Hypoxia formation and breakdown were tracked during 2015 in Muskegon Lake estuary at multiple locations, and five years (2011–2015) of time-series buoy observatory data were evaluated for the effect of episodic wind-events on lake mixing. Bi-weekly water temperature and dissolved oxygen (DO) profiles at four locations revealed that hypoxia occurred at all sites and persisted for 2–3 months during summer 2015. On one date in late-summer, up to 24% of the lake's volume was estimated to be mildly hypoxic (DO < 4 mg L\(^{-1}\)) as defined by lake sturgeon requirements. Patterns of wind speed and water column stability in late spring indicated that high winds and low stability delayed the onset of hypoxia while in late summer low winds and high stability delayed degradation of hypoxia. Wind speeds appear to play a large role in the interannual variability of stratification and subsequent hypoxia. Water temperature and DO profiles taken before and after one mid-summer mixing event (wind speed >7.7 m s\(^{-1}\) for 10 h), indicated that while the wind was unable to completely mix the entire water column, it deepened the epilimnion by ~1.5 m and sheared a thin layer from the upper hypolimnion. By entraining internally loaded nutrients, such episodic wind-events may initiate and sustain algal blooms in nutrient limited surface waters. Quantifying the variable role of wind and mixing events will be key to integrating limnological processes into climate models of the future.

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### Introduction

Lakes and estuaries are the concentration points for the runoff of entire watersheds, which makes them highly susceptible to eutrophication and subsequent bottom water hypoxia (Larson et al., 2013; Marko et al., 2013; Zhang et al., 2010). While rivers and runoff have always supplied nutrients to lakes and coastal oceans, agricultural practices that include excess nutrient additions have made eutrophication a serious problem in many areas (Foley et al., 2012; Zhang et al., 2010). Eutrophication leads to higher than normal phytoplankton biomass production at the surface, which eventually settles to the lake bottom where it is decomposed or buried (Pacheco et al., 2013). Decomposition in the hypolimnion without the input of epilimnetic oxygen, due to thermal stratification, can lead to hypoxia (Sahoo et al., 2011). Hypoxia can have negative effects on the organisms when it degrades habitat for fish and zooplankton (Ludsin et al., 2009; Weinke and Biddanda, 2018). Also, more bioavailable species of phosphorus and nitrogen are released from the sediment under anoxic or near anoxic conditions and concentrate in the hypolimnetic waters during stratification (Ostrovsky et al., 1996; Salk et al., 2016).

In typical dimictic lakes, warmer summer temperatures stabilize the thermocline, which limits mixing between the epilimnion and the hypolimnion (Dokulil, 2013; Schmid et al., 2014). Without regular mixing, the hypolimnion of stratified lakes can become hypoxic. Anthropogenic climate change is increasing air and water temperatures worldwide which contributes to intensification of stratification and the spatial and temporal proliferation of hypoxia (Dokulil, 2013; Gleckler et al., 2012; O'Reilly et al., 2015). In addition, toxin-producing cyanobacteria are 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 (Dokulil, 2013; Hong et al., 2006). Episodic precipitation events are also problematic because they may bring heavier rains and are becoming 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 (Sahoo et al., 2011; Sinha et al., 2017; Williamson et al., 2009). Episodic strong wind-events during thermal stratification that shift the thermocline downward can...
stimulate surface blooms of algae and cyanobacteria through entraining internal loaded nutrients (particularly phosphorus in freshwater systems) into the epilimnion (Crockford et al., 2014; Jennings et al., 2012; Salk et al., 2016).

