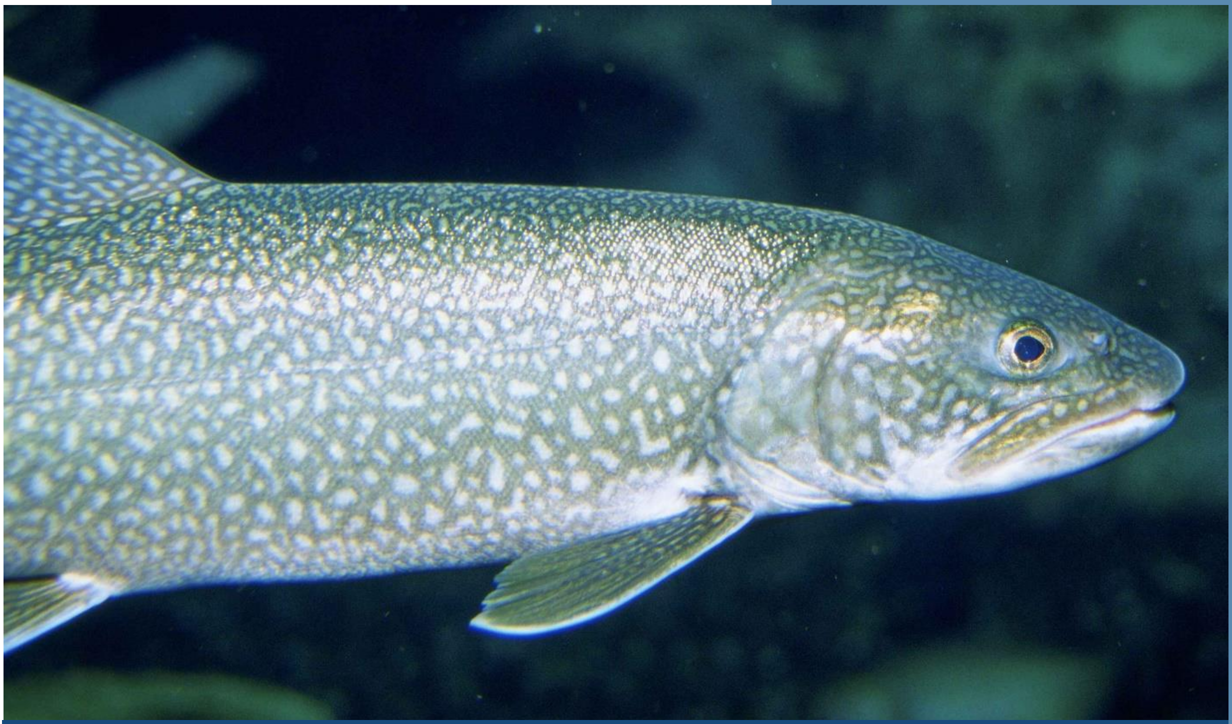

Understanding Declining Offshore Productivity in the Great Lakes

Final Report

Date: March 28, 2018

Prepared Under Contract to:

The International Joint Commission

LimnoTech
Water Environment | Scientists Engineers

Cover image: underwater close-up view of adult lake trout.
Photo source: Eric Engbretson, U.S. Fish and Wildlife Service, public domain, Wikimedia Commons.

LimnoTech
Water | Scientists
Environment | Engineers

501 Avis Drive
Ann Arbor, MI 48108
734.332.1200
www.limno.com

Understanding Declining Offshore Productivity in the Great Lakes

Final Report

Prepared Under Contract to:
The International Joint Commission

March 28, 2018

Prepared by:
LimnoTech, Ann Arbor, Michigan

Blank page

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1 Executive Summary

This assessment sought to determine the current state of knowledge of the relationship between phosphorus loading and upper food web productivity in offshore areas of the Great Lakes ecosystems. The project tasks included a literature review, an update of Bunnell et al. (2014) data, and a review of available food web models. A summary of the resulting findings, gaps, and recommendations follows.

1.1 Findings

Several important findings, particularly derived from the review of updated phosphorus concentration data and fish data from all the lakes, are itemized below.

- Changes in average spring total phosphorus concentrations and abundance of prey fish and predatory fish have shown continued variation but few strong trends from about 2005 to 2010, and continuing over the five years since the Bunnell et al. (2014) data compilation and analysis (typically including data up to 2010; new data are through 2015 in most cases). This suggests that most low-productivity lakes may be approaching a steady state with respect to dreissenid mussel populations and impacts, along with other recent drivers of primary productivity change.
- Multiple lines of evidence show a major decline in the productivity of the lower food web in Lake Michigan and Lake Huron, and to a lesser extent in Lake Ontario. Impacts on the upper food web have varied by lake and over time, and are complicated by the roles of predation and recruitment at this level.
- Trapping of nutrients by mussels has increased benthic productivity and decreased pelagic primary productivity in Lake Michigan, and in other lakes where dreissenids dominate the benthic fauna.
- Invasive round gobies continue to play an important but not well quantified role as a competitor for food with other prey fish, as well serving as a food source for upper trophic levels in the Great Lakes, partially offsetting the impacts of declining prey fish in many of the lakes, and returning some mussel biomass to upper trophic levels based on mussel predation by gobies.
- The virtual disappearance of the primary benthic food source *Diporeia* from all lakes except Superior has compounded the effects of phosphorus shunting by mussels on offshore fish productivity.
- The collaborative and cooperative management of the offshore commercial and recreational fishery is relatively healthy in most of the Great Lakes, despite ongoing variability in offshore fish productivity.
- Ecological models of increasing complexity have been successfully applied to simulate and help explain patterns observed in the Great Lakes over the last several decades, although important aspects of the full role of nutrient shunting by mussels in overall lake productivity remain to be worked out. At this time, model use to support fishery management decisions has been somewhat limited in favor of more direct measures of community and population condition (i.e., stock assessment data). Use of models within a framework that evaluates alternative fishery

management actions (e.g., stocking, harvest) and policies may enhance their usefulness and incorporation into formal adaptive management frameworks.

1.2 Gaps

Although significant progress has been made in understanding the linkage between nutrients and offshore fish productivity in the last 10 years, major gaps in understanding remain. A group of research priorities identified by the Great Lakes Fishery Commission that are broadly consistent with the topic of this assessment include, "Quantification of energy and nutrient dynamics in Great Lakes food webs, and the role of food web members in structuring resilient communities and ecosystems" (http://glfc.org/pubs/pdfs/research/FRP%20Theme%20Conceptual%20Diagram.pdf).

Some of the data and knowledge gaps identified in the current assessment are listed below.

- The scaling of grazing impacts of mussels versus nutrient load reductions on offshore primary production are not well understood, particularly on seasonally dynamic species assemblages and after summer stratification isolates phytoplankton in the upper water column from mussel grazing.
- The relative impacts of predation on prey fish (top-down) versus decreased food supply (bottom-up) are not well known in most lakes.
- In-lake TP concentrations often do not match predictions based on available loading data alone, and nutrient loading data and models need to be updated at appropriate scales. The processes by which spring phosphorus loads are transformed in summer primary productivity in offshore areas are not clear, including the transformation to bioavailable phosphorus during this lag period.
- The importance of mussel/round goby/macroalgae interactions is recognized, but not well quantified in nearshore regions; nor is its influence on offshore phytoplankton and fish productivity well constrained. Developing nutrient management approaches to control nearshore macroalgae growth may require a compromise in some lakes and basins that also allows for optimal fish production.
- Modeling methods for determining the relative effectiveness and impact of alternative phosphorus reduction strategies on offshore fish productivity are not yet well developed, so they should be applied within an adaptive management framework.

1.3 Recommendations

Areas where resources might be effectively applied and further policy development could be productively undertaken are summarized here.

- Improve coordination among water quality (bottom-up control) and fishery (top-down control) managers to clarify (i.e., reduce uncertainty in) the relationship between land and watershed controls on nutrients and their effect on offshore fishery production and conditions. Monitoring should be optimized to track lake sub-basin and lake-wide performance standards for acceptable impacts of nutrient-related actions on offshore fishery resources.
- Further development and application of well-constrained ecosystem models that link biogeochemistry, lower food web productivity, nearshore ecology, and offshore fish productivity, along with maintenance and enhancement of associated monitoring programs to meet the greater data demands of ecosystem models, would be a valuable component of an integrated ecosystem adaptive management system.

- Adding nearshore monitoring of nutrients, chlorophyll a, and zooplankton across the basin, and linking and coordinating the timing of data processing and reporting of all lower trophic level data to annual fishery stock assessment metrics, may improve our ability to connect and adapt nutrient-related actions to fishery production and conditions in the following season.
- Development of optimized monitoring for oligotrophic lakes and basins that are most at risk from changes that could be induced by nutrient management (Huron, Michigan, Ontario, and eastern basin of Erie).

2 Introduction

This technical synthesis report supports a study led by the Work Group on Declining Productivity in Offshore Regions of the Great Lakes of the Science Priority Committee of the International Joint Commission (IJC) Science Advisory Board. The report details the current state of knowledge within the Great Lakes ecosystems of the relationship between offshore nutrient concentrations and upper food web productivity. The findings are organized around the three project tasks: a literature review, an update of Bunnell et al. (2014) data, and a review of available food web and biogeochemical models. This report also identifies gaps in knowledge of the science related to nearshore-offshore nutrient gradients, and describes research topics and approaches that should be addressed to support evaluation of potential tradeoffs between phosphorus load reduction and fish productivity in the Great Lakes. The technical report includes recommendations for potential consideration by the IJC commissioners, based on further Work Group review and analysis. The report is written to inform two of the most pressing issues in the Great Lakes basin: nutrient load reduction strategies and management of the fishery. The report will support the goal of the larger IJC project to make novel contributions to the dialogue around these and related issues, and to enhance the robust scientific collaboration that exists among the IJC, agency and university researchers, and resource managers.

2.1 Project context

Phosphorus has been recognized for decades as the primary limiting nutrient for primary productivity in most freshwater systems, including the Great Lakes. Concerns about the impacts of excess nutrient loading on the lakes, including algal blooms and oxygen depletion of bottom waters, led to regulation and mitigation of total phosphorus (TP) loading to the lakes from the United States and Canada beginning in the 1970s and accelerating through the 1990s and early 2000s (Dove and Chapra 2015). Mitigation measures included upgrading of wastewater treatment plants, restrictions or bans on the use of phosphorus in detergents, and changes to agricultural tillage practices to reduce erosion and particulate phosphorus delivery to the lakes. Implementation of the Great Lakes Water Quality Agreement (GLWQA) has been overseen by Environmental and Climate Change Canada (ECCC), and the U.S. Environmental Protection Agency (USEPA), with fishery-related issues managed by the Great Lakes Fishery Commission (GLFC).

The arrival and spread of invasive filter-feeding dreissenid mussels (zebra and quagga mussels; hereafter referred to as “mussels”) throughout the lakes in the 1990s, with the exception of Lake Superior, led to trapping of phosphorus near shore (Hecky et al. 2004; Cha et al. 2011) and dramatic and persistent declines in offshore primary productivity and phytoplankton biomass in Lake Michigan, Lake Huron, eastern Lake Erie, and Lake Ontario (Fahnenstiel et al. 2010, Madenjian et al. 2015). With the exception of nearshore areas and some embayments (Figure 1), only western and to some extent central Lake Erie have persisted in a high-nutrient state (Table 2-1).

Along with the declines in offshore primary productivity in the lakes other than Superior came corresponding declines in productivity of parts of the offshore fishery, generally including lake trout, salmon, lake whitefish, and other species. The apparent cause-effect relationship between mussel increases and fish decreases is complicated by the coincident and possibly linked decline of the dominant benthic organism and important offshore food source in the lakes, the macroinvertebrate *Diporeia* (Barbiero et al. 2011a). Invasive round gobies have provided a supplemental food source for some predatory fish and bottom feeders in recent years (Pothoven and Madenjian 2013). A final complicating factor is ongoing and variable fish predation by sea lamprey (Krueger and Marsden 2007).

The patterns over time for abundance and harvest of individual offshore species in particular lakes can be complex. There is overall decline of prey fish and predatory fish in several of the lakes, compared to historical highs, but recent trends for some species show reversals. For example, a decline in alewife and Chinook in the mid-2000s in Lake Huron was followed by an increase in lake trout and lake whitefish in the main basin, and walleye in Saginaw Bay (GLFC 2013). Trout and lake whitefish increases may have been bolstered by higher densities of round gobies than are estimated by traditional prey fish survey methods; lake whitefish harvests have been decreasing dramatically in the last five years.

Efforts have intensified in recent years to reduce phosphorus (P) loading under Annex 4 of the 2012 Great Lakes Water Quality Agreement. The initial focus has been on managing non-point sources in Lake Erie to reduce harmful algal blooms and hypoxia. This effort will move next to the eastern basin of Lake Erie and Lake Ontario, where increasing nearshore macroalgae (especially *Cladophora*) has been a concern. Fishery managers in these areas and other lakes (Michigan and Huron) are seeking a better understanding about how planned nutrient loading reductions may impact offshore waters that are already oligotrophic due to previous P control efforts and mussel impacts. Because Lake Erie is nutrient rich and likely some years away from substantial offshore fish productivity declines, except perhaps for the eastern basin, it will not be considered extensively in this report. Because nutrient loading and primary productivity in Lake Superior are relatively low and stable and mussels are present only at low abundance in marginal bays, this lake will also not be emphasized except for comparative purposes. That leaves Lake Michigan, Lake Huron, and Lake Ontario as the lakes that will be treated in the most detail.

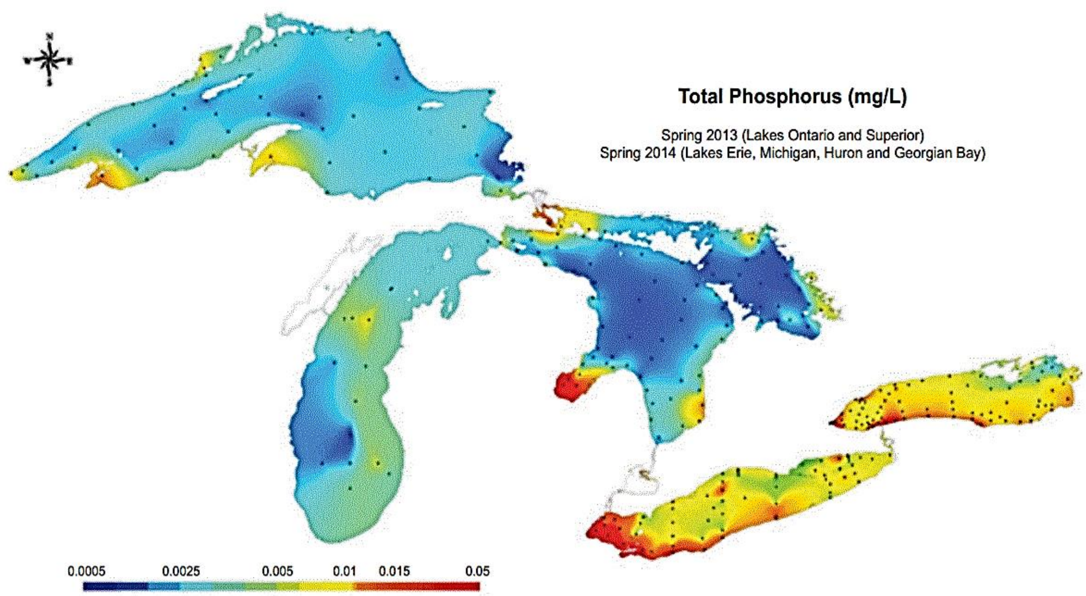

Figure 1. Spring total phosphorus concentrations for the Great Lakes, showing elevated areas in several embayments, including Saginaw Bay, as well as in western Lake Erie, and along northwestern and southern shorelines of Lake Ontario. Note that data for Green Bay are not collected or reported from these sources. Reproduced from ECCC and USEPA (2017), incorporating data from ECCC (Dove and Howell) and USEPA (Osantowski).

Table 2-1. Trophic status and trend of Great Lakes since approximately 1998 (based on ECCC and USEPA, 2017; data herein used for trends), with bounds for mesotrophy of 10 and 20 µg/L spring TP.

Lake or Basin	Offshore Trophic State	Offshore Trophic State Trend	Notes
Superior	Oligotrophic	Increasing	TP objectives consistently met
Michigan	Oligotrophic	Declining	Below TP objective
Huron	Oligotrophic	Declining	Below TP objective
Erie – Western	Eutrophic	Variable	Above TP objective, common algal blooms
Erie – Central	Mesotrophic	Stable/Declining	Above TP objective, bottom water hypoxia
Erie – Eastern	Oligotrophic	Stable	At or below TP objective
Ontario	Oligotrophic	Declining	Below TP objective

2.2 Work progress timeline

Preparation of the components of this report and interaction with the Work Group were conducted according to the following schedule:

- May 1, 2017: IJC-LimnoTech project contract finalized
- May 23, 2017: Project kickoff conference call
- June 29, 2017: Draft Literature Compilation completed (Deliverable #1)
- July 18, 2017: Work Group conference call
- August 17, 2018: Conference call with David Bunnell to discuss data sources for updates
- August 28-29, 2017: Attended and presented preliminary project results at related Great Lakes Lower Trophic Levels workshop at Cornell Biological Field Station
- August 31, 2017: Final Literature Compilation completed (Deliverable #2)
- October 3, 2017: Work Group conference call
- October 31, 2017: Bunnell et al. (2014) Data Update completed (Deliverable #3)
- December 20, 2017: Work group conference call
- December 22, 2017: Contract amendment to add supplemental data
- December 30, 2017: Model Review Memo completed (Deliverable #4)
- January 17, 2018: Outline of draft final report completed for Work Group review
- January 18, 2018: Work Group conference call
- February 19, 2018: Project abstracts submitted for IAGLR 2018 annual meeting
- March 1, 2018: Draft Final Report completed (Deliverable #5)

- March 2, 2018: Work Group conference call to review draft report (scheduled)
- March 20, 2018: Interim revision of Draft Final Report completed
- March 22, 2018: Work Group conference call to further review draft report
- March 23, 2018: Final Work Group comments on interim draft report received
- March 28, 2018: Revised Final Report completed (Deliverables #6 and #7)

Conference calls and email exchanges with Work Group leadership, members, and data suppliers took place throughout the execution of the project.

2.3 Use of the report

This report is intended to provide an objective summary of the state of knowledge within the Great Lakes ecosystems of the relationship between nutrient levels and upper food web productivity including fisheries, and to identify associated research and monitoring priorities to link nutrient management to fishery management. It is not primarily intended to describe or promote any particular policy recommendations. That said, there are multiple policy implications of the data and analysis presented in the report, most directly as this relates to priorities for ongoing investment in research and monitoring, but also for nutrient and fishery management. Although these will be broadly considered in the final sections of the report, the Work Group report that will be prepared to accompany this report may include more specific policy recommendations for consideration by the IJC commissioners.

3 Literature Review

The purpose of this section is to provide information on the current state of knowledge within the Great Lakes ecosystems with respect to the relationship between nutrient levels and upper food web productivity. The review is organized in a series of lake-by-lake trophic status reviews, followed by basin-wide discussion moving up trophic levels from primary producers to predatory fish. Discussions of invasive species and climate change conclude the section. The information was obtained from an initial literature compilation which represented a collection of relevant background materials for the IJC Declining Offshore Productivity Study. This included a synthesis of the available regional and global knowledge and literature related to how reduced phosphorus loading to lakes has affected fish biomass and communities. The sources compiled included peer-reviewed articles, conference proceedings, and government publications.

The initial literature search was completed using scientific databases (e.g., ProQuest and Google Scholar) with a pre-determined list of key words. Search strings were completed using broad terms such as "Nutrient Reduction", "Fish", and "Lakes", and further refined to include specific terms such as "Oligotrophication", "Fish Community", "Great Lakes", "Food Web", and "Impacts". We also looked specifically at articles that cited or were related to key sources (i.e., Bunnell et al. 2014). Publications that discussed the impact of nutrient reductions on the fish community were prioritized over those that discussed the trophic state or lower food web. Articles were also reviewed that discussed impacts outside the Great Lakes in order to gain an understanding of the global knowledge on the subject matter. Thus, of the 187 total references in the initial review, 28 were from outside North America. This includes data from lakes located in Denmark, France, Germany, Italy, Sweden, Switzerland, and Africa.

Although articles were included in the literature review from outside the Great Lakes, many international systems are not representative of Great Lakes conditions due to smaller size, more persistent stratification, and substantial internal loading of phosphorus from formerly hypoxic sediments after nutrient reduction. While interesting, the focus of most recent articles from outside North America (e.g., Finger et al. 2013, Caudron et al. 2014, Eero et al. 2016, Ozkan et al. 2016, Anneville et al. 2017, Noges et al. 2017) is on improvements to relatively small lakes following a concerted effort to reduce phosphorus loadings. For example, a trend towards oligotrophication caused by reducing phosphorus loading has allowed for a recovery of the whitefish fishery in Lake Geneva, Switzerland (Anneville et al. 2017). A similar situation, with some complications, has developed in the Bay of Quinte in Lake Ontario, where reduced nutrient loading has resulted in slower recovery than anticipated due to internal phosphorus release from sediment in parts of the bay (Miehls et al. 2009; Arhonditsis et al. 2016). Given these differences between the situation in many smaller lakes or even Great Lakes embayments, and the situation in the much larger and non-analogous lakes, the bulk of this report focuses primarily on the Great Lakes with minimal subsequent citation of literature from smaller lakes.

Additionally, we formatted a Google Sheet Document, titled "Literature Compilation for the IJC Declining Offshore Productivity Study". It is split into multiple categories including the Topic Heading (matching this literature review), with additional subheadings of Trophic State, Trophic Level, Taxa Group, Lake, and Indicator/Variable. A copy of the literature review was made available as a Google document: https://docs.google.com/spreadsheets/d/1dGm182e9DzLzDB4nVrWLyoGheXBFS-nFddjjj_X5UM/edit?usp=sharingSummary of recent research on fish response to nutrient management in lakes

The following sections will briefly summarize some of the pertinent articles collected as part of the literature review.

3.1 Trophic status changes in the Great Lakes

The trophic status is a useful means of classifying water bodies in terms of the primary productivity of the system. In general, watersheds with native soils that are rich in P, or agricultural watersheds with fertile soil, fertilizer and manure application, and periodic mechanical tillage produce higher sediment and nutrient loads, resulting in higher productivity and more eutrophic (even hyper-eutrophic) lake systems, whereas forested watersheds tend to result in more oligotrophic lakes.

The 2017 report on the Status of the Great Lakes (ECCC and USEPA 2017), provided a lake-by-lake assessment based on phytoplankton abundance in the open waters and associated benthic indicator (Figure 2). According to the assessment, Lake Superior remains an oligotrophic lake with generally unchanging conditions, whereas Lake Michigan and Lake Huron are listed as oligotrophic with deteriorating conditions in the 2017 report. Signs of the increasing oligotrophy in these lakes have been apparent for a number of years (Barbiero et al. 2012). This has been attributed to both the invasion of mussels reducing pelagic primary producers (Huron) and likewise a reduction in primary production in Lake Michigan. While Lake Ontario is a meso-oligotrophic to oligotrophic lake and appears to be changing more slowly than Huron or Michigan, the lake phytoplankton assemblage shows some evidence of changes driven in part by the invasive mussels. Binding et al. (2015) summarized the spatial and temporal variations in water clarity across the Great Lakes from satellite observations and long-term Secchi disk depth records (1970s-2015). Results showed increases in water clarity in Lakes Ontario, Huron, and Michigan, whereas Erie showed no trend but high variability, while Superior showed little change. Data also showed a divergence in clarity trends between nearshore and offshore areas. Coastal water quality generally contrasts with offshore conditions, especially near river mouths and other sources of sediments, nutrients, and other pollutants.

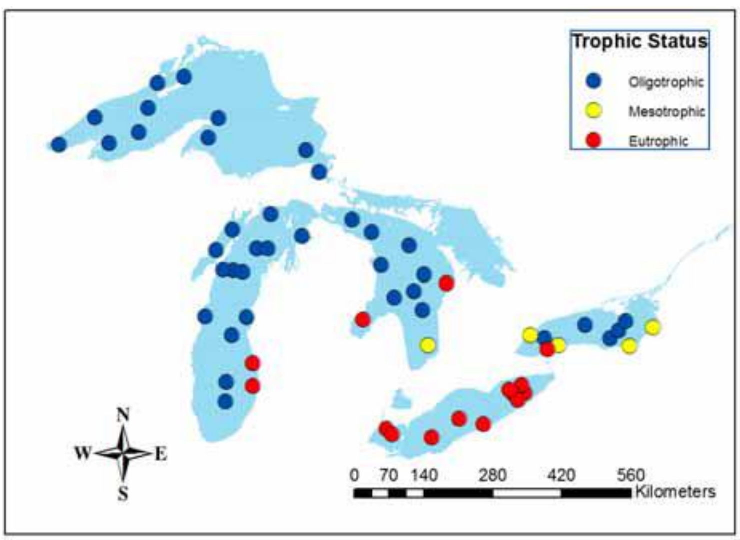

Figure 2. Great Lakes map showing the mean trophic status at sampling sites from 2010-2012 based on an index of benthic community composition (from ECCC and USEPA, State of the Great Lakes 2017 Technical Report).

The long-term trend toward more intense oligotrophy in Lake Michigan, Lake Huron, and Lake Ontario appears to be related to a reduction in phosphorus concentrations in offshore waters (Dove and Chapra 2015). Phosphorus is an essential nutrient for the growth of plants and animals, yet the levels in these lakes are generally below target levels. This trend appears to have been strongly influenced by the advent and expansion of zebra mussels around the lakes, and their later replacement by quagga mussels. Filter feeding by the mussels has trapped nutrients closer to shore, resulting in offshore nearshore enrichment, particularly in bottom waters and sediments due to mussel excretion and egestion (Hecky et al. 2004, Waples et al. 2016); the total offshore impacts of this nutrient "shunting" remain unclear, and are difficult to distinguish from reductions in nutrient loading from tributaries. Additionally, quagga mussels are able to colonize soft sediments in deeper waters than zebra mussels can access, which could represent a permanent trapping mechanism for phosphorus, termed the "mid-depth sink" hypothesis by Vanderploeg et al. (2010). The result of the combination of this redistribution of bioavailable phosphorus to the nearshore benthos (Ozersky et al. 2009), along with increased water clarity and light penetration due to mussel filtration, is expansion of macroalgae, particularly filamentous *Cladophora*, in some nearshore areas of Lake Michigan, Lake Huron, eastern Lake Erie, and Lake Ontario (Howell 2018). Habitat usage by fish associated with mussel and *Cladophora* occurrence has also been noted (e.g., Binder et al. 2017).

3.1.1 Lake Superior

Lake Superior is the largest Great Lake by volume and surface area, (82,100 km^2); it is also the coldest and deepest (maximum depth of 406 meters). Offshore Lake Superior is currently ultraoligotrophic based on Dove and Chapra's modified trophic class scheme, which utilizes spring total phosphorus (TP), summer Chl a, and summer Secchi depth (Dove and Chapra 2015). The rate of decrease in TP has slowed in Huron and Michigan; the rate and absolute values in Superior are consistently below the GLWQA target of 5 µgP/L (Dove and Chapra 2015).

Lake Superior has the lowest fish species richness of all the Great Lakes, and dreissenid mussels are rare. While many Great Lakes invaders (dreissenid mussels, alewife, sea lamprey, etc.) have not been able to invade and spread to the same extent as they have in the other lakes (Bunnell et al. 2014), there have been 20 reported invaders over the last decade. These include the Eurasian ruffe, the deadly infectious fish disease (VHS), and the Banded Mystery Snail, which was detected and reported in 2015.

Although dreissenid mussels are currently present in the lake, they are mainly restricted to a select number of harbors and nearshore areas, where their densities are low (Evans et al. 2011). Several factors appear to limit them from invading the offshore areas, including the depth, temperature and calcium limitations (Dove and Chapra 2015). Offshore water clarity has remained stable (see data in sections below).

3.1.2 Lake Michigan

Lake Michigan is the third largest Great Lake by surface area, (57,800 km^2), and has a maximum depth of 281 meters in the north, with another shallower basin in the south. Offshore waters of Lake Michigan are currently oligotrophic to ultraoligotrophic. The Dove and Chapra (2015) modified trophic class scheme, which utilizes spring TP, summer Chl a, and summer SD, has classified the open waters as ultraoligotrophic. Others have also noted that the trophic status of Lake Michigan, which has historically been mesotrophic, is similar to the historically more oligotrophic Lake Superior (Mida et al. 2010; Barbiero et al. 2012).

Lake Michigan as a whole has experienced a long-term oligotrophication trend, with higher rates of oligotrophication in recent years since the expansion of invasive mussels. Primary production across Lake Michigan has decreased substantially in response to the invasion of dreissenid mussels and their expansion into the offshore around 2005. This has significantly altered the nutrient dynamics, chlorophyll concentrations, primary production, and lower food web of the lake, causing the trophic state to converge with Lake Superior and Lake Huron (Mida et al. 2010; Barbiero et al. 2012; Fahnenstiel et al. 2016). In general, quagga mussels have replaced zebra mussels, colonized deeper depths (>100 m), and have led to a significant decline in primary production during the spring (Bunnell 2012). According to the most recent CSMI (Cooperative Science and Monitoring Initiative) surveys, the mean density of mussels in Lake Michigan at 30-90 m depth was higher than any other Great Lake. Recent data suggest that populations have stopped increasing in shallow waters (<90 m), but are still expanding in deep water (Baldridge and Nalepa 2015; Glyshaw et al. 2015).

Nearshore Lake Michigan has shown a slight increase in water clarity in recent years, but a slightly different trend from the offshore. According to Binding et al. (2015), the average nearshore water clarity has been increasing in recent years.

3.1.3 Lake Huron

Lake Huron is the second largest Great Lake by surface area, (59,600 km^2), and has a maximum depth of 229 meters. Its complex shoreline and bathymetry break the lake into multiple basins and bays (e.g., Saginaw Bay and Georgian Bay). The offshore waters of Lake Huron continue to undergo oligotrophication, with the trophic state transitioning from oligotrophic to ultraoligotrophic in recent years (Evans et al. 2011; Barbiero et al. 2012; Dove and Chapra 2015; Warner and Lesht 2015; Fahnenstiel et al. 2016). This trend is believed to be caused by a number of factors, but is dominated by both phosphorus loading declines and mussel activity (Barbiero et al. 2012). Declines in spring Chl a and TP concentrations, and gradual increases in soluble silica (indicating a reduction in diatom productivity) and water clarity are evident in offshore Lake Huron.

Like Michigan, zebra mussels initially invaded Huron, but by 2012 they were mostly replaced by quagga mussels. Peak mussel biomass is currently found at depths between 30 and 50 m; densities are continuing to increase in offshore areas. In recent years, mussel populations have increased at depths greater than 90 meters and are stable or decreasing in waters less than 90 meters deep (Horvatin presentation in ECCC 2015). Mussel filtering is believed to be the basis for recent declines in phytoplankton productivity and abundance in the lake (Fahnenstiel et al. 2016). Mussels in the offshore are also believed to be significantly reducing nutrient concentrations in the photic zone, increasing transparency to record-setting levels, and triggering the loss of the spring plankton bloom (ECCC 2015). Researchers have pointed out, however, that offshore mussel populations were most likely too low at the time of nutrient declines in the early 2000s to be the initial cause of the oligotrophication (Bunnell et al. 2014; Barbiero et al. 2012).

Nearshore Lake Huron is currently highly variable spatially, with the trophic state depending greatly on factors such as distance from shore and tributary inputs. Nearshore monitoring conducted in 2015 by the Ontario Ministry of the Environment and Climate Change found that nearshore Lake Huron is currently ultraoligotrophic to oligotrophic in most areas, but that there are mesotrophic areas with high levels of nutrient enrichment and algal growth near rivers and close to the shoreline (Howell 2015). For example, the status of the Georgian Bay is highly dependent on phosphorus loads from tributaries, and varies temporally and spatially, but has shown phosphorus enrichment along the shore and algal fouling in the eastern bay (Allerton et al. 2016; Briggs and Howell in ECCC 2015).

3.1.4 Lake Erie

Lake Erie is the fourth largest (25,700 km^2) and the shallowest Great Lake. It has three distinct basins, based on bathymetry and circulation, with average depths of 7.3 m (west), 18.3 m (central), and 24.4 m (east), and a maximum depth of only 64 m. Each basin has responded differently to changes in nutrient loading over recent years (Maccoux et al. 2016), with an overall gradient of more severe nutrient impacts in the west, and lower impacts in the east. Nutrient loads come primarily from the Maumee River, which drains a highly productive agricultural watershed, which is also the largest in the Great Lakes (16,460 km^2). Secondary contributions come from other tributaries, including the Detroit River. Winter and early spring blooms of the diatom *Aulacoseria islandica* have been documented in Lake Erie under the ice and in open water (Twiss et al. 2012); biomass from these blooms may contribute to summer hypoxia in the central basin. Dreissenid mussels are most abundant in the eastern basin; populations are limited by summer hypoxia in the central basin and to a lesser extent by frequent sediment resuspension in the western basin (Karatayev et al. 2017).

3.1.5 Lake Ontario

Lake Ontario, the smallest of the five Great Lakes (19,000 km^2), has a maximum depth of 244 m and more than three times the total volume of Lake Erie. Offshore Lake Ontario is currently believed to be in an oligotrophic state. Dove and Chapra (2015), using 2013 offshore data collected by ECCC, determined that offshore Lake Ontario is oligotrophic with low primary productivity, and that it is currently below total phosphorus and chlorophyll a targets set by the 1978 GLWQA. Additionally, recent (2013) summer phytoplankton biomass measurements indicate that Lake Ontario, as a whole, may currently be closer to an ultraoligotrophic trophic state (Munawar et al. 2016). It is believed that dreissenid mussels have caused the high water transparency, low nutrient levels, and reemergence of nuisance *Cladophora* algae (deBarros 2016, Howell 2018). Overall, the data suggest that offshore Lake Ontario is currently strongly oligotrophic, has very low primary productivity, and is phosphorus limited.

