Masters Theses   Graduate Research and Creative Practice

8-2016

Green and Choking: Exploring the Dynamics of Seasonal Productivity and Hypoxia in a Great Lakes Area of Concern and Habitat Blueprint Estuary Using Time-Series Measurements

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Green and Choking: Exploring the Dynamics of Seasonal Productivity and Hypoxia in a Great

Lakes Area of Concern and Habitat Blueprint Estuary Using Time-Series Measurements

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A Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Master of Science

Biology

August 2016

Dedication

I dedicate this thesis to Amy, Jeff, Julia, and Rebecca, for all of their love, encouragement, and support for me throughout this life and academic journey. My appreciation is beyond words.

Acknowledgements

Abstract

Although hypoxia (dissolved oxygen <4 mg L^{-1}) in the bottom waters of lakes, reservoirs, and estuaries may be a natural product of stratification in eutrophic or mesotrophic systems, there is increasing concern because the occurrence of hypoxia is spreading in many areas where hypoxia did not previously exist. Part of this new knowledge can be attributed to time-series data from buoy observatories that monitor systems in good weather and in bad, and allowing insight into the inner workings of a lake where sampling only a few times per year would not. This study made use of a five-year time-series of meteorological and water quality data in order to examine the effect of episodic wind-events on stratification and hypoxia within Muskegon Lake, Michigan, as well as performing bi-weekly lake-wide monitoring to evaluate the effects of stratification, hypoxia, and wind-events on the lake. In the wind-event portion of the study, we found that events where wind speeds were above average for an extended period of time occurred fairly frequently on the lake, but that thermal stratification allowed only the strongest events to significantly mix the water column at the buoy location a few times per year. This provided infrequent relief of hypoxia in the bottom waters. The second portion of the study found extensive effects on the water quality and biology in the bottom of the lake due to hypoxia such as increased phosphorus concentrations, enhanced phycocyanin following a strong wind-event, and decreased fish abundance, richness, and size. We also found that hypoxia occurred lake-wide at all four sample locations, but was most stable at the deepest point in the lake that was least influenced by wind-events. It is possible that the combination of hypoxia and strong episodic wind-events leads to entrainment of phosphorus-rich waters to the surface initiating or continuing an algal bloom. Hypoxia and wind-event mediated internal loading of phosphorus could be a positive feedback loop for cyanobacterial blooms and hypoxia in Muskegon Lake.

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Abbreviations

AOC-area of concern

AWRI-Annis Water Resources Institute

cm-centimeters

DO-dissolved oxygen

km-kilometer

L-liters

m-meters

mg-milligram

MLO-Muskegon Lake Observatory

NH_3-ammonia

s-seconds

SRP-soluble reactive phosphorus

TKN-total Kjeldahl nitrogen

TP-total phosphorus

YSI-Yellow Springs Instruments

Chapter 1 – Introduction

Introduction

As the problem of aquatic hypoxia continues to spread across the world's rivers, reservoirs, lakes, and coastal water bodies, scientists are concerned with questions of how and why it forms, what forces interrupt it, and what are the consequences to the ecosystems. The most common definition for aquatic hypoxia is when the dissolved oxygen (DO) concentration falls below 2 mg L^{-1}; however, the term varies with some studies citing DO concentrations less than 3 or 4 mg L^{-1} as being considered "hypoxic" as well (Diaz 2001; Ludsin et al. 2009; Larsson and Lampert 2011). DO typically decreases in the bottom waters of lakes, reservoirs, and estuaries during the summer as thermal stratification sets in, or salinity stratification in the case of some estuaries, and water column or benthic bacteria consume the remaining DO. Stratification isolates the cooler bottom waters from regular mixing with the warmer surface waters, which prevents reoxygenation of the deeper portions of the lake and allows hypoxia to develop, persist, and intensify.

Although hypoxia is most likely a natural feature in lakes as a result of stratification and the availability of organic matter to be decomposed in the bottom waters and sediment, it is clear in recent times, the areal and volumetric extent of hypoxia is expanding around the globe in freshwater and marine systems alike (Diaz and Rosenberg 2008; Zhou et al. 2013; Jenny et al. 2016). There are many consequences of hypoxia at every level within a lake ecosystem. At the chemical level, bioavailable forms of phosphorus and nitrogen are reduced and released from sediments at low DO concentrations, sometimes referred to as internal loading (Testa and Kemp 2012; Nürnberg et al. 2013). Greenhouse gases such as methane and nitrous oxide also accumulate in hypoxic waters (Chen et al. 2008). Bacterial communities under hypoxic

conditions also can change, with some species switching to more anoxic metabolic pathways, and other species that are more tolerant to low DO conditions becoming more abundant (Crump et al. 2007; Zaikova et al. 2010). The phytoplankton and cyanobacterial abundance in surface waters can be impacted by hypoxia and internal loading if nutrients reach the sunlit surface waters, forming an algal bloom (Smith et al. 2011; Michalak et al. 2013; Crockford et al. 2014). At the higher trophic levels within the ecosystem, many zooplankton and fish species are known to be intolerant of low dissolved oxygen concentrations and are forced to move vertically or horizontally to escape to more tolerable but possibly unfavorable habitat (Killgore and Hoover 2001; Ludsin et al. 2009; Roberts et al. 2009; Kraus et al. 2015).

Despite the fact that stratification makes the system stable enough for hypoxia to develop, forces such as weather make lakes hydrologically dynamic systems (Fig 1). Such meteorologically driven hydrologic events can have an influence on the chemistry and biology of a lake by bringing nutrient rich waters or resuspended sediments to plankton in nutrient poor waters (Cotner et al. 2000; Kerfoot et al. 2008; Crockford et al. 2013). Enhanced heterotrophic and autotrophic activity caused by intense weather events (increased river runoff and sediment resuspension) have been observed in Lake Michigan (Cotner et al. 2000; Johengen et al. 2008; Kerfoot et al. 2008). Similar studies on smaller lakes indicate that episodic weather events can have profound influences on the physical structure of the water column, availability of sediment derived nutrients, and plankton metabolic activity (Smith et al. 2011; Jennings et al. 2012; Crockford et al. 2014). Other studies have found that while phytoplankton could sustain most of their productivity locally through biotic mineralization, entrainment of nutrients from mixing events is needed to account for all of the phosphorus demand (Kamarainen et al. 2009).

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Purpose

The overall purpose of this project was to evaluate disturbances to and effects of bottom water hypoxia in Muskegon Lake, Michigan. Within the primary goal of evaluating disturbances to hypoxia, the secondary goal was to study episodic wind events on the lake and how they mix the water column at the Muskegon Lake Observatory location. The ultimate goal of this was to determine if Muskegon Lake experiences strong enough wind-events during summer stratification to deepen the thermocline into the hypoxic hypolimnion. The second goal of evaluating the effects of hypoxia in bottom waters was to provide evidence for ecosystem level changes by monitoring a suite of variables from nutrients to fish. The results of the second part were analyzed individually, as well as in conjunction with the first part to determine how the ecosystem responds to hypoxia and wind-events.

Scope

While this study directly pertains to Muskegon Lake; however, the methodology and results can be applied to other similar systems with suitable modifications. Results are particularly relevant to other drowned river-mouth systems along the west coast of Michigan, many of which also experience hypoxia. Lessons learned and methodology from this study can be applied not only to other drowned river-mouth lakes, but to other inland lakes, bays, and estuaries as well. In fact, a similar methodology to part one of this study is currently being applied to Callander Bay within Lake Nipissing, Canada to evaluate the effects of wind-events on water column stratification and hypoxia (Prescott, M. 2016 IAGLR abstract).

Assumptions

A major assumption of this study is that measurements being made at the Muskegon Lake Buoy Observatory are representative of the rest of the pelagic waters of Muskegon Lake. This idea was tested and evaluated through bi-weekly profiles at three additional pelagic locations in Muskegon Lake, primarily to compare water temperature and dissolved oxygen profiles, the variables of greatest interest.

In the second part of the study nutrient concentrations and bacterial abundances were assumed to be constant within the hypolimnion. On the basis of the observed homogeneity of the hypolimnetic temperatures and dissolved oxygen, as well as acoustic Doppler current profiler (ADCP) data that show comparable bottom water current speeds to that of the surface, we think this assumption is valid.

Hypothesis

The hypothesis is that while wind events are common on Muskegon Lake, most of these events are not of significant magnitude to break the summer thermal stratification and bring about relief from hypoxia. We also expect that benthic fish and hypolimnetic bacterial abundance will decrease, while nutrient levels, especially SRP, to increase in bottom waters as a result of desorption from metals in the sediment as a result of hypoxia. In addition, we anticipate that phycocyanin will increase in surface waters following periods of particularly strong wind-events to greater concentrations than before the wind-event occurred.

Significance

This work has significance in multiple areas, by helping to advance the knowledge of how wind-events influence lake mixing, as well as how the effects of hypoxia respond to lake mixing. We know of no other study in which the influence of wind-events on lake stratification has been examined in an ecological context with as much intensity as this one, which uses 5 years of time-series data to accomplish this task. The present study has helped to determine drivers of lake mixing. This study also examines the effects of hypoxia on fish at the community level, whereas many other studies only identify specific fish species of interest to study. We point out that in systems where excessive nutrient loading is not an issue, algal blooms can still occur, possibly as a result of mixing events that entrain nutrient rich water to the surface.

Definitions

Mild Hypoxia – Dissolved oxygen concentration in water is <4 mg L^{-1}.

Severe Hypoxia- Dissolved oxygen concentration in water is <2 mg L^{-1}.

Epilimnion- The upper, warmer layer of a thermally stratified lake

Hypolimnion- The lower, cooler layer of a thermally stratified lake

Metalimnion- The layer between the epilimnion and hypolimnion of a thermally stratified lake, in which a marked decrease in temperature occurs.

Thermocline- The horizontal plane within the metalimnion at which the rate of decline in temperature is maximal.

Oxycline- The horizontal plane at which the rate of decline in the concentration of dissolved

oxygen is maximal.

Figure Legends

Fig 1. Biological processes underlying the main components of lake metabolism. Oxygenic photoautotrophs use energy from photosynthetically active radiation (PAR) to produce biomass and oxygen (O_2) from water (H_2O), carbon dioxide (CO_2), and nutrients. Some of the primary production is respired by aerobic organisms, producing CO_2 and H_2O and consuming O_2. The pools of dissolved CO_2 and O_2 in the lake also exchange with the atmosphere. Figure and caption modified from McNair et al. (2013).

Figures

Figure 1
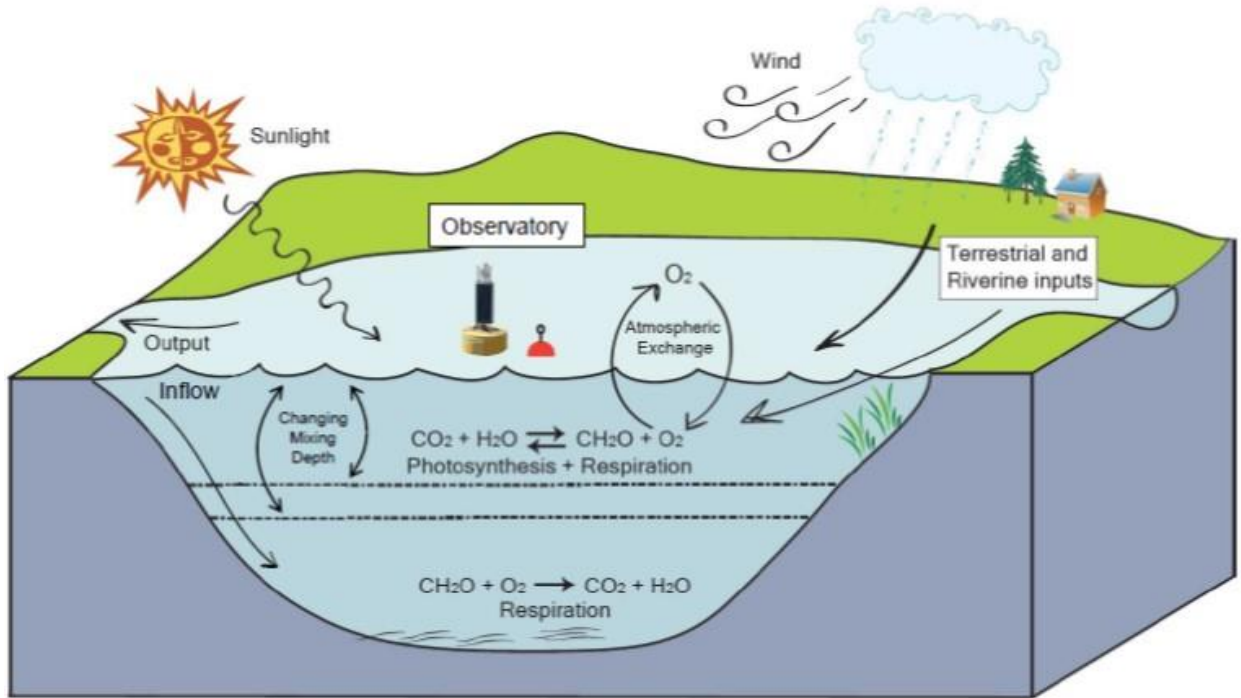
Chapter 2.1

Title

Shaken and stirred: Time-series observations reveal the influence of episodic wind events on lake stratification and bottom water hypoxia in a Great Lakes estuary (Muskegon Lake, Michigan)

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Running Head

Episodic wind events affect stratification and hypoxia

Keywords

Abstract

Hypoxia in lakes, estuaries, and coastal waters is an increasingly important issue worldwide as the climate warms and productivity accelerates, which increases microbial oxygen demand to decompose algal biomass in bottom waters. We monitored the process of hypoxia formation and degradation during 2015 in Muskegon Lake at multiple locations, and evaluated the effect of episodic wind-events on lake mixing using five years (2011-2015) of time-series observatory data. Bi-weekly water quality profiles at the center of the three sub-basins in addition to the observatory location revealed that hypoxia occurred at all four sites and persisted for 2-3 months during 2015. On one date, up to 24% of the entire lake's volume was estimated to be mildly hypoxic (DO < 4 mg L^{-1}). Based on the wind-event analysis, there was a significant relationship between the number of hours of above average wind per month and the monthly average wind-event mixing depth. Water quality profiles taken before and after one such mixing event indicated that, while the wind was unable to completely mix the entire water column, it deepened the epilimnion and sheared a thin layer from the upper hypolimnion. Wind-events may be the mechanism for entraining sediment-derived nutrients to the surface waters, fueling episodic algal blooms that would likely not occur with normal winds. It is important to determine the future of wind and mixing events in climate models as anthropogenic influences strengthen stratification and exacerbate hypoxia.

Text

Introduction

      Lakes and estuaries are the concentration points for the runoff of an entire watershed, which makes them highly susceptible to eutrophication and subsequent bottom water hypoxia (Zhang et al. 2010; Larson et al. 2013; Marko et al. 2013). While rivers and runoff have always supplied nutrients to lakes, seas, and the coastal oceans, agricultural practices that include excess nutrient additions have made eutrophication a serious problem in many areas (Steinman et al. 2008; Foley et al. 2012). Eutrophication has led to a rise in ecological issues such as algal and cyanobacterial blooms, which can give way to harmful toxins in the water supply and low dissolved oxygen (DO) in bottom waters, also known as hypolimnetic hypoxia (Nürnberg et al. 2013; Paerl and Otten 2013). Eutrophication and sinking algal blooms may sequester excess carbon dioxide into the sediments, but this only will occur if carbon in algal biomass is not reintroduced to the surface through bacterial processing as carbon dioxide in wind-driven mixing events (Pacheco et al. 2013).

      Anthropogenic global climate change is increasing air temperatures worldwide, which directly correlates to increasing water temperatures in lakes - contributing to the proliferation of hypoxia (Dokulil 2013). Warmer temperatures stabilize the thermocline, which limits normal mixing between the epilimnion and the hypolimnion (Dokulil 2013). Toxin-producing cyanobacteria are also more tolerant to growing in warmer, stable waters than other phytoplankton, which allows them to bloom under conditions that are detrimental to the growth of other algae (Hong et al. 2006; Dokulil 2013). Episodic precipitation events are also problematic because they may bring heavier rains and become more frequent. The ground is not able to completely absorb sudden heavy precipitation, so more nutrients are flushed into the

rivers and lakes than would occur under normal rain conditions (Williamson et al. 2009; Sahoo et al. 2011).

The two issues of eutrophication and climate change come together in the formation of hypolimnetic hypoxia in lakes (Williamson et al. 2009). Inland lakes receive a relatively higher concentration of nutrients from their surroundings and heat up faster than the larger Laurentian Great Lakes, which makes them very susceptible to developing hypoxia (Dokulil 2013). Eutrophication leads to higher than normal phytoplankton biomass production at the surface, which eventually settles to the lake bottom where some of it is decomposed and some is buried (Pacheco et al. 2013). Decomposition in the hypolimnion without the input of oxygen from the surface layers, due to thermal stratification, can lead to hypoxia (Sahoo et al. 2011). Hypoxia can have negative effects on the organisms of the lake when it reduces living space for fish and zooplankton (Ludsin et al. 2009). Also, more bioavailable species of phosphorus and nitrogen are released from the sediment under low oxygen conditions and build up in the hypolimnetic waters under stratification (Kamarainen et al. 2009). Abnormal wind-events during thermal stratification can mix the lake down into the hypolimnion can create blooms of primary production through internal loading of nutrients (particularly phosphorus in freshwater systems) to the epilimnion (Jennings et al. 2012; Crockford et al. 2014). The excess production then sinks to the bottom to be decomposed and further aggravates hypoxia (Testa and Kemp 2012).

Muskegon Lake, a Great Lakes area of concern (AOC), routinely experiences episodic hypoxia as a result of historic and ongoing eutrophication. The lake has a history of lumber and paper mills along the shoreline, and is the receiving basin for Michigan's second largest watershed, making it a settling area for large concentrations of organic matter (Steinman et al. 2008; Marko et al. 2013). The decomposition of excess organic matter in the sediment, along

with stratification, encourages the formation of hypoxia in the summer. The Muskegon Lake Buoy Observatory (MLO) has allowed us to intensely document the presence of hypoxia in the lake from 2011-2015 (Biddanda et al. In Review). The aim of this study is to further investigate hypoxia in Muskegon Lake with three goals: 1) to document the formation and presence of hypoxia throughout the lake's three main basins and the central buoy location during summer 2015, 2) to identify the frequency and intensity of summer mixing events during 2011-2015 using MLO data, and 3) to determine lake-wide consequences of strong wind before and after an episodic wind-event through monitoring specific wind-events in summer 2015 during hypoxia. By accomplishing these goals, we can further understand the development and disruptions of hypoxia in Muskegon Lake and apply lessons learned to other freshwater lakes, seas, and coastal areas around the world.

