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July 8, 2020

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Re: Transmittal of the Science Advisory Board Report - *Understanding Declining Productivity in the Offshore Regions of the Great Lakes.*

In June 2020, the International Joint Commission's Science Advisory Board (SAB) completed a report entitled *Understanding Declining Productivity in the Offshore Regions of the Great Lakes*. The report includes a number of findings and a recommendation aimed at improving coordination between water quality and fishery managers and improving the understanding of ecosystem impacts of nutrients in both nearshore and offshore waters of the Great Lakes.

The Great Lakes Water Quality Agreement recognizes the complexity of the Great Lakes basin ecosystem and its interacting components of air, land, water and living organisms in lakes comprised of many different types of habitat in the nearshore and offshore regions. The Agreement embraces coordination, the ecosystem approach, adaptive management and science-based management as recommended principles and approaches. We find the subject report to be in line with these principles and approaches with advice to help managers evaluate and better understand the dichotomy between excess nutrient levels in the nearshore while levels are declining in the offshore. The reductions in the nutrient levels offshore are affecting ecosystem services including restoration of fishery production. This report is a unique compilation of all available information about declining offshore productivity and shows this is a significant issue.

This report has been developed in accordance with Article 7.1(c) of the Great Lakes Water Quality Agreement. The IJC's role is to provide advice on approaches and options the Parties may consider to improve effectiveness in achieving the purpose and objectives of the Agreement. The IJC endorses this report of the SAB and its recommendation aimed at fostering an integrated ecosystem approach involving fisheries and water quality managers.

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The report identifies the need for Great Lakes water quality managers to partner with fishery managers to break down information silos and adopt an adaptive management framework that considers both the upper and lower food webs. Targets set for nutrient reductions under the GLWQA require an ecosystem-level analysis to consider potential impacts on offshore waters and strike a balance between ecosystem services. A key finding in the report describes how invasive mussels are implicated in sequestering nutrients in the nearshore. This underscores the importance of applied research and the work of the Invasive Mussel Collaborative to control invasive mussels. As such, GLEC may wish to explore with the Great Lakes Commission and the Invasive Mussel Collaborative how they might provide insight and support in addressing this issue.

The Commission will partner with the Great Lakes Fishery Commission to communicate key messages from this study to, and seek feedback from, fishery managers and other organizations in the context of other work being carried out on nutrient management. We expect that this report will be useful to governments to inform actions under Annex 2 (Lakewide Action and Management Plans), Annex 4 (Nutrients) and Annex 10 (Science) as managers strive to control excess nutrients, maintain algal species consistent with healthy aquatic ecosystems while at the same time taking steps to restore and protect native fish species.

If you have any questions or comments on the information provided in this letter or the attached report, please do not hesitate to contact us. In keeping with IJC policy, this transmittal and associated report will be posted to our website. We look forward to your feedback.

