, decreased diversity, reduced carbon cycling efficiency, and inability of phytoplankton to maintain stable populations (Bergkemper et al., 2018; Ptacnik et al., 2008; Urrutia-Cordero et al., 2017; Ye et al., 2019). As low points in the landscape that integrate changes in the watershed, lakes serve as reliable sentinels of climate change and hot spots of carbon cycling (Biddanda, 2017; Williamson et al., 2009). As such, phytoplankton are useful indicators of changing conditions due to their fast growth rates, short life cycles, high abundance, small size, and high reactivity (Cai and Reavie, 2018; Reavie et al., 2014b).

A major concern regarding climate change is the combined effects of enhanced anthropogenic nutrient loading into waterbodies and climate change-induced alterations of precipitation and temperature on cyanobacterial harmful algal bloom (HAB) development (National Office for Harmful Algal Blooms, 2021; Paerl and Otten, 2013). Most studies that investigate the multi-variable effects of global climate change on phytoplankton hinge on a scenario in which water temperatures continually warm, high-magnitude precipitation events are more frequent, and drought periods last longer (Carey et al., 2012; Havens and Paerl, 2015; Paerl and Otten, 2013). In the Great Lakes region specifically, several models have projected that climate change will manifest as higher annual mean temperatures, increased winter and spring precipitation in the short term, and eventual decreased precipitation as warming intensifies (Byun and Hamlet, 2018; McBean and Motiee, 2008; Wang et al., 2016; Zhang et al., 2020). Anthropogenic stressors have already induced quantifiable changes in the phytoplankton community of the Great Lakes. For example, warming water temperatures and extreme precipitation events have caused shifts in water quality and more frequent cyanobacterial HABs in Lake Superior (Austin and Colman, 2007; Cooney et al., 2018; Reint et al., 2020). To a more extreme extent, Lake Erie is facing recurring eutrophication events and cyanobacterial HABs due to nutrient inputs, surrounding land use, and climate change (National Office for Harmful Algal Blooms, 2021; Watson et al., 2016). Lakes Michigan and Huron have experienced changes in phytoplankton as well, most notably in the form of spring diatom declines, and Lake Ontario has seen increased summer densities of cyanobacteria (Reavie et al., 2014a).

However, it has been demonstrated that global climate change is not progressing linearly but rather manifests in extreme and record-breaking events, reduced predictability, and enhanced variability, especially at regional scales (Falvey and Garreaud, 2009; Katz and Brown, 1992; Melillo et al., 2014; Rahmstorf and Coumou, 2011; Wigley, 2009). In fact, the Midwest region of the United States experienced a 37% increase in the amount of precipitation concentrated in extreme events between 1958 and 2012 (Melillo et al., 2014). Such uncertainty in predicting future temperature and precipitation patterns warrants investigation into how potential climate scenarios will affect the phytoplankton community, and long-term studies are important in elucidating this impact (Fahnenstiel et al., 2010; Gillett and Steinman, 2011; Reavie et al., 2014a; Stockwell et al., 2020). The year 2019 was an unusually rainy year for most of the United States (NOAA, 2020; Fig. 1). In particular, the Great Lakes region experienced substantial water level rises due to frequent precipitation (US Army Corps of Engineers, 2020). Studying the year 2019 offered us a

valuable opportunity to glimpse the effects of an alternate scenario in which regional cooling and frequent precipitation prevailed.

Muskegon Lake (Muskegon, MI) is a mesotrophic drowned river mouth Great Lakes estuary. Drowned river mouths are the interface between lotic and lentic systems, creating an ecosystem in which physical and chemical properties exist along a spatial gradient. They are generally highly productive, and their wide range of habitats enables them to host a diversity of organisms and sustain high biomass (Defore et al., 2016; Dila and Biddanda, 2015; Larson et al., 2013; Marko et al., 2013). Due to a long history of anthropogenic stress, including lumber, industry, and wastewater influx, Muskegon Lake was termed an Area of Concern by the EPA in 1987 (EPA, 2020). One of the beneficial use impairments identified was the presence of nuisance algae (Steinman et al., 2008). While the lake has significantly improved in these terms due to intensive restoration efforts, isolated cyanobacterial blooms (often *Microcystis* species) still annually occur. Monitoring efforts have since been implemented, including the long-term Muskegon Lake monitoring program (2003–present; Steinman et al., 2008) and the Muskegon Lake Observatory (MLO; 2011–present; Biddanda et al., 2018). The long-term data available for Muskegon Lake make it ideal for our objective: understanding how a year of anomalous climatic variance characterized by unseasonably cool temperatures and record-breaking rainfall affected the phytoplankton community in 2019.

## Methods

### Study site

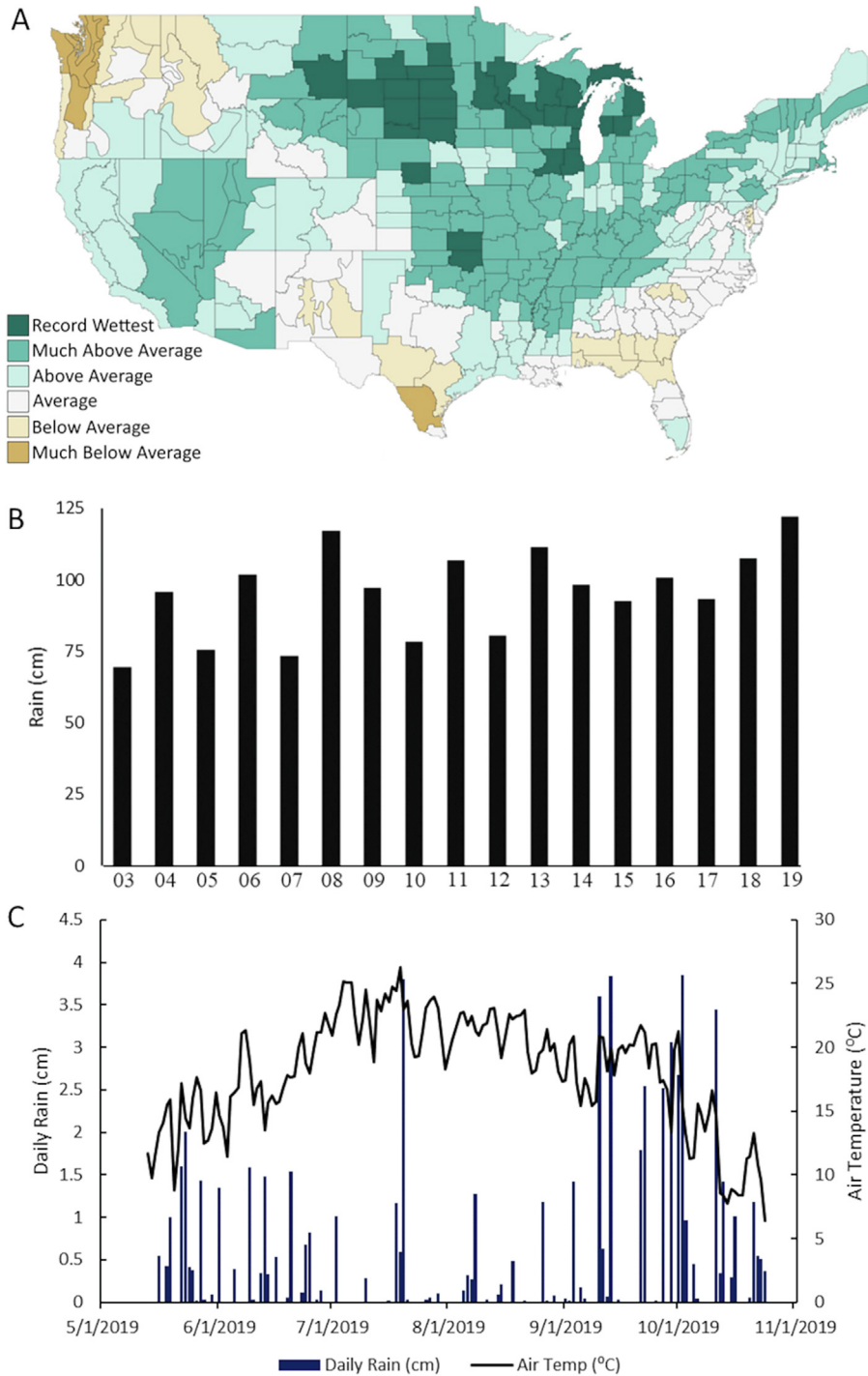
Muskegon Lake (N 43°13'59.45", W 86°17'25.42", Muskegon, MI) is a mesotrophic freshwater estuary. Its main inflow is the Muskegon River, and it drains Michigan's second largest watershed into Lake Michigan through a navigational channel. It has a surface area of 17 km<sup>2</sup>, volume of 119 million m<sup>3</sup>, mean depth of 7 m, maximum depth of 21 m, and seasonally variable hydraulic residence time of 23 days (Liu et al., 2018; Steinman et al., 2008; Fig. 2).

