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Out of oxygen: Stratification and loading drove hypoxia during a warm, wet, and productive year in a Great Lakes estuary

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ABSTRACT

Hypolimnetic hypoxia, or low oxygen in bottom waters, impairs ecosystem services of freshwater lakes and estuaries globally. Both hypoxia incidence and intensity are increasing around the world due to eutrophication and climate change. As the hypolimnion becomes hypoxic and ultimately anoxic, sediment-bound legacy phosphorus is released. Water column mixing due to large storm events or fall turnover entrains these nutrients to the surface, causing harmful algal blooms. To assess the dynamics of hypoxia throughout the growing season, we evaluated Muskegon Lake, where hypoxia recurs annually, utilizing high-frequency time-series data from the Muskegon Lake Observatory (MLO) buoy (https://www.gvsu.edu/wri/buoy/), biweekly nutrient sampling, and seasonal respiration experiments during 2021. While water-column stratification set the stage for hypolimnetic hypoxia, frequent wind-mixing events, and episodic intrusions of cold, oxygenated, upwelled Lake Michigan waters intermittently reduced the thickness or intensity of the hypoxic zone. Respiration experiments revealed that riverine and surface organic matter inputs contributed most to hypolimnetic hypoxia in the spring, whereas surface inputs did so during summer, and riverine inputs during fall, indicating seasonally variable sources drive hypoxia. Biweekly measurements indicated increased soluble reactive phosphorus in the hypolimnion during anoxia via internal phosphorus loading from the sediment with the potential for fueling surface blooms with net export of soluble reactive phosphorus and total phosphorus to nearshore Lake Michigan. Our findings on the role of seasonally changing temperature, loading, phytoplankton production, hypolimnetic respiration, and internal phosphorus loading in shaping hypoxia dynamics have relevance to similarly afflicted ecosystems in the Great Lakes Basin.

Introduction

Freshwater ecosystems provide clean drinking water, food, recreation, and jobs to millions living near the Laurentian Great Lakes. These ecosystems also provide habitat, breeding grounds, and critical food web interactions for terrestrial and aquatic organisms. However, aquatic systems across the world are experiencing hypolimnetic hypoxia, or low dissolved oxygen (DO) in bottom waters, at greater intensities than years past due to climate change and anthropogenic activities (Breitburg et al., 2018; Brewer and Peltzer, 2009; Conroy et al., 2010; Diaz and Rosenberg, 2008; Ding et al., 2018; Kane et al., 2014; Rabalais et al., 2010; Scavia et al., 2014). An aquatic ecosystem is considered hypoxic when DO concentrations are at or below 4 mg/L, with mild hypoxia prevailing at concentrations between 2–4 mg/L and severe hypoxia between 0–2 mg/L. (Biddanda et al., 2018; Rabalais et al., 2010). Hypoxia is classified in this way due to the lethal and non-lethal effects on fish at low DO concentrations, such as fish kills or deterring fish from inhabiting bottom waters, respectively (Magaud et al., 1997; Weinke and Biddanda, 2018). Protecting freshwater ecosystems from increasing eutrophication and hypoxic zones is vital to maintaining the ecological, economic, and intrinsic values and services they provide even as the climate changes.

Understanding the future effects of climate change on aquatic ecosystems is key to envisioning the future dynamics of hypoxia. A variety of studies have modeled future climate change scenarios for the Midwest and Great Lakes regions as well as globally (Byun and Hamlet, 2018; Katz and Brown, 1992; O'Reilly et al., 2015; Rahmstorf and Coumou, 2011). Katz and Brown (1992) suggest that climate extremes and the time interval between events indicate that climate could be changing in the direction of extremes. Climate change has increased global surface air temperatures between 0.1 °C and 1.8 °C over the last 100 years (Rahmstorf and

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Coumou, 2011). Byun and Hamlet (2018) determined that Midwest and Great Lakes Region air temperatures will continue to rise with overall increases between 3.31 °C and 6.45 °C by 2100 relative to a baseline period from 1971 to 2000. Meanwhile, mean water temperatures globally have increased 0.34 °C per decade. Lakes in the Great Lakes region that normally experience seasonal ice coverage are warming even faster at a rate of 0.72 °C per decade because of increased temperature and solar radiation and decreased cloud coverage (O'Reilly et al., 2015). Over the last 60 years, precipitation has increased in the United States on average by 4.5–5.7% due to higher wet day intensities (Harp and Horton, 2022). Precipitation is expected to increase by 30% during the winter and spring and decrease by 15% during the summer by 2080. As temperature and precipitation extremes continue to change over time, hypoxia and harmful algal bloom (HABs) dynamics will shift temporally and spatially in response to the changes in climate (Jane et al., 2021; Mancuso et al., 2021; Michalak, 2016; Whitney, 2021). As an additional downstream effect of hypoxia, greenhouse gas emission, methane from anaerobic respiration, occurs when organic matter, such as algal biomass, decomposes in a low oxygen environment. As the water column mixes, these greenhouse gasses can be released into the atmosphere, furthering climate change (Salk et al., 2016).

Muskegon Lake experiences hypoxia on a yearly basis (Biddanda et al., 2018; Dugener et al., 2023). Muskegon Lake is a drowned river mouth Great Lakes estuary that provides a vital connection between the lentic and lotic aquatic ecosystems of Lake Michigan and the Muskegon River, respectively (Fig. 1; Larson et al., 2013; Weinke et al., 2022). Restoration and continued research efforts intend to remove Muskegon Lake from its current standing as a designated Area of Concern (AOC) (Steinman et al., 2008). The organic matter that is decomposed and leads to hypoxia can either come from autochthonous surface algal production, or allochthonous riverine carbon. As organic matter infiltrates the hypolimnion from either source, DO is consumed by bacteria, which creates hypoxia. Earlier studies have measured respiration in the Muskegon River and Muskegon Lake surface waters; but to the best of our knowledge, there are no concurrent measures of hypolimnetic respiration, a measure that could be useful for constraining/modeling hypolimnetic oxygen depletion (Defore et al., 2016; Dila and Biddanda, 2015). Biological oxygen demand (BOD) experiments are a useful tool for understanding how different sources of carbon fuel subsequent respiration rates in the hypolimnion (Scully et al., 2022).

A previous study has shown that Muskegon Lake serves as a sink for total phosphorus (TP) and particulate organic carbon as water flows from the Muskegon River into Lake Michigan (Marko et al., 2013). Even after external nutrient loading decreases, legacy nutrients such as phosphorus (P) can be released from the sediment into the overlying water column when that water is anoxic, containing no dissolved oxygen (Anderson et al., 2021a,b; Carey et al., 2012). As anoxia occurs within a lake, legacy P that was bound with iron hydroxides or other metals in the sediment is released into the water column, as is the iron and manganese that was initially bound to the P (Mortimer, 1941; Steinman and Spears, 2020). If storms and mixing events co-occur with phosphorus release from the sediment, the unbound phosphorus is dispersed throughout the water column, where it is taken up by cyanobacteria and phytoplankton. In turn, these cyanobacterial blooms can cause contamination of municipal drinking water sources and beach closings (Ding et al., 2018; Paerl et al., 2016a,b; Watson et al., 2016). Water column mixing stirs the re-suspended P into the surface waters, instigating a positive feedback loop of cyanobacterial blooms, hypoxia, and regional climate change (Salk et al., 2016; Steinsdóttir et al., 2022; Sweerts et al., 1991). However, the positive feedback loop is nonlinear, and the subsequent impacts of hypoxia can occur in different severities and durations. Therefore, it is vital to understand the causes of hypoxia and mitigate its consequences in aquatic ecosystems where eutrophication may occur (Magaud et al., 1997; Paerl et al., 2016a).

The objectives of this study were to: 1) quantify the spatial and temporal scale of hypolimnetic hypoxia during 2021 and correlate them with shifts in environmental or meteorological patterns such as changes in stratification strength, 2) describe the effects of temporal inputs of organic matter on the drawdown of oxygen in the hypolimnion, and 3) assess internal P loading from the sediment and subsequent phytoplankton growth at the surface which may lead to further hypoxic conditions. The sediment in Muskegon Lake was expected to experience occasional, short-term exposures to hypoxia/anoxia events followed by oxic conditions replacing the hypoxic zone in a period of hours or a few days due to wind mixing events. This cycle was anticipated to repeat multiple times throughout the summer-fall period when the lake is generally stratified. The present study implemented seasonal BOD experiments to elucidate the direct inputs of organic matter into Muskegon Lake, inputs that in turn drive oxygen consumption creating hypoxia. By critically analyzing the high-frequency Muskegon Lake Observatory (MLO) environmental data, making discrete, biweekly, in situ sampling/measurements, and carrying out seasonal respiration experiments, we investigated the causes and consequences of hypolimnetic hypoxia in Muskegon Lake.

