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Review

Widespread prevalence of hypoxia and the classification of hypoxic conditions in the Laurentian Great Lakes

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ABSTRACT

Aquatic hypoxia within the Laurentian Great Lakes has contributed to various adverse ecological consequences and stimulated research interest in recent decades. An analysis of published peer-reviewed journal articles from 2000 to 2020 demonstrates an increasing trend of studies related to hypoxia in the Laurentian Great Lakes. However, the majority of these studies (78%) focus on Lake Erie and in particular the well-documented hypolimnetic hypoxic conditions that develop in the central basin of Lake Erie. This hypoxic zone is relatively large (up to 1.5 million ha), has substantial ecological effects, and motivates monitoring programs and water quality improvement initiatives. Nonetheless, the hypoxic zone in the central basin of Lake Erie is only one of over twenty documented hypoxic zones in the Laurentian Great Lakes. Moreover, hypoxic conditions in the Great Lakes are quite diverse. Here, we define and characterize a four-fold classification of Great Lakes hypoxic conditions: 1) hypolimnetic hypoxia, 2) over-winter hypoxia, 3) diel hypoxia, and 4) episodic hypoxia. We suggest that Great Lakes research and monitoring programs should seek to more broadly document hypoxic conditions and develop models to predict the temporal and spatial occurrence of hypoxia. Such efforts are particularly timely as future climatic conditions contributing to warmer temperatures, longer and more intense stratified periods, increased spring nutrient loading and more variable allocthonous inputs are expected to exacerbate three of the four hypoxic conditions described for the Great Lakes (hypolimnetic, diel, and episodic hypoxia).

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Introduction

Hypoxia is a widespread phenomenon throughout freshwater and marine ecosystems. Hypoxia is harmful to aquatic organisms that rely on aerobic respiration, from single-celled plankton to complex vertebrates (Abdel-Tawwab et al., 2019; Roman et al., 2012). The development and presence of hypoxia has long been monitored and studied in vulnerable coastal systems; for example, the Gulf of Mexico and Chesapeake Bay "dead zones" have received broad attention in both popular press and peer-reviewed journals. Both these high-profile systems are located near areas of high human population density, have potential links to climate change (Du et al., 2018; Dubravko et al., 2005, 1996; Najjar et al., 2010), and have experienced increased severity of hypoxia in recent decades (Du et al., 2018; Turner et al., 2008). However, hypoxia is also prevalent and potentially deleterious in freshwater systems (Jane et al., 2021), including the Laurentian Great Lakes (herein referred to as the Great Lakes). While select locations characterized by hypoxia in the Great Lakes have been subject to concentrated research and monitoring interest (e.g., central basin of Lake Erie), there is a paucity of programs describing and mapping the extent of hypoxia relative to the size and diversity of systems across the Great Lakes. It is therefore useful to assess the range of hypoxic conditions that occur throughout the Great Lakes and for resource managers to understand and identify the attributes of different hypoxic phenomena, the mechanisms leading to such phenomena and the potential consequences of hypoxic conditions.

Hypoxia is a naturally occurring process in many aquatic systems, but the global prevalence and extent of hypoxia has been exacerbated by nutrient loading, habitat alteration, and climate change in both marine (Altieri and Gedan, 2015; Meire et al., 2013; Rabalais et al., 2010) and freshwater (Collingsworth et al., 2017; Jenny et al., 2016; North et al., 2013) systems. Since the 1960′s, incidences of hypoxia in coastal marine systems have increased over thirtyfold, with the number of recognized dead zones doubling every ten years over the same time period (Diaz and Rosenberg, 2008). Inland water bodies throughout the world have concurrently experienced increases in the presence and severity of hypoxia (Saari et al., 2018), and the Great Lakes are no exception to this trend. Increased frequencies of hypoxia have been reported in the central basin of Lake Erie (Scavia et al., 2014) since the 1990′s, and extensive seasonal hypoxia has recently been documented in Muskegon Lake (Biddanda et al., 2018), Green Bay (Klump et al., 2018), and Saginaw Bay (NOAA GLERL Technical Report, 2013). The intensification of hypoxia in the Great Lakes has also led to new U.S. legislation and increased international efforts to improve our understanding of hypoxia in the United States and Canada, including the Harmful Algal Bloom and Hypoxia Research and Control Act (1998; Amendments: 2004, 2014) and the binational Great Lakes Water Quality Agreement (Great Lakes Water Quality Protocol, 2012), each of which explicitly list hypoxia as a major concern for ecosystem health in the Great Lakes.

Early research regarding hypoxia in the Great Lakes focused on the central basin of Lake Erie, where elevated levels of hypolimnetic hypoxia were recognized since at least the mid-20th century (Rosa and Burns, 1987). Several studies have described how low oxygen conditions may develop in the Great Lakes. Beeton (1965) recognized the connection between human-induced eutrophication of the Great Lakes and increased hypoxia severity. Charlton (1980) described the complex interactions between productivity, temperature, and hypolimnetic thickness that cause reduced hypolimnetic oxygen concentration in the Lake Erie central basin. Moreover, Charlton suggested that decreasing lake productivity alone would not be sufficient to eliminate hypoxic phenomena in Lake Erie because the unique bathymetry of the lake creates a thin hypolimnion in the central basin and this relatively small volume of bottom water is fairly readily depleted of oxygen. Patterson et al. (1985) found that dissolved oxygen dynamics within Lake Erie were largely explained by turbulent mixing, wind speeds, sediment oxygen demand, and stratification. The average hypolimnetic dissolved oxygen depletion rate in the central basin of Lake Erie increased from 1929 to 1980 (Rosa and Burns, 1987), highlighting the trend of increasing water quality deterioration during the 20th century. Recently, there has been a resurgence in research interest devoted to Great Lakes hypoxia as: a) hypoxic conditions have persisted despite overall decreases in nutrient loading (e.g., Scavia et al., 2014) and b) aquatic resource managers look to predict the impacts of potentially worsening and more widespread hypoxia under future climatic scenarios. (e.g., Ludsin and Höök, 2013; Watson et al., 2016).