### Muskegon Lake Observatory (MLO) data

The MLO ([www.gvsu.edu/buoy](http://www.gvsu.edu/buoy)) buoy is located in the geomorphic center of the lake and is managed by the Biddanda Laboratory at the Annis Water Resources Institute (Fig. 2, yellow circle). The MLO is comprised of a surface buoy that houses the meteorological station and a subsurface buoy with a string of sensors that spans the water column (roughly 12 m in this location). Since its installation in 2011, the MLO records time-series water quality data every 15 min and meteorological data every 5 min (Biddanda et al., 2018). Data used in this study were daily averaged values and included water temperature, collected at 2, 4, 6, 8, 10, and 11 m (NexSens temperature nodes); precipitation (LUFFT WS600 Meteorological Station); and chlorophyll *a* (proxy for phytoplankton abundance) and phycocyanin (proxy for cyanobacteria abundance) pigment concentrations, collected at 2 m (Turner C3 Submersible Fluorometer). Periods of missing data are due to maintenance, service, and biofouling.

### 2019 Biweekly sample collection

From 30 April to 18 October 2019, we sampled biweekly at three sites: the Muskegon River inflow (MRIV), near the MLO buoy (MLO), and in the channel outflow (CHNL; Fig. 2, red triangles). We collected a phytoplankton sample at each site using a 20- $\mu$ m mesh plankton net to sample 10 m of the water column. Due to depth differences, we sampled 2 m of the water column

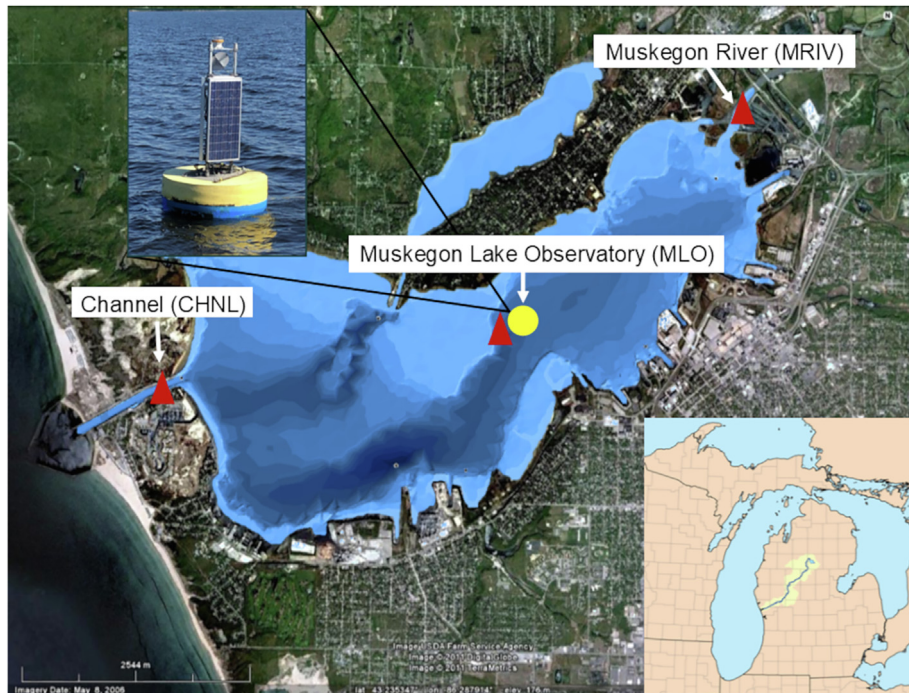


**Fig. 1.** A) A map of the conterminous United States displaying divisional precipitation ranks for 1 January through 31 December of 2019 based on long-term data from 1895 through 2019 (NOAA, 2020; <https://www.ncdc.noaa.gov/temp-and-precip/us-maps/>). Note that the Muskegon Lake watershed (Michigan, USA) is entirely within a “Record Wettest” region. B) Annual rain accumulation (1 January–31 December) for years 2003–2019 for Muskegon, Michigan (NOAA, 2020). C) Daily rain accumulation (cm) and daily average air temperature (°C); data provided by the Muskegon Lake Observatory (MLO) buoy for 2019.

five times consecutively at CHNL and MRIV and 10 m of the water column once at MLO. Each plankton tow sample was concentrated down to a final volume of 100 mL by swirling the sample around the caudal end of the plankton net while rinsing down the outside of the net with fresh site water and stored in a 125-mL brown Nalgene bottle. Upon return to the lab, 3–5% Lugol’s iodine solution was added, and samples were stored at room temperature.