Methods

Study site

Muskegon Lake (43.23^{o} N, 86.29^{o} W) is a mesotrophic drowned river mouth Great Lakes estuary located in Muskegon, Michigan (Fig. 1; Mancuso et al., 2021). Muskegon Lake drains the second largest watershed in the state of Michigan, the Muskegon River, into Lake Michigan. The estuary has three inflows including the Muskegon River, Bear Lake, and Ruddiman Creek with the Muskegon River contributing the most inflow by a considerable margin. A navigation channel on the west end of the lake serves as the outflow into Lake Michigan. Muskegon Lake has a surface area of 17 km^2 and a water volume of 119 million m^3. The estuary has an average hydraulic residence time of 23 days, mean water depth of 7 m, and a maximum water depth of 21 m (Liu et al., 2018). Muskegon Lake was listed as an Area of Concern (AOC) by the International Joint Commission due to past industrial contamination and eutrophication problems, degradation to fish and wildlife populations, degradation of benthos, and degradation of fish and wildlife habitat.

MLO buoy

The MLO is an observatory buoy operated by the Biddanda Lab at the Annis Water Resources Institute – Grand Valley State University that is deployed in a central location in Muskegon Lake. The MLO site varies in depth due to yearly changes in water levels but is stationed at approximately 11 m water depth. The MLO has been in operation since 2011, providing high-frequency, time-series meteorological and water quality data with open access to all during the ice-free season, generally from April until November, depending on weather conditions (Biddanda et al., 2021). Water quality data is collected every 15 min and meteorological data every 5 min, 24 h a day. The meteorological station sits 2 m atop of the buoy and measures wind speed and direction, precipitation, air temperature, humidity, barometric pressure. For measuring water quality, the MLO is equipped with YSI (Yellow Springs Instruments) 6600/6920 sondes at depths of 2, 5, 8, and 11 m

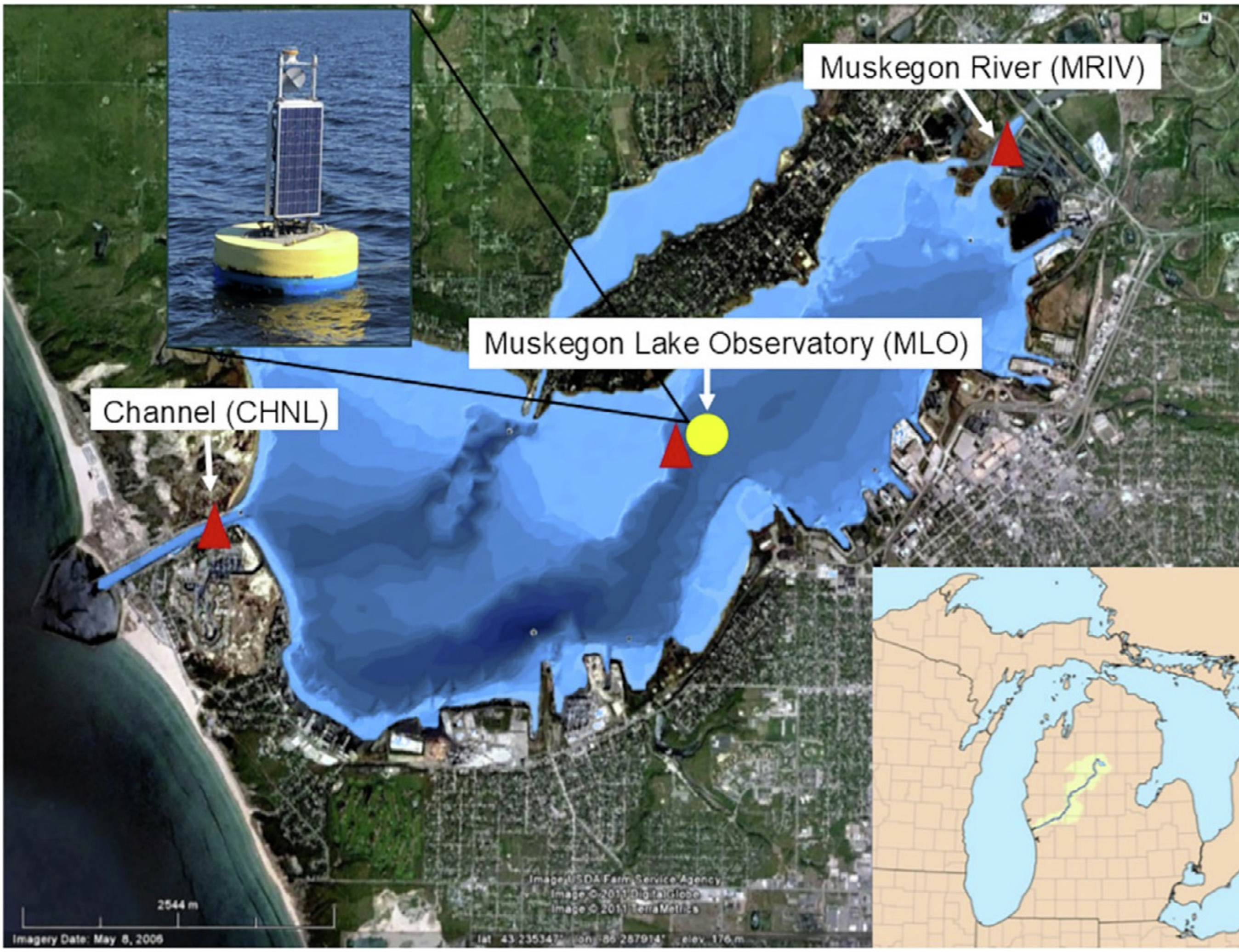

Fig. 1. A map of Muskegon Lake in the Laurentian Great Lakes basin including the location of the Muskegon Lake Observatory buoy (MLO, yellow circle). Red triangles represent in situ discrete sampling sites of nutrient analysis. The sampling sites include the Muskegon River (MRIV), MLO, and the navigation channel (CHNL). The inset is a watershed map of the Muskegon River which flows into Muskegon Lake at the lake's northeast end.

and NexSens temperatures nodes at 2, 4, 6, 8, 10, and 11 m. The YSI sondes measure chlorophyll *a*, phycocyanin, DO, and water temperature throughout the water column (Fig. 2). DO sensors were calibrated using a two-point calibration before the MLO was deployed in the spring. Data QA/QC was maintained according to the QAPP set forth under the original EPA-MLO project. A quality assurance calibration (dirty sensor check) was performed upon the retrieval of the MLO in the fall after system recovery to ensure the quality of the data throughout the year. Additionally, PME miniDOT sensors that measure DO and water temperature were placed at 0.5 m increments from 7 m to 10.5 m to provide a finer resolution of hypoxia in the hypolimnion during 2021. The data are summarized in this study as daily averages of the parameters. Missing data occurs intermittently in the data due to times of maintenance, servicing of the buoy, and heavy biofouling.

Time-series data visualization and analysis

Visual representation of thermal stratification and hypoxia in the water column was achieved using heat maps of 2021 MLO DO and water column temperature data. Schmidt stability values were also calculated for 2021, determining the strength of stratification throughout the summer and fall. Heat maps were created using daily-averaged water temperature and DO concentrations at depths of 2, 4, 6, 7, 7.5, 8, 8.5, 9, 9.5, 10, 10.5 and 11 m. The heat maps also determined the spatial extent of the hypoxic zone through the water column at the MLO. Due to the MLO's central location geographically and bathymetrically, MLO data observed in the heat map can be used as a proxy to understand hypoxia dynamics throughout Muskegon Lake (Biddanda et al., 2018; Mancuso et al., 2021). Chlorophyll-*a* and phycocyanin time-series measurements were graphed utilizing the MLO data to connect internal P loading to surface blooms. The R package RLakeAnalyzer was used to create the heat maps in RStudio Version 2021 (Wickham, 2016; Winslow et al., 2015). RLakeAnalyzer interpolates between depths of the MLO sensors by discretely calculating the vertical density gradient between the upper and lower sensors (Read et al., 2011).