The direct and indirect effects of hypoxia on aquatic ecosystems and the services provided by these ecosystems are prolific and include the degradation of benthos and zooplankton community health (Goto et al., 2012; Hale et al., 2016), loss of fish habitat (Budnik et al., 2021), changes in the efficiency of commercial fishing (Chamberlain et al., 2020), and drinking water taste and odor problems (Diaz and Rosenberg, 2011; Ruberg et al., 2008). Many of these consequences are perceived as negative, but hypoxia can have more complicated effects on organisms when it occurs at sub-lethal levels. Hypoxic zones may provide refuge for zooplankton from planktivorous fish (Vanderploeg et al., 2009a; Vanderploeg et al., 2009b), may increase feeding efficiency and consumption by piscivorous fish (Brandt et al., 2011), and may increase commercial fishing catches by concentrating target species in smaller areas (Chamberlain et al., 2020; Kraus et al., 2015). Hypoxia may rise to an issue of concern for aquatic resource managers when the duration, magnitude, or extent of the phenomenon increases beyond natural levels. The annual economic cost of elevated levels of hypoxia is difficult to estimate, but the ecosystem services (e.g., recreational boating, fishing, tourism, drinking water) that are threatened by hypoxia in Lake Erie alone generate an annual income of over $50 billion (LEIA, 2012). As such, documenting where hypoxia occurs in the Great Lakes and understanding the mechanisms by which hypoxia has developed or intensified in recent decades is informative for the management of Great Lakes ecosystems and may allow for better direction of management actions.

Several distinct types of hypoxia (alternatively, hypoxic conditions) occur throughout the Great Lakes. While the seasonal hypolimnetic hypoxia that develops annually in the central basin of Lake Erie appears to receive the greatest research and monitoring attention, other hypoxic conditions are also common. Complex combinations of physiochemical and biological phenomena result in the development of diverse hypoxic conditions with unique spatial and temporal dynamics. The purpose of this review is to categorize and describe the diversity of hypoxic conditions present within the Great Lakes and to characterize the physical and anthropogenic processes that can cause hypoxia to develop. In doing so, we hope to expand the focus of research and management effort to encompass all hypoxic conditions that affect this freshwater system. Importantly, this review examines the processes that cause hypoxia to develop but intentionally avoids discussing the ecological effects of hypoxia in order to present a more focused analysis. Specifically, our objectives are to (i) classify the different types of hypoxic conditions that occur throughout the Great Lakes, (ii) examine the documented physical extent of hypoxia and the breadth of related research within the Great Lakes region, and (iii) identify key knowledge gaps as areas for future research.

Classification of hypoxic conditions

Several studies have defined hypoxia thresholds (e.g., 2.0 mg O_2 L^{-1}, Diaz and Rosenberg, 2008; 3.0 mg O_2 L^{-1}, Howell and Simpson, 1994; 4.0 mg O_2 L^{-1}, Paerl et al., 2006), but the exact concentration below which dissolved oxygen has meaningful biological effects varies depending on the organism of interest, the environment, and the duration of exposure (e.g., Hrycik et al., 2017). In practice, the term hypoxia represents a spectrum of oxygen concentrations ranging from slightly depleted oxygen levels to complete anoxia. Hypoxia is sometimes defined in terms of measurable consequences reflected upon the ecosystem, such as the oxygen concentration at which fisheries collapse (Renaud, 1986), or a particular biological function becomes impaired (Diaz and Rosenberg, 1995). Generally, fishes experience sub-lethal effects of hypoxia (e.g., decreased consumption and growth) at oxygen concentrations much higher than those that lead to direct mortality. The range of oxygen levels likely to negatively impact the population biomass of fishes varies widely among taxa (Hrycik et al., 2017). This variation is evident even within the Great Lakes. For example, yellow perch (*Perca flavescens*) have demonstrated a relatively high tolerance for hypoxic conditions in both experimental and field studies (Almeida et al., 2017; Roberts et al., 2011), while lake trout (*Salvelinus namaycush*) are adversely affected by oxygen concentrations at or below 7.0 mg O_2 L^{-1} (Evans, 2007). The duration of exposure and the physiology of the organism are important factors in determining the impact of hypoxia on aquatic fauna. Whereas most fishes succumb to hypoxic conditions relatively quickly, many invertebrate species can survive severe hypoxia for days to weeks (Vaquer-Sunyer and Duarte, 2008). For this review, we recognize that any single dissolved oxygen concentration cannot accurately describe the scope of negative consequences for all aquatic fauna. Instead, we define the term “hypoxia” as any scenario in which decreased dissolved oxygen concentrations have demonstrable effects on the organisms or ecological functions of an ecosystem.

Hypoxic conditions in aquatic systems can develop through a variety of processes. Oxygen can be depleted, and a system can become hypoxic, if a) oxygen consumption rates exceed rates at which dissolved oxygen is generated (e.g., if aerobic respiration exceeds photosynthesis) and b) if depleted oxygen concentrations cannot be adequately replenished from external sources (e.g., if density stratification or ice cover limit oxygen replenishment through diffusion at the air–water interface). Conditions that cause hypoxia can be cyclic, recurring on a seasonal or daily basis, or highly dynamic and spatiotemporally variable. For example, rapid movement of water can lead to a given location quickly shifting from oxygenated to hypoxic conditions. Such phenomena are well-documented in nearshore marine systems where offshore hypoxic waters may rapidly intrude nearshore and displace oxygenated water (e.g., Booth et al., 2012; Fennel and Testa, 2019; Grantham et al., 2004).

Although the specific mechanisms by which hypoxia occurs depend on the system of interest, we can identify four broad categories of hypoxic conditions that occur in the Great Lakes region: hypolimnetic hypoxia, over-winter hypoxia, diel hypoxia and episodic hypoxia. Below, we describe each of these categories, as well as some of the different hypoxia manifestations within each category. Importantly, we focus on hypoxic conditions evident in the Great Lakes and do not discuss other types of phenomena that may lead to hypoxia in other systems.