Although hypoxia may be a natural feature of many freshwater systems, it is increasing in frequency and severity as nutrients accumulate in watersheds and global warming strengthens thermal stratification (Diaz and Rosenberg, 2008). In recent decades, the surface waters of lakes around the world have been warming at an alarming rate of 0.3 °C per decade (O’Reilly et al., 2015). In considering the lengthening of the “hypoxic season”, less emphasis has been placed on wind mixing than warming of waters. High winds encourage mixing in lakes through internal waves which create turbulence at the boundary between the epilimnion and hypolimnion (Imboden and Wüest, 1995). Sufficient duration of high winds causes enough turbulence and mixing so that the epilimnion deepens. While overall wind speeds are expected to stay the same or even decline with climate change, episodic events of high wind and precipitation are expected to become more common and intense (Deng et al., 2018; Gastineau and Soden, 2009; Kasprzak et al., 2017; Pryor and Barthelmie, 2011). Thus, there is a need to better understand the complex and interactive forces that drive water column stability and hypoxia formation in natural waters.

Muskegon Lake, a Great Lakes area of concern (AOC), routinely experiences episodic hypoxia as a result of historic and ongoing eutrophication (Biddanda et al., 2018; Salk et al., 2016). The aim of this study was to 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 wind, and how those winds affect stratification and hypoxia during 2011 – 2015, and 3) to determine lake-wide consequences before and after an episodic wind-event by monitoring specific wind-events in summer 2015 during hypoxia. By addressing these goals, we hope to better understand the dynamics of hypoxia in Muskegon Lake and apply lessons to other lakes and coastal waters.

**Methods**

**Study site**

Muskegon Lake is a mesotrophic drowned river-mouth lake situated on the lower peninsula of Michigan’s western coast (Fig. 1). Muskegon Lake receives water from the Muskegon River watershed, the second largest in Michigan (7302 km²), and empties into Lake Michigan via a 1.8-km long, 100 m wide, and 10 m deep connecting channel (Marko et al., 2013). The Muskegon River is the primary inflow to Muskegon Lake, but there are several much smaller tributaries directly into Muskegon Lake such as Bear Creek to the north and Ruddiman Creek to the South. Muskegon Lake has an average hydraulic residence time of ~23 days, however, this can range from 14 to 70 days depending on the season and Muskegon River discharge (Freedman et al., 1979; Marko et al., 2013). Muskegon River water temperature during the summer is typically between the surface and thermocline temperature of Muskegon Lake, thus it does not flush the hypolimnetic water. Sample sites were 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 sub-basins (Marko et al., 2013).

Muskegon Lake typically becomes ice-free in March, allowing high rates of phytoplankton growth from late spring to early fall. Most algal growth occurs in late-July to early September (Weinke and Biddanda, 2018). Stratification begins in early-June with hypoxic conditions occurring within a few weeks, and persists until mid-September with fall overturn (Biddanda et al., 2018). Total phosphorus concentrations are around 20 µg/L at the surface and bottom, with summertime bottom concentrations rising to 50–80 µg/L. Soluble reactive phosphorus (SRP) is typically 5–10 µg/L in surface waters throughout the year and as high as 50 µg/L in bottom waters during summertime hypoxia. Nitrate and TKN are abundant year-round, with ammonia sporadically available (Steinman et al., 2008; Weinke and Biddanda, 2018).
Secchi depth in the lake averages between 2 and 2.5 m year round (Steinman et al., 2008).

**Muskegon Lake Buoy Observatory**

Due to environmental issues associated with the long history of industry along the shoreline, Muskegon Lake was declared a Great Lakes AOC in 1987 by the EPA (Steinman et al., 2008). Beginning in 2011, Great Lakes Restoration Initiative funds from the EPA were used to install and operate a time-series buoy observatory on the lake to monitor water quality. The Muskegon Lake Observatory (MLO) monitors meteorological conditions every 5 min and, physical, chemical, and biological variables every 15 min 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 sondes (Yellow Springs Instruments) at 2, 5, 8, and 10–11 m, temperature (NexSens) at 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. Gaps in wind speed data were supplemented by NOAA meteorological (R.M. Young) data at the Muskegon Field Station along the channel between Muskegon Lake and Lake Michigan, 5 km west of MLO. The entire string of water quality sensors was serviced, cleaned, and recalibrated every 1–2 months during the typical operation season of May to December each year, with the exception of temperature. 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**

