

Review

The re-eutrophication of Lake Erie: Harmful algal blooms and hypoxia



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ABSTRACT

Lake Erie supplies drinking water to more than 11 million consumers, processes millions of gallons of wastewater, provides important species habitat and supports a substantial industrial sector, with >\$50 billion annual income to tourism, recreational boating, shipping, fisheries, and other industries. These and other key ecosystem services are currently threatened by an excess supply of nutrients, manifested in particular by increases in the magnitude and extent of harmful planktonic and benthic algal blooms (HABs) and hypoxia. Widespread concern for this important international waterbody has been manifested in a strong focus of scientific and public material on the subject, and commitments for Canada-US remedial actions in recent agreements among Federal, Provincial and State agencies. This review provides a retrospective synthesis of past and current nutrient inputs, impairments by planktonic and benthic HABs and hypoxia, modelling and Best Management Practices in the Lake Erie basin. The results demonstrate that phosphorus reduction is of primary importance, but the effects of climate, nitrogen and other factors should also be considered in the context of adaptive management. Actions to reduce nutrient levels by targeted Best Management Practices will likely need to be tailored for soil types, topography, and farming practices.

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1. Introduction

Lake Erie, the southernmost, warmest, shallowest, and most biologically productive of the Great Lakes, supplies drinking water to more than 11 million consumers, processes millions of gallons of wastewater, provides habitat for economically, ecologically, and culturally important biota, and supports a substantial industrial sector, with annual income to tourism, recreational boating, shipping, fisheries, and other industries of over \$50 billion (LEIA, 2012). These and other key ecosystem services are now increasingly threatened by eutrophication, manifested by increases in the magnitude, duration, and extent of harmful algal blooms (HABs; Higgins et al., 2008; Michalak et al., 2013; Steffen et al., 2014) and hypoxia (Zhou et al., 2013, 2015; Scavia et al., 2014). In recognition of these ecosystem impacts and the need to develop a sustained restoration and management programme, the International Joint Commission (IJC) commissioned the Lake Erie Ecosystem Priority (LEEP) taskforce in 2012 to evaluate current conditions, identify knowledge and monitoring gaps, provide guidance for management targets, and engage public interest and support (International Joint Commission (IJC), 2014; Watson et al., 2013). This initial IJC review, and subsequent work by binational taskforces, led to commitments for remedial action in the recently renewed Canada-USA Great Lakes Water Quality Agreement (GLWQA). Nutrients, hypoxia and algal biomass are addressed under Annex 4 of this Agreement, with specific references to setting interim total phosphorus (TP) load and basin-specific concentration targets for Lake Erie. Similarly, the 2014 renewed Canada-Ontario Agreement (COA) specifically highlights Lake Erie in the objectives to set loading and concentration targets.

Scavia et al. (2014) reviewed and evaluated recent eutrophication-related trends in Lake Erie, and developed response curves to guide hypoxia-based loading targets. Following a binational remedial effort, central basin hypoxia and west-central phytoplankton biomass showed strong declines in the late 1970s and early 1980s, followed by a general increase in these parameters since the mid-1990s which the authors attributed to increased agricultural loading of soluble reactive phosphorus (SRP). The authors also concluded that reducing central basin hypoxic area to levels observed in the early 1990s (ca. 2000 km²) requires the reduction of TP loads by 46% from the 2003 to 2011 average or SRP loads by 78% from the 2005 to 2011 average, and that

those reductions would protect fish habitat. Based on an analysis of long-term records of climate and nutrient data, however, Zhou et al. (2015) reported that a record-breaking hypoxic event in 2012 followed a period of drought and low tributary flow, while in 2011, the largest cyanobacterial bloom of the decade (as measured by remote sensing; e.g., Michalak et al., 2013) was accompanied by mild hypoxia. These and other authors have concluded that both the extent and severity of central basin hypoxia and west basin planktonic algal blooms show strong, but fundamentally different relationships with the timing and volume of spring-summer river discharge and associated nutrient inputs (Rucinski et al., 2014; Stow et al., 2015). Furthermore there is evidence that together with P, nitrogen plays an important role in planktonic bloom composition and toxicity, while light and temperature have a major effect on benthic bloom development (Auer et al., 2010; Steffen et al., 2014; Davis et al., 2015). These and other studies demonstrate that P reduction is of primary importance, but the effects of climate, nitrogen and other factors may need to be considered when developing an adaptable response which may require a tailored approach, such as the application of targeted Best Management Practices (BMPs) that account for soil types, topography, and farming practices (McElmurry et al., 2013). A proliferation of scientific and other published material has led to a global awareness of the issues challenging this lake (e.g., a Scopus database search yields >300 documents for the terms 'blooms', 'nutrients' and 'hypoxia' in Lake Erie over the past 5 years) and widespread media and website coverage (e.g., http://www.glerl.noaa.gov/res/HABs_and_Hypoxia/; <http://www.cbc.ca/news/trending/algae-blooms-lake-erie-lake-st-clair-nasa-photoshow-1.3179298>). This review presents a synopsis of past, present and future nutrient loading, HABs and other impairments in this lake and options for mitigation.

2. Signs of impairment: harmful blooms and hypoxia

2.1. Harmful algal blooms (HABs)

2.1.1. Planktonic HABs

In most regions of North America the majority of planktonic HABs are caused by cyanobacteria (cHABs), most often where surface waters receive high inputs of growth-limiting nutrients (phosphorus, P and nitrogen, N). Global climate and regional

weather patterns can also increase the risk of cHABs, which are generally favoured by nutrient-enriched runoff from intense rain events, warm temperatures, low flushing, water column stability and prolonged ice-free growing seasons (Paerl and Otten, 2013; Watson et al., 2015).

Recently, cHABs have become particularly problematic in Lake Erie, the shallowest, warmest and most populated of the Great Lakes, and most vulnerable to disturbance. Lake Erie has undergone some significant regime shifts over the past century, manifested in disturbing trends in the risk and severity of harmful algal blooms (HABs). Basin development, eutrophication, species invasion, increases in diffuse and point-source loading, climate change and restoration efforts have been accompanied by salient changes in plankton community structure and productivity (Allinger and Reavie, 2013). Analyses of long term plankton and sediment data have shown that algal blooms are not new to this Lake, but have changed dramatically in species composition and dynamics over the past fifty years (Allinger and Reavie, 2013; Steffen et al., 2014). Earlier eutrophication during the mid-late 1900s resulted in extensive cyanobacterial blooms across many of the Great Lakes, despite their size. These were occurring during a time when the threat of toxins was generally unrecognized, and the main concern was with aesthetics and taste-odour (Carmichael, 2008). Dense spring and fall blooms were driven by excessive wastewater-dominated nutrient loading, and were generally composed of eukaryotic algae (diatoms such as *Asterionella*, *Cyclotella*, *Fragilaria*, *Synedra*, *Aulacoseira*, along with chlorophytes and dinoflagellates), with outbreaks of N_2 -fixing (*Aphanizomenon* spp.; *Anabaena*)¹ and non-fixing cyanobacteria (*Coelosphaerium*, *Anacystis*, *Oscillatoria* (syn. *Planktothrix*), *Merismopedia*, *Woronochinia*, *Microcystis*, *Pseudanabaena*) in the mid-summer (Munawar et al., 2008; Allinger and Reavie, 2013). Casper (1965), for example, described a severe surface bloom that followed a period of calm weather in late summer 1964, extending across some 2000 km² of the west basin. This bloom was dominated by an assemblage of cyanobacteria (*Anacystis cynea* (syn. *Microcystis aeruginosa*), *Oscillatoria* (syn. *Planktothrix*), *Aphanizomenon holsaticum* (syn. *Aph. flos-aquae*), *Anabaena circinalis*) and the green colonial flagellate *Carteria*.

To address the advanced eutrophication of Lake Erie and the other Great Lakes, binational restoration efforts were implemented in 1972 with the signing of the Canada-US GLWQA (Hasler, 1969). Within ten years, binational remediation, aimed largely at point source municipal and industrial inputs, reduced total P loading into Lake Erie to half the peak levels observed in 1968 (Makarewicz and Bertram, 1991; Charlton et al., 1993). Total phytoplankton biomass in the lake was also significantly reduced, but species of *Aphanizomenon*, *Anabaena*, *Planktothrix* and *Microcystis* remained present in these assemblages (Kane et al., 2009; Allinger and Reavie, 2013). Since the 1990s, several other changes have occurred which have had profound effects on Lake Erie. Most notably, widespread colonization by dreissenid mussels and other invasive species, increasing non-point agricultural loading of more bioavailable P (i.e., SRP) and climate change have engineered ecosystem-wide changes in the physical, chemical and biological regimes of the Great Lakes (Hecky et al., 2004; Conroy et al., 2005; Jiang et al., 2015). In Lake Erie, this has been accompanied by a resurgence of algal biomass, particularly in the west basin, and major shift in the dominant bloom species and their spatial and temporal dynamics starting in the early 2000s (Barbiero et al., 2006; Millie et al., 2009). Planktonic blooms in this lake have since been characterized by a rise in the predominance and severity of cHABs and the dominance of more toxic taxa such as *Microcystis*

(Munawar et al., 2008; Allinger and Reavie, 2013; Kane et al., 2014).

The majority of these blooms occur in the west basin of Lake Erie, where the mid-summer cyanobacterial peaks of the late 1900s have been replaced by severe cHABs which cover large areas and can persist throughout the summer and late fall (Michalak et al., 2013; Steffen et al., 2014). Extensive cHABs dominated by *Microcystis* and other potentially toxic cyanobacteria (*Dolichospermum*, *Planktothrix*) are now an annual event across the open waters of the basin (e.g., Rinta-Kanto et al., 2009a; Steffen et al., 2014). Biomass is generally lower in the more oligotrophic offshore regions of the central and east basins, although there is some indication of a recent increase in cyanobacteria in the summer plankton assemblages in these basins (Allinger and Reavie, 2013; Kane et al., 2014), while narrow shoreline bands of dense cHABs have arisen over the past several years; for example following the 2012 upwelling and extensive fish kill along the northern shore (Rao et al., 2014).

Brittain et al. (2000) first galvanized public attention to the serious implications of the rise in predominance of *Microcystis* with their report of significant levels of the hepatotoxin microcystin-LR (MC-LR) in the west basin of Lake Erie from a 1995 bloom of *Microcystis aeruginosa*, a widespread producer of these toxins in north temperate freshwaters (Wilson et al., 2005). MC-LR is among the most toxic of the >100 different microcystin varieties (congeners) characterized to date, and has been identified in numerous bloom samples from the Great Lakes along with microcystin-LA and -RR (Dyble et al., 2008). Molecular studies have identified toxic strains of *M. aeruginosa* across the lower Great Lakes, Lake St. Clair and Lake Michigan, demonstrating a capacity for this species to form blooms that are not localized to near-shore areas, but widely distributed across Lake Erie and connected waters (Rinta-Kanto et al., 2005; Dyble et al., 2008; Rinta-Kanto et al., 2009a; Davis et al., 2014). Dyble et al. (2008) identified distinct differences in genetic coding for MC production among *M. aeruginosa* populations in Lake Erie and Saginaw Bay (Lake Huron), which may affect the congeners produced by local blooms and their associated toxicity. These studies also show that current Lake Erie *Microcystis* is genetically indistinguishable from earlier populations and not an invasive new genotype, consistent with the persistence and opportunistic population surges of this taxon throughout historical regime shifts in response to environmental influences (Rinta-Kanto et al., 2009b). Other cyanobacteria may contribute to toxin levels, notably *Planktothrix suspensa/aghardhii*, a known source of MC toxins in Lake Erie, which can predominate under turbid conditions in the nutrient-rich Maumee River and particularly Sandusky Bay (Rinta-Kanto and Wilhelm, 2006; Kutovaya et al., 2012; Davis et al., 2015).