The trophic state has been relatively stable to declining in recent years in Lake Ontario, possibly due to an apparent slowing of expansion or stabilization in dreissenid mussel densities (Bunnell et al. 2014, Baldridge and Nalepa 2015). Additionally, while there was a pronounced decline in total phosphorus in the mid-late 1990s, there was not a strong trend for the next decade or so until a more recent decline began in about 2008 (Dove and Chapra 2015, Holeck et al. 2015, data herein). Similarly, offshore Chl a concentrations have shown either a stable or slightly increasing trend in recent years (deBarros 2016; Bunnell et al. 2014), and while water clarity greatly increased in the 1980s, and into the 1990s, it has shown no trend in recent years (Bunnell et al. 2014; Binding et al. 2015).

Nearshore Lake Ontario has high spatial and temporal variability, with local conditions ranging from hypereutrophic to oligotrophic. There appear to be higher concentrations of TP in the western, more urbanized nearshore areas of Lake Ontario, with decreasing concentrations in eastern areas (deBarros 2016), although upwelling conditions often alter this state in particular areas of the lake that otherwise have limited tributary loading. Chl a and TP are both substantially higher at many nearshore sites in comparison with offshore waters (Makarewicz et al. 2012).

In terms of trophic state and offshore fishery productivity, Lake Michigan, Lake Huron, Lake Ontario, and the eastern basin of Lake Erie are the most similar to each other and will be considered in the most detail in the rest of this assessment.

3.2 Lower trophic levels

The Great Lakes lower food web (for the purposes of this report) consists of the zooplankton, phytoplankton, and benthic communities. These lower trophic levels are critical to sustaining and maintaining healthy food webs supporting fish production, and are an important component to consider with respect to changing ecosystems. Table 3-1 provides a general summary from the State of the Great Lakes report (2017), on the current status and trends of the lower food web across the Great Lakes. While this summary provides a simplified and recent overview of the status, many of the lakes have experienced significant changes over time. Some of these changes will be highlighted in the sections below.

Table 3-1. The state of the phytoplankton, zooplankton, and benthos communities across the Great Lakes (adapted from the State of the Great Lakes 2017 Report); "deteriorating" = declining, except for Lake Erie phytoplankton.

Lake	Phytoplankton – Open Water		Zooplankton – Open Water		Benthos – Open Water	
	Status	Trend	Status	Trend	Status	Trend
Across Great Lakes	Fair	Deteriorating	Good	Unchanging	Good	Unchanging
Superior	Good	Unchanging	Good	Unchanging	Good	Unchanging
Michigan	Fair	Deteriorating	Good	Unchanging	Good	Unchanging
Huron	Fair	Deteriorating	Fair (low)	Unchanging	Good	Unchanging
Erie	Poor	Deteriorating	Good	Unchanging	Poor	Deteriorating
Ontario	Good	Unchanging	Good	Unchanging	Fair	Unchanging

3.2.1 Algae and phytoplankton trends

Phytoplankton primary production is at the base of the aquatic food web and is a key driver in the health of ecosystem. Changes in the level of primary production can impact all of the other trophic levels, from zooplankton to predatory fish (Capuzzo et al. 2018). Recent observations on the state of the phytoplankton community across the Great Lakes suggest that it is continuing to change (Table 3-1). Overall it is classified as "deteriorating", although this can indicate opposite biomass trends in different lakes (i.e., increasing in Erie and declining in Michigan, Huron, and Ontario) as ideal conditions fall in a particular range. While Superior and Ontario remain "unchanging" and in good condition, they have each experienced changes to the community structure. Reavie et al. (2014) published on phytoplankton trends across all the lakes from 2001-2011, and this is used as a basis for the summary below. The importance of the very small components of the basal food web (picoplankton, viruses, bacteria) has also recently been highlighted (Vanderploeg et al. 2015, Carrick et al. 2015, Denef et al. 2017), but more exploration or this important part of the food web is merited.

In general, decreasing phytoplankton biomass with the rapid oligotrophication of Lakes Huron and Michigan has resulted in the lower food webs of these lakes resembling that of Lake Superior (Barbiero et al. 2012). Lake Michigan tends to be dominated by cyanobacteria, with a historical spring dominance (by biovolume) of diatoms. However, spring biovolume (especially in the southern basin) has declined significantly from 2001-2011 (Reavie et al. 2014). Evans et al. (2011) also showed slow declines in seasonal silica drawdown, indicating decreased primary production and utilization of silica by phytoplankton, until more recently when more abrupt declines in drawdown rate occurred . This is supported by an increase in spring soluble reactive silica concentrations in Lake Michigan over the last few decades. Soluble silica concentrations averaged 0.52 and 0.54 mg/L (southern and northern basins) in 1983-1987, and increased to 0.87 and 0.89 mg/L in 2006-2010 (Barbiero et al. 2012). Similarly, Lake Huron has seen a reduction in spring biovolume, which is generally dominated by the diatoms, blue-greens, and chrysophytes. There has been a decline in summer Chl a concentrations after nutrient loads were lowered (1970s-1990). In recent years, trends have identified a further decline in spring and summer Chl a compared to the 1990s (Barbiero et al. 2012, Dove and Chapra 2015). Additionally, there has been an increase in silica concentrations since the mussel invasion, indicating declining phytoplankton production (Evans et al. 2011; Barbiero et al. 2012; Dove and Chapra 2015).

Unlike these lakes, Lake Erie central basin phytoplankton biovolumes have generally increased over the last decade (Allinger and Reavie 2013). High spring biovolumes are mostly attributed to centric diatoms, whereas a more mixed phytoplankton sample is common during summer sampling events. Although a similar increase in spring diatom blooms was not observed in the eastern basin (Reavie et al. 2014). The western basin is also dominated by centric diatoms in the spring with an increasing trend in total cell densities in spring and summer. Summer data have also shown an increase in the number of *Microcystis*, indicative of the recent cyanobacteria algal blooms in Lake Erie (Reavie et al. 2014).

Lake Ontario showed an increase in summer cell densities, but otherwise there was no significant change over the 10-year period (Reavie et al. 2014). Lake Superior is dominated year-round by blue-green algae in terms of density, but biovolume is mostly diatoms, chrysophytes, cryptophytes and dinoflagellates. There has been a slight increase in the number of cell densities in the lake from 2001. MODIS imagery and the Great Lakes Production Model determined that lake-wide Chl a concentrations were similar before 1974, and in 2010-2013, suggesting a fairly stable long-term trend. Additionally, they found a consistent depth gradient in Lake Superior over time, with the highest Chl a concentrations in shallow areas and the lowest in deep waters, further supporting the conclusion that primary productivity in Lake Superior has not changed substantially over time (Fahnenstiel et al. 2016).

In addition, the nuisance green alga, *Cladophora* has also experienced changes across the Great Lakes. *Cladophora* is a large genus with a broad range of ecological characteristics, but in the Great Lakes *Cladophora glomerata* dominates. In general, the prevalence and biomass of this species has increased over the last decade with the eutrophication of Lake Erie and in correlation with the dreissenids. *Cladophora* can be problematic as it can foul shorelines, clog drinking water and cooling water intakes, as well as harbor organisms that are pathogenic to humans (e.g. *Salmonella*) (Bootsma et al. 2015, Higgins et al. 2008; Verhougstraete et al. 2010).

As of 2016, 40% of Lake Ontario shoreline was estimated to have nuisance levels of *Cladophora* and in general levels have been increasing since the 1990s (Kuczynski et al. 2016, Howell 2018). In Lake Huron, *Cladophora* is growing in multiple nearshore areas but the biomass is largely unknown. In a remote sensing analysis, it was estimated that about 15% of the shoreline is impacted by nuisance levels of the submerged aquatic vegetation. In Lake Michigan, Brooks et al. (2015) estimated via remote sensing surveys that 28% of the Lake Michigan shoreline is affected. Macroalgae does not appear to be present at nuisance levels in most of Lake Superior.

3.2.2 Zooplankton trends

While the current status of the zooplankton communities across the Great Lakes remains unchanged (Table 3-1), there were significant historical changes. Zooplankton are heterotrophs that are a vital component of freshwater food webs, especially for sustaining larval and juvenile fishes. Zooplankton community structure can be affiliated with the trophic status of a lake, where oligotrophic lakes are often dominated by calanoid copepods, whereas eutrophic lakes tend to have more cladocerans and cyclopoid copepods (Bunnell et al. 2011). Zooplankton community structure is also heavily regulated by the general makeup of the aquatic system, where some species will selectively feed on smaller or larger target zooplankton. Mean body size and species composition of zooplankton are also sensitive indicators of predatory pressure by planktivorous fish and large invertebrates (*Mysis* and predatory cladocerans), although such indicators need further development (ECCC & USEPA 2017). Additionally, the bottom-up relationship (declining phytoplankton prey) in the Great Lakes can also drive change in the zooplankton community (Bunnell et al. 2011, Barbiero et al. 2011b). Significant changes across the Great Lakes have been observed in part due to the introduction of the predatory cladocerans (native to Northern Europe and Asia) such as the *Bythotrephes longimanus* and the *Cercopagis pengoi,* and the introduction of dreissenid mussels, whose veligers now constitute a substantial component of the zooplankton at certain times of the year in all lakes except Superior.

In general, Lake Superior's zooplankton community has remained similar, but recent findings suggest *Bythotrephes* has had a measurable impact on the offshore cladoceran community (Pawlowski et al. 2017). The predatory *Bythotrephes* preys on a number of species, including other cladocerans (e.g., *Bosmina, Daphnia, Holopedium*) and small copepods (Pawlowski et al. 2017). Of the potential cladoceran prey species, *Bosmina* densities were also the most negatively correlated with *Bythotrephes* densities. While the overall changes to the zooplankton appear less significant than other lakes, this research suggests a need to further explore potential changes to the community structure.

The Lake Michigan zooplankton community has undergone major changes over the last few decades. A significant reduction in the native cladoceran populations (Driscoll et al. 2015) occurred in the late 1980s. The introduction of the predatory cladoceran (*Bythotrephes*) and the more recent *Cercopagis* was likely partially responsible for this decline (Witt et al. 2005; Pichlova-Ptacnikova and Vanderploeg, 2011). Zooplankton biomass also declined following the invasion of the mussels, with both the cladoceran and cyclopod copepods representing a significant portion of the lost biomass (Driscoll et al. 2015). Additionally, the calanoid copepods and *Mysis* appear to have also experienced declines (Vanderploeg et al. 2012; Driscoll et al. 2015). Despite these recent changes to its food web, driven partially by invasive species, recent reports suggest Calanoids, Cyclopoids and Cladocerans still remain the dominant zooplankton in the lake (Vanderploeg et al. 2012).

The lower food web of Lake Huron has experienced substantial changes over time (Barbiero et al. 2009). Similar to Lake Michigan, the exotic predatory cladoceran *Bythotrephes longimanus* was first detected in the lake in the 1980s and has contributed to significant shifts in the zooplankton community composition, including reductions in the populations of several native cladoceran species and a decrease in species richness, which could represent a decreasing food base for forage fish (Barbiero et al. 2009). However, exact mechanisms of these declines, and the relative strength of bottom-up versus top-down pressure, have yet to be fully determined (ECCC & USEPA 2017).

There was a significant shift in the zooplankton communities in offshore Lake Ontario between 1997 and 2011 (Barbiero et al. 2014). The shifts were attributed from an initial assemblage dominated by cyclopoid copepods, cladocerans and bosminids, to a reduction in the numbers of cyclopoids, a more variable cladoceran community, and increased biomass of calanoid copepods (Barbiero et al. 2014). But unlike Lakes Huron and Michigan, these trends were not accompanied by a trend towards increased oligotrophy, but were more likely caused by decreased vertebrate predation due to alewife declines and changes in the predatory invertebrate community (Barbiero et al. 2014).

3.2.3 Benthos trends

Benthic macroinvertebrates are organisms without backbones that live on the lake beds (rocks, sediments, debris, logs, plants, etc.). Unlike fish, they are relatively immobile and are continuously exposed to their environments, making them sensitive to water quality. Many reside in an area long enough (months to years) to reflect changing environmental conditions and serve as an important food source for fish species. In general, shorter term trends (2010-2012) suggest the status of the benthic community appears to be unchanging across the Great Lakes (Table 3-1), except in Lake Erie, where the increased eutrophication appears to have impacted the benthic community. Using an oligochaete trophic index, Lake Erie is increasing, suggesting a more tolerant (less diverse) community, specifically in the eastern basin.

Within the Great Lakes, there has been an increased realization of the importance of benthic processes and pathways within the whole-lake context (Vander Zanden and Vadeboncoeur 2002). Recent analysis of long-term dynamics of major trophic levels in Laurentian Great Lakes revealed a far greater prevalence of bottom-up regulation since 1998, emanating from long-term declines in TP inputs and the more recent proliferation of nonindigenous dreissenid mussels (Bunnell et al. 2014).

In Lake Superior, despite some invasive introductions (e.g., the mudsnail), the food web structure remains relatively unchanged from historic times (Schmidt et al. 2009; Sierszen et al. 2011), and populations of native benthic invertebrates, dominated by *Mysis* and the amphipod *Diporeia spp.,* remain healthy (Scharold et al. 2004; 2009; Sierszen et al. 2011). Diporeia is mostly abundant in colder, offshore areas and is generally absent from warm, shallow bays and basins (Landrum and Nalepa 1998).

Lake Michigan's benthic community has changed over time, mostly due to the invasion of mussels. Native mussels have been mostly displaced with the exotic quagga, and to a much lesser extent the zebra mussels (Nalepa et al. 2014, Figure 3). By 2010, the quagga mussels had attained mean densities of over 10,000 animals per m² at some water depths (Madenjian et al. 2010), which led to a substantial increase in energy flow to the macroinvertebrate community. Nalepa and colleagues have tracked the benthic community changes from the early 1990s through the present. As of 2010, there was a significant decrease in the native *Diporeia* with a subsequent increase in the quagga population.

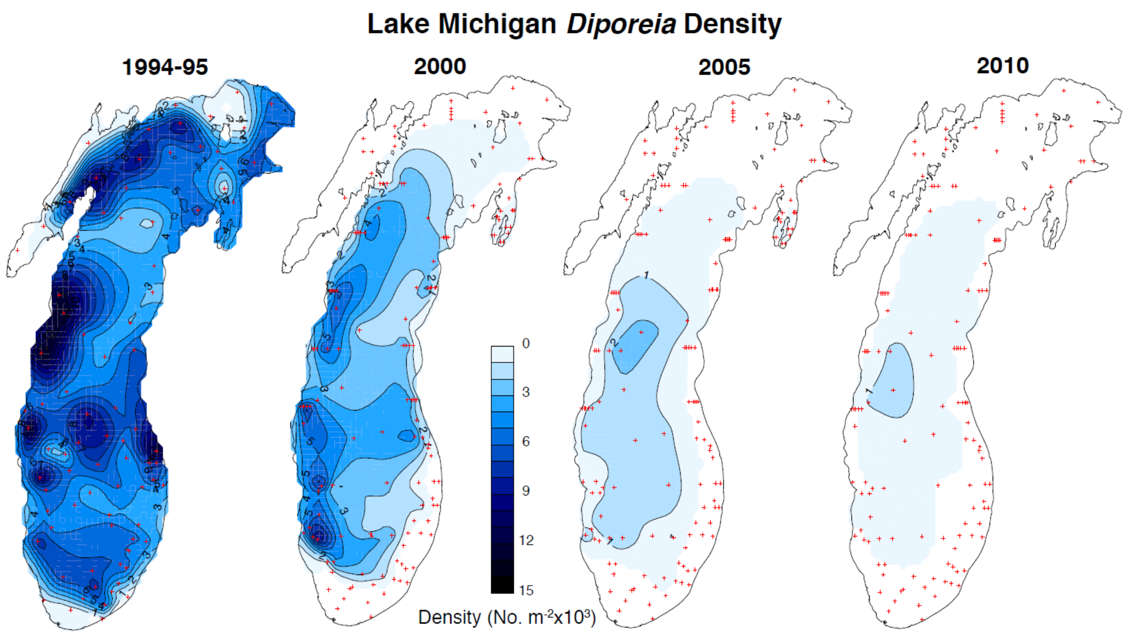

Figure 3. The mean densities of Diporeia across Lake Michigan (from Nalepa et al. 2014; NOAA Technical Memorandum GLERL-164)

Similar to Lake Michigan, there has been a change to the Lake Huron and Lake Ontario benthic community structure, with increases in the abundance of invasive mussels and decreases in abundances of the amphipod *Diporeia spp*. and oligochaetes (Nalepa et al. 2007; Barbiero et al. 2011a; Birkett et al. 2015). While the decrease in *Diporeia* is likely related to the invasive mussels, factors such as declines in the magnitude of the spring bloom, which provides a pulse of food to the deep benthic community, may be important. For example, the large declines in *Diporeia* populations across Lake Huron that occurred in the early 2000s followed a dramatic reduction in spring phytoplankton biovolumes (Barbiero et al. 2011a).

The descriptions above refer primarily to the offshore profundal benthos. Little is known about potential changes that have occurred over time around individual lakes or the entire basin in the nearshore benthos, especially in benthic invertebrates, with the exception of more localized studies on water quality indicators such as nymphal mayflies (*Hexagenia*) in Saginaw Bay and elsewhere (e.g., Siersma et al. 2014).

3.3 Prey Fish

Assessment of prey fishes within the Great Lakes have been conducted since the early 1970's. Recent assessments suggest that total prey biomass (i.e., alewife, rainbow smelt, bloater and cisco) appears to have declined in many of the lakes (Lake Superior, Lake Michigan, Lake Huron and Lake Ontario) over the 30+ years since monitoring began (Kunnenun 2017). Recent composition and abundance condition summaries of prey fish communities by lake are summarized below.

3.3.1 Composition, abundance, and biomass

Lake Huron (Riley et al. 2013)

The current state of the prey fish community in Lake Huron (Figure 4) is likely responding to the effects of invasive species like spiny water flea, dreissenid mussels, and round goby, as well as shifting predation pressure from lake trout and salmon (He et al. 2015). Assessments of the Lake Huron prey fish community have found continuing low biomass and abundance of offshore, non-native species like alewife and rainbow smelt. The abundance of native species like bloater, however, appears to be responding positively (O'Brien et al. 2016, Collingsworth et al. 2014) to the ecological changes which may also be driven by nutrient load reductions and lower trophic level shifts. Offshore habitat usage by prey fishes within Lake Huron has been altered by water quality modifications and invasives species, and appears to be in a state of flux with composition changes expected in the future. There is also evidence that changes in predation intensity are playing a role in prey fish absolute and relative abundance in Lake Huron (He et al. 2015, Clark et al. 2016 and 2017).

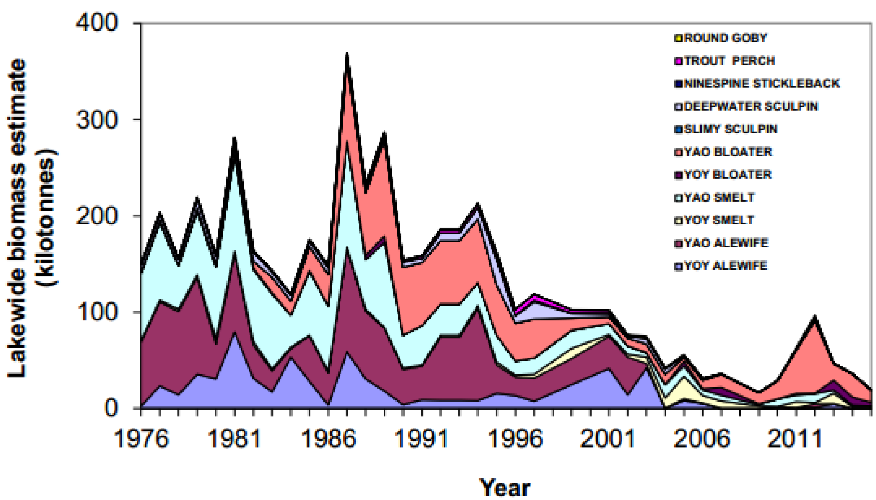

Figure 4. The 2015 main basin prey fish biomass estimate for Lake Huron was 19.4 kilotonnes, a decline of about 50% from 2014. This estimate is the second lowest in the time series, and is approximately 5% of the maximum estimate in the time series observed in 1987. Approximately two-thirds of the 2015 biomass estimate was composed of bloater (Roseman et al. 2016).

Lake Erie (Kayle et al. 2017)

The prey fish community within Lake Erie is complex because of the larger, physical and environmental differences across the lake's basins, as well as the diversity of habitats, species, and stock behaviors within. Of the three basins, the western basin fishery responds most rapidly to changes in environmental conditions including the tributary nutrient loads contributing to eutrophic conditions that may lead to an unstable food-web structure which may adversely affect the central basin as well. At present, the prey fish community is summarized as follows,

> <u>Western Basin</u> – The prey base is spiny rayed fishes and round goby. Eutrophic conditions appear to create a shifting food-web resulting in declines in prey base populations (e.g., clupeids and *Notropis)*.
>
> <u>Central Basin</u> – Trends in the central basin are somewhat similar to the western basin with increasing TP concentrations and a shift in the forage community towards spiny rayed fishes and round goby although the forage community further transitions moving eastwards to that more similar to the eastern basin.
>
> <u>Eastern Basin</u> – Oligotrophic conditions generally remain in the eastern basin. The forage base is generally stable, abundant and diverse and dominated by rainbow smelt, emerald shiners, gizzard shad, as well as round goby as the benthic species.

Lake Michigan (USGS 2017)

The prey fish community within Lake Michigan (Figure 5) continues to shift in response to reduced nutrient loading, mussel shunting of nutrients to the lakebed, and predation. At present, alewives continue to serve as the primary prey base, although their densities are declining and their age structure is truncated, indicating heavy predation pressure. Rainbow smelt and bloater remain important components of the food web, as do round goby as a benthic species. Besides bloater, other native coregonines and other native prey species are at historic low levels and comprise a relatively low proportion of the prey base, when compared to Lake Superior and Lake Huron (O'Brien et al. 2016). Changes in predation intensity may also be playing a role in Lake Michigan (Teshaye et al. 2014).

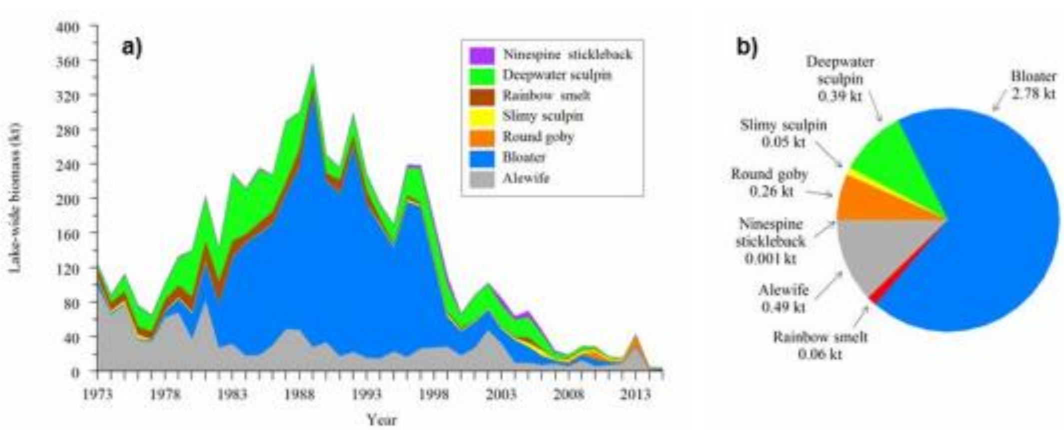

Figure 5. Biomass estimates of pelagic prey fish and total lake-wide prey fish biomass estimates (sum of alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, round goby, and ninespine stickleback) in 2015 was a record low for Lake Michigan. In 2015, bloater and deepwater sculpin, two native fishes, constituted over 78% of this total (Madenjian et al. 2016).

Lake Superior (Pratt et al. 2016)

The offshore prey fish community within Lake Superior (Figure 6) remains dominated by native species and appears to be stable in both abundance and biomass. Nutrient levels remain relatively stable although total phosphorus concentrations appear to be lower than previous estimates, possibly affecting the lower trophic levels, although not clearly evident in the prey fish community condition.

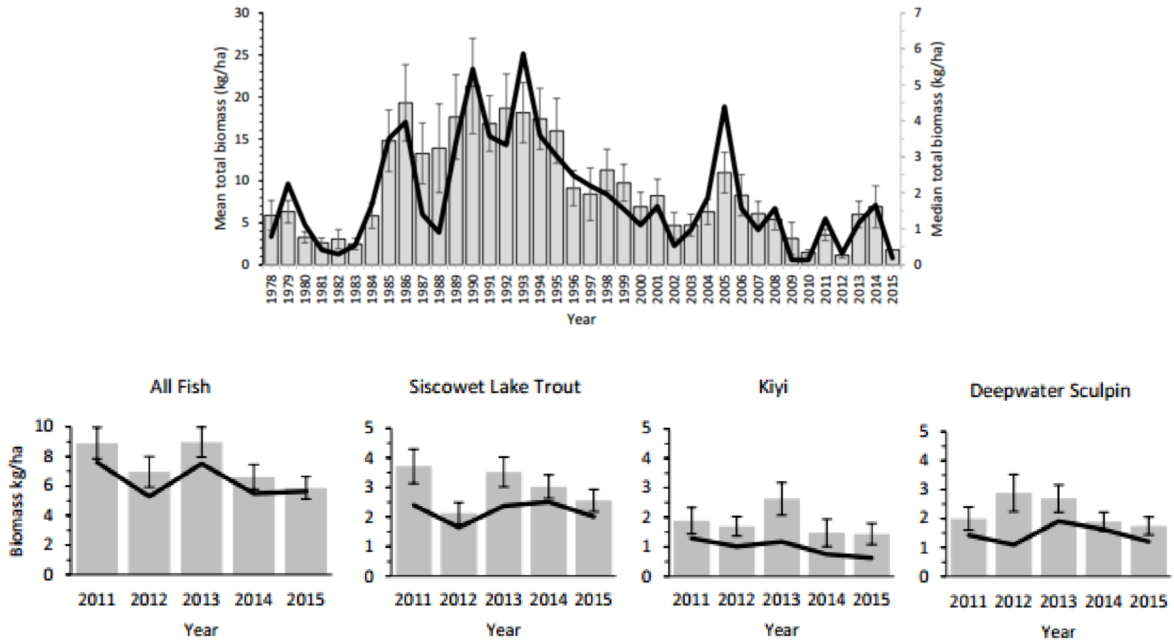

Figure 6. Nearshore lake-wide mean biomass in Lake Superior (top graph) was near the lowest biomass for this survey since it began in 1978. In the offshore zone (lower graphs), a total 12,433 individuals from eight species or morphotypes were collected in 2015; coregonines made up nearly twice the biomass collected in the previous survey (Vinson et al. 2016).

Lake Ontario (O'Gorman 2017)

The offshore prey fish community within Lake Ontario has a relatively stable to moderately increasing diversity, although it is generally generally lower than in the early 2000s reporting periods. Alewife, rainbow smelt, and cisco show positive population trends, while threespine stickleback and emerald shiner show declining population trends. Lower trophic levels differ in an onshore to offshore gradient – nearshore conditions show higher nutrient (eutrophic) concentrations while the offshore exhibits a low nutrient (oligotrophic) condition, raising management concerns about the ability of the lake to support alewife production to a level that meets salmonid demands. The Lake Ontario data are shown in comparison with data from other lakes in Figure 7.

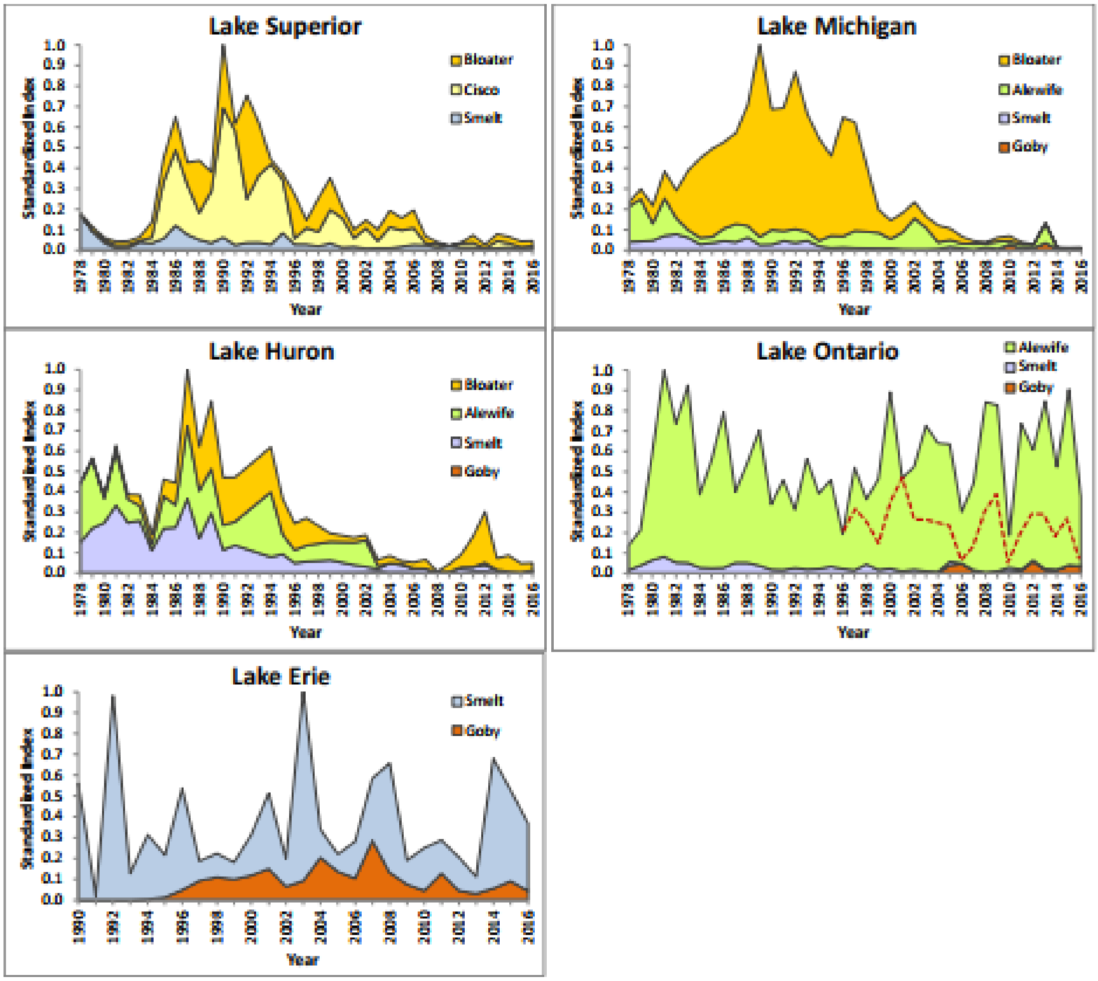

Figure 7. Lake-wide standardized indices of pelagic prey fish biomass for selected species. The red dashed line on the Lake Ontario plot represents a continuing estimate of the adjusted values corrected to the historical sampling gear configuration, which was modified in 1997 and subsequent years.

Cross-Basin Trends (Gorman and Weidel 2016)

In general, trends in biomass of prey fishes from bottom trawl data were inconsistent across the basin and only coregonids showed statistical agreement across the upper Great Lakes (data for Lake Ontario cisco were not available). The appearance of strong and moderate year-classes of bloater in Lake Huron in 2005-2013 countered the common trend of continuing weak year-classes of coregonids in Lakes Michigan and Superior. There was no agreement in cross-basin trends in biomass for rainbow smelt and alewife, although there was agreement between pairs of lakes. Hydroacoustic data were not reviewed in detail, but generally show low to moderate and variable biomass of pelagic prey fish in Lake Huron, Lake Michigan, and Lake Ontario, similar to bottom trawl data.

Although there was statistical agreement in trends of age-0 and older round goby biomass among lakes where this species has successfully invaded (Michigan, Huron, Erie, and Ontario), temporal patterns of biomass in each lake were different. Recent trends in round goby biomass remain highly variable in these lakes, although sampling methods have not generally been optimized for goby. There is widespread evidence that round goby has become increasingly important in piscivore and even non-piscivore diets (e.g., for lake trout, walleye, smallmouth bass, yellow perch, burbot, sturgeon, and lake whitefish in Lakes Michigan, Huron, Erie, and Ontario).