Hypolimnetic hypoxia

The mechanisms and factors that contribute to the development of hypolimnetic hypoxia have been understood since at least the early 20th century (e.g., Edmondson et al., 1956; Yoshimura, 1933). Warm summer air temperatures generate thermal density stratification throughout the water column, producing a distinct thermocline that separates the cooler hypolimnetic waters near the lakebed from the warmer epilimnetic waters near the lake surface, where oxygen is readily replenished through atmospheric diffusion. Mixing between the lake layers is inhibited by strong,

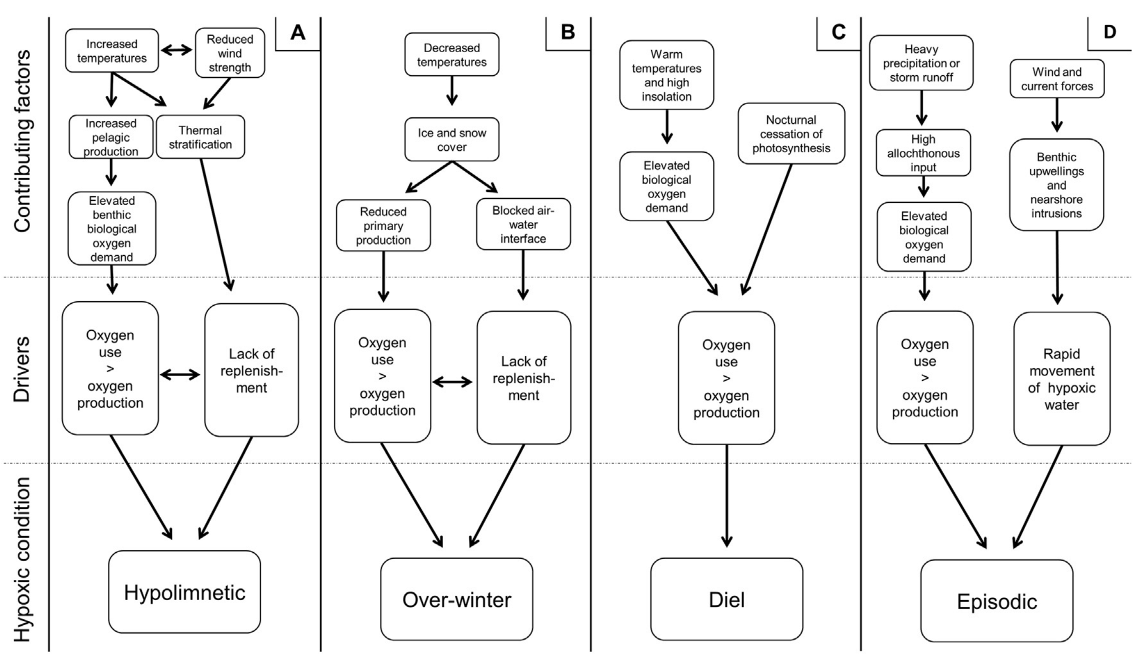

Fig. 1. Conceptual diagram illustrating the physical and biological principles driving diverse hypoxic conditions throughout the Laurentian Great Lakes, including a) hypolimnetic, b) over-winter, c) diel and d) episodic hypoxia. Vertical arrows indicate logical flow of progression from driving factors to conditions. Horizontal arrows indicate an interaction of factors within a hierarchical level.

temperature-dependent water density gradients, which suppress the transfer of heat and dissolved gas from the surface layer to the benthos. Vertical mixing is further suppressed by the characteristically weak winds that occur during the stratified summer (Cannon and Troy; 2018; Hamidi et al., 2013) and the well-mixed surface layer rarely extends to depths greater than 20 m. High primary productivity in the nutrient- and light-rich surface layer increases oxygen demand in the hypolimnion as organic material settles to the bottom. The respiratory activity of microbial decomposition depletes oxygen faster than it can be replenished due to either mixing with surface waters or primary production in the hypolimnion, which remains low due to limited light and nutrient availability. Dissolved oxygen concentrations in the hypolimnion gradually decrease as the available oxygen supply is exhausted. This decline continues throughout the stratified summer until surface waters cool and trigger a lake turnover event in the fall, allowing mixing of the stratified layers and a subsequent restoration of hypolimnetic oxygen levels. We define hypolimnetic hypoxia as a gradual, persistent reduction in the dissolved oxygen concentration of bottom waters following the development of a density gradient (e.g., thermocline) that reduces the vertical mixing of the water column (Fig. 1A).

Once established, hypolimnetic hypoxia often persists for the duration of the stratified summer period (e.g., Lake Erie central basin) but considerable variation in the spatial and temporal dynamics of the phenomenon have been reported among systems. Even relatively shallow systems (e.g., Muskegon Lake, 24 m, Biddanda et al., 2018; Western Lake Erie, 11 m, Loewen et al., 2007; Green Bay, 10 m, Fig. 2A) can develop stratification and subsequent hypoxia when wind-driven mixing is reduced and surface water temperatures rise. However, in shallow systems and systems receiving pulsed upstream discharges, stratification may not be maintained throughout the summer and therefore hypolimnetic hypoxia may establish for a period of time, then break down and subsequently reestablish. Wind and current patterns can also influence the spatial dynamics of hypolimnetic hypoxia after it develops. Seiches and gyres can drive oscillatory transport of hypoxic water over variable time scales (e.g., Saginaw Bay, NOAA, 2013; Lake Erie central basin, Bouffard et al., 2013; Saylor and Miller 1987). Fine-scale observational data and predictive models of Lake Erie's central basin show substantial inter-annual variability in the development, movement, and extent of seasonal hypolimnetic hypoxia (Del Giudice et al., 2018; Kraus et al., 2015; Zhou et al., 2013). Even the shape of the thermocline may affect the dynamics of hypolimnetic hypoxia. For example, the thermocline in the Lake Erie central basin develops a bowl-like depression in offshore waters, thereby reducing the volume of isolated hypolimnetic water and increasing the time for which oxygen is depleted (Beletsky et al., 2012). Moreover, benthic sinkholes throughout the Great Lakes are prone to stratification, which is often followed by the seepage and accumulation of hypoxic groundwater (Voorhies et al., 2012). Hypolimnetic hypoxia occurs in diverse and variable forms, and the examples given here are likely not comprehensive of the entire array of hypoxic phenomena that fall into this category.