Yours sincerely,

Jane Corwin
U.S. Chair

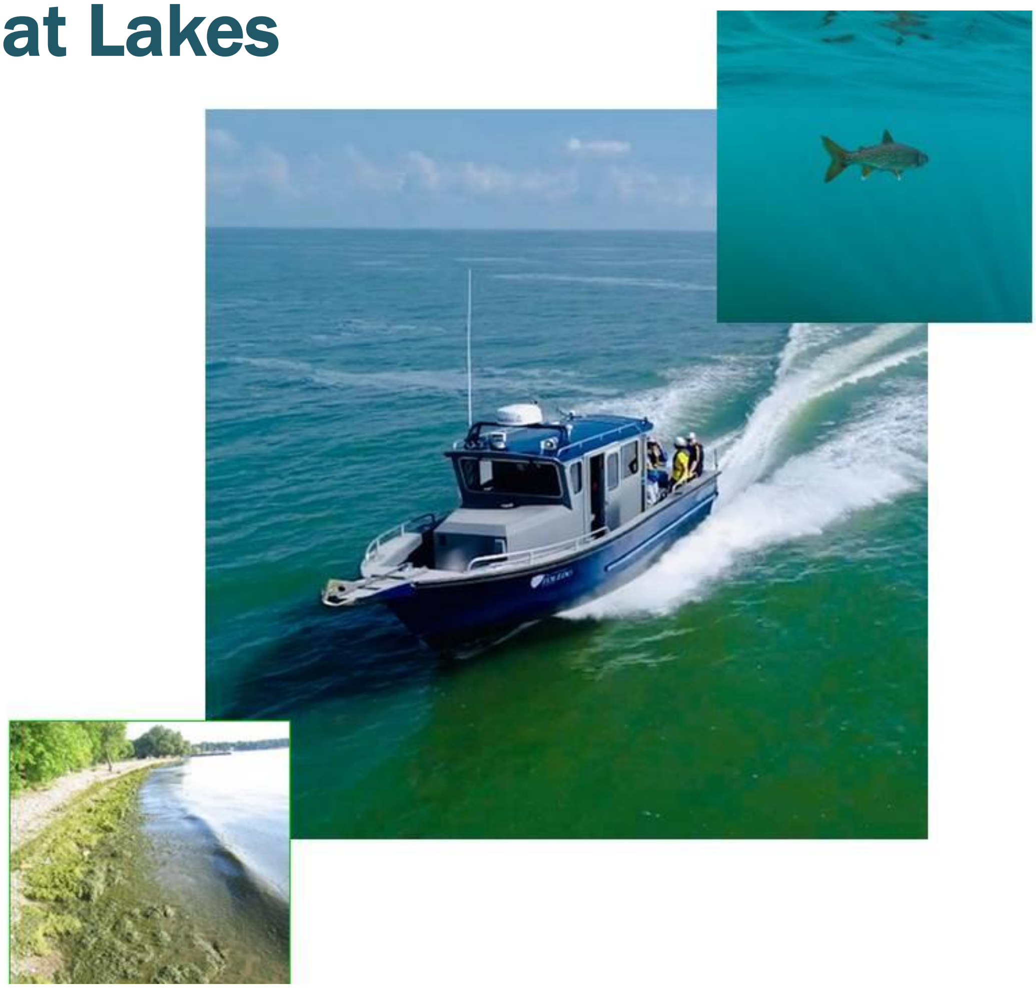
Pierre Beland
Canadian Chair

Enclosures:

1. Understanding Declining Productivity in the Offshore Regions of the Great Lakes, SAB-SPC Report, June 29, 2020.

Cc: Robert (Bob) Lambe, Executive Secretary, Great Lakes Fishery Commission
Darren Nichols, Executive Director, Great Lakes Commission

Understanding Declining Productivity in the Offshore Regions of the Great Lakes



A report submitted to the International Joint
Commission by the Great Lakes Science Advisory
Board, Science Priority Committee
Declining Offshore Productivity Work Group

June 29, 2020

Acknowledgements

The Great Lakes Science Advisory Board's Science Priority Committee would like to acknowledge the extensive efforts, input and guidance provided by the Declining Offshore Productivity Work Group, and LimnoTech for their 2018 contract report which provided source material for this report.

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Cover photo credits: Upper right solitary fish Credit: Paul Vecsei, cover photo of Journal of Great Lakes Research 42(2) 2016; Center University of Toledo vessel races between sampling locations in Lake Erie during the 2019 ECOHAB-funded HABS Grab Photo credit: David J Ruck/greatlakesoutreachmedia.com; Lower left: Cladophora on shore line Lake Erie: Scott Higgins

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List of Acronyms

A2EM	Advanced Aquatic Ecosystem Model
C	Carbon
DCL	deep chlorophyll layers
ECCC	Environment and Climate Change Canada
EFDC	Environmental Fluid Dynamics Code
EwE	Ecopath with Ecosim
GLEC	Great Lakes Executive Committee
GLFC	Great Lakes Fishery Commission
GLWQA	Great Lakes Water Quality Agreement
IJC	International Joint Commission
IISD-ELA	International Institute for Sustainable Development – Experimental Lakes Area
N	Nitrogen
P	Phosphorus
SAB	Great Lakes Science Advisory Board
TP	Total Phosphorus
USEPA	United States Environmental Protection Agency

Executive Summary

One of the most outstanding successes of the Great Lakes research and management community over the last 50 years was the establishment of targets through the Great Lakes Water Quality Agreement (GLWQA) for reduction of total phosphorus (TP) loadings to control whole lake eutrophication (i.e., nutrient over-enrichment) and the achievement of those targets by the mid-1980s. These actions reduced the frequency and severity of harmful algal blooms and other conditions associated with excess nutrient levels.

Over the past 15 to 20 years, however, the Great Lakes have seen a resurgence of serious eutrophication symptoms in nearshore areas and embayments, resulting in increased occurrences of cyanobacteria (blue-green algae) blooms and *Cladophora* (a filamentous attached algae) growth, among other impacts.

Contemporaneous with this evidence of re-eutrophication was the invasion and proliferation of zebra and quagga (dreissenid) mussels and their effects on nearshore nutrient retention, offshore nutrient and phytoplankton reductions as well as improved water clarity. In lakes Michigan, Huron, Ontario and the eastern basin of Lake Erie, the combination of long-term reductions in TP loadings and dreissenid-driven changes in nutrient cycling have caused offshore concentrations of TP to decline to unprecedented levels in the past two decades. Furthermore, there is evidence that these lower TP concentrations are reducing offshore commercial, recreational and native fish populations through food web changes.

These offshore reductions in biological productivity could be exacerbated by work being done under Annex 4 of the GLWQA to control nearshore nutrient loadings, particularly from tributaries where agricultural land uses predominate. Therefore, the International Joint Commission (IJC) Great Lakes Science Advisory Board's (SAB) Science Priority Committee has undertaken this project to advise the IJC of the potential impact of management actions to control nearshore eutrophication on the offshore biological carrying capacity of the lakes. There is a need for an ecosystem-level analysis to balance the need to reduce phosphorus load to control coastal cyanobacteria and *Cladophora* proliferation without impacting ecologically and economically important fish communities.