2021 Biweekly sampling

Sample collection

During 2021, water samples were collected from three locations within Muskegon Lake including the MLO site, the navigation channel feeding into Lake Michigan (CHNL), and the Muskegon River outflow into Muskegon Lake (MRIV) (Fig. 1). Sampling began

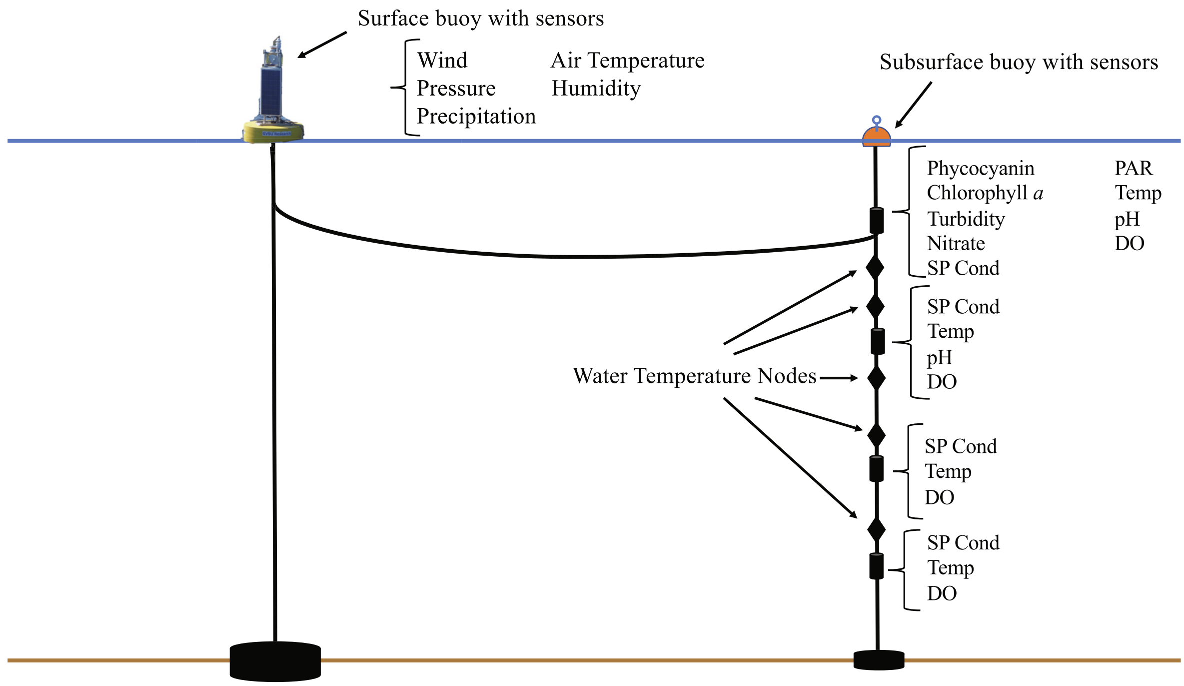

Fig. 2. Diagram of the subsurface buoy and the measurements conducted at different depths of the lake (underwater view).

on May 12 and continued biweekly until November 4. Surface water samples were collected at the CHNL and MRIV sites with a tethered bucket. At the MLO site, water samples were collected at the surface using a tethered bucket and 11 m depths using a Niskin sampler. Samples were stored in 2 L transparent Nalgene bottles inside coolers and transported back to the lab for nutrient analyses.

At each site, a YSI 6600 sonde was used to measure water temperature, chlorophyll-*a*, DO, and phycocyanin. At the MLO site, the sonde was slowly lowered over the side of the boat throughout the water column to monitor the changes in water quality. Each water column profile lasted roughly 10 min to ensure all portions of the water column were measured from the surface to the sediment. The sonde recorded an unattended sample at intervals of every two seconds during these profiles. During the sampling process, all equipment was rinsed with site water prior to data and water collection. Hydrographic profiles were not done at the Muskegon River and channel sites as the water column here is relatively shallow, fast flowing, and well mixed.

Nutrient analyses

Water samples were analyzed for TP, soluble reactive phosphorus (SRP), NO_3, and NH_3 upon return to the lab. All analyses were conducted in the Wet Chemistry Lab at the Annis Water Resources Institute. SRP, TP, and NH_3 were analyzed using a SEAL AQ2 discrete automated analyzer with the USEPA Methods 365.1, 365.1 Rev. 2.0 (EPA, 1993), and 350.1 Rev. 2.0 (EPA, 1993), respectively (AQ2 Methods NO: EPA-118-A Rev. 4, EPA-119-A Rev. 5, and EPA-103-A Rev. 6). NO_3 was analyzed using a Dionex ICS 2100 Ion Chromatograph with USEPA Method 353.2 Rev. 2.0 (EPA, 1993) (AQ2 Method NO: EPA-115-A Rev. 4).

Seasonal respiration experiments

Sample collection

Seasonal respiration experiments were conducted in conjunction with biweekly sampling. The experiment was designed to quantify the contribution of different sources of organic matter input to the seasonal drawdown of DO in the hypolimnion of Muskegon Lake. On May 24, July 6, and October 5, 2021, water samples were collected for the biweekly nutrient analyses and the seasonal respiration experiments from the MRIV and MLO sites. On these dates, 30 L of water were collected in a 10 and a 20 L carboy at 11 m depth at the MLO site, and 20 L were collected at the MRIV and MLO sites at 1 m depth. All samples were placed in coolers and transported back to the lab.

Titration process

Upon return to the lab, the water samples were dispensed into standard 300 mL BOD bottles and incubated at temperatures mimicking the bottom waters of Muskegon Lake measured by the MLO on the day of collection. Water samples were bottled into five treatments that were to be measured at three different time points. Each treatment had quadruplicates for each timepoint meaning that each of the five treatments had 12 bottles for the experiment. The treatments included Muskegon River water, Muskegon Lake surface water, and Muskegon Lake bottom water. The other two treatments were 50/50 mixtures of Muskegon River water with Muskegon Lake bottom water and the second consisting of Muskegon Lake surface water with Muskegon Lake bottom water. The bottles were incubated in the dark at near-ambient DO with a set of quadruplicates measured at 0 h, or the time of bottling, 24 h, and 48 h. We assumed that the water samples would be undergoing a one part bottom water and one part surface or river water mixing in the hypolimnion under the incubation conditions, which would serve as a rough approximation for what may be occurring within Muskegon Lake. After bottling and incubation, we measured the DO concentrations by performing Winkler titrations that were conducted using a Radiometer Analytical TitraLab 860 automatic titrator with a platinum combined Ag/AgCl reference electrode that inferred the DO concentrations from the endpoint of the titration (Carignan et al., 1998; Weinke et al., 2014). Because measurement of small changes in DO concentrations within a large pool of DO is challenging and sensitive to tiny variations in bottle handling and sample filling, we adapted the recommended practice of making

DO measurements in quadruplicate bottles and picking only the 3 closest values measured (i.e., leaving the outlier out) for use in respiration measurements (Carignan et al., 1998).

Statistical analysis

From the BOD experiments, three of the four quadruplicates were utilized while the fourth was eliminated due to its standing as an outlying data point. The outlying data point was determined by averaging the four data points together and removing the one furthest from the average. This generates a data set that is based off a significantly reduced percent coefficient of variation ($p < 0.05$). An ANOVA was generated for each treatment utilizing triplicates normalized at the average of time 0 and subtracting the triplicates at 48 h from the normalized time 0 concentrations during each season to analyze the rate of DO consumption over time. A post hoc test of two-tailed t-tests were utilized to compare the differences in slopes of the ANOVA during a given season, and a Bonferroni correction was added to the *t*-test to reduce the probability of type 1 error (Oksanen et al, 2018).

Results

Time-series data analysis

The thermal stratification and hypoxia heat maps illustrate the temperature and DO concentrations throughout the water column in 2021 from mid-May until the end of September (Fig. 3). Wind mixing events are observed as the thermal stratification and DO heat maps distinctly merge into one uniform color temperatures or DO concentrations. The MLO detected four wind mixing events, each coinciding with heavy precipitation, on June 26th, July 14th, July 22nd, and a multiple day mixing event on August 8th and 9th (Fig. 3, 4). The event on June 26th completely mixed the water column. The July 14th, July 22nd, and August 8-9th events partially mixed the water column, with the August event lasting for multiple days and restricting the hypoxic zone, although this event did not have the strength to fully mix the water column (Fig. 3, 4). Thermal stratification reestablished in the beginning of July coinciding with the onset of hypoxia on July 1st. The relationship between thermocline depth and hypoxic zone are evident in the heat maps where drastic changes in thermal structure between the hypolimnion and the epilimnion are mirrored with visual changes between oxic and hypoxic water in the hypolimnion.