Although to date, no human fatalities have been directly attributed to cHABs in North America, some cyanobacterial toxins are irritants or suspected carcinogens (notably, MC) and the health effects of sub-acute chronic exposure are difficult to resolve and largely unrecorded (Boyer, 2007; Watson et al., 2008). Microcystins are chemically stable, and the most widely reported cHAB toxins in the Great Lakes. MC levels exceeding drinking and recreational water guidance values are now detected annually across Lake Erie and eutrophic inshore areas of Lakes Ontario, Huron and recently, Lake St. Clair (Dyble et al., 2008; Davis et al., 2014; Watson and Boyer, 2014). Other cyanobacterial toxins are less frequently monitored and rarely detected, despite the often-significant presence of cyanobacterial taxa that have been reported as toxic in other surface waters. The neurotoxin anatoxin-a, for example, has been reported intermittently in Lake Erie inshore areas and the embayments of Lake Ontario (Boyer, 2007; Perri et al., 2015). The toxin cylindrospermopsin has not been found in Lake Erie waters, despite the presence of species known to produce

¹ Planktonic forms are now reclassified as *Dolichospermum*; Wacklin et al., 2009.

this toxin in other lakes such as *Aphanizomenon flos-aquae* and the congeneric taxa *Cylindrospermopsis* (Conroy et al., 2005); strains of which also produce deoxy-cylindrospermopsin. Less is known about the occurrence of the paralytic shellfish toxins (PSTs) such as saxitoxin or its analogues produced by some freshwater cyanobacteria, although more recently, monitoring has become more intensive for all cyanotoxins (Watson and Boyer, 2014). During early surveys, PSTs were detected in only 0.2% of the mid- to late-summer samples collected from the lower Great Lakes basin in the mid-2000s and analyzed using HPLC techniques (Boyer, 2007). Since 2010, however, the US Ohio-EPA has been monitoring cyanotoxins in samples collected throughout the year from an extensive network of water treatment plant intakes and sources, including sites from Lake Erie (http://wwwapp.epa.ohio.gov/gis/mapportal/HAB_Monitoring.html). The data are based on ELISA analyses, and indicate that saxitoxin or its analogues may be present in as many as 40% of the samples, most at levels well below the Ohio EPA drinking water 'Do Not Use' threshold of 0.2 µg/L, including sites directly connected with or sampled from Lake Erie (average 0.022 µg/L). The cyanobacterial sources were not identified but could include either *Lyngbya* or *Dolichospermum* species, both of which are present in Lake Erie. As noted above, several species of *Dolichospermum* have been identified from many of the recent Lake Erie blooms, while *Lyngbya wollei* is often problematic in the south-west basin as dislodged or benthic mats; saxitoxin analogues (named *Lyngbya wollei* toxins, or LWTX) were identified in populations of this cyanobacteria from Lake St. Clair and the St. Lawrence River (Lajeunesse et al., 2012; Vijayavel et al., 2013).

Early detection of cHABs is fundamental to their effective management, and diagnostic and monitoring methods have been greatly enhanced by the advancement of microscopic, molecular, and imaging techniques. The increased spatial and spectral resolution of remote sensing techniques now allows earlier warning, targeted sampling and bloom forecasting, although currently, these methods are largely limited to tracking surface material and cannot represent the often-significant biomass dispersed through the water column (Binding et al., 2012; Obenour et al., 2014). Advanced molecular methods can source-track and diagnose phenotypic and physiological traits at different levels of community resolution. This approach has allowed scientists to quantify, for example, the abundance and expression of genes coding for nutrient assimilation, toxin and taste-odour production and other key metabolic processes, and identify major taxa in a mixed bloom (Kutovaya et al., 2012, 2013; Kutovaya and Watson, 2014; Steffen et al., 2015). Genetic sequencing has further elucidated both the structure and function of individual bloom community members (Steffen et al., 2012, 2015; Harke et al., 2015), and shown that toxin-producing *Microcystis* blooms are composed of a mix of toxic and non-toxic cells (Ha et al., 2008; Rinta-Kanto et al., 2009a).

Eutrophication is widely acknowledged as a primary driver of high phytoplankton biomass. In particular, P is a key growth-limiting nutrient which reinforces cyanobacterial biomass and dominance in many freshwater systems including Lake Erie (e.g., Downing et al., 2001; Michalak et al., 2013). Nevertheless it is increasingly clear that cHAB management should consider how other factors qualify the response to P control, for example, the timing and bioavailability of this and other primary and trace nutrients, temperature, light, mixing and other physical factors, climate change, and top-down control from grazers and disease (e.g., Elser, 1999; Paerl and Otten, 2013). The recent shift in HAB characteristics has evolved with no discernible increase in total annual P loading, and instead, appears to be linked with the timing, sources and increased bioavailability of this load, coupled with other important changes (e.g. Obenour et al., 2014; Scavia et al.,

2014). Recent authors have linked the level of cHAB impairment in Erie to the volume of spring runoff in the Maumee basin, coupled with rising non-point SRP inputs from west basin tributaries (Stumpf et al., 2012; IJC, 2014; Kane et al., 2014). The rise in *Microcystis* dominance, also observed in other areas of the Great Lakes such as the Bay of Quinte (Lake Ontario), Green Bay (Lake Michigan) and Saginaw Bay (Lake Huron), has also been attributed to the enhanced water clarity, selective particle removal and soluble nutrient recycling associated with dreissenid filtering activity (Conroy et al., 2005; Munawar et al., 2008; Nicholls, 2011; Vanderploeg et al., 2013; De Stasio et al., 2014). Growing evidence now suggests that while P is a primary factor driving total phytoplankton biomass across most of Lake Erie, the supply and chemical speciation of N may play a key role in shaping the structure and abundance of this community (Dolman et al., 2012; Donald et al., 2013; Horst et al., 2014; Davis et al., 2015). The capacity to fix N₂ at low dissolved inorganic N supply is an important factor facilitating dominance by some cyanobacteria in P-enriched systems, and the basis for simple empirical models predicting cyanobacterial dominance at low N:P ratios (e.g., Smith, 1983). This paradigm has sparked significant debate, given that many cHAB taxa – including *Microcystis* – are not diazotrophs, while many heterotrophic Proteobacteria are, and benthic recruitment of *Microcystis* and other cyanobacteria from N-enriched sediments can facilitate cHABs even at low N:P ratios (e.g. Downing et al., 2001; Ståhl-Delbanco et al., 2003; Steffen et al., 2012; Davis et al., 2015). In Lake Erie, evidence points to the importance of N in cHAB events, for example, seston stoichiometric data for C:N:P indicates planktonic N limitation which varies among seasons, basins, nearshore and offshore zones, and years (Fig. 1). Taxon-specific bioassays also highlight the importance of both inorganic (NO₃, NH₄) and organic N (e.g., North et al., 2007; Chaffin and Bridgeman, 2014). Urea – increasingly used in fertilizers – can facilitate blooms of *Microcystis* and other cHAB taxa and influence toxicity (Davis et al., 2010, 2015; Finlay et al., 2010). Research also points to iron availability as a potential factor in cHABs events (Mioni et al., 2003; North et al., 2007; Molot et al., 2014) but little work has been done to evaluate this in Lake Erie.

Climate plays a large role in the inter-annual variance in the severity and spatial-temporal dynamics of these blooms (e.g., Michalak et al., 2013), affecting the timing and concentrations of nutrient loads, ice cover, storm events, water temperature, hydrodynamics and mixing patterns. Warmer temperatures have resulted in an earlier thaw or incomplete ice coverage on Lake Erie in recent years – although the record ice-cover in 2013–14 and 2014–15 highlights the significant annual variance of this cover. Higher temperatures also affect mixing, circulation and nutrient loading/internal processing, together with changes in precipitation, irradiance and storm events. This can alter aquatic community succession, and potentially facilitate extended blooms of cHAB species such as *Microcystis* (Davis et al., 2012; Koslow et al., 2013). Prolonged periods of stable thermal stratification and calm conditions can result in the rapid development of large surface blooms of large buoyancy-regulating cyanobacteria such as *Microcystis*, *Dolichospermum* and *Aphanizomenon* (Carey et al., 2012) which can become wind-blown aggregates representing a serious threat to inshore areas – as seen in the recent drinking water crisis in Toledo (Carmichael and Boyer, in press).

While non-HAB cyanobacteria such as picocyanobacteria (<2 µm) are essential food web components in more oligotrophic areas (Carrick and Schelske, 1997; Wilhelm et al., 2006), cHAB taxa are generally favoured by high nutrient levels. Current approaches reflect the historic focus on nutrients, but the science of cHABs in Lake Erie is evolving towards a more comprehensive study of bloom development and toxicity, and the importance of other factors such as climate change and other taxa. Blooms of species

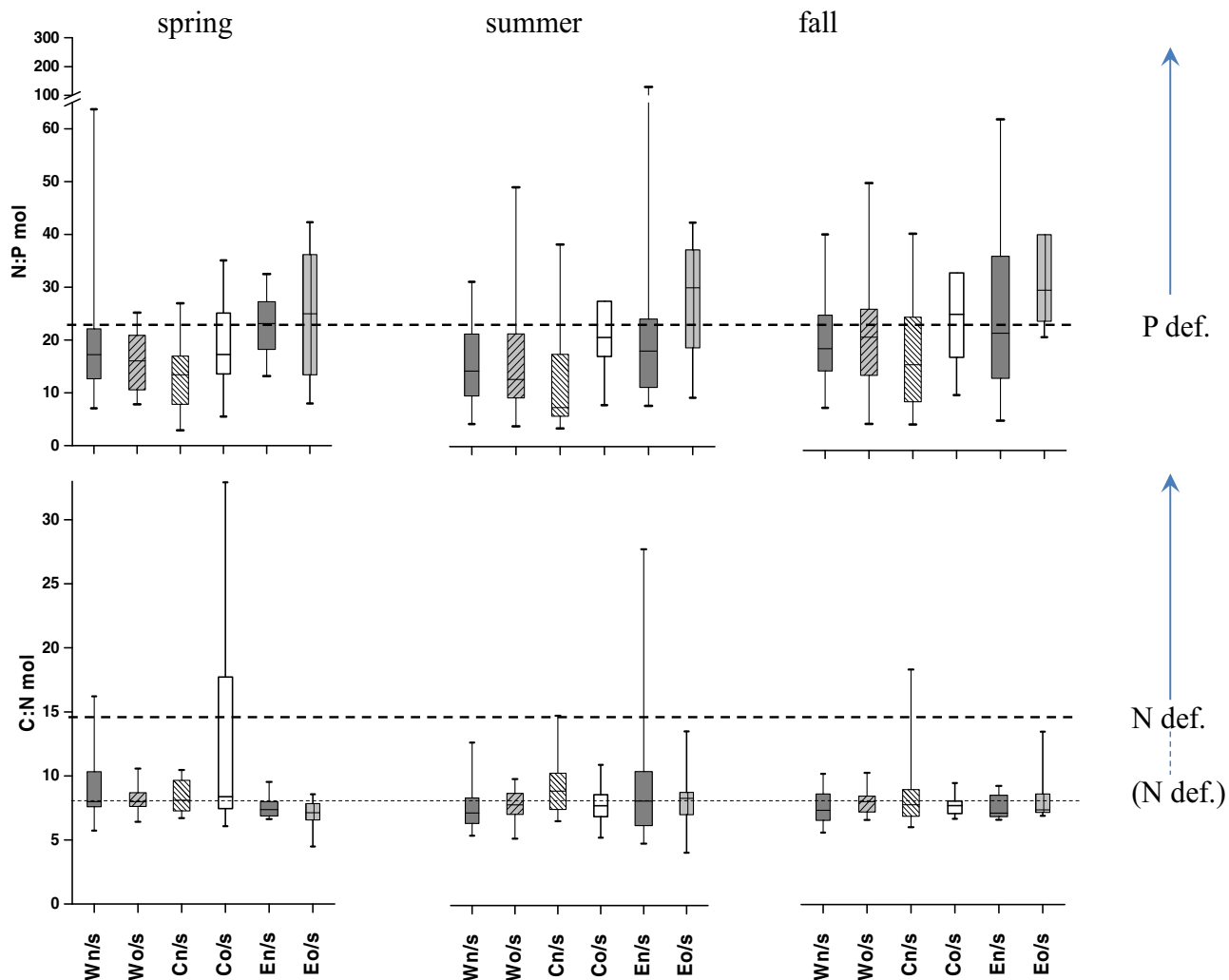


Fig. 1. Box and whisker plots showing sestonic molar ratios of N:P (top), and C:N (bottom); plots arranged left to right in order of: West Basin Inshore, West Basin Offshore, Central Basin Inshore, Central Basin Offshore, East Basin Inshore, East Basin Offshore. Data from open water (May–Oct) surface samples (1 m), 2000–2010 (S. Watson unpublished, Environment and Climate Change Canada). Boxes represent 95th percentiles. Horizontal dashed lines are indicative of moderate (---) or severe (—) P or N deficiency (Ref. Healey and Hendzel, 1980). 'Offshore' defined as approximately 20 km from closest shoreline, not by depth contour.

from other major phytoplankton groups such as the winter diatom *Aulacoseira islandica* can not only impact water quality and food web structure but also may set the stage for successive plankton communities and cHAB development by altering nutrient cycling and deposition/recycling processes (Saxton et al., 2012; Twiss et al., 2012). For example, the accumulated biomass and heightened bacterial activity in early spring may fuel spring blooms and subsequent successional development, while the accumulated live and decaying diatom cells, bacteria and organic detritus at the sediment surface may periodically seed surface populations and exacerbate bottom nutrient recycling and hypoxia (Bižić-Ionescu et al., 2014; Wilhelm et al., 2014). Bacteria and viruses are also important components of HAB communities. Heterotrophic microbiota are involved in a range of physicochemical processes such as ice nucleation, nutrient cycling and oxygen drawdown, and influence both the development and decline of cHABs (Tang et al., 2010; Wilhelm et al., 2011; Louati et al., 2015). Metagenomic, metatranscriptomic and physiological studies are now revealing the significant roles that bacteria and phages play in cell mortality, along with the functional processes of N-fixation and metabolism, toxin production and breakdown, and colony formation (Steffen et al., 2012, 2015; D'Souza et al., 2013; Davis et al., 2015; Harke et al., 2015; Wang et al., 2015). Future cHAB research should focus on identifying

and evaluating the relative importance of all key biotic and abiotic driving forces behind bloom events. This approach will improve our modelling and predictive capacity for different nutrient and climate scenarios and provide a more comprehensive approach to cHAB management practices.