This report explores the dual challenges of nearshore nutrient enrichment and reduced ecosystem productivity in the offshore, with particular emphasis on the latter, and includes the completion of three related tasks by a contractor under the guidance of a multidisciplinary SAB work group.[1] First, a literature review was completed on the global experience of how reductions in phosphorus loading to lakes has influenced upper food web organisms and fish communities, fish production, biomass and/or yield. Second, a study previously published in the journal *Bioscience* that investigated the relationship among nutrients and lower food web changes and changes in fish communities in all five Great Lakes over the period 1998 to 2010 was updated to include

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[1] The contractor report (LimnoTech, 2018) provides source material for this report is accessible at ijc.org/sites/default/files/2019-11/SAB-SPC_DecliningProductivity_ContractorReport_2018.pdf.

more recent data, in some cases up to 2016. Third, the availability and experience of appropriate models that can link phosphorus (P) concentrations to upper food web and fishery production in the pelagic (i.e., open waters) ecosystem was reviewed.

This report includes sections on a description of the problem, a literature review, an analysis of recent Great Lakes trends, an examination of various models, findings, knowledge gaps and a recommendation. A summary of key findings and the recommendation are included below; readers should review the full report for a more detailed discussion of these findings and the recommendation.

Key findings and recommendation

Key findings

In recent decades, offshore TP concentrations have fallen across lakes Michigan, Huron, Ontario and the eastern basin of Lake Erie to below GLWQA targets at least in part due to the impacts of invasive dreissenid mussels (i.e., zebra and quagga mussels), *Cladophora* growth and the resulting nearshore trapping of nutrients. Uncertainty remains about the long-term trends of TP in Lake Superior.

Trapping of nutrients by dreissenids (i.e., zebra and quagga mussels) and *Cladophora* has increased nearshore benthic productivity and decreased pelagic primary productivity in lakes where *Dreissena spp.* have become the dominant benthic fauna. The virtual disappearance of *Diporeia* (a small, energy-rich shrimp-like organism historically the primary benthic food source for fishes) from all the lakes except Superior has compounded the effects of phosphorus shunting by mussels on offshore fish productivity.

Changes in average spring TP concentrations and abundance of prey fish and predatory fish have shown continued variation but few strong trends after 2005, including the most recent five additional years analyzed as part of this study (i.e., 2005 to 2010). This suggests that most lakes may be approaching a plateau with regard to TP concentrations and external and internal P loadings, mussel populations and impacts, and other recent drivers of algal productivity change.

Monitoring of lower food web organisms (other than chlorophyll as a surrogate for phytoplankton) with standard stations and sampling protocols across all lakes only began in the Great Lakes in 1998 after the most substantial declines in TP had already occurred. During the relatively short period of record of the lower food web (1998 to present), multiple lines of evidence show a major decline in the offshore productivity of the lower food web organisms in Lake Michigan, Lake Huron and to a lesser extent in Lake Ontario. These lakes appear to be dominated by bottom-up regulation (i.e., resource limitation, as opposed to top-down regulation through predation and fish harvest), which is consistent with very low TP concentrations and the global experience with re-oligotrophication (i.e., a return to a low level of nutrients).

Fish populations, especially for large bodied top predators, were in a degraded condition because of overexploitation and invasive sea lamprey predation when the GLWQA was first implemented in 1972. Several deep water dwelling coregonid (whitefish and lake herring) species had been extirpated from all the lakes except Superior and the top predator lake trout was in low abundance in all the lakes. Some of the Great Lakes (especially Michigan and Ontario) continue to have substantial stocking of valued species (primarily salmonids) in efforts to meet lake-based Fish Community Objectives. Several introduced salmonid species have also become naturalized in some of the Great Lakes, partially reducing the effectiveness of the stocking management for fishery managers.

Salmonid stocking and piscivore restoration complicate simple interpretation of the prey fish population dynamics even though they have been monitored since the early 1970s by various agencies. Prey fish stocks have declined in all the lakes (except Erie) since historic highs in the 1980s and early 1990s to historic lows in recent years. Although contemporaneous with declining TP in these lakes, the recovery of predation pressure by piscivores would also depress prey fish biomass. Therefore, a correlation between declining TP and prey fish biomass would be insufficient to infer causality over this post-GLWQA period. Further complicating the trends in prey fish abundance is the prominence in this category of non-native invasives (i.e., alewife and round goby) in all the lakes except Superior.

The deep water coregonid fauna lost over the last century in several of the lakes may have left trophic niches vacant and contributed to the success of aquatic invasive species over the past thirty years. It is uncertain the extent to which these invasives can replace the extirpated deepwater coregonids and maintain food web efficiencies in increasingly oligotrophic lakes. Consequently, efforts are now underway to stock the extirpated native coregonids to stabilize or increase fish production in some of the lakes. Restoration of these deep water coregonids may enable increased food web efficiency to maintain or increase fish productivity in the increasingly oligotrophic offshore waters of the Great Lakes. Success in these restoration efforts may be critical to maintaining fish production in these oligotrophic lakes.

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 and spatial patterns remain to be worked out. At this time, models applied to support fishery management decisions have been somewhat limited in favor of more direct measures of fish community and population condition (i.e., stock assessment data). Use of nutrient-based models within a framework that evaluates alternative fishery management actions (i.e., stocking, harvest and habitat remediation) and policies may enhance their usefulness and incorporation into formal management frameworks.