Methods

Study Site

Muskegon Lake is a drowned river-mouth lake situated on Michigan's western coast, and connected to Lake Michigan (Fig 1). Due to the accumulation of sand dunes on Michigan's western coast, typical river flow is restrained and pools behind the dunes, forming drowned river-mouth lakes, which are a common feature along this particular coast of Michigan. Muskegon Lake receives water from the Muskegon River watershed, the second largest in Michigan (7302 km^2), and empties into Lake Michigan via a 1.8-km connecting channel (Marko et al. 2013). Muskegon Lake has an average hydraulic residence time of ~23 days, however, this can range from 14-70 days depending on the season and Muskegon River discharge (Freedman et al. 1979; Marko et al. 2013). The Muskegon River is the primary inflow with several much

smaller tributaries such as Bear Creek to the north and Ruddiman Creek to the South. The

sample sites were deliberately selected to avoid sampling too close to any one of the tributaries,

avoiding tributary-specific influences. With a mean depth of ~7 m and a maximum depth of ~21

m, Muskegon Lake also has a relatively irregular bathymetry with three apparent sub-basins

(Marko et al. 2013).

Muskegon Lake Buoy Observatory

Due to the environmental issues associated with the long history of industry along the

shoreline, Muskegon Lake was declared a Great Lakes Area of Concern in 1987 (Steinman et al.

2008). As a result, Great Lakes Restoration Initiative funds from the EPA were used to install

and operate a time-series buoy observatory on the lake to monitor its water quality. The MLO

monitors meteorological conditions every 5 minutes and, physical, chemical, and biological

variables every 15 minutes from multiple depths throughout the water column (~12 m depth) at

one location near the center of the lake (Fig 1; Vail et al. 2015). Of concern in this study are

measurements of dissolved oxygen concentration using YSI datasondes (Yellow Springs

Instruments) at 2, 5 ,8, and 10-11 m, temperature (NexSens) at roughly 2, 4, 6, 8, 9-10, and 10-

11 m, and air temperature, wind speed, and wind direction (Lufft) ~2 m above the lake surface.

The entire string of water quality sensors is serviced, cleaned, and recalibrated every 1-2 months

during the typical operation season of May to December each year, with the exception of

temperature (which cannot be calibrated). Further information on the MLO system, how it

operates and open access to data, are detailed in Vail et al. (2015) and at www.gvsu.edu/buoy.

Wind-Event Analysis

Of the entire 2011-2015 wind speed data set, the mean wind speed was 5.1 m s^{-1} (10 knots) with a standard deviation of 2.6 m s^{-1} (5 knots), thus we defined a wind-event as any time the wind was above 1 standard deviation from the mean, or 7.7 m s^{-1} (15 knots). One standard deviation away from the mean was picked, because it is statistically abnormal, so we were only looking at the effects of the upper ~15% of wind that the lake experiences. Wind-events have been studied in other systems, with effects on the water column seen with similar wind speeds (Imberger 1985; Jennings et al. 2012; Crockford et al 2014). We also decided that the wind would have to persist for at least three consecutive hours, considering preliminary analysis indicated that 1-2 hour periods of high wind had little effect on the water column. If wind speeds fell below 7.7 m s^{-1} following at least 3 hours of high wind and wind speeds picked up again, we allowed up to 2 hours of wind below 7.7 m s^{-1} between to call it a continuous event. Thus an event could be only three hours long, or could last for many days with intermittent periods of 1-2 hours of wind less than 7.7 m s^{-1}.

During the times the episodic wind-event was taking place, we evaluated the buoy water temperature profiles to see how deep the event had mixed the lake from the surface downward compared to before the wind-event. We recorded the depth to which epilimnetic water homogenized from the surface to the bottom of the deeper epilimnion for water temperature (within 1° C). The example in Figure 2 indicates that there was an event with winds in excess of 7.7 m s^{-1}, and the water temperature mixed from the surface (2 m) all the way to 11 m. In this case we would record an 11 m "event mixing depth" for temperature.

To evaluate temporal patterns in mixing events, we calculated how many hours of wind over 7.7 m s^{-1} that each month and year experienced during the time that the buoy was deployed.

The time frame for this was from May to October during 2011-2015. Thus, we were able to gather wind hour totals for 5 years and 30 months total.

Manual Monitoring

The four stations in Muskegon Lake (East, Buoy, West, and South) were sampled once every two weeks starting the first week of May 2015 until the first week of November 2015 (Fig 1). Water quality profiles were performed at each site with a YSI 6600 sonde equipped with water temperature, dissolved oxygen, specific conductivity, pH, oxidative-reductive potential, turbidity, chlorophyll *a*, and phycocyanin sensors. The sonde was allowed to equilibrate at the surface for 1 minute, and then lowered at a rate of ~1.7 cm s^{-1} while taking measurements every 2 seconds to give a nearly continuous profile of the water column. This gave the parameters enough time to respond to parameter changes. Sensors were recalibrated on a monthly basis.

Using the dissolved oxygen concentration from the profiles, we determined the percent of the water column at each site that was mildly and severely hypoxic. We defined mild hypoxia as DO < 4 mg L^{-1}, because concentrations below this level can affect Lake Sturgeon (*Acipenser fulvescens*) behavior (Altenritter et al. 2013). Muskegon Lake is an important habitat for a remnant Lake Sturgeon population, so the current definition for mild hypoxia in Muskegon Lake is ecologically relevant. We defined severe hypoxia as DO < 2 mg L^{-1}, because that is the more conventional definition for hypoxia (Diaz 2001).

Although the goal was to perform additional manual monitoring trips before and after episodic wind events, we were only able to sample before and after one event. Wind speed forecasts were difficult to monitor as they changed often, so it was difficult to identify days that

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would serve as suitable "pre-event" samples. Many times, the actual wind speeds experienced on the lake were higher than in the weather forecast, in which case we did not sample beforehand because we did not anticipate the wind being strong enough to be deemed a wind-event. The lone before/after monitoring trip was performed in late July 2015.

Results

Development of Hypoxia

Both mild and severe hypoxia were present at some point at all four of the sites in Muskegon Lake over the course of summer; however, the percent of each site's water column that was hypoxic varied seasonally (Fig 3). Mild hypoxia was first observed as a thin layer at the bottom of the South water column on 6/17/2015; however, significant hypoxia was clearly present at all four sites by the next trip on 6/30/2015. The percent of each site's water column that were mildly hypoxic on 6/30/2015 varied from 0.2% at West to 20.1% at South (Fig 3). Mild hypoxia then disappeared from all but the East site where 22% of its water column was hypoxic on 7/15/2015 (Fig 3). This interruption is thought to be due to wind-driven upwelling and intrusion of Lake Michigan water coming in through the channel and displacing the bottom hypoxic waters (Dirk Koopmans, pers comm). By 7/31/2015, mild hypoxia had returned to all four sites, varying from 3.9% at West to 32.9% at the Buoy (Fig 3). The next sample on 8/10/2015 showed the highest cumulative amount of mild hypoxia for any date ranging from 17% of the water column at East to 44.3% at South (Fig 3). By 10/5/2015 there was no mild hypoxia detected at any of the sites.

Despite some interruptions to hypoxia in the early and late summer, it persisted in the bottom of the lake for a considerable amount of time throughout the summer. Based on the dates

when mild hypoxia was detected, we can roughly calculate the length of time that hypoxia existed at each site in Muskegon Lake. The longest continuous streaks of mild hypoxia were 42, 58, 55, and 55 days at the East, Buoy, West, and South sites respectively. This does not account for samplings in which mild hypoxia was detected at a single time point, but the dates before and after did not detect hypoxia. Potentially, the added duration of short-term mild hypoxia in the bottom of the lake lengthens the hypoxic season by 15 to 30 days.

Severe hypoxia was not detected at any of the sites until 7/28/2015. On that date, severe hypoxia was detected at the East site with 14.9% of the water column (Fig 3). On 8/10/2015, severe hypoxia developed at the Buoy and South sites in addition to the East site (Fig 3). From this point on, the South site was severely hypoxic until 9/23/2015, the last day hypoxia of any kind was detected. The only time that all four sites were severely hypoxic was on 9/9/2015 (Fig 3).

Unlike mild hypoxia, severe hypoxia was not present or persistent for long periods of time at each location. Severe hypoxia was detected on continuous sampling days only the East and South sites. The East and South sites showed 14 and 45 days of uninterrupted severe hypoxia, respectively, while the Buoy had severe hypoxia on two discontinuous dates and West on one sample day.

Wind Events

The number of hours of wind over 7.7 m s^{-1} changed seasonally as well as yearly. It is clear that the spring and fall months (particularly May and October) face a longer duration and higher frequency of above average winds (Fig 4). June through September are less windy, with

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the exception of August 2012 and 2015 which were exceptionally windy. These two months included the most number of hours of wind over 7.7 m s^{-1} of all June-September 2011-2015. The two windy August months of 2012 and 2015 were far windier than August 2011, 2013, and 2014 that ranked as the three least windy months of the entire dataset. The other months tended to follow the U-shaped pattern of wind from spring to fall.

On an annual basis, 2012 and 2015 stood out as the two windiest years with 914 and 1102 total hours of above average wind respectively. The windiest June, August, and September occurred during 2012, while 2015 contained the windiest May, July, and October of the 5-year wind record. Alternatively, 2013 was the least windy year of the 5-year record, containing four of the seven least windy months.

As expected, the depth that episodic mixing events were able to homogenize the epilimnion at the Buoy location was deepest in the spring and fall, and shallowest in the summer (Fig 5). Wind-events were able to regularly homogenize the water column temperature completely to the bottom-most sensor 73.5% of the time in May and 95% of the time in October, while only 26% of the time in June-September as a whole. Even within this time-frame, the summer transitional periods of June and September mixed the lake to the bottom at the buoy 46.3% of the time; however, during the peak summer months of July and August this occurred only 7.7% of the time.

The average mixing event depth obtained from the temperature nodes were 9 m in May and 10.1 m in October (Fig 5), while the range for the summer months June and September was between 6.4 and 8.1 m. From late-June to mid-September, typical wind-events were only temporarily able to deepen the epilimnion by a few meters. More extreme wind-events were able

to mix the lake near the bottom; however, this was rare and also temporary during summer stratification.

Based on linear regression analysis, there was a statistically significant relationship between the number X of monthly hours of wind over 7.7 m s^{-1} and the monthly average mixing event depth Y (Y=0.0145X+6.38, ($F_{1,28}$=19.78, p<0.001, r^2=0.42).

Lake-Wide Monitoring of a Single Wind-Event

For one episodic wind-event in 2015, we were able to take profiles in the four locations before (7/28/2015) and after (7/31/2015) it took place. From 7/29/2015 15:00 to 7/30/2015 15:00 there were 10 hours of average wind speed over 7.7 m s^{-1} coming from 260° WSW. Three of the hours were immediately consecutive, so it was indeed a wind event according to our definition. Before the event, there was a lake-wide thermocline of roughly 5.1 m thickness and 7.3 m deep in the middle (Fig 6). Following the event, the thermocline thinned slightly to 4.9 m thickness and deepened in the center to 8.7 m (Fig 6). The buoy data taken during the wind-event indicated that the thermocline was temporarily shifted deeper than seen in the manual profiles following the event (Fig 7).

There were also slight changes in the water column temperature and dissolved oxygen concentration post-event. Following the event, the epilimnion was made much more homogenous than it was previously. The average epilimnetic and hypolimnetic temperatures were very similar (though different than each other) before and after the event; however, the metalimnetic temperature decreased from 20.8 °C to 18.9 °C across the lake on average. Interestingly, the average DO concentration of all three layers decreased, from 8.9 to 8.2 mg L^{-1}

in the epilimnion, 5.2 to 4.3 mg L^{-1} in the metalimnion, and 4.2 to 3 mg L^{-1} in the hypolimnion.

According to the DO profiles, the wind event did not relieve any of the hypoxia. The East site

even fell from an initially mildly hypoxic DO concentration (2.2 mg L^{-1}) to a severely hypoxic

concentration (1.1 mg L^{-1}) after the event.

Discussion

      Based on the manual monitoring profiles taken at four different points in Muskegon

Lake, we demonstrated that mild hypoxia occurred lake-wide and was persistent throughout the

summer, while severe hypoxia rarely occurred lake-wide and was persistent at a few sites. While

not all sites showed consistent levels or severity of hypoxia every sampling, we did see long

stretches at each site where hypoxia was detected multiple times in a row. Given the high

productivity of Muskegon Lake, it is no surprise that there is enough benthic and hypolimnetic

respiration to deoxygenate the bottom waters (Weinke et al. 2014; Dila and Biddanda 2015).

Other lakes where hypoxia commonly occurs such as Lake Simcoe, in the province of Ontario,

Canada, and Lake Erie, do not experience hypoxia across their entire lake bottoms as a result of

factors such as depth, bathymetry, and wind-mixing (Altenritter et al. 2013; Nürnberg et al.

2013; Zhou et al. 2015).

      There were two disruptions to the presence of hypoxia that are site specific. The first

major disruption occurred in mid-to-late June when a suspected mass of upwelled Lake

Michigan water wedged into the bottom of Muskegon Lake. Upwelling events of Lake Ontario

water have also been found to come into Hamilton Harbor (Bocaniov et al. 2011). The cold,

oxygen-rich water pushed the slightly warmer, hypoxic water mid water column. This

reoxygenated the hypoxic water through mixing, and diffusion. The hypoxic water was also

pushed closer to the surface, so it was more vulnerable to wind-event mixing with warmer

oxygenated waters. The intrusion water affected the West site most notably because it is closest

to the channel to Lake Michigan. Its effects were also seen as far east as the Buoy location, but

the intrusion was unable to make it all the way across the lake to the East site.

The second hypoxic disruption occurred on August 23-24 when a cold front came in

along with 34 hours of continuous wind over 7.7 m s^{-1}. The combination of air cooling and

above average winds deepened the thermocline to 10-11 m, which is equivalent to the total depth

of the East site. Because of this, hypoxia was relieved for the whole water column at the East

site, and hypolimnetic nutrients likely mixed into surface waters. The thermocline deepened to a

similar depth at the other three sites, relieving some but not all of the hypoxia as well. Strong

winds together with air cooling have been shown to significantly mix a stratified lake (Crockford

et al. 2014). Warmer air temperatures over the next few weeks warmed the epilimnion and

caused the thermocline to move higher in the water column, thus allowing hypoxia to continue to

develop at all sites.

The irregular bathymetry of the lake allowed hypoxia to persist at the deeper locations.

When the water column is much deeper than the thermocline, there is less of a likelihood to have

mixing events reach the lake bottom. Sites like the South location are markedly deeper than the

surrounding bathymetry, which cuts it off from regular surficial mixing as well as episodic

mixing (Nürnberg et al. 2013). In addition, the prevailing summertime wind direction of ~SW,

comes across the long fetch of the lake. Thus, oxygenated water is likely to pool up on the

shallower eastern side of the lake, temporarily reoxygenating the East and Buoy locations instead

of the deeper, western South and West locations (Imberger 1985). Without the disruption of

intruding Lake Michigan water, it is likely that hypoxia would have been the most persistent at these locations instead of the Buoy site.

It is important to note that there are two different types of mixing that occur in Muskegon Lake, and most typically dimictic lakes for that matter. During the spring, the air temperature warms and thus the lake does as well. Following the major spring overturn, the surface layers of the lake begin to warm; however, the lake is not quite stratified yet, so relatively weak winds, and especially wind-events, are able to completely homogenize the lake many times (Crockford et al. 2014). This results in a re-homogenization of the entire water column, which slightly cools the upper waters and warms the bottom water. This process continues throughout May into early June, and the reverse process happens typically toward the end of September into October. The many overturns are also aided by the significantly higher number of hours of above-average wind, as evidenced by the positive association of increased mixing depth as wind hours increased.

Eventually, given an extended calm period without wind-events, the upper layers become too warm to regularly mix with the bottom waters. This leads to a metalimnion that separates the upper epilimnion and lower hypolimnion (Imberger 1985). This can happen at as little as 2 °C difference between the surface and bottom waters. At the point that the thermocline forms and the upper and lower layers of the lake no longer regularly mix, the second type of mixing during a wind-event begins, called an internal seiche (Imberger 1985).

We suspect that Muskegon Lake experiences internal seiches in the thermocline on a daily period as winds strengthen during the day and weaken at night. The metalimnion tilts and becomes a "teeter-totter" (Imberger 1985). During the day, we can speculate that the westerly winds pile up the warm, epilimnetic "surface water" in the eastern portion of the lake in the

downward shift of the metalimnion, while the cooler bottom waters get pushed westward in the upward shift (Fig 8). Evidence for this also comes from Acoustic Doppler Current Profiler (ADCP) data at the MLO, that indicates bidirectional flow of surface and bottom waters. During a typical summer day, westerly winds push the surface waters back towards the east side of the lake, against the overall flow, and bottom waters flow west towards the channel (Unpublished data, Scott Kendall and Leon Gereaux). This reverses at night when the winds weaken, and the layers of the lake move the opposite ways as the tilt reverses. Unlike what Monismith (1985) and Imberger (1985) found in the Wellington Reservoir of Australia, the hypolimnion of Muskegon Lake is significantly moved by wind-event forcing. They suggest that just the epilimnion and metalimnion tilt as wind speeds increase, and that the hypolimnion is relatively unaffected. However, as Figure 2 shows as an example, wind events on Muskegon Lake can lead to significant tilting of the hypolimnion as well.

This also decreases the effect of episodic wind-events completely mixing the lake like in the spring and fall. The high winds can only extend the assumed seiche effect more dramatically due to the summer stratification. That is to say, Figure 2 does not indicate that the entire lake mixed completely, and then suddenly developed stratification again. What it means is that the event was strong and forced enough of the western epilimnetic water to nearly completely fill the eastern basin of Muskegon Lake that is shallower than the western portion. This gives the illusion that the entire lake mixed to the bottom because, according to the temperature node profile, the whole water column was homogenous for a few hours. Almost immediately after the winds let up, the lake returned to its previous state, and we see a stratified water column once again (Imberger 1985). This was, of course, an extreme case as similar situations have only happened 14 times between July and August in the past 5 years. Similar to Imberger (1985), we

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also see that once the winds let up, the next seiche under normal wind conditions did not overshoot the normal range of thermocline tilt.

Given stratification and the inability for even extreme wind-events to completely mix Muskegon Lake, this contributes to the formation and persistence of hypoxia in the hypolimnion for the duration of stratification (Dokulil et al. 2010; Sahoo et al. 2011). In fact, many aquatic systems are afflicted by summertime hypoxia, which may be a completely natural feature (Delorme 1982). Evidence suggests that hypoxia has existed in estuaries and coastal areas prior to human influence; however, the occurrence and spread of hypoxia is increasing in recent time (Diaz 2001; Zhang et al. 2010; Jenny et al. 2016). Lakes and estuaries have spring and summer blooms as well as organic matter in the sediments to decompose, drawing down dissolved oxygen in the bottom waters. Without regular mixing with the oxygenated surface waters, the bottom waters will stay hypoxic until the fall overturn (Sahoo et al. 2011).

