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ABSTRACT

We chronicled the seasonally recurring hypolimnetic hypoxia in Muskegon Lake – a Great Lakes estuary over 3 years, and examined its causes and consequences. Muskegon Lake is a mesotrophic drowned river mouth that drains Michigan's 2nd largest watershed into Lake Michigan. A buoy observatory tracked ecosystem changes in the Muskegon Lake Area of Concern (AOC), gathering vital time-series data on the lake's water quality from early summer through late fall from 2011 to 2013 (www.gvsu.edu/buoy). Observatory-based measurements of dissolved oxygen (DO) tracked the gradual development, intensification and breakdown of hypoxia (mild hypoxia <4 mg DO/L, and severe hypoxia <2 mg DO/L) below the ~6 m thermocline in the lake, occurring in synchrony with changes in temperature and phytoplankton biomass in the water column during July–October. Time-series data suggest that proximal causes of the observed seasonal hypolimnetic DO dynamics are stratified summer water-column, reduced wind-driven mixing, longer summer residence time, episodic intrusions of cold DO-rich nearshore Lake Michigan water, nutrient run off from watershed, and phytoplankton blooms. Additional basin-wide water-column profiling (2011–2012) and ship-based seasonal surveys (2003–2013) confirmed that bottom water hypoxia is an annually recurring lake-wide condition. Volumetric hypolimnetic oxygen demand was high (0.07–0.15 mg DO/Liter/day) and comparable to other temperate eutrophic lakes. Over 3 years of intense monitoring, ~9–24% of Muskegon Lake's volume experienced hypoxia for ~29–85 days/year – with the potential for hypolimnetic habitat degradation and sediment phosphorus release leading to further eutrophication. Thus, time-series observatories can provide penetrating insights into the inner workings of ecosystems and their external drivers.

Introduction

"A skillful limnologist can possibly learn more about the nature of a lake from a series of oxygen determinations than from any other chemical data." – George Evelyn Hutchinson, 1957.

The cycle of oxygen in the biosphere is intimately tied to that of carbon, which in turn is stoichiometrically linked to the cycling of all bioactive elements (Lyons et al., 2014; Schlesinger and Bernhardt, 2013; Keeling et al., 2010). By closely following oxygen, one can gain an integrated picture of ecosystem function, including carbon balance. Modern sensors, arrays, and buoy platforms, now allow us to continuously and remotely monitor the changes in dissolved oxygen (DO) concentration in aquatic systems *in situ* at high spatial and temporal resolution enabling the study of episodic phenomenon that are rarely captured by discrete sampling and monitoring methods (Porter et al., 2009; Johnson and Claustre, 2016; Aguilera et al., 2016). One such phenomenon that is amenable to tracking via time-series observations of changes in DO is bottom water hypoxia, which has been increasing both in prevalence and intensity in recent decades around the world (Diaz and Rosenberg, 2008; Gilbert, 2009; Jenny et al., 2016).

Hypoxia has many different definitions with different thresholds, but generally refers to low DO concentrations (Farrell and Richards, 2009). The more common definition of hypoxia has DO concentrations

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<2 mg/L while others have thresholds ranging from 1 to 6 mg/L (Diaz, 2001–2 mg/L; Farrell and Richards, 2009–5-6; Killgore and Hoover, 2001–5 mg/L; Ludsin et al., 2009–3 mg/L). In the present study, we distinguish between mild and severe hypoxia, with mild hypoxia at <4 mg/L but >2 mg/L – wherein most invertebrates and fish suffer stress (Hawley et al., 2006; Bręk-Laitinen et al., 2012; Altenritter et al., 2013), and severe hypoxia at <2 mg/L DO (Diaz, 2001; Scavia et al., 2014) - the more conventional definition. Hypoxia in stratified lakes occurs when a mass of water is isolated from atmospheric oxygen due to density differences caused by thermal or haline stratification, combined with oxygen drawdown by respiring organisms in the water and sediments (Zhang et al., 2010; Bouffard et al., 2013).

There are many factors that affect the spatial and temporal extent of bottom water hypoxia within a freshwater system (Zhang et al., 2010). Bathymetry mostly determines if and where the system is deep enough to stratify (Nürnberg et al., 2013). The high oxygen demand of benthic respiration in organic rich sediments is likely to quickly draw down DO in the hypolimnion (Sweerts et al., 1991). In eutrophic systems, hypoxia is amplified due to high rates of algal productivity leading to sinking/dying plankton, and the subsequent large source of carbon for water column and sediment respiration (Scavia et al., 2014; Bouffard et al., 2013; LaBuhn and Klump, 2016). In most temperate systems that experience seasonal changes, bottom water hypoxia is commonly associated with the summer thermal stratification (Zhou et al., 2014).

Muskegon Lake, a Great Lakes estuary, is one of several drowned river-mouth lakes located in West Michigan (Fig. 1). Crustal rebound during the post-glacial period caused a rise in Great Lakes water levels and the flooding of ancient river valleys (Herdendorf, 1990). Great Lakes drowned river-mouths are model examples of freshwater estuaries because of their location at the mouth of a river and their connection to one of the Great Lakes (Larson et al., 2013). The physical characteristics of drowned river-mouth lakes (small outflow, longer residence time of water, high retention of sediments, low water velocities) may make them a useful laboratory for investigating the effects of terrigenous input on coastal aquatic ecosystems. Specifically, they have the physical complexity approaching that of a marine estuary, with substantial riverine inflows, sediment deposition, and periodic inflows from downstream receiving waters. However, atypical of estuaries, they have little advection. This makes changes that are observed at a point over time more likely to be due to the evolution of biogeochemical processes in the lake, as opposed to being primarily due to advection.

The mesotrophic Muskegon Lake was designated as an Area of Concern (AOC) in 1985 by the USEPA, because of degraded water and sediment quality due to years of industrial and urban pollution (Carter et al., 2006). Although water quality has improved considerably since 1985, and invertebrate and fish populations have rebounded (Steinman et al., 2008), the lake is still affected by a number of Beneficial Use Impairments (BUI) such as eutrophication, bottom water hypoxia and harmful algal blooms (Steinman et al., 2008). As part of ongoing restoration and associated environmental monitoring, a buoy-based multi-sensor observatory was designed and deployed in 2011 to obtain high-resolution time-series data (Biddanda, 2012; Vail et al., 2015; Weinke and Biddanda, in press).

Herein, we report on the temporal dynamics and spatial extent of hypoxia in the drowned river-mouth Muskegon Lake ecosystem. We test the following hypotheses: 1) Hypoxia recurs every summer in Muskegon Lake and once it is established it is maintained as long as thermal stratification is maintained, 2) Properties measured at the Muskegon Lake Observatory buoy (MLO) are representative of properties of the lake as a whole, and 3) Severity of hypoxia will be greatest during