3.4 Predatory Fishes

3.4.1 Composition, abundance, and biomass

The SOGL (ECCC and USEPA 2017) report summarizes the status and trends of several, target predator species metrics within the region (Tables 3-2 and 3-3; Figure 8). The SOGL data, however, provide a better representation of the offshore over the nearshore environment – an important gap noted previously by Bunnell et al. (2014). Further, the SOGL summaries do not cover the full diversity of predator species managed and protected within the region, although they do offer a view into the condition of a few key species. Region-wide, fish species diversity is ranked from “fair” to “good,” although native species proportions are ranked as “poor” to “good”. For example, lake sturgeon are generally poorly distributed, although their distributions and numbers are improving basin-wide. Walleye appear to have a good status with a leveled trend, and lake trout are in fair numbers with an improving trend (ECCC & USEPA 2017). Lake-by-lake summaries are as follows:

- Superior: ECCC and USEPA (2017) noted high species diversity and high native species proportion. The diversity trend was noted as flat, although it appears to be on a slight improving trend. Lake trout (lean and siscowet) are considered the top predator in Lake Superior, with a concern that the predators may be at or near lake-wide carrying capacity. Lake Superior spring TP is quite low, but has been steady to gradually increasing in recent years (Dove and Chapra 2015; data herein).
- Lake Michigan: ECCC and USEPA (2017) noted moderate to high species diversity and moderate native species proportion. Offshore predator-prey dynamics appear unstable due to offshore lower trophic community impacts, likely created by dreissenids, declines in *Diporeia*, and lower prey biomass (Bunnell 2012). Although lake trout is singled out in the Lake Michigan salmonine objective, others such as Chinook salmon, coho salmon, rainbow trout (steelhead), and brown trout are important predators within the system.
- Lake Huron: ECCC and USEPA (2017) noted a fair species diversity and high native species proportion. Riley et al. (2013) note an increase in walleye and yellow perch biomass and production with Chinook successfully reproducing, although remaining low in numbers lake-wide.
- Lake Erie: ECCC and USEPA (2017) noted high species diversity and moderate native species proportion. Key, cool water (western basin) predators within Lake Erie include walleye while the coldwater (eastern basin) predators include lake trout and burbot (Markham and Knight 2017).
- Lake Ontario: ECCC and USEPA (2017) noted poor to low species diversity and poor native species proportion. Stewart et al. (2017) noted the need to better understand how phosphorus inputs from watersheds affect food web connections to increase Chinook production, while recognizing that declines in Chinook production may create an opportunity for positive responses from other predatory species like walleye, lake trout, and lake herring.

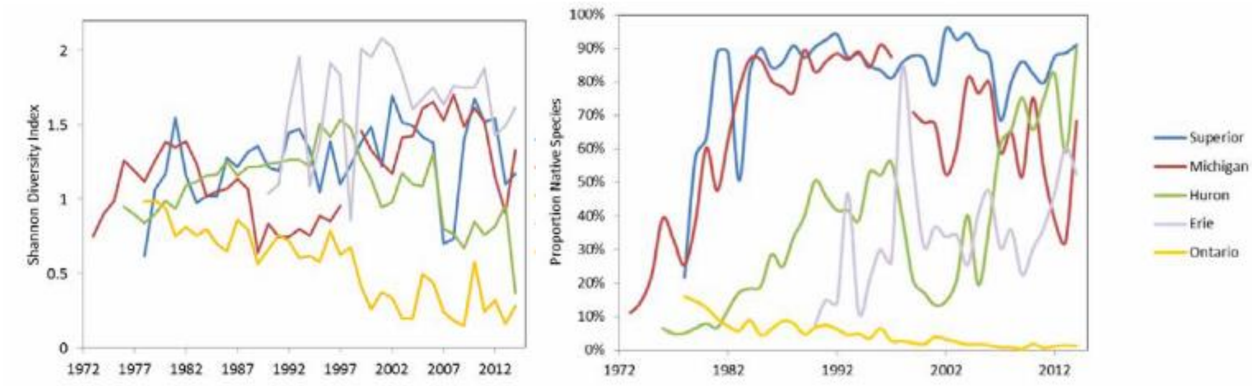

Figure 8. Overall species diversity and native species proportions as reported by lake in SOGL (2017), primarily from bottom trawl data reflecting mostly smaller prey fish.

Table 3-2. Prey and key species trends as reported by lake in ECCC and USEPA (2017).

Lake	Prey Fish – Open Water		Lake Sturgeon		Walleye		Lake Trout	
	Status	Trend	Status	Trend	Status	Trend	Status	Trend
Across Great Lakes	Fair	Undetermined	Poor	Improving	Good	Unchanging	Fair	Improving
Superior	Good	Unchanging	Poor	Improving	Fair	Unchanging	Good	Unchanging
Michigan	Fair	Deteriorating	Poor	Improving	Good	Unchanging	Poor	Improving
Huron	Fair	Undetermined	Poor	Improving	Good	Unchanging	Good	Improving
Erie	Fair	Improving	Poor	Improving	Good	Improving	Fair	Improving
Ontario	Poor	Deteriorating	Poor	Improving	Fair	Unchanging	Fair	Improving

Table 3-3. General trends for key species identified in SOGL (2017)

Lake	Prey Fish – Open Water	Lake Sturgeon	Walleye	Salmonines
Across Great Lakes	Abundance not used to assess prey fish status because successful management actions would inherently reduce prey fish biomass.	Distributed, smaller populations throughout Great Lakes. Stocking improving local populations.	Populations are variable but unchanging overall. Dependent on ecosystem health and recruitment.	Natural reproduction is variable between lakes. Some population increases observed in response to stocking and rehabilitation.
Superior	Recent fluctuations with a low overall density currently, but still able to support a healthy predator fish population. Concerns over recent declines in abundance.	Abundance is increasing through natural reproduction and limited stocking.	Variable conditions from improving to static with management actions in place.	Natural reproduction of both nearshore and offshore populations. Likely reached carrying capacity, with abundance stabilizing.
Michigan	Recent declines in prey fish abundance (primarily alewife) have led to reduced piscivore stocking.	Natural recruitment and stocking supports stable or growing local populations.	Meeting sustainable harvest goals.	Densities are stable but well below target. Some natural reproduction. Poor survival of stocked fish in northern Lake Michigan.
Huron	Recent declines in prey fish abundance have led to reduced piscivore stocking.	Natural recruitment supports growing local populations.	Recovery strong in Saginaw Bay because of alewife reductions, while depressed in Georgian Bay.	Many year classes of wild lake trout have been observed. Adult and juvenile populations abundant. Post-release survival of stocked fish is low.
Erie	NA	Natural recruitment and stocking supports stable or growing local populations.	Older cohort but improving recruitment.	Increased stocking and success of Lake Champlain strain has increased adult stocks to near rehabilitation targets. Natural reproduction not detected.
Ontario	High abundance of non-native alewife. Recent efforts have been implemented to restore native species (bloater, cisco).	Natural recruitment and stocking supports stable or growing local populations.	Meeting or exceeding performance targets with stable or improving abundances.	Abundance increased following sea lamprey control. Post-release survival has increased.

3.5 Invasive species impacts

Invasive species are among the greatest threats to freshwater ecosystems and have the capacity to rapidly change the ecosystems they invade. The abundance of non-native species can dramatically alter the structure and function of aquatic communities. Researchers have identified the Great Lakes as one of the most invaded freshwater systems across the world. At present, over 180 species have been identified as nonindigenous to the region. Table 3-4 presents a general overview of the status of invasive impacts across the Great Lakes, specifically noting changes to the dreissenid and sea lamprey communities.

Table 3-4. The state of the aquatic invasive species impacts across the Great Lakes (adapted from the State of the Great Lakes 2017 Report)

Lake	Impacts of Aquatic Invasive Species		Dreissenid mussels		Sea lamprey	
	Status	Trend	Status	Trend	Status	Trend
Across Great Lakes	Poor	Deteriorating	Poor	Deteriorating	Fair	Improving
Superior	Poor	Deteriorating	Good	Unchanging	Fair	Improving
Michigan	Poor	Deteriorating	Poor	Deteriorating	Good	Improving
Huron	Poor	Deteriorating	Poor	Deteriorating	Good	Improving
Erie	Poor	Deteriorating	Fair	Improving	Fair	Improving
Ontario	Poor	Deteriorating	Poor	Deteriorating	Good	Unchanging
Lake St. Clair, Detroit and St. Clair Rivers	Poor	Deteriorating	NA	NA	NA	NA

3.5.1 Dreissenid mussels

The dreissenid mussel invasion (Figure 9), first by zebra mussels (*Dreissena polymorpha*) and then by quagga mussels (*Dreissena rostriformis bugensis*), has caused major changes to nutrient concentrations and distributions in the waters and sediments of the Great Lakes. Zebra mussels were first detected in Lake Erie in the late 1980s, but eventually were able to spread and become established in all of the Great Lakes, except for offshore areas of Lake Superior (Dove and Chapra 2015). Dreissenid mussels spread rapidly, occur at high densities, and filter large volumes of water. They have been known to reduce phytoplankton biomass and primary production, increase water clarity and light penetration, increase phosphorus bioavailability, and increase benthic primary production (Althouse et al. 2014). They also tend to modify the cycling of nutrients, alter food webs, and cause cyanobacterial blooms and the growth of nuisance benthic algae (Cha et al. 2011). In general, mussels have dramatically changed ecosystems and driven oligotrophication in the Great Lakes where they have become strongly established (Barbiero et al. 2012). Some parts of Lake Superior have also shown evidence of recent oligotrophication despite the relative lack of mussels, suggesting that variations in nutrient loading may still be playing an important role basin-wide. Mussel abundance varies widely from lake to lake and within individual lakes depending on substrate, food supply, water temperature, and other factors. This variation, and the relative lack of high-resolution data on mussel abundance and change through time in many lake basins have important implications for possible divergence of mussel-related effects on nutrient fate and transfer among and within lakes. Such lake-wide and basin-wide variability is an important qualifier of any general statements about the role of mussels in the system.

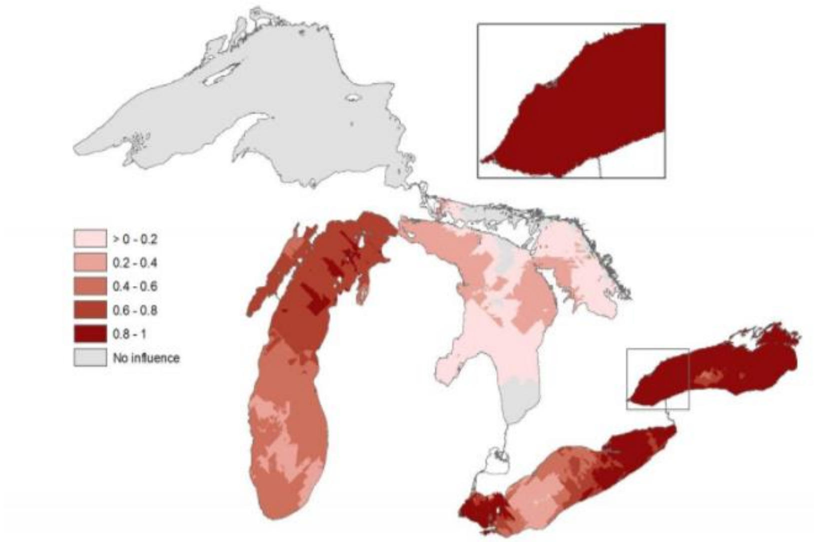

Figure 9. The spatial distribution of zebra and quagga mussels in the Laurentian Great Lakes normalized to a scale from zero to one (from GLEAM: Invasive mussels)

It has been hypothesized, with some support from recent studies, that invasive mussels have caused a nearshore phosphorus shunt in multiple lakes (Hecky et al. 2004). This suggests that mussels trap and retain phosphorus in nearshore areas and especially around tributaries, thereby increasing benthic nutrient levels in nearshore areas. Thus, as they are increasing water transparency and converting particulate phosphorus to soluble reactive phosphorus, they are also causing declines in offshore primary production and nutrient concentrations (Hecky et al. 2004; Cha et al. 2011; Stow et al. 2014; deBarros 2016). Data supporting this hypothesis suggest that mussels have caused a substantial increase in nearshore phosphorus retention (from 46% to 70%) and the reappearance of cyanobacterial blooms and nuisance algal growth in Saginaw Bay, Lake Huron (Cha et al. 2011). In Lake Ontario and Lake Michigan, mussels have also increased nearshore water clarity and led to the reemergence of nuisance *Cladophora* (deBarros 2016, Auer et al. 2010). The net long-term impact of nearshore changes on offshore nutrient delivery and primary productivity is an area of active research in the Great Lakes.

While there is a current lack of consistent lake-wide dreissenid benthic macroinvertebrate density estimates, there have been some quantitative and qualitative updates in recent years.

- Lake Superior: Dreissenid densities continue to be minimal in Lake Superior (ECCC & USEPA 2017).
- Lake Michigan: Mussel biomass appeared to peak at Lake Michigan mid-depth sites (30-90 m) in 2008 and have declined in the time since. At > 90 m deep sites, density and biomass have continued to increase, but are dominated by small mussels (Baldridge & Nalepa 2015; Elgin et al. 2017). On the other hand, the State of the Great Lakes 2017 report suggests that densities have shown a slight decline at > 90 m deep sites since 2012, but that biomass is stable (ECCC & USEPA 2017). A lake-wide survey for Lake Michigan was conducted in 2015, but the results have not been published.
- Lake Huron: In Lake Huron, between 2007 and 2012, dreissenid density stabilized at 31-90 m, but continued to increase at >90 m (ECCC & USEPA 2017).

- Lake Erie: Recent studies from Lake Erie show that densities have slightly increased in all basins since 2010. Over the long-term, densities in the central and eastern basin are significantly reduced, while densities in the western basin continue to climb (Karatayev et al. 2014; Karatayev et al. 2017).
- Lake Ontario: In Lake Ontario, dreissenid density peaked at the 31-90 m depth interval in 2003, yet continues to increase at > 90 m based on 2013 data. It should also be noted that while density has decreased, biomass has increased at 31-90 m in recent years (ECCC & USEPA 2017).

3.5.2 Round goby

The round goby is one of the most successful invaders in the Great lakes (Figure 10), reaching densities of 1-14 individuals per square meter in some areas, with maximum densities over 130 per square meter. The bottom-dwelling fish were first discovered in the St. Clair River in 1990, and by 1998, they had invaded all five Great Lakes (Charlebois et al. 1997; Walsh et al. 2007). While most studies have focused on the near-shore environment of the Great lakes where they are often most concentrated, researchers have found round gobies in over 300 feet (92 meters) of water.

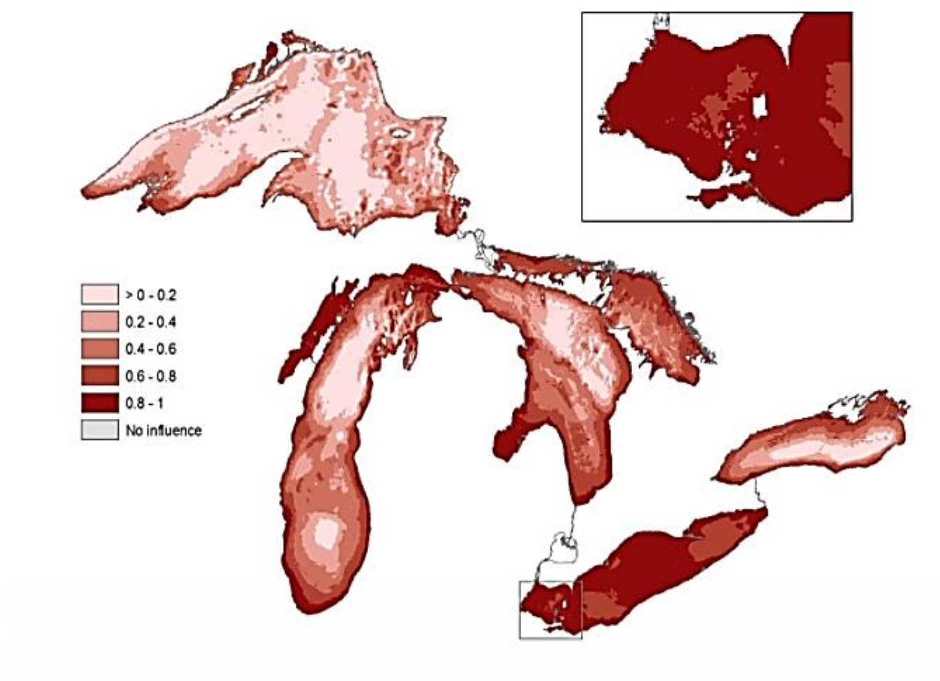

Figure 10. The spatial distribution of round goby in the Laurentian Great Lakes normalized on a scale of zero to one (from GLEAM: Round Goby).

Round gobies can compete with native fish for resources (e.g., sculpins and darters) and can significantly alter food web energy pathways, reproduction, and growth of native fish. Round gobies can also prey heavily on zebra and quagga mussels, and while they cannot eliminate the mussels completely, they can reduce mussel numbers to some extent and alter size distribution by selectively feeding on smaller mussels. Additionally, they can reduce the population of other native invertebrates through predation. Round gobies can also have significant effects on the diet of native piscivorous fishes (Crane et al. 2015, Carlsson et al. 2009). For example, Johnson et al. (2005) observed that round gobies constituted 75% of the diet of smallmouth bass (*Micropterus dolomieu*) and burbot (*Lota lota*), 30% of that of yellow perch (*Perca flavescens*) and 10% of that for walleye (*Sander vitreus*) in the central basin of Lake Erie. With respect to a shifting diet, round goby can affect the growth, fitness and mortality of fishes.

3.5.3 Others

Although invasive mussels and round gobies receive a great deal of attention, there are several other potentially harmful invaders. For example, the sea lamprey, a primitive jawless fish, parasitizes a number of economically important fish such as the lake trout, non-native salmon, lake whitefish, lake herring, rainbow trout, burbot and walleye. Other species include the rusty crayfish, and spiny water flea (*Bythotrephes longimanus*; as discussed above). Additionally there is a great deal of recent attention of the potential invasion of four Asian carp species (bighead, silver, black, and grass). If these fish establish themselves within the Great Lakes, there is a high likelihood they will outcompete some native species and threaten to have a significant ecological impact, although not all native species may be negatively impacted (Zhang et al. 2016a and 2016b, Reed 2017).

3.6 Climate impacts

Along with other stressors, changing climate is likely influencing nutrient delivery (Stow et al. 2015) and offshore fish productivity in the Great Lakes in a number of important ways. A recent review by Collingsworth et al. (2017) concluded that warming lake temperatures (Figure 11) will also produce fish habitat that is characterized by less ice cover (duration and area), and longer and more widespread stratification accompanied by more prevalent bottom hypoxia. Warm water fish were projected to have prolonged optimal growth, but impacts on specific life stages were anticipated to be more complex. The conclusion that climate change may intensify the negative impacts of eutrophication was also the finding of a national study of harmful algal blooms (Chapra et al. 2017).

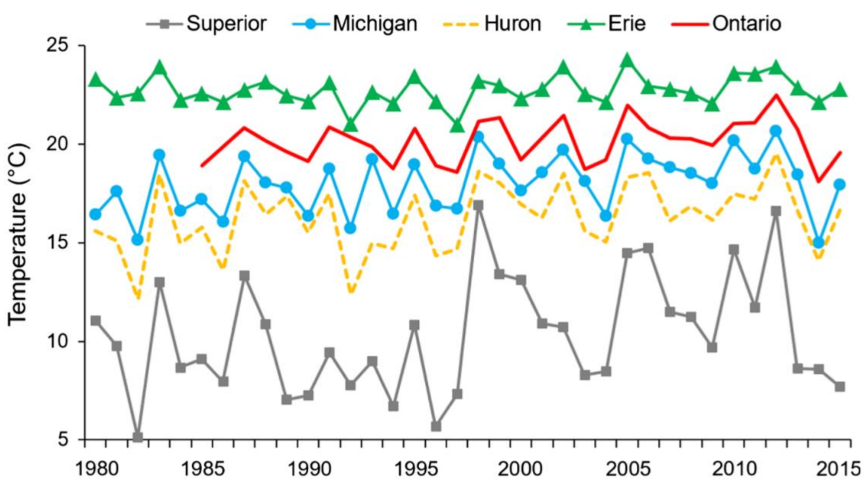

Figure 11. Mean summer (July–September) water temperatures (C) over time for each of the Great Lakes showing a very gradual warming trend, with a more pronounced trend for Lake Superior (from Collingsworth et al. 2017, based on data from NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/) and Sharma et al. (2015)).

3.7 Summary

A critical goal for fishery management within the region is to "stop invasions of aquatic species" (GLFC 2017). Invasive species impacts often cause changes in the ecosystem that can be rapid and difficult to understand and often (but not always) negatively impact desired species (Stewart et al. 2017). For example, the invasion of dreissenid mussels has resulted in increased water clarity and changed the way nutrients are cycled in the nearshore and offshore zones with additional impacts of the food web caused by species like round goby and spiny water flea (Riley 2013). The shifting equilibrium brought about by these species continues to challenge managers trying to isolate and understand impacts of watershed-based inputs of nutrients on offshore aquatic communities.

4 Data compilation

The following data compilation includes an update from the Bunnell et al. (2014) paper. This update includes plotting the relationships between total phosphorus and fishery response (relative biomass and density) for both the predatory fish and prey fish communities across all of the Great Lakes. Additionally, it updates the relationships between total phosphorus, chlorophyll *a*, Secchi depth, and zooplankton. This includes an evaluation of the strength of these relationships by looking at statistical relationships in time and space across habitat types within the Great Lakes. Additional published data from Environment and Climate Change Canada are included when appropriate to add further explanatory power.

4.1 Background

The offshore TP concentrations and water transparency in Lake Michigan and Lake Huron are now similar to those of Lake Superior (Barbiero et al. 2012), and TP declines and transparency increases have also been observed in Lake Ontario (Richardson et al. 2012). There is concern that these declining TP concentrations may be reducing pelagic and total offshore biological productivity and imposing dramatic food web changes, if not collapse, especially on Lake Huron and Lake Michigan.

In 2014, Bunnell et al. provided a thorough evaluation of the current trajectory with respect to the trophic status of the Great Lakes. The paper described the latest trends in phosphorus loads, total phosphorus, chlorophyll a, Secchi disc depth, zooplankton, benthic macroinvertebrates, prey fish, and predatory fish since the 1970s (up to 2011) across all Great Lakes to determine potential drivers of food web alterations. While the results varied by lake, in general there was a reduction in phytoplankton, native invertebrates, and prey fish, with an increase in water clarity since 1998. Evidence for bottom-up regulation was strongest in Lake Huron followed by Lake Michigan, but was present in at least one trophic interaction across all lakes.

4.2 Data sources

We began by reviewing the sources and types of data that were plotted by Bunnell et al. (2014). Through a review of the literature, evaluating sources of data from Bunnell et al. (2014) and communications with David Bunnell, we determined a list of potential data providers to obtain recent (since ~2010) total phosphorus, prey fish biomass, and piscivore fish biomass data for all five Great Lakes. These experts were contacted and relevant data were requested. The “Data Sources” tab in the compiled data workbook summarizes who was contacted and the data source for each lake and parameter. The following people are acknowledged for their assistance with acquiring updated data: Alice Dove (ECCC), Brian Breidert (Indiana DNR), Brian Lantry (USGS), Brian Weidel (USGS), David Bunnell (USGS), David Fielder (Michigan DNR), James Bence (Michigan State University), Jeremy Holden (OMNRF), Ji He (Michigan DNR), Jory Jonas (Michigan DNR), Mark Vinson (USGS), Michael Connerton (NYSDEC), Nicholas Legler (Wisconsin DNR), Owen Gorman (USGS), Stephen Riley (USGS), Stuart Ludsin (Ohio State University), Ted Treska (USFWS), and Travis Brenden (Michigan State University).

4.3 Methods and challenges

We compiled and plotted the data based on data type and lake. The original data from Bunnell et al. (2014) and the new data were tabulated and plotted. Spring total phosphorus values are tabulated and plotted for all lakes on the corresponding worksheet ("Spring TP-All Lakes" tab), and replotted (corresponding axis on right side of plots) along with fish biomass to assist in the evaluation of the data on the following worksheets. Data were plotted from 1998-present to observe the time since the dreissenid mussel invasion of most lakes. The dotted, vertical black line in each plot corresponds to the last year of data shown in Bunnell et al. (2014) figures.

Whenever possible, updated data included the same parameters and were presented in the same format as Bunnell et al. (2014) plots. Exceptions are described in the overview of each plot. Data were plotted so that the entire time series was compiled using the same methods and data sources, allowing for accurate analysis of trends. Note that there are some discrepancies between the new data and that from Bunnell et al. (2014). This is either due to different parameters (which are noted) or updates to the models that have been used to estimate biomass from sampling data (i.e., Lake Michigan piscivore biomass or Lake Erie walleye abundance models). Lake Erie was unique in that we analyzed the data within each of its three basins (where that was possible), because of their strong differences in morphometry and primary productivity (Ludsin et al. 2001).

4.4 Results

4.4.1 Water quality parameters

4.4.1.a TP

Total phosphorus data from 1998-2010 are from Bunnell et al. (2014), while 2011-2016 data were accessed via the USEPA Central Data Exchange site (https://cdx.epa.gov). For each lake (Figure 12), data represent the mean upper water column (<12 m) total phosphorus concentrations (μg/L) measured across all offshore sites (>30 m, except for western and central basins of Lake Erie). Reporting for Lake Erie is separated by basin (Figure 13).

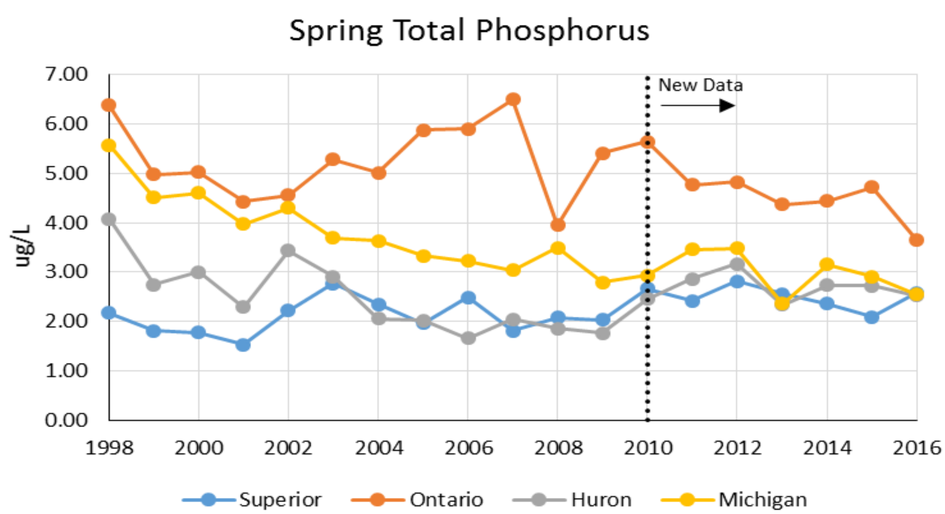

Figure 12. Spring total phosphorus concentrations (USEPA).

While there was a declining trend evident for spring TP in Lake Huron and Lake Michigan from 1998-2010, the new data shown here (2010-2016, Figure 12) suggest that the phosphorus concentrations have leveled out. Ontario was variable from 1998-2010 but since 2010, there appears to be a decreasing trend in total phosphorus. Superior has been mostly stable over the entire time period but there does appear to be a slight increase from 1998 through 2016. New data do confirm that the three upper lakes, Superior, Huron, and Michigan are now very similar with respect to spring TP. Updating earlier models (Chapra 1977) using updated loading estimates (e.g., Maccoux et al. 2016) would allow direct comparison of offshore concentrations with changing loads over time.

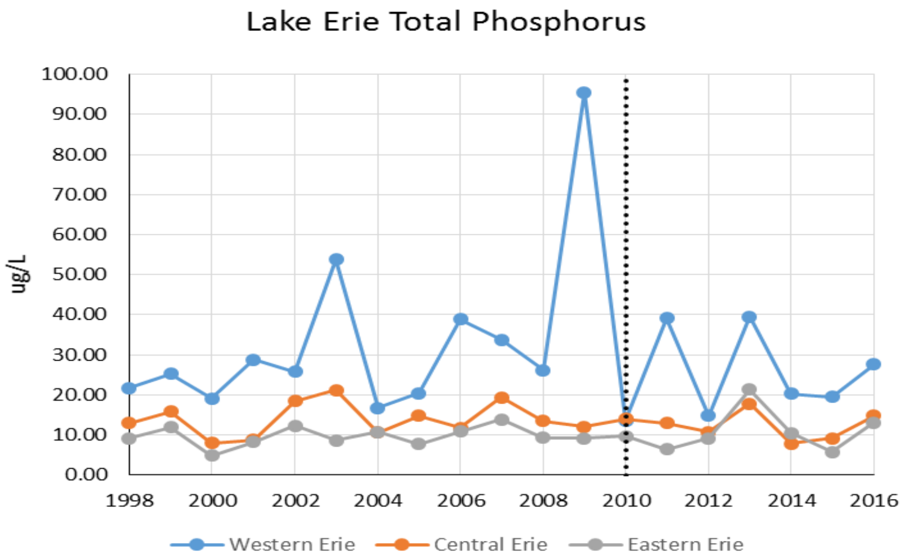

Figure 13. Spring total phosphorus concentrations are from USEPA GLNPO surveys across Lake Erie.

Lake Erie TP levels in the western basin are high and variable, likely due to the influence of dynamic river plumes and wind-induced resuspension of sediments during spring sampling. The central and eastern basin have remained relatively consistent over time and are less variable. There is limited evidence to suggest that Erie is experiencing reduced offshore phosphorus levels, and the western lake basin in particular remains eutrophic (Figure 1).

Canadian spring total phosphorus data were provided by Alice Dove (Environment and Climate Change Canada). Lake Erie data are a combination of research and monitoring cruises, whereas other lakes are mainly monitoring data. For each lake, data represent the mean surface (1 m) total phosphorus concentration (µg/L) measured across all offshore sites. Data from 1998-2012 were analyzed using acid persulfate digestion followed by automated colorimetric molybdate stannous chloride method. Data from 2013-2015 were analyzed using an acidic persulphate oxidation, continuous flow analyzer, ascorbic acid, molybdenum blue, colorimetric method (NLET Method 01-1191).

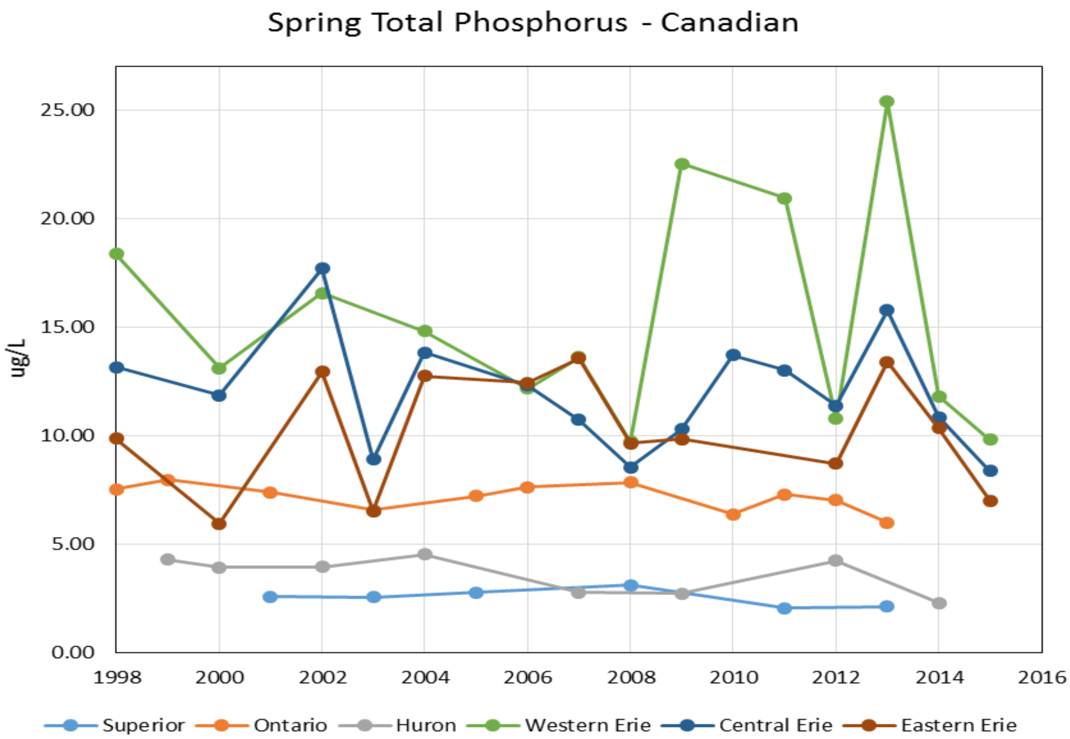

Figure 14. Spring total phosphorus concentrations are from Environment and Climate Change Canada surveys.

Canadian total phosphorus data shown here (Figure 14, note different axes from previous figures) and are compared to the USEPA data in more detail later in this section. Lake Huron showed a decreasing trend from 1999 through 2009, but has mostly stabilized in recent years. Superior appears stable over the course of 2001 through 2013 and does not appear to be increasing. Canadian data show variable phosphorus over time in all three basins of Lake Erie, but most pronounced in the western basin (Figure 14), which is strongly influenced by periodic sediment resuspension events.

4.4.1.b Chlorophyll a

Average May chlorophyll a (ug/L) data, were estimated using remote sensing data and the Great Lakes Fit algorithm (Lesht et al. 2013). Remote sensing data were drawn from 5 x 5 km squares centered on USEPA GLNPO open-lake sampling stations, although time offsets between USEPA water sampling and satellite images mean that the data are not directly analogous. Estimates from 1998-2007 utilized SeaWiFS imagery whereas 2008-2016 used MODIS imagery. Information for this work was provided in part by USEPA GLNPO's Monitoring Program, compiled by Rick Barbiero.

Chlorophyll a data, was mostly variable across the three Erie basins, with a slight decrease in the western basin (Figure 15). Superior was stable over time, whereas levels Huron and Michigan decreased from 1998 through 2016. The Lake Ontario chlorophyll a data appear to decrease from 1998 through 2010 but are variable from 2010-2016 with no evident trends.

