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Abstract

Hypoxia has been a central focus of research regarding water quality impairments throughout the world in the past century. The fresh and coastal marine waters affected by hypoxia are of great importance due to the ecosystem services and species habitat they provide, and because of the regional economic activity spurned by these waters in return. As such, a great deal of research effort has been devoted to elucidating the causes and ecological effects of hypoxia with the hopes of remediating the issue. The bulk of this effort has been directed at the role of anthropogenic allochthonous nutrient loading and algal bloom size in the development of recurring hypoxia, as these issues have been exacerbated in the past century. Less examined is the extent to which various climatological and meteorological variables influence hypoxia across temporal scales with even less examination directed towards the potential role of algal bloom community composition on hypoxia. This review summarizes the degree to which meteorological factors (air temperature, wind, precipitation, and ice cover) and community composition of algal blooms influence the development and extent of hypoxia in the hypolimnion of stratified water bodies. Special focus is given to dimictic freshwater lakes, though other marine and estuarine water bodies are discussed as well. Although not of primary importance, meteorological conditions explain much of the short-term temporal variance in hypolimnetic hypoxia and act as a vessel for nutrient transport. While receiving more attention in recent years, the explicit role of algal community composition on the development of hypoxia remains largely unexplored.

Keywords: Algae, Limnology, Hypoxia, Meteorology

Review: Influence of meteorological conditions and algal community composition on hypolimnetic hypoxia

Introduction

Freshwater and coastal marine waters are important systems of ecological productivity and economic value (Williamson et al., 2009; Barbier et al., 2011). These systems are subject to a myriad of aliments - some natural - though anthropogenic perturbations have led some systems towards undesirable and irreversible states (Jenny et al., 2014). One of these ailments, hypoxia, or a lack of oxygen (often referred to as “dead zones” when large enough), occurs when a water body is depleted of oxygen to a level detrimental to biotic survival. This threshold is often defined as dissolved O_2 concentrations at or beneath 2.0 mg L^{-1}, though the dissolved oxygen tolerance of aquatic species varies greatly (Weinke and Biddanda, 2018). Hypolimnetic hypoxia occurs when a stratified water body becomes oxygen depleted in the bottom layer (hypolimnion) through microbial respiration and reduction reactions faster than natural processes diffusion and photosynthesis can replenish the oxygen supply (Bouffard et al., 2013).

Hypoxia has been spreading globally in the past century (Jenny et al., 2016), largely the result of anthropogenic forces through increased nutrient loads (Diaz and Rosenburg, 2008). These increased nutrient loads are typically cited as the culprit for the development of expansive hypoxic zones and algal blooms across the world (Diaz, 2001) from Lake Erie (Scavia et al., 2014) to the Gulf of Mexico (Rabalais et al., 2002) to the Baltic Sea (Conley et al. 2011). As such, considerable research and effort has been put into reducing both point and non-point source nutrient loads on adjacent lands, as well as researching the ecological consequences of hypoxic conditions (Rabalais et al., 2002; Scavia et al., 2014). While initially nutrient reductions – especially phosphorous (P) – alleviated much of the algal blooms and hypoxia, a “re-eutrophication" of many lake ecosystems in light of sustained nutrient reductions has called into question the relative impact of other factors influencing the development of hypoxia (Donner and Scavia, 2007; Jenny et al., 2014; Watson et al., 2016). Although nutrient inputs have great influence and can moderate the development of hypoxia, the full picture of hypoxia cannot be portrayed by one factor as its development is determined by a combination of anthropogenic influence and natural physical processes (Carrick, 2004; Burns et al., 2005).

Another oft-studied influencer of hypoxia are several natural climatological processes – wind, precipitation, and air temperature – that act in conjunction with nutrient loading, albeit each to differing extents of examination. The effect of wind has been a focal point of these natural processes as wind can mix water columns, deepen thermoclines, distort the usual movement of water, and entrain trapped nutrients (Beletsky et al., 2012; Crockford et al 2014; Weinke and Biddanda, 2019). As the Earth's climate has begun to change, climate variables subject to change have been analyzed for their effects on aquatic systems (Nicholls, 1998; Huang et al., 2012). Precipitation is one of the variables examined, though often only as a vessel for nutrient transport from terrestrial to aquatic systems (Michalak et al., 2013; Zhou et al., 2014). Regardless, it is becoming clearer that changes in patterns of precipitation do play a substantial role in altering lake and coastal marine ecosystems whether through changes in discharge, timing, or water level (Anderson and Taylor 2001; Donner and Scavia, 2007; Jennings et al 2012). Air temperatures have continued to increase in recent decades with eight of the ten hottest years on record being in the last decade – including the five hottest as the past five years (NOAA, 2020). Changes in air temperature can hold powerful influence over aquatic systems, determining stratification, turnover, and solubility of dissolved oxygen, among other effects (Posch et al., 2012; Meire et al., 2013; Del Giudice et al., 2018). While not pertinent for tropical or sub-tropical lakes and coastal systems, a body of literature is growing on the effect of ice cover on the development of hypoxia in monomictic and dimictic lakes (Straile et al., 2003; Austin and Colman, 2008; Perello et al. 2017).