For the entire 2011–2015 wind speed data set, the mean wind speed was 5 m s\(^{-1}\) (10 knots) as determined through a 2nd order Weibull distribution. We defined a wind-event as any wind above one standard deviation from the mean. One standard deviation was chosen because it is statistically rare, so we only considered effects of the upper ~15% of wind that the lake experienced. Wind speeds were abnormally distributed, skewed right, and thus, the upper 15% of wind speed data were 7.7 m s\(^{-1}\) (15 knots) and greater. Winds above 7.7 m s\(^{-1}\) were deemed “high winds” henceforth. Wind-events have been studied in other systems, with effects on the water column had similar wind speeds (Crockford et al., 2014; Imberger, 1985; Jennings et al., 2012). Even short sustained periods (as low as 3 hrs) of these high winds showed a substantial effect on the water column by temporarily increasing hypolimnetic temperatures and DO during the event (Fig. 2).

To evaluate temporal patterns in wind speeds and stratification, we calculated the total number of hours of high wind that each month in each year experienced during the time that the buoy was deployed. This time frame for this was from May to October during 2011–2015. Thus, we were able to gather wind hour totals for 30 months within a 5-year span. We also calculated the monthly average Schmidt stability coefficients from hourly data for all 5 years from MLO water temperature data throughout the water column using R package rLakeAnalyzer (Read et al., 2011; Winslow et al., 2015). Although the MLO is not located at the deepest point in the lake, the deepest temperature node was used to represent 11 m to the bottom of the lake in the calculation of Schmidt stability. Schmidt stability is a water body’s resistance to mixing (in this case via wind) due to thermal stratification (Idso, 1973). The value of Schmidt stability is the amount of work needed to be done by the wind to mix the water body completely, thus it serves this study to evaluate the strength of stratification and how stratification is affected by episodic winds.

Spearman correlations were used to evaluate the effect of high winds on the delay and recovery of the lake from stratification and hypoxia. We compared the date the hypoxia was first and last detected in each year along with the corresponding amount of high wind and average Schmidt stability value in May and September respectively. May and September were chosen, because May is when the main setup for stratification happens while September is when stratification is broken down.

**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 and DO sensors. The sonde was...
allowed to equilibrate at the surface for 1 min, and then lowered at a rate of ~1 m min⁻¹ while taking measurements every 2 s to give a profile of the water column. This allowed sensors time to respond to changes throughout the water column. Sensors were recalibrated on a monthly basis.

Using the DO 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). The term “hypoxia” when used generally will refer to mildly hypoxic conditions. 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 most conventional definition for hypoxia (Diaz, 2001).

Although the goal was to perform additional profiles before and after many episodic wind-events, we were only able to sample before and after one event due to logistical difficulties. The lone before/after monitoring trips were performed on July 28 and 31, 2015.

**Results**

**Development of hypoxia**

Both mild and severe hypoxia were present at some point at all four of the sites in Muskegon Lake during summer; hypoxia depth varied seasonally at each site’s water column (Fig. 3). Mild hypoxia was first observed as a thin layer at the bottom of the South water column on June 17, 2015, but by June 30, 2015 mild hypoxia was present at all four sites. The amount of each site’s water column that was mildly hypoxic on June 30, 2015 varied from 0.2 m at West to 3.9 m at South (Fig. 3). Mild hypoxia then disappeared from all but the East site when 2.3 m of its water column was hypoxic on July 15, 2015 (Fig. 3). This interruption is due to wind-driven coastal upwelling and intrusion of Lake Michigan water coming in through the channel and displacing the bottom hypoxic waters (Electronic Supplementary Material (ESM) Fig. S1; Liu et al., 2018). By July 31, 2015, mild hypoxia had returned to all four sites, varying from 0.6 m at West to 3.9 m at South. The next sample on August 10, 2015 showed the highest cumulative amount of mild hypoxia for any date ranging from 1.8 m of the water column at East to 10.8 m at South (Fig. 3). By October 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 it 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 15–30 days.