Over – winter hypoxia

Water bodies located in temperate climates have the potential to experience surface freezing and ice accumulation during winter.

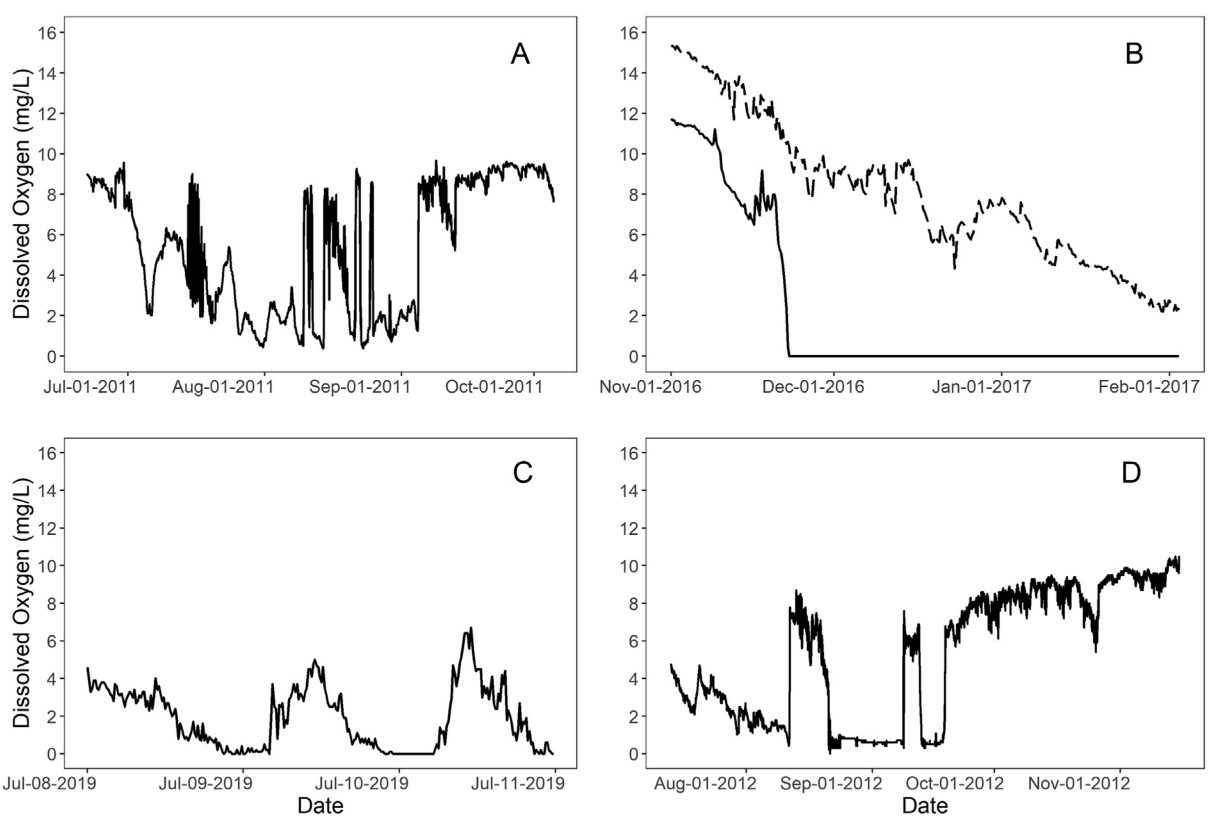

Fig. 2. Hypoxia observed in long-term monitoring datasets in various locations throughout the Great Lakes. A) Ten-minute hypolimnetic oxygen concentration (mg/L) in Green Bay, Lake Michigan from June 21st to October 5th, 2011 (data courtesy Dr. Val Klump of University of Wisconsin). B) Average 6-hour hypolimnetic oxygen concentration (mg/L) directly at the sediment–water interface (solid line) and 0.5 m above the substrate (dotted line) at Coreyon Reef in Saginaw Bay during the winter of 2016. C) Fifteen-minute dissolved oxygen values at the mouth of Old Woman Creek estuary, Huron, Ohio from July 8th to July 11th, 2019 (NOAA NERRS data). D) Ten-minute hypolimnetic oxygen concentration (mg/L) within Fairport Harbor, Ohio from July 13th to November 15th, 2012 (data courtesy Kraus et al., 2015).

Thick layers of ice and snow cover may reduce light penetration and inhibit the ability of aquatic photosynthetic organisms to produce oxygen (Greenbank, 1945). Similarly, the blocked air–water interface eliminates oxygen renewal from diffusion or wave action at the surface layer (Magnuson et al., 1985). Subsequent respiration by aquatic organisms reduces dissolved oxygen levels under the ice, sometimes generating hypoxic conditions (Greenbank, 1945; Magnuson et al., 1985; Yang et al., 2019). Some freshwater diatom species proliferate during winter months by colonizing the underside of ice (e.g., Bondarenko et al., 2006), but under-ice photosynthesis is only sufficient to meet respiratory oxygen demands in shallow, snow-free lakes with no underlying eutrophication issues (Song et al., 2019). Conversely, in nutrient-rich waters, oxygen consumption may actually increase during the under-ice period as freezing ice releases dissolved nutrients to the liquid water below, fueling increased metabolic activity (Yang et al., 2016). The subsequent rate of oxygen consumption is greater than the rate at which oxygen can be replenished due to the inhibiting characteristics of the ice layer. We define over-winter hypoxia as a reduction in the dissolved oxygen concentration in part or all of the water column following the development of a layer of surface ice at the air–water interface (Fig. 1B).