We collected physiochemical measurements using a YSI 6600 maintained at 1 m for two minutes at each site. We collected whole water samples from 1 m with a Van Dorn sampler at CHNL and MLO and from the surface with a bucket at MRIV. Samples at MRIV were collected at the surface rather than at 1 m because water here is expected to be well-mixed, and we sampled from a bridge, where it was not feasible to use a Niskin sampler. We stored samples in 2-L transparent Nalgene bottles in a dark cooler until





**Fig. 2.** Study site, Muskegon Lake, including sampling locations (red triangles) and the location of the Muskegon Lake Observatory (MLO; yellow circle). The inset in the upper left is a picture of the MLO buoy. The inset in the lower right is a map of Michigan's lower peninsula, including the Muskegon River (blue line) with the watershed delineated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

returning to the lab for nutrient and chlorophyll *a* analyses. All sample collection equipment was rinsed with site water prior to use.

### Sample analyses

For phytoplankton analyses, we gently inverted samples several times to homogenize them before settling 1 mL of sample for 10 min in a Sedgewick Rafter Counting Chamber. Using Wehr et al. (2002), Prescott (1973), and Bellinger and Sigeo (2010) as reference texts, 350 algal natural units were identified to the genus level for each sample using a Nikon Ti-U or a Nikon Eclipse Ni-U DIC/Epi-fluorescence compound microscope at 200× to 400× magnification. We then mathematically scaled each sample up to represent the number of natural algal units per L of lake water (count per L).

We prepared water samples for nutrient analyses upon return to the lab. Nitrate ( $\text{NO}_3^-$ ) and soluble reactive phosphorus (SRP) samples were filtered through a 25 mm, 0.45- $\mu\text{m}$  nitrocellulose filter, which was rinsed with 5 mL of 25% HCl (v/v) and 25 mL of deionized water followed by pushing air through the filter three times.  $\text{NO}_3^-$  samples were frozen and SRP samples were refrigerated (4 °C) until analysis. We prepared ammonia ( $\text{NH}_3$ ) samples by acidifying 250 mL of sample with 250  $\mu\text{L}$  of concentrated  $\text{H}_2\text{SO}_4$  and then refrigerating (4 °C) until analysis. SRP and  $\text{NH}_3$  were analyzed on a SEAL AQ2 discrete automated analyzer using USEPA Methods 365.1 and 350.1 Rev. 2.0 (1993), respectively (AQ2 Methods NO: EPA-118-A Rev. 4, EPA-103-A Rev. 6).  $\text{NO}_3^-$  was analyzed on a Dionex ICS 2100 Ion Chromatograph using USEPA Method 353.2 Rev. 2.0 (1993, AQ2 Method NO: EPA-115-A Rev. 4).

We prepared samples for chlorophyll *a* analysis by filtering a measured amount of less than 500 mL of each sample through a 25 mm, 0.7- $\mu\text{m}$  microfiber GF/F glass fiber filter. Filters were stored in a -80 °C freezer until analysis. Briefly, filters were prepared by

grinding the filter and 3 mL of buffered 90% acetone for one minute. The slurry was left to extract at 4 °C for 24 h and then was centrifuged for 20 min at 4000 rpm. Absorbance wavelengths were measured against a blank (buffered acetone solution) at 750, 664, and 665 nm using a UV-VIS 2450 Shimadzu dual beam spectrophotometer, and chlorophyll *a* concentration (*c*), used as a proxy for phytoplankton abundance, was calculated using the following equation (Standard Methods, APHA et al. 1992):

$$c = 26.7 * (A_{664\text{nm}} - A_{750\text{nm}}) - (A_{665\text{nm}} - A_{750\text{nm}}) \\ * \text{Vol extracted (mL) / Vol filtered (L)}$$

### Statistical analysis

Heat maps were used to display temperature profiles of the lake for May through October of each year (2011–2019). Rows that had missing data at all depth sensors were removed, and data was interpolated by the program to fill values for those dates. Additionally, we assumed water temperature values 0 through 2 m were the same and extended the 2 m measurements to the surface. Dates of onset and termination of thermal stratification were determined as the date a thermocline at any depth was recorded and maintained for at least 3 consecutive days thereafter and the first date of the last 3-day consecutive period a thermocline was detected, respectively. However, for years 2011 and 2013, we used a 2-day criterion because both years had a period of missing data immediately following a 2-day period of thermocline detection in which the onset of stratification date likely occurred. To determine whether water temperature in 2019 was significantly different from other years, we performed one-sample t-tests to compare average 2 m water temperature values in the spring (20 May–19 June), summer (20 June–22 September), and fall (23 September–20 October) of 2011–2018 to those of 2019. Normality of data was confirmed using the Shapiro-Wilk test. To further explore the extent of the difference between 2019 and other years, we

summed the daily average 2, 4, 5, 6, and 8 m water temperature values on days for which all nine years had data (i.e., days for which any year was missing data were omitted). This resulted in 81 days between 30 May and 20 October for each year included in the analysis. Depths below 8 m were omitted from the analysis due to their subjectivity to influence from episodic Lake Michigan intrusion events of cold upwelled waters along the coast (Weinke and Biddanda, 2018). Data from 2018 was omitted from the analysis due to a substantial amount of missing data caused by sensor equipment malfunctions and resulting interruptions for observatory maintenance.

We created stacked bar graphs using phytoplankton abundance data to visualize community composition at the division level for each sampling day at each site. Data is displayed in terms of algal natural units per liter of sample water. We plotted chlorophyll *a* values measured from water samples collected at each site and water temperature (average of 1 m water temperatures recorded at each site) on a time-series graph.

A PCA correlation biplot was created using environmental data collected at each site during biweekly sampling to visualize and interpret temporal and spatial variation. Samples with missing data due to equipment malfunctions were removed, as PCA cannot be run on a matrix including missing observations. Variables included were dissolved oxygen (DO), pH, chlorophyll *a*, temperature, specific conductivity (SpCond), SRP, NH<sub>3</sub>, and NO<sub>3</sub><sup>-</sup>, and none were removed from the PCA, as they all had similar eigenvector lengths.

Non-metric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity matrix was used to visualize and interpret spatial and seasonal phytoplankton community variation in 2019. We performed a post-hoc adonis test to determine if significant differences existed between seasons and sites. If significance was detected, a pairwise permutation multivariate analysis of variance (PERMANOVA) was performed to locate the significant differences using the Benjamini and Hochberg adjustment method after 999 permutations. Subsequently, we ran a similarity percentage (SIMPER) analysis to determine the contribution of each phytoplankton genus to the dissimilarity matrix.

All analyses were performed in RStudio (R version 4.0.2; R Development Core Team, 2018) using the following R packages: rLakeAnalyzer for heat maps (Winslow et al., 2019), devtools for t-tests (Wickham et al., 2020), ggplot2 for stacked bar graphs (Wickham, 2016), vegan for PCA (Oksanen et al., 2018), and vegan and RVAideMemoire for NMDS (Hervé, 2020; Oksanen et al., 2018).

## Results

### MLO data trends

Our data suggest 2019 to be an unusually cool and wet year in Muskegon Lake. At 36.88 cm above the long-term average, 2019 had the highest annual rainfall accumulation of the past 115 years in Muskegon, Michigan (Fig. 1A, B). Of the 165 days of MLO operation in 2019, 79 days experienced rainfall, totaling 65.05 cm (Fig. 1C). This value is 56.90 cm less than the yearly rain accumulation for 2019, which was 121.95 cm (NOAA, 2020), indicating the remaining rainfall occurred before 30 April and after 18 October.