Schmidt stability values of Muskegon Lake during 2021 showed that the estuary was moderately stratified from the beginning of July until the end August and into early September (Fig. 4). Muskegon Lake was slightly stratified by the time the MLO was deployed. Schmidt stability values at 0 J/m^2 depict a fully mixed estuary, whereas Schmidt stability values greater than 300 J/m^2 illustrate a moderately stratified estuary. Maximum stratification in Muskegon Lake was observed on August 28th at 340 J m^{-2}. Schmidt Stability values declined to slightly above 0 J/m^2 on September 13th, showing the first signs of fall turnover within Muskegon Lake, whereas the lake fully mixed on September 18th for the first time since the June 26th wind mixing event.

Biweekly sampling

SRP concentrations started increasing on July 6th at the MLO bottom site as SRP levels were nondetectable at any of the sites until this date (Fig. 6, Electronic Supplementary Material (ESM) Table S1). After July 6th, SRP concentrations continued to increase in the MLO bottom water. On August 10th, SRP increased to 0.048 mg/L from the first detected 0.014 mg/L on July 6. SRP concentrations continued to rise, and the maximum was recorded on September 9 with a concentration of 0.052 mg/L. As the stratification in Muskegon Lake began to break down in mid-September due to fall turnover, SRP was detected at the MLO surface at 0.006 mg/L while SRP at the MLO bottom dropped to 0.013 mg/L. These measurements indicated water mass mixing of the lake, an observation reflected by a concurrent increase in phycocyanin and chlorophyll *a* sensed by the MLO at 2 m (Fig. 5). SRP was detected into late October and early November at all four sites.

The prolonged duration of surface phytoplankton productivity corresponded with bottom water hypoxia. As an increase in phytoplankton biomass on June 30th was detected by the MLO, hypoxia followed behind immediately with the onset of hypoxia on July 1st. Surface production remained high throughout the summer and into September, leading to continued hypoxia with minimal disruptions. As fall turnover began in September and the lake fully mixed on September 18th, hypoxia diminished, but surface production continued to rise peaking at 30 μg/L of chlorophyll *a* on October 3rd (Fig. 5).

TP concentrations were lowest during the late spring and early summer. After the onset of hypoxia in early July, TP trends showed an increase in concentrations at all four sites, peaking in September and October for all sites around 0.7 mg/L. The TP trends were reliant on the increase in SRP throughout the year at the MLO bottom and Muskegon River, and in the fall at the navigational channel and MLO surface. NO_3 concentrations were highest in the late spring and early fall and lowest during the summer and peak growing season. NO_3 peaked around 0.6 mg/L with lowest concentrations of 0.04 mg/L. NH_3 was relatively stable throughout the sampling season at all sites fluctuating between 0.01 mg/L and 0.1 mg/L with an outlier of 0.25 mg/L recorded at the Muskegon River site on June 8th (Fig. 6).

Seasonal respiration experiments

The change in DO concentrations in BOD bottle incubation triplicates (after removing the largest outlier to reduce coefficient of variation) over 48 h expressed as the slope of linear regressions were considered the rate of DO drawdown due to the decomposition of organic matter in each of the treatments (Carignan et al., 1998; Weinke et al., 2014). These DO drawdown rates could be underestimates of oxygen consumption in the hypolimnion as diffusion into the sediment was not measured in the BOD bottle measurements that contain only the overlying water and not the sediment.

The ANOVA of BOD experiments produced varying results across the seasons. During spring, the admixtures of river + bottom and surface + bottom did not significantly change the DO drawdown in comparison to the non-mixed treatments (ESM Fig. S1). Riverine inputs had the fastest rate of DO decline over 48 h during the spring (Table 1). During this season, the rates of DO decline in the river and surface water were statistically faster than the rate of DO decline bottom water (ESM Table S2). In the summer and fall, riverine and surface water inputs into the hypolimnion drove oxygen consumption at differing rates (ESM Fig. S1). Table 1 provides an overview of the rate of DO consumption in all treatments over the 48 h experiment. In the summer, surface and the surface + bottom mixture had a statistically faster DO drawdown rate compared to river + bottom. In the fall, the addition of river water mixed with bottom water had the fastest DO drawdown rate in the hypolimnion followed by the surface water (ESM Table S2).

Discussion

Hypoxia dynamics linked to stratification

The onset of stratification in lakes occurs due to low winds, high air temperatures, and direct solar radiation; this can result in

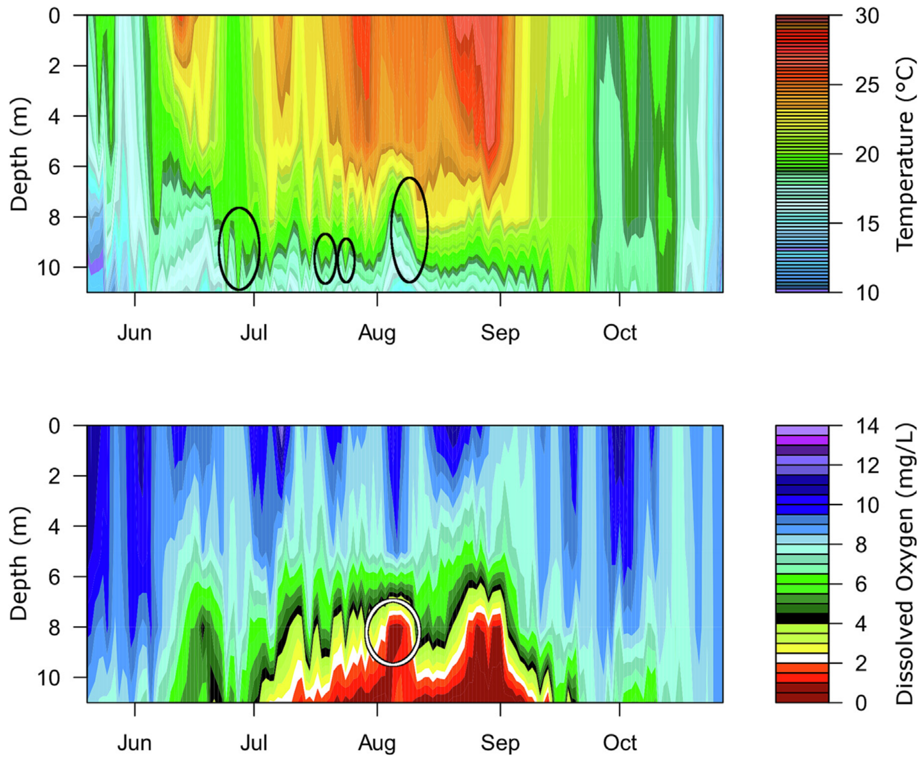

Fig. 3. Heat map of temperature and DO measurements at varying depths throughout the water column from late May until the end of September 2021. Temperature and DO data were collected by the MLO's NexSens T-Nodes. Hypoxia is denoted as the orange and red coloration, respectively, which corresponds to DO concentrations at or below 2 mg/L. Black circles represent wind-mixing events. The white circle encompasses the floating hypoxia event.

subsequent hypoxia (Bouffard et al., 2013; Bravo et al., 2015; Edwards et al., 2005; Hamidi et al., 2015; Nakhaei et al., 2021). Muskegon Lake, as with other systems, experiences hypoxia because of seasonal thermal stratification (Bocaniov et al., 2020; Weinke and Biddanda, 2019). Environmental data from the MLO demonstrated that hypoxia was sustained and severe throughout the summer months of 2021. A lack of thermal stratification disruption and warm spring and summer air temperatures coincided in considerably warmer Muskegon Lake surface water temperatures compared to the bottom waters which created a high stratification strength that did not break up during the summer (Weinke and Biddanda, 2019).

Hypoxia dynamics in Muskegon Lake during 2021 varied compared to other previously reported hypoxic zones in the Laurentian Great Lakes basin. In Muskegon Lake, the onset of hypoxia occurred in early July, peaked in early August and then again in late August, and eventually broke down fully in early September. Xu et al. (2021) utilized a spatio-temporal geostatistical interpolation framework to determine that the hypoxic zone in Lake Erie emerged in early August or late July, peaked in mid-August or September, before breaking down in October in the years 2014–2016. The delay in hypoxia in Lake Erie compared to Muskegon Lake could be due to the sheer size and volume of the Lake Erie or the differences in regional climatological events between years (Katz and Brown, 1992; Wigley, 2009). However, in Green Bay, Wisconsin from the years 2009–2015 stratification occurred from late June until early September, similar to Muskegon Lake in 2021 (Klump et al., 2018). Hypoxia duration ranged from 2 weeks in more offshore sites in Green Bay to 3 months closer towards the outlet of the Fox River, which again is similar to the 2-month time period experienced in Muskegon Lake (Klump et al., 2018). Hypolimnetic and sediment oxygen demand contribute to hypoxia in Muskegon Lake, similar to how it contributes to hypoxia in Canadian inland lakes, Green Bay and Lake Erie (Nakhaei et al., 2021). Although the timelines of hypoxia may be slightly altered between Green Bay, Lake Erie, and Muskegon Lake, Muskegon Lake may serve as a sentinel warning system for other Great Lakes regional bodies of water as each lake experiences similar constructs of the hypoxic zone, while Muskegon Lake tends to do so slightly earlier in the summer. There are 20 hypoxic zones documented in the Laurentian Great Lakes. Of these, five are drowned river mouth Great Lakes estuaries, including Muskegon Lake (Tellier et al., 2022). Three of the five drowned river mouth estuaries are located along the west coast of Michigan with Pentwater Lake, White Lake, and Muskegon Lake experiencing annual hypolimnetic hypoxia (Tellier et al., 2022; Weinke et al., 2022). Although similar trends can be drawn between Muskegon Lake and other systems, the data for Muskegon Lake in this study is from the singular year of 2021 and trends may differ based on the environmental characteristics of that specific year.