Climatological factors influence hypoxia both directly and indirectly through their influence on phytoplankton blooms. The general size and occurrence of algal blooms, particularly harmful algal blooms (HABs), have been examined thoroughly with respect to their influence on hypoxia (Rabalais et al., 2002; Watson et al., 2016). Large phytoplankton blooms contribute to hypoxia mainly through water column respiration and the ensuing microbial respiration from the decomposition of this productivity (Anderson and Taylor, 2001; Diaz and Rosenburg, 2008). Large algal blooms have increased throughout the past century (Paerl and Huisman, 2008) and the composition of the algae within these blooms has changed with time (Allinger and Reavie, 2013). Whether these compositional changes have an influence on hypoxia is a subject which has received very little attention relative to other factors.

This review examines the role that meteorological conditions and algal community composition have in the development of hypolimnetic hypoxia. While some attention is directed to coastal marine systems (namely the northern Gulf of Mexico), the bulk of this paper focuses on hypolimnetic hypoxia in moderate to large, stratified, dimictic lakes typified by the Laurentian Great Lakes region of North America. Further, the effects of hypoxia on aquatic biota are substantial, but there exists a large body of work devoted to the synthesis of these impacts in both freshwater and marine ecosystems, and as such no attempt is made to discuss these issues at length (Diaz and Rosenberg, 1995; Wienke and Biddanda, 2018). Also, while climatological factors will be discussed in relation to changes that have occurred in the past century, no attempt is made to extrapolate future climate conditions. Rather, changes up to 2020 will discussed.

Climatological Influence

Wind and Storms

Stratification

Winds exert a near constant pressure on all water bodies with the power to create significant changes to any established thermal and chemical structure. Moderate to deep temperate lakes generally stratify during the summer, forming an upper, warm, oxygenated layer (epilimnion) with a thin layer of rapid temperature change (thermocline) leading to the bottom, colder layer (hypolimnion). In coastal systems this same layering occurs, but instead of a thermocline, a pycnocline is formed when a rapid change in density occurs. In both situations, vertical transport is restricted, leaving the hypolimnion largely as a closed system (Bouffard et al., 2013). As a system stays in this stratified state, oxygen depletion continues until all oxygen is consumed and an anoxic state is reached. Because of this potential to devoid the hypolimnion of oxygen, the structure of stratification has been found by some to be more influential to hypoxia than the timing of nutrient deliveries (Rucinski et al., 2016). Wind has great influence over this structuring, with wind events leading to vastly different outcomes between deeper systems and shallower systems (Crockford et al., 2014; Rao et al., 2014; Jabbari et al., 2019).

Perello et al. (2017) found that in the typically well-mixed shallow western basin of Lake Erie, when stratification did occur, storm events were enough to thoroughly mix the water column, reintroducing oxygen to the thin hypolimnion. Similarly, Kamarainen et al. (2009) found that during the stratified summer period in Lake Mendota, Wisconsin winds periodically had the strength to entrain phosphorous from the hypolimnion back throughout the water column. This entrained phosphorous was plentiful enough to theoretically sustain algal blooms for a period up to 19 days with no other sources of phosphorous. These algal blooms inevitably fall, initiating microbial decomposition in the lake once the wind has ceased, and stratification returns. In the open waters on Lake Huron, winds were able to maintain enough turbulent mixing to entrain phosphorous throughout the winter and into the spring diatom bloom (Nicholls, 1998). Although the effects of wind events can be long-lasting, the change imparted on the physical structure of stratification by wind are generally are short-lived (Jennings et al., 2012).

In deeper systems, often full water column mixing is more difficult to achieve through wind-induced mixing, altering the position of the thermocline within the water body instead (Bouffard et al., 2013). The central basin of Lake Erie has served as model example of this process, with some years having winds that lead to downwelling that served to deepen the thermocline (Conroy et al. 2011; Bouffard et al. 2013; Rowe et al., 2019). Compared with shallower systems, a deepening of the thermocline does not replenish the hypolimnion with oxygen, but rather reduces the volume of the layer, accelerating oxygen depletion and driving a system towards hypoxic conditions more quickly (Conroy et al. 2011; Bouffard et al. 2013). To emphasize the importance of a deepened thermocline, Bouffard et al. (2013) also determined that vertical turbulent diffusivity was more important to hypolimnion reoxygenation than molecular transfer of O_2 (which is limited by the separation between epilimnion and hypolimnion). The deeper the thermocline lies in the water column, the less likely vertical turbulent diffusivity will occur, further relegating the hypolimnion to a state of hypoxia in some instances.

Wind Direction

Influence on the state of stratification is the overarching effect of wind on hypoxic water bodies. However, all wind is not created equal with respect to its impact on stratification. Predominant winds and the general direction of water flow have substantial influence on the formation of the thermocline position and shape (Beletsky et al., 2012). Changes in these dominant wind direction patterns can act to alter the development and relief of hypoxia, often depending on the shape, bathymetry, and orientation of a water body (Zhou et al., 2015).