Ecosystem models that link biogeochemistry, lower food web productivity, nearshore ecology and offshore fish productivity are currently under development. These aquatic ecosystem models can best be attained by coupling nutrient - lower food web eutrophication models with upper food web fish production models at the zooplankton level of the food web. Such models would benefit 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). These complex ecosystem models will be an essential component of an integrated ecosystem adaptive management system.

Further enhancement and coordination of monitoring in support of management and modeling are required, especially for lakes Huron, Michigan, Ontario and the eastern basin of Lake Erie. Monitoring that is optimized for ecosystem modeling and adaptive management should include increased spatial and temporal resolution for external nutrient loading and primary productivity, including the seasonal deep chlorophyll layers (DCL) and winter seasons. Most importantly, the monitoring data generated should be reported annually in an integrated format to enable rapid management response to ecosystem change.

Currently, Lake Ontario nutrient targets are being reviewed under Annex 4 of the GLWQA; this process will be an important test case for current ecosystem modeling capabilities. Major reductions in upstream nutrient loading to Lake Erie together with stakeholder concerns about increased coastal, nuisance *Cladophora* growth and declining salmonid biomass (LimnoTech 2018) present a ‘nearly-perfect storm’ for both water quality and fisheries managers. The Great Lakes Fishery Commission (GLFC) and its partner agencies could team up with Annex 4 subcommittee members working on nutrient targets to avoid unintended consequences that may result from a focus on a single aspect of the ecosystem. Adopting a true ecosystem analysis approach (i.e., a fully coupled lower-upper food web model) and adaptive management may lead to an optimum balance between nutrient loads and offshore fishery production.

The collaborative and cooperative management of the offshore commercial and recreational fisheries has been proactive across fisheries agencies in response to the declining offshore fish productivity. Management actions have been informed through review of stocking rates, information on the possible impacts of disrupted food webs and supporting new modeling research to address the linkages between P and fish abundance and productivity. However, nutrient management lies outside the sole responsibility of the fisheries agencies and even greater cooperation between water quality and fisheries agencies will be essential to maintaining a healthy and valuable fishery in the lakes.

Recommendation

The Great Lakes Executive Committee (GLEC) should explore and implement opportunities and capacities for cooperative application of ecosystem forecasting science addressing nutrient and fisheries management in the Great Lakes. In order to address this recommendation, GLEC should engage and partner with state and provincial fisheries and environmental agencies as well as other national and binational agencies involved with monitoring and managing Great Lakes aquatic resources.

To initiate comprehensive engagement, the GLEC should form a multiagency Cooperative Ecosystem Monitoring and Modeling Advisory Committee ("Committee"). This Committee could be an *ad hoc* or standing committee focusing on:

- Reviewing ecosystem forecasting science and its potential application to current and emerging issues confronting environmental and fisheries managers in the Great Lakes;

- Identifying key data requirements for the effective use of ecosystem modeling and forecasting science by managers in the Great Lakes and fostering the exchange of such data, especially among fishery and water quality programs to support integrative decision support;

- Evaluating potential benefits from, as well as tradeoffs between, nutrient management and fisheries within and among the Great Lakes, especially for lakes Huron, Michigan, Ontario and the eastern basin of Erie where changes in fisheries could be induced by enhanced nutrient management under the Annex 4 process;

- Identifying and implementing strategies to enhance collaborative decision making and adaptive management of the Great Lakes ecosystems among water quality and fisheries managers through existing administrative structures or, if necessary, new collaborative structures;

- Enabling and promoting consistency and clarity of public communications from water quality and fisheries agencies regarding current and potential interactions between these resources and their management; and

- Other aspects that arise during discussions.

The Committee should be established within two years along with its terms of reference, multiagency composition, procedures and work plan (to be reviewed annually). The Committee should use the ongoing Annex 4 assessment on Lake Ontario as a test bed for integrating and instituting coordinated data/information management aimed at reducing eutrophic conditions nearshore while sustaining healthy fish populations offshore. Progress on measures, analysis and outcomes should be shared publicly at annual Lake Committee meetings hosted by the Great Lakes Fishery Commission. After the next two consecutive five-year Cooperative Monitoring and Science Initiative cycles, the Parties should report on their success in connecting and adapting nutrient-related actions to fishery management through effective information flow and decision support, modeling and forecasting.

Perspective

The success of point source nutrient controls in the 1970s and 1980s resulted in a remarkable recovery of the lakes, with continued declines in TP concentrations in the open waters of all of the lakes (except Lake Erie) to well below target levels. However, ongoing nutrients loads from primarily nonpoint sources to the nearshore, likely mediated by dreissenid mussels, has resulted in a proliferation of cyanobacteria (blue-green algae) in shallow embayments and *Cladophora* growth in many coastal areas. The consequences of these dual changes are taking the offshore waters of the lakes into unknown territory in terms of ecosystem productivity and fisheries changes.

Calls for further reductions in P loading may have unintended consequences in offshore waters, thus requiring an ecosystem-level analysis prior to making a decision for further reductions. This complex challenge will require that we fully utilize our collective science capabilities and apply them directly to evaluating ecosystem services and the tradeoffs between them. The IJC SAB offers this analysis in the hope that it will inform the discussion and compel a careful and detailed evaluation of nutrient reduction tradeoffs by the governments of Canada and the United States in collaboration with all relevant stakeholders.