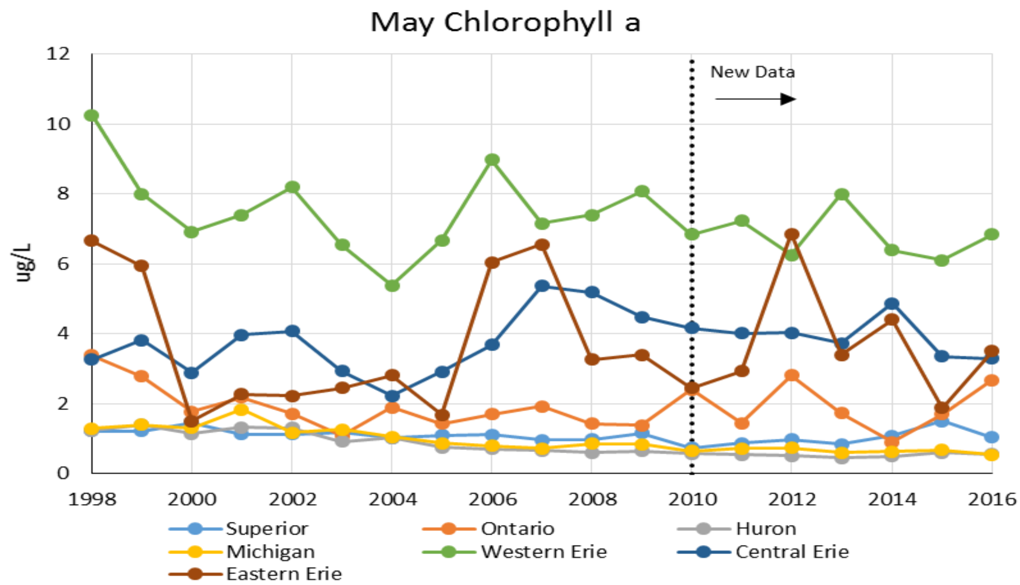

Figure 15. Spring chlorophyll a data estimated using remote sensing data and the Great Lakes Fit algorithm.

Canadian summer chlorophyll a data for offshore sites were provided by Alice Dove (Environment and Climate Change Canada) and are presented in Figure 16. Lake Erie data are from a combination of research and monitoring cruise samples, whereas other lakes are mainly monitoring data. For each lake, data represent the mean integrated surface (1 m) chlorophyll a concentration (µg/L) measured across all offshore sites.

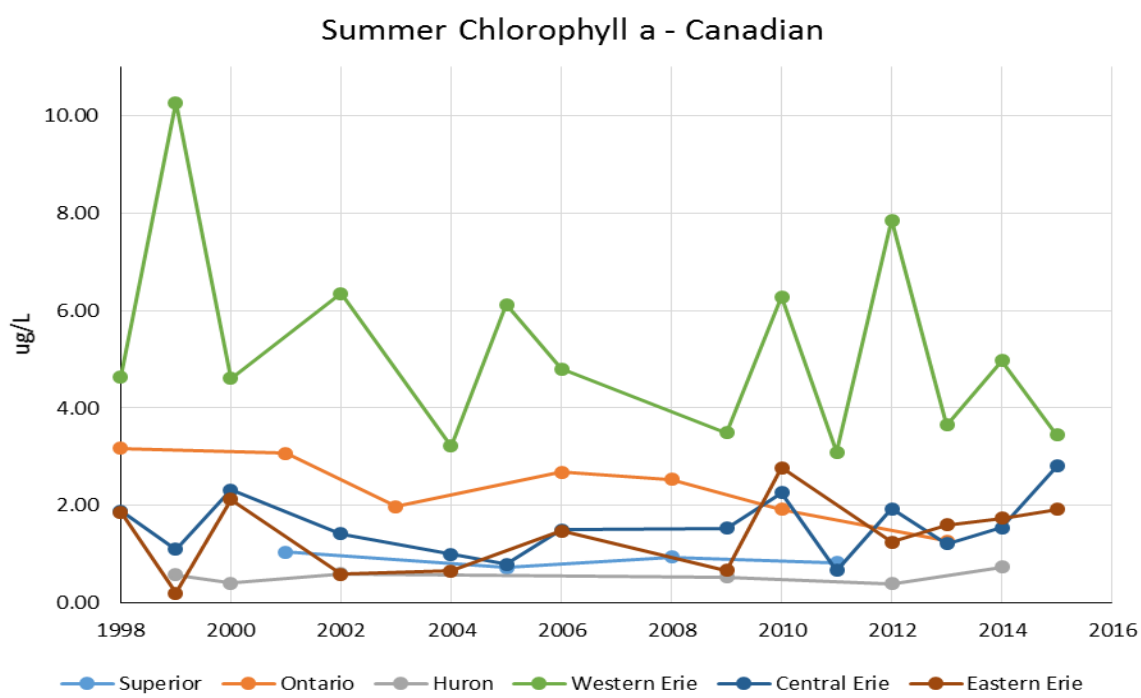

Figure 16. Summer offshore chlorophyll a data, from Environment and Climate Change Canada surveys.

The Ontario data showed a gradual decrease in chlorophyll a from 1998 through 2013. This suggests that the lake is moving towards greater oligotrophy. There was a variable but decreasing trend in the western basin of Lake Erie, while no trend was evident in the other basins. Superior remained stable over time, with no evident trends.

4.4.1.c Secchi depth

Spring Secchi disc depth (m) measurements were averaged across all USEPA GLNPO open-lake stations sampled during the day (Figure 17). Information for this work was provided in part by USEPA GLNPO's Monitoring Program, with data compiled by Rick Barbiero.

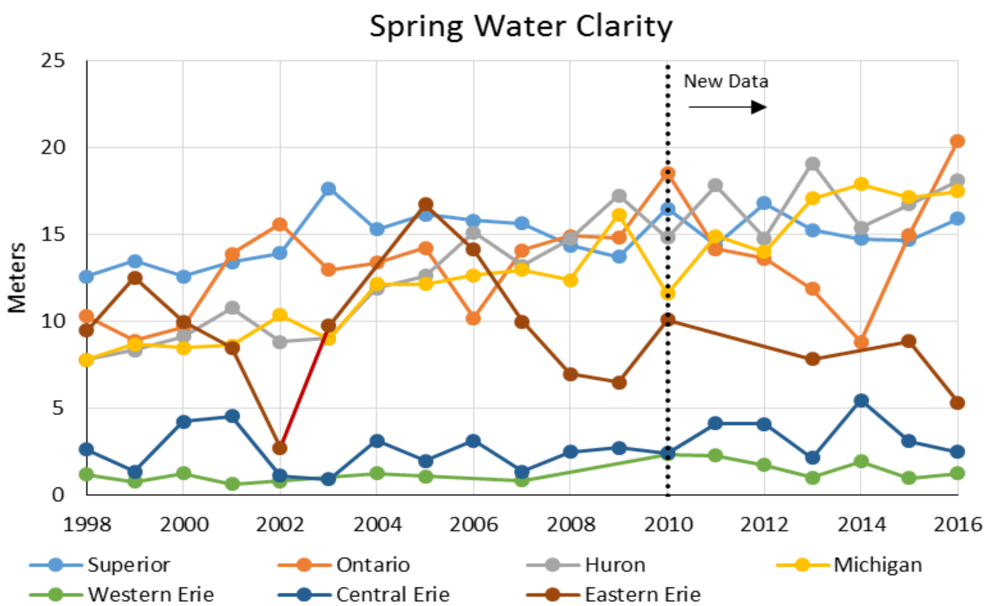

Figure 17. Spring Secchi disc depth (m) measurements, averaged across all USEPA GLNPO open-lake stations

Water clarity (measured by the depth to which the Secchi disc is no longer visible) increased in Michigan and Huron from 1998 through 2016. Ontario showed an increasing trend from 1998 through 2010 but has been mostly variable since 2010. The eastern basin was variable over time whereas the western and central basins remain stable. Visibility in the western basin was consistently the lowest among the three basins and other lakes over time. The central basin had relatively low clarity compared to the eastern basin which was more similar to the other lakes. Superior clarity increased in the late 90s, early 2000's but has remained stable since.

Canadian summer Secchi disc depth data were provided by Alice Dove (ECCC) and are presented in Figure 18 for comparison. Lake Erie data are a combination of research and monitoring cruises, whereas other lakes are mainly monitoring data. For each lake, data represent the mean Secchi disc depth (m) measured across all offshore sites. Note that there are no data for western Lake Erie for 2015 because sampling occurred after dark, and that Secchi data were collected in the spring in the USEPA program, whereas Canadian data were collected in the summer.

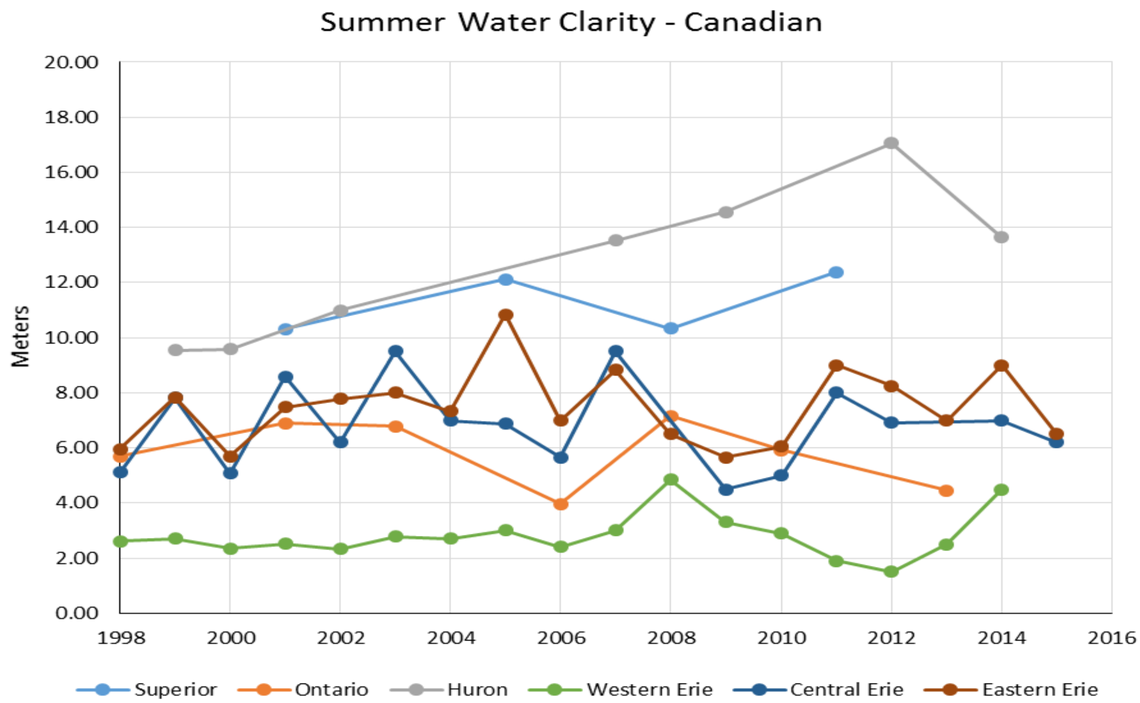

Figure 18. Canadian summer Secchi disc depth data (ECCC; no Lake Michigan data).

Overall, the trends in the Canadian summer data were fairly consistent with those of the U.S. spring data, except for Lake Ontario, where summer Secchi depth was relatively stable from 1998 through 2013 in Canadian data, but spring depths were increasing in U.S. data. Unlike the U.S. data, the eastern basin and central basin of Lake Erie had similar clarity over time; the eastern basin had consistently greater Secchi depths in U.S. data.

4.4.1.d Zooplankton

Total areal crustacean zooplankton biomass (g DW/m^2) data, averaged by lake (basin for Erie) from USEPA GLNPO open-lake stations are presented in Figure 19. Data were collected by 153 µm mesh nets from the shallower of 100 m or bottom minus 2 m (bottom minus 1 m in Lake Erie) and drawn from zoo database v. beta 2.70. Data are limited to cladocerans, cyclopoids, and calanoids, and exclude rotifers, veligers, and nauplii. Information for this work was provided in part by USEPA GLNPO's Monitoring Program, compiled by Rick Barbiero. Note that biomass formulas and flow meter data have been updated in recent years, resulting in different values as compared to Bunnell et al. (2014).

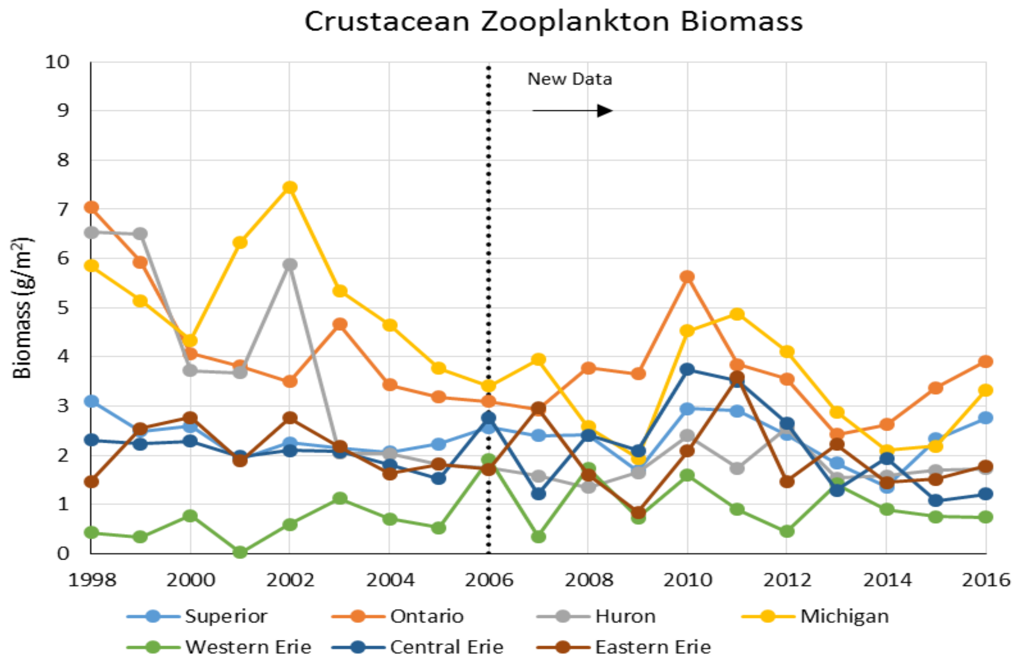

Figure 19. Total areal crustacean zooplankton biomass (g DW/m²) data, averaged by lake (basin for Erie) from USEPA GLNPO open-lake stations.

Zooplankton biomass decreased from 1998 through 2016 in Huron and Michigan. A decrease was also observed in Ontario where levels dropped sharply from 1998 through 2006 but may have stabilized since this period. Superior remained stable over time, consistent with the overall lake trends. While variable, there may be an overall increase in zooplankton biomass in the western basin of Lake Erie.

4.4.2 Lake-by-lake fish data

4.4.2.a Lake Superior

Lake Superior prey fish nearshore biomass estimates were sampled by the U.S. Geological Survey and compiled by Mark Vinson and are presented in Figure 20. Species included rainbow smelt, cisco, bloater, and sculpin. Estimates were based on May/June nearshore bottom trawl samples at up to 82 sites per year that began around 16 m and ended around 54 m depths (Vinson et al. 2017).

The general trend across the Superior prey fish (Figure 20) remained similar to what Bunnell et al. (2014) observed. There was a significant decrease in prey fish biomass from 1998 through 2010, with an apparent steadying at the lower level since then. Despite the lower levels, Lake Superior is considered healthy due to it having the highest proportion of native prey fish across the Great Lakes.

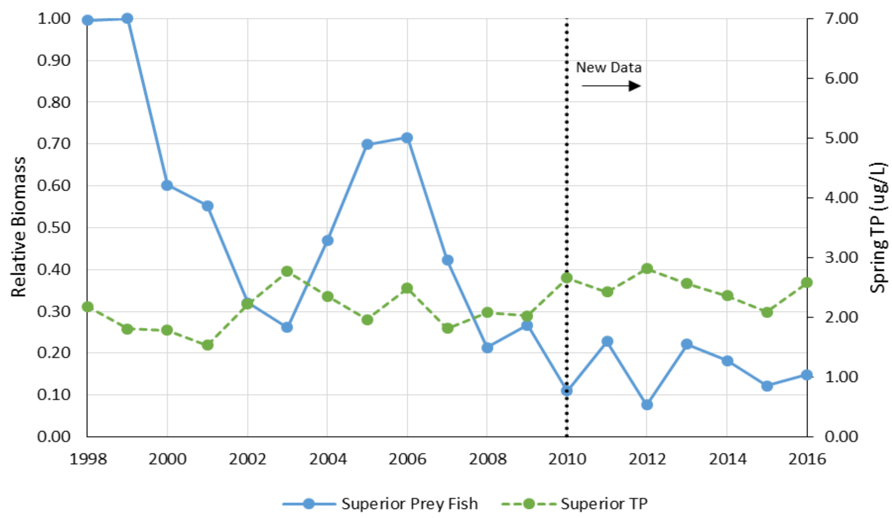

Figure 20. Lake Superior prey fish nearshore biomass estimates plotted against total phosphorus concentrations.

Lake Superior lean lake trout catch per unit effort (catch per km of net) data from 1998-2016 were derived from sampling by eight agencies around the lake, compiled by Ted Treska, and are presented in Figure 21. Data were based on May gillnet collections, with the geometric mean catch per unit effort of lake trout (>532 mm total length) being scaled by available lake trout habitat in the area. Calculations were based on work by Julie Nieland and Michael Hansen to incorporate net saturation adjustments and other variables (Bunnell et al. 2014; Ted Treska, personal communication, 10/26/17). In general, the fluctuating but generally flat lake trout pattern appeared to be consistent with Bunnel et al. (2014) findings.

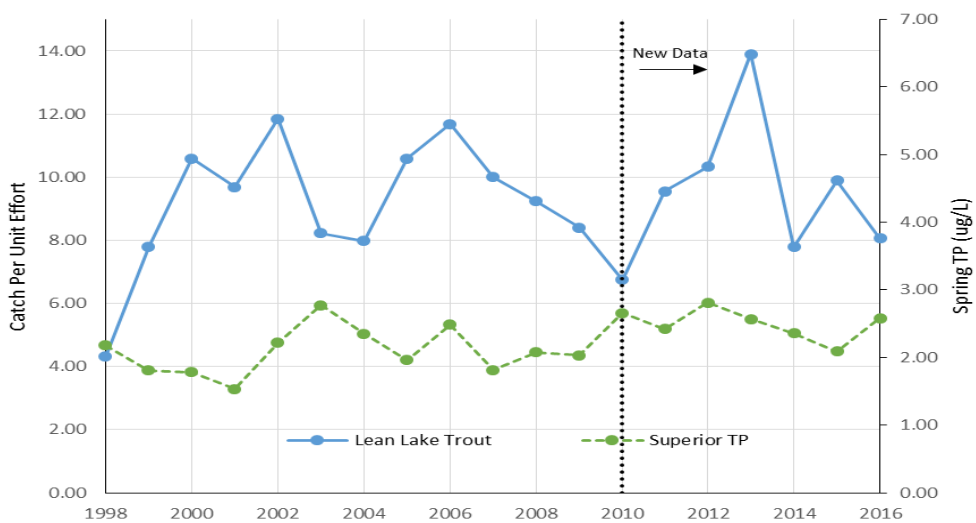

Figure 21. Lake Superior lean lake trout catch per unit effort (catch per km of net) data from 1998-2016.

Nearshore lake-wide mean biomass estimates for lake trout (lean, siscowet, and hatchery; Figure 22) in Lake Superior were estimated from bottom trawls (Vinson et al. 2017). The method varied from the Bunnell et al. (2014) summary which plotted catch per unit effort of lean lake trout (>532 mm total length) from gillnet surveys. However, a comparison between the two datasets showed minimal differences (2% average percent difference, 12% maximum).

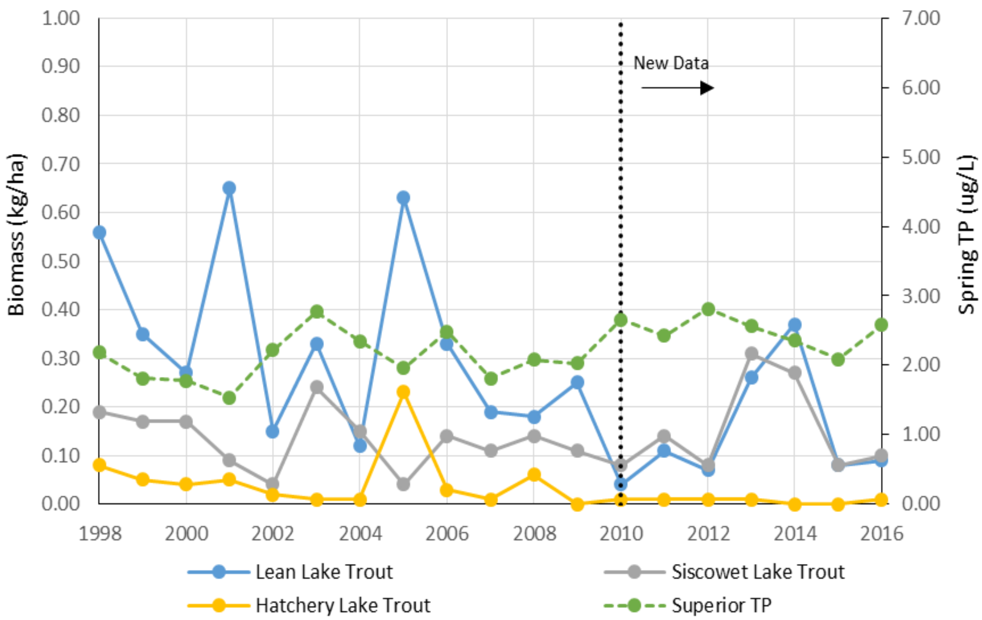

Figure 22. Lake Superior nearshore lake-wide mean biomass estimates for lake trout (lean, siscowet, and hatchery).

While the relative biomass of siscowet lake trout remained similar across time, the lean lake trout biomass, although highly variable, has decreased over time.

4.4.2.b Lake Michigan

Lake Michigan prey fish relative biomass estimates were compiled by David Bunnell, U.S. Geological Survey and are presented in Figure 23. Estimates were based on bottom trawl surveys and included alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, round goby, and ninespine stickleback (David Bunnell, personal communication, 8/22/17). The relative biomass in Michigan prey fish has significantly decreased over time. As shown in Figure 23, this decrease was consistent with a decrease in total phosphorus over the same time period, although the decline is greater than expected based on phosphorus decrease alone suggesting the importance of predation as well (Tsehaye et al. 2014). Based on the recent data (2010-2016), there has been no recovery in the prey fish population.

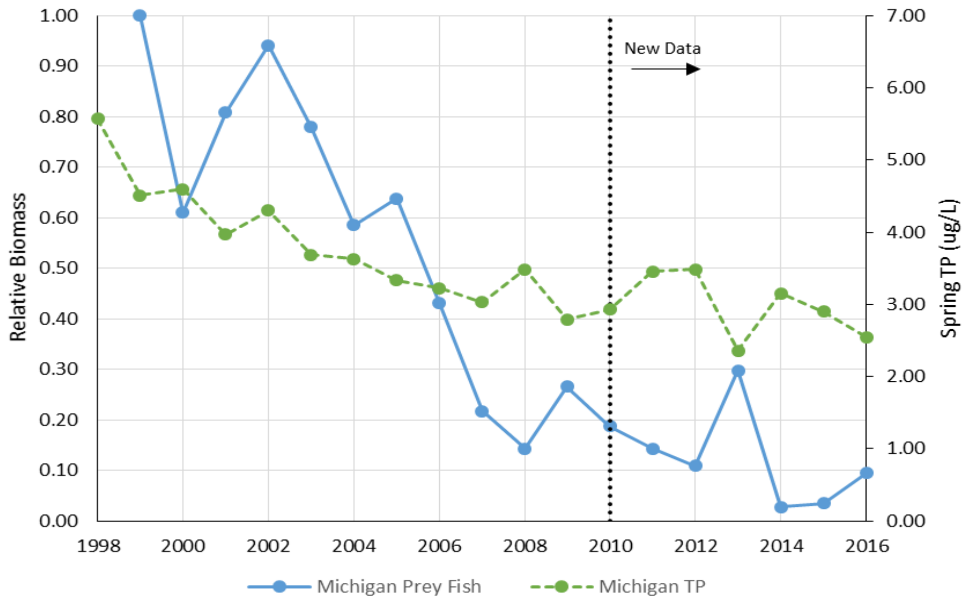

Figure 23. Lake Michigan prey fish relative biomass estimates compared with spring TP.

Lake Michigan piscivore biomass (Figure 24) includes estimates from 2016 statistical catch at age models for lake trout, Chinook salmon, coho salmon, brown trout, and steelhead trout. These data were compiled from Nicholas Legler (Wisconsin DNR), Brian Breidert (Indiana DNR), and Jory Jonas (Michigan DNR). Estimates for lake trout, coho salmon, brown trout, and steelhead trout should be used with caution due to assumptions in the current models (Nicholas Legler, personal communication, 10/19/17). Note the differences between the biomass estimates from the 2016 model (blue) and the biomass estimates from Bunnell et al. (2014) for 1998-2010 (yellow).

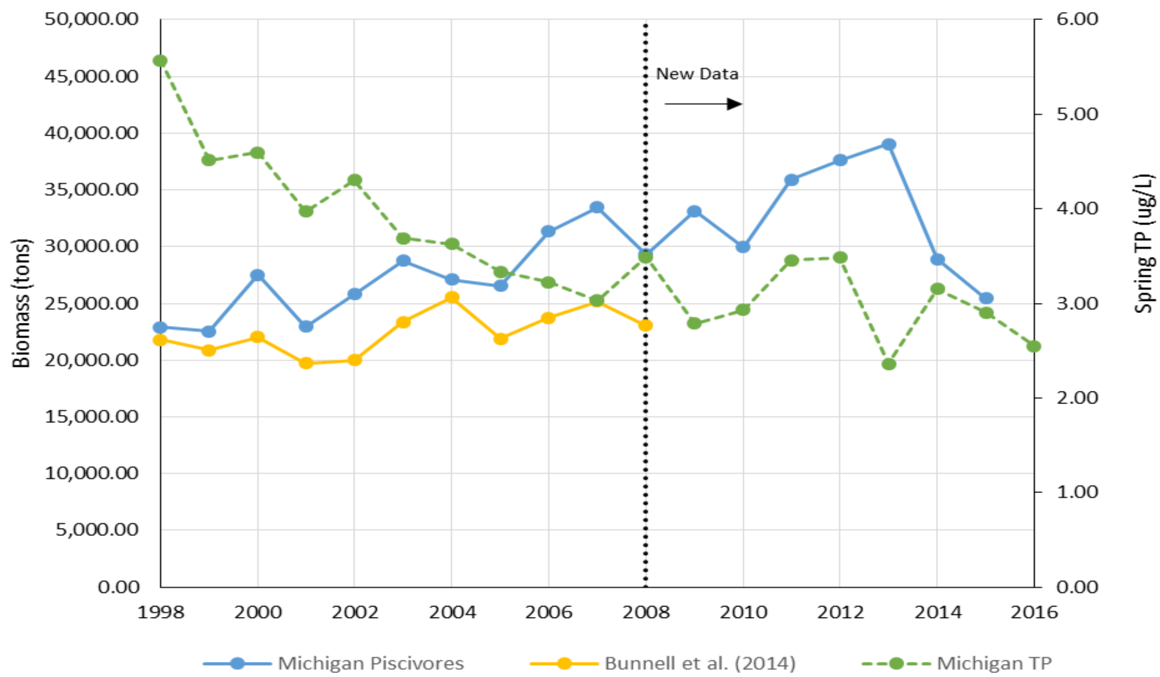

Figure 24. Lake Michigan piscivore biomass includes estimates from 2016 statistical catch at age models for lake trout, Chinook salmon, coho salmon, brown trout, and steelhead trout.

While the data are estimates, it appears Lake Michigan piscivore biomass increased from 1998 through 2013. This trend was more evident in the current dataset than that of Bunnell et al. (2014). While expected year to year variability is high, the last two years of data (2014-2015) showed a significant reduction in biomass, more consistent with the early-mid 2000s.

4.4.2.c Lake Huron

Lake Huron prey fish (Figure 25) were sampled by the USGS and compiled by Stephen Riley. Relative biomass estimates were calculated from estimates of total prey fish biomass, based on autumn bottom trawl samples. Species include rainbow smelt, bloater, deepwater sculpin, slimy sculpin, ninespine stickleback, round goby, alewife, trout-perch, and spottail shiner. Data are lacking for 1998, 2000, and 2008. Note that recent estimates may be biased due to the relative inability of the trawl survey to sample round gobies (Stephen Riley, personal communication, 8/22/17). See Riley et al. (2017) for more information. While prey fish abundance decreased over the 2000s, they appear to have stabilized at the lower levels since 2010. The anomalous peak in prey fish abundance since 2010 was reportedly driven by an excess of bloater in mid-water trawls during that survey period (USGS 2017), and is not considered representative based on Work Group discussions.

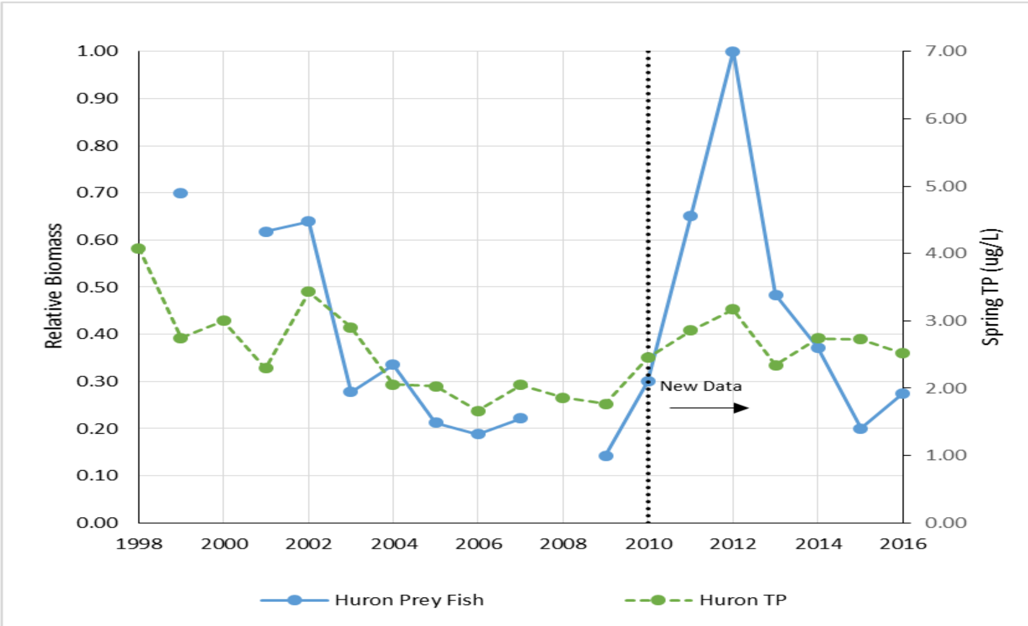

Figure 25. Lake Huron main basin prey fish plotted with TP.

Lake Huron piscivore (lake trout and Chinook salmon) biomass estimates (Figure 26) were compiled from multiple sources. Bunnell et al. (2014) provided estimates for 1998-2009, which were derived from an age-1+ statistical-catch-at-age (SCAA) model developed by Ji He and Travis Brenden. Updated estimates were provided for age-1+ Chinook salmon (James Bence, personal communication, 11/3/17) and age-3+ lake trout (hatchery and wild; Ji He, personal communication, 10/24/17) from the most up-to-date assessment models. Prey fish, piscivores, and TP all show a moderate to large peak around 2012.

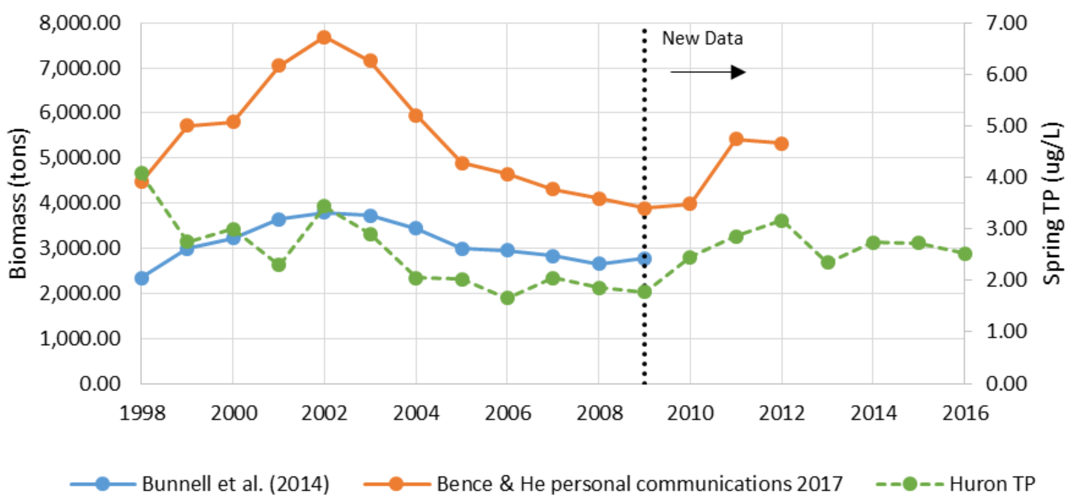

Figure 26. Lake Huron main basin piscivore (lake trout and Chinook salmon) biomass estimates.

Total biomass estimates for age 2-13+ walleyes in Lake Huron (excluding North Channel, Georgian Bay, and Ontario waters of the northern main basin) were compiled by David Fielder, Michigan DNR (Figure 27). Juvenile walleyes and those migrating from Lake Erie were not included (David Fielder, personal communication, 10/16/17). High walleye biomass in 2006-2008 was not sustained or repeated in the new data.