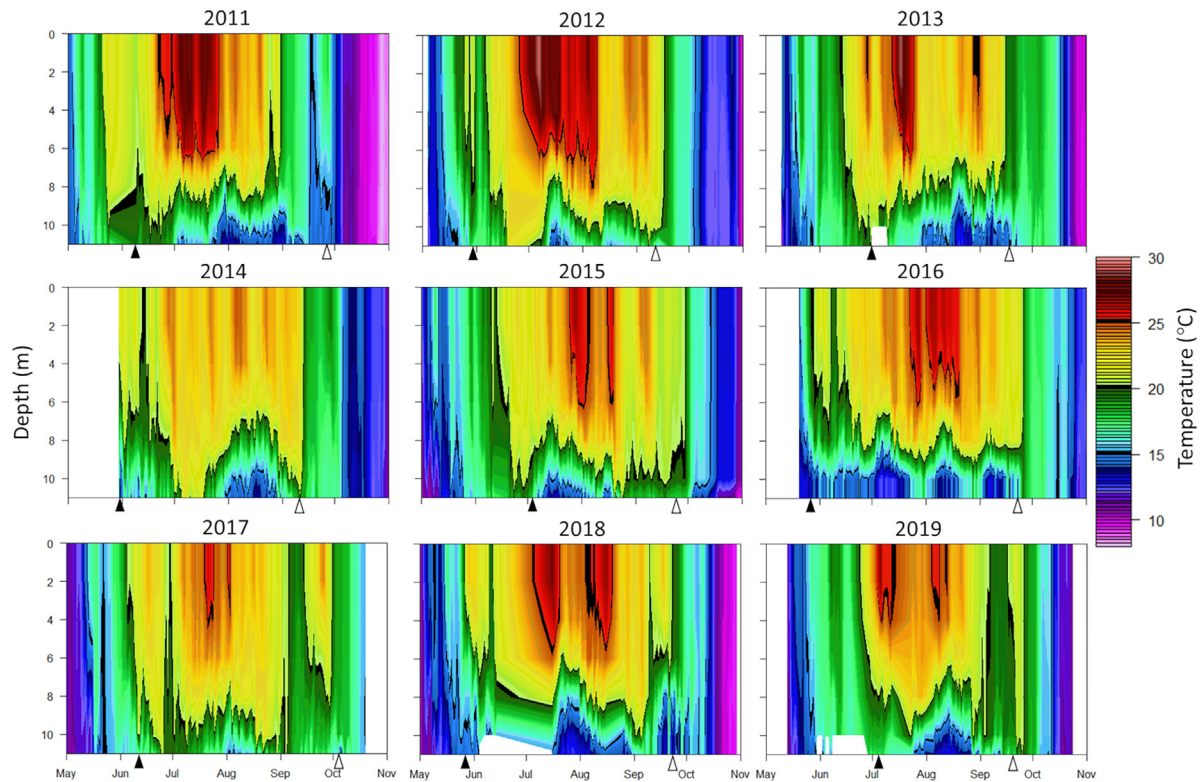
Heat maps and time-series data reveal 2019 as an anomalous year in terms of temperature for Muskegon Lake (Fig. 3). One-sample t-tests performed on time-series temperature data corroborate these observations: the average spring water temperature at 2 m in 2019 (17.14 °C) was significantly lower than that of 2011–2018 ( $t = 6.471$ ,  $p$ -value < 0.0005; Table 1) and was outside of the 95% confidence interval (18.70–20.49 °C). The average summer water temperature at 2 m in 2019 (22.84 °C) was also significantly

lower than that of 2011–2018 ( $t = 3.336$ ,  $p$ -value < 0.05) and was outside of the 95% confidence interval (23.07–24.21 °C). The fall average water temperature at 2 m in 2019 (16.38 °C) was not significantly different from that of 2011–2018 ( $t = 0.281$ ,  $p$ -value = 0.787) and was within the 95% confidence interval (15.27–17.79 °C). Thermal stratification began later in 2019 than in previous recorded years (Fig. 3). Date of initiation, considered as the date a thermocline at any depth was detected and maintained for at least 3 consecutive days thereafter (except for 2011 and 2013, in which a 2-day criterion was used due to missing data), was an average of 25 days later in 2019 than in 2011–2018. Additionally, 2019 had the shortest period of stratification of any other year, at 77 days (Table 2). However, thermal stratification ended around the same time as previous recorded years, with the last 3-day period a thermocline was detected beginning an average of 1.67 days earlier in 2019 than in 2011–2018. Additionally, water temperature at 2 m took an average of 10.10 days longer to reach 15 °C in 2019 than it did in 2011–2018. Similarly, it took 9.86 days longer to reach 19 °C and 7.88 days longer to reach 23 °C in 2019 than it did in 2011–2018. In 2019, average water temperature at 2 m reached over 25 °C on only 15 days, the fewest number of days in all but two other years on record (2014 and 2017). It was above 20 °C for only 69 days, the fewest number of days on record, with the next shortest being 78 days in 2018 (Table 1). Summing the 2, 4, 5, 6, and 8 m water temperature values for 81 days between 30 May and 20 October for each year, excepting 2018 (due to missing data – see above), revealed 2019 to be notably cooler than other years with a value of  $8.165 \times 10^3$  compared to a range of  $8.343 \times 10^3$ – $8.867 \times 10^3$  in 2011–2017 ( $8.539 \times 10^3 \pm 1.799 \times 10^2$ , mean  $\pm 1$  SD; Table 2; Electronic Supplementary Material (ESM) Fig. S1).

Chlorophyll *a* concentrations (a proxy for phytoplankton abundance) measured by the MLO demonstrate that 2019 had relatively low values compared to previous recorded years (Fig. 4A). Notably, the first peak occurred several weeks later than in previous years, and the three-peak pattern (mid-June, early August, late September) typical for chlorophyll *a* concentration in Muskegon Lake was absent. Rather, after the first peak in early July, chlorophyll *a* concentration steadily declined throughout the remainder of the growth season, excepting a slight peak in late August. Phycocyanin concentrations (a proxy for cyanobacterial abundance) measured by the MLO in 2019 generally followed a similar pattern to previous recorded years, with peak values occurring during the month of July and a steady decline thereafter, but values were noticeably lower (Fig. 4B).