Harmful cyanobacteria blooms have significant socioeconomic effects (e.g. Steffensen, 2008; Smith et al., 2015), and have been reported from all states and provinces in the Great Lakes basin, with several regions recording animal illness and death, primarily of dogs and livestock. A recent review by Carmichael and Boyer (in press) evaluated the risk to human health across the Great Lakes from Federal, state and provincial case reports of cyanobacterial illness and death among animals and humans for all areas adjoining the Great Lakes. These data showed that only Lake Erie had probable or suspect cases of human and animal poisoning and that these were few in number. Ohio reported two probable and seven suspect cases of human illness associated with exposure to Lake Erie water in 2010, but none in the severe bloom year of 2011. No other provinces or states demonstrate cHAB-related health issues. All other Great Lakes experience periodic cHABs but no reports of human or animal illness, although there have been multiple beach postings and advisories, for example, in Hamilton Harbour (Watson et al., 2012).

In 2014, the first reported major impairment of Lake Erie drinking water supplies by cyanobacterial toxins affected a large population base. The source of the toxins was a *Microcystis* bloom in the west basin of Lake Erie, which although not exceptionally toxic or large in size, was driven towards the drinking water intake by strong winds from the north. As noted above, toxin-producing cHABs have occurred regularly in Lake Erie over the past 20 years dominated by *Microcystis* (Brittain et al., 2000; Watson et al., 2008; Steffen et al., 2014). Intermittently elevated toxin levels have also been reported from the west basin for more than a decade, for example, in 2000, toxin concentrations in *Microcystis* blooms exceeded 25 µg MC-LR/L (Brittain et al., 2000) and have since ranged from 1 to 200 µg MC-LR/L in surface water samples (Watson et al., 2008). While relatively minor compared to some cHAB-related drinking water events across the world (e.g., Lake Taihu; Qin et al., 2015), the 'Toledo incident' served to illustrate the challenges of predicting and managing such an event (Carmichael and Boyer, in press). In prompt response to the incident, there has been new US legislation which has included the passage of Ohio Senate Bill 1, regulating fertilizer application and the disposal of dredged lake sediments, and H.R. 212, *The Drinking Water Protection Act*, a United States federal bill which charges the US EPA to develop a strategic plan to assess and manage the risk associated with algal toxins.

2.1.2. Benthic HABs

The variety of physical habitat features in Lake Erie contributes to the rich diversity of benthic algae documented in Lake Erie since the late 1800s (>200 distinct taxa; Stewart and Lowe, 2008). Despite this apparent richness, detailed ecological study has been largely confined to two benthic HAB species responsible for the development of blooms that can foul beaches, shorelines and water intakes in Lake Erie: the chlorophyte *Cladophora glomerata* and cyanobacterium *Lyngbya wollei*. The spatial distribution of these blooms in Lake Erie is largely controlled by gradients in habitat features that exert control on growth. In the east basin, expansive areas of hard substratum, moderate to high water turbulence, high water clarity and adequate P supply, provide optimal conditions for *Cladophora* (Davies and Hecky, 2005; Higgins et al., 2008). In contrast, despite higher P levels in the west basin, the higher turbidity and relatively limited availability of hard substrate restrict the potential growth habitat of *Cladophora* to the splash zone. These conditions appear to provide favourable conditions for *L. wollei*, which achieves optimal photosynthetic rates at relatively low light (<50 µmol m⁻² s⁻¹; Pinowska et al., 2007; Bridgeman et al., 2012) and is often found associated with unconsolidated substrates such as mixtures of dreissenid shell fragments and sand (Bridgeman and Penamon, 2010).

The negative economic, aesthetic and recreational use impacts from benthic HABs are well documented, and include the fouling of beaches and residential shorelines, clogging of industrial water intakes, and unpleasant odours associated with decaying organic matter (Carmichael et al., 1997; Higgins et al., 2008). Ecological impacts are not well characterized owing to their transient nature, but nonetheless exist. For example, expansive standing crops represent a significant nutrient sink over much of the growing season (Higgins et al., 2005; Bridgeman et al., 2012), yet neither *Cladophora* nor *Lyngbya* are considered ideal food resources for grazers (Dodds and Gudder, 1992; Hudon et al., 2012). Large accumulations of attached or drifting algal biomass can result in transient hypoxic conditions in shallow littoral regions (Gubelit and Berezina, 2010) which have deleterious impacts on invertebrate communities (Berezina and Golubkov, 2008). Potential risks to fish and other aquatic wildlife also exist, as some *Lyngbya wollei* populations are

reported to produce paralytic toxins (Carmichael et al., 1997; Lajeunesse et al., 2012; Vijayavel et al., 2013) and dense stands of *Cladophora* in the lake and deposited on beaches often harbour *Clostridium* bacteria that produce type E botulism toxins (Chun et al., 2015).

2.1.2.1. Eastern Erie: *Cladophora*. The severe blooms of *Cladophora* that were a persistent feature along much of the northern shore and isolated locations along the southern shore of the east basin through the 1950s to late 1970s were largely a symptom of eutrophication (Taft and Kischler, 1973; Mantai et al., 1982; Millner et al., 1982). Control of point-source P discharges to Lake Erie is generally credited with reducing the extent and severity of *Cladophora* blooms (Higgins et al., 2008), however, since the mid-1990s, expansive blooms of *Cladophora* have returned along much of the northern shores of the east basin (Higgins et al., 2005). Attached biomass observed in these contemporary blooms is generally lower than recorded historically, but growth extends deeper into the lake (Higgins et al., 2008). This change in growth pattern is thought to be largely driven by increased water clarity and an increase in suitable substrate following the advent of significant dreissenid mussel populations (both *Dreissena polymorpha* and *Dreissena bugensis*) in the east basin (Higgins et al., 2005). Mussels may also alleviate nutrient shortages through the excretion of metabolic wastes and/or increasing the amount of particulate matter available for re-mineralization through egestion of non-edible algae and other detritus in the benthic environment (Hecky et al., 2004). While it has been challenging to demonstrate this concept on a broad scale, recent in situ studies have demonstrated increases in SRP concentrations above mussel beds (Martin, 2010; Dayton et al., 2014), and P excretion rates are estimated to meet *Cladophora* growth requirements over the growing season (Ozersky et al., 2009). This is supported by observations of increased primary production rates by these macroalgae in the presence of mussels (Davies and Hecky, 2005) and a positive spatial association with dreissenid mussel abundance both within (Wilson et al., 2006) and across the lower Great Lakes (Depew et al., 2011).

2.1.2.2. Western Erie: *Lyngbya*. Blooms of *Lyngbya wollei* in the west basin are a more recently recorded phenomenon, with severe blooms first noted in 2006 (Bridgeman and Penamon, 2010; Bridgeman et al., 2012). While *Cladophora* in the Great Lakes is generally considered to represent one cosmopolitan species (Ross, 2006), it is unclear if recent blooms of *L. wollei* in the west basin are the result of a native strain or one recently introduced from elsewhere in North America (Bridgeman and Penamon, 2010). It is important to note, however, that *L. wollei* can often be mistaken for *Plectonema wollei* when based on morphological assessment (Stewart and Lowe, 2008), and *P. wollei* has been documented in Lake Erie since the late 1890s (Pieters, 1902; Taft, 1942; cited in Stewart and Lowe, 2008). Detailed study of *L. wollei* in western Lake Erie is limited, but it is most frequently found growing on substrates composed of dreissenid shell fragments and sand in close proximity to P-rich waters with high turbidity (e.g., Maumee Bay; Bridgeman and Penamon, 2010). This is consistent with conditions associated with other reported occurrences of this benthic cyanobacterium in the Great Lakes – St. Lawrence River system (Vis et al., 2008). In general, *Lyngbya* blooms are most common in nutrient enriched waters, including those with limited water exchange or flushing (Paerl et al., 2006). The recent increases in bioavailable P inputs to the western basin (Scavia et al., 2014) remains the most parsimonious explanation for their development in the western basin of Lake Erie at present (Bridgeman and Penamon, 2010; Bridgeman et al., 2012).

2.1.2.3. Climate change and benthic HABs. Forecasting the trajectory for benthic HABs under climate change in the Great Lakes region is challenging. The extent and severity of blooms under a warmer climate – and ultimately their ecological, economic and societal impacts – will also depend on both the species in question and the associated hydrologic changes that are likely to affect the physical–chemical environment (Bennington et al., 2010; Hayhoe et al., 2010) and biological processes such as metabolism and growth rate. While it is anticipated that warming water temperatures will facilitate an earlier start to growth and thus bloom formation, this is more likely to favour prokaryotes such as *Lyngbya*, because their growth rates are optimized at relatively higher temperatures (Speziale and Dyck, 1992) compared to eukaryotes such as *Cladophora* (Graham et al., 1982).

Insight into the anticipated response of benthic HABs to increased warming can be gleaned from existing studies of growth dynamics (Malkin et al., 2008), studies of algal communities impacted by artificially warmed habitats such as thermal effluent plumes (Kirby and Dunford, 1982), and application of growth models to warming scenarios (Malkin et al., 2008; Higgins et al., 2012). For example, in Lake Ontario, Malkin et al. (2008) observed *Cladophora* growth over two years with contrasting thermal regimes (average difference of 4.2 °C in water temperature between 2004 and 2005). Although attached biomass did not differ substantially between years (~120 g m⁻² dry wt in 2004, ~100 g m⁻² dry wt in 2005), peak biomass was attained much earlier (Julian Day 170) in the warmer year (2005) than in the cooler year (2004; Julian Day 204). Similar phenology has been observed when comparing *Cladophora* growth in the vicinity of thermal effluent plumes from power generating stations with growth observed remote from the thermal influence (Kirby and Dunford, 1982). Malkin et al. (2008) also applied the *Cladophora* Growth Model (CGM; Higgins et al., 2005) to simulate growth dynamics with up to an additional 2.5 °C of warming, but found only minor changes in predicted attached biomass (~+8%) with a warming of 1.0 °C, and no increases beyond 2.0 °C, as respiration rates increased to a greater degree than production rates. The applicability of these results to Lake Erie is uncertain given that this lake is on average, warmer than Lake Ontario. Nonetheless, both direct observation and modelling suggest that *Cladophora* is fundamentally constrained by P and light availability, so warming temperatures alone are not anticipated to have major impacts on biomass accrual unless accompanied by alterations in the timing of P availability and the benthic light climate.

2.1.2.4. Summary. The issue of benthic HABs in Lake Erie merits sustained integrated research and monitoring, because the symptoms of coastal impairment cannot be easily ignored. While it is generally accepted that the overabundance of algal species that constitute benthic HABs is primarily controlled by bottom-up processes (i.e. nutrient and light availability), the importance of top-down processes (i.e. grazers or physical detachment/sloughing) are not well characterized, particularly in the Laurentian Great Lakes. Given that the production and accrual of biomass can be quite variable over both temporal and spatial scales, definitive conclusions regarding the proximate factors responsible for the development and maintenance of contemporary benthic HABs in Lake Erie have been elusive, to a large extent because of infrequent and irregular measurements of standing crop (e.g., Higgins et al., 2005; Bridgeman et al., 2012) and an incomplete understanding of the impacts of recent ecological disturbance (e.g. impact of dreissenid mussels; *sensu* Hecky et al., 2004) and the changing nature of nutrient loads to the lake (Dolan and Chapra, 2012). Alternative monitoring and assessment approaches such as remote imaging (Shuchman et al., 2013) and acoustic survey methods (Depew et al., 2009, 2011) have recently demonstrated success at incorporating

natural variability into synoptic assessments, and offer the ability to extend assessment of benthic HABs to broader areas.

2.2. Hypoxia

The reduction of hypoxic conditions (i.e. <2 mg/L dissolved oxygen, DO) in the central basin of Lake Erie has long been a goal of international remedial efforts, which was first identified in the 1972 GLWQA, and re-stated in the recently renewed (2012) agreement. Concern with this issue was heightened during the late 1960s and early 1970s, with the publication of maps showing an anoxic area (i.e. <0.2 mg/L) in the bottom layer (hypolimnion) of the lake linked by the public media to the phrase “Lake Erie is Dead”, which became a common misconception (Sweeney, 1993; Ludsin et al., 2001). At the time, the scientific belief was that P loading had a significant and direct effect on the severity of hypoxia, and the 1972 GLWQA sought to bring about a large improvement in DO depletion by reducing P loads by approximately 50%. The initial post-remedial declines in hypoxia and anoxia during the early 1990s – which were associated with improved biological communities (Ludsin et al., 2001) – were thus attributed to these P abatement programs, but the response was less than initially desired (Charlton, 1980a; Bertram, 1993; Burns et al., 2005). To understand why hypoxia never fully disappeared and has recently re-emerged as an issue in Lake Erie (Hawley et al., 2006; Scavia et al., 2014), this section re-examines the causes of hypoxia, how it may be altered by climate change, and its documented and potential effects on food webs.