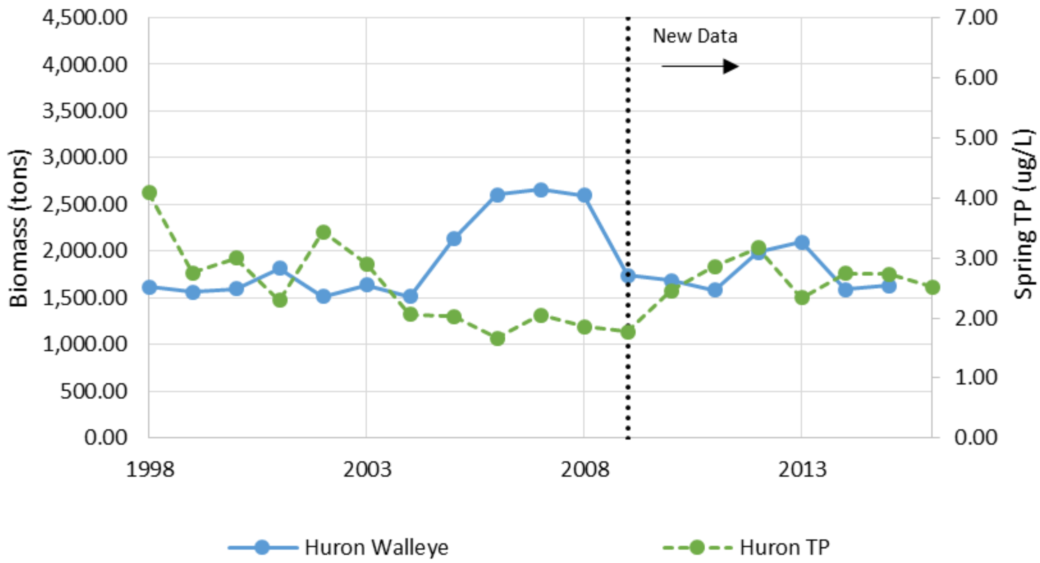

Figure 27. Total biomass estimates for age 2-13+ walleyes in Lake Huron (excluding North Channel, Georgian Bay, and Ontario waters of the northern main basin),

4.4.2.d Lake Erie

The relative biomass of prey fish in western Lake Erie was estimated (in tons; Figure 28) from Figure 2.4.3 in the Report of the Lake Erie Forage Task Group. These estimates were based on August interagency trawling program data (FTG 2016).

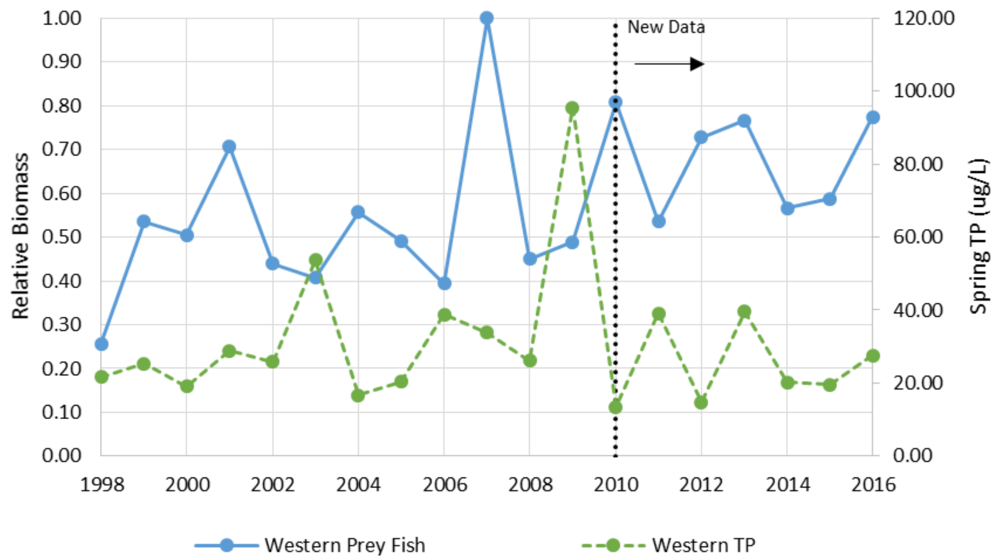

Figure 28. Relative biomass of prey fish in western Lake Erie.

It appears the prey fish are variable but increasing with time from 1998-2010, but new results from 2010-2016 are mostly consistent at the higher relative biomass.

Central Lake Erie prey fish relative density were digitized from the mean density of prey fish (number per hectare) in Ohio waters of the central basin (Figure 2.3.2 in the Report of the Lake Erie Forage Task Group) and are presented in Figure 29. Biomass estimates were not available for the central basin of Lake Erie. These data were based on bottom trawl surveys, with 48 trawl tows conducted in 2016. Data were also available for Pennsylvania waters of the central basin for some years, but trawl surveys were not conducted in 2006, 2010, 2011, 2013, and 2014, so these data were not used. There are no annual trawl surveys in Ontario waters of the central basin (FTG 2016). With high variability, there has been a consistent up and down trend in central prey fish with the lowest number across the time period reported recently in 2016 (Figure 29).

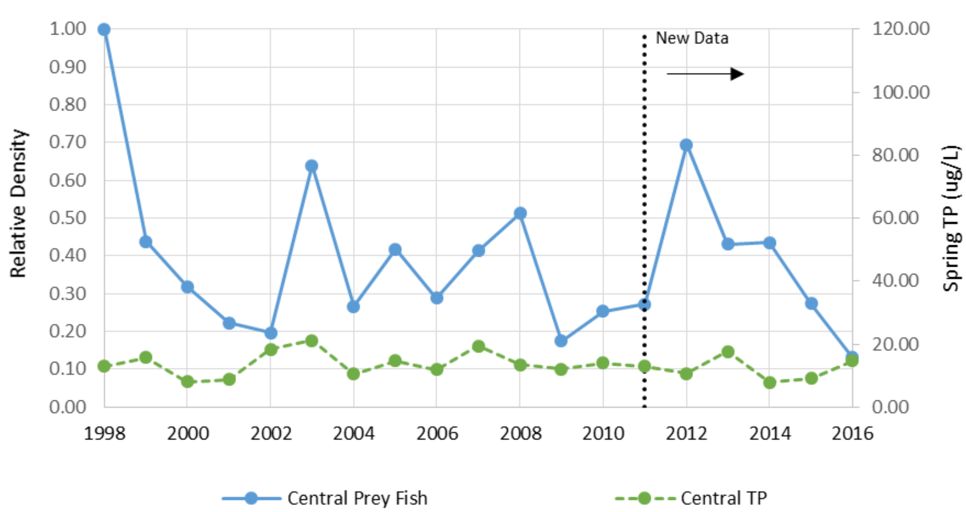

Figure 29. Relative density of fish in central Lake Erie.

Eastern Lake Erie prey fish relative biomass (Figure 30) was digitized from forage fish biomass data collected with a bottom trawl in the New York waters of Lake Erie. Species include rainbow smelt, emerald shiner, and round goby (Figure C.7 in NYSDEC 2017). While variable there was an increase in eastern basin prey fish from 1998 through 2011, when biomass dropped in 2012, but have since increased (2016).

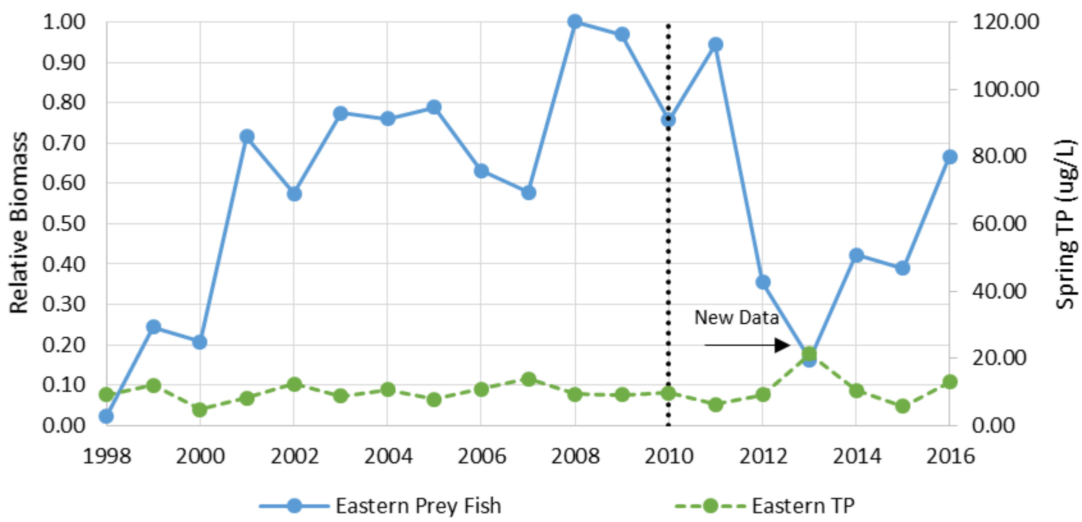

Figure 30. Relative biomass of the eastern Lake Erie prey fish.

Lake Erie (whole lake) prey fish relative density was digitized from standardized pelagic prey fish (rainbow smelt and round goby) data in Figure 2 of Gorman (2017) and presented below in Figure 31. Biomass data for Lake Erie prey fish are not consistently available, so relative density was used to display the trends in prey fish. The whole lake prey population is variable across time.

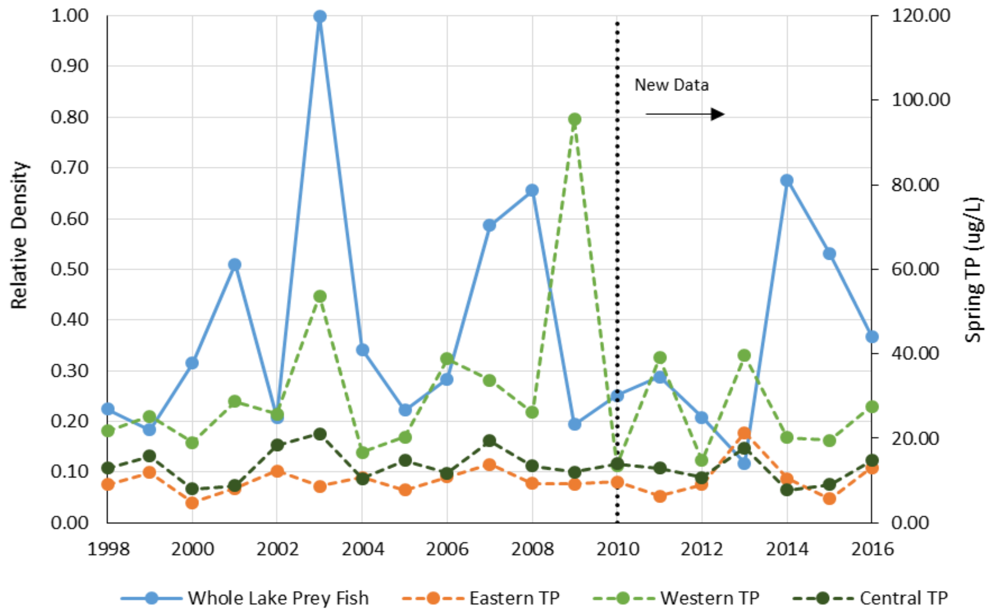

Figure 31. Lake Erie (whole lake) prey fish relative density.

Lake Erie walleye abundance was estimated by the Lake Erie Walleye Task Group and is presented in Figure 32. An SCAA model was used to estimate the abundance of age-2 and older walleye in Lake Erie using fishery-dependent and fishery-independent data sources (Lake Erie Walleye Task Group 2017). The whole lake walleye abundance peaked in 2005 but remains consistent over the time period.

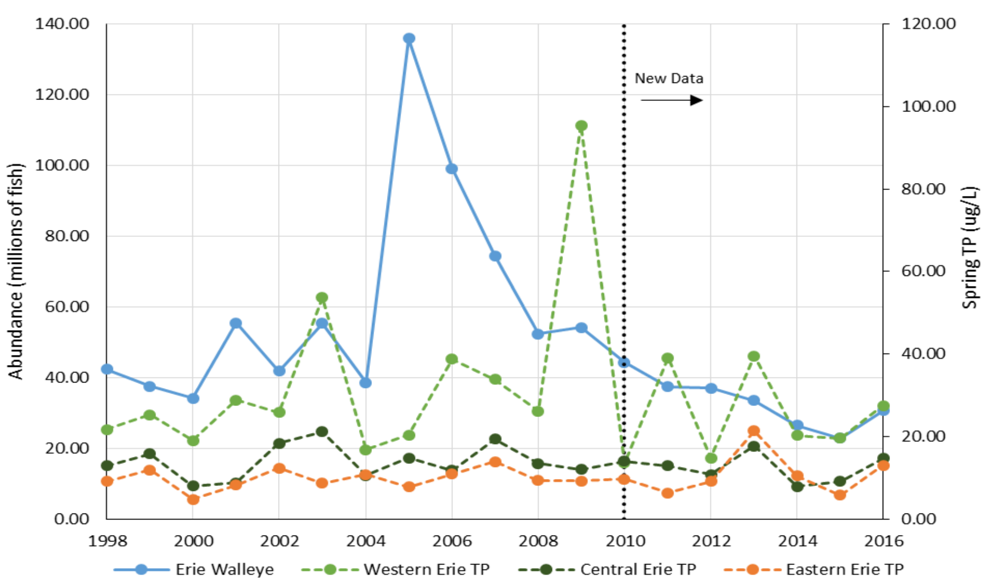

Figure 32. Lake Erie walleye abundance over time compared with TP concentrations in the three basins of the lake.

4.4.2.e Lake Ontario

Lake Ontario prey fish relative biomass was calculated from biomass estimates for alewife, rainbow smelt, and all benthic or demersal species captured in bottom trawls and is presented in Figure 33. For most species, a seasonal-specific estimate (stratified by depth) was reported as the vulnerability to the trawl differs widely across season. Data were provided by Brian C. Weidel (USGS), Michael J. Connerton (NYSDEC), and Jeremy P. Holden (OMNRF), with funding from the following sources: USGS Ecosystems mission area, Status and Trends & Fisheries Programs; Sport Fish Restoration Act to the NYSDEC; and Province of Ontario. Significant differences between these data and the prey fish data used in Bunnell et al. (2014) exist because a number of important assumptions regarding survey biases have been validated since that time. Benthic prey fish densities from 1978-2014 are based on sampling U.S. waters, whereas the whole lake has been sampled since 2014. Rainbow smelt and alewife biomass densities from 1978-2015 are based on sampling U.S. waters, whereas the whole lake has been sampled since 2016 (Brian Weidel, personal communication, 10/16/2017). The relative biomass in prey fish was variable but mostly stable over time.

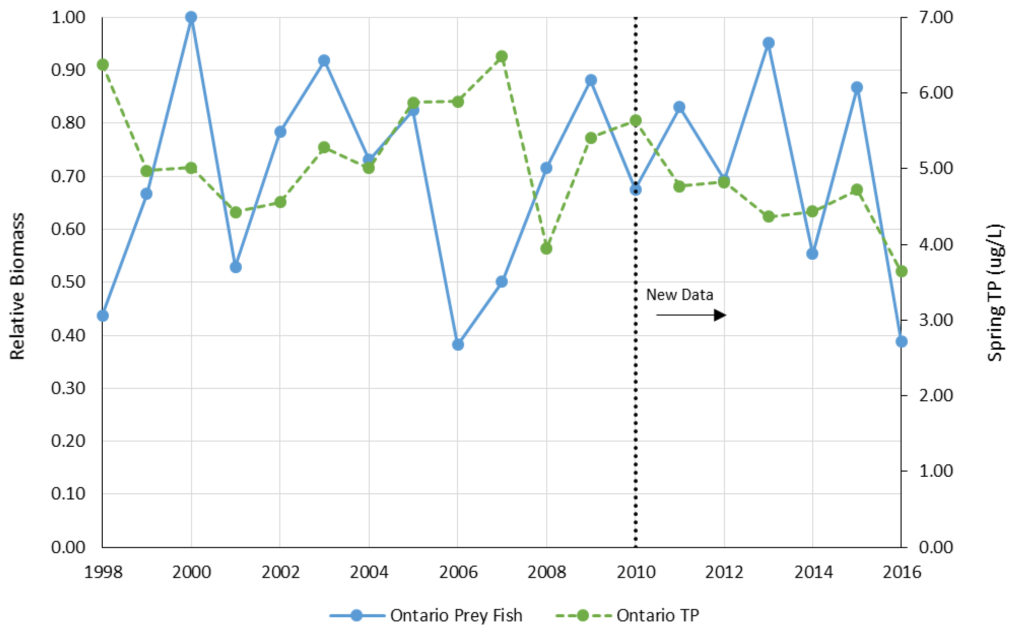

Figure 33. Lake Ontario prey fish abundance over time plotted with spring TP for comparison.

Lake Ontario lake trout and Chinook salmon biomass (age 1 and older) 1998-2007, were derived from Bunnell et al. (2014) and are presented in Figure 34. Updated data are not yet available. Data from 1998 through 2007 showed a consistent decreasing trend in piscivore biomass.

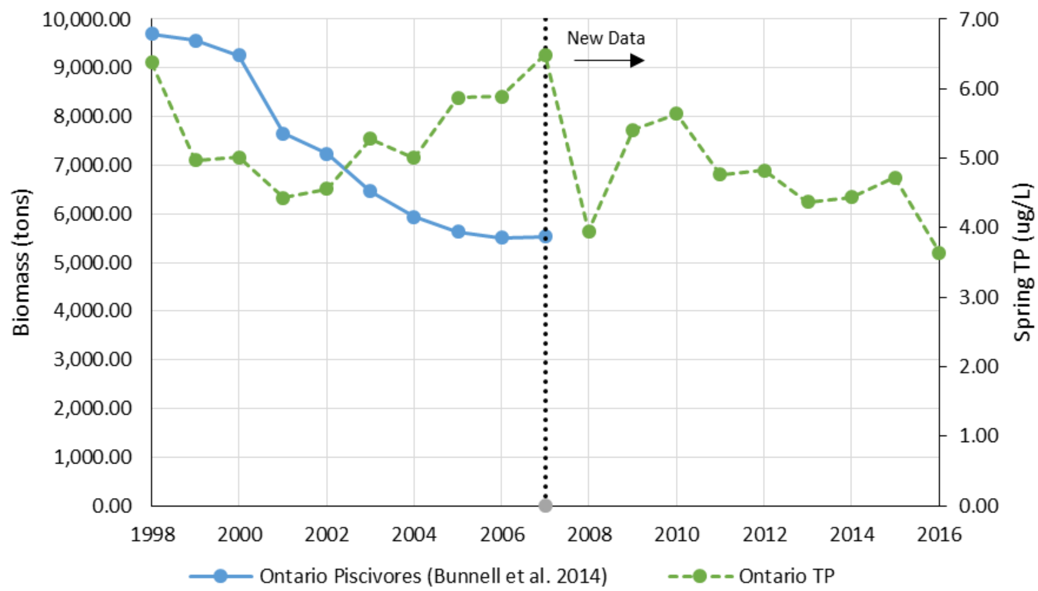

Figure 34. Lake Ontario piscivore data reported by Bunnell et al. (2014), plotted along with historical and more recent TP data for the lake for comparison.

4.5 Data Analysis

Spearman's nonparametric correlation analysis was used, as by Bunnell et al. (2014), to determine if there was a correlation between the time series (1998-2016), and a given trophic level or attribute (spring TP, chlorophyll a, water clarity, zooplankton, prey fish, and predatory fish) across each lake. The results of the analysis are presented below in Table 4-1. The data were analyzed using GraphPad Prism 7.02. With 13 or fewer XY pairs, Prism computes an exact P value for nonparametric (Spearman's) correlation, looking at all possible permutations of the data. With 14 or more pairs, Prism computes an approximate P value for nonparametric correlation.

Table 4-1. Spearman's rank correlations between specific biotic or physicochemical attributes and the year in each of the five Great Lakes, including the three basins of Lake Erie. Each time series spans 1998-2016. Results with significant p-values (<0.05) are noted with asterisks.

vs. Time	Western	Central	Eastern	Superior	Ontario	Huron	Michigan
Total Phosphorus	0.01	-0.1	0.15	**0.51***	-0.43	-0.21	**-0.86***
Water Clarity	0.38	0.18	-0.32	**0.47***	0.39	**0.91***	**0.94***
Chlorophyll a	-0.41	0.32	0.14	**-0.49***	-0.24	**-0.92***	**-0.93***
Zooplankton	-0.25	-0.28	-0.13	-0.45	**-0.73***	**-0.72***	**-0.72***
Prey Fish	**0.55***	-0.21	0.14	**-0.84***	0.032	-0.2	**-0.91***
Piscivore	-	-	-	0.052	**-0.99***	-0.5	**0.64***

We also used Spearman's nonparametric correlation analysis to determine whether there was a relationship between adjacent trophic levels (or attributes). This can provide evidence for bottom-up or top-down regulation across the lakes and in each basin of Lake Erie.

Table 4-2. Spearman's nonparametric correlations between trophic levels and/or attributes for each Great Lake and the three basins of Lake Erie. Results with significant p-values (<0.05) are noted with asterisks.

	Western	Central	Eastern	Superior	Ontario	Huron	Michigan
Total Phosphorus x Chlorophyll a	**0.53***	0.11	**0.50***	-0.44	0.097	0.13	**0.88***
Zooplankton x Chlorophyll a	0.34	-0.056	0.17	0.31	**0.58***	**0.67***	**0.66***
Prey Fish x Zooplankton	-0.37	-0.15	-0.16	0.16	-0.1	**0.59***	**0.68***
Piscivore Biomass x Prey Fish	-	-	-	0.067	0.15	0.54	**-0.54***

Consistent with the figures presented above, the correlation analysis identified some trends in Lake Superior (Table 4-1). There was a positive increase in total phosphorus over time, albeit levels still remain among the lowest across the Great Lakes (but now similar to Lake Huron and Lake Michigan). Even so, chlorophyll a was reduced and water clarity was enhanced across the period. There was a slight decline in zooplankton biomass along with declines in prey fish biomass (driven by bloater, cisco, and rainbow smelt). Catch per unit effort of lean lake trout in Superior was used for the predatory fish correlation, and did not show any change.

There was a negative relationships between total phosphorus and chlorophyll in Lake Superior, which seems counter to the idea that phytoplankton biomass should be increasing with increasing phosphorus (Table 4-2). Bunnell et al. (2014) suggested this relationship to be spurious and likely an outlier. No other pairs appeared to have strong relationships within Lake Superior.

Lake Huron exhibited time trends across most parameters (Table 4-1) from 1998-2016. There was a significant increase in water clarity along with decreases in chlorophyll a and zooplankton (Table 4-1). While there was evidence for a decrease in prey fish and predatory fish, the correlation across time was not significant. As observed by Bunnell et al. (2014), several trophic levels were positively correlated with one another, consistent with bottom-up control. These included significant relationships between zooplankton to chlorophyll a, prey fish to zooplankton, and piscivore biomass to prey fish. No top-down control was evident in Lake Huron.

Similar to Lake Huron, Lake Michigan exhibited strong negative relationships across time in total phosphorus, chlorophyll a, zooplankton, and prey fish. Water clarity increased from 1998 to 2016. As observed by Bunnell et al. (2014), several trophic levels were positively correlated with one another, consistent with bottom-up control. These included significant positive relationships between zooplankton to chlorophyll a, and prey fish to zooplankton. However, there was a negative relationship between piscivore biomass and prey fish, suggesting top-down control at this level.

While concentrations of total phosphorus in Lake Ontario appear to be trending downward since 1998, there was no significant correlation between time and phosphorus. The biomass of zooplankton declined over time. While predatory fish appear to have declined each year, data for predatory fish were only available for Lake Ontario up to 2007. The only significant relationship in Lake Ontario was evidence of bottom-up control between zooplankton and chlorophyll a.

Lake Erie yielded few time trends across all attributes and basins. The only significant trend that Spearman's analysis identified was an increase in prey fish in the western basin. Similarly, there was no significant relationships when comparing trophic levels, except for total phosphorus and chlorophyll a in the western and eastern basins. Data were not correlated for predatory fish, but some trends can be observed as described in other sections of this report. Overall, the trends from 1998-2016 remained similar to Bunnell et al. (2014) findings with respect to most time trends and trophic level relationships.

4.6 Comparison between Canadian and U.S. Data

Figures 35 and 36 display boxplots of long-term total phosphorus concentrations for Lake Superior, Lake Michigan, Lake Huron, Lake Erie (western, central, and eastern basins), and Lake Ontario. Figure 35 shows the upper Great Lakes (Lakes Superior, Michigan, and Huron) while Figure 36 presents the lower Great Lakes (Lakes Erie basins and Ontario). The data for these boxplots was obtained from the USEPA GLNPO and ECCC long-term monitoring programs. The solid line within each box corresponds to the median value for the year, the upper and lower ends of the box represent the 75th and 25th percentile values, and the ends of the "whiskers" show the minimum and maximum values measured. The horizontal dashed line within each plot indicates the target open water concentration of total phosphorus for each lake from the 1978 GLWQA (IJC 1978). Note that values for all lakes except Erie now consistently fall below these targets, and there is some concern that concentrations may be approaching a lower threshold where offshore fish productivity could be impacted (e.g., Yurk and Ney 1989, Jeppesen et al. 2005). Experimental fertilization of low-productivity lakes in western Canada has taken place with the intention of enhancing fishery productivity (e.g., Ashley et al. 1997).

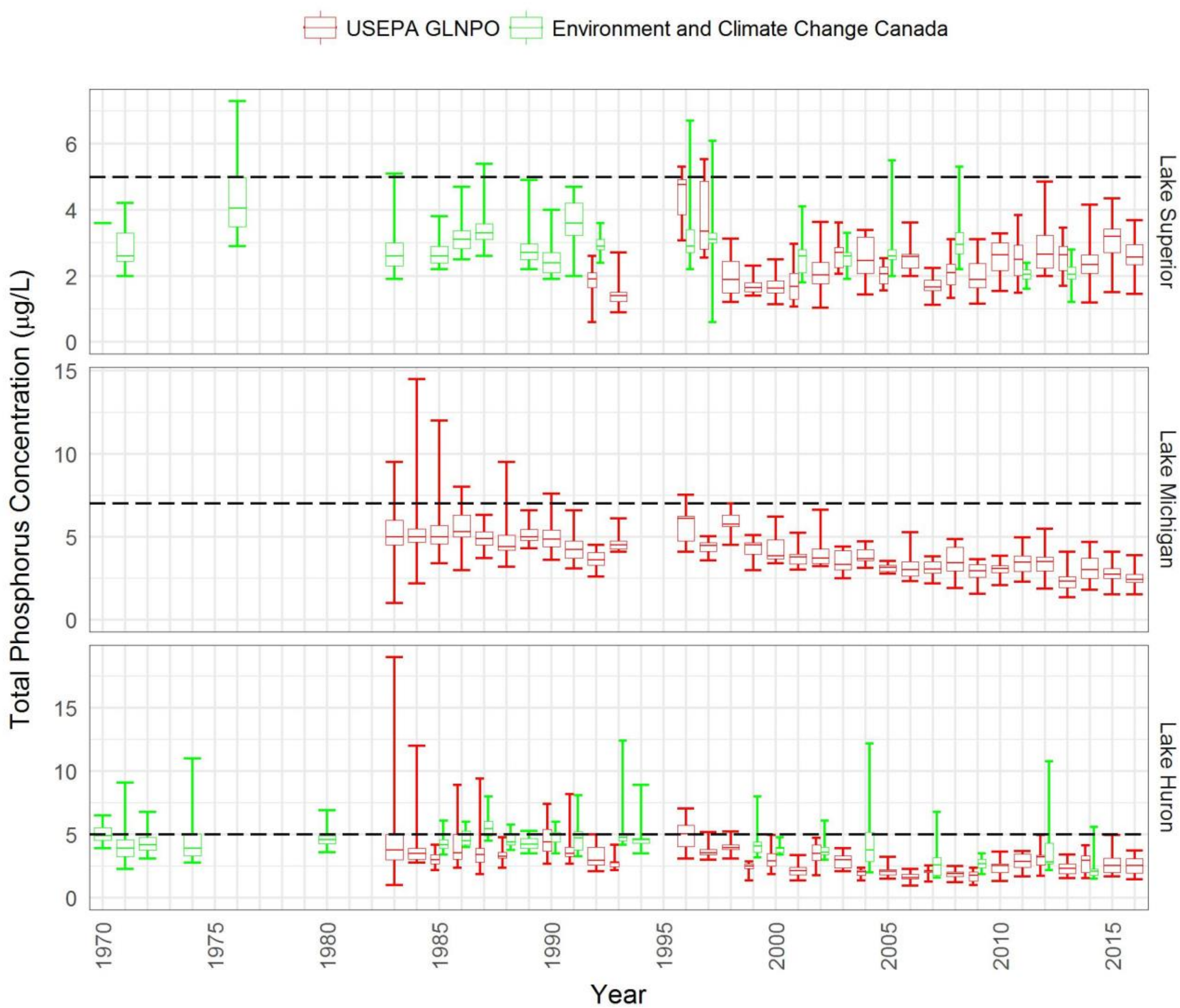

Figure 35. Time series of total phosphorus in the upper Great Lakes. Data are limited to spring TP measurements from surface waters (top 3 m) at offshore locations. U.S. data are from the U.S.

Environmental Protection Agency's Great Lakes National Program Office (GLNPO). Canadian data are from Environment and Climate Change Canada's Great Lakes Surveillance Program (GLSP). The horizontal dashed line within each plot indicates the target open water TP concentration for each lake from the 1978 GLWQA (5 µg/L for Lakes Superior and Huron; 7 µg/L for Lake Michigan). Note that there are differences in the scale of the vertical axis of each plot.

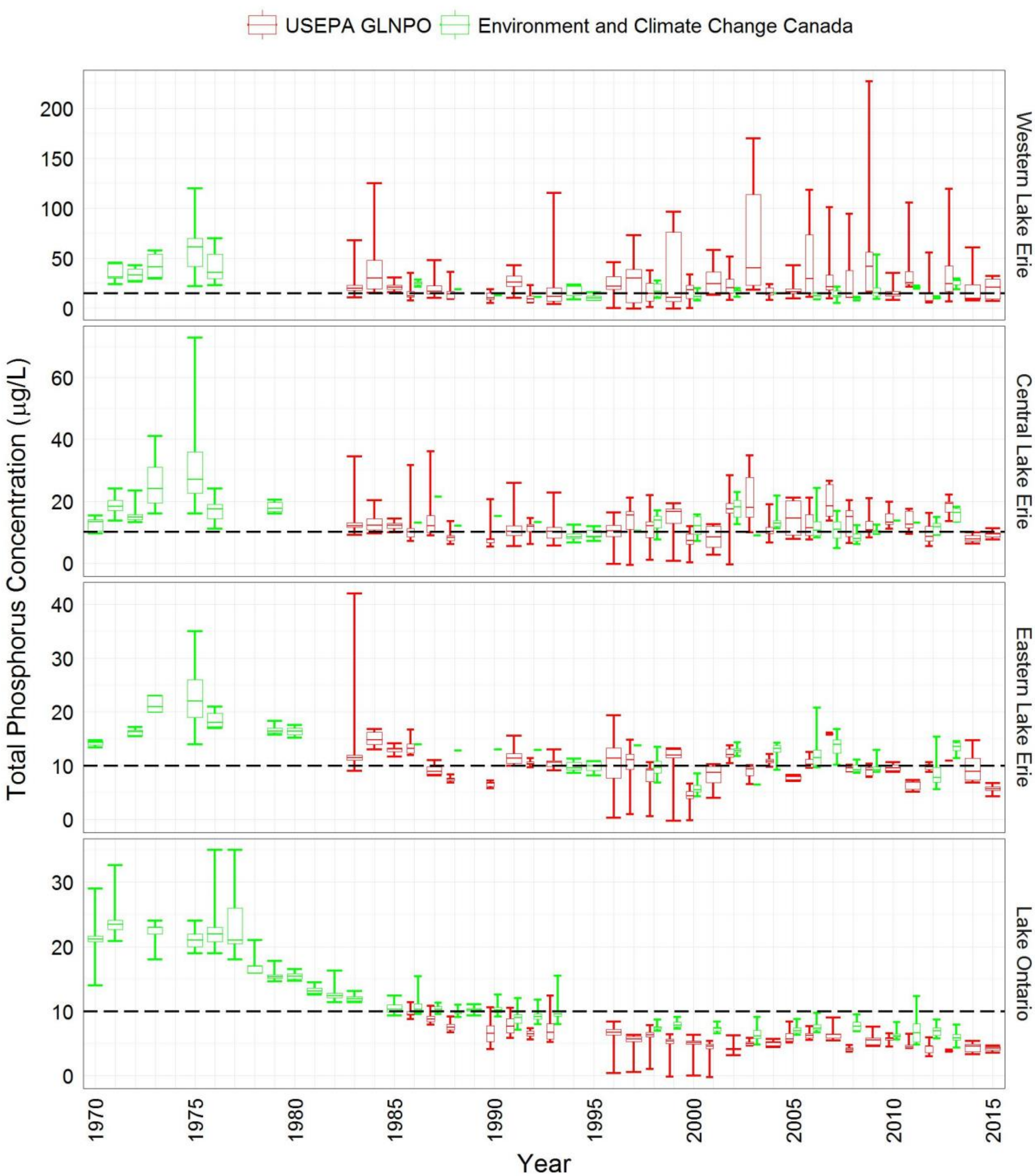

Figure 36. Time series of total phosphorus in the lower Great Lakes. Data are limited to spring TP measurements from surface waters (top 3 m) at offshore locations. U.S. data are from the U.S. Environmental Protection Agency's Great Lakes National Program Office. Canadian data are from Environment and Climate Change Canada's Great Lakes Surveillance Program. The horizontal

dashed line within each plot indicates the target open water TP concentration for each lake from the 1978 GLWQA (10 µg/L for Central Lake Erie, Eastern Lake Erie, and Lake Ontario; 15 µg/L for Western Lake Erie). Note that there are differences in the scale of the vertical axis of each plot.