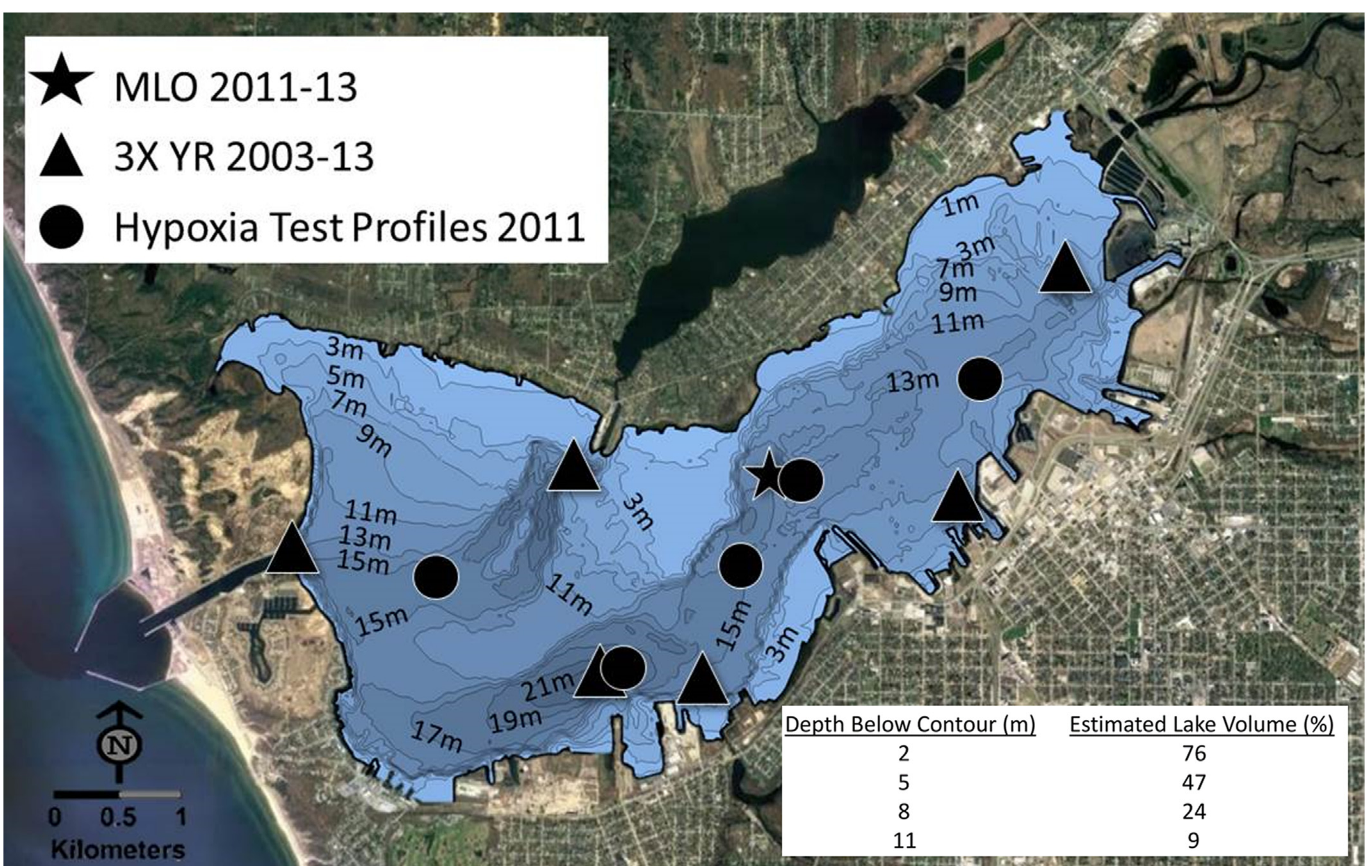

Fig. 1. Bathymetry map of Muskegon Lake showing location of MLO (star), six long-term monitoring sites (triangles), and five hypoxia test profiles (circles). Contour lines are every 2 m. Satellite imagery is from Google. The estimated lake volume below isobaths corresponding to MLO dissolved oxygen sensors are located in the lower right corner.

years with wet springs – similar to hypoxia in Lake Erie, when the greatest springtime nutrient delivery via suspended sediments occurs. To test these hypotheses, we used: 1) Time-series observatory data to detect and track temporal variability and estimate vertical spatial extent (2011–2013), 2) Discrete lake-wide profiles to corroborate assumptions of lake-wide hypoxia based on observatory data (2011–2012), and 3) Time-series and discrete seasonal data to see if the occurrence of hypoxia was changing over time (2003–2013). Lessons learned should be applicable to lakes, estuaries and coastal waters undergoing change around the world.

Materials and methods

Study site

Muskegon Lake is a mesotrophic drowned-river mouth on the west coast of Michigan's lower peninsula (Fig. 1). It is directly connected to Lake Michigan through a navigation channel, which allows Muskegon Lake to function as a freshwater estuary, with occasional inflows of Lake Michigan water back into Muskegon Lake. Muskegon Lake covers an area of ~17 km^2, has a mean water depth of 7 m with a maximum depth of 23 m, and a volume of ~120 million m^3 (Carter et al., 2006; Steinman et al., 2008; Defore et al., 2016). It has an average hydraulic residence time of 21 days; however, this time-frame can vary widely over the year depending on discharge from the Muskegon River watershed (~7000 km^2; Steinman et al., 2008; Defore et al., 2016). Most of the watershed that contributes to Muskegon Lake is forested (53.2%), with the remainder being 23% agricultural, and 4.2% urbanized (Marko et al., 2013). The lake has water quality issues from the logging and foundry industries beginning in the 1800s.

Data acquisition

Muskegon Lake Observatory buoy

The Muskegon Lake Observatory buoy (MLO), located at 43.238239° N, 86.280532° W, has delivered high-frequency time-series meteorological and water quality data throughout the water column from April/May to November/December since 2011 (Biddanda, 2012; Figs. 1, 2, Electronic Supplementary Material (ESM) Fig. S1), and all current and historical data are available online (www.gvsu.edu/buoy, Fig. 2). Data quality is assessed in part by frequent lab-based sensor checks and calibrations, and removal of biofouling is performed periodically throughout the deployment for quality assurance measures. For the MLO data used in this paper, water temperature data was measured by temperature nodes (NEXSENS) at 2, 4, 6, 8, 10, and 11 m depths, and DO and Chlorophyll data were measured by YSI (Yellow Springs Instruments) 6600/6920 datasondes at 2, 5, 8, and 11 m depths equipped with YSI ROX 6150 DO sensors (Vail et al., 2015). All DO, chlorophyll and water temperature data from the MLO used in the present study are daily averaged data gathered at 15-min intervals – except for May and early June 2011 when data were measured at 1 and 2-h intervals, respectively.

Lake-wide test profiles

After we first noticed persistent hypolimnetic hypoxia in the MLO data stream in 2011, we performed water column profiles at five locations around Muskegon Lake during July and August 2011 and July 2012 to confirm the lake-wide presence of hypoxia (Fig. 1). One site was at the MLO to provide additional confirmation of the accuracy of the MLO sensors, and the other four sites represent the four major sub-basins of the lake (West, South, Central and East). DO/temperature profiles were performed at each location by slowly lowering (~1 m/min) a YSI 6600 datasonde equipped with a YSI temperature and ROX 6150 DO sensor to the lake bottom.

Long-term seasonal monitoring

Seasonal shipboard monitoring began in 2003 at six locations three times per year: Spring (May), Summer (July), and Fall (September) (Steinman et al., 2008). At each of the six monitoring locations (Fig. 1), temperature and DO concentrations were taken at 1 m below the surface, the middle of the water column, and 1 m above the bottom using a YSI 6600 datasonde equipped with sensors that included a YSI ROX 6150 optical dissolved oxygen sensor. The sensor was allowed to equilibrate at each location within the water column and was calibrated in the morning before the cruise. All site and water column measurements were taken on the same day between the hours of 8 a.m. and 2 p.m. Only summer/ July data is featured in this study.