2.2.1. Causes of hypoxia

All temperate lakes that stratify during summer will have some degree of DO depletion in the hypolimnion, and in some cases, this can lead to hypoxic conditions that can negatively affect biota (Arend et al., 2011; Scavia et al., 2014). The bathymetry of Lake Erie renders it particularly prone to seasonal hypoxia. This is true of the central basin, which is deep enough to stratify during the summer (mean depth (Z_m) = 18.3 m), and typically develops a “thin” hypolimnion with a small volume relative to the epilimnion owing to the establishment of the thermocline close to the lake bottom (generally <6 m above the sediment surface; Rosa and Burns, 1987). Even under relatively unproductive conditions (e.g., pre-settlement), the small volume of hypolimnetic water cannot accommodate the DO demand generated by a combination of the diffusion of reduced substances (e.g., methane) from the sediment and the degradation of organic detritus from the surface layer. The resulting DO depletion leads to hypolimnetic hypoxia, often established early in the summer and extending through to the fall turnover. Thus seasonal hypoxia has most likely occurred in the central basin of Lake Erie for thousands of years before the settlement of the basin (Delorme, 1982). By contrast, the shallow west basin (Z_m = 7.3 m) usually does not develop sustained hypoxia, owing to strong wind-induced mixing that keeps the basin from stratifying for long periods of time during summer, while the hypolimnetic volume of the deeper east basin (Z_m = 24.4 m) is large enough that there is insufficient DO depletion before fall turnover to cause hypoxia.

Owing to the bathymetry of central Lake Erie, the severity of hypoxia can vary both within and among years in response to meteorological conditions (e.g., wind, temperature). Local weather can drive physical processes such as mixing, within and between-basin circulation, and water-column stratification (strength, depth), all of which can influence the rate of DO depletion and concentrations by regulating hypolimnetic thickness, temperature, sediment-associated DO demand, and its transfer across the thermocline (Charlton, 1979, 1980a, 1980b; Cornett and Rigler, 1979; Burns et al., 2005; Mueller et al., 2012; Zhou et al., 2013; Rucinski et al., 2014). In this way, hypoxia can be problematic in

one year (e.g., a warm year with deep thermocline and thin hypolimnion) but not the next (e.g., a colder year with a shallower thermocline and thicker hypolimnion), regardless of allochthonous nutrient loading. To illustrate, no hypoxia was detected in central Lake Erie during 1975, a year of excessive P loading (Scavia et al., 2014), owing to the formation of an unusually thick, cold hypolimnion that was driven by meteorological conditions (Charlton, 1979). These phenomena can account in part for the presence of hypoxia in Lake Erie during pre-settlement times, and its high variance during periods of both eutrophication (1970s; Charlton, 1979) and oligotrophication (early 1990s; Bertram, 1993). Early oxygen data which pre-date nutrient controls suggested a large and direct effect of increasing P loads on hypoxia (Dobson and Gilbertson, 1971) and led to expectations of a large response to decreased P loads. Those data, however, represented intermittent and biased sampling, and the effect of increased P load was much less than previously believed, once hypolimnion thickness and temperature were accounted for (Charlton, 1979, 1980a). This is consistent with the persistence of hypoxia subsequent to P load reduction.

Despite the importance of weather-induced physical processes, humans have influenced the severity of hypoxia in central Lake Erie indirectly through excessive nutrient loading (i.e., cultural eutrophication; Rosa and Burns, 1987; Bertram, 1993; Burns et al., 2005; Rucinski et al., 2014). Historically, P has limited primary production in Lake Erie (Vollenweider et al., 1974), and large increases in loading have led to excessive production of phytoplankton and inedible cyanobacteria. For these reasons, a correlation between annual P loading and seasonal hypoxia has been documented, although as mentioned above, the full potential of hypoxia in Lake Erie is dependent on lake physical processes (Burns et al., 2005; Rao et al., 2008; Rucinski et al., 2014). This suite of findings highlights the need to consider both physical processes and allochthonous nutrient inputs when attempting to understand and predict hypoxia in Lake Erie. Failure to account for stochastic physical processes associated with weather can help to explain why nutrient loading alone is not an effective predictor of hypoxia and why hypoxia remained a sporadic problem both before and after TP loading targets (11,000 MTA) were met as a result of point-source P abatement programs under the 1972 GLWQA.

To illustrate the importance of considering both physical processes and allochthonous P loads when predicting hypoxia, DO depletion rates from 1970 to the present were analyzed (Fig. 2). These rates, based on the EPA monitoring data, were obtained by adjusting in situ DO depletion rates for differences in hypolimnion thickness and temperature, and DO transfer across the thermocline using the methods of Burns et al. (2005). The adjusted depletion rates capture trends in the organic decomposition in water and sediment, as well as the oxidation of reduced compounds in sediment, both of which relate to primary production, and in turn, to P loads. Using this approach, as higher temperatures increase bacterial decomposition rates, for example, the adjusted depletion rates would not change for a given P load (due to the Q_{10} temperature correction), but the in situ rates would increase and DO concentrations would be reduced. The adjusted data (Fig. 2) are reminiscent of a flattened version of the TP loading trend for Lake Erie (IJC, 2014; Scavia et al., 2014), showing an initial response to reduced loads up to about 1990, followed by variability and some tendency to increase later. In 1970, the P load was about 23,000 MTA and the adjusted oxygen depletion rate was 3.8 mg/L/month. By the period from 1990 to 2000, the depletion rate average was 3.1 mg/L/month at a nominal P load of 11,000 MTA. Following the regression in Burns et al. (2005), the depletion rate would be approximately 3 mg/L/month at a P load of 5000 MTA or a 21% decrease in oxygen depletion rate for a 75% decrease in P load from 1970. These new rates, which again consider many important

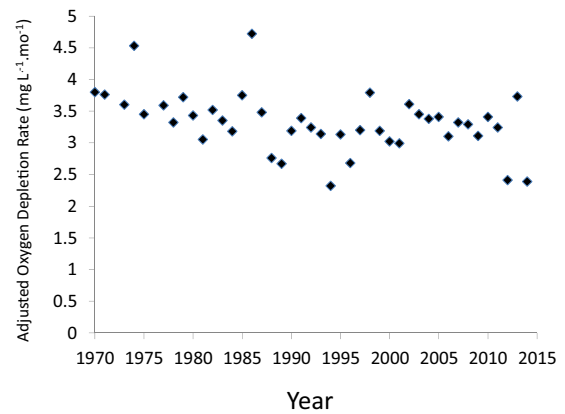


Fig. 2. Adjusted oxygen depletion rates in the central basin of Lake Erie (1972 and 1976, missing data). Data courtesy Great Lakes National Program Office, U.S. EPA.

physical processes in addition to oxygen concentrations, minimize the effects of stochastic variability and represent central basin DO depletion processes better than in situ DO depletion rates. In addition, the 1987–1996 post-remedial improvements and subsequent worsening of central basin hypoxia that were suggested by short-term measures of DO concentration (as in, for example, Scavia et al., 2014), may have been affected by other factors. For example, Burns et al. (2005) considered two of the improvement years with higher oxygen concentrations as anomalous, and perhaps due to hypolimnetic primary production. Further research is needed on how to derive and represent DO concentrations over time in a way that is not confounded by physical and other factors.

2.2.2. Climate change and hypoxia

Predictions made for other temperate freshwater ecosystems indicate that climate change may exacerbate the magnitude, duration, and frequency of hypoxia via a number of different mechanisms such as deeper and longer stratification, increased water temperature, and increased nutrient runoff during winter and spring (Kling et al., 2003; Ficke et al., 2007; Fang and Stefan, 2009; Jiang et al., 2012). To date, few modelling studies have attempted to predict the effects of climate change on Lake Erie hypoxia. For example, Schertzer and Sawchuk (1990) modelled the effect of doubling atmospheric CO₂ on stratification, predicting only slight hypolimnetic anoxia in the central basin of Lake Erie during late fall. Assuming that the warming and stratification trends in Lake Erie would be similar to those seen in Lake Ontario (Huang et al., 2012), the earlier development of a longer summer stratification period, with a later fall turnover is expected. As shown in other freshwater systems, these conditions would result in earlier bottom DO depletion, and hypoxic conditions are likely to be present over an extended time period (Fang and Stefan, 2009). Hypoxia could also be exacerbated by continued increases in multi-day storm events during winter and spring (Kunkel et al., 1999), which have been predicted to increase nutrient runoff in highly agricultural watersheds such as the Maumee River Basin during winter and spring (Cousino et al., 2015).

Water level is a key factor that is likely to affect future hypoxia formation, but much uncertainty exists in predicting the effects of climate change on Great Lakes water levels. For example, Angel and Kunkel (2009) predicted a decline of 0.61 m in Lake Erie water level, whereas MacKay and Seglenicks (2013) predicted much less drastic decreases in average water levels. If the projected water level reductions are realized (e.g., as in Angel and Kunkel, 2009) or reduced levels occur even sooner owing to natural climate variability (Gronewald and Stow, 2014), bottom hypoxia could be exacerbated further. This could happen because a reduced water

volume would allow the lake to warm more rapidly during spring and attain higher surface and hypolimnetic temperatures. In turn, the thermocline could develop closer to the bottom, resulting in intensified DO depletion.

2.2.3. Effects on foodwebs

Hypoxia can affect the structure and composition of the biological communities present in the hypolimnion. Most aquatic organisms require DO to meet their basal metabolic needs (Wu, 2002; Ekau et al., 2010; Pörtner, 2010), and sustained low DO levels can affect them directly by causing mortality (i.e., fish kills: e.g., Rao et al., 2014; benthic macroinvertebrate kills: Bridgeman et al., 2006) or indirectly by modifying movement and foraging behaviour, growth, and reproduction (Eby and Crowder, 2002; Wu, 2002; Ludsin et al., 2009; Domenici et al., 2013). Benthic invertebrates, particularly those with limited mobility (e.g., dreissenid mussels), would be expected to be affected negatively by hypoxia in the central basin, as boundary layer DO gradients may form close to the bottom under calm conditions. A 50-year historical dataset (Burlakova et al., 2014) supports this tenet by showing that dreissenids, which have dominated benthos in the west and east basins during the past few decades, were not detected in the offshore area of the central basin affected by hypoxia. For this reason, Burlakova et al. (2014) suggested that dreissenid density may be useful as an indicator of the severity of oxygen depletion, because of the limited tolerance of these organisms to hypoxia. Similarly, it has been suggested that hypoxia may regulate the distribution, abundance, and population dynamics of burrowing mayflies (*Hexagenia* spp.) in western Lake Erie (Bridgeman et al., 2006); however the central basin hypolimnion is too cold to allow development of a population of these organisms in the offshore areas, regardless of oxygen concentrations (Krieger et al., 2007).

Hypoxia may affect fish species or age classes differentially, and coupled with changes in predator-prey interactions, alter the food web structure and function (e.g., Breitburg et al., 1997; Brietburg, 2002; Eby and Crowder, 2002; Ludsin et al., 2009). It may also have a more generalized effect; acute, lethal effects of hypoxia have been documented, for example, in sporadic multi-specific fish kills associated with upwellings of hypolimnetic water on the north shore of Lake Erie (Rao et al., 2014). Nevertheless these acute effects are likely to be rare, given that fish can generally detect and avoid hypoxia (Wannamaker and Rice, 2000). Instead, non-lethal (indirect) effects would be expected to predominate and be manifested as changes in the behaviour of fish and their benthic and planktonic prey.

Towards the end of summer, bottom DO concentrations in the central basin of Lake Erie can exclude most fish from the hypolimnion and at the same time decrease the availability of zooplankton prey (Vanderploeg et al., 2009a,b; Pothoven et al., 2009). In turn, individuals may be exposed to increased predation risk (Vanderploeg et al., 2009a; Brandt et al., 2011) or excluded from optimal areas for foraging and growth (Roberts et al., 2009, 2012; Arend et al., 2011), thus forcing them to make energetically expensive foraging forays into the bottom sediments for food (Roberts et al., 2009, 2012). Some species are expected to be affected negatively by hypoxia (e.g., rainbow smelt, *Osmerus mordax*; round goby, *Neogobius melanostomus*; lake whitefish, *Coregonus clupeaformis*; Ludsin et al., 2001; Arend et al., 2011; Pothoven et al., 2009), others only affected in a minor fashion or not at all (e.g., yellow perch *Perca flavescens*; emerald shiner, *Notropis atherinoides*; Arend et al., 2011; Pothoven et al., 2009). Still others may even benefit indirectly from hypoxia (e.g., walleye, *Sander vitreum*; Brandt et al., 2011; Pandit et al., 2013). At present, however, the population-level effects of hypoxia on Lake Erie fishes remain largely hypothetical (Ludsin et al., 2001; Scavia et al., 2014)

which is consistent with the current level of understanding for nearly all other ecosystems in this respect (Breitburg et al., 2009). Given this uncertainty and the importance of sub-lethal effects of hypoxia, it is clear that more research is required to evaluate the short- and long-term effects on fish populations.

Lake Erie hypoxia encompasses considerable uncertainty in terms of both biological and nutrient control outcomes (Rucinski et al., 2014; Scavia et al., 2014). Nevertheless, if some of the predicted climate change scenarios are realized (e.g., warming, increased winter and spring precipitation), preventative nutrient controls will likely be needed simply to maintain the status quo in the lake, despite some uncertainty regarding the short term effects of these measures on hypoxia. Ongoing monitoring from different agencies provides data to meet the needs of the models with respect to hypoxia in the central basin; however, more research is required to quantify the sediment oxygen demand as nutrient load reductions are applied.