Once Muskegon Lake stratified, wind mixing events affected the thermal structure by temporarily alleviating some hypoxia in the middle of the water column but did not fully break up the hypoxic hypolimnion. A previous study in Muskegon Lake quantified a wind mixing event that deepened the epilimnion by approximately 1.5 m when westerly or southwesterly winds persisted at 7.7 m/s and for at least 10 h. (Weinke and Biddanda, 2019). A 2021 example of this is the August 8th and 9th storm event that had maximum wind speeds reaching 33 m/s and winds above 7.7 m/s for ~30 h. Prior to this storm event, hypoxia occupied the water column from 8 m to 11 m. Afterwards, the hypoxic zone was compressed to 10 m to 11 m depth but was not fully mixed. As the summer ends, atmospheric temperatures decrease, in turn dropping surface temperatures and weakening the thermal structure in Muskegon Lake. Wind mixing and storm events eventually degrade the hypoxic zone when the thermal structure of the lake

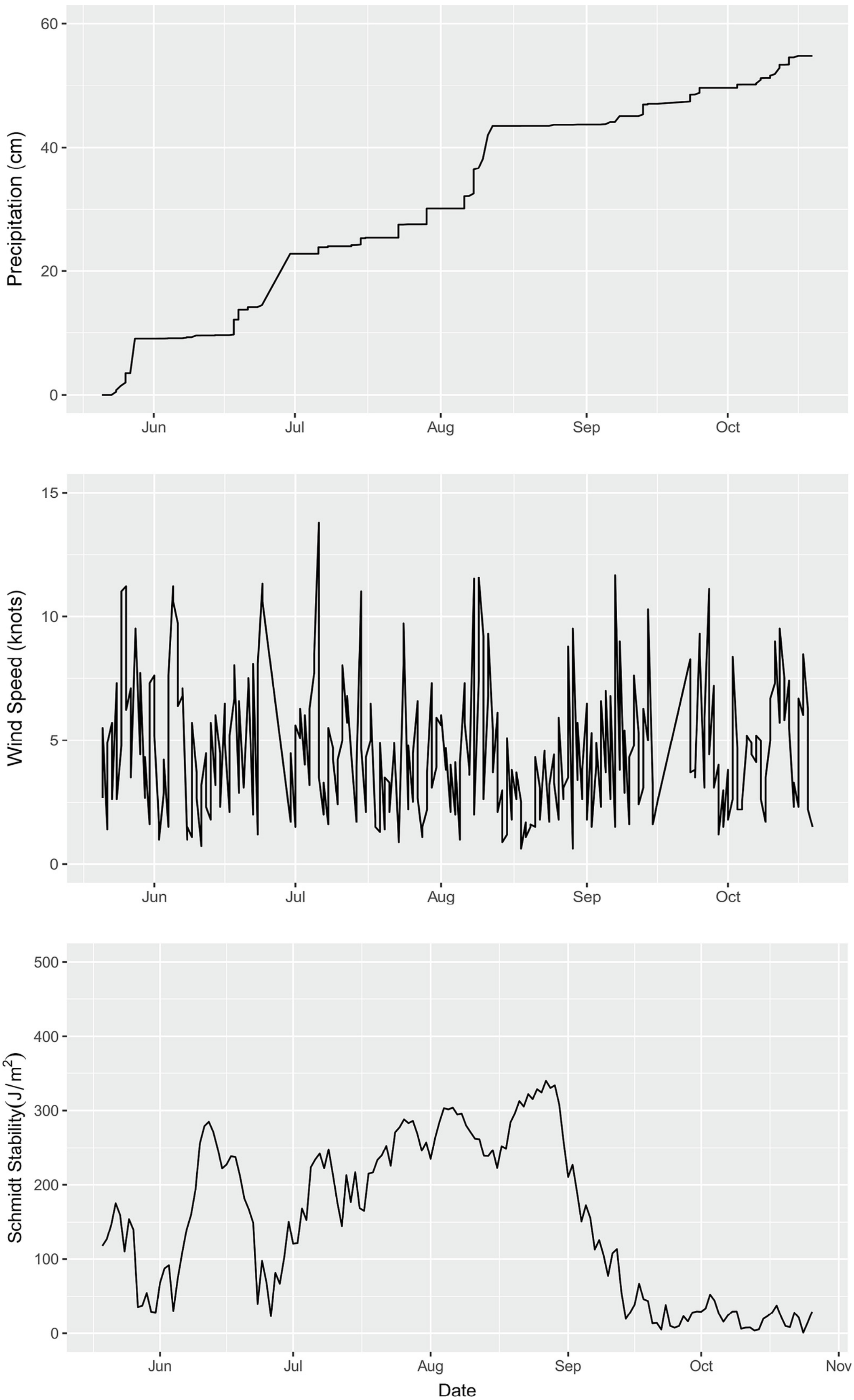

Fig. 4. Time-series graphs of cumulative precipitation, wind speed, and Schmidt stability detected by the MLO buoy for 2021.