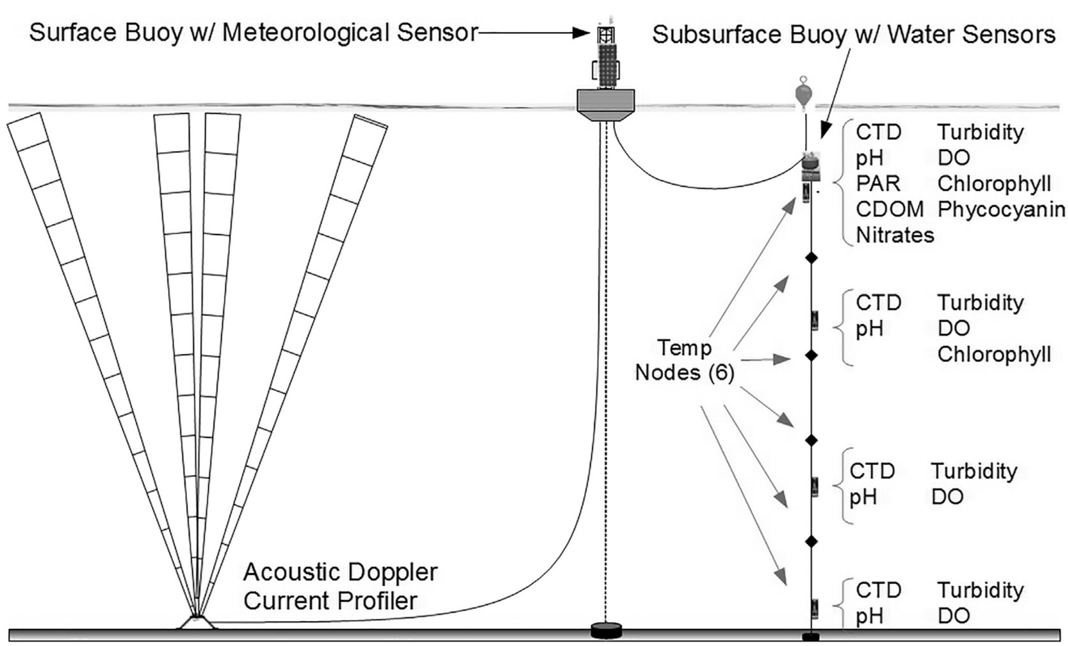

Fig. 2. Observatory layout. MLO design consisted of three main parts that are cabled together: (1) surface buoy, (2) subsurface buoy and sensor string, and (3) the acoustic Doppler current profiler (ADCP). The surface buoy supports a meteorological station, the master data logger, solar panels and battery power. The subsurface buoy supports the water chemistry sensors with YSI sensors (e.g., DO) fixed at 2, 5, 8 and 11 m while temp sensors occur at more depths (~2 m). An acoustic Doppler current profiler is also attached to the surface buoy.

Data analysis

Mild vs. severe hypoxia

We differentiate two thresholds of hypoxia for ecological and comparative reasons. Mild hypoxia is defined as DO <4 mg/L. This definition of mild hypoxia is ecologically relevant, as invertebrates and fish become stressed under these conditions (Hawley et al., 2006; Diaz and Breitburg, 2009), and in Muskegon Lake it has been found to be the cut-off point at which threatened juvenile Lake Sturgeon do not inhabit such waters (Altenritter et al., 2013). Severe hypoxia is defined as DO <2 mg/L and serves as a comparative threshold as most studies use this as definition for hypoxia – levels below which water and habitat quality as well as ecosystem structure and function are severely impacted (Diaz, 2001; Scavia et al., 2014).

Seasonal monitoring

DO profiles from the archived Muskegon Lake long-term seasonal (spring, summer and fall) monitoring data set were analyzed for mild and severe hypoxia during summer (July) sampling trips from 2003 to 2013. Of the six monitoring sites, the total number of sites that showed mild and severe hypoxia was counted, and a trend analysis over the years was plotted.

Depth of mixed layer (Z_{mix}) calculation

In order to determine the depths of the two layers from our spaced sensors, we calculated the depth of mixed layer (Z_{mix}) following the recommendation by Staehr et al. (2010). Staehr states that Z_{mix} starts at the surface and ends at the metalimnion (where temperature decreases by 1° Celsius or more per meter). As water temperature data were acquired from temperature sensors located at every 1 m depth in the water column, we calculated Z_{mix} of Muskegon Lake and rounded to the nearest meter. The depth of Z_{mix} was calculated for every 30-min interval, and then averaged to find the mean Z_{mix} for each day. This depth is what we defined as the thermocline. Using DO and water temperature from a time-series sensor string, makes it easy to estimate where the epilimnion turns into the hypolimnion. Water temperatures and DO concentrations taken by sensors at a particular depth were extrapolated upwards to the next highest sensor in the water column, or to the surface. Also, for the closest sensors above the thermocline and above the lake bottom, extrapolations were downward as well.

Hypoxic factor (HF) and Hypolimnetic oxygen depletion rate (HOD) estimates

We also used the 2011–2013 MLO DO data to calculate several different factors with respect to hypoxia in order to compare with other lakes in the region and around the world, while differentiating between mild and severe hypoxia in applicable cases. As a basic analysis, we calculated the number of days when the daily average DO concentration was hypoxic anywhere in the water column as well as noting the number of days each of the individual four DO sensors located at different depths in the MLO detected hypoxia. In ESM Fig. S2, only common days where DO was measured between all three years were used.

MLO DO data were also used to calculate the areal and volumetric hypoxic factors (AHF and VHF, respectively) according to Nürnberg, 2004. Areal hypoxic factor (AHF) is the number of days per year that hypoxic or severely hypoxic water covers a sediment area that is equal to the lake's surface area (Nürnberg, 2004). Similar to the AHF, the VHF, gives the number of days per year that a volume equal to the entire lake volume is hypoxic or severely hypoxic. VHF was determined in the same manner as AHF, the difference being that volumetric values are substituted for area values (Foley et al., 2012; ESM Table S1). A measurement of hypoxia at one depth was assumed to apply across the entire lake for the surface area and volume at that depth. In calculating these factors, we did not determine if the oxycline was above the highest sensor to detect hypoxia (i.e., if hypoxia was detected at 8 m and not 5 m, we assumed the water was hypoxic only below 8 m and not above it). Thus, our findings provide a conservative estimate of areal and volumetric hypoxic factors.

Finally, the rates of areal and volumetric hypolimnetic oxygen depletion (AHOD and VHOD, respectively) were calculated based on Matthews and Effler (2006) and Foley et al. (2012), respectively. VHOD rate estimates are based on change in volume-weighted oxygen concentrations in the hypolimnion (VHODobs – observed rates based on raw DO concentrations measured by sensors; VHODvm – vertical mixing, which is VHODobs accounting for vertical mixing of DO; and VHODadj – adjusted, which is VHODvm accounting for temperature effects on metabolism). First, the VHODobs were calculated for each year, and then the rates of VHODvm and VHODadj were derived from it to correct for vertical mixing and hypolimnetic temperature differences, respectively (see below).

We calculated the VHODobs as well as the rates corrected for VHODvm, and VHODadj. The observed rate is obtained by calculating the volume-weighted average DO concentration in the hypolimnion each day during the establishment of hypoxia. The VHODobs is the slope of the volume-weighted DO over time during the nearly linear decrease in hypolimnetic DO. DO concentrations below 2 mg/L were not used in these estimates of depletion rates as DO concentrations below this DO level are not expected to be linear (Burns, 1995). VHODvm is adjusted for vertical mixing by calculating a vertical heat exchange coefficient, which is used to calculate the DO flux during the period of near-linear decrease. The DO flux value is added to VHODobs to become VHODvm. All the VHODvm's for each year are standardized to one temperature to account for how temperature influences metabolism. The average temperature of the hypolimnion during all three years was 18.8 °C, so all years were standardized to an even 19 °C. This new temperature standardized rate is called VHOD adj. Calculations of AHOD were inconclusive and did not reveal any significant patterns, and therefore are not included or discussed.

Quantifying lake volume at isobaths for estimating duration and extent of hypoxia

The pre-existing 2006 National Hydrography Dataset (NHD) GIS feature data for the Muskegon Lake shoreline was adjusted to an updated 2008 format using ESRI™ ArcGIS software and high resolution (6″ pixel) leaf-off aerial orthophotography. Historic mean water level for the Lake Michigan was then used to estimate the Muskegon Lake water level for April 2008 at 176.4 m. This water level was used as the base elevation and adjustment point for correcting all relevant lake bathymetric data, taken from the recently published February 2008 NOAA electronic bathymetric chart for Muskegon Lake.