1.0 Background and Problem Statement

Under the initial GLWQA of 1972 and its amendments in 1978, targets were set for TP loadings and open (pelagic) lake concentrations of TP in the lakes. By the mid-1980s, these targets were being met or exceeded (lower than targeted) in all the lakes (DePinto et al. 1986; Dove and Chapra, 2015; **Figure 1**).

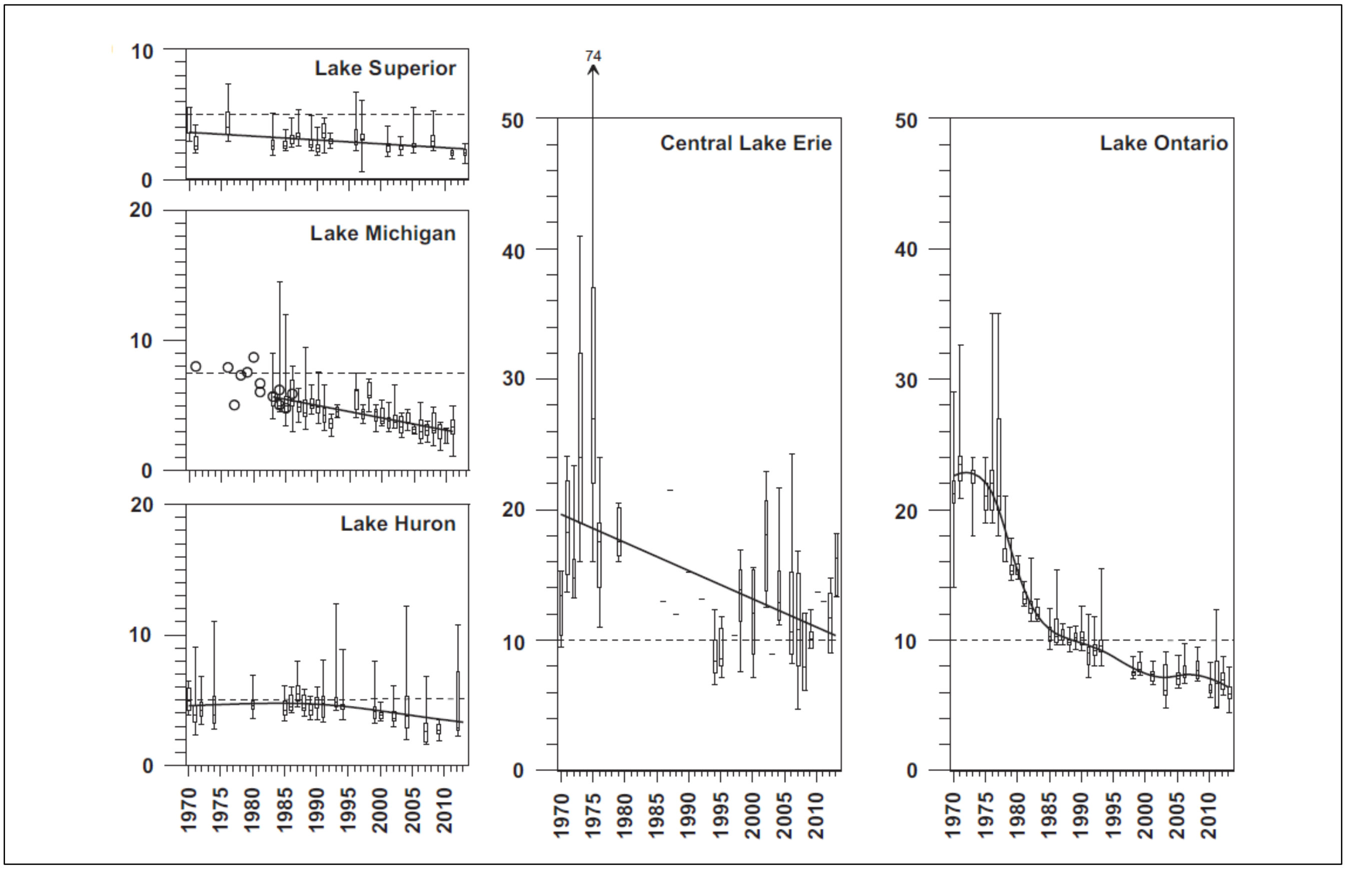

Figure 1: Pelagic total phosphorus (TP) concentrations (from Dove and Chapra, 2015). Pelagic TP concentrations are declining across all the Great Lakes and are well below targets set under the GLWQA. The GLWQA (Canada and the United States, 2012) has called for these targets to be revisited and possibly lowered in response to nearshore water quality issues in particular excessive growth of *Cladophora*. These declining concentrations have had substantial impact on food webs and fish biomass in offshore waters. Reducing these concentrations further may pose unacceptable risk to upper food web organisms and particularly fisheries. Horizontal axis is total phosphorus (TP) concentrations (µg P/L). Horizontal dashed lines are existing GLWQA TP target concentrations.