One of the biggest effects of hypoxia in the bottom waters is the release of nutrients, particularly phosphorus in freshwater systems, from the sediments (Nürnberg et al. 2013). This process is called internal loading. Normally, much of the phosphorus in the sediments is bound to metal particles under oxidative conditions (Smith et al. 2011). Lower dissolved oxygen concentrations create a reducing environment, whereby soluble reactive phosphorus (SRP) is released from the sediment into the hypolimnetic water above. High rates of release occur when DO of overlying water is < 2 mg L^{-1}, but elevated concentrations of SRP are also seen when DO of overlying water is between 3-4 mg L^{-1} (Nürnberg et al. 2013). Continual stratification and hypoxia, can lead to a build-up of SRP in the hypolimnetic waters. Muskegon Lake shows evidence of internal loading due to extensive, persistent hypoxia during summer. Seasonal sampling on Muskegon Lake, typically once in May, July, and September, indicates two times

higher concentrations of SRP in the bottom waters compared to surface waters (Steinman et al. 2008).

During episodic wind-events, there is the potential for these nutrients to be brought to the surface waters (Kamarainen et al. 2009). As the above-average winds cause extreme seiches, there is slight mixing where the epilimnion and hypolimnion meet the metalimnion. Wind-events increase the movement of water and increase the mixing and diffusion that happens within these boundary layers. Also, due to the stress on the metalimnion (shear), small billows of these metalimnetic and hypolimnetic waters may burst into the epilimnion (Imberger 1985). Thus, extreme winds may help the epilimnion pick up nutrients from the metalimnion and upper hypolimnion, and entrain them to the surface where phytoplankton and cyanobacteria are likely to use the increased nutrients to grow and bloom (Imberger 1985; Kamarainen et al. 2009). Also, during the previously mentioned Lake Michigan intrusion, nutrient-laden hypolimnetic water is pushed closer to the surface, by the more dense Lake Michigan water underlying it. As nutrient-rich water comes closer to the surface, weaker wind-events could be capable of bringing nutrients to the phototrophs at the surface.

It is easy to see that given a total cutoff of external nutrient loads, a eutrophic system can maintain its trophic status and productivity through internal loading and biotic mineralization (Kamarainen et al. 2009). While there is likely still some nutrient mixing into the epilimnion during normal winds, the effect could be amplified during episodic wind-events. In these cases, a larger burst of nutrients could be supplied suddenly to potentially harmful algal blooms in eutrophic systems during the prime growing season of the calm, hot, late summer (Michalak et al. 2013).

It is important to take stratification, hypoxia, mixing events, and internal loading into consideration when thinking about the future of lakes as they relate to climate change. In the temperate regions, there is expected to be an increase in air temperature, which will translate to warmer lakes (Sahoo et al. 2011; Dokulil 2013). A warmer epilimnion will create a stronger degree of stratification, further limiting regular and episodic lake mixing from at least partially reoxygenating the bottom water (Sahoo et al. 2011). We are already seeing the stratification and hypoxic seasons expanding in many lakes (Paerl and Huisman 2008; Dokulil et al. 2013). Lakes are now stratifying earlier and staying stratified longer, which allows hypoxia to develop and persist in the bottom of lakes (Dokulil 2013). A longer duration of hypoxia will promote a great release of nutrients from the sediments under the now reducing conditions (Nürnberg et al. 2013). This could potentially further concentrate these nutrients in the hypolimnion.

While no increase or decrease for wind speeds is expected according to current climate models (Pryor and Barthelmie 2011), the weather is supposed to become more episodic (Jennings et al. 2012). A greater frequency of episodic events could potentially create a situation in which nutrients are more frequently supplied in a higher concentration from the hypolimnion to the epilimnion, without hypolimnetic reprieve from hypoxia (Crockford et al. 2014). Given cyanobacterial propensity to grow in warmer waters compared to phytoplankton, such as diatoms and green algae, episodic supplies of nutrients could enhance already problematic blooms of cyanobacteria (Paerl et al. 2011; Crockford et al. 2014). In addition, while mixing does lead to a temporary decrease in cyanobacteria at the surface, intermittent mixing has been shown to be ineffective at permanently mitigating blooms of *Microcystis* (Jöhnk et al. 2008).

This complex system has the potential to influence trophic levels in the lake beyond that of phytoplankton. Decaying algal blooms haven been shown to exacerbate hypoxia in lakes

(Paerl et al. 2011). Hypoxic water has been indicated as both a refuge and a hazardous zone for zooplankton. Some can tolerate low oxygen and use it as a hideaway from hypoxia intolerant fish (Larsson and Lampert 2011), while other intolerant zooplankton become concentrated above the hypoxia into the mouths of intolerant fish (Goto et al. 2012). Longer extents and expanded areas of hypoxia will also eliminate more habitat that cold, deep dwelling fish prefer. This forces them to move to warmer water above the hypoxia or to shallower, oxygenated littoral zones (Zhang et al. 2010). Overall, hypoxia can have profound effects on organisms from the biochemical level to the community level (Zhang et al. 2010).

All of this information together stresses the importance of continuous monitoring of our lakes and reservoirs. Lakes have been shown to be integrators, regulators, and sentinels of change within watersheds and the climate (Williamson et al. 2009). Particularly this study indicates that monitoring buoys, such as the Muskegon Lake Observatory, are invaluable in improving our understanding of how these vital systems operate (Jennings et al. 2012). Observatories can deliver higher frequency, time-series data from throughout the water column to off-site locations (Porter et al. 2009). This means that we can know what is happening within the lake system during these episodic storms, which we would otherwise not see by sampling once on a sunny day to avoid bad or dangerous weather conditions (Jennings et al. 2012).

Conclusion

Using time-series observatory data and discrete measurements, we monitored the spread of hypoxia in the deepest areas of Muskegon Lake, and evaluated the effect of episodic wind-events on mixing the lake before, during, and after stratification. It is evident that both mild and severe hypoxia were a lake-wide phenomenon during summer stratification, and that mild

hypoxia persisted for at least 2-3 months continuously in 2015, barring an intrusion of upwelled water from Lake Michigan or an extreme wind-event combined with substantial cooling of the overlying air mass. Additionally, episodic wind-events occurred quite frequently on Muskegon Lake; however, the spring and fall periods experienced more hours of above average wind speeds that have the potential to mix the lake. Spring and fall events tended to mix the entire lake many times, but wind-events during the summer could not completely mix the lake due to stratification. We suspect, summer wind-events exaggerated the seiche of the thermocline within the lake, but stratification soon returned as the winds weakened. Close monitoring around the lake during one particular wind event indicated that wind-events homogenize and deepen the epilimnion, which shifted the metalimnion slightly deeper as well. This indicated that during the event, the upper hypolimnion was sheared off, which could potentially bring nutrients like SRP to the surface waters, given their release into the water column during hypoxic, reducing conditions. While we cannot control the weather to prevent stratification related hypoxia and internal loading, efforts need to be made to reduce the loads of external nutrients that promote aquatic eutrophication. At the broader scale, we should take steps to mitigate climate change to prevent stratification from intensifying in the future.

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Figure Legends

Figure 1. (Left) Map of the Great Lakes region with arrow pointing to the location of Muskegon Lake, Michigan, USA. (Right) Bathymetric map of Muskegon Lake indicating the locations of sub-basin sampling and red ring for the Muskegon Lake Observatory (MLO) locations with site names and approximate depths. Boxes with white arrows indicate tributaries to Muskegon Lake.

Figure 2. (A) Graph of water column temperature data measured by the Muskegon Lake Observatory (MLO) from 8/2/15 to 8/4/15. (B) Wind speed measurements taken during the same time period. The horizontal line defines the 7.7 m s^{-1} point, above which we have defined as above average wind speeds.

Figure 3. Percent of each site's water column that is mildly (DO < 2 mg L^{-1}) hypoxic (A) and severely (DO < 4 mg L^{-1}) hypoxic (B). No bar representation for a site on a sampling date indicates that hypoxia was not detected during that period.

Figure 4. Average number of hours of above average wind speeds (>7.7 m s^{-1}) during each month 2011-2015 (*N=5* for all months except May when no buoy meteorological data was reported in 2014 until June). The thick lines inside the bars represent the median of the data. The tails represent the minimum and maximum number of hours, while the bars represent the inner 25-75th percentile.

Figure 5. Average depths by month that mixing events homogenize the epilimnion.

Figure 6. Average water temperature profile taken at the four sampling sites on 7/28/15 (Solid Line) and 7/31/15 (Dashed Line).

Figure 7. Muskegon Lake Observatory measurements of water temperature (Top) and dissolved oxygen concentration (Bottom) during a wind-event. Grey vertical bars indicate times when the wind speeds were over 7.7 m s^{-1}.

Figure 8. Conceptual representation of mixing in a rough west-to-east cross-section of Muskegon Lake. On the top row, is a wind-mixing event during no or weak stratification. There is essentially no thermocline, so the lake wind mixes easily and completely. On the bottom row, is a wind-mixing event during strong stratification.