Zhou et al. (2015) found that the duration of predominantly northwest winds in the month of June in Lake Erie increases eastward flow, carrying nutrient-rich water along with it, but the explanatory power of wind direction on hypoxia in July and August was limited. Conversely, Rowe et al. (2019) observed that years with predominantly southwesterly winds on Lake Erie caused substantial downwelling, resulting in a thinner thermocline and an earlier initiation of stratification. A reversal of this wind direction shifted the lake from downwelling to upwelling – relocating potentially damaging hypoxic waters.

Wind direction also controls the shape of the thermocline (Beletsky et al., 2012). Cyclonic winds tilt the isotherms away from the center of moderate and large lakes, creating a dome-shaped thermocline that is “pushed up” in the lake’s center. Conversely, anti-cyclonic winds lead to a mid-lake convergence which forces water down, reversing the thermocline to a bowl shape. In Lake Erie, this wind-driven change in water flow was enough to lower the thermocline of the central basin of Lake Erie by five meters (~50% of the average thermocline depth at this location) (Beletsky et al., 2012). If this deepened thermocline persists, the reduced volumetric area can increase the time the hypolimnion spends in a hypoxic or anoxic state (Bouffard et al., 2013; Perello et al. 2013). Zhou et al. (2014) had the opposite findings in the Chesapeake Bay, with down-estuary (cyclonic) NE winds increasing vertical stratification and thusly hypoxic volume, while up-estuary (anti-cyclonic) SW winds alleviated hypoxia by reversing gravitational flow and disrupting the formation of stratification. While wind direction had an appreciable effect on hypoxia, it represented only a small fraction of the interannual variability in Chesapeake Bay (Zhou et al., 2014). These contrasting findings suggest that the end result of wind direction on hypoxia is largely system-to-system, with differences between systems making overall generalizations difficult.

Wind Intensity

The intensity of wind is perhaps the most important aspect with regards to influence on the water column (Bouffard et al., 2013). The intensity and frequency of wind events greatly influence the structure of stratification and contributes to changes in hypolimnetic oxygen demand (HOD), or the dissolved oxygen required by oxygen-consuming processes in the water column and sediments (Carrick, 2004; Conroy et al., 2011).

Generally, the effects of moderate and strong wind events are analyzed for their influence on aquatic systems. Quiescence – calm periods with little winds - too, however, can alter these systems (Paerl and Huisman, 2008; Huang et al., 2010). In Lake Ontario, Huang et al. (2010) had to account for declining surface wind speeds in a model of atmospheric forcing since this decline has resulted in a shallower surface mixed layer and more stable summer stratification. Furthermore, Huang et al. (2012) observed a decline in wind speeds throughout the last 40 years over Lake Huron that was partially responsible for a 12-day increase in the period of stratification over the same timeframe. This increase in duration and stabilization of stratification from quiescent winds generally leads towards conditions favorable to the development of hypoxia, though the shallower surfaced mixed layer described by Huang et al. (2010) may actually serve to delay hypoxic conditions due to the higher hypolimnetic volume (Bouffard et al., 2013).

Often, small changes in the intensity of wind are sufficient to alter the structure of stratified water bodies. Kamarainen et al. (2009) found that two weeks in June and September with only slightly above average winds were sufficient to mix the water column. These weeks experienced an average wind speed of 5.3 m s^{-1}, compared with an average wind speed of only 4.5 m s^{-1}during those months. This increase of only 0.8 m s^{-1} was enough to entrain phosphorous in the water column, stimulating phytoplankton blooms. In a smaller European lake, Crockford et al. (2014) observed total lake turnover with wind events of just over 5 m s^{-1}, similarly stimulating the epilimnion with sediment-derived phosphorous.

Although total water column mixing is possible, a more likely result of moderate to intense winds is a deepening of the thermocline in moderate and large water bodies. In Lake Erie, multiple studies described sustained wind events of > 6 m s^{-1} causing the thermocline to decline (Conroy et al., 2011; Bouffard et al., 2013). As HOD depletion rates have been relatively stable in the face of anthropogenic changes, the effect of winds events above this threshold in Lake Erie may have substantial influence on the rate of HOD (Conroy et al., 2011). However, strong winds in June and July prior to the onset of stratification both delayed the development of stratification and may facilitate the vertical transfer of oxygen (Conroy et al., 2011; Zhou et al., 2015). This delay reduces the time that the hypolimnion is separated and is partially responsible for the decreased hypoxic extent described by Zhou et al. (2015).

Upwelling Events

The combination of favorably directed and particularly strong winds alters hypoxia through mass movements of waters (Millie et al., 2009), often in the form of upwelling events. Upwelling events are relatively common events in coastal marine systems (Grantham et al., 2004; Feng et al. 2014), though these events have been found to occur in stratified freshwater lakes as well (Biddanda et al., 2018; Liu et al., 2018). The outcomes of upwelling on hypoxia are dichotomous, with some systems being released from hypoxia via upwelling, while other systems are quickly moved into hypoxic conditions.