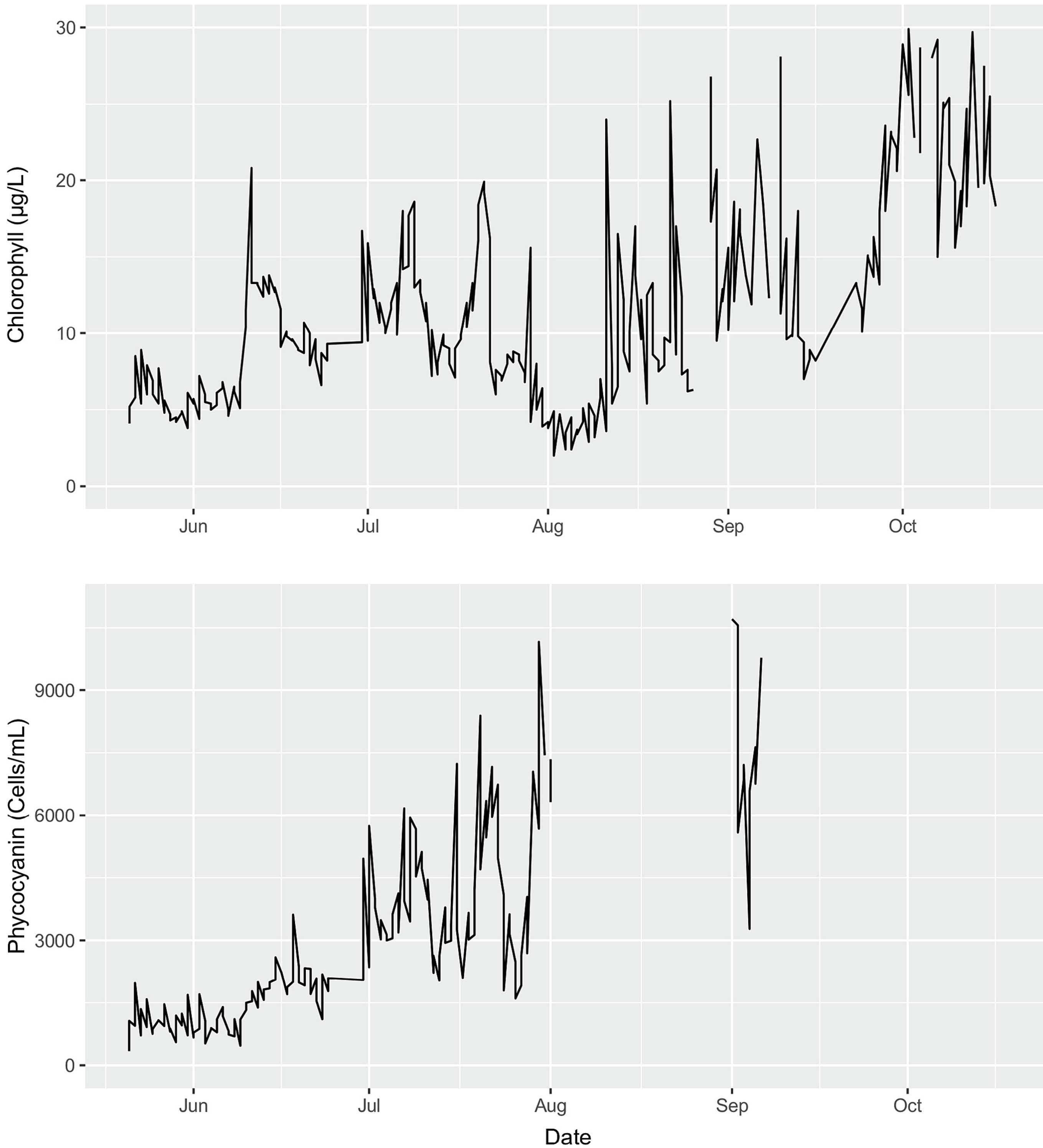

Fig. 5. Chlorophyll (µg/L) and phycocyanin (Cells/mL) time-series measurements from May 23rd until mid-October of 2021 depicting an increase in primary production and cyanobacteria HABs throughout the growing season. Missing data points in both graphs are attributed to biofouling and maintenance trips that temporarily paused the operation of the MLO.

becomes isothermal in the fall. This phenomenon tends to occur towards the end of September or early October as seen in Muskegon Lake in 2021 (Biddanda et al., 2018; Dugener et al., 2023; Weinke and Biddanda, 2018, 2019).

Upwelling and the movement of water plays a large role in hypoxic alleviation in the Laurentian Great Lakes basin (Liu et al., 2018). In early August 2021, a cold-water, oxygenated intrusion from Lake Michigan entered Muskegon Lake, creating a mid-depth hypoxia at 8 m that was separated from the sediment (Fig. 3). The Lake Michigan water is oxic and creates a temporary layer of suitable hypolimnetic habitat for some fish species. However, the hypoxic zone directly above it limits fish movement between zones, further shrinking the habitable water column. Fish abundance, number of species, and maximum length all decreased

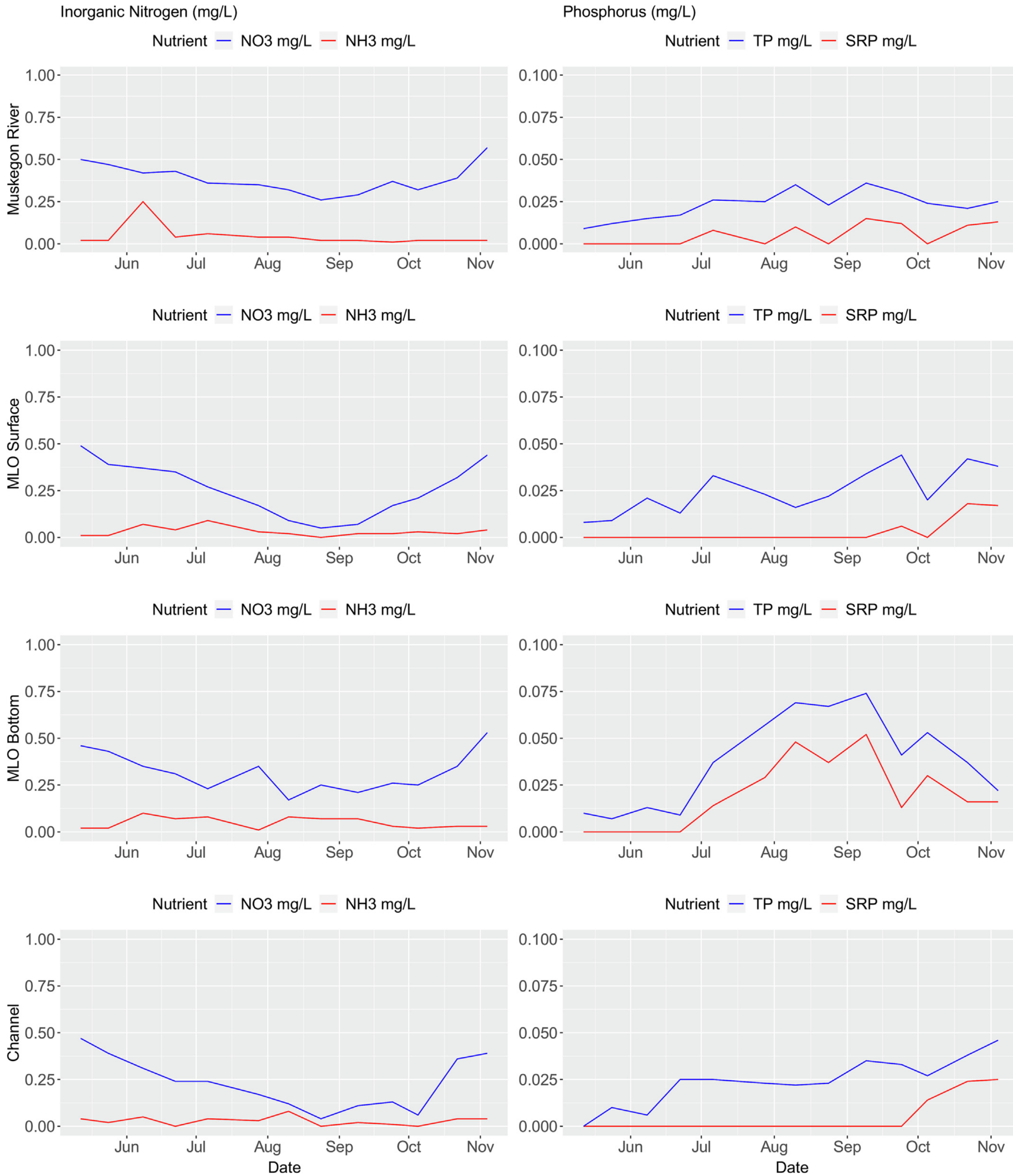

Fig. 6. Time-series graphs of biweekly nutrient sampling at the Muskegon River, MLO Surface, MLO Bottom, and Channel sites. Note the difference of scales between inorganic nitrogen and phosphorus graphs.

in catch because of hypoxia (Weinke and Biddanda, 2018; Altenritter et al., 2013). Intrusions and mid-depth hypoxia can last from a day to several weeks. Intrusions can also temporarily alleviate hypoxia if a wind mixing event overlaps with an intrusion, or if the temperatures and densities of the Lake Michigan and Muskegon Lake water are similar and conducive to mixing. This reintroduces oxic conditions to the bottom water for a short time. This phenomena can occur anywhere from six or seven times a year to not occurring in a year at all based on the strength of stratification within Muskegon Lake during the event, and mainly takes

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Table 1
List of slopes of the seasonal BOD experiment. The slopes are the rate of decline of DO seasonally from each site and the admixture between the river and bottom water (R + B) and surface and bottom water (S + B). A more severe negative slope corresponds with a higher rate of oxygen consumption in that water sample. Slopes with an asterisk are statistically significant from at least one other slope in that season.

Season	Treatment	Slope (mg/L/d)
Spring	Bottom	−0.55*
	River	−0.87*
	Surface	−0.79*
	R + B	−0.76
	S + B	−0.79
Summer	Bottom	−0.74
	River	−0.7
	Surface	−0.89*
	R + B	−0.68*
	S + B	−0.9*
Fall	Bottom	−0.52*
	River	−0.35*
	Surface	−0.58*
	R + B	−0.65*
	S + B	−0.44*

place in the late spring or early fall when stratification is strong (Liu et al., 2018).

Intrusions in Lake Erie are more variable in nature compared to that which occurs in Muskegon Lake. Extreme winds can push P-rich, hypoxic water from the central basin of Lake Erie towards the southern shoreline creating nearshore hypoxia (Jabbari et al., 2021; Jabbari et al., 2019; Rowe et al., 2019). Neither of these phenomena occur in Muskegon Lake as the hypoxic water tends to remain in the hypolimnion. Rather, the intrusions of Green Bay tend to align more similarly with occurrences in Muskegon Lake where upwelling can help alleviate hypolimnetic hypoxia. Southerly winds in Green Bay and north and northwesterly winds in Muskegon Lake push upwelled water into the hypoxic zone, respectively (Grunert et al., 2018; Liu et al., 2018). With climate change and more variable and extreme wind patterns, Muskegon Lake, Lake Erie, and Green Bay could variably experience either years with plentiful upwelled intrusions or years without a single intrusion.