Kendall's nonparametric rank correlation analysis was used to determine if there were differences in the slope of the TP data regression line between the Canadian and U.S. data for three time periods; 1998-current, 1998-2010, and 2010-current. Data analysis was performed using R version 3.4.2, with the statistical package EnvStats. The slopes and statistical significance are presented below in Table 4-3, and shown graphically with confidence intervals in Figure 37.

Table 4-3. Kendall's rank correlations comparing the slope of the TP regression line for three time periods, for the USEPA and ECCC data. Significant p-values (>0.05) are noted with asterisks and the slope is bolded.

Lake	Agency	Slope		
		1998-current	1998-2010	2010-current
Central Lake Erie	USEPA	-0.05	0.17	-0.12
Central Lake Erie	ECCC	**-0.26***	**-0.40***	**-1.13***
Eastern Lake Erie	USEPA	0.020	0.02	0.31
Eastern Lake Erie	ECCC	-0.05	0.20	-1.30
Lake Huron	USEPA	-0.01	**-0.10***	-0.02
Lake Huron	ECCC	**-0.12***	**-0.15***	**-0.48***
Lake Michigan	USEPA	**-0.10***	**-0.14***	**-0.10***
Lake Ontario	USEPA	**-0.08***	0.004	**-0.23***
Lake Ontario	ECCC	**-0.08***	**-0.04***	-0.20
Lake Superior	USEPA	**0.05***	**0.04***	0.04
Lake Superior	ECCC	**-0.04***	**0.06***	0.00
Western Lake Erie	USEPA	-0.03	0.23	1.07
Western Lake Erie	ECCC	-0.20	-0.09	-1.68

The individual TP data points are presented in Figure 37 from 1998 through the most recent available data. The left hand panel plots the data, slope of the regression line, and confidence intervals using the U.S. EPA GLNPO data, whereas the right hand panel presents the plots using the ECCC data. Michigan is not presented as no data are available from the Canadian monitoring program. Based on Table 4-3, however, Lake Michigan showed a significant decreasing trend in spring total phosphorus concentrations across all three time periods.

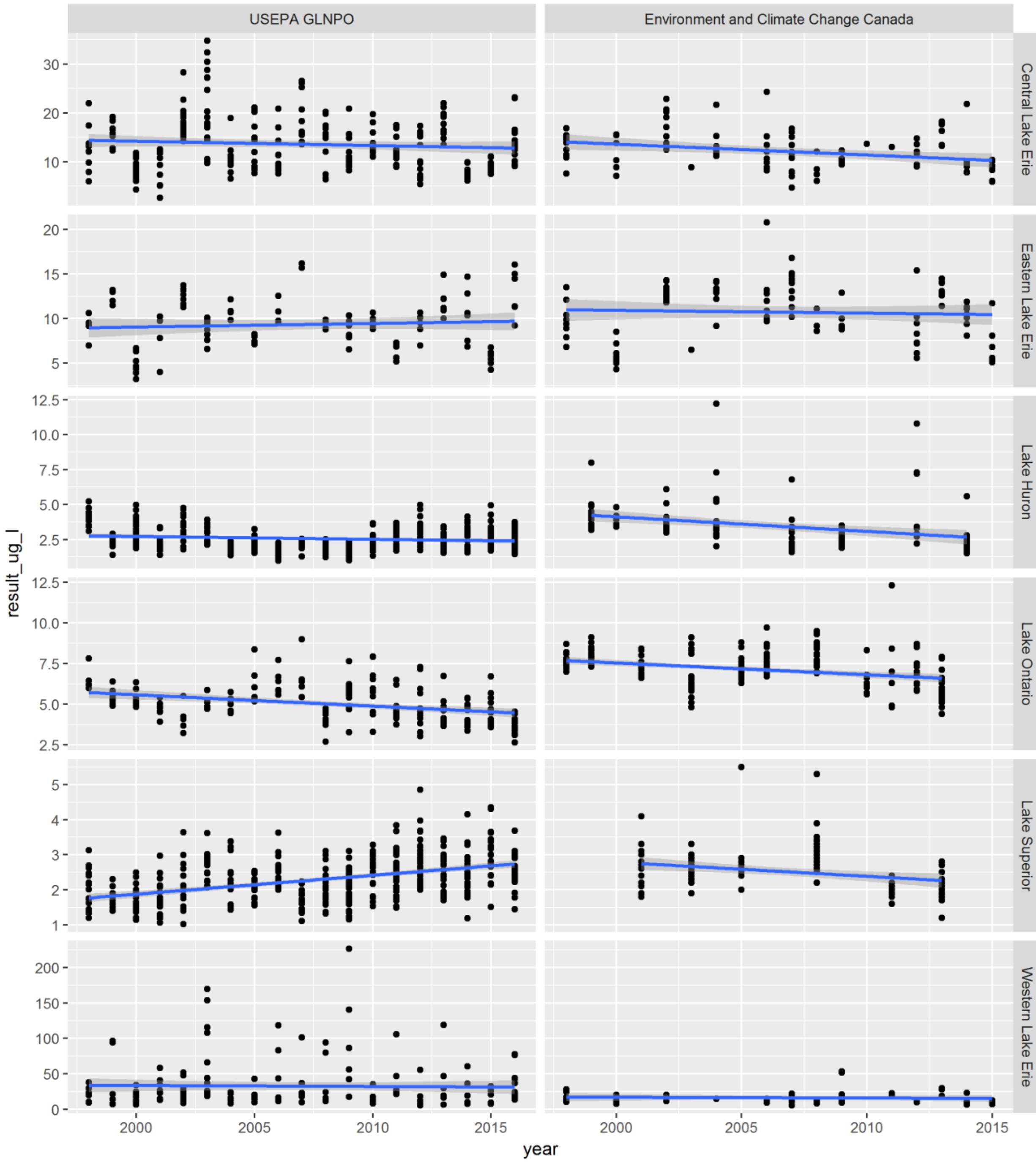

Figure 37. Time series of raw TP data in µg/L for all Great Lakes (except Lake Michigan), comparing the USEPA and ECCC data from 1998 through the most currently available data. The slope of the line is presented in blue, and the grey shading represents the 95% confidence intervals.

Figure 37 demonstrates the number of data points available from each monitoring program. More data were generally collected and at a higher frequency in the USEPA GLNPO program compared to the ECCC program, although more sampling points are represented in some years from ECCC than from USEPA.

This can impact the significance and direction of trends. For example, while Lake Superior data produced a significant positive slope across time for the USEPA data, the Canadian data show a significant decreasing trend. The high variability in total phosphorus levels across seasons and years, and less frequent sampling years in the Canadian monitoring program likely explain the variable results. As mentioned above, while Lake Superior is showing gradually increasing TP concentrations, the values still remain among the lowest across all the lakes (similar now to Huron and Michigan [not shown in Figure 37; see Figure 35]).

The slopes of the Lake Ontario total phosphorus data were the same (slope = -0.08) across the two monitoring programs, with both showing a statistically significant decrease in levels from 1998 to present. Additionally, the most recent USEPA data from 2010-present, show a significant decline. While the slopes are consistent across the Lake Ontario data (USEPA slope = -0.23 and ECCC slope = - 0.20), the trend was insignificant in the ECCC data. This lack of significance was likely due to the limited number of years (n = 4), compared to the USEPA data (n = 7). Overall, the results from both monitoring programs suggest a long-term (1998-present) and near-term (2010-present) drop in total phosphorus levels in Lake Ontario.

5 Model Review

This assessment is a synthesis of the available regional and global knowledge related to how reduced phosphorus loading to lakes has affected fish biomass and community structure. Quantitatively approaching a set of ecological questions with this level of complexity is often done most effectively with a numerical model that combines data and process understanding across temporal and spatial scales. This section of the report presents a review of numerical ecological models by (1) summarizing the classes of models that have been applied generally to fishery research and management since approximately 2005, and (2) providing more specific information on the collection of biogeochemical and food web models that have been applied to Great Lakes ecosystems over that period. The sources considered for this compilation included primarily peer-reviewed journal articles, conference proceedings and presentations, and government publications.

5.1 Background

Traditional management of fisheries in the oceans and Great Lakes was oriented toward stocks of individual species, somewhat in isolation from other species and larger ecosystem drivers such as nutrient loading, invasive species, and climate change. Ecosystem-based management concepts for fisheries, understood in contrast to species-specific management approaches, were first developed in the 1970s and 1980s (Christenson et al. 1996; Pikitch et al. 2004), although it could be argued that sea lamprey control in the Great Lakes beginning in the 1950s anticipated this development. Further refinement and implementation of ecosystem-based management in subsequent decades, especially in Europe and Canada, created corresponding demand for tools to support complex multi-species data integration, quantitative simulation of ecological processes and interactions, and development of predictive scenarios for support of management decisions. At the same time, increasing computer processing speeds facilitated the creation of aquatic environmental models of greater complexity and resolution that could be run on desktop computers by individual researchers in many cases.

The Revised 1978 Great Lakes Water Quality Agreement, and the 1981 Joint Strategic Plan for Management of Great Lakes Fisheries, both prioritized ecosystem-based management concepts and Lake Ecosystem Objectives (LEOs; Hartig et al. 1998; Slocombe 1998; Guthrie 2017). Management agencies have been incorporating increasingly quantitative and integrative approaches to Great Lakes fishery management since then. In 1987, the Modeling Task Force of the IJC Science Advisory Board published a report that provided an overview of the status and future of large lake models for management and other purposes (Sonzogni et al. 1987).

Numerical ecosystem modeling in the Great Lakes was first applied to management of eutrophication in western Lake Erie, with development of the seven-compartment LAKE1 model (Di Toro et al. 1973) and a later ensemble of companion models for all lakes (Bierman 1980). Chen et al. (1975) expanded Great Lakes water quality models to include fish for Lake Ontario. More intensive Great Lakes ecosystem modeling that included the upper food web was initiated in the early 2000s by updating the old NETWRK FORTRAN code (Ulanowicz and Kay 1991) into a Windows-compatible form (EcoNetwrk). This was done to apply it to understanding the current and future impacts of invasive invertebrates (mussels, zooplankton) on Great Lakes fish communities (Shuter and Mason 2001; Miehls et al. 2009). Subsequent modeling work on a lake-basin scale to simulate Great Lakes ecosystems from nutrients to fish has mostly consisted of adapting models that were originally developed for marine systems to applications in these freshwater inland seas, rather than integrating the approaches from the numerous lake models that had been developed from the 1970s through the early 2000s in Europe and elsewhere (Mooij et al. 2010).

DeVanna-Fussell et al. (2016) recently reviewed modeling and management approaches that can be applied to benefit decision-making regarding the dynamic Great Lakes fishery.

5.2 Classes of Ecological Models

Aquatic ecosystem models for fishery applications can be broadly classified into bioenergetic predator-prey models, individual-based models, and whole ecosystem/dynamic system models (Plagányi 2007; see Figure 38 below). Statistical catch-at-age (SCAA) models used to develop single-species stock assessments from field survey data and harvest data, which are then used to guide the setting of catch limits and stocking decisions, are not considered further here. Biogeochemical models of the lower food web (nutrients to zooplankton) will be discussed, as several new modeling efforts in this category have recently published their results, which are relevant to models that include upper trophic levels regarding findings on nearshore nutrient trapping.

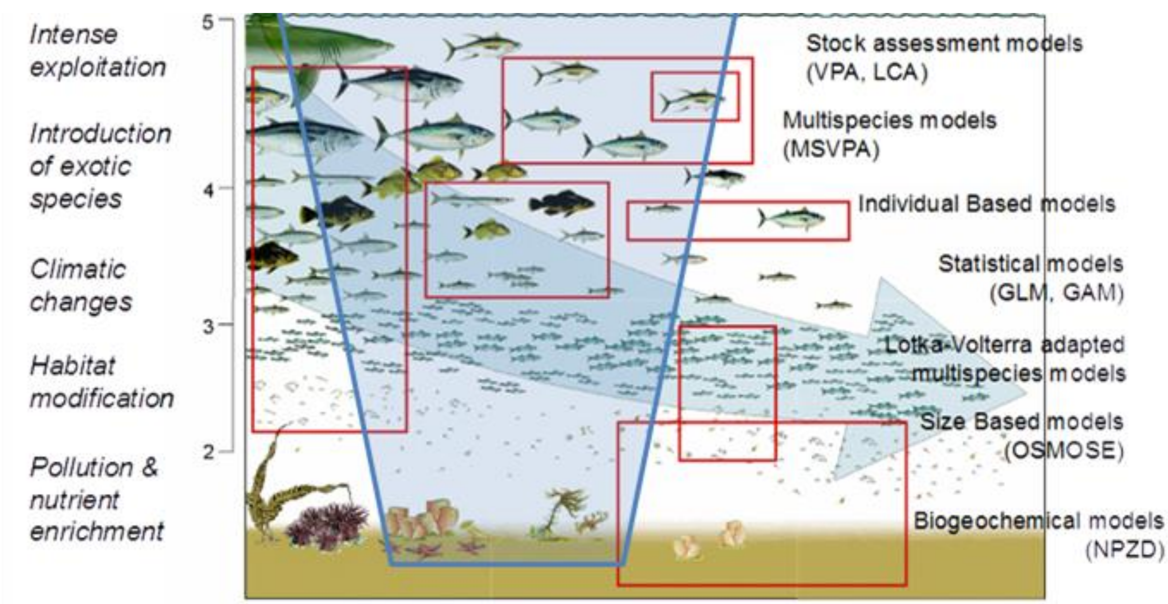

Figure 38. Schematic diagram developed from Plagányi (2007; Figure 3) showing hierarchy of ecosystem model complexity for a marine system; axis scale (approximate trophic levels [numbers] with example human impacts [text labels] for each) is from Pauly et al. (2003) and artwork is by Rachel Atanacio. Red boxes correspond to example domains of listed model types to the right. The large blue trapezoid contains all trophic levels in the ecosystem, similar to what a full ecosystem model would capture. The large arrow in the background represents the concept of fishing down the food chain (sensu Pauly).

5.3 Summaries of Specific Models and their Applications

Specific ecosystem models that have been applied in the Great Lakes in recent years are described in the following section. This is not a comprehensive review of all such models, but rather a representative sample of the kinds of modeling projects that have been recently completed or are underway, and which are most relevant to the objectives of this summary. The summary table below (Table 5-1) compares attributes and lists applications of the models described.

5.3.1 Ecosystem Models of the Lower Food Web

Several nutrient cycling or lower food-web models of whole lakes or embayments in the Great Lakes have been developed in recent years. These include the Advanced Aquatic Ecosystem Model (A2EM), which was applied recently as the Western Lake Erie Ecosystem Model (WLEEM; Verhamme et al. 2016), and was previously linked to an Individual-Based Model in Saginaw Bay (Sesterhenn et al. 2014). The Estuary, Lake and Coastal Ocean Model-Computational Aquatic Ecosystem Dynamics Model (ELCOM-CAEDYM) was used in Lake Erie by Oveisy et al. (2014) to simulate winter conditions, including simple water quality parameters, and by Bocaniov et al. (2014) to simulate nearshore shunting of nutrients by mussels. Shen et al. (2018) simulated quagga mussel impacts in Lake Michigan in 1D, and Pilcher et al. (2017) and Rowe et al. (2017) simulated nutrient cycling in Lake Michigan, including mussel grazing impacts in 3D, using NPZD models linked to MITgcm and FVCOM circulation models, respectively. Models that simulate *Cladophora* have not generally been linked with broader ecosystem models in the past, but researchers are now beginning to do this (e.g., Valipour et al. 2016).

These models have produced robust results that are generally in good agreement with observations, but they have generally not yet been linked to upper food web models (with some exceptions), although proposals have been developed to further explore such linkages.

5.3.2 Statistical-Based Models

A statistical-based platform using a multispecies statistical age-structured model to assess predator–prey balance was applied to Lake Michigan (Tsehaye et al. 2014). This work was among, “recent studies [which] have begun incorporating predation interactions into statistical catch-at-age (SCAA) models, which allow the application of statistical estimation procedures in a multispecies context.” The model was applied to inform the management of top predators. The study examined the balance between the predation and productivity of alewives and rainbow smelt, and the response of salmonids. The modeling study found that the feedback mechanisms are not likely to keep a predator-prey balance with Chinook salmon and lake trout. This is because of “consumption declining only at the lowest prey densities, while the other salmonines consumed prey at a maximum rate across all observed prey densities.”

Middle-upper food web (prey fish/piscivore) simulations such as these can test hypotheses about interactions among and within these trophic levels, but cannot account for other factors such as changing nutrient loads or climate.

5.3.3 Individual/Agent-Based Models (IBMs)

These models simulate behavior of single populations of individuals/agents over the course of their life cycles. The model output can be statistical and spatially explicit, but also can be somewhat challenging to visualize given the large numbers of individuals that are typically modeled.

This type of model has been used to simulate alewife populations in Lake Michigan (Höök et al. 2008). An IBM was also used to assess the survival and possible establishment of non-native grass carp in the Great Lakes Basin and coastal wetlands (Jones et al. 2017). A recent study compared lake-specific and general IBMs for yellow perch growth for Lake Erie (Marin Jarrin et al. 2017). The study found that sparse zooplankton data, which is the situation for most of the Great Lakes, impacted the performance of the IBM.

Table 5-1. Model review summary.

Model Type	Capabilities	Strengths	Weaknesses	Recent Applications
Lower Food Web/ Biogeo-chemical Models (A2EM, MITgcm-NPZD, FVCOM-NPZD, ELCOM-CAEDYM)	Simulate nutrient, phytoplankton, zooplankton, and detritus cycling in water column and sediment; some include benthos; spatially explicit; balance element masses	Constrain elemental mass balances and spatio-temporal variability in phenomena	Do not include upper trophic levels; nearshore and embayment interactions are focus	Eutrophication (Lake Erie, Green Bay, Saginaw Bay); Lake Michigan mussel impacts
Statistical-Based Models (not SCAA)	Multispecies statistical age-structured models to assess predator–prey balance	Good for predicting predation impacts	Cannot incorporate lower food web, physical factors	L. Michigan salmonines and prey
Individual or Agent-Based Models (IBMs)	Simulate behavior of single populations of individuals/ agents over the course of their life cycles; output can be statistical and spatially explicit	Useful where behavior is believed to have a strong influence on dynamics	Typically not applied to multiple species or multiple populations	L. Erie: yellow perch growth; Great Lakes Basin and wetlands: grass carp establishment and survival, impacts on wetlands
Individual-Based Community Models	Combine Individual-Based Models for multiple species	Allow for consideration of greater complexity than IBMs	Require process understanding of interactions among species	L. Michigan, L. Huron, and L. Erie: invasive species, climate change, contaminant accumulation
Bioenergetic Models	Based on bioenergetic and allometric reasoning, parameterized using power functions of individual body mass, constrained by diet data from gut contents	Balance ecosystem energy flow, which constrains shifts in diet and health	Require intensive laboratory experiments and empirical data on diets to constrain algorithms	L. Michigan, L. Huron: lake whitefish impacts of *Diporeia* decline; alewife impacts of mussel invasion; yellow perch/walleye
Whole Ecosystem Models: ATLANTIS	End-to-end approach which includes nutrient cycling, ecological processes (competition, predation), and anthropogenic processes	Attempts to create a holistic representation of the system, including human factors	Many parameters; hard to constrain; insufficient data; uncertainty	L. Michigan, L. Erie, L. Huron (in progress): Asian carp/ invasive impacts
Whole Ecosystem Models: Ecopath with Ecosim	Used for trophic models of ecosystems, stressors (nutrient loading, invasive species); biomass-based; can be linked to economics model	Moderate complexity; User-friendly interface; most widely used model	Limited spatial capabilities; limited by incomplete knowledge of ecosystem functioning	L. Superior: lake trout; L. Michigan, Saginaw Bay, L. Ontario, and L. Erie: Asian carp and invasives impacts

5.3.4 Individual-Based Community Models

Individual-Based Community Models (IBCMs) combine multiple IBMs into an integrated framework that allows for simulations of interspecies interactions. Community models like this represent an intermediate level of complexity between IBMs and the more comprehensive ecosystem models described below. IBCMs can be combined with bioenergetics models or other approaches based on the research or management question of concern, and availability of data. An example of an IBCM that was developed to explore potential impacts of phytoplanktivorous and zooplanktivorous Asian carp (Silver and Bighead carp, respectively) on Saginaw Bay and Lake Huron food webs is illustrated in Figures 39 and 40 (Ivan et al. 2012). The research team also included complementary modeling approaches (i.e., Ecopath with Ecosim) described below.

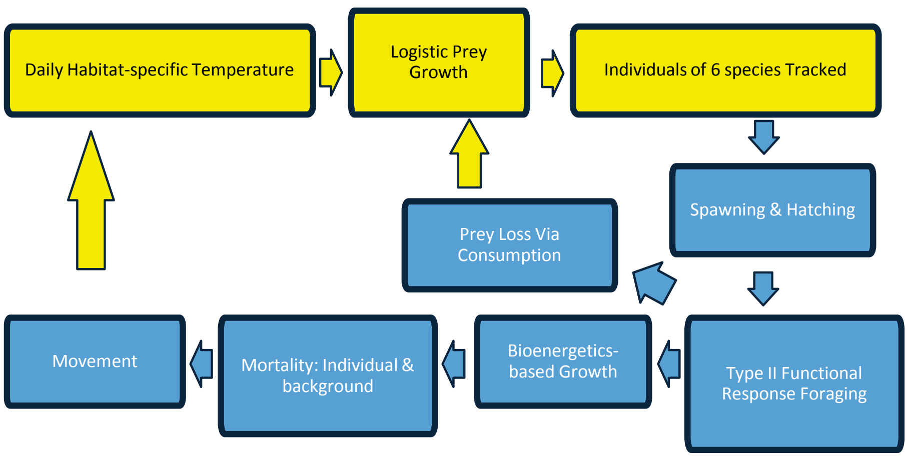

Figure 39. Schematic diagram of Individual-Based Community Model used to explore potential Asian carp impacts in Saginaw Bay and Lake Huron (Ivan et al. 2012 and subsequent presentations).

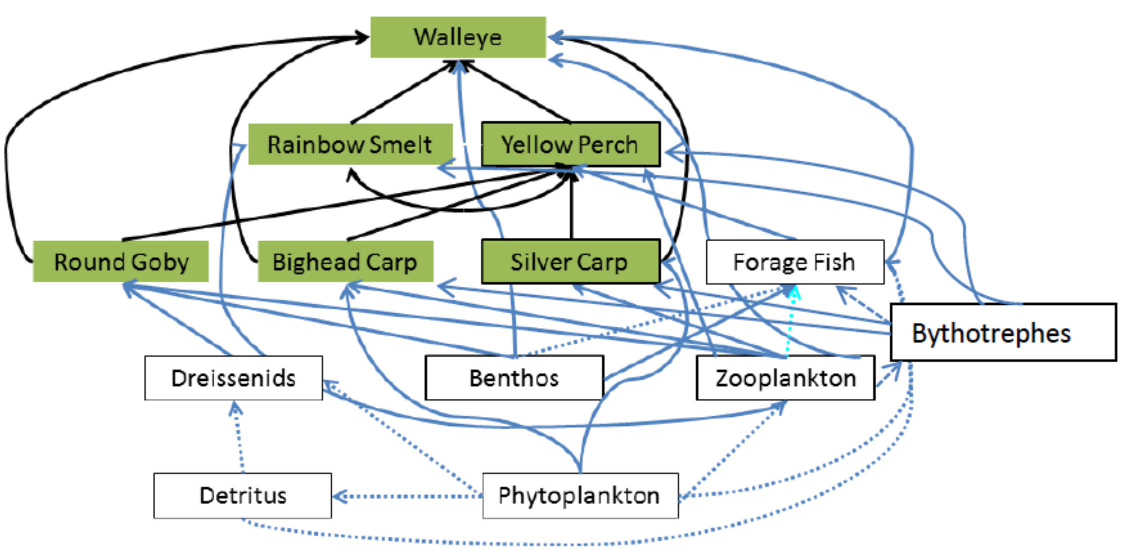

Figure 40. Food web diagram of the Asian carp IBCM study described above: green boxes indicate species tracked as individuals; white boxes indicate species tracked as biomass pools; lines indicate interactions among species only (black), species and pools (blue solid), and pools only (blue dotted).

5.3.5 Bioenergetic Models

Bioenergetic models provide a way to estimate consumption to assess the impact of individual species on an ecosystem based on organismal energy balances (Hanson et al. 1997, Deslauriers et al. 2017, van der Lee et al. 2017). Energy is consumed by metabolism, growth, and waste. In a widely-cited paper, Kitchell et al. (1977) developed bioenergetic models for yellow perch and walleye, and showed a strong dependence of growth rate for both on temperature. Madenjian et al. (2013a) performed laboratory experiments to test a widely used bioenergetics model for lake whitefish and lake trout (the Wisconsin model), and found that it performed well for lake trout, but needed to be modified to better match lake whitefish results. Bioenergetics were used recently in predicting the impacts of the invasion of grass carp in the Great Lakes (van der Lee et al. 2017, Jones et al. 2017). Such predictive studies tend to have large uncertainties, given the need to make multiple assumptions about the feeding behavior of a species in a new habitat with few empirical constraints.

A bioenergetics approach was linked with numerical models of temperature and dissolved oxygen in Lake Erie by Arend et al. (2010). Fish habitat quality for rainbow smelt, emerald, shiner, yellow perch, and round goby was assessed in the study and showed degradation from -8% to -35% due to hypoxia impacts, depending on the species. Foley et al. (2017a, 2017b) recently applied a bioenergetics approach to determine the importance of dreissenid mussels in round goby diets in Saginaw Bay. He et al. (2015) coupled age-structured stock assessment models and fish bioenergetics models to quantify piscivory patterns during the rapid trophic shift in the main basin of Lake Huron after the alewife decline.

Bioenergetics models have been widely used in single-species management, but need to be linked with other approaches for more integrated management of whole ecosystems, particularly in the face of rapidly changing conditions.

5.3.6 Atlantis Ecosystem Model

The Atlantis Ecosystem Model was developed in Australia by Beth Fulton and her collaborators (https://research.csiro.au/atlantis/) (Fulton et al. 2011). It has now been applied to over 30 marine and freshwater ecosystems around the world, including operational applications by the National Oceanic and Atmospheric Administration in multiple marine systems in the Atlantic, Pacific, and Gulf of Mexico. The processes in this model include an end-to-end approach with a representation of nutrient cycling, ecological processes including competition and predation, and anthropogenic processes (see Figures 41 and 42). This model can represent a three-dimensional, spatially explicit domain. Once the model is calibrated, it can be used to evaluate scenarios of ecosystem response to understand management options and likely responses to various current or future ecosystem stressors.

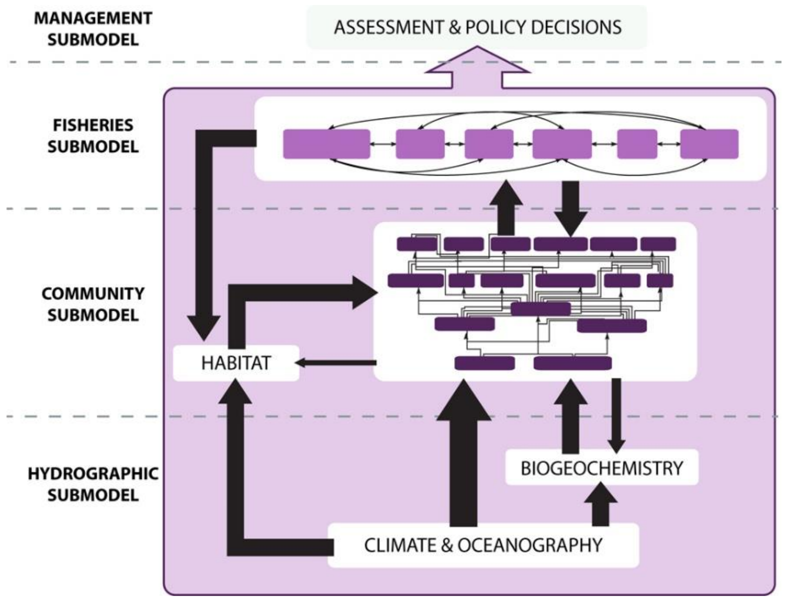

Figure 41. Schematic wiring diagram of the Atlantis model and submodels.
***Source*: https://www.pifsc.noaa.gov/cred/img/framework_of_atlantis_model_med.jpg**

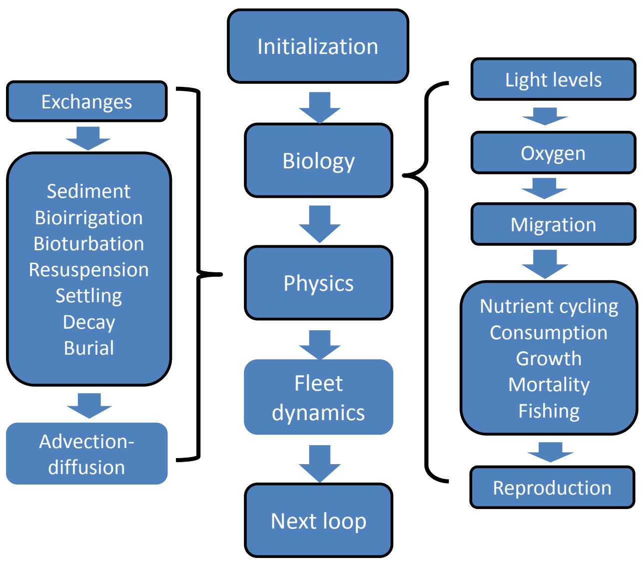

Figure 42. Processes and system components that can be simulated in the Atlantis model.

Lake Michigan is the first freshwater ecosystem where Atlantis has been applied. The grid system used in the model configuration is shown in Figure 43. The model has been used to forecast the invasion and establishment of Asian carp and hydrilla in Lake Michigan. Simulations were of the current conditions without Asian carp and with the carp at three population levels (none, low, high; Zhang et al. 2016a). Atlantis was also used to simulate oxygen concentrations and seasonal depletion in Lake Michigan.

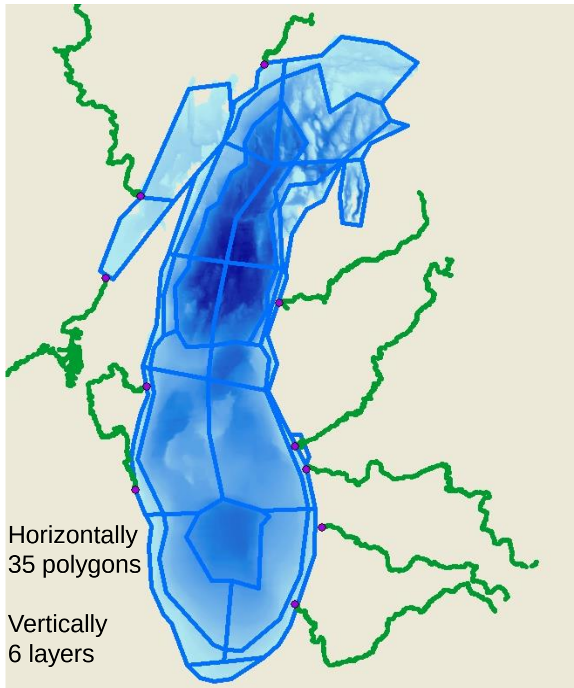

Figure 43. Atlantis model horizontal grid cells used by Zhang et al. (2016a) for Lake Michigan simulations.

An Atlantis model is also in development by the same group for Lake Erie with similar modeling objectives; the model grid is shown below (Figure 44). Another Atlantis model for Lake Huron is in the early stages of development by these researchers.

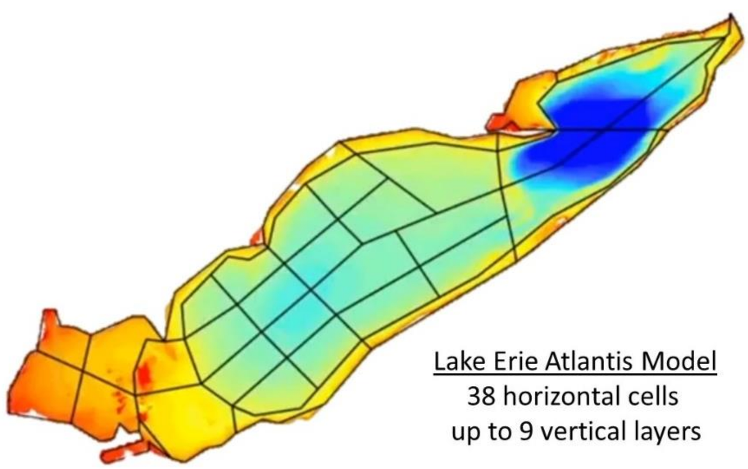

Figure 44. Atlantis model grid for Lake Erie. Source: Zhang, personal communication.

5.3.7 Ecopath with Ecosim

Ecopath with Ecosim (EwE) is free software developed at the University of British Columbia (http://ecopath.org/) that has been downloaded by over 5,000 users over the last 20 years. It has been applied to simulate trophic processes in ecosystems around the world, including the Great Lakes, since the late 1990s. Applications often combine the equilibrium mass balance module (Ecopath) with the dynamic food web module (Ecosim). These process simulations can be used to study the effects of various stressors on a system. For example, the models have been used to study the effects of excessive nutrient loading and invasive species in the Great Lakes (Zhang et al. 2016a). Kitchell et al. (2000) used EwE to evaluate the ecological consequences of a suite of alternative management strategies for Lake Superior predatory fish, incorporating two different sets of life history characteristics.