3. Nutrient loading to Lake Erie

3.1. External loading: nutrient management and models

3.1.1. Advancements in our understanding of the role of phosphorus loading

As a result of the lake-wide remedial actions taken to meet the 1972 GLWQA objectives, TP inputs declined precipitously from 1972 to meet the annual target loading level of 11,000 metric tonnes per annum (MTA) by the early 1980s, and remained below this target in most years up to 2011 (Scavia et al., 2014). These reductions largely stemmed from the progress made with the control of point sources (e.g., upgrading of the wastewater treatment plants (WWTPs), restrictions in commercial detergents), whereas more recently, the non-point source contribution has become the primary external factor modulating the ecosystem dynamics of Lake Erie (e.g., Dolan and McGunagle, 2005; Stow et al., 2015). For example, in several monitored tributaries draining into the western and central basins, the most bioavailable P fraction (SRP) has more than doubled since the 1990s, rising from ~11% to 24% of the TP load, e.g., Maumee River, Sandusky River, Honey Creek, and Rock Creek (Baker et al., 2014; Stow et al., 2015; locations of major tributaries are shown in Fig. 3). Scavia et al. (2014) also estimated that the west, central, and east basins of the lake received approximately 60%, 30%, and 10% of the (2003–2011) lake-wide TP loads and ~68%, 24%, and 8% of the whole-lake SRP loads, respectively. Although these estimates do not consider the inter-basin nutrient transport, they do provide evidence that nutrient loads from several tributaries in the western half of the lake (particularly from Maumee, Detroit, Sandusky and Cuyahoga Rivers) are the predominant drivers of the severity of eutrophication symptoms in Lake Erie.

An updated estimate of the P inputs and outputs for U.S. and Canadian watersheds showed that human sources dominate in the Lake St. Clair, Clinton, Detroit, Huron, Cuyahoga, Ashtabula watersheds; agricultural fertilizers in Ottawa-Stony, Raisin, Maumee, Cedar-Portage, Sandusky, Huron-Vermilion, Cedar Creek input; and manure in the Grand (Ontario) and Thames loads (Scavia et al., 2014). In the same context, Daloğlu et al. (2012) and Bosch et al. (2013, 2014) used the Soil and Water Assessment Tool (SWAT) to evaluate P sources within several watersheds, and showed that approximately 40% of the TP load from the Maumee, Sandusky, and Cuyahoga watersheds originates from 25% of the basin, suggesting the need for designing BMPs to alleviate the impact of non-point source loading (see Section 3.2). It has been shown that the intensity of spring storms in the Lake Erie watershed has increased, and precipitation patterns are predicted to show more intense late-winter and early spring events in the

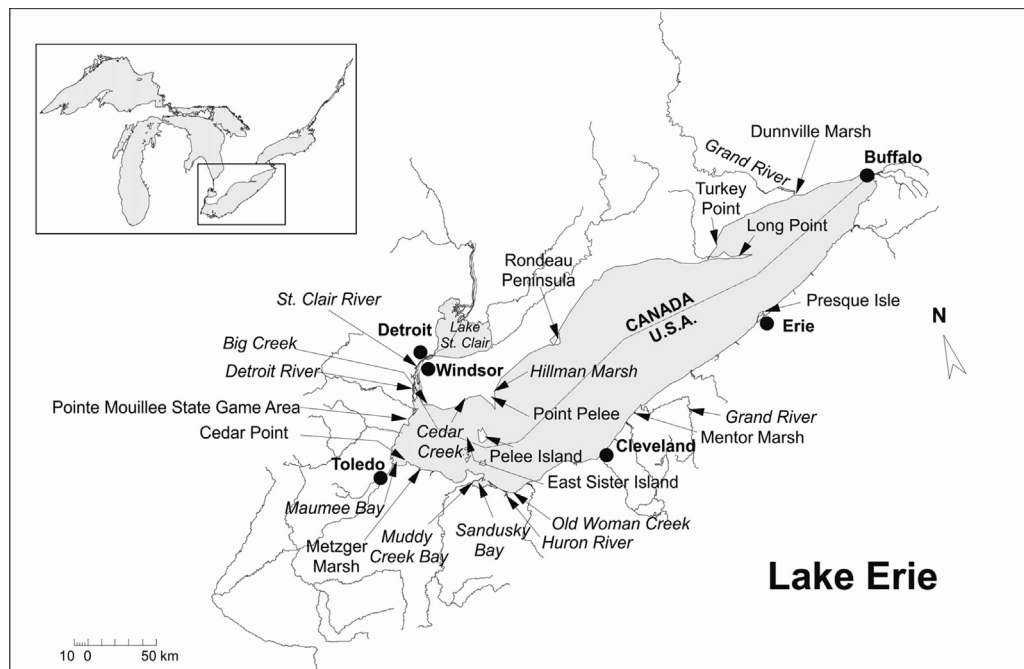


Fig. 3. Map of Lake Erie showing major tributaries and wetland complexes (the latter based on Maynard and Wilcox, 1997).

future (Hayhoe et al., 2010; Bartolai et al., 2015). Daloğlu et al. (2012) demonstrated with a SWAT model of the Sandusky watershed that the more recent increase in intense spring storms, coupled with changes in tillage and fertilizing practices, is a likely driver of the increase in SRP loads from agricultural watersheds. The frequency of extreme rain events has increased since the early 1900s in this region, as has the duration of wet periods. Bosch et al. (2014) further showed that climate change will make load reductions even more difficult, highlighting the importance of adaptive management.

3.1.2. Recent modelling work in Lake Erie

A variety of empirical and process-based models has been developed to examine ecological mechanisms and predict the response to nutrient management actions for Lake Erie (Kim et al., 2014). The simplistic nature of empirical models typically does not allow the prediction of conditions induced by episodic events or internal loading (Cheng et al., 2010). As an alternative, process-based (or mechanistic) models mimic the role of individual ecological processes through mathematical description and realistic parameter specification to depict ecosystem dynamics. Based on a general set of equations, these models aim to describe key physical, chemical, and biological processes with site-specific parameters, initial conditions, and forcing functions which are then used to reproduce observed system dynamics and project future system response to different nutrient or climate scenarios (Arhonditsis and Brett, 2004). In Lake Erie, both types of models have been used to examine different ecological responses in the lakes. Some of the recent process-based models, however, are over-parameterized and therefore do not have the capacity to support robust predictive capability (Kim et al., 2014).

The selection of mathematical equations and parameters must be ecologically defensible and linked tightly to the contemporary understanding of the system. Nonetheless, differences in both mathematical assumptions and parameter specification of existing Lake Erie modelling constructs can conceivably yield significantly different projections under alternative management scenarios (Zhang et al., 2008; Leon et al., 2011; Rucinski et al., 2014). For example, models differ on their description of phytoplankton

functional groups and values for maximum growth rates, which are based on literature not necessarily derived from Lake Erie. The maximum growth rate is an influential parameter that aims to characterize the average patterns of diverse assemblages of phytoplankton species. The control of this maximum potential growth by resource (temperature, light, and nutrient) limitations determines the growth rates predicted by the phytoplankton simulations. In this regard, algal growth rates have been modelled as a single function of ambient nutrient concentrations, or as a two-step process that considers nutrient uptake rate in relation to the ambient supply, and subsequently, growth rate as a function of cell nutrient storage. Likewise, several of the existing modelling efforts have not explicitly simulated top-down processes (Zhang et al., 2008; Leon et al., 2011). Both intracellular storage and top-down control are key factors to predicting phytoplankton responses to ambient nutrient variability, and may have profound implications in the predictive statements when examining lake dynamics under alternative management scenarios. Given that several of the existing mechanistic models have relevant modules (Zhang et al., 2008; Leon et al., 2011), the impact of top-down processes will be addressed in the near future. The updated models have to accurately reflect the current understanding of the interplay between bottom-up and top-down forces in shaping phytoplankton dynamics in the system.

Many recent modelling studies have highlighted the need to include multiple nutrients along with the finer representation of phytoplankton communities to elucidate key issues such as cyanobacteria dominance. Nevertheless because of the unresolved ecology of plankton assemblages, the development of robust group-specific parameterizations to support such scenario-based predictions is highly uncertain (Watson et al., 2008) and the capacity of current models to simulate the dynamics of individual species or genera is far from established (Anderson, 2005). For example, the reproduction of seasonal phytoplankton succession is very sensitive and only occurs within a fairly narrow window of the model parameter space (Zhao et al., 2008). The effect of dreissenids is another critical aspect that requires robust modelling, yet existing sub-models lack the ability to predict changes in spatiotemporal mussel densities and age group distributions

(Bierman et al., 2005). As an alternative, statistical models provide straightforward relationships coupled with uncertainty estimates (e.g., response curves), founded upon data from the system. Despite their simplicity, these models offer a screening level insight into predicted Lake Erie response to external and internal changes, but they have major limitations outside the range of the dataset used.

Sediment diagenesis is a critical facet of nutrient biogeochemistry that has received little attention from both empirical (e.g., pore water analysis, P fractionation, organic matter profiles) and modelling points of view (McCulloch et al., 2013). Sediments are an important factor influencing lake water quality and recovery time, acting as a source or sink for numerous chemicals, including nutrients. Proximal to the sediment-water interface, intensive microbiological, geochemical and physical processes determine the release of organic matter, nutrients, and pollutants into the overlying water. Detailed knowledge of these processes is thus essential for the assessment of water quality, understanding the impacts of hypoxia, and managing surface water quality. Where measurements are impossible or expensive, diagenetic modelling is a valuable tool to investigate the interplay among the sediment processes, verify concepts, and potentially predict system behaviours (Boudreau, 1997). This approach can help to address questions such as whether sediment P retention can be predicted from sediment mineralogy, substance inputs, and catchment type and how this may be influenced by human activities and/or climate change.

In Lake Erie, models with different strengths and weaknesses offer a unique opportunity for synthesis and improvement of contemporary modelling. Collective Lake Erie mechanistic and empirical models can be integrated to guide the decision-making process, provide a framework for improvement of contemporary modelling practices, compare alternative ecological structures, challenge existing ecosystem conceptualizations, and synthesize different (and often conflicting) paradigms. One of the overlooked aspects of the existing local modelling work involves the rigorous assessment of model structural and parametric uncertainty (Arhonditsis et al., 2007). Recognizing the importance of the uncertainty problem, the recent model calibration practices tend to change from seeking a single “optimal” value for each model parameter, to seeking a distribution of parameter sets that all meet a pre-defined fitting criterion (Stow et al., 2007). These acceptable parameter sets may then provide the basis for estimating model prediction error associated with the model parameters.

3.2. External loading: effectiveness of urban and agricultural BMPs in reducing phosphorus loads

Although BMPs are most often employed to reduce peak flow and suspended solids, they are increasingly designed for pollutant reductions. This section focuses on BMPs that have been scientifically evaluated for their efficacy in P reduction, and highlights practices that have been implemented within the U.S. portion of the Great Lakes watershed.

3.2.1. Urban BMPs

Urban P loads can represent a disproportionately large fraction of a drainage basin's TP loading. For example, the urbanized fraction of the Lake Champlain watershed constitutes only 3% of the area but is estimated to contribute 18% of the P load (Meals and Budd, 1998). Due to the multitude of land uses within urban watersheds, it is often difficult to pinpoint P loads from specific urban land cover, and holistic management/control of urban P loads with distributed BMPs at a majority of urban sub-watershed discharge points may be required (Winter and Duthie, 2000). The selection of BMPs for P removal in urban settings is often based on

general classification of perceived BMP utility (Gibb et al., 1999) and is used in the following discussion of urban BMPs.

3.2.1.1. Non-structural (alternative behaviour/management) BMPs. Non-structural BMPs include educational outreach and municipal ordinances focused on behaviour modification to reduce P loadings from activities such as the use of lawn fertilizers, better management of litterfall and pet wastes in urban environments. Educational outreach alone has demonstrated only minor improvements in reducing P loadings related to fertilizer use (Dietz et al., 2004). On the other hand, adoption of municipal ordinances that limit P-containing lawn fertilizer application resulted in significant reductions in TP and a trend of dissolved P reductions in Ann Arbor, MI (Lehman et al., 2009). Considerable reductions in P loads may also be realized through the use of soil chemistry testing to optimize fertilizer addition (Erickson et al., 2005). An additional practice that has been successful is the use of composted manure as a fertilizer, which provides a source of slow release P, and generally reduces TP loadings to urban streams compared to conventional commercial turf-grass sod maintained with inorganic P fertilizer (Richards et al., 2008). Nevertheless, results from these approaches have been mixed and are dependent on the scope of adoption.

3.2.1.2. Non-point source structural or engineered BMPs. Engineered BMPs include a full spectrum of approaches (Fig. 4; Table 1) such as porous pavements, media filters, bioswales, rain gardens, green roofs, detention biofiltration, and bioretention basins, constructed wetlands and various commercial devices. Structural or engineered BMPs typically employ filtration and/or detention (allowing settling of sorbed material), and many BMPs combine several different filtration and removal devices. The following section outlines the utility and limitations of these technologies as they pertain to urban P loadings (Table 2).