Severe hypoxia was not detected at any of the sites until July 28, 2015. On that date, severe hypoxia was detected at the East site over 1.6 m of the water column (Fig. 3). On August 10, 2015, severe hypoxia developed at the Buoy and South sites in addition to the East site. From this point on, the South site was severely hypoxic until September 23, 2015, the last day hypoxia of any kind was detected. The only time that all four sites had severe hypoxic was on September 9, 2015.

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 (Fig. 3). 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 date.

**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 high winds (Fig. 4). June through September are less windy, with the exception of August 2012 and 2015 which were exceptionally windy. These two months were two of the three that included the most number of hours of high wind 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. August 2012 and 2015 accounted for 80% of high winds during August 2011–2015 alone. The other months tended to follow the U-shaped pattern of wind from spring to fall as indicated in Fig. 4.

On an annual basis, 2012 and 2015 were 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 monthly average Schmidt stability coefficient at the Buoy location was lowest in the spring and fall, and highest in the summer months (Fig. 4). There was little variability in stability during May and October, with values averaging quite low. June had similar averages to May, but 2014 was approximately twice as stable as the other years. July, August, and September had the highest stabilities and greater variability between years. Several outliers occurred in July 2014 and August 2012 and 2015.

Time series development of hypoxia in relation to stability and wind events

Spearman correlation coefficients indicated there was a strong positive correlation between the number of hours of high wind in May and the first annual detection of hypoxia (Fig. 5). Furthermore, there was a strong negative relationship between the average water column stability in May and the first detection of hypoxia, as expected. This means that low late-spring wind speeds and high May water column stability correlated to earlier development of hypoxia. Additionally, the relationships hold for the last annual detection of hypoxia, where high winds and low water column stability in September correlated to an earlier reprieve from hypoxia. Despite the strong correlation coefficients, none of the four tests yielded statistically significant p-values. Because data were limited by a sample size of 5 years, we concluded that these are strong trends, but statistically insignificant.

Lake-wide monitoring of a single wind-event

Profiles in the four locations before (July 28, 2015) and after (July 31, 2015) were observed for one episodic wind-event in 2015. From July 29, 2015 15:00 to July 30, 2015 15:00 there were 10 h of average wind speed over 7.7 m s⁻¹ from 260° WSW. Three of the hours were consecutive, so it was a wind event according to our definition. Before the event, there was a lake-wide metalimnion of roughly 5.1 m thickness and 7.3 m deep in the middle (Fig. 6). Following the event, the metalimnion thinned slightly to

![Fig. 4. a) Number of hours of monthly above average wind speeds (>7.7 m s⁻¹) and b) Average Schmidt stability coefficients during May to October 2011–2015 at the Muskegon Lake Observatory (MLO). May 2014 only represented by 2 days of data due to late buoy deployment.](image1)

![Fig. 5. Plots showing how the timing of the first (a) and last (b) annual detections of hypoxia can be altered by May and September (respectively) wind speeds and water column Schmidt stability. Wind speed correlations are accompanied by the double line and stability correlations values by the solid black line. Spearman ρ and p-values for each correlation are given in the graphs.](image2)
4.9 m thickness and deepened in the center to 8.7 m (Fig. 6). The buoy data during the wind-event indicated that the metalimnion 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 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 (Fig. 7). 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. The DO profiles indicated the wind-event did not relieve any of the hypoxia. The East site hypolimnion 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.

Despite the relatively small changes in the water column as a result of this event, these types of events were quite frequent on Muskegon Lake (10 h duration, 8.1 m s⁻¹ average wind speed). Shorter and weaker wind events, such that occurred between July 28 and July 31, 2015, were more common than longer and stronger events (Fig. 8). Almost all events that occurred from 2011 to 2015 had an average wind speed during the event of 7.7 to 10.3 m s⁻¹ (15–20 knots). Additionally, most wind events had high winds for 10 or fewer hours. Strong wind events like that seen in Fig. 2 (13 h continuous duration at 11.1 m s⁻¹) were not as common, but can have larger impacts on water column structure.