### Biweekly sample data trends

Diatoms were the dominant division throughout all seasons and sites, especially in the spring and fall (Fig. 5). Diatoms comprised over 75% of the phytoplankton community by count in 10 of the 13 sampling days at CHNL and MLO and 12 of the 13 sampling days at MRIV. The three most numerous genera in the spring at MRIV were *Fragilaria* Lyngbye, *Melosira* Agardh, and *Navicula* Bory (Fig. 5A); at MLO were *Fragilaria*, *Aulacoseira* Thwaites, and *Melosira* (Fig. 5B); and at CHNL were *Fragilaria*, *Aulacoseira*, and *Dinobryon* Ehrenberg (Fig. 5C). In the summer, the three most numerous genera at all three sites were *Aulacoseira*, *Fragilaria*, and *Melosira*. In the fall, the three most numerous genera at MRIV were *Aulacoseira*, *Fragilaria*, and *Planktothrix* Anagnostidis & Komárek; at MLO were *Aulacoseira*, other centric diatoms (namely *Cyclotella* Brébisson and *Stephanodiscus* Ehrenberg), and *Fragilaria*; and at CHNL were *Aulacoseira*, *Cyclotella/Stephanodiscus*, and *Melosira*. Also apparent in the chlorophyll *a* time-series graph (ESM Fig. S2), MRIV had substantially lower phytoplankton abundance than CHNL and MLO overall and did not display the bell-shaped



**Fig. 3.** Time-series MLO water temperature data displayed as heat maps for each year of operation (2011–2019). While the deployment and retrieval dates for each year vary, the x-axis was standardized to 1 May–1 November; as such, some graphs have missing periods of data at the beginning and end of the time frame. White gaps within the heatmaps indicate dates with partial data. Dates of onset and termination of thermal stratification are denoted by solid and open triangles along the x-axis, respectively. Water temperature values at 15, 20, and 25 °C are displayed in black.

**Table 1**

Water temperature data from the MLO at 2 m depth in Muskegon Lake from 2011 to 2019 for comparing 2019 (bolded) to other years. Included are maximum recorded temperature (20 May–20 October), spring average (20 May–19 June), summer average (20 June–22 September), fall average (23 September–20 October), number of days above 20 °C and 25 °C (20 May–20 October), first date (as Julian day) over 15, 19, 23, and 25 °C. All values were calculated using daily-averaged water temperature (°C) values.

| Year        | Max. Temp.   | Spring avg.  | Summer avg.  | Fall avg.    | # Days > 25 | # Days > 20 | 1st Day > 15 | 1st Day > 19 | 1st Day > 23 | 1st Day > 25 |
|-------------|--------------|--------------|--------------|--------------|-------------|-------------|--------------|--------------|--------------|--------------|
| 2011        | 28.01        | 18.50        | 23.87        | 15.95        | 35          | 89          | 139          | 153          | 185          | 188          |
| 2012        | 29.25        | 20.72        | 24.90        | 14.45        | 36          | 91          | 132          | 140          | 171          | 187          |
| 2013        | 28.99        | 18.74        | 23.47        | 17.37        | 21          | 97          | 136          | 142          | 175          | 179          |
| 2014        | 24.95        | 21.10        | 23.25        | 14.84        | 0           | 94          |              |              | 176          | 217          |
| 2015        | 26.61        | 18.18        | 23.22        | 17.07        | 18          | 106         | 127          | 156          | 193          | 206          |
| 2016        | 26.79        | 20.07        | 24.07        | 17.45        | 28          | 121         | 141          | 146          | 170          | 204          |
| 2017        | 25.82        | 19.31        | 22.62        | 19.05        | 9           | 111         | 133          | 154          | 166          | 200          |
| 2018        | 27.10        | 20.11        | 23.73        | 16.06        | 19          | 78          | 129          | 146          | 149          | 197          |
| <b>2019</b> | <b>26.85</b> | <b>17.14</b> | <b>22.84</b> | <b>16.38</b> | <b>15</b>   | <b>69</b>   | <b>144</b>   | <b>148</b>   | <b>181</b>   | <b>185</b>   |

temporal pattern of abundance seen at the other sites. Alternatively, MRIV had higher phytoplankton abundance in the spring than the other two sites, but abundance values declined and were subsequently variable in the summer and fall. While the diatoms were overwhelmingly the dominant phytoplankton division at all three sites, other divisions were present in the summer and fall. At MRIV, dinoflagellates (e.g., *Peridinium* Ehrenberg), chlorophytes (e.g., *Gloeocystis* Nägeli, *Sphaerocystis* Chodat), cyanobacteria (e.g., *Planktothrix*, *Microcystis*, *Chroococcus*), and chrysophytes (e.g., *Dinobryon*, *Mallomonas* Perty) appeared in the summer, and cyanobacteria increased in abundance in the fall. At MLO, chrysophytes (*Dinobryon*, *Mallomonas*), cyanobacteria (e.g., *Dolichospermum* Wacklin, Hoffman, & Komárek, *Planktothrix*, *Aphanizomenon* Morren ex Bornet & Flauhault, *Microcystis*), chlorophytes (e.g., *Gloeocystis*, *Pandorina* Bory, *Pediastrum* Meyen), and, in small numbers,

dinoflagellates (e.g., *Cryptomonas*) appeared in the summer, and at CHNL, chrysophytes (e.g., *Dinobryon*, *Mallomonas*), cyanobacteria (e.g., *Planktothrix*, *Dolichospermum*, *Microcystis*, *Aphanizomenon*), and chlorophytes (e.g., *Pandorina*, *Pediastrum*, *Scenedesmus*) appeared in late summer, and their relative abundance at each site held steady throughout the fall.

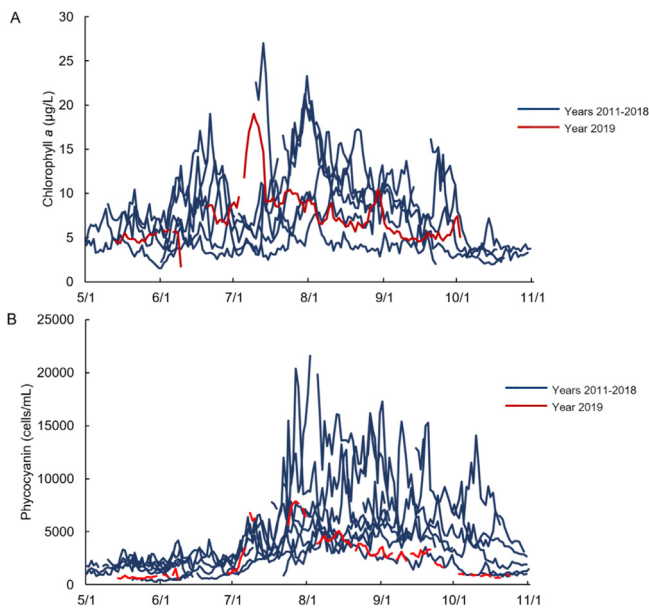
The PCA and NMDS demonstrated spatial and temporal variation in environmental variables and the phytoplankton community, respectively. The first two axes of the PCA explained a cumulative 62.86% of variation in environmental data (PC1 = 39.66%, PC2 = 23.20%; **ESM Fig. S3A**). Spring data associated with higher NH<sub>3</sub> and DO; summer data tended towards higher chlorophyll *a*, pH, and temperature; and fall data tended towards higher NO<sub>3</sub><sup>-</sup> and SRP. Both fall and summer data had higher SpCond than spring data. Regarding sites, CHNL and MLO grouped together,