The variability and dynamics of over-winter hypoxia are not often investigated given the difficulty involved in accessing and monitoring the under-ice aquatic environment. Over-winter hypoxia seems to present in one of two ways in freshwater systems. Within shallow or inland systems, the interruption of oxygen transfer at the air–water interface may be sufficient to produce hypoxia throughout most of the water column (Magnuson et al., 1985; Marshall et al., 2021). This can have a devastating effect on aquatic biota, often resulting in substantial winterkills (Greenbank, 1945). However, in deeper systems, over-winter hypoxia only develops near the sediment while waters closer to the surface maintain higher dissolved oxygen concentrations (Epstein et al., 1974; Kalejs, 2017; Fig. 2B). As with hypolimnetic hypoxia, this trend is likely related to seasonal mixing and thermal stratification. Although primary production and oxygen renewal may still occur near the surface, where light penetrates the ice, the absence of wind-induced mixing limits oxygen renewal at depth, with weak inverse stratification near the ice-water interface further restricting mixing due to radiative convection (e.g., Yang et al., 2019) While this form of near-bottom, over-winter hypoxia may not present a high risk of direct mortality to most fishes, it has been implicated in the degradation of spawning habitat, affecting egg survival and recruitment for fall-spawning species (e.g., Kalejs, 2017; Madenjian et al., 2008).

Diel hypoxia

Diel hypoxia is a natural phenomenon that can develop in highly productive, shallow, aquatic habitats during warmer months. It is a common occurrence in wetlands and estuaries where it is driven by the interaction between variable rates of primary production and consistently high respiration-induced oxygen demand (Cheek et al., 2009). During the day, high levels of photosynthesis can adequately offset the oxygen consumed during respiration. However, as photosynthesis ceases at night, the high biological oxygen demand rapidly depletes dissolved oxygen concentrations to low levels, and atmospheric diffusion cannot adequately keep pace with demand. Dissolved oxygen is then replenished the next day when photosynthesis resumes. Furthermore, warm temperatures experienced in shallow waters limits oxygen solubility and contributes to rapid deoxygenation. The rates of oxygen consumption and renewal within these shallow, isolated systems are in such delicate balance that the nocturnal cessation of photosynthesis results in decreased dissolved oxygen within hours of sunset (Cornell and Klarer, 2008). We define diel hypoxia as a daily pattern of oscillating dissolved oxygen concentrations driven by rapidly fluctuating levels of oxygen demand and production within a shallow aquatic system (Fig. 1C).

The typical presentation of diel hypoxia is less variable than the other hypoxic conditions described above because the specific conditions required to produce diel hypoxia only occur in shallow, productive environments throughout the Great Lakes (e.g., Old Woman Creek estuary, Huron, Ohio). However, temporal variations in the severity of daily dissolved oxygen oscillations have been observed. After severe rainfall or flooding events, changes in water depth and hydrodynamic mixing may reduce the severity of diel hypoxia for several days (Cornell and Klarer, 2008). Coastal inlets are often transformed by nearshore currents and sedimentation patterns. As such, the connections between coastal wetlands and the main lakes are in a constant state of flux, altering the susceptibility of these systems to the development of diel hypoxia.

Episodic hypoxia

All of the forms of hypoxia described thus far develop because of seasonal or diurnal patterns. However, there are two mechanisms which cause hypoxia to arise suddenly in a less periodic, and therefore less predictable, manner. Rapid oxygen depletion may occur in slow-flowing systems that experience a sudden influx of organic material following heavy precipitation (e.g., combined sewer overflow events), especially in urban systems with high densities of impervious drainage areas and channelized tributaries (Gaulke et al., 2015; Kreutzberger et al., 1980). The acute pulse of nutrient-rich water leads to a strong increase in biological oxygen demand and hypoxia. Locally reduced oxygen concentrations can persist for several days to weeks after instances of sudden allochthonous input (Gaulke et al., 2015). The severity of these events depends largely on the duration of exposure, water depth, and the nutrient load into the system (Bell, 2008). In addition, abrupt nearshore intrusions of hypoxia can occur when strong winds generate coastal upwellings, where warm, oxygen-rich water is pushed offshore and replaced by cooler, potentially hypoxic waters from the offshore hypolimnion. (Kraus et al., 2015; Rao et al., 2014). Such events usually occur between lake layers within a single basin, but examples of inter-basin transfer of oxygen depleted waters have been documented (Jabbari et al., 2019). We define episodic hypoxia as a reduction in dissolved oxygen concentration following a discrete event that results in the sudden intrusion of hypoxic water or allochthonous nutrients into a system (Fig. 1D).

Hypoxia throughout the Great Lakes

Individual studies have documented occurrences of hypoxia throughout the Great Lakes since the early 20th century. However, to our knowledge, there is no comprehensive assessment of the extent of hypoxia within the Great Lakes and surrounding wetlands. As such, researchers and managers may not be aware of the widespread prevalence of hypoxia phenomena. To evaluate recent patterns of research related to hypoxia in the Great Lakes, we conducted an analysis of published papers. On March 8, 2021, we searched all databases of ISI Web of Science using the topic search query for hypoxia and specific Great Lakes ((“Lake Erie” OR “Lake Huron” OR “Lake Michigan” OR “Lake Ontario” OR “Lake Superior”) AND hypoxia) over the period of 2000–2020. This search demonstrated a general increase in the number of Great Lakes hypoxia papers published over this time period (Fig. 3A). We corrected for the general trend of increasing number of indexed publications and found a gradual increase in the proportion of Great