Grunert et al. (2018) found that upwelling events occurred from Lake Michigan into Green Bay when strong southernly winds occurred. Whether these intrusion events contributed to the initiation or alleviation of hypoxia was dependent on the temperature of the upwelling waters, which in turn was controlled by a number of other factors (see: Ice Cover). Similarly, Muskegon Lake, Michigan experienced annual upwelling intrusion events of cold water from Lake Michigan (Liu et al., 2018; Weinke and Biddanda, 2019). These events occurred during summer stratification, and the oxygen-rich cold Lake Michigan waters pushed hypoxic waters up from the hypolimnion (temporarily creating “floating hypoxia”) where these waters were subject to molecular and vertical oxygen diffusion, alleviating hypoxia. Upwelling occurred during periods of sustained (~ 2 days) strong northernly winds (> 5 m s^{-1}; Liu et al., 2018). Further modelling showed that strengthening winds from 5–7 m/s increased the size of intrusions, while extreme winds (> 15 m/s), though temporarily offset by full water column mixing, eventually led to even greater sized intrusions (up to 13% of Muskegon Lake’s water volume) as upwelling continues to occur long after winds subside (Lui et al., 2018). Lake Ontario has been shown to have recurring upwelling events into Hamilton and Toronto harbors triggered by strong and sustained westerly winds (Bocaniov et al., 2012; Hlevca et al., 2018). Here too, upwelling transferred cool, oxygenated water to the harbors that alleviated hypoxic conditions.

In other lake systems, upwelling can have the opposite effect and serve to suddenly transfer hypoxic waters to new areas. Lake Erie occasionally experiences strong winds that move hypoxic water found in the central basin into the typically homogenous western basin, with potentially drastic ecological consequences like the 2012 fish kill observed along the lake’s northern shore (Rao et al., 2014; Jabbari et al. 2019). Similarly, strong, predominantly northernly winds on Lake Erie resulted in upwelling of hypoxic waters along the southern coast (Rao et al., 2014; Rowe et al., 2019).

Coastal marine systems experience upwelling similar to that discussed in Lake Erie. In the northern Gulf of Mexico, upwelling-favorable winds diverted riverine discharge in a manner that increased stratification, resulting in high organic matter deposition and a rapid expansion of the hypoxic area (Feng et al., 2014). Along the coast of California, upwelling brought nutrient-rich, oxygen-deficient water that stimulated surface production and simultaneously encouraged hypoxic waters (Grantham et al., 2004).

Beyond transferring waters in mass from one location to another, upwelling events in both freshwater and coastal marine ecosystems can often mix the water column (Grantham et al., 2004; Hlevca et al., 2018). In some systems, this mixing can immediately decrease light availability and lower P:R ratios (Hlevca et al., 2018). Furthermore, the upwelling-induced water column mixing can resuspend resting algal cells, promoting the proliferation of blooms after winds have subsided and the water column re-stratifies (Bocaniov et al., 2013; Hlevca et al., 2018).

Precipitation

Precipitation has received less attention with regards to its potential influence on hypolimnetic hypoxia (Zhou et al., 2014) largely because nutrient inputs and meteorological conditions like precipitation are difficult to truly decouple (Michalak et al., 2013). While much effort has been put into quantifying, modelling, and addressing the impact of nutrient inputs on hypoxia and algal blooms (Rabalais et al., 2002; Watson et al., 2016), few studies have tried to decouple precipitation from nutrient loading (Zhou et al., 2014). Recent re-eutrophication of waters (Allinger and Reavie, 2013) in light of minimal land use changes and nutrient reductions goals being met has brought forth the role of climatic variability in determining hypoxic variability (Donner and Scavia, 2007). Though perhaps not as influential as general nutrient inputs, changes in the quantity and timing of precipitation events may play a significant role in this hypoxic variability (Michalak et al., 2013; Zhou et al., 2014).

Large precipitation (and resulting high discharge) events may be particularly influential in the transfer of nutrients (Richards et al., 2001) and the alteration of stratification structure and water chemistry (Jennings et al., 2012). Large, precipitation-driven nutrient loading events, though not solely responsible, were required to initiate hypoxia in a moderately sized European lake (Lake Bourget; Jenny et al., 2014). Similarly, extreme precipitation events increased dissolved organic carbon to a series of globally dispersed lakes (Jennings et al. 2012).

The effect of these inputs on hypoxic development is both immediate (Jenny et al., 2014) and delayed (Paerl and Huisman, 2008; Michalak et al., 2013). Short-term increases in discharge may act to immediately resolve or delay the onset of stratification and hypoxia (Paerl and Huisman, 2008). High discharges in Lake Erie and Lake Geneva correlate with reduced hypoxia for that season, potentially due to higher oxygen inputs associated with the increased discharge (Zhou et al. 2015; Jenny et al. 2014, respectively). High discharges when coupled with high wind events are also able to disrupt stratification for a longer period than from either event alone (Jennings et al., 2012). In western Long Island Sound, heavy precipitation events facilitated the input of NH_4^+ and subsequent phytoplankton blooms, causing hypoxia to fluctuate on a near weekly basis (Anderson and Taylor, 2001). In contrast to these precipitation-driven phytoplankton blooms, high discharge can result in delayed, expansive algal blooms in Lake Erie though perhaps surprisingly, these blooms were not associated with large hypoxic extents (Michalak et al., 2013; Zhou et al., 2015).