The corrected GIS shoreline boundary and the supplemental NOAA bathymetric point data was used to generate a new bathymetric grid (raster) feature for Muskegon Lake from which, contours were created at 2, 5, 8, and 11 m depths (the target boundaries for the volumetric analysis). The Polygon Volume tool in ArcGIS was then applied to determine the remaining lake volume beneath each of these specified boundaries (2, 5, 8, and 11 m; Fig. 3, Fig. ESM S1 and ESM Table S1).

Combining lake volume below the 2, 5, 8, and 11 m isobaths with MLO DO data at corresponding depths enabled us to estimate the number of days hypoxia prevailed below these depths and the volume of the lake that experienced hypoxia in each of the 3 years of studied. Layers of hypoxia and severe hypoxia were determined by daily average DO values at 2, 5, 8, and 11 m. DO measurements were interpolated between the sensor depths using step-wise integration (Chin-Leo and Benner, 1992). The data obtained at the 2 m sensor was also applied upwards to the top 2 m as well as down to the 5 m depth. By assuming that possibly higher DO measurements extend all the way down to the next sensor when the thermocline or oxycline is between the sensors, the present study reports conservative estimates of the extent of hypoxia in the lake.

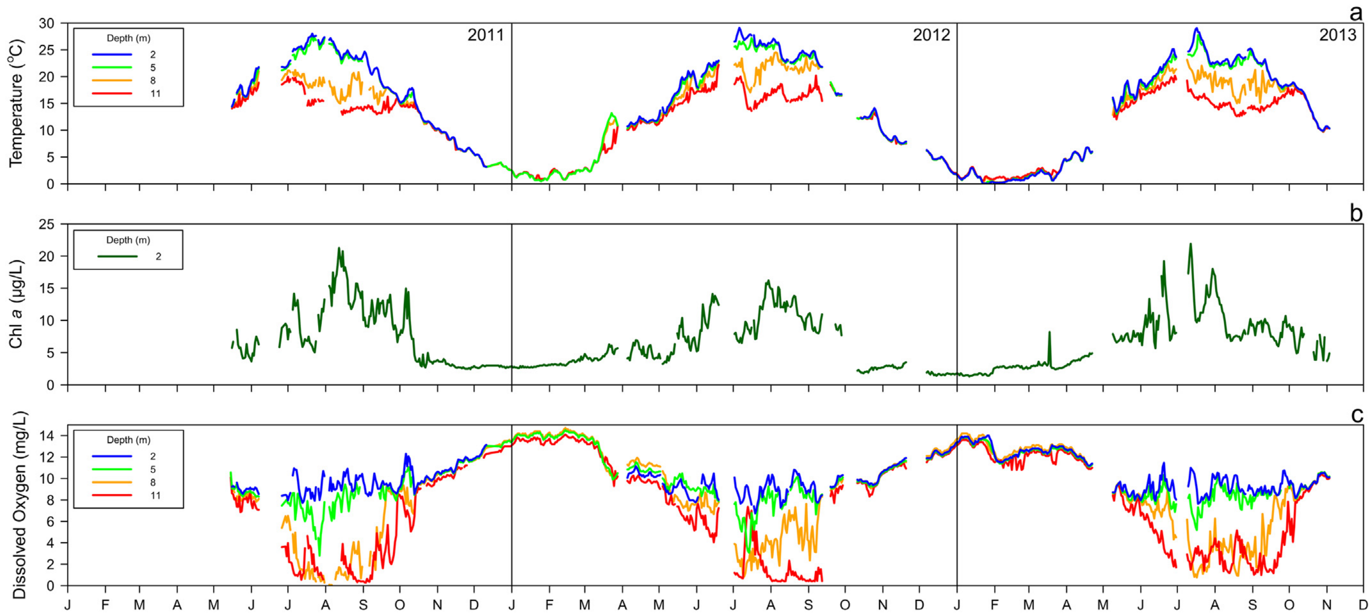

Fig. 3. Daily averaged temperature (a), chlorophyll (b), and dissolved oxygen (DO; c) at the MLO station from 2011 to 2013. These data show the development of stratification, onset of hypoxia, and associated phytoplankton blooms as indicated by chlorophyll fluorescence changes as measured by a YSI sonde.

Results

High-frequency MLO data

Based on meteorological data from the MLO, prevailing weather during each of the three study years were quite different. For air temperature, 2012 was the warmest year, while 2011 and 2013 were not as warm with 2011 being slightly warmer than 2013. The year 2012, for the most part, had above average temperatures January through July; whereas, 2011 had a very cool late-winter, but a very warm summer and early-winter. 2013 had a cool late-winter and early-spring, followed by average temperatures through the rest of the year. Based on recorded precipitation, 2013 was slightly wetter than 2011, and both were much wetter than 2012. Years 2013 and 2011 had high precipitation in winter and spring, while 2012 had a dry spring and summer. Wind speeds during June–September when hypoxia was typically present varied as well. 2011 and 2013 were very calm compared to 2012, which was very windy – especially during August 2012.

Stratification in Muskegon Lake follows a unique trajectory (Fig. 3a). As surface waters warmed during the summer, bottom waters surprisingly grew colder. Water temperatures at the bottom of Muskegon Lake fell from ~19 °C to ~14 °C during the warmest months of the summer. As a result, stratification in Muskegon Lake grew stronger during the summer months due not only to warming of surface waters but also due to cooling of bottom waters.

The DO sensor data from the MLO revealed that both mild and severe hypoxia occur frequently in Muskegon Lake at the buoy location. Both types of hypoxia were detected in all three years of data for long periods of time (Figs. 3). DO concentrations were typically drawn down to hypoxic levels in late June and oxygenated conditions return following fall overturn in mid to late September. Over the years, mild hypoxia was detected as early as June 13th (as observed in 2012) and as late as September 30th (as observed in 2013), whereas severe hypoxia occurred as early as June 24th (as observed in 2013), and as late as September 29th (as observed in 2011). Hypoxia occurred in conjunction with strong thermal stratification (Fig. 3a) and high algal biomass (Fig. 3b). There are momentary disruptions of hypoxia that are coincident with decreased temperature and increased DO in the bottom waters of Muskegon Lake that suggest significant episodic intrusions of cold, DO-rich Lake Michigan water upwelling through the channel into Muskegon Lake (Weinke and Biddanda, in press). During these hypoxia-disruption moments, one can temporarily observe "floating hypoxia" - a condition where cold and dense DO-rich offshore waters displace Muskegon Lake bottom waters to intermediate depths, such that the water mass at intermediate depth is more DO-depleted than the bottom waters (Fig. 3c).

The average mild AHF was 30.8 days while the severe AHF was 17.0 days (Table 1). The average mild VHF was 15.4 days while the severe VHF was 8.2 days. The VHODobs is the slope of the volume-weighted DO over time during the nearly-linear decrease in hypolimnetic DO, and this decrease typically took place from late May to early July in Muskegon Lake. VHODvm and VHODadj rates were approximately 150% higher than VHODobs following corrections for vertical mixing and

Table 1
Lake system descriptors based on DO concentration for years 2011–2013. Areal Hypoxic factor (AHF) represents the number of days in a year that an area equal to the lake sediment surface area experiences hypoxia. Volumetric hypoxic factor (VHF) represents the number of days in a year that a volume equal to the lake volume experiences hypoxia. Volumetric Hypolimnetic Oxygen Depletion rate (VHOD) estimates are based on change in volume-weighted oxygen concentrations in the Hypolimnion (obs = observed rates based on raw DO concentrations measured by sensors, vm = vertical mixing, which is VHODobs, but accounting for vertical mixing of DO, and adj = adjusted, which is VHODvm, but accounting for temperature effects on metabolism). Mild hypoxia refers to oxygen depletion below 4 mg DO l^{-1}, whereas severe hypoxia refers to DO concentrations below 2 mg DO l^{-1}.