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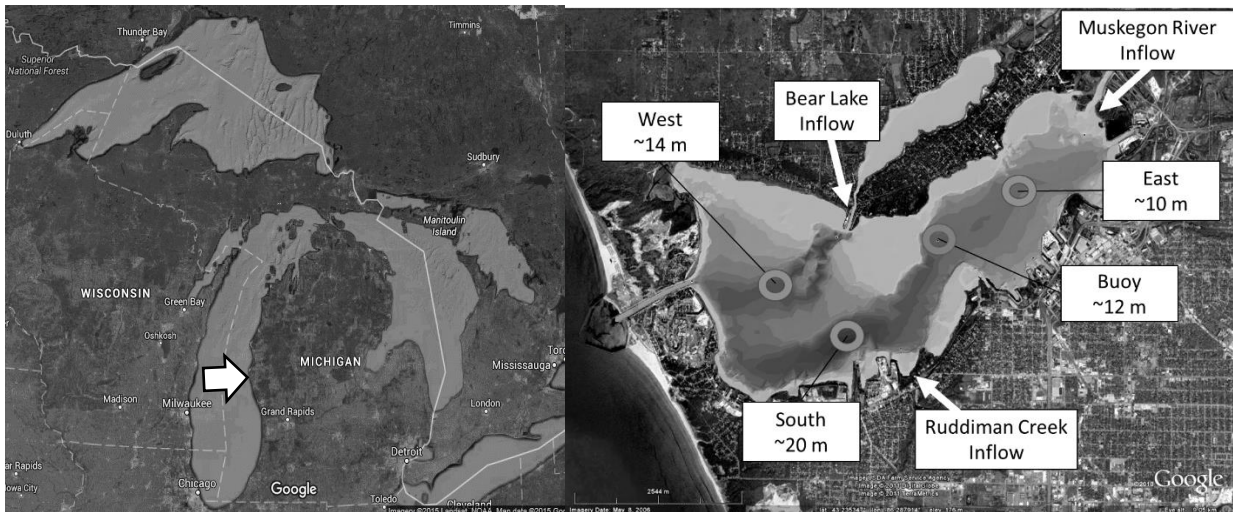
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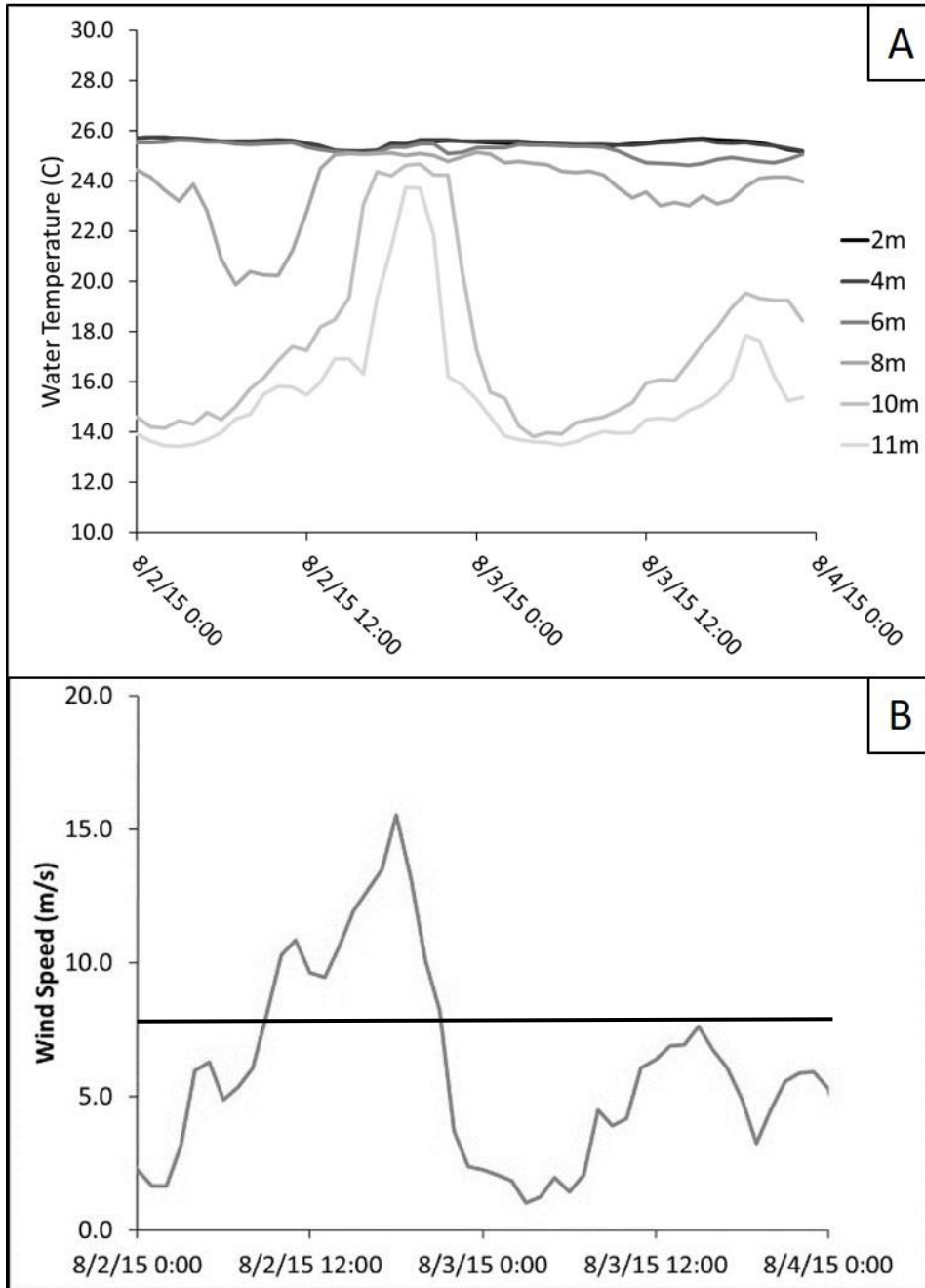
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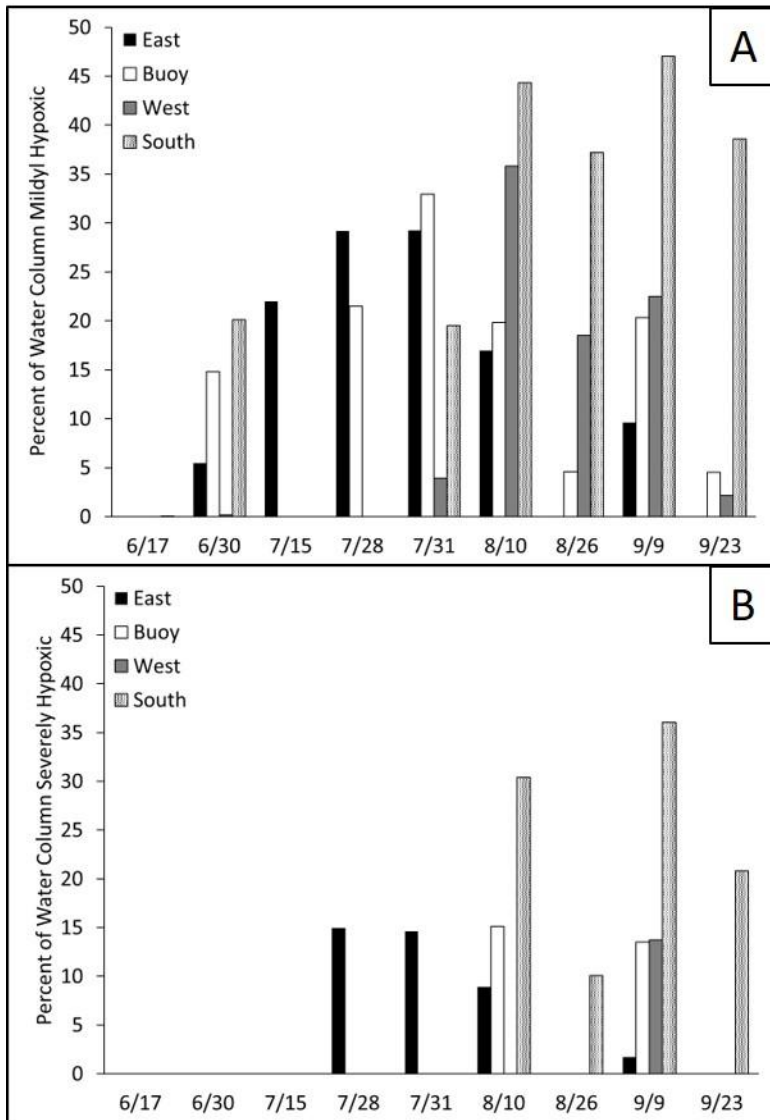
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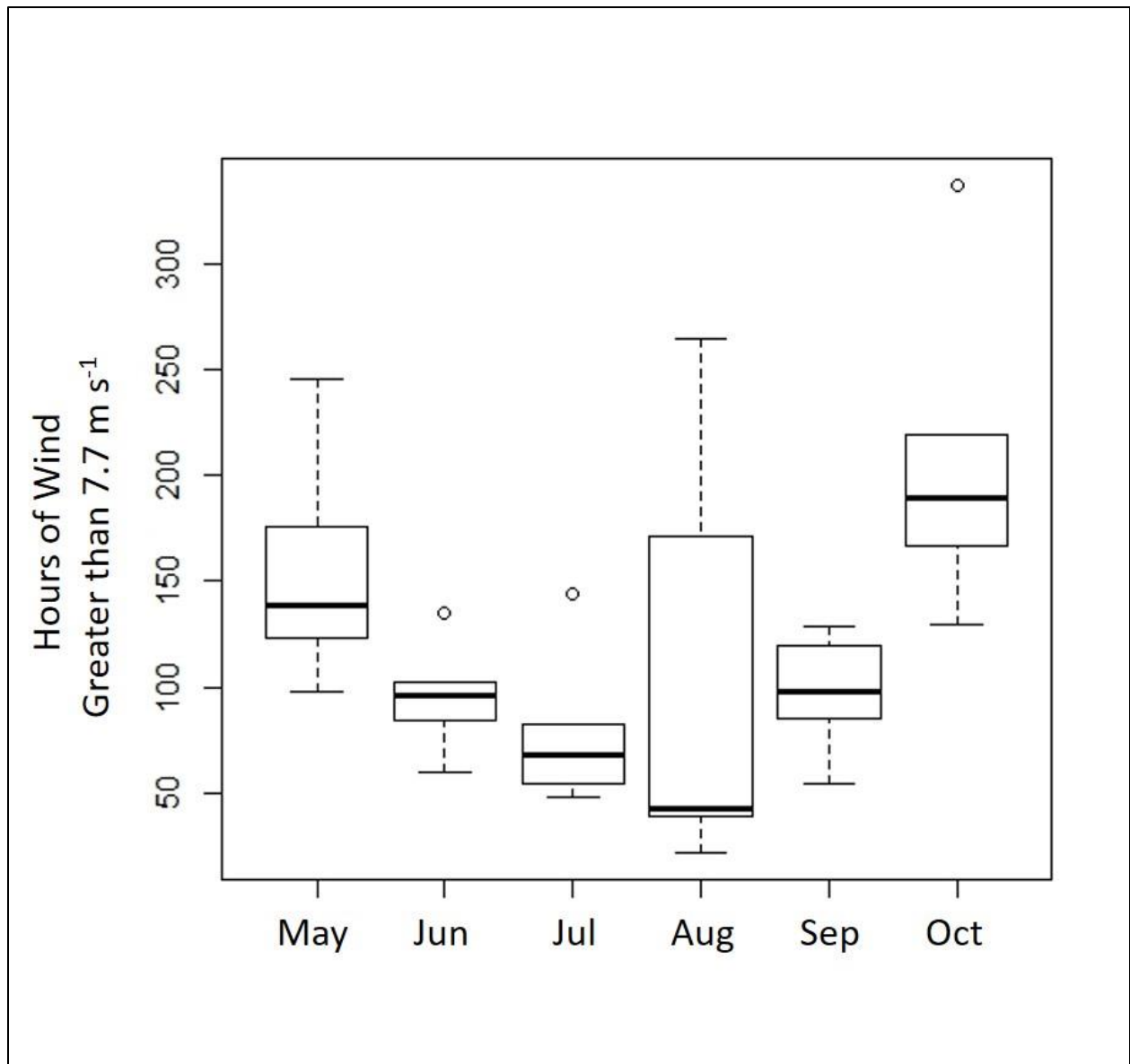
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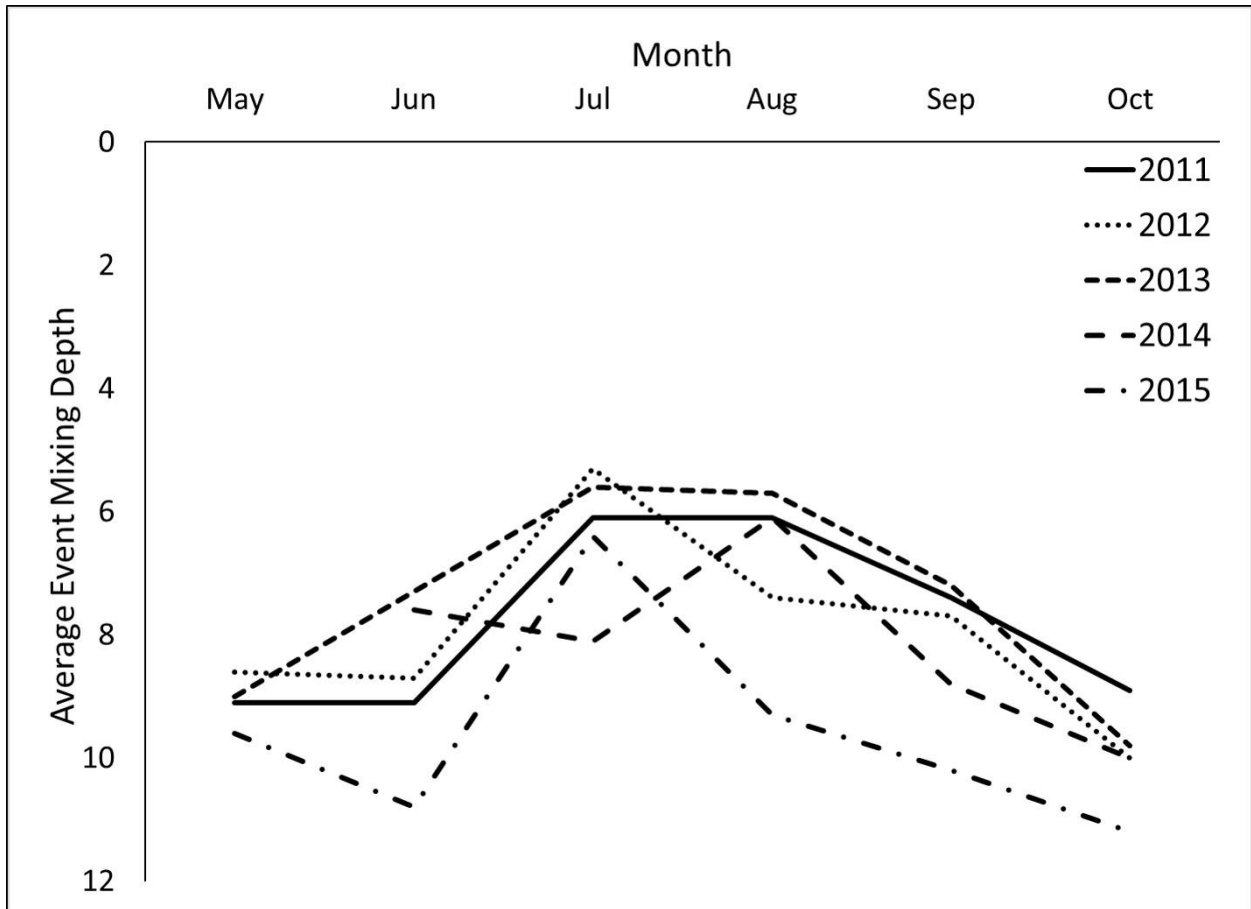
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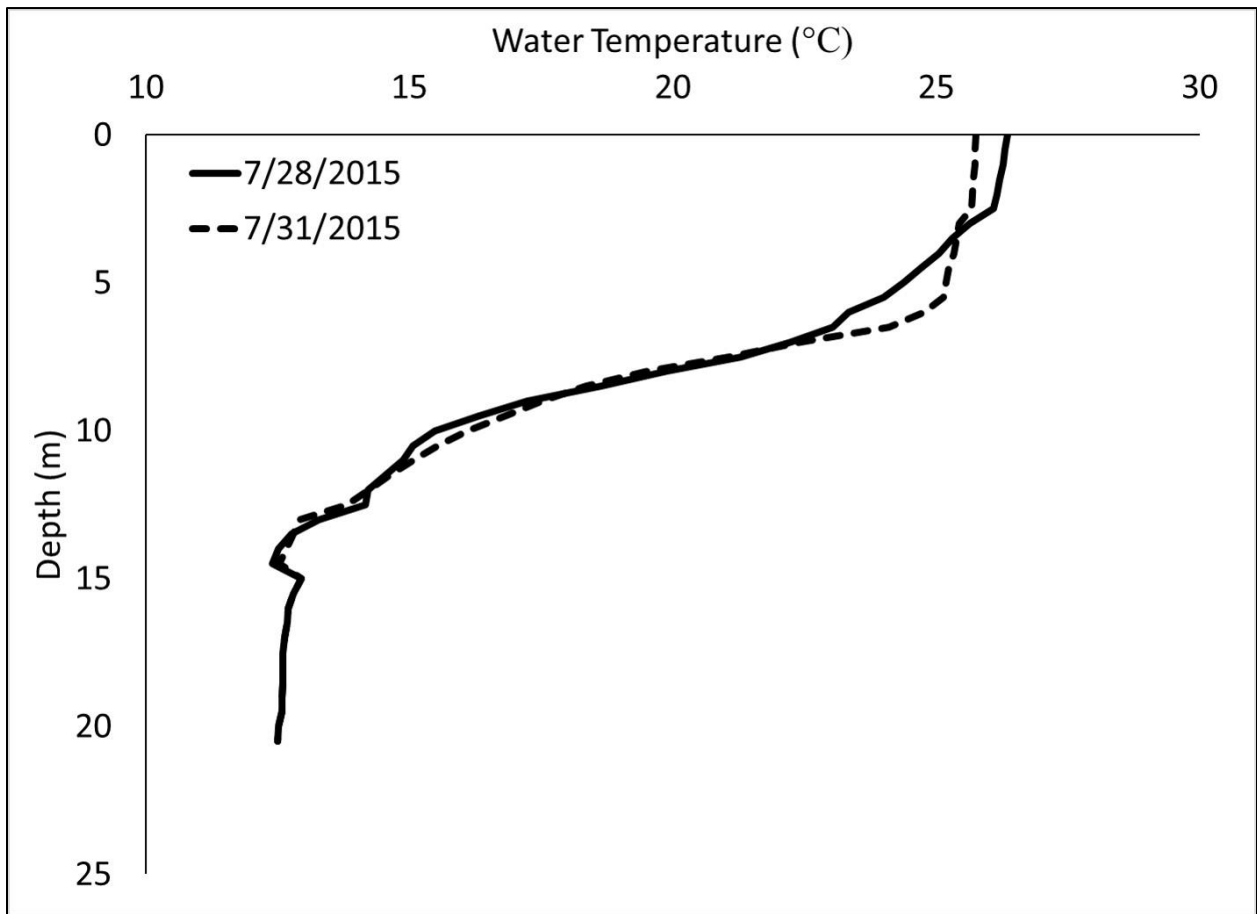
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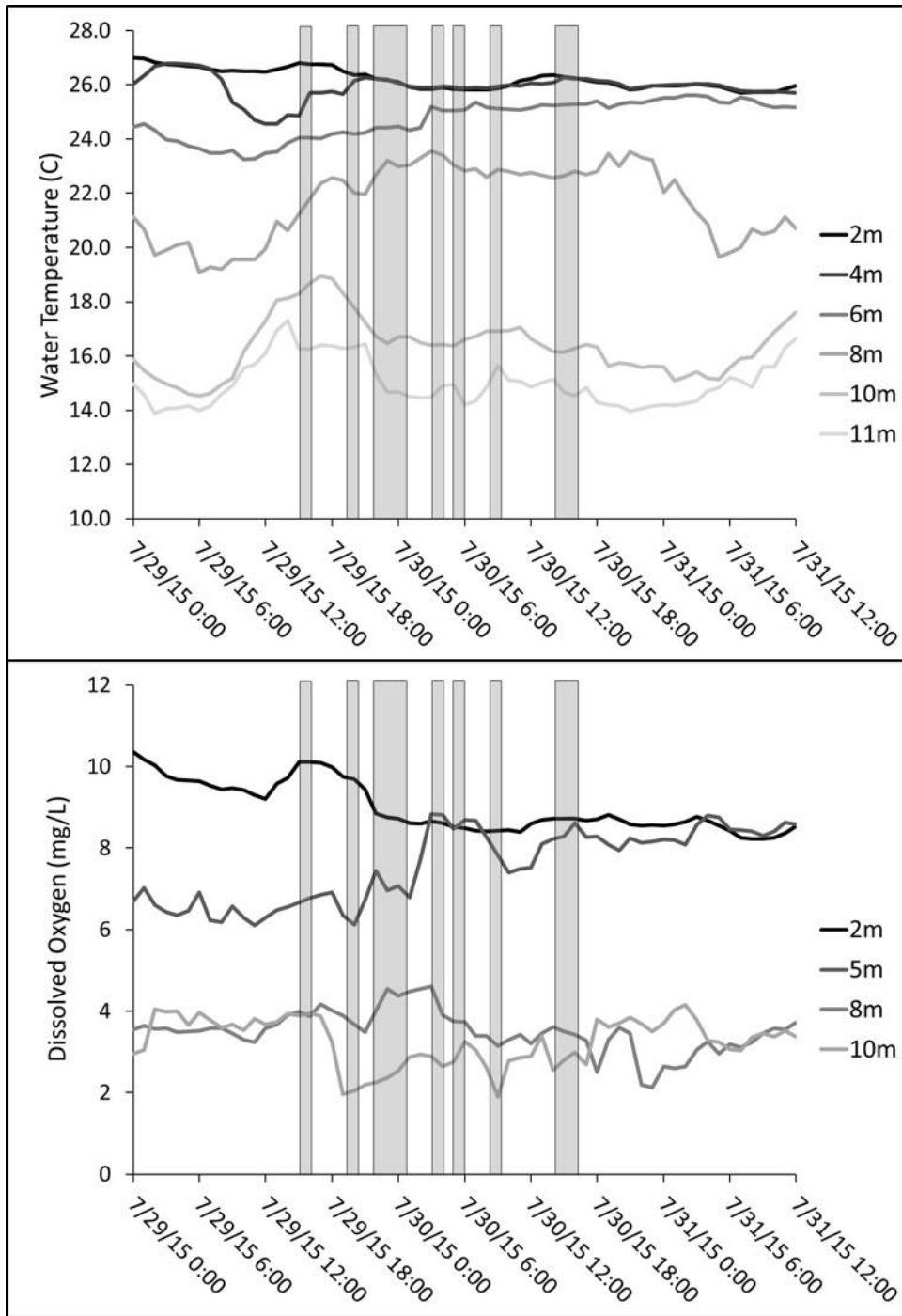
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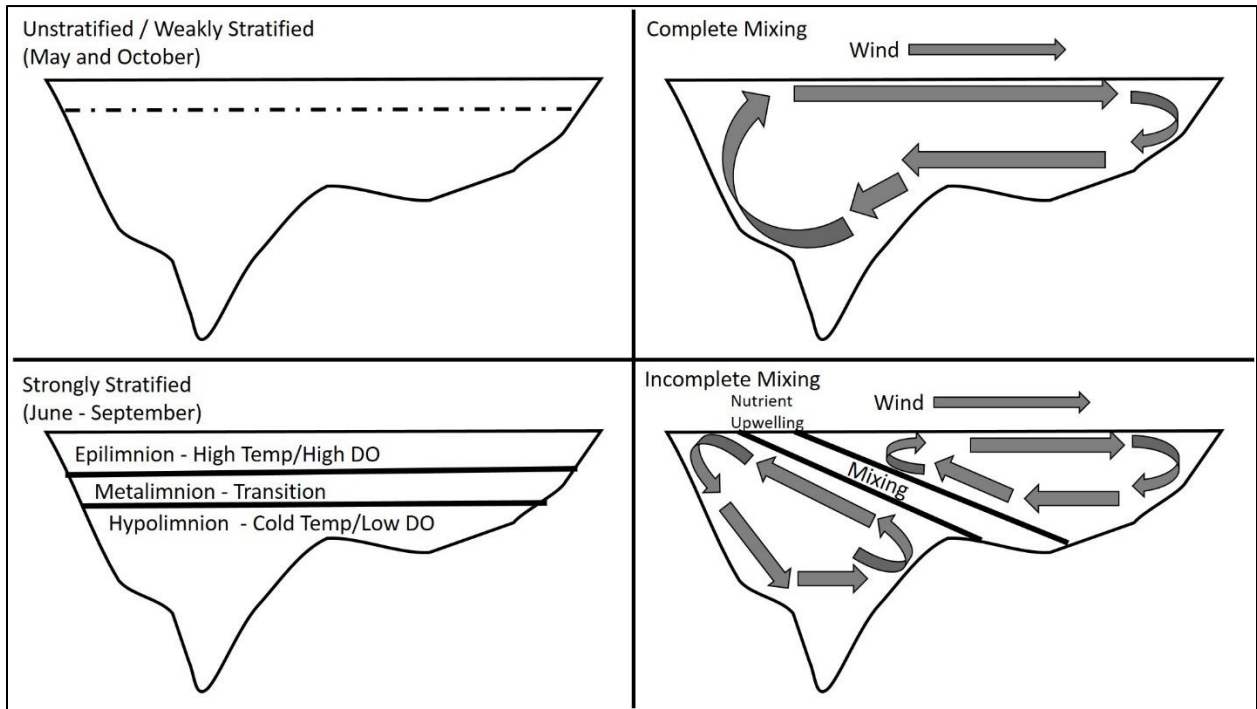
Chapter 2.2

Title

From Bacteria to Fish: Ecosystem level consequences of seasonal hypolimnetic hypoxia in

Muskegon Lake, Michigan

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Running Head

Ecosystem consequences of hypoxia

Abstract

The occurrence of bottom water hypoxia is increasing in many bodies of water around the world.   Hypoxia is of concern due to the way it negatively impacts lakes and estuaries at the whole ecosystem level. We examined the influence of hypoxia on the Muskegon Lake ecosystem by collecting nutrient samples and bacterial abundance counts from the surface and bottom waters, fish community information from the bottom waters, and performing profiles of chlorophyll and phycocyanin as proxies for phytoplankton and cyanobacterial growth, respectively. Significant changes occurred in Muskegon Lake as a result of hypoxia. Lake-wide concentrations of soluble reactive phosphorus (SRP) and total phosphorus increased in bottom waters, and were significantly higher than in the bottom before hypoxia and surface waters during hypoxia. Bacterial abundance decreased in the bottom waters from the pre-hypoxic period to post-hypoxia. There were no drastic changes in surface chlorophyll *a* concentration through the season; however, phycocyanin increased three-fold following a major wind-mixing event, and remained elevated for over 1.5 months despite several strong wind-events. The high SRP concentrations in the bottom waters may have mixed into the surface waters, sustaining the bloom. The fish assemblage in the hypolimnion changed in association with hypoxia. Overall fish abundance, species richness, and maximum length all decreased in catch as a function of bottom dissolved oxygen concentrations. The link between hypoxia and wind-events appears to serve as a positive feedback loop by continuing internal loading and cyanobacterial blooms in the lake, while simultaneously decreasing habitat quality for benthic fish.

Text

Introduction

Aquatic hypoxia is expanding its extent around the globe, which has many consequences for the ecosystems it affects (Diaz 2001). While most of the attention is on marine systems, where there are estimated to be over 400 hypoxic zones globally, freshwater hypoxia is increasing as well (Diaz and Rosenberg 2008; Jenny et al. 2016). Hypoxia is thought to be natural in many systems as a result of thermal stratification and excess organic matter decomposition (Zhou et al. 2013; Jenny et al. 2016). However, in a study of 365 lakes distributed around the world, 71 recently developed hypoxia within the last 300 years (Jenny et al. 2016). Many studies attribute the development of hypoxia within freshwaters systems to eutrophication (Diaz 2001; Scavia et al. 2014; Jenny et al. 2016), but global climate change also is suspected to play a role in increasing the strength of stratification and bacterial metabolic rates while decreasing dissolved oxygen solubility (Sahoo et al 2011; Dokulil et al. 2013).