3.2.1.3. Structural BMP treatment systems. These BMPs cover a wide array of types and varying levels of performance (Table 1). Of the references reviewed, most focus on TP with only a few including dissolved P (DP) metrics. It is worth noting that none of the BMPs reviewed were found to have consistently high removal efficiency. To provide an illustrative example, over 6000 records from the International Stormwater BMP Database (www.bmpdatabase.org) were queried (downloaded Jan. 4, 2013) to evaluate the treatment efficiency of structural BMPs, using Event Mean Concentrations (EMCs) to quantify pollutant load. This exercise included over 216 different BMP installations. To measure the BMP performance, the fraction discharged after treatment (β) was quantified by comparing the mass load of P being discharged from a BMP structure (M_{out}) relative to the mass load entering the structure (M_{in}) per individual storm event:

$$\beta = \frac{M_{out}}{M_{in}} \quad (1)$$

According to this equation, if the mass of P leaving the BMP structure is less than that entering, the fraction β is <1 (i.e. the BMP is effective). When the mass of P leaving the structure is greater than the mass entering, the fraction β is >1 and the BMP contributes to P loading. The logarithm of the fraction (β) discharged following treatment is negative in cases of P removal, while a positive $\log \beta$ indicates the BMP contributes to P loading.

TP was removed by detention basins in slightly more than half of the cases analyzed (Fig. 5), likely attributed to the removal of PP (while few cases, this curve plots to the left in the negative $\log \beta$ range). In contrast, DP was removed in fewer than 40% of the cases

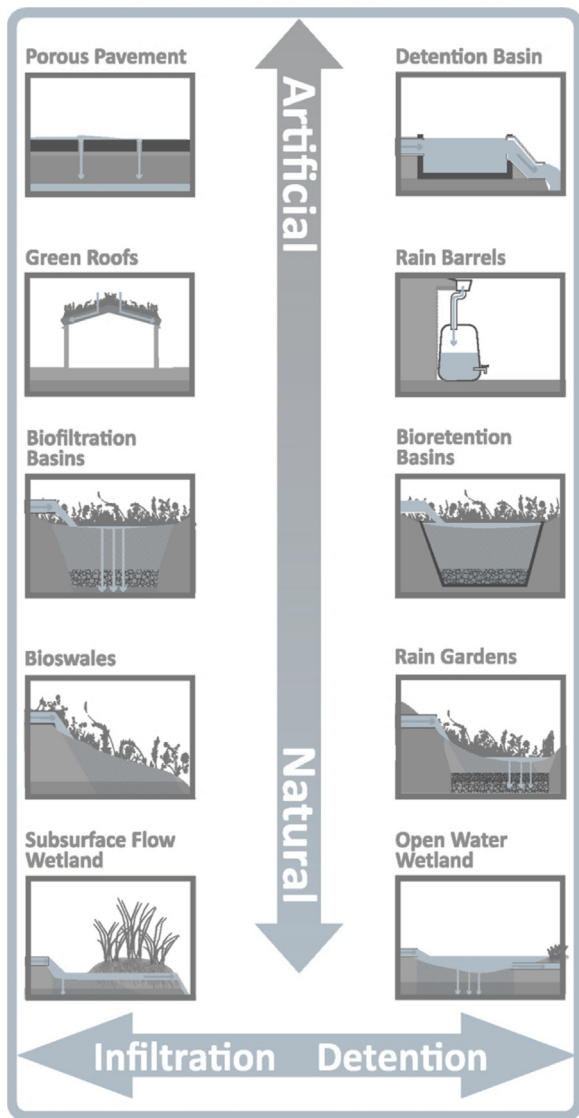


Fig. 4. Spectrum of urban structural BMPs.

analyzed. Detention basins, biofilters and wetland systems (basins and channels) resulted in notably different removal efficiencies associated with each P fraction, and the fraction of P removed tended to follow the order: PP > TP > DP.

Reductions in P discharges from large point sources are responsible for the majority of decreases in P loads to Lake Erie since the 1970s (Dolan and McGunagle, 2005). While large-scale WWTPs have been nearly 100% compliant since the 1990s, Lake Erie receives the largest municipal P load of the Great Lakes. Combined sewer overflows (CSOs) deliver some 90.4 MTA of TP to Lake Erie from Ohio alone (Ohio EPA, 2010). Nineteen CSOs discharge untreated sewage directly into the Lake, while 107 other CSOs discharge to receiving waters that empty into Lake Erie (e.g. Mill Creek, Cuyahoga River, Rocky River, Big Creek; Gomberg, 2007).

Urban BMP performance metrics can vary dramatically, depending on the metric used (Lenhart and Hunt, 2011). Evaluations based on concentrations alone may be misleading, because performance varies during and between stormwater runoff events (Lenhart and Hunt, 2011). On the other hand, percent removal is also problematic as a metric because it can vary with the influent concentration (Zhang et al., 2010) and does not account for

background water quality, eco-region differentiation, and background, or “irreducible” concentrations. Percent removal further assumes an association between influent and effluent concentrations, which may not exist (for example, due to the treatment media contributing rather than removing the pollutant) (McNett et al., 2011).

Regardless of the BMP type, three main mechanisms are responsible for P removal in stormwater: bio-uptake, sorption and precipitation. Ultimately P is retained via physical processes, by attaching to BMP materials (e.g. sorption to wetland plants) or by settling out – directly as a precipitate or indirectly, in association with biological material or suspended solids. Of these mechanisms, sorption reactions are the most common mechanism employed by BMPs. On average, ~70% of P in storm-water is removed by the elimination of particles >20 µm in diameter; and 90% of P is associated with particles (>0.45 µm) (Johnson et al., 2003). Nevertheless, because P partitioning between particulate and soluble forms varies with the solution chemistry and the amount and type of solids present, and furthermore can convert rapidly, BMPs need to address both P fractions in order to achieve consistent and high removal (Leisenring et al., 2010).

To assess the effectiveness of urban BMPs, appropriate and rigorous metrics should be used that include both dissolved and particulate fractions of P and flow-weighted EMCs for loading estimates, and account for the variability inherent to these dynamic systems. An important example is seen in the high spatiotemporal variance in water quality and nutrients measured in the Detroit River by a joint EC-USEPA sampling study (Burniston et al., 2009). Additionally, if systems are large or contain sufficient vegetation (e.g. constructed wetlands), an assessment will likely also need to consider the diurnal and seasonal variation induced by biological cycling of P.

3.2.2. BMPs in agricultural and rural environments

The Ohio Lake Erie Phosphorus Task Force (OH-LEPFT) provides agricultural BMP recommendations to reduce the amount of P, N and sediment exports to Lake Erie (Ohio EPA, 2010). BMP effectiveness is site-specific, and depends on local topography, climate, cropping systems maintenance, selection, and installation (Alfera and Weismiller, 2002). Several review articles have evaluated a suite of BMPs implemented simultaneously (Bishop et al., 2005) which makes it difficult to discern the effectiveness characteristics of an individual BMP within the suite. Many of the BMPs reviewed by these papers were outside the Lake Erie basin, but can be reasonably applied to the Lake Erie watershed. Assessments were done at different scales (plot, field, and watershed scale), using either field studies or simulation modelling. Most BMP assessments at watershed scale have been carried out as modelling studies or as a trend analysis of temporal changes in water quality parameters at the watershed outlet (e.g., Bosch et al., 2013). The BMP effectiveness tool created by Merriman et al. (2009; available online: Gitau, 2013) has been used in many of these BMP assessments.

Some of the agricultural BMPs cited by Sharpley et al. (2006) are now mandatory in Ohio, in particular western Lake Erie watersheds. An Ohio state law that took effect in July 2015 restricts manure and fertilizer application: (1) on frozen or snow-covered soil, (2) on moisture-saturated soil (top 2 in.), and (3) when a weather forecast calls for more than 50% chance of 1-in. precipitation in 12 h before commercial fertilizer application and 0.5-in. of precipitation in 24 h for manure. Subsurface application and incorporation of manure and fertilizer within 24 h of precipitation are exempted from this restriction.

In-field control BMPs minimize nutrient and sediment transport and include controlled drainage, conservation tillage, 2-stage ditch, grassed waterways, etc. BMPs designed to remediate and

Table 1

Urban structural/constructed BMPs and associated removal effectiveness.

BMP	Removal	Comments
Porous pavements	TP: 60–71% ^{1–3}	Variable performance reported Inflow TP versus outflow TP not statistically different ⁴
Media filters (sand filters, infiltration trenches, etc.)	TP: 43–82% ^{3,5–9}	Filter material selection critical Organic content of media does not appear to enhance P reductions ^{10–12} Statistically significant decreased observed for TP and PO ₄ ⁴
Filter strips/bioswales	TP (LSGFS): ~48% ^{13,14} TP (bioswales): 0–85% ^{10,15–20}	Length of LSGF is important ²¹ Based on EMC, removal still varies but appears to be around 50% ²² Increases in TP, PO ₄ and DP, likely due to fertilizer application, are reported ⁴
Green roofs	Initial increase in TP ²³	Limited data also suggests differences in short- versus long-term performance ²⁴ More rigorous long-term monitoring required
Bioretention basins	TP: 20–90% ^{3,7,16,18,19,25–28,29} DP (wet ponds): ~51% ³⁰ DP (wet ponds): ~60% ¹³	Removal efficiency depends on design ³¹ Large difference observed between “wet” and “dry” basins ^{13,30,32} Better mechanistic understanding needed ³³
Wetlands	TP (constructed): 25–70% ^{22,34} TP (channels): 51% ³⁵ DP (channels): 39% ³⁵	Performance varies widely depending on surface or subsurface flow ^{30,32} Removal efficiencies in subsurface flow and open surface wetlands hampered by low oxygen conditions that induce P release ³⁶ A better understanding of the geochemical processes in these systems is required
Commercial devices	TP (oil and grit separator): <10% TP ³ (sedimentation basins): ~50% removal ³⁷	Many commercial devices claim to remove P but lack rigorous external evaluation

References: ¹Hogland et al. (1987); ²MWCOG (1983); ³Young et al. (1996); ⁴Leisenring et al. (2010); ⁵Bell et al. (1995); ⁶Horner and Horner (1995); ⁷City of Austin (1990); ⁸Welborn and Veenhuis (1987); ⁹Maniquiz et al. (2010); ¹⁰Claytor and Schueler (1996); ¹¹Stewart (1992); ¹²Stormwater Management (1994); ¹³Horner et al. (1994); ¹⁴Reeves (1994); ¹⁵Yousef et al. (1985); ¹⁶Yu et al. (1993); ¹⁷Yu and Kaighn (1995); ¹⁸Yu et al. (1994); ¹⁹City of Austin (1995); ²⁰Khan et al. (1992); ²¹Winston et al. (2011); ²²Zhang et al. (2009); ²³Hathaway et al. (2008); ²⁴Berndtsson (2010); ²⁵Gain (1996); ²⁶Harper and Herr (1993); ²⁷Martin and Smoot (1986); ²⁸Yu and Benelmouffok (1988); ²⁹Gibb et al. (1999); ³⁰Schueler (1999); ³¹Hogan and Walbridge (2007); ³²Shaver and Maxted (1994); ³³Roy-Poirier et al. (2010); ³⁴US EPA (1993); ³⁵Schueler (1999); ³⁶Van de Moortel et al. (2009); ³⁷Zhang et al. (2010).

Table 2Agricultural phosphorus (P) – Transport Best Management Practices; TP: total phosphorus; PP: particulate P; SRP: soluble reactive P (i.e. PO₄).

BMP	Overview	Loading reductions	References
Residue and tillage management (conservation tillage) practices	Soil surface remains partially covered with crop residue after tillage and planting to reduce soil erosion.	Up to 60–80%; TP and SRP reduction range widely (–390% to 91%)	Galloway et al. (1981), Mostaghimi et al. (1988), Schreiber and Cullum (1998)
Conservation cropping	Includes crop rotation, cover crops conservation, and double cropping.	Estimated 74% SRP, 73–88% NO ₃ .	Bosch et al. (2009), Jiao et al. (2011)
Conservation buffers	Includes contour buffer strips of permanent, herbaceous vegetative cover, riparian forest buffers dominated by trees or shrubs adjacent to and up-slope of watercourses or water bodies, and filter strips of herbaceous vegetation.	2–93% TP, –103 to 93% SRP, 48–92% PP	McElmurry et al. (2013; Table 8)
Constructed/restored wetlands	Designed to treat wastewater and runoff primarily from agricultural processing, livestock, and aquaculture facilities, and to improve storm runoff or other flows lacking specific water quality discharge criteria.	Highly variable	Hoffmann et al. (2012), Rogers et al. (2009)
Grassed waterways	Shaped or graded vegetated channels designed to carry surface water at a non-erosive velocity to a stable outlet.	Not quantified	USDA-NRCS (2010)
Emerging technologies	Includes two-stage ditches; controlled drainage; and treatment of tile outlets with bioreactors, filters, etc.	Not quantified	Powell et al. (2007), Kroger et al. (2011), Nistor and Lowenberg-DeBoer (2007), McDowell et al. (2008)

intercept pollutants at the edge of field include filter strips, wetlands, sediment basins, bio-filters/reactors (US EPA, 2010; Miller et al., 2012). BMPs related to nutrient management have both environmental and economic benefits: off-farm nutrient transport is an investment loss for the farmers (Mullen et al., 2009). The effect of fertilizer application rate on P loss at a farm scale is related directly to application method, the hydrologic soil group, and crop type. The method of nutrient application is also related to tillage methods (Andraski et al., 1985). Nutrient management in combination with tillage and erosion practices may reduce TP loads by more than 80% but in some cases may increase the loads (Cestti et al., 2003). BMPs currently promoted in the Lake Erie U.S. watersheds are cover crops, conservation and no-tillage systems, the “4R” (right source, rate, timing, and application method) fertilizer principle, and drainage water management (McElmurry et al., 2013).