DO condition	Year			
	2011	2012	2013	Average (STDev)
Days mild hypoxia was detected	87	73	94	84.7 (10.7)
Mild areal hypoxic factor (days year^{-1})	35.1	24.2	33.1	30.8 (5.8)
Mild volumetric hypoxic factor (days year^{-1})	17.7	12.0	16.6	15.4 (3.1)
Days severe hypoxia was detected	67	62	51	60 (8.2)
Severe areal hypoxic factor (days year^{-1})	22.5	15.9	12.5	17.0 (5.1)
Severe volumetric hypoxic factor (days year^{-1})	11.7	6.2	6.8	8.2 (3.0)
VHODobs (mg O_2 l^{-1} d^{-1})	0.148	0.071	0.086	0.102 (0.041)
VHODvm (mg O_2 l^{-1} d^{-1})	0.273	0.212	0.267	0.251 (0.034)
VHODadj (mg O_2 l^{-1} d^{-1})	0.285	0.212	0.266	0.254 (0.038)

yearly temperature differences in the hypolimnion. However, the VHODvm and VHODadj rates were not meaningfully different. The highest VHOD rates with corrections were in 2011 and 2013, which were not meaningfully different, while 2012 was much lower. The VHODobs rates for 2012 and 2013 were not different, while 2011 was approximately twice as high (Fig. 4). The overall average corrected VHOD was ~0.250 g m^{-3} d^{-1}. These graphs show that oxygen is being used up faster than it can be replaced, and therefore there is a decline in oxygen content of the hypolimnion.

Overall, by raw days of hypoxia detection, 2013 leads in mild hypoxia, followed by 2011 and 2012 (Table 1). 2011 had the most days of severe hypoxia, followed by 2012 and 2013. The average number of days with mild and severe hypoxia was 84.7 and 60.0 days, respectively. Looking at each of the individual DO sensor detection of hypoxia by percent of monitoring days by years showed some interesting patterns. Severe hypoxia also never occurred at 2 m, and only once at 5 m in 2013 compared to all three years for mild hypoxia (Fig. 5). 2012 had the least amount of severe hypoxia at 8 m, but had the most at 11 m. 2011 and 2013 had similar amounts of severe hypoxia at 8 m and 11 m. Mild hypoxia never occurred at 2 m, but occurred at 5 m in all three years for short periods of time (Fig. 5). Mild hypoxia for both 8 m and 11 m occurred most frequently in 2011, followed by 2013 and 2012. In all 3 years of time-series observations, there was always a higher occurrence of mild hypoxia at 11 m than 8 m, and more severe hypoxia was detected at 11 m than 8 m.

By the measure of number of days of hypoxia detection at and below a depth, 2011 was the most severe followed by 2013 and then 2012 (Tables 1 and 2; Fig. 5 and ESM Fig. S2). The average number of days that mild hypoxia was detected at 8 m and 11 m were 78 and 46 days, respectively. An estimated ~25% of the lake volume was mildly hypoxic for ~1.5 months each year, and ~10% of the volume was mildly hypoxic for ~2.5 months. The average number of days of severe hypoxia was 47 days at 8 m and 13 days at 11 m, which again reflects ~25% and 10% of the lake volume respectively. Severe hypoxia at and below 8 m was only continuously persistent in 2011. Year 2011 experienced similar numbers of days of mild and severe hypoxia at and below 11 m (Table 2, Fig. 5 and ESM Fig. S2).

Lake-wide hypoxia confirmation

The lake-wide profiles on several occasions confirmed the presence of hypoxia across Muskegon Lake on days when the MLO detected hypoxia. The DO profiles indicated that all 5 test-sites were fairly comparable (Fig. 6). The first profile date shows a similar oxycline across the lake. All 5 sites had mild and severe hypoxia in late July 2011 (Fig. 6a). The second profile date occurred roughly a week after the first trip in early August, which again showed hypoxia at all 5 sites and comparable DO profiles among the sites (Fig. 6b). A year later in mid-July 2012, mild hypoxia was shown to occur at all 5 sites, with all profiles comparable (Fig. 6c). The profiles also show higher DO concentrations in the bottom waters, and overall higher bottom water DO concentrations in the western part of the lake compared to the eastern side, lending credence to the idea that very-cold, high DO water from Lake Michigan was intruding into the bottom of Muskegon Lake during that period.

Seasonal monitoring

The 11 years of long-term seasonal shipboard monitoring revealed that Muskegon Lake has had at least a decade long history of mild and severe hypoxia during the summer (Fig. 7). Both types of hypoxia have been detected in at least 0–4 of the 6 sites every year since 2003. We did not expect hypoxia to occur at all of the 6 sites since 2–3 of the 6 sites in the long-term seasonal survey were too shallow to experience prolonged stratification; hence these are quite conservative estimates of hypoxia incidence. Nevertheless, it is becoming clear that during this decade-long seasonal observation period one can discern an overall trend of increasing occurrence of both mild and severe hypoxia regardless of season. The highest occurrence of hypoxia of any kind in July was 4 sites in 2011 and 2013. Overall, mild hypoxia was seen at more sites than the severe hypoxia, and the incidence of both mild as well as severe hypoxia showed an increasing trend since 2003, suggesting that the occurrence of summer time hypoxia in this ecosystem may be increasing through the years.

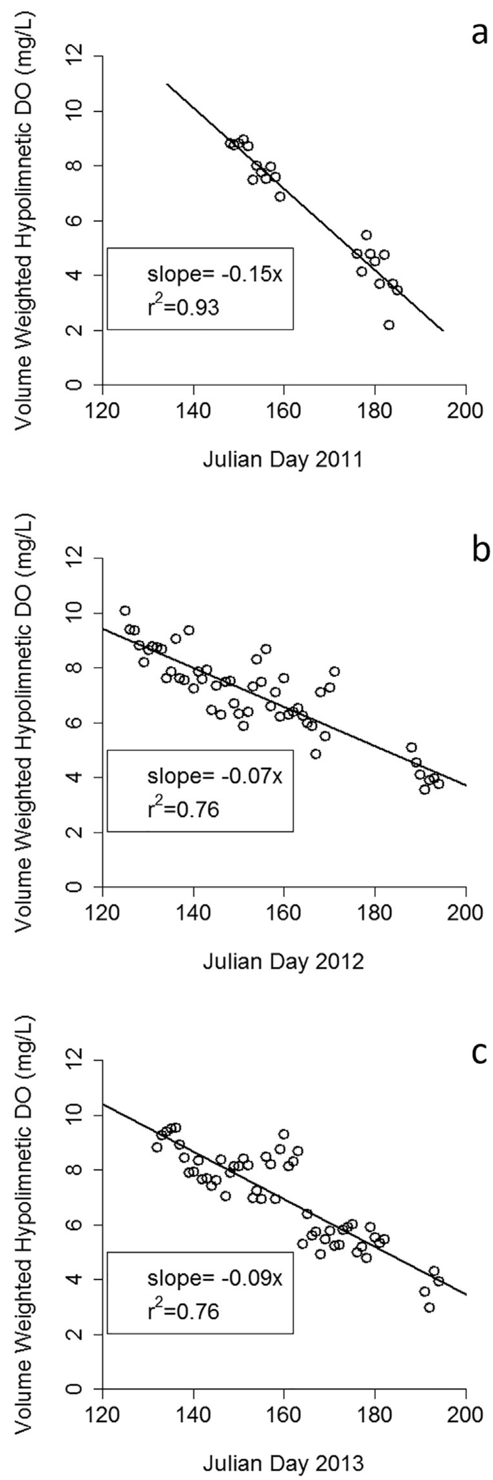

Fig. 4. Volumetric Hypolimnetic Oxygen Depletion estimates (VHODobs) during 2011 (a), 2012 (b) and 2013 (c), based on measured change in volume-weighted DO in the hypolimnion. Rate units are in mg O_2 l^{-1} d^{-1} as represented by the regression slope of DO over Julian days.