An intensely studied consequence of hypoxia is the effect it has on fish due to their economic and food importance. At the cellular level, hypoxia has been shown to be an endocrine disruptor, impairing the ability for fish to reproduce, as well as a teratogen, leading to malformed embryos (Wu et al. 2003; Shang and Wu 2004). While many laboratory studies indicate decreased consumption and growth as a result of hypoxia exposure, some indicate that these effects may not be seen in the wild because fish have the ability to detect and avoid hypoxia (Burleson et al. 2001; Roberts et al. 2011; Vanderplancke et al. 2015). However, numerous studies also show the impacts of hypoxia on fish because they must move to higher oxygenated areas that may not be preferred habitat, (Eby et al. 2005; Ludsin et al. 2009; Roberts et al. 2009; Brown et al. 2015; Kraus et al. 2015). Not only does hypoxia cause fish to move, but

zooplankton and prey fish may be forced to move. Hypoxia intolerant species must move to shallower water, to the same areas that the larger fish have also been restricted, which increases trophic interactions to a perhaps unnatural level (Eby and Crowder 2002). Those that are fairly tolerant of hypoxia can actually use it to their advantage, swimming down into water that larger fish are unwilling to venture into (Ludsin et al. 2009; Larsson and Lampert 2011). This, of course comes at the cost of living in hypoxia (Larsson and Lampert 2011; Goto et al. 2012). Dissolved oxygen is one of the major factors that shapes fish assemblages (Killgore and Hoover 2001; Eby and Crowder 2002; Bhagat and Ruetz 2011; Altenritter et al. 2013).

Another concern with bottom water hypoxia is the internal regeneration or loading of nutrients. External loads of phosphorus are the primary cause of eutrophication of freshwater systems, which helps initiate algal blooms and subsequent hypoxia (Scavia et al. 2014). In efforts to reverse eutrophication, watershed managers often point to reducing phosphorus loads to lakes in order to improve water quality; however, systems can maintain their eutrophic status through hypoxia mediated internal loading (Nürnberg et al. 2013). Phosphorus is normally oxidized and bound to metals under oxic conditions, but under low-oxygen conditions, the system becomes reducing and releases bioavailable forms into the water column (Smith et al. 2011). Once concentrated in the bottom waters, they are typically isolated until the fall turnover. However, during extreme wind-events, these nutrients may be entrained into the surface waters (Jennings et al. 2012; Crockford et al. 2014). Episodic influxes of nutrients to surface waters may be a mechanism for stimulating algal blooms, especially cyanobacteria, during the late-summer period where water temperatures are warmest, stratification is strongest, and hypoxia is the most severe of the season (Crockford et al. 2014). Algal blooms as a result of these nutrient supplies could potentially sustain themselves for weeks (Kamarainen et al. 2009).

The main objective of this study was to evaluate the ecosystem level changes that occurred in Muskegon Lake during 2015 as a result of bottom water hypoxia. Secondary objectives were to: 1) measure surface and bottom nutrient concentrations of four locations in Muskegon Lake to find evidence of nutrient regeneration in bottom waters and episodic transport to surface waters, 2) measure bacterial abundance at the surface and bottom for changes in overall abundance correlated with hypoxia, 3) identify what benthic fish species are present during hypoxia and in what abundances, 4) study chlorophyll *a* and phycocyanin pigment measurements in the surface waters to correlate blooms with major episodic wind-events. With the results of this study, we hope to understand the concurrent changes that take place in Muskegon Lake as a result of hypoxia, to better inform us as to what occurs in similar lakes that experience hypoxia.

Methods

Study Site

Muskegon Lake is located midway up Michigan's western coast, and is one of many drowned river-mouth lakes that naturally occur along this specific coast (Fig. 1). Normally, river-mouths end in a delta-like fashion; however, the build-up of sand dunes has impeded natural flow, and led to a back-up forming a drowned river-mouth. Its primary inflow is on the west side from the Muskegon River watershed, which is the second largest in Michigan (7302 km^2; Marko et al. 2013). It has additional smaller tributaries of Ruddiman Creek to the south and Bear Lake to the North. The mean hydraulic residence time changes seasonally (14-70 days) and with the weather, and averages ~23 days. (Freedman et al. 1979; Marko et al. 2013). Sample

locations in Muskegon Lake were purposefully chosen because they represented the center of the lake's three sub-basins, and were located away from any tributary inflows.

Manual Monitoring

        Manual monitoring was done at four sites in Muskegon Lake (East, Buoy, West, and South) and were visited bi-weekly in 2015 starting on May 6th and ending on November 4th (Fig. 1). The sites were sampled in the morning hours between approximately 8 a.m. and 11 a.m. in order of East, Buoy, West, and then South. Order of sampling was not randomized in order to sample all four locations in the least time possible and avoid too much influence of changing time of day. At each site, a YSI datasonde (Yellow Springs Instruments), equipped with temperature, dissolved oxygen (DO), chlorophyll a, and phycocyanin sensors, was used to perform a profile of the water column. It was allowed to equilibrate as close to the surface as possible for 1 min, then lowered at a rate of roughly 1m/min to the previously measured depth using a drop rope and weight. DO was not calibrated each trip because these sondes are calibrated monthly.

Nutrients

        At each site, water for nutrient analysis was gathered bi-weekly using a Van Dorn bottle from 1 m below the surface and 1 m above the sediment. Water was dispensed from the sampler into acid washed Nalgene bottles. Bottles were kept on ice in a cooler until the return to the laboratory, where they were immediately transported to the in-house chemistry lab at the Annis Water Resources Institute, Muskegon, Michigan (AWRI). Samples were collected for soluble

reactive phosphorus (SRP), total phosphorus (TP), ammonia (NH_3), and total Kjeldahl nitrogen

(TKN). They were analyzed in-house at the AWRI, according to EPA (1993) methods. Samples

that were below the detection limit were assumed to be 50% of the detection limit (SRP=0.05 mg

L^{-1}, NH_3=0.01 mg L^{-1})

For the four types of nutrients, comparisons were made between the top and bottom

samples for each period of pre, during, and post hypoxia, as well as a comparison between just

the bottom samples pre, during, and post hypoxia. In order to justify pooling data, sites were

compared to one another for the same time period (pre, during, and post-hypoxia) and location in

the water column (top or bottom) using ANOVA (all pre-hypoxia surface samples were

compared between sites for example).

When comparing the groups for SRP to evaluate the ability to pool them across sites,

only sites during post hypoxia taken from the bottom water were significantly different. They

were still pooled together, because the other five groups were not different. Not all of the pooled

groups were normally distributed, so non-parametric tests were used. A Kruskal-Wallis test was

used to compared the bottom samples pre, during, and post hypoxia, and a pairwise Wilcoxon

test with Holm's correction was used for post-hoc testing. A sign test was used to compare the

top and bottom samples for each period relative to hypoxia, due to non-normality and

asymmetric distribution about the median.

For TP, no sites were statistically significant from one another by way of ANOVA.

Though all pooled bottom samples were normally distributed (Shapiro-Wilk normality test),

bottom pre, during, and post hypoxia TP samples were still compared using Kruskal-Wallis with

post-hoc pairwise Wilcoxon signed ranks using Holm's correction so that all comparisons are

consistent. Given the three surface groups were not normally distributed, surface and bottom samples during the three periods were compared using a paired Wilcoxon signed ranks test.

In the analysis of NH_3, only one pair of sites were different from one another in the bottom during hypoxia using an ANOVA test, thus all groups were still pooled. When comparing the bottom for pre, during, and post hypoxia, during hypoxia was not normal, so the three groups were compared using a Kruskal-Wallis. A pairwise Wilcox with Holm's correction was used to differentiate the three groups. Since all surface and bottom groups were not normal, paired Wilcoxon signed ranks tests were used.

Only the bottom during-hypoxia group of TKN concentrations show significant differences between some sites using an ANOVA, so groups were still pooled. All bottom groups for pre, during, and post hypoxia were normal, but for consistency they were also compared using Kruskal-Wallis and post-hoc comparisons were done using a pairwise Wilcoxon signed ranks test with Holm's correction. All top and bottom groups were normally distributed so surface and bottom groups were compared using paired Wilcoxon signed ranks tests.

Bacteria

We preserved the bacteria with 2% formalin, followed by an acridine orange stain. We then filtered them using black 25 mm (0.2 μm pore size) polycarbonate Millipore filters. Prepared slides were frozen and stored in the freezer until enumeration. Bacterial enumeration was done via standard epifluorescence microscopy (1000x Magnification) (Hobbie et al. 1977; Dila and Biddanda 2015).

For bacterial abundance, only one group of sites out of six showed significant differences between sites by ANOVA, so sites were still grouped depending on surface or bottom and period in relation to hypoxia. All bottom groups were not normally distributed so they were compared using a Kruskal-Wallis and a post-hoc pairwise Wilcoxon signed ranks test with Holm's correction. Surface and bottom groups were compared using a paired Wilcoxon signed ranks test.

Chlorophyll a and Phycocyanin

To analyze the ability for major mixing events to initiate algal blooms, we compared near-surface chlorophyll and phycocyanin concentrations before and after the first major mixing event of the summer on 8/2/15. Chlorophyll *a* and phycocyanin from profiles were averaged for each site between 1 and 2 m, which encompasses the maximum concentration ranges for the water column. The sites and dates were pooled for before and after 8/2/15 and compared.

Fish

We collected fish using gill-nets at the Buoy location. The fish were caught in two 38.1 m long by 1.8 m tall experimental gill-nets, with 5 mesh sizes ranging from 2.54 cm up to 12.7 cm bar measure by increments of 2.54 cm (Sanders et al. 2011; Altenritter et al. 2013). Nets were deployed at approximately 8 a.m. and recovered 3 hours later. Fish were identified to species and total length measured. Nets were placed on the bottom of the northeast and southwest sides of the MLO at a depth of approximately 12m. Nets were always deployed with the smallest mesh size facing North for consistency.

Linear regressions were used to investigate the relationship of fish abundance, species richness, and maximum length to the lowest DO concentration measured in the water column during the day of sampling. Normality was tested using a Shapiro-Wilk test. Abundance and richness were not normal, but were square-root transformed and were then normally distributed. Maximum lengths were normal and linear regressions were performed accordingly. Regressions were considered significant at $\alpha < 0.05$.

Results

Nutrients

There were similarities and significant differences in SRP concentrations between the top and bottom samples, and this changed when hypoxia was or was not present (Fig. 2). SRP concentrations were highest in the bottom during hypoxia with a median of 0.0189mg L^{-1}, and lowest at the top during hypoxia when no sample was above the detection limit. Following the fall overturn, SRP concentrations in the top and bottom were relatively similar at 0.008 and 0.010 mg L^{-1}, respectively. A significant difference was found for the bottom SRP concentrations pre, during and post hypoxia ($\chi=9.0674$, df=2, p<0.05). Post-hoc testing revealed that pre and during concentrations were significantly different (p<0.01), while pre vs post and during vs post concentrations were not different. Pre-hypoxia (s=9, p<0.01) and during-hypoxia (s=26, p<0.001) concentrations were significantly higher at the bottom, but concentrations post hypoxia were no different top vs bottom.

Similar to SRP, TP concentration peaked in the bottom waters during hypoxia at 0.366 mg L^{-1}, while concentrations in the other 2 periods at the bottom and the 3 at the top were all similar. There were significant differences between the bottom TP concentrations during the

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three periods (χ=11.745, df=2, p<0.01), and bottom concentrations during hypoxia were found to be significantly higher than pre (p<0.01) and post hypoxia (p<0.05; Fig. 2). Pre and post hypoxia concentrations were not different. Bottom TP concentrations during hypoxia were found to be significantly higher than surface concentrations (V=48, p<0.001).

Contrary to what we expected, NH_3 concentrations in the surface waters during hypoxia were very similar to the bottom (0.167 mg L^{-1} and 0.193 mg L^{-1} median). The highest NH_3 concentrations (0.043 mg L^{-1}) occurred prior to hypoxia in the bottom. NH_3 concentrations indicated a significant difference when comparing pre, during, and post hypoxia (χ=9.3384, df=2, p<0.01). NH_3 concentrations were significantly higher in the bottom waters prior to hypoxia compared to during hypoxia (p<0.05), while pre-hypoxia concentrations were no different than post, and during hypoxia concentrations were no different than post hypoxia (Fig. 2). Prior to hypoxia, concentrations of NH3 at the bottom were higher than at the surface (V=4, p<0.001), but there were no differences between the surface and bottom during or post hypoxia.

TKN concentrations in the pre and post hypoxia periods were all relatively similar ranging from 0.429 to 0.493 mg L^{-1}. The highest concentration occurred in the surface waters during hypoxia (0.593 mg L^{-1}), which also created the biggest difference in surface and bottom concentrations between the three periods. In the bottom, there were no differences in TKN with relation to hypoxia with pairwise tests despite the Kruskal-Wallis test indicating a difference (χ=7.1177, df=2, p<0.05). Interestingly, surface TKN concentrations during hypoxia were actually higher than those of the bottom waters (V=401, p<0.001; Fig. 2). Comparisons between surface and bottom groups indicate that during hypoxia TKN concentrations were higher at the surface than at the bottom (V=401, p<0.001).

Bacterial Abundance

Bacterial abundances changed in the surface and bottom of Muskegon Lake throughout the summer. Median surface abundances pre and during hypoxia (903,300 and 946,300 cells mL^{-1}) decreased to 392,400 cells mL^{-1} in the post hypoxia period. Bottom bacterial abundance decreased consistently throughout the season from 662,200 to 550,100, to 368,900 cells mL^{-1}. When comparing pre, during, and post hypoxia bacterial abundances in the bottom waters, all three periods were significantly different from one another (χ=18.58, df=2, p<0.001). Pre was significantly higher than during (p<0.02), pre was significantly higher than post (p<0.001), and during was significantly higher than post (P<0.01; Fig. 3). Pre was the highest and post was lowest, with during falling between them. In the comparisons of top and bottom abundances, pre (V=109, p<0.01) and during (V=387, p<0.001) were both significantly different, while top and bottom were not different in the post hypoxia period.

Chlorophyll a and Phycocyanin

Three separate strong wind-events occurred on 8/2, 8/20, and 8/23-24, which homogenized the water column at the buoy location to the bottom-most sensors. The event on 8/23-24 led to a late summer turn-over event, whereby nearly the entire lake was mixed. The lake-wide average of phycocyanin concentrations (3579 $\pm$ 491 cells mL^{-1}) in the three samples (6/30, 7/15, 7/28) before 8/2 were significantly lower (W=0, P<0.001) than phycocyanin concentrations (11232 $\pm$ 760 cells mL^{-1}) afterwards (8/10, 8/26, 9/9; Table 1, Fig. 4). Chlorophyll *a* concentrations were not significantly different before (6.7 $\pm$ 0.3 µg L^{-1}) or after

(7.8 ± 0.5 μg L^{-1}) 8/2, and water temperatures also were also not significantly different prior to (23.8 ± 0.5 °C) or following (22.8 ± 0.4 °C) the 8/2 event (Table 1, Fig. 4).

Fish

The catch of benthic fishes in the vicinity of the MLO in Muskegon Lake changed drastically as seasonal hypoxia developed within the lake's hypolimnion. Total catch over the 11 sampling dates yielded 201 fish comprised of 11 different species. The overall most abundant fish species in the catch were yellow perch (*Perca flavescens*), spottail shiner (*Notropis hudsonius*), white perch, (*Morone americana*), and walleye (*Sander vitreus*) (Table 2). During peak DO on November 4, 2015, 67 fish comprised of 9 species were caught. This represented the highest abundance and species richness of all sampling trips. During the lowest period of DO, no fish were caught. This represented the lowest abundance and species richness of all sampling trips. Catch during hypoxia was almost entirely composed of yellow perch, with only three other species (white perch, walleye, and alewife) captured in low abundances under the same conditions. Fish total length also changed with decreasing DO (Fig. 5). Maximum fish lengths tended to decrease as hypoxia formed. In contrast, minimum fish size changed very little over the course of the season.

All regressions yielded significant relationships with DO. Benthic fish abundance near the MLO increased as DO increased ($p<0.001$, R^2=0.74, $F_{1,9}$=26.06, Abundance=0.6034(DO)+0.7763; Fig. 5). Species richness increased as DO increased ($p<0.001$, R^2=0.81, $F_{1,9}$=38.16, Number of Species=0.2570(DO)+0.4555; Fig. 5). Minimum fish length was fairly consistent across DO concentrations, ranging between 9 and 11 cm. Maximum

($p<0.00001$, $R^2=0.91$, $F_{1,9}=91.06$, Maximum Length=+0.2570(DO)+0.4555; Fig. 5) fish lengths increased as DO increased.

Discussion

Internal Loading of Phosphorus

SRP and TP were both significantly higher in the bottom in the summer hypoxia compared to the springtime during oxygenation. Although the bottom SRP concentrations of during hypoxia and post hypoxia were not statistically different, 17 of the 28 measurements during hypoxia were higher than the maximum concentration measured post hypoxia. This suggests that they might have been different if not for several extremely low concentrations caused by a Lake Michigan intrusion of low nutrient water and episodic wind mixing. This also is supported by the comparisons for TP that show during hypoxia, bottom TP concentrations were higher than pre or post hypoxia. While Steinman et al. (2008) also indicate that bottom water SRP concentrations were higher than surface in Muskegon Lake from 2003-2005, the same pattern is observed in 2015, although bottom SRP concentrations range much higher in the current study.

The high SRP concentrations of bottom waters during hypoxia suggest that even mild hypoxia is causing internal loading from the sediments or mineralization from algal decomposition. Rates of release of inorganic phosphorus from sediments are known to increase under low oxygen conditions, so the high SRP in hypoxic waters of Muskegon Lake come as no surprise (Zhang et al. 2010; Smith et al. 2011; Nürnberg et al. 2013). Typically, higher SRP release rates from sediments occur when the DO concentration in the overlying water is < 2 mg

L^{-1}, however studies have noted increased SRP concentrations in hypolimnetic water even when DO concentration 1 m above the sediment is 3-4 mg L^{-1} which is a common occurrence during the summer in Muskegon Lake. The sediments of Muskegon Lake are organically rich due to high productivity within the lake and supply from the Muskegon River, which means there is a lot of carbon to be respired, drawing down DO concentrations quickly (Marko et al. 2013; Dila and Biddanda 2015). Under these hypoxic conditions, SRP would be reduced and released from the sediments. Respiration and nutrient mineralization in the water column, specifically the hypolimnion, also may be a source of SRP, as water column respiration has been shown to be the main source of hypoxia generation in Lake Erie and The Gulf of Mexico (Conroy et al. 2011; McCarthy et al. 2013). Although several studies have indicated that summer is a period of high internal phosphorus loading in two nearby drowned river-mouth lakes (Steinman et al. 2004; Steinman et al. 2009), another indicates that there is relatively little internal load compared to external load in a different nearby lake (Steinman et al. 2006). More experiments using hypolimnetic water and sediment core incubations would be needed to further determine what the exact internal source of the SRP is in Muskegon Lake.

The patterns with the nitrogen species of NH$_3$ and TKN were less clear and seemed to not be related to hypoxia formation. We would expect the nitrogen form of NH$_3$ to increase similarly to reduced phosphorus SRP with hypoxia formation (Zhang et al. 2010). Unlike SRP and TP, NH$_3$ and TKN did not increase in concentration in the hypoxic period. In fact, surface TKN during hypoxia was actually higher in concentration than the bottom. While not all studies agree on the exact DO concentration at while P and N release from sediments, the suggested range goes from below 2 mg L^{-1} to below 0.5 mg L^{-1} (Mortimer 1941; Schön et al. 1993; Testa and Kemp 2012). All sites reached DO concentrations where N should have been released as well as

P. Other nitrogen species such as Nitrite-NO_2, Nitrate-NO_3 could be measured in the future - which could reveal more about the presently missing details in Nitrogen cycling under hypoxia.