Aside from the intensity of precipitation events, the timing of precipitation also has bearing on the development of hypoxia. Typically, studies on precipitation timing have focused on the spring season (Donner and Scavia, 2007; Paerl and Huisman, 2008; Michalak et al., 2013), since this coincides with fertilization of agricultural fields across the United States (Donner and Scavia, 2007). Record-setting algal blooms did not correspond with a greater extent of hypoxia in Lake Erie in 2011 when early spring precipitation was extreme throughout the watershed (Michalak et al., 2013; Zhou et al., 2015), although high spring and early summer (April-June) precipitation the following year was found to predict a substantial portion of the development of that year’s large hypoxic extent (Zhou et al., 2015). In the Mississippi River watershed, land cover, land use, and nutrient applications remained relatively stable in the 20 years prior to 2007, but changes in the previous year’s precipitation and subsequent increases in nitrogen indicated hypoxia would be an issue (Donner and Scavia, 2007). To emphasize that point, this study concluded that years in which November-December and March-April-May were unusually wet necessitated a 50–60% nitrogen application reduction (nearly 2× less than the recommended target) to keep hypoxia in check in the Gulf of Mexico. A study in Chesapeake Bay also indicated the importance of the timing of precipitation, with April-May precipitation predicting nearly a third of yearly hypoxic variability (Zhou et al., 2014). Paerl and Huisman (2008) also noted that in lakes across the world, high winter and spring precipitation promoted high discharge that can result in large algal blooms.

Although the majority of literature points towards the intensity and timing of discharge having a quantifiable effect on the development of hypoxia (Donner and Scavia, 2007; Michalak et al., 2013; Zhou et al., 2014), at least one large-scale analysis of freshwater lakes refutes this (Jenny et al., 2016). In this study of 365 freshwater lakes’ sediment samples worldwide dating back to 1700, no correlation was found between changes in precipitation (or air temperature) and hypoxia, but hypoxia was attributed to anthropogenic causes around the turn of the 20th century (Jenny et al., 2016).

Air Temperature

Anthropogenic sources of greenhouse gas emissions have begun to rapidly warm global air temperatures, and in response, water temperatures (Jenny et al., 2014). In stratified water bodies, rises in water temperature alter hypoxia through several mechanisms including reduced O_2 vertical transport, reduced O_2 solubility, increased biological oxygen demand (Meire et al., 2013), and extension of the stratified season (Austin and Colman, 2008). These warmer conditions influence stratified systems not only through these mechanisms, but also by promoting conditions favorable to ecologically detrimental cyanobacterial blooms (Paerl and Huisman, 2008).

Warmer-than-typical air temperatures often relate directly to the thermal stratification of coastal marine (Meire et al., 2013) and freshwaters (Hondzo and Stefan, 1991). In the waters of Mobile Bay, Alabama and the surrounding coastal shelf, the strength of stratification was more important to HOD than organic loading or sediment oxygen demand, accounting for 36–80% of changes in hypolimnetic oxygen content (Turner et al., 1987). In the North Sea, future modelling predicted an 11.5% decrease in late-summer hypolimnetic dissolved oxygen concentration induced by intense stratification, reduced O_2 solubility, and increased biological oxygen demand accounting for 58%, 27%, and 15% of the 11.5% decrease, respectively (Meire et al., 2013). In freshwater systems, warm winter and spring temperatures were shown to promote an earlier onset of stratification and deeper thermoclines in both moderate (Hondzo and Stefan, 1991) and large (Del Giudice et al., 2018) temperate dimictic lakes, with Lake Ontario gaining 12 days of stratification over a 40-year period (Huang et al., 2012). In the monomictic Lake Constance, warmer winter temperatures resulted an array of physiochemical effects, including a reduced temperature gradient at the lake surface that resisted complete water column mixing, failing to mix nutrients and replenish hypoxic waters with oxygenated water (Straile et al., 2003). Some buffer to hypoxia can be achieved in stratified waters with heightened discharge (Zhou et al., 2014), though the smaller these inputs are, the more susceptible a lake becomes to the warmth-induced hypoxia and stratification (Jenny et al., 2014).

The influence of air temperatures may also be slightly magnified in water temperatures (Austin and Colman, 2008; Huang et al., 2010). Lake Huron (King et al., 1997), Lake Ontario (Huang et al. 2010, 2012), and Lake Superior (Austin and Colman, 2008) have all shown increases in water temperature with increases in air temperature. Although water temperatures increase in parallel with air temperature (Huang et al., 2012; King et al., 1997), surface water temperatures increase nearly twice that of regional air temperature, leading to increased stratification and subsequent hypoxia (Austin and Colman, 2008; Huang et al. 2010).