**Discussion**

The construction and disruption of hypoxia

Based on the manual monitoring profiles taken at four different sites in Muskegon Lake, we demonstrated that mild hypoxia occurred lake-wide and was persistent throughout the summer. While severe hypoxia rarely occurred lake-wide, it was persistent at a few sites. Not all sites showed consistent levels or severity of hypoxia every sampling, but long stretches were observed 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 (Dila and Biddanda, 2015; Salk et al., 2016; Weinke et al., 2014). 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 major disruptions to the presence of hypoxia that were site specific. The first major disruption occurred in mid-to-late June when a suspected mass of upwelled Lake Michigan water created an underflow into the bottom of Muskegon Lake. This type of upwelling event is confirmed through analysis of water profiles (temperature, DO, and specific conductivity), as well as hydrodynamic modelling efforts using time-series water quality data around Muskegon Lake and nearby Lake Michigan (Liu et al., 2018). The dense, cold, oxygen-rich water pushed the slightly warmer, hypoxic water to 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. But its effects were also seen as far east as the East location.

Lake Michigan coastal upwelling occurs frequently along the Muskegon shoreline during the summer following northerly winds (Liu et al., 2018; Plattner et al., 2006). The upwellings translate to intrusions into the bottom of Muskegon Lake at least once every year, according to MLO data (Biddanda et al., 2018; Liu et al., 2018). This 2015 intrusion event was especially strong considering the East site showed signs of intrusion, but intrusions don't always affect the East and Buoy locations (Liu et al., 2018). Upwelling events of Lake Ontario water have also been found to come into Hamilton Harbor (Bocaniov et al., 2011; Lawrence et al., 2004; Yerubandi et al., 2016), and into Toronto Harbor (Hlevca et al., 2018), as well as Lake Michigan into Green Bay (Gr uncert et al., 2018). Similar to Hamilton Harbor and Green Bay, the intrusions in Muskegon Lake result in upwelling from and movement of hypoxic water (Gr uncert et al., 2018; Yerubandi et al., 2016). On the contrary, episodic upwelling in the central basin of Lake Erie has been observed forcing its hypoxic, hypolimnetic water into the bottom of Lake Erie's western basin which is normally a well-mixed system and free of hypoxia (Jabbari et al., 2019).

The second major hypoxic disruption occurred on August 23–24 when a cold front passed through with 34 h of continuous high winds. The combination of air cooling and high winds deepened the thermocline to 10–11 m, which was 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 (Ostroovsky et al., 1996). 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 well-stratified lake (Crockford et al., 2014; Kuha et al., 2016). Warmer air temperatures over the next few weeks warmed the epilimnion that caused the thermocline to move higher in the water column, thus allowing hypoxia to develop at all sites.

The irregular bathymetry of the lake allowed mild and severe hypoxia to persist at the deeper locations. When the water depth is much deeper than the thermocline, there is less likelihood that 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, transects the long fetch of the lake. Thus, oxygenated high 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. Without the disruption of intruding Lake Michigan water, it is likely that hypoxia would have been most persistent at these locations instead of the Buoy site.

The stratification and the inability for extreme wind-events to completely mix Muskegon Lake during the summer contributes to the formation and persistence of hypoxia in the hypolimnion for the duration of stratification (Dokulil, 2013; Sahoo et al., 2011). In fact, many aquatic systems are affected 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 has increased in recent time (Diaz, 2001; Jenny et al., 2016; Zhang et al., 2010).

Do episodic wind events lead to episodic algal blooms?