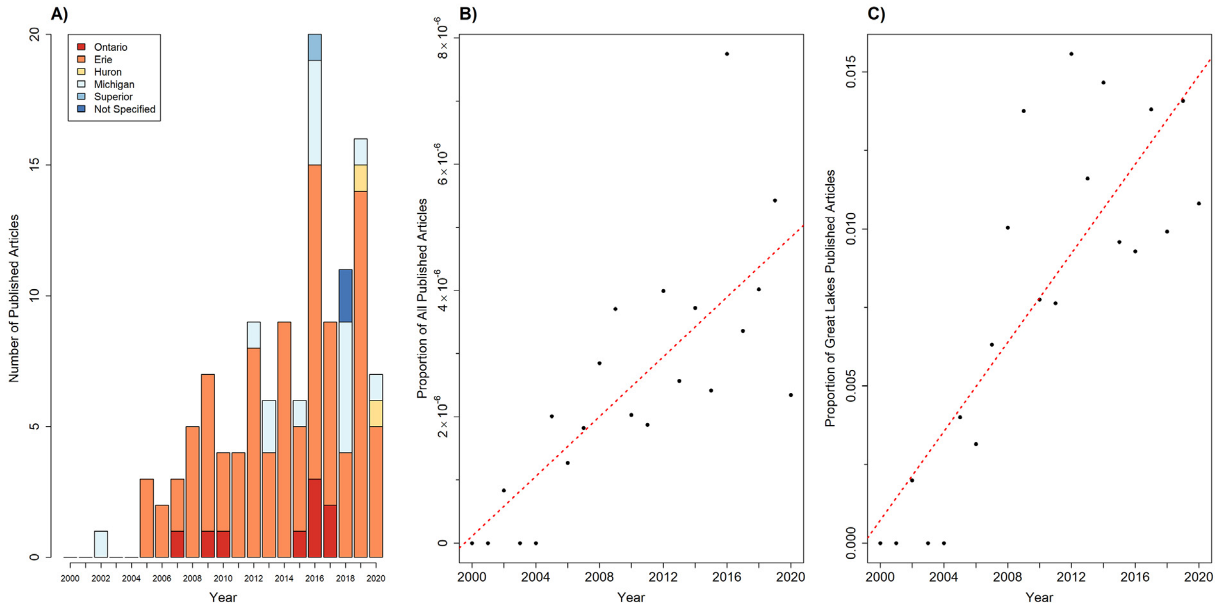

Fig. 3. A) Number of published articles related to hypoxia returned by the topic search query "Lake X hypoxia" (where X is one of: Ontario, Erie, Huron, Michigan, or Superior) per year, separated by lake of interest, from all databases accessible by ISI Web of Science from 2000 to 2020. B) Yearly proportion of hypoxia articles relative to all published articles returned from all databases accessible by ISI Web of Science from 2000 to 2020. C) Yearly proportion of hypoxia articles relative to all Great Lakes articles (as defined by the search query "Lake Erie OR Lake Huron OR Lake Michigan OR Lake Ontario OR Lake Superior") in all databases accessible by ISI Web of Science from 2000 to 2020.

Lakes hypoxia articles published over the period (+2.4x10^{-7} % of all published articles per year, Adj. R^2 = 0.553, p < 0.001; Fig. 3B). We then normalized by including only Great Lakes articles (as defined by the search query "Lake Erie OR Lake Huron OR Lake Michigan OR Lake Ontario OR Lake Superior") and still found an increase in the proportion of hypoxia articles among Great Lakes articles published each year (+0.07% of all Great Lakes articles per year, Adj. R^2 = 0.658, p < 0.001; Fig. 3C). Not surprisingly, Lake Erie was overrepresented among these articles, with 78% of articles specific to Lake Erie. (Fig. 3).

The central basin of Lake Erie is the most intensively studied hypoxic system within the Great Lakes region, and perhaps all the inland waters of North America. Poor water quality and hypoxia have been a major problem in Lake Erie for decades (Conroy et al., 2011; Edwards et al., 2005), with phosphorous-induced eutrophication considered the main driver of central basin hypolimnetic hypoxia since the late sixties (Mortimer, 1987; Vollenweider, 1968). Despite Lake Erie receiving the majority of the research effort, hypolimnetic hypoxia has been identified in other areas of the Great Lakes region (e.g., Lake Simcoe, Nuernberg et al., 2013; Green Bay, Hamidi et al., 2013, 2015; Muskegon Lake, Biddanda et al., 2018; Onondaga Lake, Tango and Ringler, 1996) and the phenomenon is likely present, but generally underrepresented, in many more Great Lakes systems.

Compared to hypolimnetic hypoxia, relatively few studies have attempted to document the presence of over-winter hypoxia in the Great Lakes. This is likely due, at least in part, to the difficulty associated with taking accurate measurements of the under-ice environment and the hazards of field sampling in freezing conditions. Recent advances in optical dissolved oxygen loggers have made it possible for researchers to conduct water quality sampling throughout the under-ice period and recent studies have explored the presence of over-winter hypoxia on coregonine rocky reef spawning grounds (e.g., Kalejs, 2017). Conversely, diel hypoxia has been observed in several shallow and semi-isolated Great Lakes coastal wetlands, such as those associated with the drowned river mouth lakes of eastern Lake Michigan (Parker et al., 2012) and river mouths of southern Lake Erie (NOAA, National Oceanic and Atmospheric Administration, 2021 data; Fig. 2C).

Episodic hypoxia in the Great Lakes occurs in response to storm-driven upwellings, longshore currents, severe rainfall runoff events, and direct nutrient input in and around population centers. Offshore hypolimnetic hypoxic water occasionally intrudes into nearshore areas of central Lake Erie when strong wind events displace the surface layer through Ekman transport (Fig. 2D; Kraus et al., 2015; Valipour et al., 2021). Upwellings of hypoxic water can be induced or exacerbated elsewhere within the system by large storms or cross-basin currents (Dunstall et al., 1990; Jabbari et al., 2019; Rao et al., 2014). River-input nutrients have also been identified as the cause for severe algal blooms and subsequent episodic hypoxia in several coastal urban centers (Bellinger et al., 2016; Gaulke et al., 2015; Zhang et al., 2016). Lake Erie experiences the greatest abundance and diversity of hypoxic phenomena and so is afforded the majority of research and management focus. However, hypoxia occurs in all five of the Great Lakes and novel hypoxic phenomena have been documented within many systems historically assumed to be normoxic (free of hypoxia) as the practice of regularly monitoring dissolved oxygen conditions has become more affordable and commonplace (Fig. 4, Table 1).