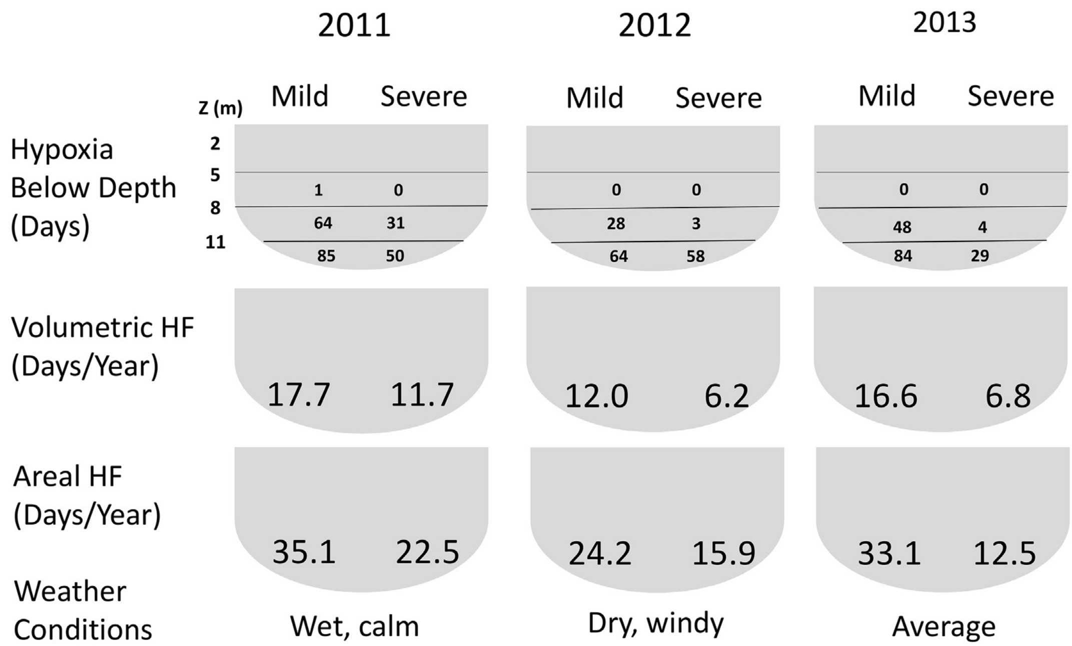

Fig. 5. Duration, intensity and distribution of hypoxia in Muskegon Lake during 2011–2013 as measured by the MLO. The first row shows the number of days that hypoxia was detected at each depth. In the second row are shown yearly, volumetric mild and severe hypoxia factor (VHF in days year^{-1}) and in the third row, areal mild and severe hypoxic factor (AHF in days year^{-1}). Average weather conditions during each year are described in the bottom row.

Discussion

Hypolimnetic hypoxia is a recurring annual feature of Muskegon Lake

This study and others have shown that bottom water hypoxia was a consistent, annual feature within Muskegon Lake (Biddanda, 2012; Vail et al., 2015; Salk et al., 2016; Weinke and Biddanda, in press). Due to the large temporal variability in hypolimnetic hypoxia observed in the time-series buoy data during 2011–2013 (Fig. 3), earlier discrete seasonal monitoring may have missed the incidence of hypoxia at the deeper locations during seasonal monitoring (Fig. 7). For example, time-series observations in the present study has shown that while hypoxia did occur every summer, the spatio-temporal dynamics of hypoxia in Muskegon Lake was complicated by episodic inflow of cold and oxygenated upwelled coastal waters from Lake Michigan (Weinke and Biddanda, in press). Although we discuss the recurrence of hypoxia from 2002 to 2013 and during the 3 years (2011–2013) in the present study, we also have evidence that it has been occurring in more recent years of 2014–2017 (www.gvsu.edu/buoy; Weinke and Biddanda, in press). From these data, it is quite clear that the occurrence of hypolimnetic hypoxia is an annually recurring summer-time event in this lake ecosystem over the past decade or more.

The persistence of hypoxia in Muskegon Lake is troubling, considering the improvements and remediation that has been implemented as part of the AOC-GLRI efforts. Steinman et al. (2008) showed the improvements in water quality as far as nutrients and chlorophyll, which tend to be correlated with hypoxia in inland lakes and estuaries. However, despite decreasing nutrients and chlorophyll over the past 30–40 years, hypoxia is still a feature of the bottom waters of Muskegon Lake. This allows us to speculate that, like other systems such as Lake Erie, perhaps hypoxia is a natural feature of Muskegon Lake (Zhou et al., 2012); or the lake has not had enough time to recover from the internal loading of legacy P from the sediments that promotes eutrophication and allows hypoxia to develop each year.

Table 2
Duration of hypoxia in the interior of the lake in years 2011–2013 expressed as the number of days in the year hypoxia was experienced below a certain depth in the lake. The first row shows the number of days hypoxia was detected at each depth. At 5 m, mild hypoxia was only detected once and not at all during 2012 or 2013. At 8 and 11 m, mild and severe hypoxia was detected every year. Average conditions for each year is described in the bottom row. Over the years 2011–2013, on average (1SD) mild hypoxia prevailed at depths 5, 8 and 11 m, for 0.3 (0.6), 47 (8), and 78 (12) days, respectively. Over the same years severe hypoxia prevailed at 5, 8, and 11, for 0 (0), 13 (16), and 46 (15) days, respectively.

Year	Type of hypoxia	# days hypoxic below depth		
		5 m	8 m	11 m
2011	Mild	1	64	85
	Severe	0	31	50
2012	Mild	0	28	64
	Severe	0	3	58
2013	Mild	0	48	84
	Severe		4	29
Average # days (SD)	Mild	0.3 (.6)	46.7 (18)	77.7 (11.8)
	Severe	0 (0)	12.7 (15.9)	45.7 (15)
% lake volume below depth		47	24	9

Hypoxia is variable in duration

Hypoxia has a long duration in the bottom waters of Muskegon Lake each year. Once DO trends lower in concentration in mid to late-June following thermal stratification, DO concentrations fall to hypoxic levels consistently until mid-September. It is persistent, and despite occasional disruptions, likely due to major mixing events and intrusion of oxygenated Lake Michigan water, hypoxia can quickly redevelop within 1–2 weeks in the hypolimnion (Salk et al., 2016). From these observations, we could estimate that the hypolimnion of Muskegon Lake is hypoxic for 2–3 months every year. Similar durations of hypoxia have been seen in numerous other lakes (Foley et al., 2012).

Hypoxia is a lake-wide phenomenon

On an areal basis, hypoxia is also expansive across Muskegon Lake. DO profiles from the seasonal monitoring program show that on average, hypoxia can be detected almost every year despite the temporal limitations of the study program. Test profiles performed at the same time that the MLO detected hypoxia, showed that hypoxia occurred at similar depths and levels at four other locations in Muskegon Lake.