The conditions reached with warmer temperatures not only promote hypoxia through direct interference of oxygen transfers and lengthened stratification, but also by creating conditions favorable for nuisance cyanobacterial blooms, the senescence and decomposition of which further hypoxia (Paerl and Huisman, 2008). In Lake Nieuwe, Netherlands, the water column stability provided by warmer summer air temperature and reduced winds created conditions directly beneficial to cyanobacteria (Jöhnk, 2008). Cyanobacteria outcompete other algae at higher temperatures and regulate buoyance to take advantage of nutrient-deficient epilimnetic water (Mantzouki et al., 2015). Another European Lake, Lake Zurich, exemplified this process further (Posch et al., 2012). Although nutrient inputs had declined in the previous 40 years by 5-fold, favorable water conditions created by warm temperatures have made the cyanobacteria *Planktothrix rubescens* the dominant algal species in the lake (Posch et al., 2012).

Ice Cover

Warm winter temperatures may be especially influential on the development of summer hypoxia in dimictic lakes through control on the extent of ice coverage (Perello et al., 2017). Ice cover has direct control on the initiation of stratification (Austin and Colman, 2008) and indirect controls on the formation of substantial diatom blooms (D’Souza et al., 2013).

Often the link between winter ice coverage and the onset of stratification is quite straightforward, with ice coverage increasing reflectance and delaying the surface warming in spring. Over a 100-year period in Lake Superior, an average reduction in lake ice coverage from 23 to 12% stemming from a ~1.5 ˚C increase in regional air temperatures resulted in a 25-day increase in the length of stratification (Austin and Colman, 2008). A similar trend was observed in Lake Erie with an increase in the stratification period in the lake’s central basin with reductions in ice cover, increasing the time that hypolimnetic oxygen depletion could occur (Perello et al., 2017). In other systems, a reduction in ice coverage has acted to reduce summer thermal stratification. A warm winter in the Lake Michigan area (2012) lead to little ice cover and caused upwelling events into Green Bay to be warmer, reducing the thermal gradient of the bay and resulting in reduced stratification (Grunert et al., 2018). A colder winter (2013) with increased ice extent conversely caused these summer intrusions to be with much colder water, intensifying stratification and aiding the development of hypoxia in the summer.

Ice coverage (or lack thereof) may also control the development of phytoplankton growth throughout the winter and spring (Nicholls, 1998; Twiss et al., 2012). The presence of winter ice may support large diatom blooms that have traditionally gone unnoticed or underappreciated compared with spring diatom blooms (Twiss et al., 2012). D’Souza et al. (2013) observed *in situ* concentrations of chlorophyll-*a* as much as 100× greater on floating ice than in surrounding open waters. In addition, diatoms themselves may be partially responsible for the nucleation of ice (D’Souza et al., 2013), further strengthening the relationship between diatoms and ice coverage. The presence of ice may also provide a substrate that diatoms can attach to and proliferate (Twiss et al., 2012), resulting in winter under-ice blooms of diatoms that can have greater biomass than spring diatom blooms (Twiss et al., 2012) and 1.5–6× greater than summer blooms of *Microcystis* Lemmermann (Reavie et al., 2016). These winter diatom blooms were subsequently shown to account for a substantial portion of the organic matter in the benthos, contributing to sediment oxygen demand during decomposition (Carrick et al., 2005; Reavie et al., 2016). A lack of ice coverage may also promote spring blooms by allowing winds to keep nutrients entrained in the water column (Nicholls, 1998), whereas the presence of ice coverage results in quiescent under-ice conditions that reduce sediment suspension, and entrap nutrients in the sediment, reducing spring primary productivity (Nicholls et al., 1998; Twiss et al., 2016).

Although some have hypothesized that greater ice coverage may reduce summertime hypoxic extent (Twiss et al., 2012), this remains a largely untested hypothesis with more recent findings about the extent of winter under-ice blooms relative to summer blooms bringing into question the impact of different sources of organic matter on summer hypoxia (Reavie et al., 2016).

Algal Community Compositional Influence

Bacillariophyta

Compared with the thorough examinations of nutrient loading (Rabalais et al., 2002; Scavia et al., 2014; Watson et al., 2016) and meteorology, much less research effort has been devoted to identifying the role algal bloom community composition plays in influencing hypoxia (Reavie et al., 2016). Benthic and pelagic algal decomposition accounts for a large portion of hypolimnetic oxygen depletion (Carrick et al., 2005), and in some systems planktonic respiration itself can dominate oxygen depletion during the summer months (Kemp et al., 1992). Bacillariophyta, or the diatoms, can proliferate rapidly under the right environmental conditions, resulting in large blooms (Reavie et al., 2016). Moreover, diatoms often constitute a large proportion of the total phytoplankton composition, in one instance representing over 40% of the annual phytoplankton biomass (Makarewicz, 1993). Although diatoms blooms have been observed prior to the development of hypoxia (Allinger and Reavie, 2013), direct contribution of winter and spring diatom production has not been explicitly described (Twiss et al., 2012). Regardless of direct description, some inferences can still be made regarding the effect of diatom blooms on hypolimnetic hypoxia via connections to lake ice (in freshwater systems) and diatom biology.