EwE was used to simulate the effects of changing phosphorus loads, and the effects of dreissenid mussel and reduced alewife biomass on the Saginaw Bay foodweb (Kao et al. 2014; see Figure 45**)**. Scenarios of high, medium, and low phosphorus loads, alewife, and dreissenid biomass (low and no dreissenids) were simulated. This study found that dreissenids have a large impact on lower tropic levels, but a small impact on fish when compared with the impacts of nutrients or alewife biomass changes. The researchers found that with the removal of alewives and reduced dreissenids, the target nutrient loads from 1978 would not sustain the current fishery in Saginaw Bay. In a subsequent study of Lake Huron, Kao et al. (2016) "assess[ed] these [top-down (predation) and bottom-up (resource)] controls on the Lake Huron main basin food web and the 2003 collapse of an invasive pelagic prey fish, alewife," with EwE simulations. Results showed that a combination of top-down and bottom-up controls triggered the alewife collapse. With the current conditions of low nutrients and relatively high quagga mussel densities, it is unlikely that salmonines in Lake Huron will recover.

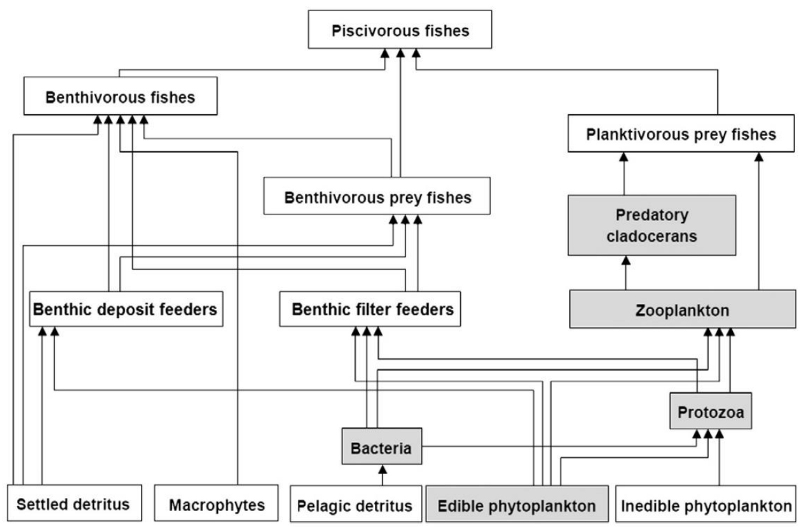

Figure 45. Saginaw Bay food web simulated using Ecopath with Ecosim by Kao et al. (2014).

Zhang et al. (2016b) studied the impact of the possible invasion of Asian carp in Lake Erie. In this study, they simulated 16 fish species (including multiple life stages of walleye, yellow perch, lake trout, and rainbow trout), and other parameters (e.g., birds, benthos, zooplankton, protozoa, bacteria, algae, and detritus), for a total of 47 groups. This study concluded that the lower trophic levels of the food web would be most affected by Asian Carp, but they also pointed out that there is high uncertainty in these forecasts.

Hossain et al. (2012) used EwE to simulate round goby interactions in areas of high and low sediment contamination in Hamilton Harbor on Lake Ontario (results shown in Figure 46). They concluded that "most of the trophic flows are concentrated within the first two trophic levels, while mass fluxes at the higher trophic levels are significantly lower." Hossain et al. (2017) attempted to constrain the uncertainty of the prior EwE model output for the harbor using a simplified version of the model. Based on this analysis, they concluded that microbial recycling of detritus may be more important in this system than previously recognized (see also Vanderploeg et al. 2015).

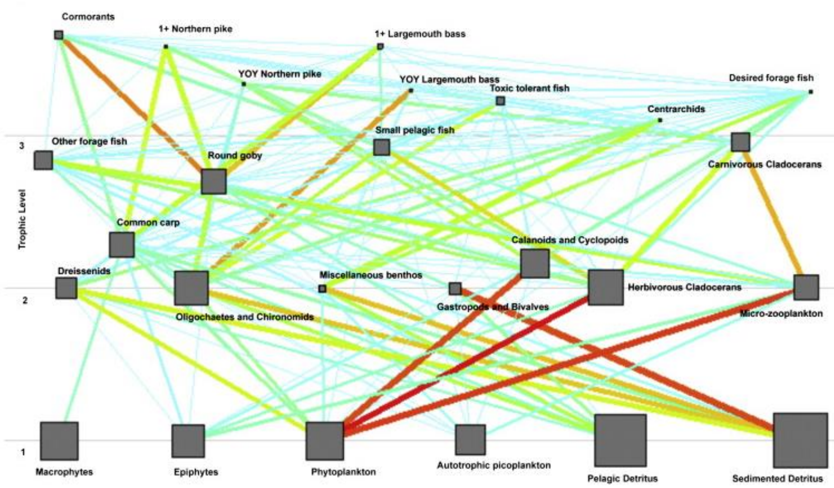

Figure 46. Ecopath with Ecosim topology results for Hamilton Harbor in Lake Ontario (Hossain et al. 2012).

5.4 Summary of Model Review Findings and Recommendations

5.4.1 Findings

- Ecological models of increasing complexity have been applied in the Great Lakes over the last several decades.
- Whole ecosystem models now exist (EwE, Atlantis) that can simulate the full system from nutrients to offshore pelagic predatory fish reasonably well, although data limitations impact the uncertainty of model outputs. Such models can be used to explore bottom-up and top-down relationships.
- Whole ecosystem models have not been routinely applied to offshore fish communities in recent years; the focus has rather been on potential impacts of nearshore invasive species in embayments. In this sense, such models have not actually simulated “whole ecosystems”, but rather relatively homogenous embayments of larger lake ecosystems.
- Research groups that have applied whole ecosystem models in the Great Lakes mostly operate within academia and federal research laboratories, rather than within fishery management agencies, resulting in some incomplete technology transfer to management applications, although agency personnel often participate in the modeling projects.

5.4.2 Recommendations

- Efforts should be made to link the biogeochemical/lower food web modeling and fishery modeling research communities more closely, along with their models.
- Ongoing investment in whole ecosystem modeling (including coupled lower food web-upper food web models), and the essential monitoring efforts that feed the models, is likely to be very useful for evaluating linkages between various nutrient management approaches and corresponding fishery impacts.
- Approaches that better constrain and communicate uncertainty in model outputs should be pursued by researchers in collaboration with resource managers.

- Models that have been developed for recent invasive species research projects should be maintained and adapted for application to other research topics and management applications.

6 Management Implications

As understanding of the evolving relationship between nutrient loading and offshore fish productivity in the Great Lakes has grown, the sophistication and integration of the linked management actions that influence these ecosystems have also increased. Although there is still substantial room for improvement, asking the right questions, updating policies and procedures, and constantly seeking to improve have served the management community well. Here we will discuss a subset of the actions being taken or considered by Canada and the U.S. that are directly related to the topic of this report.

6.1 Nutrient load target setting

The primary drivers for nutrient load reductions in the Great Lakes have been concerns about eutrophication impacts such as harmful algal blooms and low oxygen in bottom waters. Their effects have generally been the most pronounced in shallow embayments such as Green Bay in Wisconsin, Saginaw Bay in Michigan, and the Bay of Quinte in Ontario, as well as Lake St. Clair, although phosphorus that passes through these and similar smaller embayments is an important driver for offshore phytoplankton and fish productivity in the lakes. Lake Erie is unique in that the impacts occur at the basin scale, with harmful algal blooms in the western basin and low oxygen in the central basin common in summer. Toxins produced by blooms in western Lake Erie in August 2014 resulted in the issuance of a "do not drink" order by the City of Toledo, based on concerns about the safety of drinking water for over 400,000 customers. This incident triggered intensified attention to the issue of nutrient loading and eutrophication in the Great Lakes. The occurrence of dense nuisance macroalgae such as *Cladophora* has also become a problem in nearshore areas of what are otherwise low-productivity lakes or basins such as Michigan, Huron, Ontario, and eastern Lake Erie. Development of nutrient management policies aimed at reducing *Cladophora* abundance in these oligotrophic lakes or basins is likely to involve greater consideration of possible offshore impacts on fishery productivity than has been the case for western and central Lake Erie.

6.1.1 Current policy context

Point source reductions in phosphorus loading have not prevented the return of eutrophic conditions to Great Lakes nearshore waters and embayments, so attention has now shifted to mitigation of non-point phosphorus from agriculture. Binational research and policy development have been underway in recent years, including intensive water sampling in lakes and rivers, deployment of monitoring instruments and development of new satellite products to link water quality with algal blooms and hypoxia, modeling to understand drivers and the relative impacts of different load reduction scenarios, and policy development to allocate mitigation resources and create effective incentives and commitments for load reductions across multiple political jurisdictions.

6.1.1.a GLWQA Annex 4

In 2016, responding to commitments made under Annex 4 of the 2012 Great Lakes Water Quality Agreement and based on the results of an ensemble of numerical models, Canada and the U.S. adopted a 40% target for phosphorus load reductions for Lake Erie. This target was based on the results of an ensemble modeling exercise (Annex 4 Objectives and Targets Task Team Final Report to the Nutrients Annex Subcommittee, June 11, 2015). Each country, along with surrounding states and the province of Ontario, have developed domestic action plans that lay out strategies for meeting the new targets. The U.S. Action Plan summarizes the actions that federal agencies and states are taking in the western Lake Erie basin, and provides a means of tracking and reporting progress. As Lake Erie plans are being completed and implemented, attention is shifting to Lake Ontario, where nearshore macroalgae issues will be addressed under Annex 4. Because of the oligotrophic state of offshore waters in Lake Ontario, potential impacts on offshore fish productivity of nutrient reductions to control nearshore *Cladophora* in the basin will be a more important consideration than in western and central Lake Erie; similar concerns exist in eastern Lake Erie.

6.1.1.b Domestic action plans

Draft domestic action plans for Lake Erie were initially released in March and August 2017, for Canada and the U.S., respectively. The U.S. plan included major contributions to load reductions from enhanced agriculture conservation practices (approximately 2/3 of load reduction), along with upgrades to wastewater treatment plants (approximately 1/3 of load reduction), particularly in Detroit. Canada and Ontario released their revised plan in February 2018 (see: https://www.canada.ca/content/dam/eccc/documents/pdf/great-lakes-protection/dap/action_plan.pdf); the final U.S. Action Plan for Lake Erie was released in March 2018 (https://www.epa.gov/sites/production/files/2018-03/documents/us_dap_final_march_1.pdf). The Canadian plan identifies more than 120 actions that are intended to reduce nutrient loads from rural and urban sources, but particular commitments to load reductions associated with the actions are generally not specified.

6.1.1.c Total Maximum Daily Loads

Under the U.S. Clean Water Act, state waters that do not meet certain water quality criteria can be listed as "impaired," which can then trigger a process of determining how the water quality can be improved and the setting, allocation, and enforcement of Total Maximum Daily Loads (TMDLs) for pollutants. A relatively recent and regional-scale example of this is Chesapeake Bay, for which nutrient and sediment TMDLs were finalized in 2010, requiring load reductions of 20% to 25%. Michigan listed its portion of western Lake Erie as "impaired" in 2016. Ohio did the same in 2016 for nearshore waters of the lake, and areas around drinking water intakes, but not for offshore waters. USEPA subsequently reconsidered this decision, after initially approving Ohio's designation. On March 22, 2018, Ohio EPA announced that it was declaring the offshore waters of western Lake Erie impaired as well as the nearshore waters, after consulting with academic and federal experts.

6.2 Fishery management implications

Fish production and fishery yields generally depend on lake primary productivity with highest yields in eutrophic systems and lower yields in oligotrophic areas. Note that this report does not address or give data on fish production per se, nor on yields, which typically refers to harvest. We have presented data on primary production using diagnostic correlates of productivity in each case. Fishery managers generally attempt to balance extractions (yield) and losses (natural mortality) against the complex and varying levels of fish production (recruitment and growth, which rely on food resources). Offshore fishery management for sustainable yields has improved immensely because of coordinated, inter-jurisdictional management. Fishery management is now largely responding to complex changes in fish production, as driven by changes in environmental conditions and habitats that can be directly influenced by the actions of water quality and land management practices. This management is most effective with coordinated commitments of all relevant agencies to a formal, basin-wide, common goal under the Joint Strategic Plan for Management of Great Lakes Fisheries, as implemented through lake committees with coordination by the GLFC to achieve fish community objectives (FCOs) in each lake.

Watershed features and locations affect nutrient delivery and nearshore environmental conditions affecting essential habitats (or functional habitats) for fish production. These habitats are affected by land management practices. Nutrient load management can indirectly affect fishery management in various ways such as influencing quantity and size composition of targeted fish species produced from essential habitats. Behavior or distribution of targeted fish under varying environmental conditions is affected by nutrient-driven changes in water clarity, hypoxic zones, and prey availability. For example, fishery managers in Lakes Huron and Michigan are especially concerned about nutrient levels given declines in lake whitefish populations from poor recruitment under existing environmental conditions (dreissenid feeding). Lake whitefish are a key species for commercial fisheries in these lakes and managers would likely welcome increases in nutrient levels to support fish production in the presence of dreissenids. Fishery managers in Lake Ontario and eastern Lake Erie have similar concerns about lake productivity and fish production.

6.3 Invasive species management implications

Distinct from the management of nutrients and the Great Lakes fishery are the attempts to protect the lakes from new non-native species that could damage their food webs, or to reduce the negative impact of species that have already become established. Several species and classes of organisms that currently impact or threaten to impact offshore fish productivity are briefly described here, along with implications of nutrient reduction for their management.

6.3.1 Dreissenid mussels

As described previously, dreissenid mussels have had a major impact on Great Lakes nutrient transport, trapping substantial nutrients on the lake bed in the nearshore and deep offshore zones of all lakes except Superior. Despite research and recent approved use of mussel control agents for environmental application, no economically viable and ecologically acceptable means currently exists for reducing mussel abundance at scale in the Great Lakes. Application of mussel control agents at more local scales is being discussed (e.g., spawning habitat used by lake trout, lake whitefish, cisco). There is interest in learning more about its efficacy in Great Lakes settings and about possible indirect effects of mussel die-offs. Despite these possible local applications, mussels are likely to persist indefinitely into the future in the lakes. In order to effectively manage systems that are strongly influenced by mussels, it is important to continue to monitor their distribution and abundance in order to predict their changing role in disruption of nutrient transport to offshore regions and to research the effectiveness of their nutrient sequestration at various scales of time and space. This information is critical for constraining ecosystem models that link lake biogeochemistry with the lower and upper food webs. Mussel abundance and grazing data do not currently exist at adequate resolution to drive models that can incorporate them for most parts of the lakes.

6.3.2 Sea lamprey

Sea lampreys, which prey as parasites on most species of large Great Lakes fish, have been actively managed by annual application of lampricides to tributaries (now approximately 200 to 250) that serve as spawning sites and larval habitat beginning in 1958. Nutrient reduction in tributaries may have several interactions with lamprey populations and activity that could complicate their management and impacts on offshore fisheries. First, improved water quality in tributaries themselves may enhance the habitat of lamprey early life stages, leading to higher recruitment. This effect would be working in tandem with barrier removal for increased fish habitat, which also can open more habitat to lamprey reproduction in some areas. Second, decreased nutrient delivery to the lower food web in the offshore of lakes can stress or reduce fish populations, which in turn can make them more vulnerable to lamprey predation based on shifting predator-prey ratios. Third, fluctuations in funding for lamprey control programs could combine with offshore primary productivity reduction due to low nutrient delivery to amplify fishery impacts in low-resilience systems.

6.3.3 Round goby

Round gobies have effectively colonized much of the Great Lakes nearshore habitat since their appearance in the lakes in 1990. In the process, they have become an important food source for predatory fish in all of the lakes. Future fishery management must necessarily include consideration of round gobies at this point, although monitoring their abundance has proven challenging given the differences in their habitat and behavior from other Great Lakes prey fish. As with mussels, which are also an important part of their diet, accurate and timely round goby data are important for constraining ecosystem models that span nutrients to predatory fish. Any impacts on nearshore prey fish productivity, including that of round gobies, caused by reduced nutrient loading, are likely to impact offshore species as well that now prey on round gobies.

6.3.4 Watch list species

The Great Lakes Aquatic and Nonindigenous Species Information System (GLANSIS; https://www.glerl.noaa.gov/glansis/index.html) provides profiles, lists, and maps for species present in the Great Lakes basin. GLANSIS information and approaches have recently been applied to identification and risk analysis of "watch list" species that pose a threat to the Great Lakes, but are not yet present in the basin (Davidson et al. 2017). Along with this activity, there have also been developments in the reduction of risk as well as preparation for rapid response to new introductions at the state and regional level (Lodge et al. 2016)). As noted above for the species discussed, nutrient management and fishery management actions should be developed in an integrated way, with full consideration of positive or negative feedbacks driven by expanding ranges or populations of existing non-native species in the lakes. Along with this, risk reduction and quantitative impact analysis of new species introductions, such as has been done for Asian carp (Zhang et al. 2016a and 2016b)), should be pursued.

7 Findings and Recommendations

This assessment sought to determine the current state of knowledge of the relationship between phosphorus loading and upper food web productivity within the Great Lakes ecosystems. The project tasks included a literature review, an update of Bunnell et al. (2014) data, and a review of available food web models. A high-level summary of the resulting findings, gaps, and recommendations follows.

7.1 Findings

Several important findings, particularly derived from the review of updated phosphorus concentration data and fish data from all the lakes, are itemized below.

- Changes in average spring total phosphorus concentrations and abundance of prey fish and predatory fish have shown continued variation but few strong trends from about 2005 to 2010, and continuing over the five years since the Bunnell et al. (2014) data compilation and analysis (typically including data up to 2010; new data through 2015 in most cases). This suggests that most lakes may be approaching a steady state with respect to mussel populations and impacts, along with other recent drivers of primary productivity change.
- Multiple lines of evidence show a major decline in the productivity of the lower food web in Lake Michigan and Lake Huron, and to a lesser extent in Lake Ontario. Impacts on the upper food web have varied by lake and over time, and are complicated by the roles of predation and recruitment at this level.
- Trapping of nutrients by mussels has increased benthic productivity and decreased pelagic primary productivity in Lake Michigan, and in other lakes where dreissenids dominate the benthic fauna.
- Round gobies continue to play an important but not well quantified role as a competitor for food with other prey fish, as well serving as a food source for upper trophic levels in the Great Lakes, partially offsetting the impacts of declining prey fish in many of the lakes, and returning some mussel biomass to upper trophic levels based on mussel predation by gobies.
- The virtual disappearance of the primary benthic food source *Diporeia* from all lakes except Superior has compounded the effects of phosphorus shunting by mussels on offshore fish productivity.
- The collaborative and cooperative management of the offshore commercial and recreational fishery is relatively healthy in most of the Great Lakes, despite ongoing variability in offshore fish productivity.
- Ecological models of increasing complexity have been successfully applied to simulate and help explain patterns observed in the Great Lakes over the last several decades, although important aspects of the full role of nutrient shunting by mussels in overall lake productivity remain to be worked out. At this time, model use to support fishery management decisions has been somewhat limited in favor of more direct measures of community and population condition (i.e., stock assessment data). Use of models within a framework that evaluates alternative fishery management actions (e.g., stocking, harvest) and policies may enhance their usefulness and incorporation into formal management frameworks.

7.2 Gaps

Although significant progress has been made in understanding the linkage between nutrients and offshore fish productivity in the last 10 years, major gaps in understanding remain. A group of research priorities identified by the GLFC that are broadly consistent with the topic of this assessment include, "Quantification of energy and nutrient dynamics in Great Lakes food webs, and the role of food web members in structuring resilient communities and ecosystems" (http://glfc.org/pubs/pdfs/research/FRP%20Theme%20Conceptual%20Diagram.pdf).

Some of the data and knowledge gaps identified in the current assessment are listed below.

- The scaling of grazing impacts of mussels versus nutrient load reductions on offshore primary production are not well understood, particularly on seasonally dynamic species assemblages and after summer stratification isolates phytoplankton in the upper water column from mussel grazing.
- The relative impacts of predation on prey fish (top-down) versus decreased food supply (bottom-up) are not well known in most lakes.
- In-lake TP concentrations often do not match predictions based on available loading data alone, and nutrient loading data and models need to be updated at appropriate scales. The processes by which spring phosphorus loads are transformed in summer primary productivity in offshore areas are not clear, including the transformation to bioavailable phosphorus during this lag period.
- The importance of mussel/round goby/macroalgae interactions is recognized, but not well quantified in nearshore regions; nor is its influence on offshore phytoplankton and fish productivity well constrained. Developing nutrient management approaches to control nearshore macroalgae growth may require a compromise in some lakes and basins that also allows for optimal fish production.
- Modeling methods for determining the relative effectiveness and impact of alternative phosphorus reduction strategies on offshore fish productivity are not well developed, so they should be applied within an adaptive management framework.

7.3 Recommendations

Areas where resources might be effectively applied and further policy development could be productively undertaken are summarized here.

- Improve coordination among water quality (bottom-up control) and fishery (top-down control) managers to clarify (i.e., reduce uncertainty in) the relationship between land and watershed controls on nutrients and their effect on offshore fishery production and conditions. Monitoring should be optimized to track lake sub-basin and lake-wide performance standards for acceptable impacts of nutrient-related actions on offshore fishery resources.
- Further development and application of well-constrained ecosystem models that link biogeochemistry, lower food web productivity, nearshore ecology, and offshore fish productivity, along with maintenance and enhancement of associated monitoring programs to meet the greater data demands of ecosystem models, would be a valuable component of an integrated ecosystem adaptive management system.
- Adding nearshore monitoring of nutrients, chlorophyll a, and zooplankton across the basin, and linking and coordinating the timing of data processing and reporting of all lower trophic level

data to annual fishery stock assessment metrics, may improve our ability to connect and adapt nutrient-related actions to fishery production and conditions the following season.

- Development of optimized monitoring for oligotrophic lakes and basins that are most at risk from changes that could be induced by nutrient management (Huron, Michigan, Ontario, and eastern basin of Erie).

8 References Cited

Allerton, M. L., Gudimov, A., Cheng, V., Richards, A., and Arhonditsis, G. B. 2016. Bayesian watershed modelling to support adaptive management in the southeastern Georgian Bay Area. International Association for Great Lakes Research 59th Annual Conference on Great Lakes Research: Abstracts, June 6-10, 2016, University of Guelph, Ontario.

Allinger, L.E., and E.D. Reavie. 2013. The ecological history of Lake Erie as recorded by the phytoplankton community. *Journal of Great Lakes Research*, 39(3):365-382.

Althouse, B., Higgins, S., and Vander Zanden, M. J. 2014. Benthic and planktonic primary production along a nutrient gradient in Green Bay, Lake Michigan, USA. *Freshwater Science*, 33(2): 487-498.

Anneville, O., C. Vogel, J. Lobry, and J. Guillard. 2017. Fish communities in the Anthropocene: detecting drivers of changes in the deep peri-alpine Lake Geneva. *Inland Waters*, 7(1):65-76.

Arend, K.K., Dmitry Beletsky, Joseph V. Depinto, Stuart A. Ludsin, James J. Roberts, Daniel K. Rucinski , Donald Scavia, David J. Schwab, and Tomas O. Höök. 2010. Seasonal and interannual effects of hypoxia on fish habitat quality in central Lake Erie. *Freshwater Biology*. 1-18.

Arhonditsis, G.B., Kim, D.K., Shimoda, Y., Zhang, W., Watson, S., Mugalingam, S., Dittrich, M., Geater, K., McClure, C., Keene, B. and Morley, A. 2016. Integration of best management practices in the Bay of Quinte watershed with the phosphorus dynamics in the receiving waterbody: What do the models predict? *Aquatic Ecosystem Health & Management*, 19(1):1-18.

Ashley, K., Thompson, L.C., Lasenby, D.C., McEachern, L., Smokorowski, K.E. and Sebastian, D. 1997. Restoration of an interior lake ecosystem: the Kootenay Lake fertilization experiment. *Water Quality Research Journal of Canada*, 32(2):295-323.

Auer, M.T., L.M. Tomlinson, S.N. Higgins, S.Y. Malkin, E.T. Howell, and H. A. Bootsma. 2010. Great Lakes Cladophora in the 21st century: same algae—different ecosystem. *J. Great Lakes Research*, 36:248–255.

Baldridge, A.K., and T.F. Nalepa. 2015. The status of dreissenid mussels in the Great Lakes and suggested future research directions. Presentation at International Association for Great Lakes Research Conference on Great Lakes Research, May 27, 2015.

Barbiero, R., K. Schmude, B. Lesht, C. Riseng, G. Warren, and M. Tuchman. 2011a. Trends in Diporeia populations across the Laurentian Great Lakes, 1997-2009. *J. Great Lakes Research*, 37(1): 9-17.

Barbiero, R.P., B.M. Lesht, and G.J. Warren. 2011b. Evidence for bottom-up control of recent shifts in the pelagic food web of Lake Huron. *J. Great Lakes Research*. 37(1):78-85.

Barbiero, R.P., B.M. Lesht, and G.J. Warren. 2012. Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. *J. Great Lakes Research*, 38(2):368–380.

Barbiero, R.P., B.M. Lesht, and G.J. Warren. 2014. Recent changes in the offshore crustacean zooplankton community of Lake Ontario. *J. Great Lakes Research*, 40(4):898-910.

Barbiero, R. P., Balcer, M., Rockwell, D. C., & Tuchman, M. L. 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(5), 816-828.

Bence, James (Michigan State University). "Lake Huron Chinook Salmon Biomass Estimates Request." Personal communication received by Nate Jacobson, 11/3/17.

Bierman, V.J., Jr., 1980. *A comparison of models developed for phosphorus management in the Great Lakes. Phosphorus Management Strategies for Lakes*. R.C. Loehr, C.S. Martin, W. Rast, (eds.). Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

Binder, T.R., Farha, S.A., Thompson, H.T., Holbrook, C.M., Bergstedt, R.A., Riley, S.C., Bronte, C.R., He, J. and Krueger, C.C. 2018. Fine-scale acoustic telemetry reveals unexpected lake trout, *Salvelinus namaycush*, spawning habitats in northern Lake Huron, North America. *Ecology of Freshwater Fish*, 27(2):594-605.

Binding, C.E., T.A. Greenberg, S.B. Watson, S. Rastin, and J. Gould. J. 2015. Long term water clarity changes in North America's Great Lakes from multi-sensor satellite observations. *Limnology and Oceanography*, 60:1976-1995.

Birkett, K., Lozano, S.J. and Rudstam, L.G. 2015. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994–2008. *Aquatic Ecosystem Health & Management*, 18(1):76-88.

Bocaniov, S.A., R.E. Smith, C.M. Spillman, M.R. Hipsey, and L.F. Leon. 2014. The nearshore shunt and the decline of the phytoplankton spring bloom in the Laurentian Great Lakes: insights from a three-dimensional lake model. *Hydrobiologia*, 731(1):151-172.

Bootsma, H.A., Rowe, M.D., Brooks, C.N., Vanderploeg, H.A. 2015. Commentary: The need for model development related to Cladophora and nutrient management in Lake Michigan. *J. Great Lakes Res*. 41 (Supplement 3), 7–15.

Briggs, T. and T. Howell. 2015. Investigations into Water Quality and Ecological Conditions in Eastern Georgian Bay (Research Presentation 9). Abstract in ECCC (Environment and Climate Change Canada). 2015. State of Lake Huron Workshop Proceedings, Great Lakes Maritime Heritage Center, Alpena, Michigan, U.S.A., November 4-5, 2015.

Bunnell, D.B. [ed.]. 2012. The state of Lake Michigan in 2011. Great Lakes Fish. Comm. Spec. Pub. 12-01.

Bunnell, D.B., R.P. Barbiero, S.A. Ludsin, C.P. Madenjian, G.J. Warren, D.M. Dolan, T.O. Brenden, O.T. Gorman, J.X. He, T.H. Johengen, B.F. Lantry, B.M. Lesht, T.F. Nalepa, S.C. Riley, C.M. Riseng, T.J. Treska, I. Tsehaye, M.G. Walsh, D.M. Warner, and B.C. Weidel. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *BioScience*, 64:26-39.

Bunnell, David (USGS). "Lake Michigan Data." Personal communication received by Doug Bradley, 8/22/17.

Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S.M. and Engelhard, G. H. 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24(1).

Carlsson, N. O., Sarnelle, O., and Strayer, D. L. 2009. Native predators and exotic prey–an acquired taste? *Frontiers in Ecology and the Environment*, 7(10), 525-532.

Carrick, H.J., Butts, E., Daniels, D., Fehringer, M., Frazier, C., Fahnenstiel, G.L., Pothoven, S. and Vanderploeg, H.A. 2015. Variation in the abundance of pico, nano, and microplankton in Lake Michigan: Historic and basin-wide comparisons. *Journal of Great Lakes Research*, 41(3):66-74.

Caudron, A., E. Lasne, C. Gillet, J. Guillard, and A. Champigneulle. 2014. Thirty years of reoligotrophication do not contribute to restore self-sustaining fisheries of Arctic charr, *Salvelinus alpinus*, in Lake Geneva. *Fisheries Research*, 154:165-171.

Cha, Y., C.A. Stow, T.F. Nalepa, and K.H. Reckhow. 2011. Do invasive mussels restrict offshore phosphorus transport in Lake Huron? *Environmental Science & Technology*, 45(17):7226-7231.

Chapra, S.C. 1977. Total phosphorus model for the Great Lakes. *Journal of the ASCE Environmental Engineering Division,* 103(2):147-161.

Chapra, S.C., Boehlert, B., Fant, C., Bierman Jr, V.J., Henderson, J., Mills, D., Mas, D.M., Rennels, L., Jantarasami, L., Martinich, J. and Strzepek, K.M. 2017. Climate change impacts on harmful algal blooms in US freshwaters: A screening-level assessment. *Environmental Science & Technology*, 51(16), pp.8933-8943.

Chapra, S. C., Dove, A., & Warren, G. J. 2012. Long-term trends of Great Lakes major ion chemistry. *Journal of Great Lakes Research*, 38(3), 550-560.

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J., and Rudnika, S. 1997. The Round Goby, *Neogobius melanostomus* (Pallas), a Review of European and North American Literature. Zion, IL: Illinois-Indiana Sea Grant Program and Illinois Natural History Survey.

Chen, C.W., M. Lorenzen, and D.J. Smith. 1975. A comprehensive water quality-ecological model for Lake Ontario. Tetra Tech, Incorporated.

Christensen, N.L., A. Bartuska, J.H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee, 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecological Applications*, 6:665-691.

Clark, R.D., Bence, J.R., Claramunt, R.M., Clevenger, J.A., Kornis, M.S., Bronte, C.R., Madenjian, C.P. and Roseman, E.F. 2017. Changes in movements of Chinook Salmon between Lakes Huron and Michigan after alewife population collapse. *North American Journal of Fisheries Management*, 37(6):1311-1331.

Clark, R.D., Bence, J.R., Claramunt, R.M., Johnson, J.E., Gonder, D., Legler, N.D., Robillard, S.R. and Dickinson, B.D. 2016. A spatially explicit assessment of changes in Chinook Salmon fisheries in Lakes Michigan and Huron from 1986 to 2011. *North American Journal of Fisheries Management*, 36(5):1068-1083.

Collingsworth P.D., D.B. Bunnell, C.P. Madenjian, and S.C. Riley. 2014. Comparative recruitment dynamics of alewife and bloater in Lakes Michigan and Huron. *Trans Am Fish Soc*, 143:294–309. doi:10.1080/00028487.2013.833986.

Collingsworth, P.D., D.B. Bunnell, M.W. Murray, Y. Kao, Z.S. Feiner, R.M. Claramunt, B.M. Lofgren, T.O. Höök, and S.A. Ludsin. 2017. Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America. *Rev. Fish. Biol. Fisheries*, 27(2):363-391.

Crane, D. P., Farrell, J. M., Einhouse, D. W., Lantry, J. R., & Markham, J. L. 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. *Freshwater Biology*, 60(1):111-124.

Davidson, A.D., Fusaro, A.J., Sturtevant, R.A., Rutherford, E.S. and Kashian, D.R. 2016. Development of a risk assessment framework to predict invasive species establishment for multiple taxonomic groups and vectors of introduction. *Management of Biological Invasions*, 8(1):25–36

deBarros, C. 2016. *Lake Ontario – State of Nutrient Science*. Prepared for the Lake Ontario Nutrient Task Team.

Denef, V.J., Carrick, H.J., Cavaletto, J., Chiang, E., Johengen, T.H. and Vanderploeg, H.A. 2017. Lake bacterial assemblage composition is sensitive to biological disturbance caused by an invasive filter feeder. mSphere, 2(3):e00189-17.

Deslauriers, D., Chipps, S.R., Breck, J.E., Rice, J.A. and Madenjian, C.P. 2017. Fish Bioenergetics 4.0: An R-based modeling application. *Fisheries*, 42(11):586-596.

DeVanna-Fussell, K.M.D., R.E. Smith, M.E. Fraker, L. Boegman, K.T. Frank, T.J. Miller, J.T. Tyson, K.K. Arend, D. Boisclair, S.J. Guildford, and R.E. Hecky. 2016. A perspective on needed research, modeling, and management approaches that can enhance Great Lakes fisheries management under changing ecosystem conditions. *J. Great Lakes Research*, 42(4):743-752.