Implications of phosphorus increases

An earlier study of internal P loading using sediment cores collected from Muskegon Lake that were experimentally exposed to oxic and anoxc conditions recorded some release of P under anoxia, but not enough to account for more than ~26% of the lake's total P load under the most extreme models (Steinman et al., 2020). However, all these sediment cores came from less than 8 m depth within the lake, depths that do not consistently experience hypoxia for more than a few weeks at a time during the summer. Thus, the study could have underestimated the potential of internal P loading in Muskegon Lake. Given the spatial heterogeneity of the sediment contents and hypoxic water contact, future studies should include sediment cores collected from deeper waters to test the net release of legacy P from the sediments that experience hypoxia for several months during the summer. Similar previous studies of internal P loading in the nearby drowned river mouth estuaries of Mona Lake and Spring Lake determined that internal P loading was substantial (~50–70% of P loading), but not in White Lake (~7% of P loading) suggesting variable contribution of internal P loading to these coastal ecosystems (Steinman et al., 2009; Steinman and Ogdahl, 2006).

In the present study, internal P loading was indicated in Muskegon Lake during 2021 based on bottom water SRP samples. Surface phytoplankton biomass corresponded with bottom water hypoxia as increases in phytoplankton at the surface coincided with the onset of hypoxia on July 1st. As phytoplankton productivity remained high throughout the summer, oxygen levels remained low. Eventually, Muskegon Lake fully mixed, and oxic conditions reestablished throughout the water column. However, surface phytoplankton biomass as measured by chlorophyll increased drastically as the SRP from the bottom water mixed into the surface waters due to the internal P loading within the lake. In turn creating a positive feedback loop between surface phytoplankton production, hypoxia, internal P loading, and stimulation of fall HABs (Fig. 7). We hypothesize that the release of P from the decomposition of settling phytoplankton would not make a major contribution to the hypolimnion. For example, an increase of SRP concentration was detected only after the onset of hypoxia (July 6th) despite stratification being present for a month prior (June 1st), indicating that the SRP in question is a product of internal P loading from the sediment and not settling phytoplankton although settled phytoplankton that are already part of the sediment may contribute to the release P over the long term (Fig. 6). Thus, it appears that in the present study, the release of P from sediments into the hypolimnion occurs during periods of anoxia – given how quickly SRP shows up in measurable amounts in the hypolimnion following the onset of not just stratification, but hypoxia.

SRP was first detected on July 6th in the hypolimnion at the MLO site, approximately one month after the onset of stratification and five days after the onset of hypoxia. A brief reduction in SRP occurred on August 24 due to horizontal displacement as a large storm event in between sampling trips disrupted the anoxic zone at the bottom of Muskegon Lake. However, the fall turnover event on September 18th mixed the SRP-rich bottom waters up to the surface where it was detected by the surface nutrient analysis. SRP was released from the sediment during the long mixing event which increased water column SRP and helped maintain an abnormally long cyanobacterial bloom in Muskegon Lake into November, well after the growing season should have subsided. Similar internal P loading dynamics have been documented in Lake Erie where mixing of legacy P from sediments has stimulated new primary production in the surface waters (Burns, 1976). Continued internal P loading can create, maintain, or intensify the cyanobacterial HABs in an ecosystem depending on the time of year and the amount of P released from the sediment (Ding et al., 2018; Paerl et al., 2016a). It appears that riverine inputs of SRP were rapidly taken up by surface phytoplankton as observed by the low surface concentrations. Internal P loading generated from bottom waters accumulated in the hypolimnion and was not simultaneously consumed upon release from the sediment, whereas riverine SRP was consumed almost immediately. It is difficult to infer relative contributions of SRP from internal P loading vs. riverine loading to surface productivity throughout the entire growing season. Riverine SRP contributes to surface production more than occasional internal P loading. Nitrate was higher in the Muskegon River site compared to all other sites in each season, indicating that the Muskegon River was a high source of nitrogen to the system. To limit internal P loading, alleviating hypoxic zones or capping P-rich sediments is needed to reduce cyanobacteria HABs which continue the hypoxia cycle (Paerl et al., 2016b). Studying the concentrations of molybdenum in the estuary's sediments can also yield a glimpse of the past hypoxic zones and redox conditions of P in Muskegon Lake (Boothman et al., 2022).

As Schmidt stability values drop and Muskegon Lake becomes isothermal, there was an increase in P concentrations at the surface and channel sites (Figs. 4, 6). These results suggest that SRP and TP build-up from the bottom water that has mixed to the surface is being exported from Muskegon Lake, through the navigational channel, into Lake Michigan. TP loading in 2003 from the

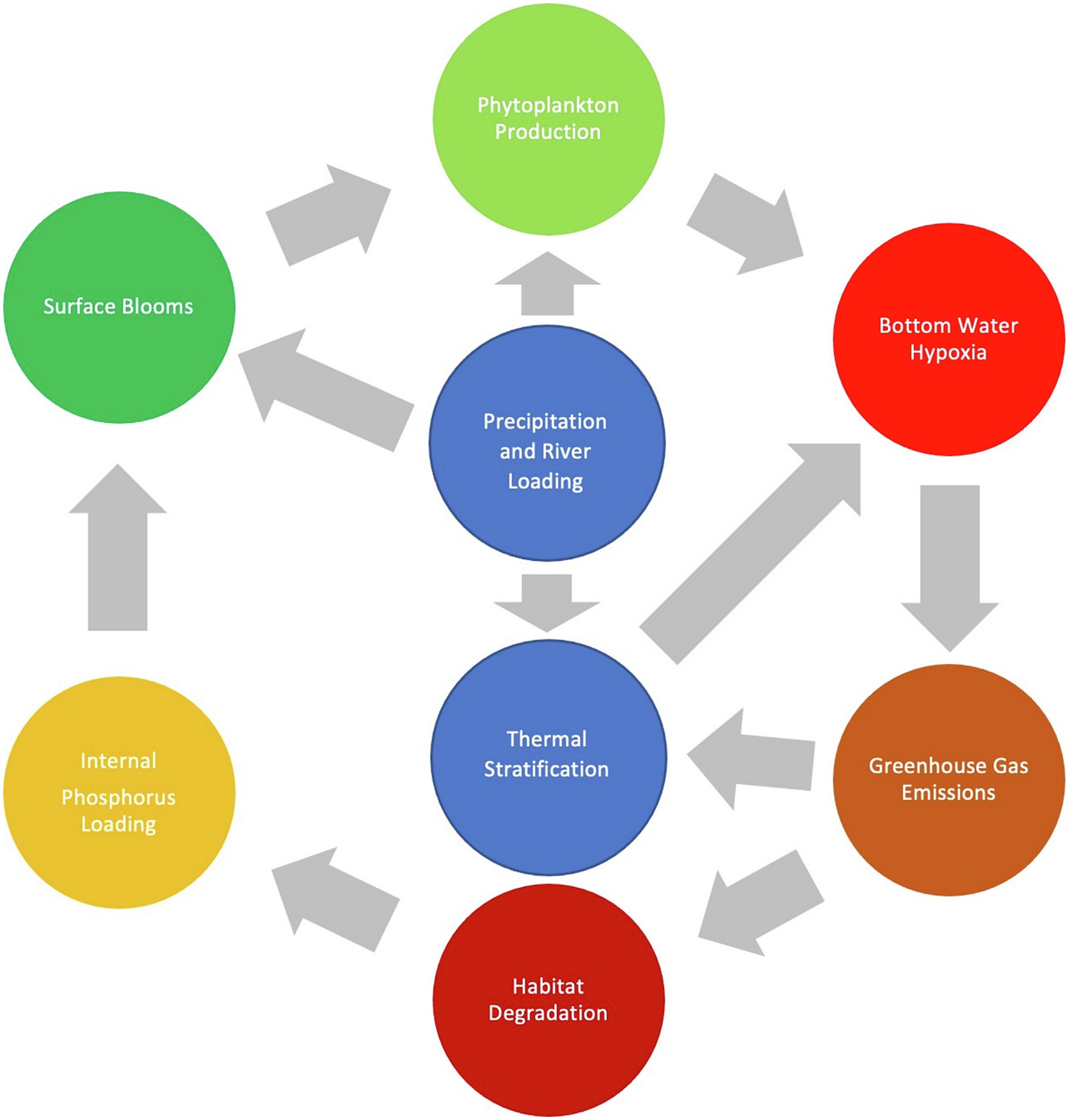

Fig. 7. A schematic diagram of a positive feedback loop of hypoxia, internal phosphorus loading, and eutrophication occurring in Muskegon Lake.

beginning of March to the end of October from the Muskegon River to Muskegon Lake was 24 metric tons (Marko et al., 2013). Using discharge rates from earlier studies of 3.5–4.9 million m^3 of water per day, our results suggest a net flux of ~66–94 kg/d of SRP and ~112–160 kg/d of TP from Muskegon Lake to nearshore Lake Michigan, during October (Liu et al., 2018; Marko et al., 2013). A previous study estimated that TP was exported at a rate of 44 kg/d from Muskegon Lake into Lake Michigan from May to October in 2003 (Marko et al., 2013). Thus, seasonal anoxia in this drowned river mouth may be leading to net export of bio-available P to Lake Michigan at amounts that could have potential consequences in the nearshore oligotrophic ecosystem. While maximal export seems to be occurring during the fall overturn, we expect a sustained low load of nutrient export to nearshore waters from Muskegon Lake to be occurring throughout the year based on relatively higher concentrations in Muskegon Lake relative to Lake Michigan. Such that constant year-round loading of TP as well as a seasonal net export of SRP may support significant offshore primary production in Lake Michigan (Biddanda and Cotner, 2002).