As discussed previously (see Ice Cover), there is an apparent 2-way relationship between the formation of lake ice and the presence of diatoms (D’Souza et al., 2013). Although the exact culprit is not clear, either diatoms themselves or associated *Pseudomonas* bacteria are effective in ice nucleation. In an experiment conducted by D’Souza et al. (2013), fresh phytoplankton (mostly diatoms) samples were evaluated for their ability to nucleate ice compared with heat-treated phytoplankton. Fresh samples were significantly better ice nucleators, demonstrating the potential ability of diatoms to accelerate the growth of ice, which then creates a favorable microclimate for the growth of diatoms in a positive feedback loop (D’Souza et al., 2013). These favorable light climates stimulate diatom growth that can reach considerable biomass, which in turn accounts for a significant portion of the organic matter input into the benthos (Reavie et al., 2016). In Lake Erie, the biomass of these winter and spring diatom blooms accounted for 11–33% of the total hypolimnetic oxygen demand during summer stratification (Lashaway and Carrick, 2010).

The biology of diatoms may further influence their relative contribution to hypolimnetic oxygen depletion through structural (Strathmann, 1967) and life history attributes (Lund, 1954; Sicko-Goad et al., 1989). Two key characteristics of diatoms are the presence of large vacuoles and a silica cell wall (Strathmann, 1967). These two features in combination are largely responsible for diatoms containing a lower carbon content per volume than other algal classes, a trend observed in both marine (Moal et al., 1987) and freshwater (Rocha and Duncan, 1985) plankton assemblages. Similarly, in marine systems the relationship between the size of algal cells and carbon density is not linear, with carbon density decreasing exponentially for biovolumes of 0.2–300 μg^{3} cell^{-1} and the smallest cells having carbon densities 2–3× greater than cells with biovolumes over 200 μg^{3} cell^{-1} (Verity et al., 1992). However, freshwater systems did not show this same carbon density-volume relationship, rather showing carbon densities relatively stable at 0.2 pgC μg$^{3-1}$ (Rocha and Duncan, 1985). In at least one instance, warming air temperatures have resulted in decreasing planktonic diatom size in a freshwater lake (Winder et al., 2009), a trend that, if true in marine ecosystems where the nonlinear relationship exists, could spark a quicker initiation of hypoxia upon decomposition (Reavie et al., 2016).

The silica cell wall that contributes to lower carbon densities in diatoms is also partially responsible for diatom's quick-sinking nature in stable waters (Sicko-Goad et al., 1984). Both the type and sinking of phytoplankton have a substantial effect on the formation of hypoxia (Zhao et al., 2018). Sinking rates in diatom-dominated blooms (1.56 m day^{-1}) are nearly double that of dinoflagellate-dominated blooms (0.87 m day^{-1}), which correlated strongly with hypolimnetic low-oxygen zones at diatom-dominated stations compared with the oxygen-levels of dinoflagellate-dominated stations. Diatoms also produce resting cells that sink to the benthos until favorable conditions initiate their rejuvenation (Sicko-Goad et al., 1989). These resting cells further contribute to hypolimnetic oxygen demand (Lashaway and Carrick, 2010), and along with decomposition of other diatom cells may have considerable effect on hypoxia (Carrick et al., 2005).

Cyanobacteria

Cyanobacteria (or Cyanophyta) have become increasingly problematic throughout the last century (Paerl and Huisman, 2008), forming large blooms that are economically and ecologically damaging (Michalak et al., 2013). Initial efforts to reduce external nutrient loads have limited these blooms in many systems (Rabalais et al., 2002; Scavia et al., 2014; Watson et al., 2016). However, lasting community composition shifts (Posch et al., 2012) and recent re-eutrophication (Scavia et al., 2014) of aquatic systems has occurred, even while external nutrient inputs and surrounding land uses have remained stable over the same period (Donner and Scavia, 2007). Cyanobacterial blooms impart numerous water quality changes on systems (Watson et al., 2016), and their unique physiology provides them a competitive advantage under recent changes in climate (Pearl and Huisman, 2008; Posch et al., 2012). However, like other algal groups, the relative contribution of various algal groups to carbon content in benthic organic matter is relatively unexplored (Reavie et al., 2016).

The timing and location of cyanobacterial blooms may have indirect controls on the development of hypoxia. The largest early summer blooms of *Dolichospermum* (Ralfs ex Bornet & Flahault) P.Wacklin et al. in Lake Erie reduced water clarity, with cyanobacterial biomass both contributing to light reduction and benefiting competitively from sediment loading-driven clarity reductions, but no relationship was found between the timing of the blooms and hypolimnetic dissolved oxygen concentrations (Chaffin et al., 2019). However, hypothetically, early season surface blooms of cyanobacteria and hypolimnetic dissolved oxygen may reduce water clarity and therefore, limit primary productivity of algae at other levels of the water column (Bridgeman and Penamon, 2010; Wilhelm et al., 2006). Blooms of cyanobacteria can produce significant biomass throughout the water column (Wilhelm et al., 2006) and on the benthos, with benthic species like *Lyngbya wollei* (Farlow ex Gomont) Speziale & Dyck having the potential to offset oxygen declines in the hypolimnion during blooms (Bridgeman and Penamon, 2010). Thus, reductions in water clarity by large cyanobacterial blooms may limit oxygen-producing primary production in the hypolimnion, though this may be beneficial in the long-term since water column and benthic algal biomasses later contribute to further hypolimnetic oxygen drawdown during their decomposition (Diaz and Rosenberg, 2008).