One of the biggest effects of hypoxia in bottom waters is the release of nutrients, particularly phosphorus in freshwater systems, from sediments through internal loading (Nürnberg et al., 2013). Much of the phosphorus in sediments is bound to metal oxides 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 and 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 (Weinke and Biddanda, 2018). Seasonal sampling from 2003 to 2005 in Muskegon Lake, typically once in May, July, and September, indicates two times higher concentrations of SRP in the bottom waters (10 µg/L) compared to surface waters (5 µg/L) (Steinman et al., 2008). Another study also found the accumulation of nutrients such as SRP in low DO waters on Muskegon Lake, noting a strong correlation between nutrient concentrations and DO (Salk et al., 2016). More recent nutrient data from 2015 found that the hypolimnion near the MLO can have SRP concentrations as high as 40 µg/L (Weinke and Biddanda, 2018).

During episodic wind-events, there is the potential for hypolimnetic nutrients to be brought to the surface waters (Planas and Paquet, 2016; Ostroovsky et al., 1996). As above-average winds cause extreme seiches, mixing occurs where the epilimnion and hypoxia...
limnion meet the metalimnion. Wind-events increase the movement of water and increase the mixing and diffusion that happens within these boundary layers (Imboden and Wüest, 1995). Also, due to shear stress on the metalimnion, 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; Ostrovsky et al., 1996). Wind-events also cause turbulence at the hypolimnetic-sediment interface, encouraging enrichment of the water with nutrient rich pore water and sediment (Imboden and Wüest, 1995). Additionally, during the previously mentioned Lake Michigan intrusion, nutrient-laden hypolimnetic water is pushed closer to the surface, by the denser 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.

Muskegon Lake is already heavily influenced by external loading, as it is a site of high deposition and retention of carbon and phosphorus from the watershed (Carter et al., 2006; Marko et al., 2013). Despite even 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; Søndergaard et al., 2003). While there is likely still some slight nutrient mixing and diffusion 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 produce harmful algal blooms in eutrophic systems during the prime growing season of the calm, hot, late summer (Michalak et al., 2013; Wilhelm and Adrian, 2008). During August of 2015, large Microcystis cyanobacteria blooms occurred in Muskegon Lake following a series of especially strong wind-events (Weinke and Biddanda, 2018). These occurred during a time when hypolimnetic SRP concentrations were high (~20 μg/L) as a result of stable hypoxia and decreased at the East and Buoy locations due to deepening of the epilimnion (<5 μg/L).

How will wind and stratification regimes change due to the climate?

Stratification, hypoxia, mixing events, and internal loading are considerations linked to the future of lakes as they relate to climate change (Snortheim et al., 2017). In the temperate regions, there is expected to be an increase in air temperature, which is currently translating to warmer lakes (Dokulil, 2013; O'Reilly et al., 2015; Sahoo et al., 2011; Schmid et al., 2014). A warmer epilimnion creates stronger stratification, and stratification and hypoxic seasons have already expanded in many lakes (Dokulil, 2013; Paerl and Huisman, 2008; Sahoo et al., 2011). A longer duration of hypoxia will promote a greater release of nutrients from the sediments under reducing conditions (Nürnberg et al., 2013). This could potentially further concentrate these nutrients in the hypolimnion.

In specific regard to the intrusions, the future of hypoxic reprieve is in question. In 2015, as well as in every other year of MLO deployment, intrusions of very cold, highly oxygenated Lake Michigan water gave Muskegon Lake a temporary break from hypoxia (Biddanda et al., 2018; Liu et al., 2018; Weinke and Biddanda, 2018). We expect Muskegon Lake and Lake Michigan to follow global surface water warming patterns similarly (O’Reilly et al., 2015). The future question is how will intrusions (which seem vital to resupply dissolved oxygen in the summer) respond to Muskegon Lake’s own warming as well as that of Lake Michigan’s. In Green Bay, Grunert et al., 2018 found that similar to Muskegon Lake, intrusions play a large role in determining the temperature of the hypolimnion during the summer, which drives stratification. In a year with fewer intrusions, the hypolimnion of Green Bay was warmer than in the following year with more intrusions. They suggest that a coastal system’s reaction to climate change may depend less on climate warming, but more on wind speed and direction to influence their thermal structure. The future ecological directions of Muskegon Lake, as well as other estuaries and coastal embayments like Hamilton Harbor (Yerubandi et al., 2016), could rely at least partly on more or fewer summertime intrusions for better or for worse (Grunert et al., 2018).