Hypolimnetic DO drawdown rates

BOD experiments revealed that seasonally distinct sources of organic matter input into the hypolimnion fueled the drawdown of DO. Surface and river water had high potential to increase oxygen consumption in the spring in the hypolimnion, but dilution of both within bottom waters may lessen the ability to differentiate oxygen consumption rates when mixed with bottom waters. The statistical significance between treatments showed that riverine and surface productivity inputs drove oxygen consumption in the hypolimnion at different rates in the summer and fall. This suggests that inputs from outside of the hypolimnion could influence DO drawdown in the springtime due to higher discharge. Applications of fertilizers on agricultural fields in the Muskegon Lake watershed can help stimulate growth within Muskegon Lake also leading to quicker DO depletion rates (Kane et al., 2014).

The surface water had the highest DO consumption rate in the summer in Muskegon Lake, and this coincides with the summer having the highest amount of sinking surface production and dissolved organic matter already present in the hypolimnion as observed in the expansive hypoxic zone at the mouth of the Mississippi River in the Gulf of Mexico (Rabalais et al., 2010). The mixing dynamics of riverine organic matter and bottom water in the summer lowered the rate of DO consumption, indicating that the riverine organic matter may be refractory during this season, inhibiting DO consumption (Asmala et al., 2013). Fall dynamics of oxygen consumption were opposite from the summer, possibly because surface productivity was no longer supported by the lake (Biddanda et al., 2018; Defore et al., 2016). Riverine organic matter, which may have been refractory during the summer, mixed with bottom water and stimulated DO consumption. When surface and bottom waters mixed, DO consumption was reduced. This could in part be caused by the development of cyanobacterial blooms in October which may be decomposed slowly in the bottom water (Shi et al., 2017).

A previous study demonstrated that ~33% of Muskegon River P was retained in Muskegon Lake (Marko et al., 2013). The study also measured Muskegon River carbon isotopes signatures in both Muskegon Lake and nearshore Lake Michigan and found that Muskegon River carbon was only found in Muskegon Lake and not nearshore Lake Michigan, suggesting that the carbon entering Muskegon Lake from the Muskegon River is utilized well before it exits into the nearshore Lake Michigan ecosystem (Marko et al., 2013). Thus, the Muskegon River nutrients and organic matter are variably contributing to primary production or hypoxia in Muskegon Lake. Muskegon Lake experiences differing impacts to its DO consumption based on the timing, frequency, and duration of autochthonous primary production or riverine input via agricultural or urban runoff from the Muskegon River (Conroy et al., 2010).

Although most DO drawdown rates were similar, seasonal comparisons between treatments illustrate a seasonal shift between treatments in which sinking surface production contributes most to hypoxia in the summer while riverine organic matter contributes most to hypoxia in the fall (ESM Table S2). In the spring, a combination of both riverine and surface derived organic matter fueled hypolimnetic hypoxia. These results demonstrate that hypolimnetic hypoxia in this estuary was influenced by variable sources of organic matter over the seasons.

Hypoxia, HABs, and internal P loading

Within the Laurentian Great Lakes Basin, there are 3 ecosystems that are known to experience hypoxia, HABs, and internal P loading simultaneously, Hamilton Harbour in western Lake Ontario, Muskegon Lake, and Green Bay (Biddanda et al., 2018; Gertzen et al., 2016; Lin et al., 2016). Muskegon Lake and Hamilton Harbour are two comparably sized Great Lakes AOCs where eutrophication and degradation of benthos due to hypoxia are beneficial use impairments. Green Bay is about eight times the size of Muskegon Lake and Hamilton Harbour. Nevertheless, these three ecosystems are similar in the formation of hypoxia and HABs in which thermal heating of surface waters coincides with influx of nutrients and organic matter from the surrounding watershed leading to a similar onset of thermal stratification and subsequent hypoxia (Bravo et al., 2015; Hamidi et al., 2015). Hypoxia is rarely disrupted within these ecosystems due to their large sizes and separation from the larger Great Lakes. However, these three ecosystems experience local disruption of hypoxia from wind mixing events as well as cold, oxygenated intrusions from their corresponding Great Lake counterpart (Grunert et al., 2018; Lawrence et al., 2004; Weinke and Biddanda, 2019). Internal P loading in Muskegon Lake, Hamilton Harbour, and Green Bay occurs within a couple of weeks of one another as conditions conducive to internal loading, such as anoxia, occur at similar timescales (Lin et al., 2016; Markovic et al., 2019). Therefore, as we continue to expand our understanding of Muskegon Lake, Hamilton Harbour, and Green Bay, comparisons can be drawn to one another on the annual formation and breakdown of hypoxia and the consequences that follow. Gaining a better understanding of the similarities and contrasts among hypoxia affected ecosystems may aid in management of hypoxia in well-known sites such as the central basin of Lake Erie. There are clear limitations of the study design such as not involving multiple years and multiple sites to compare the findings in Muskegon Lake to other similar systems. Another limitation is that there were not similar studies along similar time scales in other drowned river mouth lake ecosystems in the Great Lakes that would have clarified our findings on the one year scale. Additionally, we recognize that a limitation of the BOD drawdown experiment is that it does not represent a lake that is thoroughly mixed, while a 1:1 mixing of different water masses in nature is likely but unlikely to be sustained over long periods of time. However, these limitations do not take away from the main findings of the present study but point out potential for future approaches. Indeed, there are over 100 drowned river mouth estuaries in the Great Lakes basin with ~24 drowned river mouth ecosystems along the eastern shore of Lake Michigan alone, many of which experience summertime hypoxia and present new opportunities for comparative studies across the Great Lakes Basin (Dugener et al., 2023; Weinke et al., 2022).

Conclusions

Previous MLO observations suggest that meteorological phenomena such as episodic wind events, extreme precipitation occurrences, and intrusion of cold upwelled waters from Lake Michigan influence the dynamics of hypoxia in Muskegon Lake (Biddanda et al., 2018; Dugener et al., 2023; Liu et al., 2018; Weinke and Biddanda, 2019). In 2021, the hypoxic zone in Muskegon Lake persisted from early-June until mid-September. A warm spring allowed for an early onset of summer stratification that gained strength throughout the summer as surface temperatures did not cool throughout the season. A relatively calm summer further limited mixing events from occurring due to storms and precipitation events. The present study provides insight into how the effects of nutrient loading interact to lengthen hypoxic periods in the Great Lakes region. Seasonal differences in organic matter input into the hypolimnion changes the rate of respiration where both surface and riverine inputs were equally influential in the spring, surface inputs were most influential in the summer, and riverine inputs were most influential in the fall. As hypoxia persists throughout the summer, hypolimnetic SRP concentrations increase due to internal P loading, which creates a delayed positive feedback loop of HABs which further deplete the hypolimnion of oxygen upon their deposition to bottom water. In a world experiencing changing weather patterns, increasing anthropogenic pressure, and an uncertain future in the face of climate change, understanding the causes and consequences of hypoxia and anoxia on a spatiotemporal scale may provide clues to how future climate change scenarios will impact temperate freshwater lakes. Under the context of ongoing climate change, consequences of changing hypoxia to consider include the shifts in the food web and carbon cycle as well as recreational and social reliance upon freshwater ecosystems (Biddanda, 2017; Fergen et al., 2022; Schlesinger and Bernhardt, 2013; Weinke et al., 2022). Findings from intensive observational and experimental studies of hypoxia dynamics in Muskegon Lake may serve as a useful model for other hypoxia-afflicted Great Lakes estuaries, lakes, and coastal waters, and their associated ecological and socioeconomical resources.

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.2023.06.007.

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