Bacteria

We were unable to see a change in bacterial abundance as a result of hypoxia formation in the hypolimnion. Pre-hypoxia abundances were different between surface and bottom groups, as were during-hypoxia abundances. The average abundance of bacteria in bottom waters from pre to during hypoxia did decrease, although the statistical comparison indicates this was not significant. We expected to see bacterial abundance decrease when more anaerobic bacteria become numerous compared to aerobic bacteria, but we did not see this. In fact, the bacterial abundance was significantly lower for both surface and bottom groups from the post hypoxia period when compared to the pre and during hypoxia periods. Surface abundances across all seasons were similar to that seen by Steinman et al. (2008) for Muskegon Lake.

The similarity in bacterial abundances in pre and during hypoxia periods suggest that the bacterial community in the spring already has the potential to decrease bottom waters to hypoxic levels; however, spring mixing and lack of stratification continually supply the bottom with DO. This may explain why DO in the hypolimnion immediately starts to decrease following even weak thermal stratification. Their pre and during hypoxia bacterial abundance similarity is also puzzling considering the high productivity in the surface waters during the summer (Weinke et al. 2014; Dila and Biddanda 2015). However, it's possible that there is enough excess algal production in the surface waters that sinks to the bottom to be decomposed. The bacterial abundance during summer at the surface is roughly 36% higher than at the bottom, which

suggests perhaps much of the bacterial processing of algal production occurs in the surface

waters. About 60% of surface algal production was estimated to have been broken down in

Morgan et al. 2006. Thus, the high bacterial abundance in the surface waters during the summer

is logical, as many other systems have noted higher abundance in the oxic surface waters

(Morgan et al. 2006; Zaikova et al. 2010). Perhaps enough surface production is sinking down to

fuel the hypolimnetic bacterial community since chl *a* has been shown to be a predictor of the

BOD that depletes DO to hypoxic levels (Mallin et al. 2006). Although the current study did not

attempt to evaluate if there was a change in the bacterial community composition as a response

to hypoxia, other studies have shown that the hypolimnetic bacterial community does transition

to more hypoxia and anoxia tolerant species (Crump et al. 2007; Zaikova et al. 2010). In Lake

Tahiu, China, the bacterial community composition changed along with dissolved oxygen, and

was dominated during hypoxic times by different species than during pre or post hypoxic times

(Li et al. 2012). These species are evne suspected to be related to decomposition of *Microcystis*.

Cyanobacterial Blooms During and Following Major Mixing Events

Despite the slight increases in phycocyanin through July before the August mixing

events, there were significant differences between the phycocyanin concentrations of the three

sampling periods before the 8/2/15 event and the three sampling periods following. Surface

scums of *Microcystis* were not visible on Muskegon Lake until the August and September

sampling trips.

We investigated several possible causes for the cyanobacterial blooms to form, such as

temperature, runoff of nutrients from the river, and entrainment of hypolimnetic nutrients due to

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mixing events (Paerl and Huisman 2008; Nürnberg et al. 2013). Cyanobacteria often bloom under warm water conditions that prevail in the late summer (Paerl and Huisman 2008); however, a comparison of the air temperatures measured by the MLO from before and after the 8/2/15 wind event shows no significant change in air temperature. In fact, several of the wind events that occurred in August were accompanied by ~10°C drops in air temperature. In order to evaluate the influence of nutrients delivered by the river, we looked at the surface nutrient concentrations. There were no visually obvious trends of increasing surface nutrients that were worth investigating for the four nutrient species measured that would help fuel a cyanobacterial bloom.

The last and most plausible cause of the cyanobacterial bloom was wind induced mixing events. It is important to note that wind mixing has often been cited as the algal equalizer, because the buoyancy control by some cyanobacteria cannot overpower wind mixing (Huisman et al. 2004). During periods of high wind, cyanobacteria are circulated and mixed throughout the water column. However, this is only effective if the mixing is continuous. Periodic mixing of the water column can be ineffective at mitigating cyanobacterial blooms (Jöhnk et al. 2008). Nutrients, specifically phosphorus in freshwater systems, are regenerated in bottom waters during hypoxia through decomposition/mineralization and anoxic sediment release (Paerl et al. 2011; Nürnberg et al. 2013). These nutrients that are normally isolated in these bottom waters due to stratification, can then be mixed into the surface waters during strong episodic mixing events – fueling surface blooms (Kamarainen et al. 2009; Crockford et al. 2014).

While no obvious trends of decreasing nitrogen species occurred in the bottom waters in the study following the strong mixing events of August, both SRP and TP show decreases in the bottom waters at the two shallowest sites, East and Buoy, on the eastern side of the lake. MLO

water profile data from the Buoy site indicate that the thermocline was significantly deepened by these mixing events, especially the event over the course of 8/23 and 8/24 that kept the thermocline around 10 m for a few days. Studies of thermal profiles from the East and Buoy locations indicate that through August into early September, the thermocline was almost 10 meters deep. Thus the wind mixing events caused significant mixing and deepening of the thermocline at the East and Buoy locations, leading to a decrease in bottom SRP and TP. These nutrients were potentially mixed into the surface waters during the wind-events, supplying the needed limiting phosphorus for cyanobacteria to bloom (Kamarainen et al. 2009; Nürnberg et al. 2013; Crockford et al. 2014). Due to the fact that surface SRP decreases in the summer to undetectable levels, while nitrogen species stay the same or increase, we can hypothesize that the surface algal community is P-limited. This only increases the important of episodic supplies of phosphorus-rich water to a phosphorus-limited system,

Additionally, there were only a few weaker wind-events that occurred between or after the 3 significant ones noted here. This gave the cyanobacteria calm periods between the wind events, enough time for them to rise back to the surface and continue to bloom. Calm conditions following wind-events are especially important to allow the cyanobacteria to bloom (Paerl and Huisman 2008; Paerl and Otten 2013), which further strengthens the notion that while mixing events do spread cyanobacteria throughout the water column and bring some DO to the hypoxic waters, temporary mixing may be ineffective at mitigating HAB's and hypoxia (Jöhnk et al. 2008).

Disappearance of fish from the hypolimnion

Overall there was a dramatic difference in the abundance, species richness, and size of benthic fish that were caught in the hypolimnion near the MLO during hypoxia compared to

before or after hypoxia. Although we only caught fish at one relatively deep location in Muskegon Lake, there was a strong correlation between DO and benthic fish presence in the hypolimnion. DO profiles at the other three locations in the lake show similar hypoxic conditions throughout the summer. Given these observations, we expect a similar pattern of lake-wide summer migration of benthic fish out of the hypoxic hypolimion, which is similar to what was reported for juvenile lake sturgeon in Muskegon Lake (Altenritter et al. 2013).

Many other studies have examined fish behavior, mostly those of economic importance, to hypoxia and found similar results. In a laboratory experiment using chambers and gradients of DO saturation, largemouth bass (*Micropterus salmoides*) actively avoided low saturations of DO (Burleson et al. 2001), which is comparable to the species seen in Muskegon Lake. The study also showed that smaller fish stayed in lower DO than larger fish that stayed in higher DO water (Burleson et al. 2001). Our results also indicate that smaller fish inhabit lower DO water, and that longer fish prefer high DO. While numerous laboratory experiments have shown that fish avoid hypoxic water (Burleson et al. 2001), there are also *in situ* observations that corroborate these results. Tagged largemouth bass in tributaries of the Chowan River on the US east coast, were shown to avoid water less than 1.8 mg L^{-1} (Brown et al. 2015). In the Neuse River Estuary in North Carolina, Atlantic Croaker *Micropogonias undulatus* were found to avoid hypoxic waters that compressed their habitat to shallow, warm, oxygenated waters (Eby et al. 2005). This compression can be vertical as well as horizontal, as trawls in Lake Erie indicate that fishing along the edge of a hypoxic zone results in a higher catch (Kraus et al. 2015). The need to actively avoid hypoxia showed that the bay anchovy *Anchoa mitchilli* occupied shallower waters, which isolated it from its preferred zooplankton prey that could tolerate the hypoxic conditions.

The benthic fish in Muskegon Lake could also move upwards or horizontally to avoid hypoxia. Sampling fish communities in the mid-water column would provide more information on the potential for benthic fishes to simply move vertically to avoid hypoxia. At the Buoy location, there is a nearby shelf immediately to the west that is only a few meters deep, and may provide a refuge via horizontal migration. Lake sturgeon (*Acipenser fulvescens*) in Muskegon Lake are known to migrate from the deeper portions of the lake to the shallower mouth of the Muskegon River during the summer, so horizontal migration has been seen before in Muskegon Lake (Altenritter et al. 2013). With so many options available for hypoxia-sensitive fish to go, the change in species and abundances seen at the Buoy, possibley reflects a change in fish distribution as opposed to a change in the fish community as a whole.

There have been relatively few studies looking at the response of benthic fish species compositions to hypoxia in freshwater systems or estuaries. A study by Eby and Crowder (2002) showed that all 10 species they looked at avoided DO less than 2 mg L^{-1} in the Neuse River Estuary. Interestingly, they also found that their avoidance of hypoxia was context dependent, because when hypoxia was spatially expansive fish would go into the hypoxic zone. Similarly, we only captured one species, yellow perch when the DO was less than 2 mg L^{-1}, but these were in extremely low abundances compared to well-oxygenated times. In a study done in Mercer Bayou, Arkansas, fish species richness, abundance, and size were all significantly reduced at DO concentrations < 0.5 mg L^{-1} (Killgore and Hoover 2001).

One of the more interesting findings from the fish catches was that yellow perch was the only species found in the hypoxic waters below 2 mg L^{-1} and was the most abundant species overall. Previous studies have found that in the wild, yellow perch avoid waters below 2 mg L^{-1}, and in the laboratory, consumption of food and overall growth decreases in hypoxic water

(Roberts et al. 2009; Roberts et al. 2011). In the current study, one yellow perch was caught in our study when the DO was less than 2 mg L^{-1}, while 24 were caught when the DO was between 2 and 3 mg L^{-1}. This suggests than indeed 2 mg L^{-1} is an acceptable definition of hypoxia for Yellow Perch. As to why a yellow perch was caught in water less than 2 mg L^{-1}, one study in Lake Erie showed that although yellow perch avoid hypoxia, some make frequent dives into hypoxia in order to feed on benthic macroinvertebrates (Roberts et al. 2009). This could also explain why even so many yellow perch were caught in 2-3 mg L^{-1} water, considering only three other species (3-white perch, 1-walleye, 1-alewife) were captured when DO was that low. Muskegon Lake appears to be an important site for yellow perch, even during times of mild hypoxia (DO < 4 mg L^{-1}) when all other fishes avoided this zone at the MLO. Additionally, another study on fish communities in Muskegon Lake also found yellow perch to be the most abundant species in the littoral areas (Bhagat and Ruetz 2011). Their studies also show a significant decrease in littoral yellow perch abundance in the summer, ~25% of the abundance of either spring or fall, as well as in length range (Bhagat and Ruetz 2011; Janetski et al. 2013). Considering yellow perch have been show to migrate either horizontally or vertically to avoid hypoxia in Lake Erie, decreases in yellow perch abundance in both the benthic and littoral areas of Muskegon Lake suggest that they may occupy the limnetic/pelagic areas above the hypoxia in open water (Roberts et al. 2009).

Conclusion

There are many changes that occur in the bottom waters Muskegon Lake as a result of the development of summertime hypolimnetic hypoxia. We observed a drastic change in the benthic fish assemblage near the MLO that can be correlated with low dissolved oxygen concentrations

such as decreases in abundance, species richness, and size. There appears to be internal loading of phosphorus in bottom waters during hypoxia, however the same cannot be said for nitrogen. It is also possible that these phosphorus rich waters can be entrained to the surface, during episodic wind mixing events, which would provide cyanobacteria the fuel to continue the bloom that started during an initial calm, warm period. While bacterial abundance did not show a pattern with respect to hypoxia, further work should be done to characterize the bacterial community to identify which, if any, changes occur in species and abundances of specific species.

Although hypoxia may be an entirely natural feature of many freshwater systems, it is becoming increasingly more common and increasing in severity (areal and volumetric) as nutrients accumulate at confluences of watershed and global climate change strengthens thermal stratification. Conditions that promote internal loading of nutrients and global climate change are only continuing to accelerate, making it difficult for Earth's freshwater systems to recover. Despite potential reductions of external loads of nutrients, internal loading and climate change could allow unnatural levels of hypoxia to persist for years (Allan et al. 2012). This could have many consequences for the entire ecosystem from nutrient cycling to primary production, and bacteria to fish.

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Figure Legends

Figure 1. (Left) Map of the Great Lakes region with arrow pointing to the location of Muskegon Lake, Michigan. (Right) Bathymetric map of Muskegon Lake, Michigan with three green rings indicating the basin sampling and red ring for the Muskegon Lake Observatory (MLO) locations with site name and approximate depths. Boxes with white arrows indicate tributaries to Muskegon Lake.

Figure 2. A) Soluble Reactive Phosphorus (SRP), B) Total Phosphorus (TP), C) Ammonia (NH_3), and D) Total Kjedahl Nitrogen (TKN), concentrations in Muskegon Lake. Groups are representative of all four sites by time in relation to hypoxia (pre, during, and post) and location of sample in the water column (surface or bottom).

Figure 3. Bacterial abundance in surface and bottom waters in relation to hypoxia.

Figure 4. 1-2 m average A) Chlorophyll and B) Phycocyanin concentrations from 3 sample dates before and after the 8/2/2015 mixing event.

Figure 5. Linear regressions of A) fish abundance (total catch), B) number of species, and C) maximum length, against dissolved oxygen concentration in the hypolimnion of Muskegon Lake, Michigan.

Table 1: Water Temperature, Chlorophyll *a*, and Phycocyanin averages from 1-2 m depth duing summer 2015 in Muskegon Lake, Michigan. White dates are prior to a series of major wind-events during August, while shaded dates are during and after the wind-events.

	Temperature (°C)	Chlorophyll ($\mu g\ L^{-1}$)	Phycocyanin (cells mL^{-1})
6/30	21.7	6.0	1952
7/15	23.3	7.4	3983
7/28	26.1	6.9	4801
8/10	23.9	9.7	12369
8/26	21.1	7.4	10749
9/9	23.3	6.4	10578

Table 2: Dissolved oxygen concentration and fish caught in experimental gill nets on different sampling dates during 2015 in Muskegon Lake, Michigan at approximately 12 m depth.

|	6/17	6/30	7/15	7/28	8/10	8/26	9/9	9/23	10/5	10/23	11/4	Total Catch Per Species
Dissolved Oxygen (mg L^{-1})	5.65	2.65	4.26	3.13	1.43	2.58	0.65	2.6	8.78	9.93	10.09	
Yellow Perch (*Perca flavescens*)	28	14	10	5	1	4		6	1	4	16	89
Spottail Shiner (*Notropis hudsonius*)	3								2	9	19	33
White Perch (*Morone americana*)	1					2		1	4	12	8	28
Walleye (*Sander vitreus*)								1	1	1	15	18
Alewife (*Alosa pseudoharengus*)								1	1		6	8
Channel Catfish (*Ictalurus punctatus*)									2	5	1	8
Freshwater Drum (*Aplodinotus grunniens*)									2	4	2	8
Northern Pike (*Esox lucius*)	2								2	1	1	6
White Sucker (*Catostomus commersonii*)	1											1
Longnose Gar (*Lepiosteus osseus*)										1		1
Smallmouth Bass (*Micropterus dolomieu*)										1		1
Total Catch Per Date	35	14	10	5	1	6	0	9	15	37	69	201