Key knowledge gaps

The study of aquatic hypoxia is inter-disciplinary and the potential knowledge gaps span a broad range of categories (e.g., ecological interactions, municipal water treatment, land-use and nutrient runoff, etc.). Various municipal, state, provincial, tribal and federal agencies are involved with monitoring water quality, including dissolved oxygen, in the Great Lakes, with different agencies fulfilling distinct monitoring aspects; e.g., the EPA Great Lakes National Program Office conducts monitoring and surveillance activities in the US offshore waters of the Great Lakes in support of the U.S. – Canada Great Lakes Water Quality Agreement. Given limited resources, these agencies must make trade-offs when prioritizing monitoring activities. To this end, we draw attention to

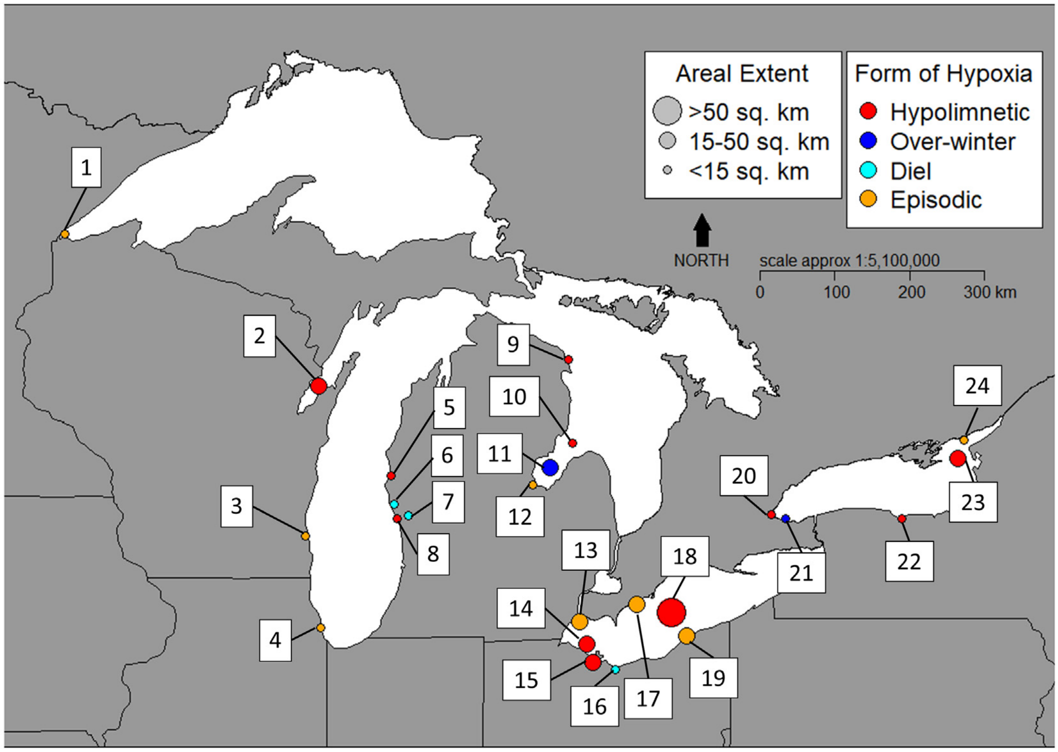

Fig. 4. Select examples of systems throughout the Great Lakes with documented hypoxia from a primary literature source. Numbers on points correspond to the relevant paper in Table 1. Size of circle denotes relative areal extent of hypoxic phenomena.

three frontiers in monitoring and research that are directly related to the occurrence and prevalence of Great Lakes hypoxia in an effort to encourage further study and broaden awareness of the need to investigate the true breadth of hypoxia within the region.

Spatial and temporal extent

The extent and magnitude of hypoxia outside of the Lake Erie central basin currently represents a major knowledge gap for the Great Lakes. It is likely that many locations throughout the Great Lakes periodically experience hypoxic conditions despite the lack of scientific reporting, with adverse consequences for the aquatic environment and a potential mismatch between present and best-course management practices. For example, current nutrient management plans focus mainly on the reduction of phosphorus to inhibit eutrophication and combat hypoxia (U.S. EPA, 2018). However, some studies have indicated that nitrogen, not phosphorous, limits primary production in Great Lakes coastal wetlands (Cooper et al., 2016; Hill et al., 2006; McCarthy et al., 2007). Anaerobic processes occur naturally in wetlands, which act as global reduction areas for the biosphere, offsetting and balancing terrestrial oxidation reactions. Nutrient enrichment can cause extreme diel fluctuations in oxygen saturation and depletion that disturb this biogeochemical process (Zhang et al., 2015). As such, regulations may need to be adapted to also address anthropogenic nitrogen contributions to more effectively manage naturally occurring hypoxia in coastal wetlands. Similarly, hypoxic phenomena may detract from recent research and management efforts focused on the conservation of habitats that sustain recruitment of native species (e.g., Kalejs, 2017; McLean et al., 2015). Undetected or underestimated hypoxia affecting rocky reefs or other critical spawning habitats may drastically reduce the effectiveness of current and planned improvements to habitat quality, mitigating any potential benefit such measures may have for ecologically and economically important species. The ability to enact informed and effective management strategies is predicated on improved understanding of the breadth of Great Lakes ecosystems and organisms that are currently experiencing or vulnerable to hypoxia.

Key considerations in monitoring potential hypoxic systems will include both how to measure oxygen concentrations and how to summarize hypoxic measurements. Traditionally, oxygen has been monitored using punctuated point or vertical profile measurements. More recently, oxygen concentrations in the Great Lakes have been quantified using towed sensors (e.g., Xu et al., 2017), autonomous vehicles (e.g., Dawson and Allison, 2021) or longer term, *in situ* loggers (e.g., Karatayev et al., 2018), thereby facilitating broader spatial and temporal quantification of oxygen conditions. Such data can be summarized in a variety of ways to index the magnitude, frequency, spatial coverage and temporal extent of hypoxia. Again, we suggest that setting a strict threshold for hypoxia may not always be appropriate given that organisms differ greatly in terms of their response to low oxygen. Nonetheless, if a single threshold or multiple thresholds are selected, data could be presented based on oxygen concentrations dropping below a threshold, for example, amount of time below threshold, frequency of events below threshold, and spatial area or volume below threshold. Data could also be presented as mean values across time or space. Alternatively, models can be used to represent the combined effects of oxygen and temperature on habitat quality for specific organisms (e.g., Arend et al., 2011). Ultimately, a combination of indices may be most appropriate to summarize oxygen conditions in a particular system as no single index may adequately capture all aspects of hypoxia.