3.2.3. Summary

The design and evaluation of BMPs for P reduction in the Lake Erie watershed is complicated by the large variation in land use and soil types dispersed through the drainage basin, as well as by the multiplicity of governmental units (and duality of federal governments) responsible for water quality regulation. The BMPs recommended at one point in time may require adjustment as the exposed soil is modified in a dynamic fashion; for example in agricultural soils where the original organic matter and loam-rich topsoil have changed, the same BMPs applied to these areas may not have the same degree of effectiveness as in the past. The transition away from small family-owned operations to large-scale tenant farming and the associated changes in the way these farms are managed will also merit consideration. Until recently, most assessments of BMP effectiveness have focused on TP and sediment reduction, where a common assumption was that the

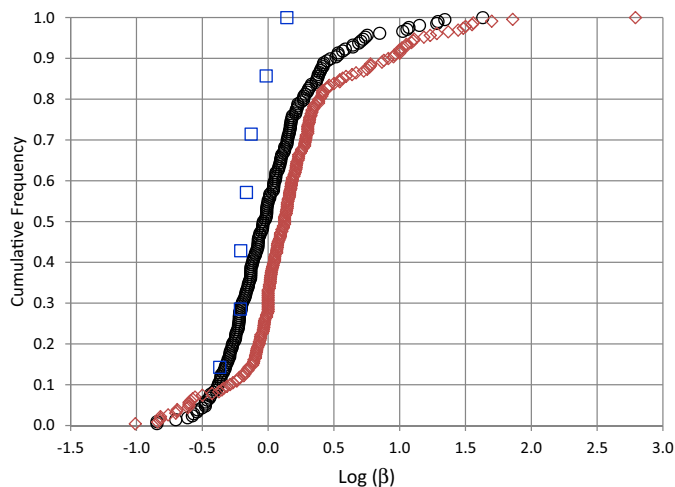


Fig. 5. Cumulative frequency of the fraction of P discharged after treatment (β) for urban detention basins, reported in the International Stormwater Database (as of Jan. 4, 2013): total P (\circ), dissolved P (\diamond), particulate P (\square).

majority of P losses occur as particulate P attached to sediments. As noted above, it is now increasingly apparent that more attention should be directed towards the concurrent removal and fate of dissolved P. Furthermore, P export via tile drains cannot be neglected in systematically-drained watersheds, such as the Maumee River watershed that drains to Lake Erie (King et al., 2014). The implications of this recent finding are not yet well-understood and pose additional challenges in controlling P exports.

The use of a suite of BMPs (or toolbox) may offer an appropriate approach to reducing P loading, however, as discussed above, separating the relative effectiveness of individual BMPs when applied in a suite is difficult (Bishop et al., 2005) and additional work will be required at varying scales (field to watershed) in order to provide an integrated assessment of multiple BMPs applied in concert. Modelling offers one potential approach to assess BMPs or suites of BMPs within a watershed. For example, as noted in an earlier section of this paper, Bosch et al. (2013) used the Soil Water Assessment Tool (SWAT) to evaluate the impacts of expanding the current use of filter strips, cover crops, and no-till BMPs in controlling runoff in six watersheds draining into western Lake Erie. Implemented singly and in combination, these BMPs reduced sediment and nutrient yields by 0–11%, and further reductions were observed by targeting BMPs in high source locations. Bosch et al. (2014) also evaluated the impacts of climate change induced alterations in precipitation and runoff and found that while BMPs could partially offset increased sediment and nutrient yields from agricultural watersheds, responses varied.

3.3. Coastal wetlands

Coastal wetlands affect nutrient cycling, offer important habitats for fish and wildlife, stabilize water supplies (both during floods and drought) and affect downstream water quality. This section briefly reviews coastal wetland issues in Lake Erie with emphasis on natural systems and wetland restoration; constructed wetlands are discussed in the BMP Section 3.2.1.2, and by McElmurry et al. (2013). Coastal wetlands can be categorized as lacustrine, riverine, and barrier-protected, based on the dominant water source, geomorphic position, and hydraulic connectivity to the lake (Albert et al., 2005). The Lake Erie watershed has a diversity of coastal wetland types, including

embayments, estuarine or drowned river-mouth (common in most of the tributaries entering the WB), and coastal lagoon wetlands (e.g., Presque Isle) (Herdendorf, 1992; Maynard and Wilcox, 1997), amounting to an earlier estimate of 530 km² of wetlands (Herdendorf, 1992; Maynard and Wilcox, 1997; Fig. 3). Coastal wetland loss in the Lake Erie watershed has been significant since European settlement, including ~90% in western LE/Maumee River basin (Maynard and Wilcox, 1997) and >97% for the Detroit River (Hartig et al., 2007). Key factors affecting Lake Erie coastal wetlands include water level fluctuations, seiches, sediment transport, upstream nutrient loading and artificial dikes (Mitsch, 1992), all of which can change over time.

Lake Erie water levels can vary short term (e.g. due to seiches), seasonally, annually and over longer periods with changes in net basin supplies (Quinn, 2002). Annual water level cycles typically show a peak in June (Keough et al., 1999), while longer term changes are driven in particular by climate factors (e.g. Wilcox et al., 2007; Fig. 6), though upstream contributions from the Detroit River (which supplies over 90% of the Lake Erie inflow; Herdendorf, 1992) are also affected by glacial isostatic rebound and alterations to bed geometry in the connecting rivers (IUGLS, 2009). Water level changes are important in determining wetland biotic communities, promoting higher plant diversity (e.g. Maynard and Wilcox, 1997; Wilcox and Nichols, 2008), while water level regulation (with lower year-to-year variation) can decrease wetland extent, diversity, and resilience (Maynard and Wilcox, 1997; Smith et al., 2008), and facilitate highly competitive species (e.g. cattails) and invasive species (e.g. purple loosestrife; Keough et al., 1999). Lake seiches have the potential to affect short-term wetland water balance and movement of dissolved and particulate constituents (Trebitz, 2006; Morrice et al., 2004; Bouchard, 2007). Human alterations to coastal environments affect water levels and/or nearshore processes more locally, for example through breakwalls and other structures affecting sediment supply, and artificial dikes (common along the southwest shore) that can affect water level patterns, nutrient transport and processing, plant diversity, and fish movement (Smith et al., 2008).

In addition to wetland extent, an additional important broad ecological consideration is wetland condition, which can be diminished by factors such as excessive loading of sediments and nutrients, contaminants, shoreline modification, diking, and invasive species (Maynard and Wilcox, 1997). Wetland impairment has occurred in Lake Erie with agriculture activity,

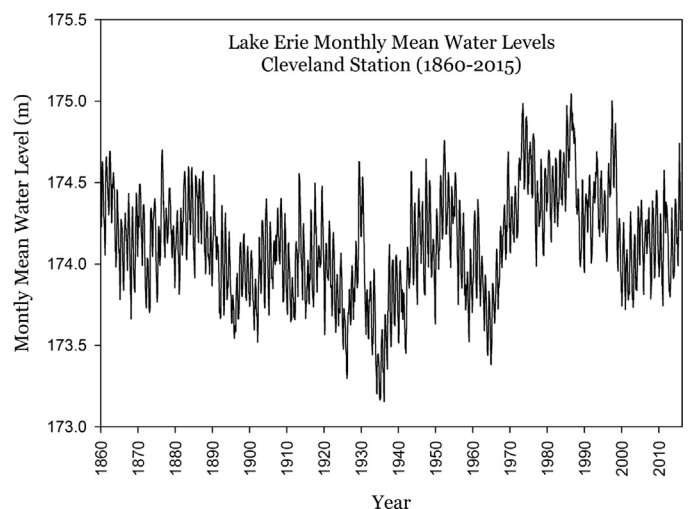


Fig. 6. Lake Erie monthly mean water levels measured at Cleveland (Station ID 9063063) (NOAA, 2015).

dredging, diking or other physical modifications, shoreline modification, and introduction of non-native species (e.g. common carp); the west basin has been particularly affected by these activities (Maynard and Wilcox, 1997). A recent assessment of Lake Erie wetlands overall showed “fair” scores (relating species-habitat specificity) and generally deteriorating conditions, and with Lake Ontario and the upper St. Lawrence River, common causes of degradation were water level control, nutrient enrichment, sedimentation, or some combination of these factors (EC and USEPA, 2014). A comprehensive Great Lakes basin-wide coastal wetland monitoring effort has been underway (<http://glri.us/projects/epa.html>), which will help to address gaps in condition assessment for coastal wetlands in the Lake Erie basin.

Wetland nutrient retention and processing is influenced by nutrient chemistry and inputs, hydrology, plant/microbial uptake, redox conditions and extent of oxidized and reduced soil layers. In part due to the wide diversity of wetland types, nutrient budgets (considering inflows, outflows, and internal cycling) can vary significantly and lead to variations in nutrient cycling both seasonally and between years within the same wetland. Earlier studies have identified several types of wetlands (including freshwater marshes, forested swamps) that acted as yearly, seasonal or inconsistent sinks, for P, N, or both (Mitsch et al., 1989; Mitsch and Gosselink, 2000). Intensive studies in Old Woman Creek National Estuarine Research Reserve (near Sandusky Bay) found variable DP and TP removal, which ranged up to 80% for SRP in one month (Heath, 1992) while overall TP removal was lower (~36%), especially during drought (Mitsch and Reeder, 1992). Reviews of this research have emphasized climate (including drought) and other drivers of hydrology that can influence wetland characteristics (e.g., transitioning from barrier-protected to embayment type) and nutrient transport (Heath, 1992), and the importance of considering loads and concentrations when evaluating nutrient reduction effectiveness (Krieger, 2003).

The potential for larger-scale wetland restoration to contribute to nutrient reduction for Lake Erie has been assessed in several studies. Mitsch et al. (1989) estimated that remaining wetlands in western Lake Erie retained up to 5% of nonpoint source P loading, and a broader restoration to 1000 km² of wetland coverage could increase this to 24–33%. Modelling also suggests the potential nutrient reduction benefits of large-scale wetland restoration (Wang and Mitsch, 1998; Mitsch and Wang, 2000); however, several issues need to be borne in mind. Wetlands need to be hydrologically connected to the waterbody, which may entail partial or full removal of dikes, with implications for wetland management (Wang and Mitsch, 1998). Many sub-basins are well upstream of Lake Erie (e.g. Han et al., 2012), and nutrient reduction would benefit by wetland restoration efforts closer to these sources. An additional issue is that restoration of historic wetland sites that had been converted to agriculture may mobilize nutrients, at least initially; for example, a Lake Michigan tributary showed up to 2.6 times higher SRP and TP levels downstream of restored agricultural system (Steinman and Ogdahl, 2011), while a restored North Carolina riverine wetland showed elevated SRP export and potential to continue for a significant period following flooding (Ardon et al., 2010). Additionally, there is the potential for conflict in multiple restoration objectives (Euliss et al., 2008) – for example, nutrient retention in the wetland may be achieved at the expense of improved fish and wildlife habitat. Indeed broader wetland restoration efforts often target excessive nutrient levels in the wetlands themselves through upstream activities (e.g. on agricultural fields) or in situ techniques (Wilcox and Whillans, 1999).

Climate change has important implications for nutrient cycling and coastal wetland condition, including winter storm damage with decreased ice cover, vegetation community changes or shifts with decreased lake levels or warmer temperatures, changes to barriers beaches, and increased spread of invasive species (Mortsch et al., 2006). Potential effects on wetland nutrient cycling include increased watershed nutrient export (and loading to downstream wetlands) via spring storms (Michalak et al., 2013), and P mobilization in coastal sediments from desiccation and inundation episodes (Steinman et al., 2012).

Overall, wetlands restoration has the potential to contribute to Lake Erie nutrient reduction goals. Such efforts would benefit from appropriate targeting, more systematic research and monitoring, and consideration of broader wetland management objectives. Several issues should be considered in wetland restoration aimed at nutrient reduction to Lake Erie, notably the potential for initial increased nutrient export, nutrient saturation, effects of climate change and the need to situate nutrient reduction amongst the broader suite of wetland services and values. Further research is needed, including identifying priority locations for wetland restoration and how restoration efforts can meet multiple objectives in the basin, including nutrient reduction.