However, over the past 15 to 20 years the Great Lakes have seen a resurgence of serious eutrophication symptoms in nearshore areas and embayments that were not evident since the implementation of TP load reductions of the 1970s. This ‘re-eutrophication’ has been exemplified by the occurrence of large cyanobacterial (Michalak et al. 2013) and diatom (Reavie et al. 2016) blooms in Lake Erie and major embayments (i.e., Green Bay, Saginaw Bay, Bay of Quinte), an increase in hypoxia in the central basin of Lake Erie and Green Bay, and a plague of *Cladophora* growth in nearshore, especially rocky shoreline areas of the lower four Great Lakes that may be more severe in terms of areal coverage than that experienced in the 1970s (Auer et al. 2010; Higgins et al. 2008; IJC 2014; Michalak et al. 2013; Scavia et al. 2014; Smith et al. 2015). These problems have adversely affected ecosystem services (i.e., beach closures, restrictions on drinking water, effects on fishery performance) in the basin. They have also prompted the establishment of a new nutrient eutrophication Annex (Annex 4) in the 2012 GLWQA Protocol (Canada and the United States, 2012) that calls for setting new, revised TP loading and in-lake concentration targets. The invasion of dreissenid mussels in the 1990s has also been implicated in the re-eutrophication and *Cladophora* resurgence in coastal areas (Hecky et al. 2004).

Contemporaneously with the nearshore and embayment re-eutrophication problems and the invasion of dreissenid mussels with their impacts on water clarity and nutrient cycling, offshore concentrations of TP have declined to approximately 50 percent of GLWQA targets in Lake Michigan, Lake Huron and Lake Ontario (Dove and Chapra 2015; **Figure 1**). These increased nearshore to offshore nutrient gradients have caused the offshore TP concentrations and transparency in Lakes Michigan and Huron to be similar to those of Lake Superior (Barbiero et al. 2012) which has always been considered the most oligotrophic of the Great Lakes and closest to a natural condition. Also, similar TP declines and transparency increases have also been observed in Lake Ontario (Dove and Chapra, 2015). There is concern that these declining TP concentrations may be reducing pelagic biological productivity and imposing dramatic food web changes on Lake Huron and Lake Michigan (Bunnell et al. 2014; **Figure 2**).

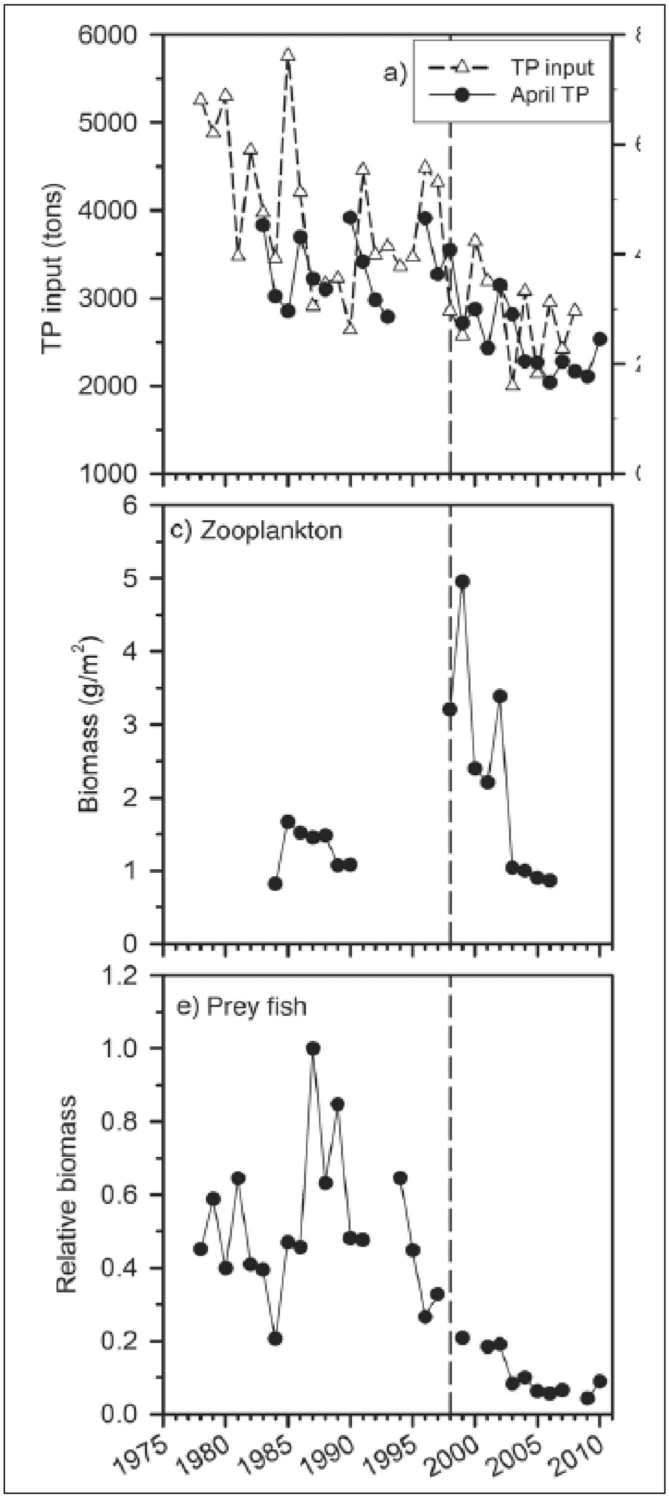

Figure 2: TP and prey fish in Lake Huron (from Bunnell et al. 2014). The vertical dash line shows the point after which within-lake Spearman's rank correlations were analyzed in Bunnell et al. (2014).