Di Toro, D.M., D.J. O'Connor, J.L. Mancini, and R.V. Thomann. 1973. A preliminary phytoplankton-zooplankton-nutrient model of Western Lake Erie. In *Systems Analysis & Simulation in Ecology*. Volume 3. Academic Press.

Dove, A. and S.C. Chapra. 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. *Limnology and Oceanography*, 60:696-721.

Dove, Alice (ECCC). "Data Request for IJC_Funded Project." Personal communication received by Nate Jacobson, 2/12/2018.

Driscoll, Z.G., H.A. Bootsma, and E. Christiansen. 2015. Zooplankton trophic structure in Lake Michigan as revealed by stable carbon and nitrogen isotopes. *J. Great Lakes Research*, 41(Supplement 3):104-114.

ECCC and USEPA (Environment and Climate Change Canada and the U.S. Environmental Protection Agency). 2017. *State of the Great Lakes 2017 Technical Report*. Cat No. En161- 3/1E-PDF. EPA 905-R-17-001. Available at binational.net

ECCC (Environment and Climate Change Canada). 2015. State of Lake Huron Workshop Proceedings, Great Lakes Maritime Heritage Center, Alpena, Michigan, U.S.A., November 4-5, 2015.

Eero, M., H.C. Andersson, E. Almroth-Rosell, and B.R. MacKenzie. 2016. Has eutrophication promoted forage fish production in the Baltic Sea? *Ambio.*, 45(6):649-660.

Elgin, A.K., Burlakova, L.E., Karatayev, A.Y., Mehler, K., and Nalepa, T.F. 2017. Quagga mussel body condition and size distribution inform recent Lake Michigan population trends. Abstract. In: International Association for Great Lakes Research Conference on Great Lakes Research, May 15-19, 2017, Detroit, MI.

Environment and Climate Change Canada. 2015. *Lake Huron Partnership Cooperative Science and Monitoring Synthesis*. Prepared by LimnoTech.

Environment and Climate Change Canada. 2015. State of Lake Huron Workshop Proceedings, Great Lakes Maritime Heritage Center, Alpena, Michigan, U.S.A., November 4-5, 2015. Prepared by LimnoTech.

Environment and Climate Change Canada. 2017. Canadian Environmental Sustainability Indicators: Phosphorus levels in the offshore waters of the Great Lakes. Available at: http://www.ec.gc.ca/indicateurs-indicators/default.asp?lang=en&n=A5EDAE56-1.

Evans, M.A., G. Fahnenstiel, and D. Scavia. 2011. Incidental oligotrophication of North American Great Lakes. *Environ. Sci. Technol.*, 45(8):3297-3303.

Fahnenstiel, G.L., S. Pothoven, T. Nalepa, H. Vanderploeg, D. Klarer, and D. Scavia. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *J. Great Lakes Research,* 36(Supplement 3):20–29.

Fahnenstiel, G.L., M.J. Sayers, R.A. Shuchman, F. Yousef, and S.A. Pothoven. 2016. Lake-wide phytoplankton production and abundance in the Upper Great Lakes: 2010-2013. *J. Great Lakes Research*, 42(3): 619-629.

Fielder, David (Michigan DNR). "Lake Huron predatory fish data for Bunnell et al (2014) update task in IJC project." Personal communication received by Nate Jacobson, 10/16/17.

Finger, D., A. Wuest, and P. Bossard. 2013. Effects of oligotrophication on primary production in peri-alpine lakes. *Water Resources Research*, 49:4700-4710, doi:10.1002/wrcr.20355.

Foley, C.J., S.R. Andree, S.A. Pothoven, T.F. Nalepa, and T.O. Höök. 2017a. Quantifying the predatory effect of round goby on Saginaw Bay dreissenids. *J. Great Lakes Research*, 43(1):121-131.

Foley, C.J., M.L. Henebry, A. Happel, H.A. Bootsma, S.J. Czesny, J. Janssen, D.J. Jude, J. Rinchard, and T.O. Höök. 2017b. Patterns of integration of invasive round goby (Neogobius melanostomus) into a nearshore freshwater food web. *Food Webs*, 10:26-38.

Forage Task Group. 2016. Report of the Lake Erie Forage Task Group, March 2017. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor, Michigan, USA.

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D. and Smith, D.C. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries*, 12(2):171–188.

GLFC (Great Lakes Fishery Commission). 2013. *The state of Lake Huron in 2010*. Riley, S.C. (ed.), Great Lakes Fish. Comm. Spec. Pub. 13-01. 106 p. http://www.glfc.org/pubs/SpecialPubs/Sp13_01.pdf

Glyshaw, P. W., Riseng, C. M., Nalepa, T. F., and Pothoven, S. A. 2015. Temporal trends in condition and reproduction of quagga mussels (*Dreissena rostriformis bugensis*) in southern Lake Michigan. *J. Great Lakes Res*. 41 (Supplement 3), 16-26.

Gorman, O.T. 2017. Great Lakes Prey Fish Populations: A Cross-Basin Overview of Status and Trends Based on Bottom Trawl Surveys, 1978-2016. In USGS, Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016 (pp. 13-24). Available at http://www.glfc.org/pubs/lake_committees/common_docs/Compiled%20Reports%20from%20USGS%202017.pdf.

Gorman, O.T., and B.C. Weidel. 2016. Great Lakes Prey Fish Populations: A Cross-Basin Overview of Status and Trends Based on Bottom Trawl Surveys, 1978-2015. In USGS (U.S. Geological Survey). 2016. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2015. Available from http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2016.pdf

Great Lakes Fishery Commission. 2017. A mid-decade review of progress under a Strategic Vision of the Great Lakes Fishery Commission 2011-2020 [online]. Available from: http://www.glfc.org/pubs/misc/SVReview2017-01.pdf [accessed 07 June 2017].

Great Lakes Fishery Commission. 2016. *Lake Erie Committee Forage Fish Task Group Executive Summary Report*. http://www.glfc.org/pubs/lake_committees/erie/FTG_docs/annual_reports/ExeSummaryFTG2016.pdf

Great Lakes Fishery Commission. 2017. *Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016*. Prepared by the U.S. Geological Survey, Great Lakes Science Center.

Guthrie, A.G. 2017. *Assessing Ecosystem-Based Management in the Great Lakes Basin*. M.S. thesis, Michigan State University, ProQuest Dissertations Publishing, 10641079.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison, Wisconsin.

Hartig, J.H., Zarull, M.A, Heidtke, T.M. and Shah, H., 1998. Implementing ecosystem-based management: Lessons from the Great Lakes. *Journal of Environmental Planning and Management*, 41:45-75.

He, Ji (Michigan Dept. of Natural Resources). "Lake Huron predatory fish data for Bunnell et al (2014) update task in IJC project." Personal communication received by Nate Jacobson, 10/24/17.

He, J.X., J.R. Bence, C.P. Madenjian, S.A. Pothoven, N.E. Dobiesz, D.G. Fielder, J.E. Johnson, M.P. Ebener, R.A. Cottrill, L.C. Mohr, and S.R. Koproski. 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(1):7-23.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: A consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci*., 61: 1285–1293.

Higgins, S., S. Malkin, Y., E.T. Howell, S.J. Guildford, L.M. Campbell, V. Hiriart-Baer, and R.E. Hecky. 2008. An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. *J. Phycol*., 44:839-854.

Holeck, K. T., Rudstam, L. G., Watkins, J. M., Luckey, F. J., Lantry, J. R., Lantry, B. F., and Johnson, T. B. 2015. Lake Ontario water quality during the 2003 and 2008 intensive field years and comparison with long-term trends. *Aquatic Ecosystem Health and Management*, 18(1), 7-17.

Höök, T.O., E.S. Rutherford, T.E. Croley, D.M. Mason and C.P. Madenjian. 2008. Annual variation in habitat-specific recruitment success: Implications from an individual-based model of Lake Michigan alewife. *Canadian Journal of Fisheries and Aquatic Sciences*, 65:1402-1412.

Horvatin, P. 2015. Long-term Trends in Lake Huron's Lower Food Web (Research Presentation 14). Abstract in ECCC (Environment and Climate Change Canada). 2015. State of Lake Huron Workshop Proceedings, Great Lakes Maritime Heritage Center, Alpena, Michigan, U.S.A., November 4-5, 2015.

Hossain, M., Stewart, T.J., Arhonditsis, G.B., van Oevelen, D., Minns, C.K. and Koops, M.A. 2017. Uncertainty assessment of trophic flows in Hamilton Harbour: A linear inverse modelling analysis. *Aquatic Ecosystem Health & Management*, 20(3):265-277.

Hossain, M., Arhonditsis, G.B., Koops, M.A. and Minns, C.K. 2012. Towards the development of an ecosystem model for the Hamilton Harbour, Ontario, Canada. *Journal of Great Lakes Research*, 38(4):628-642.

Howell, T. 2015. Monitoring of Water Quality in the Nearshore of Eastern Georgian Bay by the Great Lakes Group of MOECC. Presented at the State of Lake Huron Meeting, November 4 and 5, 2015. Available at ftp://ftp.cciw.ca/incoming/New%20Folder%20(4)/10_EMRB_GLunit_Lake_Huron_GB_work_2015draft.pdf

Howell, T. 2018. Cladophora (green algae) and dreissenid mussels over a nutrient loading gradient on the north shore of Lake Ontario. Journal of Great Lakes Research, 44(1):86-104.

Ivan, Lori, Edward S. Rutherford, Doran Mason, Hongyan Zhang, Michael Hoff. 2012. Potential impact of Asian carps in the Great Lakes: An IBM Community Model approach. 142nd Annual Meeting of the American Fisheries Society, Minneapolis–St. Paul, MN, August 19-23, 2012, abstract # W-B-7.

Jeppesen, E., M. Søndergaard, J.P. Jensen, K. Havens, O. Anneville, L. Carvalho, et al. 2005. Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology*, 50(10):1747-1771.

Johnson, T. B., Bunnell, D. B., & Knight, C. T. 2005. A potential new energy pathway in central Lake Erie: the round goby connection. *Journal of Great Lakes Research*, 31, 238-251.

Jones, L.A., Drake, D.A.R., Mandrak, N.E., Jerde, C.L., Wittmann, M.E., Lodge, D.M., van der Lee, A.S., Johnson, T.B., and Koops, M.A. 2017. Modelling Survival and Establishment of Grass Carp, Ctenopharyngodon idella, in the Great Lakes Basin. *DFO Can. Sci. Advis. Sec. Res. Doc*. 2016/101, 52 p.

Kao, Y.C., S. Adlerstein, and E. Rutherford. 2014. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: An Ecopath and Ecosim analysis. *J. Great Lakes Research*, 40 (Supplement 1):35-52.

Kao, Y.C., S.A. Adlerstein, and E.S. Rutherford. 2016. Assessment of top-down and bottom-up controls on the collapse of Alewives (*Alosa pseudoharengus*) in Lake Huron. *Ecosystems*, 19:803-831.

Kao, Y. C. 2015. *Modeling the Effects of Climate Change, Nutrients, and Invasive Species on Lake Huron Food Webs* (Doctoral dissertation, University of Michigan).

Kao, Y.C., M.W. Rogers, and D.B. Bunnell. 2017. Evaluating stocking efficacy in an ecosystem undergoing oligotrophication. *Ecosystems*. doi: 10.1007/s10021-017-0173-5.

Karatayev, A. Y., L.E. Burlakova, K. Mehler, S.A. Bocaniov, P.D. Collingsworth, G. Warren, R.T. Kraus, & E.K. Hinchey. 2017. Biomonitoring using invasive species in a large Lake: Dreissena distribution maps hypoxic zones. Journal of Great Lakes Research, In Press, Corrected Proof.

Karatayev, V.A., L.G. Rudstam, B.C. Weidel, J. Watkins, and M.G. Walsh. 2014. Monitoring the ecological impacts of Dreissena: characterizing drivers and gradients of density, biomass, and population structure in Lake Ontario. In Abstracts of Lake Ontario 2013 CSMI Papers submitted to the IAGLR 2014 Conference. ftp://ftp.dec.state.ny.us/dow/GreatLakesProgram/LOWG2014-03-05/10.CSMI%20abstracts%20for%20IAGLR%202014.pdf

Kayle, K.A., and Murray, C. 2017. Lake Erie's central basin. *In The state of Lake Erie in 2009. Edited by* J.L. Markham and R.L. Knight [online]. Available from: http://www.glfc.org/pubs/SpecialPubs/Sp17_01.pdf [accessed 25 July 2017]

Kayle, K, K. Oldenburg, C. Murray, J. Francis, and J. Markham. 2015 Lake Erie Walleye Management Plan : 2015-2019. Lake Erie Committee, GLFC, 2015.

Kinnunen, Ronald. Great Lakes prey fish populations declining. http://msue.anr.msu.edu/news/great_lakes_prey_fish_populations_declining_msg17_kinnunen17. Posted February 28, 2017, Michigan State University Extension, Michigan Sea Grant.

Kitchell, J.F., Cox, S.P., Harvey, C.J., Johnson, T.B., Mason, D.M., Schoen, K.K., Aydin, K., Bronte, C., Ebener, M., Hansen, M. and Hoff, M. 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. *Ecosystems*, 3(6):545-560.

Kitchell, J.F., Stewart, D.J. and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Board of Canada*, 34(10):1922-1935.

Krueger, C.C. and Marsden, J.E. 2007. Sea lamprey research: balancing basic and applied research, and using themes to define priorities. *Journal of Great Lakes Research*, 33(sp2):1-6.

Kuczynski, A., Auer, M.T., Brooks, C.N. and Grimm, A.G. 2016. The Cladophora resurgence in Lake Ontario: characterization and implications for management. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(6):999-1013.

Lake Erie Walleye Task Group. 2017. Report for 2016 by the Lake Erie Walleye Task Group. Presented to: Standing Technical Committee, Lake Erie Committee, Great Lakes Fishery Commission, Ypsilanti, Michigan; March 23-24, 2017. Available at http://www.glfc.org/pubs/lake_committees/erie/WTG_docs/annual_reports/WTG_report_2017.pdf.

Landrum, P. F., & Nalepa, T. F. 1998. A Review of the Factors Affecting the Ecotoxicology of Diporeia spp. Journal of Great Lakes Research, 24(4), 889-904.

Legler, Nicholas (Wisconsin DNR). "Lake Michigan predator fish data for Bunnell et al (2014) update task in IJC project." Personal communication received by Nate Jacobson, 10/19/17. Included data and feedback from Brian Breidert (Indiana DNR) and Jory Jonas (Michigan DNR)

Lodge, D.M., Simonin, P.W., Burgiel, S.W., Keller, R.P., Bossenbroek, J.M., Jerde, C.L., Kramer, A.M., Rutherford, E.S., Barnes, M.A., Wittmann, M.E., Chadderton, W.L., et al. 2016. Risk analysis and bioeconomics of invasive species to inform policy and management. *Annual Review of Environment and Resources*, 41:453-488.

Ludsin, S. A., Kershner, M. W., Blocksom, K. A., Knight, R. L., & Stein, R. A. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. Ecological Applications, 11(3), 731-746.

Maccoux, M.J., A. Dove, S.M. Backus, and D.M. Dolan. 2016. Total and soluble reactive phosphorus loadings to Lake Erie: A detailed accounting by year, basin, country, and tributary. *J. Great Lakes Research*, 42(6):1151-1165.

Madenjian, C.P., D.B. Bunnell, T.J. Desorcie, M.J. Kostich, M.A. Chriscinske, and J.V. Adams. 2016. Status and Trends of Prey Fish Populations in Lake Michigan, 2015. In USGS (U.S. Geological Survey). 2016. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2015. Available from http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2016.pdf

Madenjian, C.P., D.B. Bunnell, D.M. Warner, S.A. Pothoven, G.L. Fahnenstiel, T.F. Nalepa, H.A. Vanderploeg, I. Tsehaye, R.M. Claramunt, and R.D. Clark Jr. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: A synthesis. *J. Great Lakes Research*, 41 (Supplement 3):217-231.

Madenjian, C.P., S.A. Pothoven, and Y.C. Kao. 2013a. Reevaluation of lake trout and lake whitefish bioenergetics models. *Journal of Great Lakes Research* 39:358-364.

Madenjian, C. P., Pothoven, S. A., Schneeberger, P. J., Ebener, M. P., Mohr, L. C., Nalepa, T. F., & Bence, J. R. 2010. Dreissenid mussels are not a "dead end" in Great Lakes food webs. Journal of Great Lakes Research, 36(1), 73-77.

Makarewicz, J. C., T. W. Lewis, C. M. Pennuto, J. F. Atkins, W. J. Edwards, G. L. Boyer, E. T. Howell, G. Thomas. 2012. Physical and chemical characteristics of the nearshore zone of Lake Ontario. J. Great Lakes Res. 38: 21-32.

Marin Jarrin, J.R., Johnson, T.B., Ludsin, S.A., Reichert, J.M. and Pangle, K.L. 2017. Do models parameterized with observations from the system predict larval yellow perch (*Perca flavescens*) growth performance better in Lake Erie? *Canadian Journal of Fisheries and Aquatic Sciences*.

Markham, J.L., and Knight, R.L. [EDS]. 2017. The state of Lake Erie in 2009 [online]. Available from: http://www.glfc.org/pubs/SpecialPubs/Sp17_01.pdf [accessed 25 July 2017].

Mida, J. L., Scavia, D., Fahnenstiel, G. L., Pothoven, S. A., Vanderploeg, H. A., and Dolan, D. M. 2010. Long-term and recent changes in southern Lake Michigan water quality with implications for present trophic status. J. Great Lakes Res. 36:42-49.

Miehls, A.L.J., Mason, D.M., Frank, K.A., Krause, A.E., Peacor, S.D. and Taylor, W.W. 2009. Invasive species impacts on ecosystem structure and function: A comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. *Ecological Modelling*, 220(22): 3182-3193.

Mooij, W.M., Trolle, D., Jeppesen, E., Arhonditsis, G., Belolipetsky, P.V., Chitamwebwa, D.B., Degermendzhy, A.G., DeAngelis, D.L., Domis, L.N.D.S., Downing, A.S., Elliott, J.A., and 20 others. 2010. Challenges and opportunities for integrating lake ecosystem modelling approaches. *Aquatic Ecology*, 44(3):633-667.

Munawar, M., Munawar, I.F., Fitzpatrick, M., and Niblock, H. 2016. Structure and Function of Lake Ontario Phytoplankton Communities: Long Term Changes, 1970 to 2013. International Association for Great Lakes Research 59th Annual Conference on Great Lakes Research: Abstracts, June 6-10, 2016, University of Guelph.

Nalepa, T.F., D.L. Fanslow, G.A. Lang, K. Mabrey, and M. Rowe. 2014. Lake-wide benthic surveys in lake michigan in 1994-95, 2000, 2005, and 2010: abundances of the amphipod diporeia spp. and abundances and biomass of the mussels dreissena polymorpha and dreissena rostriformis bugensis. NOAA Technical Memorandum GLERL-164. US Department of Commerce, National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 2014.

Nõges, T., O. Anneville, J. Guillard, J. Haberman, A. Järvalt, M. Manca, G. Morabito, M. Rogora, S.J. Thackeray, P. Volta, I.J. Winfield, and P. Nõges. 2017. Fisheries impacts on lake ecosystem structure in the context of a changing climate and trophic state. *Journal of Limnology*, accepted article. doi:10.4081/jlimnol.2017.1640.

NYSDEC. 2017. Lake Erie 2016 Annual Report. New York State Department of Environmental Conservation, Albany, New York, USA.

O'Brien, T.P., P.C. Esselman, S. Lenart, S. Farha, . Armenio, C. Olds and L. Ogilvie. 2017. Status and Trends of Pelagic Prey Fish in Lake Huron, 2016. In: USGS (U.S. Geological Survey). 2017. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016.

O'Gorman, R., [ED]. 2017. The state of Lake Ontario in 2014 [online]. Available from: http://www.glfc.org/pubs/SpecialPubs/Sp17_02.pdf [accessed 13 November 2017]

Oveisy, A., Rao, Y.R., Leon, L.F. and Bocaniov, S.A. 2014. Three-dimensional winter modeling and the effects of ice cover on hydrodynamics, thermal structure and water quality in Lake Erie. *Journal of Great Lakes Research*, 40:19-28.

Ozersky, T., Malkin, S.Y., Barton, D.R. and Hecky, R.E. 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. *Journal of Great Lakes Research*, 35(3):321-328.

Ozkan, K., E. Jeppesen, T.A. Davidson, R. Bjerring, L.S. Johansson, M. Sondergaard, T.L. Lauridsen, and J. Svenning. 2016. Long-term trends and temporal synchrony in plankton richness, diversity and biomass driven by re-oligotrophication and climate across 17 Danish lakes. *Water*, 8(10). 23 pp.

Pauly, D., J. Alder, E. Bennett, V. Christensen, P. Tyedmers, and R. Watson. 2003. The future for fisheries. *Science*, 302:1359-1361.

Pawlowski, M. B., Branstrator, D. K., Hrabik, T. R., & Sterner, R. W. 2017. Changes in the cladoceran community of Lake Superior and the role of Bythotrephes longimanus. Journal of Great Lakes Research, 43(6), 1101-1110.

Pichlová-Ptáčníková, R., & Vanderploeg, H. A. 2011. The quick and the dead: might differences in escape rates explain the changes in the zooplankton community composition of Lake Michigan after invasion by Bythotrephes?. Biological invasions, 13(11), 2595.

Pikitch, E., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P.A.O., Doukakis, P., Fluharty, D., Heneman, B. and Houde, E.D. 2004. Ecosystem-based fishery management. *Science*, 305(5682):346-347.

Pilcher, D.J., G. A. McKinley, J. Kralj, H.A. Bootsma, and E.D. Reavie. 2017. Modeled sensitivity of Lake Michigan productivity and zooplankton to changing nutrient concentrations and quagga mussels. *Journal of Geophys. Research: Biogeosciences*, 122(8):2017-2032.

Plagányi, É.E., 2007. Models for an ecosystem approach to fisheries. *Food and Agriculture Organization of the United Nations, Fisheries Technical Paper 477.*

Pothoven, S.A. and Madenjian, C.P. 2013. Increased piscivory by lake whitefish in Lake Huron. *North American Journal of Fisheries Management*, 33(6):1194-1202.

Pratt, T.C., O.T. Gorman, W.P. Mattes, J.T. Myers, H.R. Quinlan, D.R. Schreiner, M.J. Seider, S.P. Sitar, D.L. Yule, and P.M. Yurista. 2016. The state of Lake Superior in 2011. *Great Lakes Fish. Comm. Spec. Pub. 16-01.*

Reavie, E.D., R.P. Barbiero, L.E. Allinger, and G.J. Warren. 2014. Phytoplankton trends in the Great Lakes, 2001-2011. *J. Great Lakes Research*, 40:618-639.

Reed, E.M. 2017. Nearshore zooplankton communities of Lake Michigan and implications for invasibility by Asian carp. M.S. thesis, University of Illinois at Urbana-Champaign, 50 p.

Richardson, V., Warren, G., Nielson, M., Horvatin, P.J., 2012. Cooperative Science and Monitoring Initiative (CSMI) for the Great Lakes — Lake Ontario 2008. J. Great Lakes Res. 38 (Suppl. 4), 10–13.Richardson et al. 2012

Riley, Stephen (USGS). "Lake Huron prey fish data for Bunnell et al (2014) update task in IJC project." Personal communication received by Doug Bradley, 8/22/2017.

Riley, S.C., E.F. Roseman, D.W. Hondorp, M.A. Chriscinske, E. Galassini, and M. Smith. 2017. Status and Trends of the Lake Huron Offshore Demersal Fish Community, 1976-2016. A report to the Great Lakes Fishery Commission, Lake Huron Committee, Ypsilanti, MI, March 21, 2017.

Riley, S.C. [ed.]. 2013. The state of Lake Huron in 2010. *Great Lakes Fish. Comm. Spec. Pub. 13-01.*

Roseman, E.F., M.A. Chriscinske, D.K. Castle, and C.G. Prichard. 2016. *Status and trends of the Lake Huron offshore demersal fish community, 1976-2015*. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys, 2015.

Rowe, M.D., E.J. Anderson, H.A. Vanderploeg, S.A. Pothoven, A.K. Elgin, J. Wang, and F. Yousef. 2017. Influence of invasive quagga mussels, phosphorus loads, and climate on spatial and temporal patterns of productivity in Lake Michigan: A biophysical modeling study. *Limnology and Oceanography*, doi:10.1002/lno.10595.

Schmidt, S. N., Vander Zanden, M. J., & Kitchell, J. F. 2009. Long-term food web change in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences, 66(12), 2118-2129.

Sesterhenn, T.M., Roswell, C.R., Stein, S.R., Klaver, P., Verhamme, E., Pothoven, S.A. and Höök, T.O. 2014. Modeling the implications of multiple hatching sites for larval dynamics in the resurgent Saginaw Bay walleye population. *Journal of Great Lakes Research*, 40:113-122.

Sharma, S., Gray, D.K., Read, J.S., O'Reilly, C.M., Schneider, P., Qudrat, A., Gries, C., Stefanoff, S., Hampton, S.E., Hook, S. and Lenters, J.D. 2015. A global database of lake surface temperatures collected by in situ and satellite methods from 1985–2009. *Nature: Scientific Data*, *2*, p.150008.

Shen, C., Liao, Q., Bootsma, H.A., Troy, C.D. and Cannon, D. 2018. Regulation of plankton and nutrient dynamics by profundal quagga mussels in Lake Michigan: A one-dimensional model. Hydrobiologia, https://doi.org/10.1007/s10750-018-3547-6.

Shuter, B., and D.M. Mason. 2001. Exotic invertebrates, food-web disruption, and lost fish production: understanding impacts of dreissenid and cladocerans invaders on lower-lakes fish community and forecasting invasion impacts on upper-lakes fish communities. Report to the Great Lakes Fishery Commission, 16 p.

Siersma, H.M., Foley, C.J., Nowicki, C.J., Qian, S.S. and Kashian, D.R. 2014. Trends in the distribution and abundance of *Hexagenia spp*. in Saginaw Bay, Lake Huron, 1954–2012: Moving towards recovery? *Journal of Great Lakes Research*, 40:156-167.

Sierszen, M. E., Kelly, J. R., Corry, T. D., Scharold, J. V., & Yurista, P. M. 2011. Benthic and pelagic contributions to Mysis nutrition across Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences, 68(6), 1051-1063.

Slocombe, D.S. 1998. Lessons from experience with ecosystem-based management. *Landscape and Urban Planning*, 40(1):31-39.

Sonzogni, W.C., Canale, R.P., Lam, D.C.L., Lick, W., Mackay, D., Minns, C.K., Richardson, W.L., Scavia, D., Smith, V. and Strachan, W.M.J. 1987. Large Lake models-uses, abuses, and future. *Journal of Great Lakes Research*, 13(3):387-397.

Stewart, T.J., Todd, A., and LaPan, S. 2017. Fish community objectives for Lake Ontario [online]. Available from: www.glfc.org/pubs/FisheryMgmtDocs/Fmd17-01.pdf [accessed 27 July 2017]

Stow, C.A., J. Dyble, D.R. Kashian, T.H. Johengen, K.P. Winslow, S.D. Peacor, S.N. Francoeur, A.M. Burtner, D. Palladino, N. Morehead, D. Gossiaux, Y. Cha, S.S. Qian, and D.Miller. 2014. Phosphorus targets and eutrophication objectives in Saginaw Bay: A 35 year assessment. *J. Great Lakes Research*, 40 (Supplement 1):4-10.

Stow, C.A., Y. Cha, L.T. Johnson, R. Confesor, and R.P. Richards. 2015. Long-term and seasonal trend decomposition of Maumee River nutrient inputs to Western Lake Erie. *Environ. Sci. Technol.*, 49(6):3392-3400.

Treska, Ted (USFWS). "GLFC Database Request." Personal communication received by Nate Jacobson, 10/26/17.

Tsehaye, I., M.L. Jones, J.R. Bence, T.O. Brenden, C.P. Madenjian, and D.M. Warner. 2014. A multispecies statistical age-structured model to assess predator-prey balance: application to an intensively managed Lake Michigan pelagic fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(4):627-644.

Twiss, M.R., McKay, R.M.L., Bourbonniere, R.A., Bullerjahn, G.S., Carrick, H.J., Smith, R.E.H., Winter, J.G., D'souza, N.A., Furey, P.C., Lashaway, A.R., Saxton, M.A., and Wilhelm, S.W. 2012. Diatoms abound in ice-covered Lake Erie: An investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010, Journal of Great Lakes Research, 38:18–30.

Ulanowicz, R.E., and J.J. Kay, 1991. A package for the analysis of ecosystem flow networks. *Environmental Software*, 6:131-142.

U.S. and Canada. 2012. Great Lakes Water Quality Agreement, entered into force February 12, 2013. Accessed at http://www.ijc.org/en_/Great_Lakes_Water_Quality , June 20, 2017.

U.S. Department of Agriculture, Natural Resources Conservation Service. 2017. Conservation Practice Adoption on Cultivated Cropland Acres: Effects on Instream Nutrient and Sediment Dynamics and Delivery in Western Lake Erie Basin, 2003- 06 and 2012. 77 pp.

USGS (U.S. Geological Survey). 2017. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016 [online].

Valipour, R., León, L.F., Depew, D., Dove, A. and Rao, Y.R. 2016. High-resolution modeling for development of nearshore ecosystem objectives in eastern Lake Erie. *Journal of Great Lakes Research*, 42(6):1241-1251.

van der Lee, Adam S., Timothy B. Johnson, Marten A. Koops. 2017. Bioenergetics modelling of grass carp: Estimated individual consumption and population impacts in Great Lakes wetlands. *Journal of Great Lakes Research*, 43(2):308-318.

Vanderploeg H.A., J.R. Liebig, T.F. Nalepa, G.L. Fahnenstiel, and S.A. Pothoven. 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Research*, 36:50-59.

Vanderploeg, H.A., S.A. Pothoven, G.L. Fahnenstiel, J.F. Cavaletto, J.R. Liebig, C.A. Stow, T.F. Nalepa, C.P. Madenjian, D.B. Bunnell. 2012. Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J. Great Lakes Research*, 38:336-352.

Vander Zanden, M. J., & Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, 83(8), 2152-2161.

Verhamme, E.M., T.M. Redder, D.A. Schlea, J. Grush, J.F. Bratton, and J.V. DePinto. 2016. Development of the western Lake Erie ecosystem model (WLEEM): application to connect phosphorus loads to cyanobacteria biomass. *Journal of Great Lakes Research*, 42(6):1193-1205.

Verhougstraete, M. P., Byappanahalli, M. N., Rose, J. B., & Whitman, R. L. 2010. Cladophora in the Great Lakes: impacts on beach water quality and human health. Water Science and Technology, 62(1), 68-76.

Vinson, M.R., L.M. Evrard, O.T. Gorman, and D.L. Yule. 2017. Status and Trends in the Lake Superior Fish Community, 2016. In USGS, Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016 (pp. 13-24). Available at http://www.glfc.org/pubs/lake_committees/common_docs/Compiled%20Reports%20from%20USGS%202017.pdf.

Vinson, M. R., L. M. Evrard, O. T. Gorman, and D. L. Yule. 2016. Status and trends in the Lake Superior fish community, 2015. In USGS (U.S. Geological Survey). 2016. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2015. Available from http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2016.pdf

Walsh, M. G., Dittman, D. E., & O'Gorman, R. 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. Journal of Great Lakes Research, 33(1), 83-92.

Waples, J.T., Bootsma, H.A. and Klump, J.V., 2017. How are coastal benthos fed? *Limnology and Oceanography Letters*, 2(1):18-28.

Warner, D.M., R.M. Claramunt, S.A. Farha, D. Hanson, T. Desorcie, and T.P. O'Brien. 2016. Status of Pelagic Prey Fishes in Lake Michigan, 2015. In USGS (U.S. Geological Survey). 2016. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2015. Available from http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2016.pdf

Warner, D.M., Lesht, B.M. 2015. Relative importance of phosphorus, invasive mussels, and climate for patterns in chlorophyll a and primary production in lakes Michigan and Huron. Freshwater Biology 60, 1029–1043.

Watson, S. B., Miller, C., Arhonditsis, G., Boyer, G. L., Carmichael, W., Charlton, M. N., Confesor, R., Depew, D.C., Hook, T.O., Ludsin, S.A., Matisoff, G., McElmurry, S.P., Murray, M.W., Richards, R.P., Rao, Y.R., Steffen, M.M.,and S.W. Wilhelm. 2016. The re-eutrophication of Lake Erie: harmful algal blooms and hypoxia. Harmful Algae, 56, 44-66.

Weidel, Brian (USGS). "Lake Ontario All Prey Fish Biomass Density." Personal communication received by Doug Bradley, 10/16/17.

Witt, A. M., Dettmers, J. M., & Cáceres, C. E. 2005. Cercopagis pengoi in southwestern Lake Michigan in four years following invasion. Journal of Great Lakes Research, 31(3), 245-252.

Yurk, J.J., and J.J. Ney. 1989. Phosphorus-fish community biomass relationships in Southern Appalachian reservoirs: Can lakes be too clean for fish? *Lake and Reservoir Management*, 5(2):83-90.

Zhang, H., E.S. Rutherford, D.M. Mason, J.T. Breck, M.E. Wittmann, R.M. Cooke, D.M. Lodge, J.D. Rothlisberger, X. Zhu, and T.B. Johnson. 2016a. Forecasting the Impacts of Silver and Bighead Carp on the Lake Erie Food Web. *Transactions of the American Fisheries Society*, 145(1):136-162. DOI:10.1080/00028487.2015.1069211

Zhang, H., L. Boegman, D. Scavia, and D.A. Culver. 2016b. Spatial distributions of external and internal phosphorus loads in Lake Erie and their impacts on phytoplankton and water quality. *J. Great Lakes Research*, 42:1212-1227.