Overall, worldwide and Great Lakes regional wind speeds are expected to stay the same or even decrease according to current climate models (Deng et al., 2018; Gastineau andoden, 2009; Pryor and Barthelmie, 2011). Without considering increasing temperatures, the timing and intensity of wind matters. Lower wind speeds in the spring have the potential to allow earlier stratification and lower summer/fall winds allow for stratification to persist later (Fig. 9). The lengthening of stratification only serves to extend the inevitable hypoxic season in lakes that are already susceptible to its formation. While we do note that even extreme wind events can’t completely relieve a system like Muskegon Lake from hypoxia, the weak period of stratification is vulnerable to wind mixing

**Fig. 9.** Conceptual representation of how spring and fall wind speeds affect the annual duration of hypoxia in a lake by altering the timing of stratification and subsequent hypoxia.
during the spring and fall. Thus, wind during periods that are not shallow, well mixed systems to temporarily develop stratification andhypoxia (Jabbari et al., 2019). On the other hand, the weather in the near future is expected to be more episodic, with extremely high wind speeds in extratropical regions increasing in occurrence (Gastineau and Soden, 2009; Jennings et al., 2012) A greater frequency of summertime episodic events could potentially create a situation in which nutrients are more frequently supplied in a higher concentration from the hypolimnion to the epilimnion via seiching and upwelling, without complete hypolimnetic reprieve from hypoxia (Crockford et al., 2014; Pöschke et al., 2015). Given cyanobacterial propensity to grow in warmer waters compared to phyto plankton such as diatoms and green algae, episodic supplies of nutrients in the summer-time could enhance already problematic blooms of cyanobacteria (Crockford et al., 2014; Paerl et al., 2011). In addition, while mixing does lead to a temporary decrease in cyanobacteria at the surface by dilution, intermittent mixing has been shown to be ineffective at permanently mitigating blooms of Microcystis (Jönköh et al., 2008).

There is an emerging need for reliable monitoring and sustainable restoration of our afflicted lakes and reservoirs (Conner et al., 2017). Lakes have been shown to be integrators, regulators, and sentinels of change within watersheds and the climate playing a globally significant role in the cycling of carbon (Biddanda, 2017; Williamson et al., 2009). The present study indicated that monitoring buoys, such as the MLO, were invaluable for improving our understanding of how these vital ecosystems continually and dynamically operate (Jennings et al., 2012). Observatories can deliver higher frequency, time-series data from throughout the water column to off-site locations and enable a more rigorous study of interaction of multiple stressors on ecosystems (Porter et al., 2009; Wachowiak et al., 2017). Time-series observatories can expand our understanding of what happens within a lake ecosystem during episodic events such as storms—ephenomenal but crucial ecosystem-wide events which would have been missed previously by discrete measurements made only on fair-weather days (Jennings et al., 2012).

Conclusion

A series of episodic events in the spring and summer can have lasting consequences for hypoxia in a water body, and changes in the annual number of these short term events can be signals of long-term change both in the climate and subsequently in the hydrosphere. As anthropogenic forcing inexorably continues to strengthen stratification, exacerbate hypoxia and alter the productivity of aquatic systems, quantifying and forecasting the ecosystem consequences of mixing events by analyzing and modeling the underlying patterns of ever-changing environmental variables and their complex interactions will become increasingly vital.

In the emerging Anthropocene, it will be essential to grasp not only the long-term patterns of change occurring in the background, but also of the role of high-impact episodic short-term events that occur superimposed on them.

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Appendix A. Supplementary data

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References