Figure 1
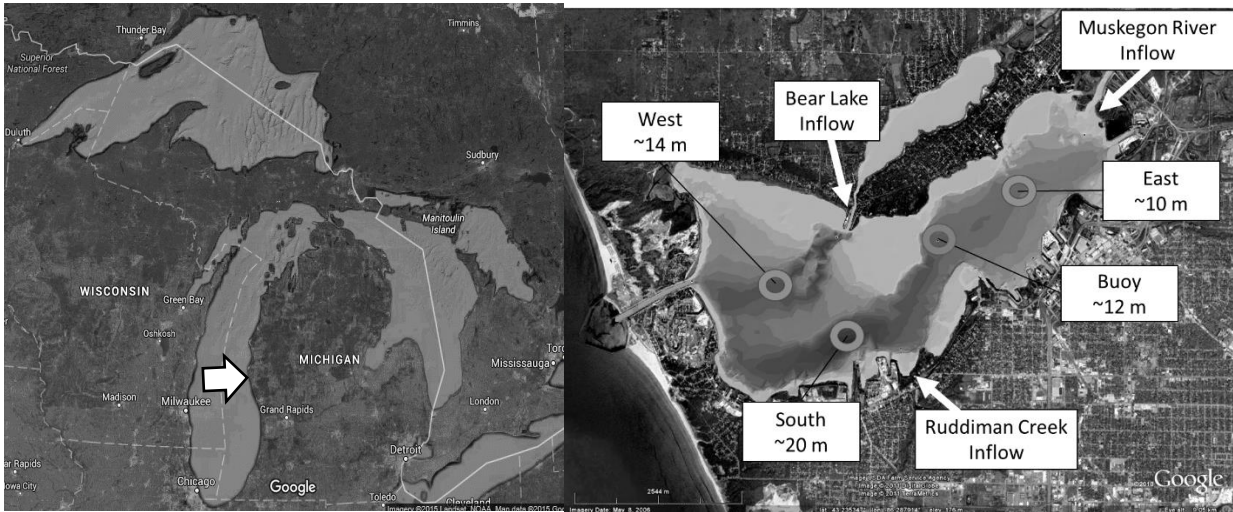
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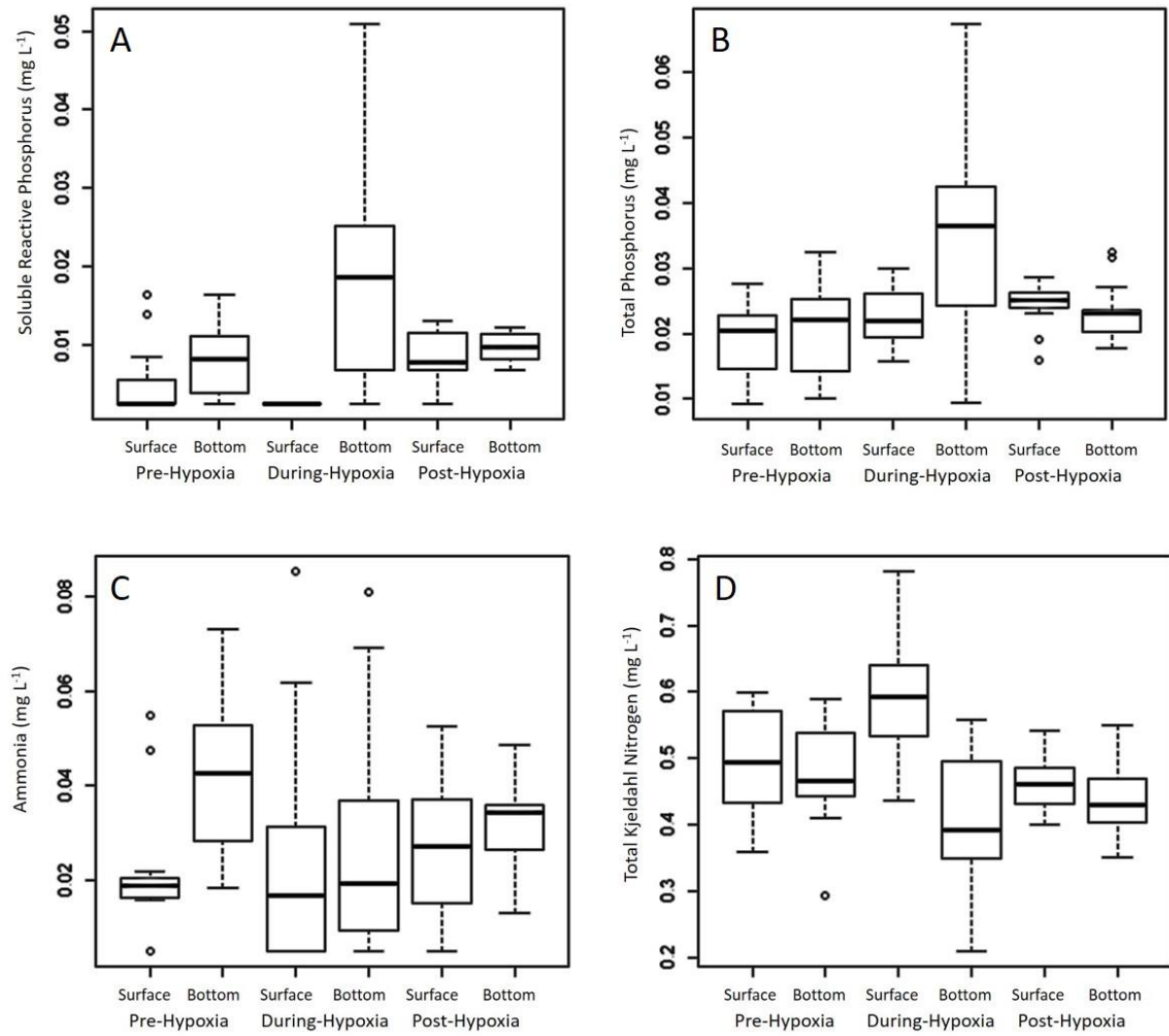
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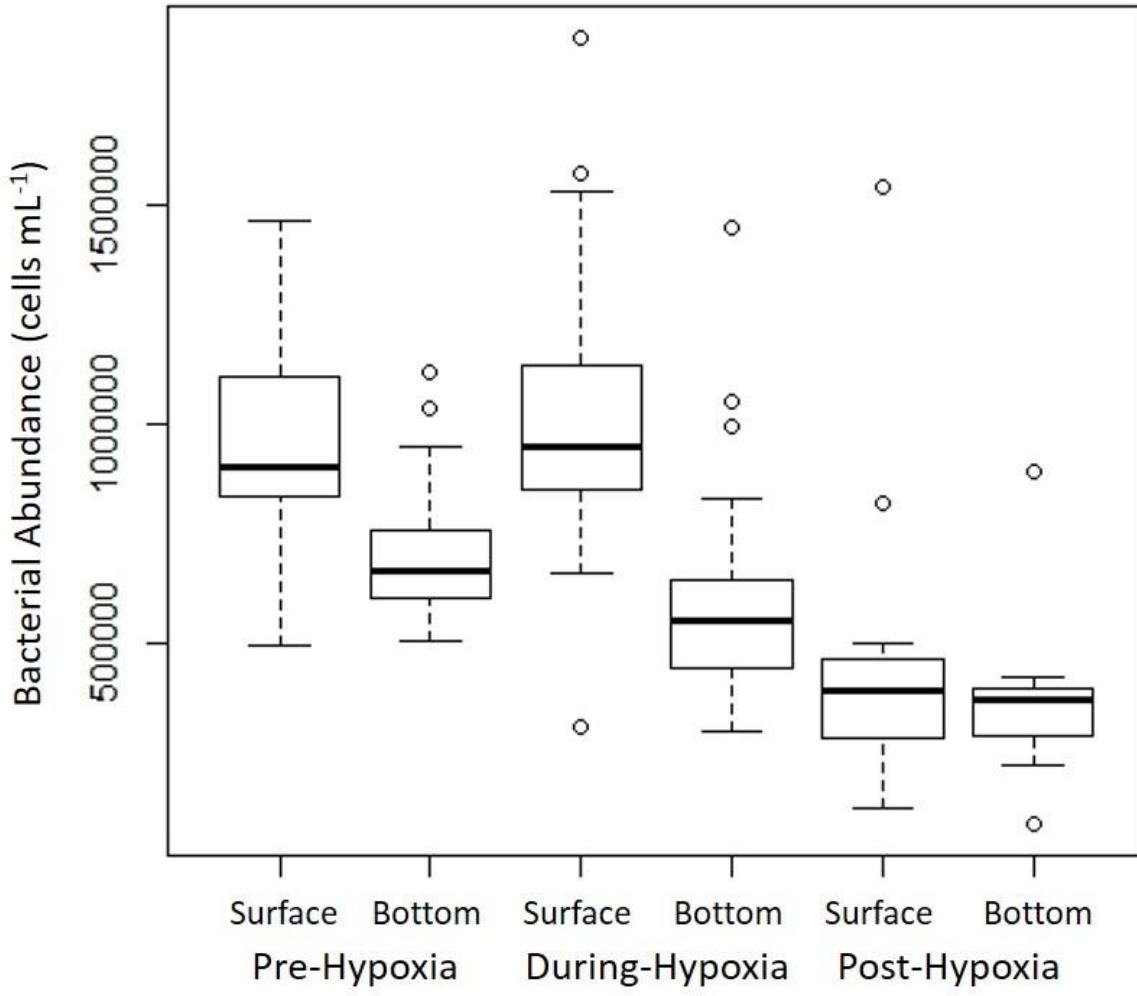
Figure 4

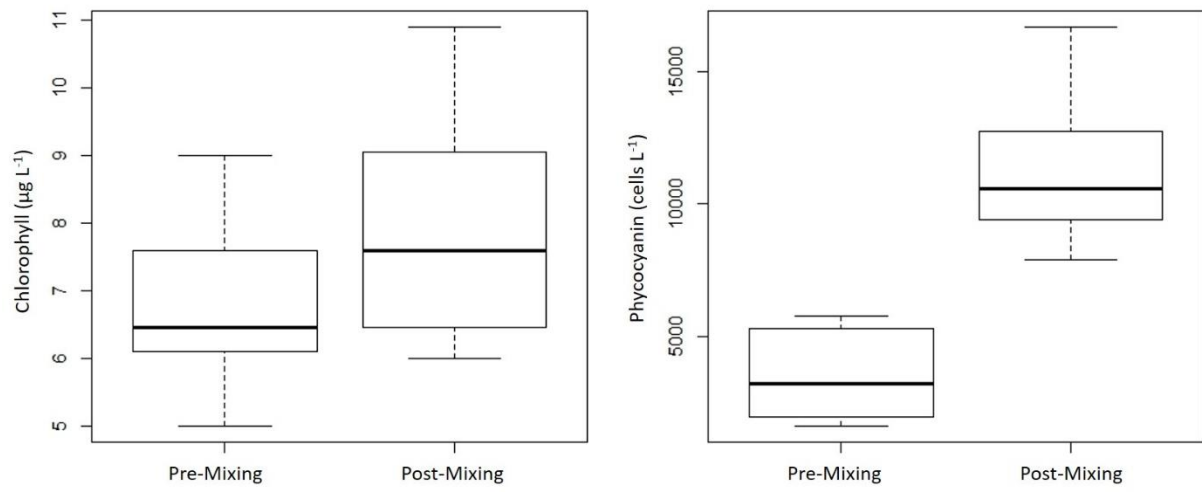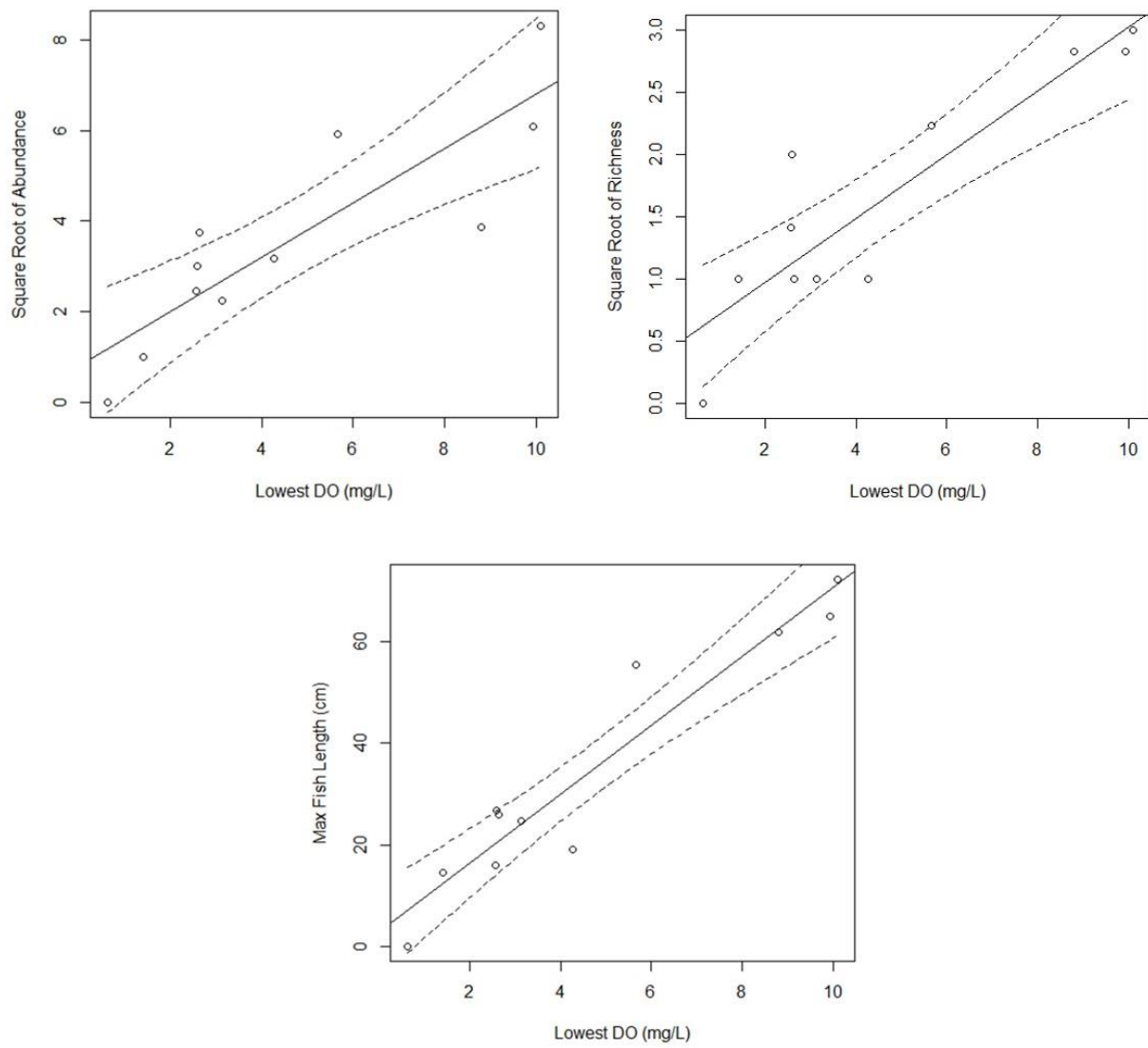Figure 5

Chapter 3

Extended Literature Review

A Review of Hypoxia in Lakes: Development, Effects, Disruptions

Abstract

In modern times, human influence has put stress on the environment, and changed the way it functions. While is it easy to see the influence on the land through deforestation and cities, the issues caused in lakes are harder to identify as we can only see so deep. One of the most important problems facing our lakes today is low oxygen in the bottom waters (hypolimnetic hypoxia). Humans have intensified hypoxia in recent times through eutrophication and global climate change. Hypoxia has significant consequences on the food web, from the smallest bacteria and phytoplankton up to zooplankton and fish. Attempting to control and reverse hypoxia is a difficult job once a lake has settled into that state and may take many years of remediation to recover. From all of the research done on the causes and effects of hypoxia, we can draw inferences about other lakes where we suspect or know hypoxia occurs.

Introduction

Role of Lakes

Due to their relatively small size compared to the oceans, lakes have received comparatively less attention for their role in global nutrient cycles (Cole et al. 2007). However, inland freshwater systems play an extraordinary role in regional and global cycling. Inland lakes and rivers significantly change the amounts and types of material that are transported from land to lake (Marko et al. 2013). For example, research indicates that our inland freshwaters process

nearly half of the carbon that they receive from the terrestrial ecosystem, which shows that they play a disproportionately important role in the global carbon cycle (Cole et al. 2007).

More recently, the large role that lakes and rivers play is being altered through anthropogenic pressure in many ways. Arguably, the most pressing issues impacting our inland waters are eutrophication and climate change, and these are taking place largely because of human development (Jenny et al. 2016). Serving as sentinels of change, our inland waters allow us to see what is happening, because the content of a lake represents the influence of an entire watershed and regional climate (Williamson et al. 2009). Williamson et al. (2009) makes the argument that lakes can tell you about what has happened, is happening, and projected to happen in the climate and watershed based on the data gathered from a lake. From data collected in the past few decades we can tell that lakes are suffering as a result of eutrophication and global climate change, and one of the main ailments is aquatic hypoxia.

What is Hypoxia?

Aquatic hypoxia is when the concentration of dissolved oxygen in the water fall below a threshold. Generally, this occurs in the bottom waters of a lake when excess organic matter in the epilimnion sinks to the hypolimnion and is decomposed by bacteria. The issue with decomposition in the hypolimnion is that there is only respiration occurring, without inputs of oxygen from photosynthesis. Also, if a lake has a defined epilimnion and hypolimnion, then the lake will be stratified with limited mixing and inputs of oxygen to the bottom from the top. So oxygen is consumed through respiration with little input, leading to depletion in the hypolimnion (Diaz 2001).

Up to this point the word hypoxia has been used to talk about low oxygen, but there are actually two different terms relating to low oxygen conditions. The thresholds that are set by these two terms change depending on which literature you are looking at. The first and most extreme is "anoxia". The term anoxia really means zero oxygen, but in some literature anoxia is defined as below 1-2 mgO_2 L^{-1} (Nürnberg 2004). The definition of "hypoxia" is even more arbitrary, because the term is reserved for defining low oxygen conditions tailored to the specific water body that is undergoing study (Nürnberg 2004). Thresholds of hypoxia range from 2 mg O_2 L^{-1} (Diaz 2001; Zhou et al. 2013), 3 mgO_2 L^{-1} (Ludsin et al. 2009), to 4 mgO_2 L^{-1} (Altenritter et al. 2013). For the purposes of this review, the term "hypoxia" will be used to describe generally low oxygen conditions.

Considering that hypoxia is becoming increasingly common around the world (Diaz and Rosenberg 2008; Jenny et al. 2016), these areas are receiving increased attention to quantify and compare aspects of their hypoxia (Nürnberg 2004). Every lake is different, so indeed lakes vary with respect to how they develop and sustain hypoxic conditions. Thus, various calculations have been performed to standardize and compare lakes through such terms as the hypoxic factor (HF) (Nürnberg 2004), which indicates the hypoxic extent on an areal and temporal basis in a lake, and volumetric or areal hypolimnetic oxygen demand (VHOD or AHOD) (Matthews and Effler 2006; Foley et al. 2012), which indicates the rate of depletion of oxygen in the hypolimnion on a volumetric or areal basis respectively.

Causes of Hypoxia

Eutrophication

The first ingredient of hypoxia is eutrophication, which occurs mainly through excess nutrient additions. These nutrients can come from a variety of sources such as agriculture, lawn fertilization, and sewage (Scavia et al. 2014?). Although phosphorus is the main nutrient of concern in freshwaters, nitrogen is of concern as well considering many cyanobacteria that are becoming more common are not nitrogen fixers (Paerl et al. 2011; Scavia et al. 2014). When the excess nutrients are added to the water, they bloom until the nutrients are used up. Once the bloom is no longer sustainable, many will die and those who are not recycled at the surface sink to the bottom and are decomposed or buried in the sediments (Paerl and Huisman 2008). When there is an excess of organic matter to be broken down in the hypolimnion, there will be a constant drawdown of oxygen. With little input of oxygen from surface waters, hypoxia is allowed to persist (Diaz 2001).

There are a few other things to consider with the detection and future of eutrophication as it relates to hypoxia in our waters. Research has shown that large watersheds and the concentration of phosphorus that comes from them, are positively correlated with rates of production and respiration in the receiving waters (Hoellein et al. 2013). Also, with eutrophication almost inevitably comes cyanobacterial blooms. Eutrophication has been found to promote the growth of cyanobacteria, and this causes problems on two fronts (Paerl and Huisman 2008). Firstly, as previously discussed, blooms will eventually sink and be decomposed in the bottom (Havens 2008). This further worsens the hypoxia situation and leads to internal loading of nutrients, which will be discussed in detail later. Secondly, some cyanobacteria such as *Microcystis* also produce toxins that are harmful to the water supply (Paerl and Otten 2013). In the future, all of these problems could become worse as global climate change increases the intensity of rain events. More intense rain events could create situations

where the land cannot absorb sudden large inputs of water, so many nutrients run off the land into the lakes and streams (Michalak et al. 2013). This would give the aquatic system a sudden input of nutrients that had little chance to be used within the terrestrial ecosystem, exacerbating eutrophic conditions (Sahoo et al. 2011).

Stratification and Global Climate Change

Thermal stratification is the other main ingredient that hypoxia needs in order to develop and persist (Diaz 2001). Increased temperatures, mainly during the summer, warm the epilimnion of the lake and create a stabilized thermocline (Paerl and Huisman 2008). The thermocline essentially helps to isolate the hypolimnion from the epilimnion (Foley et al. 2012). When the hypolimnion is isolated from mixing with the well oxygenated epilimnion, the consumption of oxygen by bacteria draws down dissolved oxygen to hypoxic levels (Nürnberg et al. 2013).

While warmer summer temperatures will lead naturally to thermal stratification in the majority of lakes, the strength of stratification is increasing due to warmer air temperatures that create a stronger thermocline and associated issues. Lake Tahoe is just one example of a lake that has become more resistant to mixing in recent years due to warmer temperatures (Sahoo et al. 2011). Research also has shown that the hypoxic season in lakes has increased as a result. The onset of stratification is coming earlier and the fall overturn is coming later, which increases the hypoxic season (Foley et al. 2012). Additionally, increased water temperatures have an effect on the solubility of oxygen and metabolic rates. Warmer water holds less oxygen, so when the lake does manage to mix, less oxygen in transported down into the hypolimnion, thus

hypoxia sets up faster (Sahoo et al 2011). Increased metabolic rates through increases in temperature cause dissolved oxygen to be used up faster as well.