**Table 2**

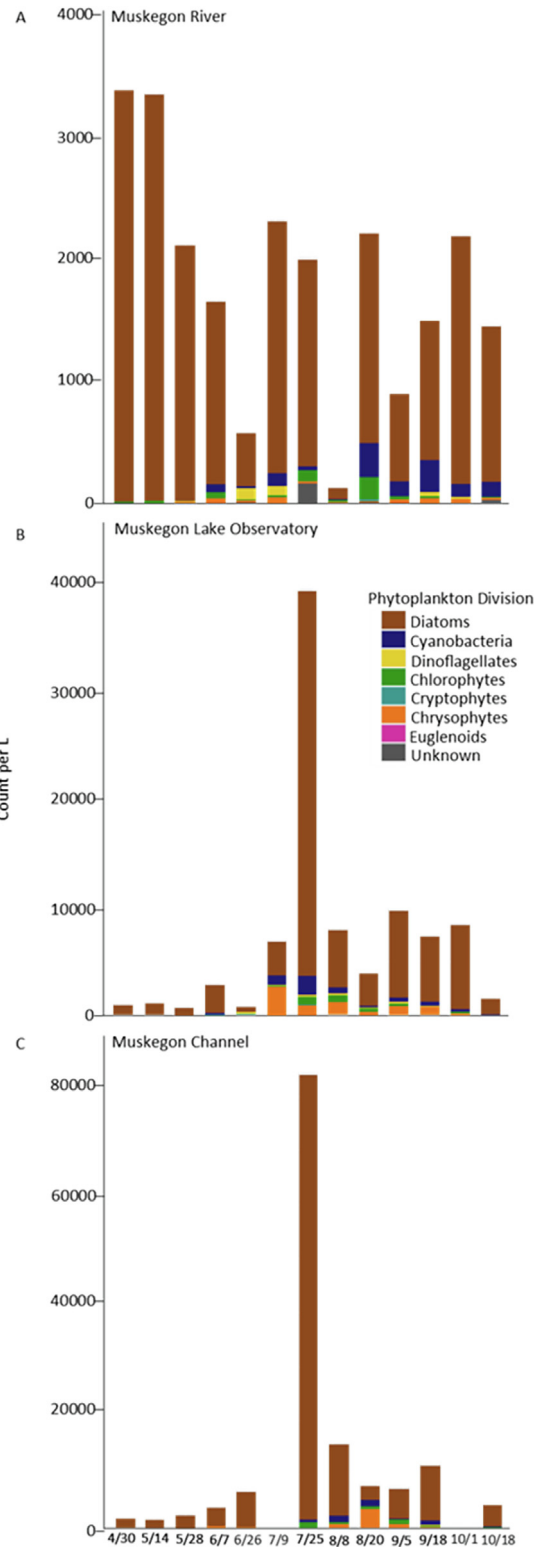
Summed daily average 2, 4, 5, 6, and 8 m water temperature values (°C), including days for which all included years (2011–2019, 2018 omitted) had data between 30 May and 20 October (i.e., days for which any year was missing data were omitted; n = 82). Duration of thermal stratification for each year (days), with dates of onset and termination determined as the date a thermocline at any depth was recorded and maintained for at least 3 days thereafter and the first date of the last 3-day period a thermocline was detected, respectively (except for 2011 and 2013, in which a 2-day criterion was used).

| Year | Sum of 2–8 m Water Temperature Values | Length of Stratification (days) |
|------|---------------------------------------|---------------------------------|
| 2011 | $8.552 \times 10^3$                   | 110                             |
| 2012 | $8.544 \times 10^3$                   | 105                             |
| 2013 | $8.343 \times 10^3$                   | 79                              |
| 2014 | $8.357 \times 10^3$                   | 102                             |
| 2015 | $8.640 \times 10^3$                   | 82                              |
| 2016 | $8.867 \times 10^3$                   | 119                             |
| 2017 | $8.467 \times 10^3$                   | 115                             |
| 2018 |                                       | 119                             |
| 2019 | <b><math>8.165 \times 10^3</math></b> | <b>77</b>                       |



**Fig. 4.** A) Time-series MLO chlorophyll a pigment concentration data at 2 m, used as a proxy for phytoplankton abundance. Years 2011–2017 are blue and 2019 is highlighted in red to compare to previous years. Note that 2016 and 2018 are not included due to insufficient data. B) Time-series MLO phycocyanin pigment concentration data at 2 m, used as a proxy for cyanobacteria abundance. Years 2011–2018 are blue and 2019 is highlighted in red to compare to previous years. For both graphs, periods of missing data are due to maintenance, service, and biofouling. Note that the x-axes only display the day and month due to there being multiple years of data included in the graph. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sharing little overlap with MRIV, driven by higher DO at CHNL and MLO and higher  $\text{NO}_3^-$ , SRP, and SpCond at MRIV. The phytoplankton community NMDS (stress value = 11.94; ESM Fig. S3B) and post-hoc adonis test displayed a significant difference in composition between seasons ( $F = 3.82$ ,  $R^2 = 0.177$ ,  $p\text{-value} = 0.001$ ), a marginally significant difference between sites ( $F = 1.74$ ,  $R^2 = 0.088$ ,  $p\text{-value} = 0.051$ ), and no significant interaction. Pairwise PERMANOVA tests revealed a significant difference between spring and fall ( $p\text{-value} = 0.003$ ), spring and summer ( $p\text{-value} = 0.003$ ), and



**Fig. 5.** Bar graphs representing phytoplankton community composition at the division level on each sampling day (30 April–18 October) for each site A) Muskegon River, MRIV; B) Muskegon Lake Observatory, MLO; C) Muskegon Lake Channel, CHAN. Abundance values are represented in algal natural units per liter of Muskegon Lake water.

CHNL and MRIV ( $p\text{-value} = 0.015$ ). SIMPER analyses revealed higher abundances of diatoms and, secondarily, cyanobacteria genera in the summer and fall than in the spring and at CHNL than MRIV.

## Discussion

Our objective was to understand how a year of anomalous weather patterns characterized by unseasonably cool temperatures and frequent precipitation affected the phytoplankton community of Muskegon Lake. The especially cool spring water temperatures delayed the first peak of phytoplankton abundance by several weeks, delaying it until early July when surface water temperature increased above 20 °C rather than mid-June when it normally occurs (Fig. 4A; ESM Fig. S2). In addition to continuously cool water temperatures, the delayed onset of stratification until late June paired with frequent rain and mixing events precluded epilimnetic phytoplankton growth and limited their abundance in comparison to other years. The driving mechanisms were likely high sedimentation risk and diluted nutrients due to mixing and high-water levels. In particular, lower water temperatures disadvantaged cyanobacteria in 2019 due to a suboptimal growth range and turbulence disrupting bloom formation (Paerl and Huisman, 2008; Robarts and Zohary, 1987; Visser et al., 1996; Fig. 4B). Overall, the temperature and precipitation regime of 2019 lowered phytoplankton abundance and disrupted the normal three-peak growth pattern in Muskegon Lake.