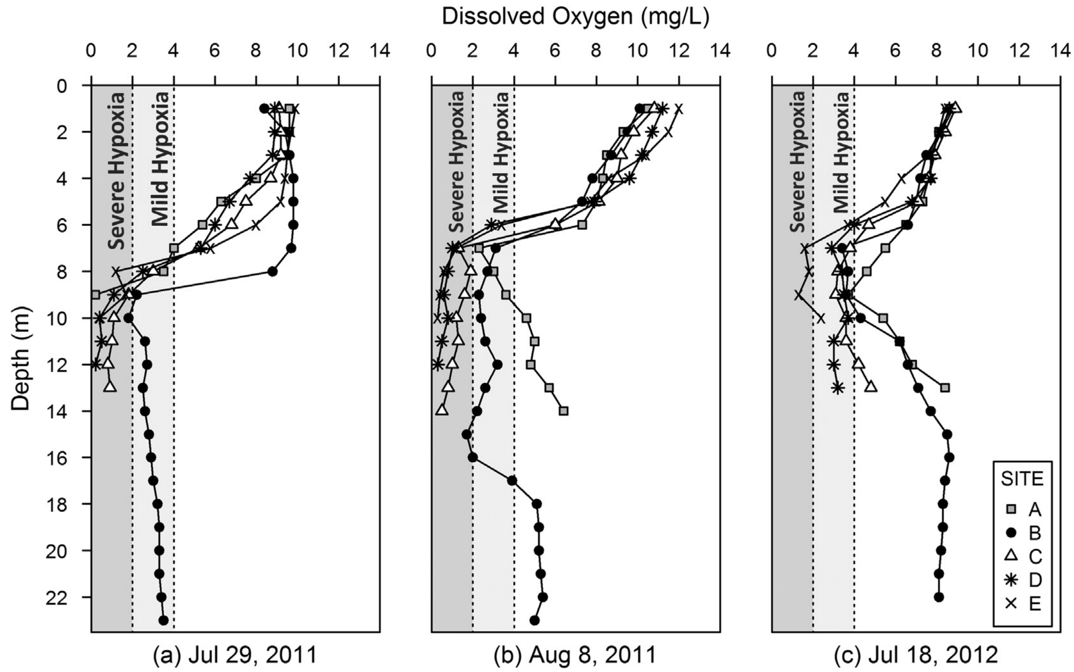

Fig. 6. Discreet hand-lowered sensor profiles of DO at five locations in July 2011 (a), August 2011 (b) and July 2012 (c). Data shows how oxygen levels changed with depth causing mild/severe hypoxia in the hypolimnion. Sites A, B, C, D and E refer to West basin, South basin, Central basin, MLO and East basin, respectively (shown as Hypoxia Test Profile sites in Fig. 1).

Strikingly similar patterns of hypoxia were observed at the West, South, Central, and East Basins. The relatively small size of the lake basin and low advection rates (water flow) may help explain this lake-wide occurrence of hypoxia. However, hypoxia is also spatially expansive across other much larger hypoxic systems like Lake Erie (Zhou et al., 2012).

Hypoxia is variable in intensity over time and space

Despite the persistence of hypoxia in Muskegon Lake over time and space, hypoxia is a variable feature on intra-annual and inter-annual timescales (Zhou et al., 2012). The high frequency MLO data have revealed these changes, and allows us to analyze and make inferences about why those differences occur. Daily changes in the amount of DO can be seen due to wind directional changes, periodic short-term changes via episodic wind-events, and weekly and monthly changes by shifting weather patterns and seasonal progression (Weinke and Biddanda, in press). In Lake Erie, the central basin hypoxia can be variable depending on the bathymetry and thickness of the hypolimnion (Bouffard et al., 2013; Zhou et al., 2012). The bathymetry of Lake Simcoe also seems to limit the formation of hypoxia, as only Kempenfelt Bay thermally stratifies enough for hypoxia to form in the bottom waters (Nürnberg et al., 2013). Drought, extreme precipitation, nutrient loading, and wind are also variables found to explain variability in hypoxic extent (Zhou et al., 2014).

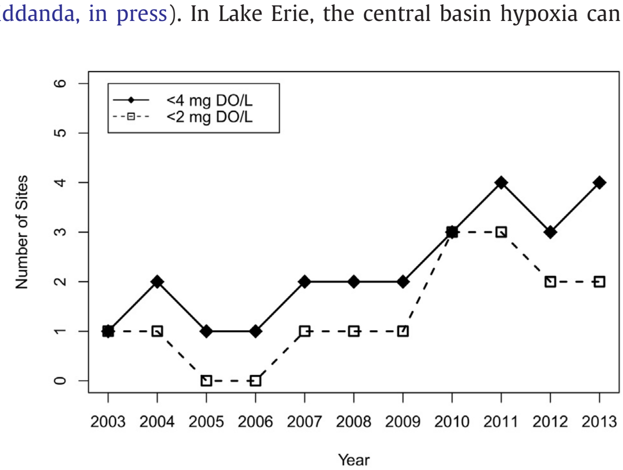

Fig. 7. Number of sites in the month of July (summer) where bottom water was either mildly hypoxic (<4 mg DO $^{-1}$) or severely hypoxic (<2 mg DO l^{-1}) during seasonal monitoring of 6 sites through years 2003–2013 in Muskegon Lake. Note: We did not expect hypoxia to occur at all 6 sites since 2–3 sites in the long-term seasonal survey are too shallow to experience hypolimnion.

More specifically, periodic intrusions of cold oxygenated upwelled water from Lake Michigan interrupts bottom water hypoxia in Muskegon Lake. During these times, the dense Lake Michigan water pushes the hypoxic water bottom water in Muskegon Lake upward in the water column causing hypoxia to be disconnected from the sediment and become detected at 5 and 8 m instead of the usual 8 and 11 m DO sensors. This leads to a temporary “floating” of hypoxic water within the water column across Muskegon Lake (Weinke and Biddanda, in press). Intrusions causing similar “floating” effects have also been observed and mapped between other bodies of water: Lake Michigan water into Green Bay (Hamidi et al., 2015), Lake Ontario water into the bottom of Hamilton Harbor (Bocaniov et al., 2012), and Mediterranean Sea waters into the Black Sea (Glazer et al., 2006; Falina et al., 2017).

Hypoxia is also variable interannually for various reasons (Nürnberg, 2004). Visually in graphs of the high-frequency DO data from 2011 to 2013, differences can be seen as far as when hypoxia is first detected, how long it takes to develop, its persistence through summer into fall, depth in the water column, and when it is finally relieved by the fall overturn. From three years of time-series meteorological data, we can start piecing together the picture of what role climate and weather play in assisting hypoxia formation each year. Based on multiple metrics of hypoxic intensity in Tables 1, 2011 was the most severe year with 2013 not that far behind. Air temperatures, which typically match closely with surface water temperature, should have indicated 2012 as the most severe year for hypoxia (Weinke and Biddanda, in press). Year 2012 had above average water temperatures from January through July which should have set the lake up to stratify earlier and stronger compared to the other years. However, 2013 had average summer water temperatures, and 2011 only had above average temperatures from May through July during the hypoxia set up period. Increasing temperatures and stratification are one of the biggest causes of hypoxic intensification (Sahoo et al., 2011; Foley et al., 2012).

Why was 2012 a less severe year for hypoxia than 2011 or 2013? Schmidt stability coefficients and wind speeds (data not shown here), which are important to hypoxia formation and persistence, illustrate that during the months of June–September the water column was much less stable in 2012 compared to 2011 and 2013 (Read et al., 2011). High wind speeds that are capable of mixing the lake were more common in 2012, which translated to lower Schmidt Stability coefficients during the months that hypoxia would occur. So not only is water temperature important to hypoxia formation and persistence, as the warmer 2011 was more severe for hypoxia than 2013, but the wind regime and water column stability play important roles as well. In addition, 2011 and 2013 had above average precipitation in late-winter and early spring, while 2012 had average to below average precipitation during this same period. It is possible that the increased precipitation may have supplied the lake with more inorganic nutrients and organic matter from runoff, which are important components of hypoxia formation as the former can fuel excess phytoplankton production in surface waters and the latter can cause fueling increased respiration in bottom waters, respectively.

All this, in turn, affects calculations that we make based on the data such as HF, VHOD, etc. Variations in VHOD rate were related to eutrophication and thermal stratification (Foley et al., 2012). Decrease in AHOD in Onondaga Lake was attributed to decrease in organic matter deposition into hypolimnion (Matthews and Effler, 2006). All these factors change from year to year depending on winter temperatures, summer temperatures, El Nino/La Nina cycles, wind speeds and directions, and algal biomass/ productivity (Hänninen et al., 2000 from Zhang et al., 2010).