With the exception of Lake Erie, prey fish biomass is near record low levels in the Great Lakes, raising concern for the sustainability of valued sport and commercial fisheries. Although the GLWQA successfully motivated jurisdictions in both countries to initiate phosphorus control programs in the 1970s and 1980s, the TP concentrations in the offshore waters of all the lakes (except Lake Erie) are now well below targets expected from reducing loadings and may be related to increased P sedimentation mediated by dreissenid mussels (Chapra and Dolan, 2012; Dove and Chapra, 2015). The consequences of these dual changes are taking the pelagic waters of the lakes into unknown territory in terms of ecosystem productivity and fisheries changes, which some researchers have referred to as 'biological deserts.'

The success of dreissenids in dominating nearshore benthic communities, thereby increasing water transparency and increased cycling of P in the littoral zone, has led to the reemergence of large *Cladophora* stands (extending over more area and to deeper water than observed in the 1970s) and public concern about related beach conditions of all the lakes with the exception of Lake Superior (Hecky et al. 2004). The resurgence of benthic algae in the nearshore zone has sparked interest in further reducing nutrient loadings to the lakes. Consequently, as the Annex 4 work moves from Lake Erie to Lake Ontario and then to the other lakes, there is a perceived risk that phosphorus load reduction to address the nearshore *Cladophora* problem may exacerbate the decline in offshore productivity (Pilcher et al. 2017).

It is incumbent on the SAB to advise the IJC of this risk that may result from taking a narrow view of the coastal *Cladophora* issue while neglecting possible impacts on pelagic food webs and ecosystem productivity. In short, further reductions in P loading may have unintended consequences in offshore waters, thus requiring an ecosystem-level analysis prior to making a decision for further reductions.

1.1 Confounding stressors

The Great Lakes management community should also determine whether lowering the productivity of the pelagic food webs may negatively influence desired recovery of lake biota from elevated concentrations of persistent legacy chemicals such as polychlorinated biphenyls and mercury (Jeremiason et al. 1999; Kidd et al. 1999; Larson et al. 1992; Swackhamer and Skoglund, 1993). Reduced organism growth rates (and also reduced sedimentation and burial of toxic chemicals) because of declining primary productivity in offshore waters may lead to higher concentrations and/or slower removal of contaminants in those food webs, and thereby offset anticipated and desired further reductions in contaminant concentrations in those food webs. Recent observations indicate that declining mercury in Great Lakes waters has not been consistently matched by a decline in fish mercury concentrations, and this may be in part due to falling productivity levels in the lakes (Zananski et al. 2011). Similarly, Murphy et al. (2017) found that slowing predatory fish growth rates in Lake Huron are associated with a reduced rate of decline of contaminants in fish monitored by United States Environmental Protection Agency's (USEPA) Great Lakes Fish Monitoring and Surveillance Program.

There also is clear evidence that the Great Lakes are warming, with shorter periods of ice cover and longer periods of summer stratification, which could induce further nutrient stress on primary productivity and aquatic food webs (Lehman 2002). On the other hand, warmer temperatures could increase abundance of bloom-forming cyanobacteria (Paerl and Huisman, 2008), thus confounding the net effect on food webs. It has already been recognized that physical changes to Great Lakes pelagic environments caused by atmospheric warming are forcing reorganization of phytoplankton communities to species that are more tolerant of longer summers and stronger stratification (Reavie et al. 2017). In any event, these climate driven changes will be superimposed on already reduced nutrient availability because of GLWQA and dreissenid impacts.

1.2 Relevance to Annex 4 process

Great Lakes phosphorus management strategies have demonstrated the strong connectivity between phosphorus load and algal productivity and biomass (DePinto et al. 1986; Dove and Chapra, 2015: Fahnenstiel et al. 2010). Since the 1970s, a series of global studies have demonstrated in freshwater systems the dependence of fish yield, fish production and biomass on TP concentration, chlorophyll and primary productivity with high statistical significance, i.e., Oglesby (1977), Hanson and Leggett (1982), Downing et al. (1990) and Downing and Plante (1993). Although aggregate biomass and growth rates increase with TP, the species composition of the fish community also changes generally with different and less valued species increasing in dominance (Jeppesen et al. 2005; Ludsin et al. 2001). Much of this global definition of the relationship between TP concentration and fish production has derived from data on smaller lakes rather than the Great Lakes which—because of their size, habitat diversity, food web complexity, invasive species and the highly selective nature of their fisheries—pose challenges to defining yield, production and biomass for their multispecies fisheries, as well as defining appropriate values for limnological characteristics. However, these statistical regression analyses have been specifically applied to the Great Lakes by Matuszek (1978) and Leach et al. (1987) with mixed results. It should be noted that these attempts to apply these statistical models to the Great Lakes fisheries preceded the dramatic declines in TP, but to our knowledge no one has determined to what extent these simple regression models might predict the recent decline in fish production. However, fisheries modeling has made substantial advances since these earlier statistical models, becoming more process oriented and specific in predicted responses of benthic invertebrates (such as *Diporeia*) and fish species to declining productivity.