Conditions characteristic of summer, such as increased temperatures and decreased water column mixing, favor cyanobacteria over other types of phytoplankton (Jöhnk et al. 2008). Cyanobacteria are better adapted to dealing with elevated temperatures than other competitors (Paerl and Huisman 2008). Reduced mixing promotes the growth of cyanobacteria as they grow best in stable, warm conditions (Paerl and Huisman 2008). Increased water residence time, which typically occurs during the later summer months, also has been shown to assist the growth and blooms of cyanobacteria (Paerl and Otten 2013). Cyanobacterial blooms can potentially play a huge role in the development of hypoxia too (Havens 2008). The blooms form large pools of dissolved organic carbon, which fuel a large portion of bacterial metabolism when released upon cell death (Paerl and Otten 2013). The accelerated bacterial metabolism not only can consume oxygen in surface waters, but in the hypolimnion as well. All in all, the tops and bottoms of lakes are intimately connected to one another despite separation by the thermocline.

Effects of Hypoxia

Internal Loading

One of the primary effects that hypoxia has on a lake is that it can help to enrich the lake with nutrients from within (Nürnberg et al. 2013). Under normal oxygen conditions, nutrients like nitrogen and phosphorus are oxidized and bound to metals in the sediment (Smith et al. 2011). However, under hypoxic conditions, nitrogen and phosphorus are reduced and released into the water column (Nürnberg and Peters 1984). Once reduced and released, they are

accessible in the water as the highly bioavailable forms of nitrogen and phosphorus (Testa and

Kemp 2012).

During the summer hypoxia when mixing is limited, these nutrients can build up in the

hypolimnion of a lake. Research on Muskegon Lake, Michigan has shown that during the

summer, levels of total phosphorus are greater than during the spring or fall (Steinman et al.

2008). Also during this time, Muskegon Lake shows higher levels of soluble reactive

phosphorus (SRP) in the hypolimnion compared to the epilimnion, which indicates a buildup of

SRP in the bottom and that the available SRP in the surface is rapidly used up and converted into

other forms. Nutrient examinations of Chesapeake Bay, which demonstrates a gradient of

hypoxia from land to ocean, shows that there is also a gradient of bioavailable nutrients along the

same gradient. In hypoxic areas, they observed higher measurements of ammonium and SRP but

just the opposite in oxic areas (Testa and Kemp 2012). A discussion of how these nutrients reach

the surface will be discussed later on.

Zooplankton

Normally, organisms such as zooplankton that operate primarily by aerobic means will be

negatively affected by hypoxia; however, this may not always be the case. Depending on the

species, they have varying survival in hypoxic zones. Goto et al. 2012 found that 50% of

Daphnia mendotae died within 4 hours of being in hypoxic waters, which indicates a very

limited tolerance to hypoxic conditions. On the other hand, *Daphnia pulcaria* seem to be

unaffected by hypoxia, as they will go into a hypoxic hypolimnion if there is more food available

than in the epilimnion (Larsson and Lampert 2011). Similar results have been seen in the

mesozooplankton of Chesapeake Bay (Ludsin et al. 2009). Although some can tolerate the

hypoxia for some amount of time, there are many negative consequences for living in cold

hypoxic water such as reduced reproduction, growth, and feeding rates (Larsson and Lampert

2011).

Fish

Similar to zooplankton, fish have varying responses to hypoxia. Many fish will actively

avoid hypoxia by either swimming towards the shore or positioning themselves just above the

hypolimnion (Ludsin et al. 2009; Larsson and Lampert 2011; Roberts et al. 2011; Altenritter et

al. 2013). Laboratory based experiments and in-situ studies also have shown that largemouth

bass (*Micropterus salmoides*) will actively avoid hypoxia (Burleson et al. 2001; Brown et al.

2015). Along a gradient of dissolved oxygen concentrations, larger largemouth bass will stay in

higher dissolved oxygen water, whereas smaller largemouth bass will live in lower oxygenated

waters (Burleson et al 2001). Avoidance of hypoxia happens for good reason as there are

numerous negative effects on fish. Yellow perch (*Perca flavescens*) food consumption and

growth rates decline in hypoxic zones (Roberts et al. 2011), and hypoxia also has been shown to

act as a teratogen and endocrine disruptor, which has consequences for fish reproduction and

embryonic development (Wu et al. 2003; Shang and Wu 2004). Fish that cannot escape the

hypoxia are likely to die, as seen with the collapse of benthic-dwelling fish populations in the

Black Sea (Mee 1992). Some fish show behavior or adaptations to deal with hypoxia though

(Xiao 2015). Yellow perch in Lake Erie will take short trips into the hypolimnion in order to

feed on benthic food sources (Roberts et al. 2009). Some other species of fish that may more

commonly experience hypoxia have special adaptations to live in hypoxic waters, such as "rough" fish like carp and catfish (Killgore and Hoover 2001; Xiao 2015).

Food Webs

All of the effects, behaviors and adaptations to hypoxia shape the communities in which they live. Species richness in fish communities has been found to decrease along a gradient of normoxia to hypoxia in a vegetated impoundment (Killgore and Hoover 2001). The diel vertical migration of planktivorous fishes in Chesapeake Bay is constrained by hypoxia, so that they can only occupy the epilimnion or the shore. This can be beneficial or harmful to fish and zooplankton though. In a laboratory experiment with fish and zooplankton in the same tank, fish avoided the hypoxic water while zooplankton used the hypoxia as a refuge (Larsson and Lampert 2011). A similar situation occurs in Chesapeake Bay between the planktivorous fishes and their mesozooplankton prey (Ludsin et al. 2009). Hypoxia can actually limit the interactions of the predator fish and prey zooplankton, which is harmful to the fish and improves the survivorship of the zooplankton. However, if zooplankton are also intolerant of hypoxia, then they are concentrated in the epilimnion with their predators (Goto et al. 2012). This reduces their survival and average body size as smaller individuals are favored under heavy predation conditions.

Role of wind events

While it may seem like mixing events that bring oxygen down to the hypolimnion would be good for a lake and its organisms, mixing events can actually make conditions worse. Mixing

can bring nutrients from the bottom (Nürnberg et al. 2013) to fuel further blooms of algae in three ways that will be discussed in detail here. The three are episodic wind events/entrainment, benthic resuspension, and seasonal overturn.

Episodic Wind Events

Even though stratification acts as a barrier to mixing and has become stronger in recent years, there are still episodic wind events during the stratified season that can temporarily break down and deepen the thermocline (Jennings et al. 2012). While Testa and Kemp (2012) say that the nutrients must be transported upwards without bringing oxygen down to the hypoxic zones, data from Muskegon Lake show how nutrients can be transported upwards without relieving hypoxia for any significant amount of time (Bopi Biddanda, personal communication). In mixing events on Muskegon Lake, hypoxia is relieved for only less than a day before low oxygen conditions return, while nutrients are presumably mixed into the epilimnion in the process possibly leading to blooms (Chapter 2.1). Other studies indicate that summertime deep-mixing events may become more common as weather becomes more episodic, and that they may offset the reduction of external nutrient loads (Crockford et al. 2014).

A similar mixing situation has been studied in Lake Mendota, Wisconsin. In a study of where phytoplankton derive their phosphorus during the summer, Kamarainen et al. (2009) looked at mineralization and entrainment. They found that mineralization was enough to sustain phytoplankton populations, but entrainment was also important to consider in order to meet phosphorus demand when episodic algal blooms occurred. The problem with these mixing events is that even though they temporarily supply the bottom with oxygen, the phytoplankton are supplied with an excess of SRP. The excess leads to an increase of overall biomass and an increase of phosphorus uptake by the phytoplankton. On this luxury uptake, the phytoplankton

can sustain a bloom for one to two weeks. While one bloom may be fine, if another mixing event occurs within that two weeks then blooms can potentially sustain for long periods of time. It is important to note that although wind-events can supply the surface waters with nutrients, an extended calm period is necessary to give cyanobacteria the competitive advantage over other types of phototrophs (Jöhnk et al. 2008).

Benthic Resuspension

Another type of episodic input of nutrients is "benthic resuspension", whereby strong storms create turbulence near the shore and then currents carry water with suspended shoreline sediment out to deeper waters (Cotner et al. 2000). The suspended sediments typically contain high levels of organic and inorganic nutrients relative to the surface waters (Cotner et al. 2000). Due to the light that is blocked by the sediment particles, heterotrophic bacterial growth decouples from autotrophic phytoplankton growth, because the bacteria have a source of food that doesn't have to come from the phytoplankton (Cotner et al. 2000). However, when phytoplankton are relatively nutrient starved, resuspension events can also stimulate their production despite less light availability (Kerfoot et al. 2008). This has also been shown to stimulate the growth of zooplankton, possibly explaining how they survive through winters with low food availability (Kerfoot et al. 2008). Research has also shown that the currents that carry suspended sediment offshore can also be transporting nutrient rich river water, of which net primary production and ecosystem respiration are actually increased more so by a combination of suspended sediment and river water than by either source individually (Johengen et al. 2008).

The last mixing event related to hypoxia that will be covered here is the fall overturn, which, in most cases, brings the final relief from hypoxia to the lake until next spring/summer in temperate climates. Despite the hypolimnion returning to oxic conditions, the fall turnover can still have negative effects on the lake if the bottom was previously hypoxic. During the summer hypoxia ammonium and SRP are released from the sediment and build up in the hypolimnion, and the fall overturn mixes the lake completely distributing these nutrients throughout the water column. This helps stimulate algal blooms at the border between summer and fall, and maintain them well into the fall (Nürnberg et al. 2013). In Lake Simcoe, Ontario, fall overturn increases phosphorus levels in the photic zone and chlorophyll concentrations, while decreasing light levels (Nürnberg et al. 2013). The overturn also appears to stimulate cyanobacterial blooms, and lead to their dominance of the phytoplankton community in the fall (Biddanda et al. 2008; Nürnberg et al. 2013). Additionally, late-fall and winter blooms of diatoms have been indicated as a major source of hypoxia for the next summer in Lake Erie (Reavie et al. 2016).

What is the future of hypoxia and what do we do about it?

Changing times

Due to human influence, hypoxic zones are spreading rapidly in lakes and coastal areas around the world (Diaz 2001). While humans have been adding fertilizer that stimulates algal blooms, global climate change has increased air and water temperatures as well. Research has found that many lakes are becoming gradually warmer at the surface, and are having a more difficult time mixing as a result (Sahoo et al. 2011). Studies are also finding that the onset of

stratification is coming earlier in the year, while the departure of stratification is coming later (Sahoo et al. 2011). Lakes with reduced mixing have seen hypoxic measurements steadily increase such as the hypoxic factor in Lake Simcoe, Ontario, and hypolimnetic anoxia in Blelham Tarn, UK (Foley et al. 2012; Nürnberg et al. 2013).   Lack of mixing not only lends itself to the formation of hypoxia, but also leads to the dominance of possibly toxic cyanobacteria in the phytoplankton community (Huisman et al. 2004; Sahoo et al. 2011).

Remedies

There are many different approaches that we can take in order to fix hypoxia. One of the most important ways is to reduce hypoxia through reversing eutrophication (Testa and Kemp 2012). Agriculture is one of the largest contributors to eutrophication (Scavia et al. 2014). Thus, nutrients can be cut off at the source through using feed that is lower in phosphorus, limiting the application of nutrients to crops to as little as is necessary, and building buffer zones around lakes and rivers so that terrestrial plants can use up nutrients before they get into the water (Daniel et al. 1998). That would lower inputs from external sources, but as previously discussed, internal loads are also significant (Nürnberg et al. 2013). The sediments of lakes can be treated with Alum to lock up phosphorus so that it is no longer available to plankton, even under hypoxic conditions (Reitzel 2003). Marko et al. (2013) even suggests that resrtictive channelized outflow of drowned river mouth lakes prevents biomass and nutrients from leaving, so they become more concentrated in the lake over time. Turning reservoirs and drowned river mouth lakes back to faster flowing systems may reduce the hypoxic conditions. In the future, sensor buoys may play a critical role in identifying hypoxic lakes, since high intensity, time-series data at multiple depths can give insight into the health and operation of lakes (Porter et al. 2009).

Conclusion

In recent times, researchers have started to realize what a critical role our inland waters play in global cycles of carbon and nutrients (Cole et al. 2007), even as their roles are being altered through human activity (Diaz 2001; Biddanda and Koopmans 2016). Global climate change and mass eutrophication have changed the amount of materials they process, how they process it, and where they process it (Dokulil 2013; Pacheco et al. 2013). Warming waters are preventing upper and lower layers from mixing, while excess algal productivity sinks and is decomposed which leads to hypoxia (Diaz 2001). The situation promotes the dominance of cyanobacteria, while zooplankton and fish further up the food web suffer from reduced habitat (Paerl and Huisman 2008; Ludsin et al. 2009; Goto et al. 2012). While lake mixing may relieve hypoxia temporarily, it may do more harm than good by bringing nutrients to the surface and fueling blooms (Kamarainen et al. 2009). Without significant remediation, eutrophic, hypoxic lakes may get stuck in a positive feedback cycle of excess productivity and hypoxia (Diaz 2001).

Extended Methodology

Study Site

Muskegon Lake is a 17 km^2 drowned-river mouth lake that connects the second largest watershed in Michigan, the Muskegon River Watershed, to Lake Michigan (Marko et al. 2013). The Muskegon River enters Muskegon Lake on the northeast end of the lake, and the Lake empties into eastern Lake Michigan through a ~2 km long shipping channel. The average hydraulic residence time of Muskegon Lake is ~23 days, but changes depending on the time of year and precipitation (Freedman et al. 1979; Marko et al. 2013). Through remediation efforts, the once eutrophic lake is now classified as mesotrophic; however, it's surface waters are still productive, leading to summertime hypoxia and *Microcystis* blooms.

Muskegon Lake Buoy Observatory

The Muskegon Lake Buoy Observatory (MLO) is a stationary water quality monitoring buoy in Muskegon Lake. It is located near the middle of the lake at ~12 m depth. It has a meteorological station ~2m above the water surface, which measures atmospheric variables (air temperature, humidity, wind speed and direction, precipitation, and barometric pressure) at 5 minute intervals. The MLO also monitors a suite of water quality variables at varying depths in the water column at 15 minute intervals. The water quality data used in this study were mainly the water temperature data from Nexsens T-nodes at 2,4,6,8, and 10-11 m. More data and information about the MLO are available online at www.gvsu.edu/buoy, and in Vail et al. 2015.

Wind Event Analysis

Since there is no common definition about what a wind-event was, we decided upon what characteristics would qualify a period of elevated wind speed as a wind-event. The average wind speed of all data points collected by the MLO from 2011-2015 was 5.1 m s^{-1} and a standard deviation of 2.6 m s^{-1}, so we defined the wind speed threshold of a wind-event as 7.7 m s^{-1} which is 1 standard deviation above the mean. We also decided that a wind-event would have to last for at least 3 consecutive hours in order to have the duration necessary to mix Muskegon Lake. Preliminary analysis confirmed that this definition was sufficient to cause a visible disturbance to the water temperature structure of Muskegon Lake. We analyzed the impact of wind-events on the temperature structure of the Lake using the MLO water temperature data. We studied the time-series data for water temperature, before, during, and after each event to identify the depth to which a wind-event homogenized the epilimnion to within 1 °C of the 2m temperature node. Thus if an event homogenized the epilimnion from 6 m to 10 m, we said the event mixing depth was 10 m. To calculate the average event mixing depth for each month (May-October) from 2011-2015, we averaged all event mixing depths for that month. We also totaled the number of hours of wind that was > 7.7 m s^{-1} each month through the five-years as well. A linear regression of number of hours of elevated wind vs. average event mixing depth was performed.

Manual Monitoring

Sampling and monitoring of Muskegon Lake was conducted biweekly at four different sites, named in order of depth East (10.5 m), Buoy (12 m), West (14.5 m), and South (21 m). Sites were selected to be at the center of one of the three sub-basins of the lake (except the Buoy

which was an established location) and also located away from the direct influence of any tributary. Sampling started in the first week of May 2015, and continued to the first week of November 2015. 2 sampling trips were conducted within the same week (July 28 and 31), to identify influences of a wind-event that occurred between those dates. The 4 sites were sampled in order of depth between 8 and 11 a.m.

Experimental gill nets (2) were set first at approximately 8 a.m. on the southwest and northeast sides of the Buoy at ~12 m depth. They are each 38.1 m long and 1.8 m tall, and contain five different equal length panels of different mesh sizes ranging from 2.54 cm to 12.7 cm by increments of 2.54 cm. Nets were pulled 3 hours later where fish were identified to species and length measured to the nearest millimeter and released.

In the meantime, the four monitoring sites were visited, where water column water quality profiles were conducted and waters samples were taken. For water quality profiles, a YSI 6600 data sonde (Yellow Springs Instruments) was equilibrated at the surface for 1 min and lowered to the bottom at a rate of ~ 1 m per min to allow adequate time for sensors to adjust. The sonde measured water temperature, dissolved oxygen, chlorophyll *a,* and phycocyanin every 2 seconds. Water samples were collected 1 m below the surface and 1 m off the bottom using a VanDorn bottle. Samples were dispensed into 500 mL bottles for nutrient analysis (total phosphorus -TP, soluble reactive phosphorus -SRP, ammonia-NH_3, and total Kjeldahl nitrogen-TKN), and 1 L bottles for bacterial abundance enumeration.

Sample bottles were put into a cooler with ice, and were prepped for analysis in the laboratory at AWRI. SRP samples were filtered and frozen. NH_3 and TKN samples were acidified and were put into the refrigerator with the TP samples. All nutrients were analyzed according to EPA (1993) methods at the Annis Water Resources Institute (AWRI) in Muskegon,

Michigan. Bacterial enumeration slides were made by preserving bacterial water samples in 2%

formalin and stained with Acridine Orange. Samples were filtered onto 25mm (0.2 μm pore

size) black polycarbonate Millipore filters. Filters were placed onto slides and put in the freezer.

Using standard epifluorescence microscopy, we enumerated the bacteria at 1000X magnification

(Dila and Biddanda 2015; Hobbie et al. 1977). Appropriate calculations were made to scale up

from the viewing area on the microscope to 1 mL.

Statistical Methods

In order to compare nutrient concentrations and bacterial abundances, the 4 sites were

pooled based on position in the water column (top or bottom) and time period (pre, during, or

post hypoxia). Thus 6 groups were compared (top-pre hypoxia, bottom-pre hypoxia, etc). We

tested the ability to pool the four sites using ANOVA. Groups were tested for normality using

Shapiro-Wilk normality test. Bottom groups were compared across periods using Kruskal-

Wallis with a pairwise Wilcoxon test and Holm's correction. Top and bottom groups of the 3

periods were compared using sign test (SRP) and paired Wilcoxon signed ranks test for the rest.

Fish catch data were analyzed using linear regressions that related total fish catch

(abundance), number of species (richness), and maximum fish length to the lowest DO

concentration measured during the water column profile of the Buoy site.

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