Multiple factors drive the dynamics of hypoxia in Muskegon Lake

The two main factors that drive hypoxia in general are thermal stratification and oxygen demand. It is evident that like most northern temperate lakes, Muskegon Lake becomes intensely stratified in the summer as seen by temperature profiles throughout the lake. Also Muskegon Lake used to be eutrophic (now mesotrophic), with high phosphorus concentrations and algal productivity (Steinman et al., 2008). It is also evident that there are high rates of current productivity (Weinke et al., 2014; Dila and Biddanda, 2015), albeit possibly less than there used to be as nutrient conditions have improved (Steinman et al., 2008). Thus the legacy of high organic matter (e.g.lumber mill debris) in the sediments of Muskegon Lake is compounded each year by that year's still excessive productivity (Defore et al., 2016). The degradation of this organic matter (legacy wood debris and settling plankton) within the lower water column and the sediment is consuming DO through hypolimnetic oxygen demand. With the subsequent drop in DO within the bottom waters, the environment is more reducing which allows internal loading of nutrients back into the water column (Nürnberg et al., 2013; North et al., 2014). Future studies should examine the relative contributions of respiration in hypolimnetic water and the sediment and the sources of organic matter fueling hypoxia in Muskegon Lake.

Muskegon Lake may also develop hypoxia as a result of being a drowned river-mouth. Constrained flow conditions from Muskegon Lake to Lake Michigan are a common characteristic of the many drowned river-mouths along the east shore of Lake Michigan (Larson et al., 2013). Muskegon River, draining the second largest watershed in Michigan, delivers large amounts of nutrients to Muskegon Lake (Marko et al., 2013). The lake is also constrained on the western side by a narrow shipping channel causing a longer residence time that enables nutrients delivered by the river to be processed within the lake. Thus, the longer residence time, amplified by reduced river-loading during the summer stratified months, may be the main reason that this drowned river-mouth lake has such high productivity combined with hypoxia during the summer–fall period (Dila and Biddanda, 2015; Defore et al., 2016; Weinke and Biddanda, in press). The constrained flow may cause nutrients to get trapped in the drowned river mouth supporting more eutrophic conditions and enabling hypoxic events (Sanger et al., 2012; Marko et al., 2013). Ten other drowned river-mouth lakes along Michigan's western coast also experience hypoxia once they are thermally stratified in the summer (Carl Ruetz and Greg Chorak, Grand Valley State University, pers. comm.), so hypoxia may be a natural feature of these types of Great Lakes estuaries.

Muskegon Lake's hypoxia is comparable to other hypoxic environments

Calculations of areal and volumetric hypoxic/anoxic factors and VHOD rates all fell within ranges seen in other lakes where these calculations have been performed. Our aerial and volumetric severe hypoxic factors are again representative of DO <2 mg/L, while most papers calculate only an anoxic factor, representative of DO <1 mg/L. Our areal severe hypoxic factors fall within and above the range seen in Nürnberg et al. (2013), which ranged from 4 to 16 days. Our areal severe hypoxic factors fall on the low end of those reported in Nürnberg (1995), which ranged from 0 to 83 days. Our volumetric severe hypoxic factors relatively low for a eutrophic lake, which range from 27 to 168 days (Foley et al., 2012), far exceeding that of mesotrophic Muskegon Lake at 6–12 days.

The VHOD calculations from the MLO data give rates of oxygen depletion (0.07–0.3 mg O_2 l^{-1} per day) that are well within what have been reported for other lakes and reservoirs around the world that range from 0.001–0.6 mg O_2 l^{-1} per day (Fulthorpe and Paloheimo, 1985; Rutherford et al., 1996; Hawley et al., 2006; Beutel, 2003; Foley et al., 2012). It is interesting to note that our VHOD rates nearly double when a correction for vertical mixing is introduced, which suggests that despite stratification forming a barrier to regular mixing between the epilimnion and hypolimnion, there is still some DO delivered or diffused between the two layers. Therefore, the VHODobs, calculated from only the observed depletion of DO, underestimates the estimated VHOD by roughly half in Muskegon Lake indicating that the net change in DO in ecosystems is a result of multiple interactions. VHODadj, which is adjusted for the differences in inter-annual hypolimnetic temperature, resulted in minimal change in rate (Matthews and Effler, 2006; Foley et al., 2012).

Role of time-series lake observatories in advancing ecosystem science, restoration and education

There is a growing body of evidence suggesting that lakes play a disproportionately large role in the global carbon cycle and climate (Cole et al., 2007; Tranvik et al., 2009). Early models saw inland waters as passive conduits, delivering terrestrially derived organic matter to the sea. Recent studies find that only around one third of this terrigenous carbon reaches the oceans; the balance is returned to the atmosphere as CO_2 or buried in freshwater sediments (Biddanda, 2017). In addition, the globally distributed lakes serve as effective indicators of global climate change due to their sensitivity to change in surrounding atmosphere and terrestrial catchments (Biddanda and Cotner, 2002; Adrian et al., 2009; Schindler, 2009; Williamson et al., 2009).

Globally, aquatic systems are increasingly suffering from the growth of human population, industrialization, invasive species, land use and climate change (Vitousek et al., 1997). Responses to these stressors can be highly nonlinear and therefore unpredictable (Scheffer et al., 2001). Long time series high-resolution data have the potential to give early warning signs of such state shifts before they occur (Wang et al., 2012). Observatories such as MLO, can measure a variety of physical, chemical, and biological properties of natural waters (Porter et al., 2009; Johnson and Claustre, 2016; Vail et al., 2015), providing a data stream that can analyze, in real-time, events such as metabolic balance, algal bloom dynamics, and response to climate forcing and episodic weather events (Staehr et al., 2010; Jennings et al., 2012). With the availability of such time-series data, students can test hypotheses, explore seasonal patterns, and develop a fuller understanding of ecosystem dynamics (Sagarin and Pauchard, 2010; Vail et al., 2015). Additionally, the recreational and economic impact of fisheries can be enhanced by access to real-time lake conditions.

Widespread DO reductions in the world's freshwater bodies may be exacerbating hypoxia and resulting in reduced habitat for fish and invertebrates and altering primary productivity and microbial life (Weinke and Biddanda, in press), but also may be increasing the emission of potent greenhouse gasses such as CO_2, CH_4 and N_2O from hypoxic zones globally further exacerbating the situation via a positive feedback loop to climate (Zhang et al. 2010; Bastviken et al., 2011; Salk et al., 2016). Indeed, coincident with bottom water hypoxia in Muskegon Lake, we have recorded high bottom water P concentrations as evidence of internal loading (Weinke and Biddanda, in press). 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 the confluences of watersheds and global warming strengthens thermal stratification negatively affecting water quality and other ecosystem services (Allan et al., 2012; Michalak, 2017; Steinman et al., 2017).

Conclusions

The present study used high-resolution spatio-temporal data acquisition to assess the state of a stressed Great Lakes estuarine ecosystem that is undergoing restoration. Sensors deployed throughout the water-column successfully detected and tracked hypoxia during summer stratification in Muskegon Lake and made the following key findings: 1) Hypoxia did occur every summer, however the timing and intensity of hypoxia was complicated by episodic inflows of cold and oxygenated waters from Lake Michigan, 2) Observations made at MLO were representative of the lake as a whole, and 3) Contrary to expectations, hypoxia was more or less similar in each of the observed 3 years but with a tendency for more intense hypoxia in years with greater spring precipitation. Furthermore, a decade-long discrete monitoring study suggested that the incidence of hypoxia has been increasing in recent years. Scattered field sampling of Muskegon Lake had occasionally detected hypoxia in the past; however, the present study was the first to provide proof of sustained and persistent seasonal hypoxia and its recurring appearance each year. Episodic rises in deep water DO in Muskegon Lake after summer stratification has set in, suggests that there is possible significant intrusion of cold and oxygenated coastal Lake Michigan water entering through the navigation channel. Empirical measurements and modeling studies are underway to assess the net year-long and lake-wide effect of such intrusions on stratification as well as hypolimnetic hypoxia. Lessons learned from analysis of time-series empirical data coupled with hydrodynamic modeling of the Muskegon Lake system, could be applied to other coastal and estuarine systems to help solve emerging problems of societal significance and assist with improved ecosystem restoration and forecasting practices to protect and conserve essential ecosystem services.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2017.12.008.

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