Structural features of cyanobacteria provide a competitive advantage under warm, calm, and stratified conditions (Reynolds et al., 1987), where their ability to regulate their position in the water column through buoyancy control creates a positive feedback loop between cyanobacterial biomass and hypoxia (Smith et al., 2011). In this situation, hypoxic conditions change the water-sediment interface from an oxidizing state that buries oxidizing metals and nutrients into the sediment to a reducing state that releases these metals and nutrients back into the hypolimnion (Mortimer, 1941). Cyanobacteria in shallow and moderately deep stratified systems are then able to exploit their buoyancy control to access these nutrients that would otherwise remain isolated, ultimately resulting in further proliferation and decomposition of cyanobacteria which exacerbate the hypoxic conditions and internal loading even further (Smith et al., 2011). Fall cyanobacterial blooms as a result of internal loading from hypoxic conditions occur in deeper systems as well, although in these systems external forces are required to entrain hypolimnetic nutrients back into the water column (Nürnburg et al., 2013b). Hypoxia-driven internal loading often is not sufficient to trigger cyanobacterial blooms by itself (Matisoff et al., 2016) but can still be quite influential as internal P loading has been shown to be as much as 45–89% of external P loading in some eutrophic lakes (Nürnburg et al., 2013a).

Compared to diatoms, cyanobacteria may have higher carbon densities relative to biovolume (Reavie et al., 2016). In a study of marine phytoplankton, at least one genus, *Synechococcus* C.Nägeli, had a carbon density (0.47 pgC μm$^{3-1}$) close to double that of other examined nanoplankton (0.13–0.31 pgC μm$^{3-1}$; Verity et al., 1992). Conversely, Rocha and Duncan (1985) found relatively consistent densities between cyanobacteria (0.156 pgC μm$^{3-1}$) and other algal classes (0.154–0.319 pgC μm$^{3-1}$) in freshwater phytoplankton. When comparing blooms dominated by one class or another, understanding the relative contribution of a particular bloom to the benthic organic matter may be valuable information when evaluating hypolimnetic and sediment oxygen demand, especially if small cyanobacteria have high carbon densities (Verity et al., 1992; Reavie et al., 2016).

Other Algal Classes

Diatoms and cyanobacteria have been the focal point of most research concerning the influence of algal composition on the development of hypoxia because of their propensity to form large blooms, though some other classes have received some limited attention more recently (Zhao et al., 2018). The majority of these studies have used interspecies differences between algae to analyze nutritional quality and its effect on aquatic food webs (Rocha and Duncan, 1985), rather than *in situ* observation of interspecies effects on hypoxia development. An early study by Strathmann (1967) demonstrated that diatoms tend to have significantly lower carbon densities than chrysophytes, chlorophytes, and dinoflagellates that all had similar carbon densities, but specific values for these classes was not mentioned. High carbon densities relative to other algae have been found in cryptophyceae by Moal (1987) and Verity (1992), both of which examined marine phytoplankton, while freshwater cyptophyceae showed moderate carbon densities in freshwater ecosystems (Rocha and Duncan, 1985). In a study analyzing thirteen algal species across 5 algal classes, differences were found between algal classes with Xanthophyceae having the highest densities (0.319 pgC μm^{3-1}), followed by Cryptophyceae, and Chlorophyta (0.181 pgC $\mu m^{3-1}$and 0.163 pgC μm^{3-1}, respectively; Rocha and Duncan, 1985). These variances suggest blooms dominated by different algal classes could result in different quantities of organic matter to the benthos, though whether this has a quantifiable effect on the development of hypoxia largely remains to be seen. Examinations beyond that of Zhao et al. (2018) (see: Bacillariophyta) are limited, though this provides some evidence that the type of bloom can be of importance in the formation of hypoxia.

Conclusion

Hypolimnetic hypoxia, although often a naturally occurring phenomenon, has been exacerbated in recent decades. Anthropogenic nutrient loading has been widely documented as the factor largely responsible for these increases in hypoxia, but an increasing body of literature has clarified the role of meteorological conditions in directly and indirectly controlling hypoxia. Nutrients have garnered this interest largely because it is the most easily manipulated variable in controlling hypoxia and because of its place as a limiting factor in the proliferation of algal blooms. Regardless, it is highly likely that meteorological variables have independent control over hypoxia. Climate change and alterations in nutrient loads have manifested in changes to algal communities, often favoring a shift towards cyanobacterial species. Even with changing climate and nutrients inputs altering the composition of algal blooms, whether community changes have any bearing on the formation or severity of hypoxia remains largely unexplored in an explicit manner. Limited research and biological differences between classes (and species) of algae suggest that the composition of algal blooms do, at least in some limited capacity, have influence on the formation of hypoxia.

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