Predictive modelling

Large-scale monitoring programs often present logistical and budgetary challenges as they span great distances and require

Table 1
Select primary literature articles documenting the presence of hypoxia in various systems throughout the Great Lakes region. Numbers in the first column correspond to identifying markers on Fig. 4.

ID Number	Paper	Location	Condition
1	Bellinger et al., 2016	St. Louis River Estuary	Episodic
2	Hamidi et al., 2013, 2015; Klump et al., 2018	Green Bay, Lake Michigan	Hypolimnetic
3	Kreutzberger et al., 1980	Milwaukee River	Episodic
4	Gaulke et al., 2015	Chicago River	Episodic
5	Chubb and Liston, 1986	Pentwater Lake Estuary	Hypolimnetic
6	Nelson et al., 2009	White Lake Estuary	Diel
7	Parker et al., 2012	Muskegon Lake Estuary	Diel
8	Biddanda et al., 2018; Weinke and Biddanda, 2018	Muskegon Lake	Hypolimnetic
9	Voorhies et al., 2012	Lake Huron sinkhole	Hypolimnetic
10	NOAA GLERL Technical Report, 2013	Saginaw Bay, Lake Huron	Hypolimnetic
11	Kalejs, 2017	Saginaw Bay, Lake Huron	Over-winter
12	Voss et al., 2014	Kawkawlin River	Episodic
13	Jabbari et al., 2019	Lake Erie western basin	Episodic
14	Loewen et al., 2007	Lake Erie western basin	Hypolimnetic
15	Conroy et al., 2011	Lake Erie Sandusky subbasin	Hypolimnetic
16	Cornell and Klarer, 2008	Old Woman Creek Estuary	Diel
17	Rao et al., 2014; Rowe et al., 2019; Valipour et al., 2021	Lake Erie central basin	Episodic
18	Conroy et al., 2011; Edwards et al., 2005; Smith and Matisoff, 2008; Zhou et al., 2013; among others	Lake Erie central basin	Hypolimnetic
19	Kraus et al., 2015	Near Fairport Harbor, Lake Erie	Episodic
20	Bowen and Currie, 2017; Flood et al., 2021; Hiriart-Baer et al., 2009	Hamilton Harbour	Hypolimnetic
21	Marshall et al., 2021	Lake Ontario coastal wetlands	Over-winter
22	Klumb et al., 2004	Irondequiot Bay, Lake Ontario	Hypolimnetic
23	Ahrnsbrak and Wing, 1998	Lake Ontario Kingston Basin	Hypolimnetic
24	Marshall et al., 2021	Lake Ontario coastal wetlands	Episodic

expensive equipment and maintenance. Recent advances in hydrological modeling have allowed researchers to circumvent these issues by projecting hypoxia risk given a suite of physical and biological variables (e.g., Bocaniov et al., 2016). Hydrological predictive models have been applied to both large (e.g., Rucinski et al., 2014) and small (e.g., Liu et al., 2018) systems throughout the Great Lakes, with varying degrees of success and accuracy. All models require periodic cross-referencing with observational data to ensure their validity and it is important for models to demonstrate agreement with historical data. Specialized hypoxia forecast models would allow researchers to identify systems that are potentially vulnerable to hypoxia using a set of commonly measured environmental variables. An improved ability to quantify hypoxia risk without committing the funds necessary for *in situ* monitoring would be a valuable tool for resource managers looking to allocate finite effort over a large area or among many systems.

Climate change

Much work is needed to accurately forecast the effect of projected climate change on hypoxia in the Great Lakes. Precipitation and average water temperature in the region have increased over the last century (Barlage et al., 2002; Collingsworth et al., 2017; Höök et al., 2020; McBean, 2008; Trumpickas et al., 2009) and are expected to continue increasing in the future due to climate change (Fang and Stefan, 2009; Kalcic et al., 2019; Trumpickas et al., 2009; Wuebbles and Hayhoe, 2004). Warmer temperatures stimulate biological activity, reduce the solubility of oxygen in water, and lead to longer and more intense periods of stratification. Coupled with intensive land use and widespread use of fertilizers in agricultural areas, these changes will likely increase the extent, severity, and duration of bouts of hypoxia (Bendtsen and Hansen, 2013; Darko et al., 2019; Ludsin and Höök, 2013). Moreover, warming temperatures may reduce the spring mixing potential of large lakes (Anderson et al., 2021), increasing the likelihood of persistent offshore hypoxia in the absence of full lake turnover events. Given these trends, some systems that do not have a history of hypoxia may develop hypoxic conditions in the future. Specifically, given the direction of predicted future climatic trends, the prevalence of hypolimnetic, diel, and episodic hypoxia will likely increase, while the prevalence of over-winter hypoxia may decrease as warming temperatures reduce the extent of ice- and snow-cover. Increased research effort toward the development of models that track the predicted changes in hypoxia strength with climate change could be useful tools to ensure that management practices will remain beneficial under future conditions.

Conclusion

Hypoxia is potentially much more widespread throughout the Laurentian Great Lakes than currently reported. Furthermore, climatic shifts in prevailing temperature and precipitation patterns will likely increase the prevalence and severity of hypoxic phenomena, particularly in temperate regions. Contemporary gaps in knowledge combined with the threat of more common and pervasive hypoxia could negatively affect the ecological integrity of the Great Lakes. The first step toward increased appreciation of hypoxia in the Great Lakes is an increased awareness of the range and extent of hypoxic phenomena that occur throughout the system. Our review suggests that the current focus and intensity of research effort does not accurately characterize the magnitude or diversity of hypoxic conditions affecting the Great Lakes. Rather, the relative scarcity of studies investigating hypoxia outside of the Lake Erie central basin may currently limit the ability of resource managers to apply effective conservation measures within systems experiencing unreported hypoxia or those vulnerable to the development of hypoxia.

Declaration of Competing Interest

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

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