3.4. Internal loading: phosphorus

3.4.1. Underlying mechanisms of internal loading and their importance in Lake Erie

A better understanding of the nutrient dynamics within Lake Erie is required in order to forecast future water quality and to target remedial actions and Best Management Practices more effectively. In particular, one of the poorly known components of the nutrient dynamics is the amount of P that is recycled to the water column by internal loading. This unknown loading creates uncertainty in the determination of the quantity of P delivered to the lake, and in estimates of the lag time between reductions in tributary loading and expected improvements in lake water quality. Externally delivered P to any lake undergoes a complexity of in-lake processes, including physical transport, biological uptake and chemical transformations before deposition onto the sediment. Much of the P deposited on the bottom is regenerated by microbial degradation of organic matter and migrates upward to the sediment surface where it is partially retained on iron and manganese oxyhydroxides under aerobic conditions (Søndergaard et al., 2003) and partially fluxes into the water column. As a result, many lakes exhibit a delayed response to reductions in external loading (Søndergaard et al., 2003), and thus quantifying these recycling processes will provide a better understanding of system response times and expectations for recovery. There are three general types of internal P cycling in Lake Erie: inter-basin transfer, biological transformation and sediment regeneration. First, much of the externally loaded P is delivered to the west basin, a portion of which is cycled while the remainder is transported as loading to the central and eastern basins. Second, numerous biological transformations recycle P to various trophic levels, the water column and the sediment. Third, P may be released from anoxic sediment (Mortimer, 1941), or from sediments that have become resuspended due to wind, waves or anthropogenic activities such as dredging (e.g. for the Toledo Shipping Channel).

3.4.2. Inter-basin transfers

There is currently insufficient information to evaluate the magnitude of these transfers within Lake Erie and whether they have changed over time. Sediment cores from the 1970s indicated a large discrepancy between net sedimentation rate in the west basin and the mass balance of external P inflows. It was proposed

that this reflected an unsampled flux of material along the bottom into the central basin (Burns et al., 1976), which has never been verified.

3.4.3. Biological recycling

This process is highly complex and may include uptake and excretion by all levels of the aquatic foodweb, as well as through decay, sedimentation, and bioturbation. Early empirical management models (e.g., Vollenweider, 1968) used simple linear model fits of annual or spring P concentrations or load, and seasonal average measures of total algal biomass. The unknown underlying processes of internal P recycling were integrated as a 'sedimentation coefficient'. These models were largely successful, albeit with a large uncertainty around their predictions, and none of the underlying complexities of internal loading prevented the success of 1970s nutrient load reductions. Since then, however, fundamental changes in the nature of the inputs (from point source to diffuse) and trophic structure of the Lake Erie biological community has invoked major changes in biological P sequestration and exchange and the recent resurgence of algal blooms has stimulated interest in the key details of P recycling, including sediment chemistry, to help evaluate the effects of load variations. In polymictic lakes with iron poor sediments, for example, internal P loading can lower the N:P ratio and may stimulate cyanobacterial blooms (Orihel et al., 2015).

Perhaps one of the most widely acknowledged changes in Lake Erie occurred with the widespread colonization by invasive dreissenid mussels, which profoundly altered the light and nutrient regimes, and the foodweb structure and response to nutrient inputs. Dreissenid veligers represent a relatively new sedimentation vector in Lake Erie which may also affect inter-basin transfers, although this process may not be easily discriminated. Dreissenids have increased the efficiency of internal P recycling and altered the inshore-offshore exchange of materials and nutrients, trapping these in the warmer and shallower nearshore zones in what is termed as the 'nearshore shunt' (Hecky et al., 2004). Zhang et al. (2011) modelled dreissenid P uptake and excretion and concluded that currently, Lake Erie may be more sensitive to P inputs than during the pre-mussel period. Mussel grazing can be equivalent to that of zooplankton but in addition, dreissenids also recycle detrital seston which would otherwise form sediment. Mussel excretion from colonized lake bottom areas can therefore return more P to the water than non-colonized substrates. Nevertheless, Zhang et al. (2008) asserted that algal productivity is "ultimately regulated by external P loads" (but see Section 2.1.2 on benthic HABs).

3.4.4. Sediment P regeneration to the water column

Sediment regeneration includes sediment release (as SRP) during hypolimnetic hypoxia (mainly in the central basin), aerobic decomposition of organic matter from the sediment-water interface, and resuspended material in the water column. Most interest has been in the first, because the degree of hypoxia is influenced by organic inputs from both external sources and lake productivity. Both are related to external P loading, one of the few controllable factors in this series. Benthic P release may also occur under oxic bottom water conditions, driven by resuspension events, organic matter degradation and biologically enhanced transport from greater sediment depths (Slomp et al., 1998; Meile and Van Cappellen, 2003; Katsev et al., 2006; Kim et al., 2013). In this case, benthic release is influenced by P retention in the underlying anoxic sediment (Gächter and Müller, 2003; Moosmann et al., 2006).

An early study by Burns and Ross (1972) concluded that the rate of hypoxic sediment P regeneration in the central basin can be as high as the rate of external loading over a two month period. Data

from later studies suggest, however, that while hypoxic sediment P regeneration in the central basin occurs, its significance and frequency is unclear and should be examined in detail. High SRP concentrations in hypolimnetic water are observed intermittently, but not commonly reported. Burns (1976) found about half of the central basin in 1970 was covered by an anoxic hypolimnion layer with up to 93 $\mu\text{g/L}$ SRP; long term monitoring data collected from samples 1–2 m above the bottom since then suggest that this degree of P release does not occur with high frequency (e.g. Environment Canada and EPA data; 1970–present). Less dramatic events may be identified with future efforts using probes that provide a greater temporal resolution. Such higher resolution sampling could be used to test for P release that may vary on a diurnal basis and/or may be rapidly dissipated into the water column by bottom currents (Rao et al., 2008) or rapidly consumed by algal and/or bacterial uptake. Incorporation of epilimnetic water into the hypolimnion or the advent of fall de-stratification can produce an oxygen flux that can re-precipitate iron-phosphorus complexes previously released as SRP and ferrous iron from anoxic sediment (Burns and Ross, 1972).

Under anaerobic conditions in the water overlying the sediment, the oxyhydroxides are reduced and release their sorbed P (Boström et al., 1998). A number of different techniques have been employed to quantify this internal P loading. For example, in Haringvliet Lake (The Netherlands) biogeochemical modelling showed that ~56% of the total P deposited on the sediment was returned to the overlying water through diffusion and bio-irrigation (the pumping of pore water by benthic macroinvertebrates through their burrows) (Canavan et al., 2006). Studies by Nürnberg et al. (2013) and Loh et al. (2013) used hypolimnion TP concentration changes and core incubations (respectively) and estimated the internal P loading in Lake Simcoe (Ontario) to be 45–89% of the external load. James (2012) incubated intact sediment cores from Lake of the Woods (Minnesota) under both aerobic and anaerobic conditions, and found that the diffusive P flux ranged from 8.3 to 12.5 $\text{mg m}^{-2} \text{d}^{-1}$ under anaerobic conditions and from 0.2 to 0.6 $\text{mg m}^{-2} \text{d}^{-1}$ under aerobic conditions. He concluded that the diffusive flux can represent an important contribution to the P cycling in this multi-basined lake. North et al. (2015) reported that under anoxic conditions internal P fluxes from Lake Diefenbaker, Saskatchewan are about 9 times higher than those under aerobic conditions, and that the internal loads in the winter are about the same as in the summer. The benthic P flux as a function of bottom water oxygen concentrations has also been measured using in situ bottom chambers (Noffke et al., 2012). In Lake Erie, Matisoff et al. (2016) used a variety of techniques to estimate the amount of P that is recycled to the water column by internal loading from the bottom sediments in the western basin. Fluxes under aerobic conditions at summertime temperatures averaged 1.35 $\text{mg P/m}^2/\text{d}$ and displayed spatial variability on scales as small as a centimetre. Using two different temperature correction factors the flux was adjusted to mean annual temperature yielding average annual fluxes of 0.43–0.91 $\text{mg P/m}^2/\text{d}$ and a western basin-wide total of 378–808 Mg P/y as the diffusive flux from sediments. This is 3–7% of the 11,000 Mg P/y IJC target load for P delivery to Lake Erie from external sources. Based on these average aerobic fluxes, the sediment contributes 3.0–6.3 $\mu\text{g P/L}$ as a background internal contribution that represents 20–42% of the GLWQA interim Target Concentration of 15 $\mu\text{g P/L}$ for the western basin. The implication is that this internal diffusive recycling of P is unlikely to trigger cyanobacterial blooms by itself but is sufficiently large to cause blooms when combined with external loads. This background flux may also contribute to a delayed response of the lake to any decrease in the external loading.

Other mechanisms may contribute to sediment P recycling in Lake Erie. Biologically enhanced transport of dissolved or adsorbed

PO₄ from sediment (i.e. bio-translocation) can play a significant and often overlooked role in sediment P exchange: migrating algae or cyanobacteria may incorporate P in deeper strata and transport it as particulate P (PP) into the epilimnion (Spears et al., 2007). Wind/wave action and resuspension of sediment P around the edges of the hypolimnion may produce prolonged increases in epilimnetic TP and DP in late summer, as occurred in 1970 (Burns, 1976) and 1968–1982 (Rosa and Burns, 1987). Sediment pore water SRP concentrations can reach over 1 mg/L or ~1000 times those in lake water (Azcue et al., 1996) while resuspended TP can be 40% soluble (Burns, 1976). The quantity of P released during resuspension depends on the frequency and depth of disturbance of the sediment bottom, the concentration and form of P in the sediment, partitioning between DP and PP, and whether the bottom waters are oxic or anoxic. Recently, Matisoff and Carson (2014) estimated that 68–86% of the sediment in suspension in the west basin is resuspended from the bottom. Under aerobic conditions, and assuming a phosphate exchange between the resuspended sediment and the lake water, this translates to an internal loading of about 300–400 MTA P (Hummel, 2014). Hummel (2014) obtained internal P loads as high as 9000 MTA under anoxic conditions and with sediments from the central basin. Aerobic decay of biological material can occur anywhere in the water column or in shallow sediments – as seen, for example, in the Bay of Quinte (Nicholls, 1999). As the process is somewhat temperature dependent, this would be a negative factor in the west basin if water temperatures increase under climate change.

3.4.5. Implications of internal loading/recycling

Internal loading is sometimes discussed as a mechanism that would delay a response to costly nutrient controls, which can generate debate on the rationale for such controls and stall management action. Nevertheless an understanding of the expected response time of the lake to changes in external loadings is essential to evaluate the effectiveness of management actions. It can also be argued that prolonged delay in nutrient management is likely to further extend the lag before any sustained improvement occurs. Regardless of whether P is regenerated during hypoxia or by resuspension, excessive accumulation of sediment P can be limited through management of external nutrient loads. Once in the lake, there are no management options to eliminate P from a lake the size of Erie, except to wait for natural processes to take their course. Earlier remedial efforts under the GLWQA resulted in a 50% reduction in TP in Lake Erie within about 10 years, despite internal recycling. Burns et al. (1976) estimated that ~92% of the P entering Lake Erie is retained in the lake, but the proportion recycled as internal loading has yet to be directly quantified, hence it is difficult to estimate the likely delay in response to management actions. A simple calculation, assuming that 92% of the P is recycled each year, indicates that only 30–50% of the external P input will remain after about 10 years. A recent review showed that most European shallow lakes reached equilibrium with reduced P loads in 10–15 years (Jeppesen et al., 2007) – consistent with the response time of Lake Erie to the 1972 GLWQA loading reductions and with the simple calculation of P retention above. It may thus be reasonable to expect that the response of Lake Erie to P management actions would not be unduly delayed past 10–15 years, but regime shifts, changes in the nature and timing of the external loading and climate change may moderate the lake's response and prompt a re-evaluation of expected response times.

4. Conclusions

Lake Erie is the most vulnerable and impacted of the Great Lakes, and the re-eutrophication and extensive algal blooms and

severe hypoxia in this important waterbody have seen much national and international attention in recent years. In 2012, the International Joint Commission convened a task team to evaluate the conditions in Lake Erie and develop mitigation strategies (e.g. IJC, 2014). Although HABs and hypoxia in Lake Erie are influenced by the natural variability of hydro-meteorological conditions in the basin, it is clear that changes in agricultural practices have contributed to a significant increase in bio-available phosphorous loading to the lake. A suite of agricultural best management actions in the watershed may offer an appropriate approach to reducing P loading to the lake. Further, proliferation of dreissenid mussels and their influence on ecological changes in the lake requires further assessment. Most recently, the governments of Canada and the United States have adopted revised P loading targets for Lake Erie, designed to reduce the extent and severity of cyanobacterial blooms as well as the extent of hypoxia in the central basin (Binational.net, 2015). P targets designed to reduce *Cladophora* growth in the east basin remain unresolved (Binational.net, 2015) but once defined, may also be incorporated. The success story of the 1970s and 1980s for the Great Lakes provides a clear and inspirational example of effective, science-based remedial action, based on active engagement by all sectors at local, regional, national and binational levels. The recent changes in Lake Erie nevertheless illustrate a need for continued vigilance and an adaptive management strategy – which integrates monitoring, research, and modelling and is based on sound science and a standardized, targeted monitoring of key measures of ecosystem response.

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