MRIV had far lower phytoplankton abundance and a community composition slightly skewed towards more epiphytic and single-celled taxa than the other two sites, CHNL and MLO (e.g., *Cocconeis* Ehrenberg, *Diatoma* Bory). Though MRIV had higher nutrient concentrations (ESM Fig. S3A), likely derived from upstream sources (Marko et al., 2013), it is probable that phytoplankton were unable to establish a strong population in the river due to high flow rates, short residence times, and high turbidity that diminished the photic zone. While these attributes are inherent characteristics of river mouths, the frequent precipitation of 2019 likely created a particularly unfavorable environment for phytoplankton in the river. It is possible that single-celled forms were favored at MRIV due to their high surface area to volume ratio and small size, which provides them with advantages in a turbulent, nutrient-rich river, such as high nutrient uptake rates and entrainment in the water column (Abonyi et al., 2014; Stockwell et al., 2020). Additionally, it is likely that the epiphytic taxa had been detached from their substrate during high-flow conditions. The slower water velocity, longer residence times, influx of nutrients from the Muskegon River, and lower turbulence at MLO and CHNL allowed for higher phytoplankton growth rates and a different assemblage to establish than at MRIV, namely filamentous and bloom-forming genera that benefit from water column stability and reduced water velocity (Mantzouki et al., 2015). Overall, the differences in environmental conditions and phytoplankton community composition between MRIV and the other two sites were expected but were likely exaggerated by the aberrant weather patterns of 2019 (Dodds and Whiles, 2019).

The most obvious and interesting finding was that the diatoms were the dominant algal division throughout the entire study period, with their abundance rarely dipping below 75% of total phytoplankton counts (Fig. 5). Through the Muskegon Lake monitoring program, which was initiated in 2003 and is performed by the Steinman Laboratory at the Annis Water Resources Institute, we have an extensive historical seasonal account of phytoplankton community composition. Muskegon Lake typically has a diverse phytoplankton community, comprised of relatively comparable amounts of chrysophytes, euglenoids, chlorophytes, dinoflagellates, cryptophytes, diatoms, and cyanobacteria (Gillett and Steinman, 2011; Mark Luttenton, Grand Valley State University, personal communication 2019). The continual dominance of diatoms in 2019 clearly deviates from the typical phytoplankton assemblage of Muskegon Lake as well as the seasonal successive

pattern posited for temperate dimictic lakes, in which diatoms are dominant in the spring and moderately abundant in the fall but largely absent in the summer (Dodds and Whiles, 2019; Sommer, 1989).

In broad terms, it is hypothesized that phytoplankton bloom development, coexistence among taxa, and single-taxon domination are largely driven by competition for light, which is directly influenced by mixing of the water column, in turn reliant on water temperature and precipitation or wind events (Huisman et al., 1999; Mur and Schreurs, 1995). In effect, a bloom can develop in a deep lake if the turbulent mixing does not exceed the critical turbulence of the phytoplankton species present. While turbidity was not exceptionally high in Muskegon Lake, nor light availability exceptionally low, we posit that the high mixing and low temperature conditions, enhanced by frequent meteorological events, provided diatoms with the advantage necessary to competitively exclude other phytoplankton divisions in 2019 (Huisman et al., 1999).

Diatoms' silica cell wall makes them prone to sinking (Hansen and Visser, 2019; Sicko-Goad et al., 1984), and they are competitive at a variety of nutrient concentrations, lower temperatures, and low light intensity. Thus, they are favored by frequent mixing of the water column, as it reduces sedimentation risk via turbulent resuspension, moderates water temperature in the photic zone, and entrains nutrients (Huisman et al., 1999, 2004; Rothenberger et al., 2009). Stockwell et al. (2020) posit that diatoms are benefited by the nutrient loading, reduced temperature and thermal stratification, and strong mixing fostered by storm events; therefore, the high frequency of the precipitation events in Muskegon Lake in 2019 created continuously favorable conditions. Additionally, in estuaries in particular, diatoms benefit from high rainfall, high river discharge rates, and short residence times, a phenomenon that is well-documented in the Neuse River Estuary, North Carolina, USA (Rothenberger et al., 2009; Paerl et al., 2010). The frequent precipitation throughout the Muskegon River watershed likely decreased water residence time in Muskegon Lake, favoring fast-growing taxa, such as diatoms, and disadvantaging taxa that require stable water columns for bloom formation, such as colonial cyanobacteria (Paerl et al., 2010; Stockwell et al., 2020). Therefore, we reason that the cool water temperatures of Muskegon Lake in 2019, long spring, and late onset of stratification provided the temperature regime necessary for diatoms to dominate through June. Subsequently, the frequent storm and wind events provided sufficient water column mixing to keep diatoms entrained throughout the summer and fall. Concurrently, insufficient temperatures, frequent mixing, and high flushing rates prevented other genera from outcompeting diatoms (Huisman et al., 1999).

Diatoms utilize silica for cell growth; therefore, it is often a limiting nutrient for their populations (Klemer and Barko, 1991; Moon and Carrick, 2007). The high abundance of diatoms relative to any other group in Muskegon Lake during 2019 suggests that silica was not limiting. The potential high abundance of silica may have been made possible by the intense precipitation in 2019, and increased runoff of silicic acid in the watershed via enhanced weathering of sedimentary and crystalline rocks, enriching the Muskegon River with silica (Tréguer et al., 1995). As such, silica in 2019 was likely abundant, while previous years with lower precipitation potentially had lower silica concentrations that limited diatoms.

Within the diatoms, shifts in genus-level composition corresponded with seasonal shifts in environmental conditions (ESM Fig. S3B). The spring community was dominated by *Fragilaria* and, secondarily, *Aulacoseira* and *Melosira*, which are all filamentous diatoms. These results are unsurprising for pelagic-zone spring sampling, and *Fragilaria* is often an abundant genus in the region (Reavie et al., 2014a). *Fragilaria* benefit from high light

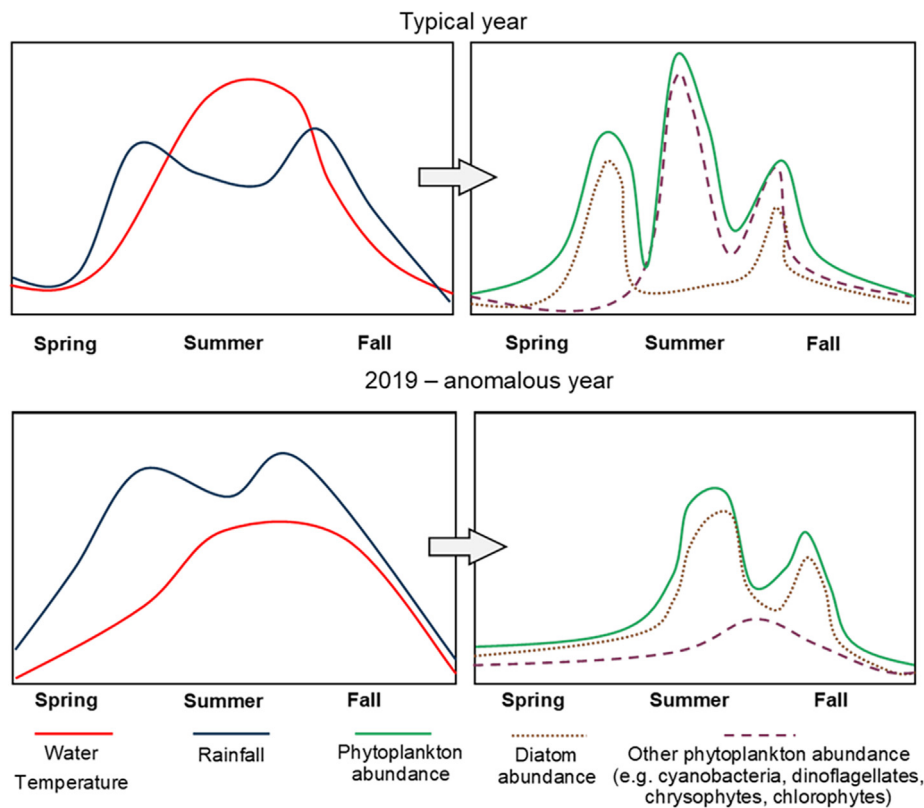


conditions, in contrast to most diatoms, and high N:P ratios, which likely drove their success here (Saros et al., 2005; Stoermer et al., 1978). The diatom bloom persisted and grew in the summer, driven by increases in *Fragilaria*, *Aulacoseira*, and *Melosira* and unusually mild increases in chrysophytes (*Dinobryon* and *Mallomonas*) and cyanobacteria (*Dolichospermum*, *Planktothrix*, and *Microcystis*) genera. However, there was a notable shift in diatom dominance from *Fragilaria* to *Aulacoseira* and *Melosira*. *Fragilaria* likely lost its advantage due to a diminishing light environment as phytoplankton growth increased (Horn et al., 2011). *Aulacoseira* has been noted to benefit from long, cold springs, late onset of stratification, and low light conditions (Horn et al., 2011). *Melosira*, often absent in the presence of stratification, has also been noted to appear in the summer if mixing is sufficient (Lund, 1971). Therefore, *Aulacoseira* and *Melosira* increased over *Fragilaria* due to conditions sustained by frequent precipitation, such as water column mixing, that prevented sinking. The fall also saw an increase in diatoms relative to spring: *Aulacoseira*, other centric diatoms (mainly *Cyclotella* and *Stephanodiscus*), and *Melosira*. *Fragilaria*, however, was significantly less abundant in the fall than spring, indicating its continued decline. One cyanobacteria genus, *Planktothrix*, was significantly more abundant in fall than spring. While a resurgence of diatoms is a familiar scenario in the fall, they are usually substantially accompanied by other divisions, such as cyanobacteria, which was not the case here. The lack of differentiation in community composition between the summer and fall further indicates a persistent presence of diatoms and surprising lack of other divisions.

Gillett and Steinman (2011) discussed a similar situation in Muskegon Lake during the year 2008, which was also a cold and wet year, but not to the extent of 2019. Comparably to 2019, the

phytoplankton community of 2008 saw significant diatom abundance, which the authors similarly attributed to turbulent conditions created by meteorological events. In contrast to 2019, 2008 had substantially higher phytoplankton biovolume than did previous years and a strong cyanobacteria presence, which the authors hypothesize was a result of increased nutrient influx due to precipitation events. However, the authors do not report any outstanding deviations in water quality parameters for that year and indicate that climatic variables may have been the driving factor. It is possible that the effect of increased precipitation and cooler water temperature on the composition of the phytoplankton community is contingent on the severity of those variables in their effects on water column stability, light environment, and phytoplankton growth optima. Studies have shown that warm temperatures and extended drought periods promote cyanobacteria abundance (Havens et al., 2019; Jöhnk et al., 2008; Lehman et al., 2017); Gillett and Steinman (2011) discussed a year in which moderately cool and wet conditions lead to both diatoms and cyanobacteria being dominant divisions; the present study found that a year of record-breaking precipitation and substantially cooler temperatures wholly favored diatoms and severely disadvantaged cyanobacteria.

Together, these phenomena support the idea that drastic, short-term climatic oscillations, such as that of 2019, have the potential to override long-term trends (Stockwell et al., 2020). If increased frequency of extreme rainfall events is a persistent pattern in the future, as is suggested by some climate models (Huntingford et al., 2003), specifically one calibrated for the Great Lakes region (Byun and Hamlet, 2018), and regional cooling prevails, diatom domination may occur more frequently with potential ecosystem impacts (Harvey et al., 2019; Fig. 5). However, future research



**Fig. 6.** Schematic diagram conceptualizing the main findings of the study, comparing environmental conditions and phytoplankton blooms during typical years (top panels) and the anomalously cold and wet 2019 (bottom panels). In general, typical years tended to have greater phytoplankton abundance, including HABS, and a three-peak growth pattern relative to 2019. The cool, long spring of 2019 delayed stratification and this, coupled with frequent precipitation, increased water column mixing and decreased residence time, allowing the spring diatom bloom to persist through the summer and fall and preventing cyanobacterial dominance. Note: these conceptual figures are based off visual assessments of long-term data and were not created using actual data.

should explore the possibility of top-down mechanisms influencing the phytoplankton community in unusual years, such as if viruses, zooplankton, and fish were also affected by the changed trophic structure resulting from the aberrant weather, and the extensive remediation efforts on the lake have likely reduced cyanobacterial abundance over time by reducing nutrient concentrations (Benndorf et al., 2002; Hanson et al., 2017; Villar-Argaiz et al., 2002).

## Conclusion

One year of anomalous weather patterns, 2019, resulted in an anomalous phytoplankton community in Muskegon Lake. The cool, long spring that delayed stratification coupled with frequent precipitation that increased water column mixing and decreased residence time created an environment in which diatoms were continually competitive, and the spring diatom bloom persisted and grew throughout the summer and fall (Fig. 6). In a world experiencing extreme oscillations in weather patterns and an uncertain future in the face of uneven climate change (Falvey and Garreaud, 2009; Zellweger et al., 2020), understanding anomalous regional events is critical for informing how various climate change scenarios will impact the water quality of temperate freshwater lakes and, in turn, advising management strategies. While no single climatic event can be confidently attributed to climate change, it is of paramount importance to recognize the mounting evidence that suggests extreme events are increasingly common and have ecosystem-level implications (Trenberth, 2012). Such significant shifts in the phytoplankton community in the world's lakes and estuaries not only serve as sensitive sentinels of anthropogenic change but have vast implications for the rest of the aquatic food web and the global cycling of elements (Biddanda, 2017; Downing, 2010; Harvey et al., 2019).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2021.07.003>.

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