There is a clear need for deeper analysis of the relationship between historic declines in TP and fish biomass and yield in the Great Lakes, and the extent to which past experience globally can guide future estimations of biomass and yield. Such analysis should certainly be informative and be included in Annex 4 modeling soon to be undertaken for Lake Ontario in order to ensure that any identification of a need to reduce P loading to address concerns about *Cladophora* also recognizes that valued species in the upper food web, for example the highly valued salmonid sport fishery, may be at risk from declining productivity.

1.3 This project

To this end, the SAB formed a multidisciplinary work group that undertook a study to address the impact of multiple possible stressors on lake productivity. This objective was accomplished through three tasks in order to provide advice to the IJC on the risks that declining offshore productivity from future phosphorus load reduction might pose for Great Lakes fisheries. First, a literature review of the global experience of how reductions in phosphorus loading to lakes has impacted upper food web organisms and fish communities, specifically fish production, biomass, and/or yield. Secondly the work group updated the prior report by Bunnell et al. (2014) of available Great Lakes data on the impact of nutrients and lower food web changes on fish communities and fishery response (biomass and yield) to evaluate the strength and form of any statistical relationships in time and space within the Great Lakes focusing on the pelagic offshore environment. This study did not address nearshore communities, which are historically less well monitored and studied. Thirdly, the availability and experience of appropriate models that can link P concentrations to upper food web and fishery production in the pelagic ecosystem was reviewed. In all three of these tasks, the work group was informed by a contract report[1] by LimnoTech (2018) which produced the most comprehensive dataset yet available for the offshore ecosystems of the Great Lakes. The work group is familiar with the jurisdictional authorities responsible for fisheries and lakewide management and provides a recommendation which is practical and within the mandate provided by the GLWQA. This dataset and report are valuable products that provide a baseline for further study and guidance to lake and fisheries managers across the lakes.

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[1] Accessible at ijc.org/sites/default/files/2019-11/SAB-SPC_DecliningProductivity_ContractorReport_2018.pdf.

2.0 Relevant Literature

2.1 Recognition of eutrophication's impacts

The impacts of cultural eutrophication, excessive and problematic algal growth and ecosystem change resulting from anthropogenic nutrient enrichment, had become broadly evident and the stimulus for aquatic resource management and public awareness by the 1960s in North America. This broad concern led to the United States National Academy of Sciences – National Research Council convening an International Symposium "Eutrophication: causes, consequences and correctives" (National Academy of Sciences 1969). This symposium had participants from 11 countries in addition to the United States. The organizers were determined to bring the most knowledgeable experts together, but also recognized that eutrophication was a growing global problem and that European countries because of their denser populations had a longer experience with eutrophic lakes. The consensus from that symposium and subsequent research in Canada and the United States identified phosphorus as a limiting nutrient for algal growth which could be effectively managed. The GLWQA was signed in 1972 and was amended in 1978 with objectives for reducing loadings of phosphorus to the Great Lakes in order to achieve target concentrations and allow for restoration of the lakes to a condition of improved ecosystem health. By the late 1980s (Makarewicz and Bertram, 1993) these targets were largely being met. However, despite this remarkable accomplishment in large ecosystem management, since the turn of the century, there has been a resurgence of cyanobacterial blooms in western and central Lake Erie and major Great Lakes embayments because of excessive nonpoint nutrient loading from agricultural lands and the resurgence of fouling of shorelines by dying *Cladophora* in all the lakes with the exception of Lake Superior. The emergence of these nearshore issues while the offshore was meeting or exceeding targets led to the call for a Nearshore Framework and also for a review of the nutrient objectives for the lakes (Canada and the United States, 2012), with the possible consequence of lowering target concentrations below the already historically low concentrations in the lakes. This review of targets has been completed for Lake Erie and new objectives have been set for loading reductions, with the exception of the north shore of its eastern basin. Both Lake Ontario and the eastern basin of Lake Erie are next for review. In both systems there may be an important tradeoff between phosphorus load reduction for *Cladophora* control and the impact on offshore productivity.

2.2 Fisheries and eutrophication

In 1971, another international symposium, "Salmonid Communities in Oligotrophic Lakes" was held in Canada (Loftus and Regier, 1972). Its stated purpose according to Stevenson (1972), "was to seek to identify the separate and joint effects of cultural eutrophication, fisheries exploitation, and introduction of nonnative fish species on the salmonid communities of recently glaciated oligotrophic lakes," which included specifically the North American Great Lakes. Once again, there was recognition that drawing on international experience was important and that eutrophication had received more attention, as early as the 1950s, in Europe for its impacts on fish communities. Some European countries had already at the time of the symposium taken steps to reduce TP loading to their lakes to reduce the impact of eutrophication. The symposium recognized that eutrophication clearly led to changes in fish communities that were unfavorable for native salmonid communities. There were examples of increased fish growth of desirable species during the early stages of enrichment of oligotrophic lakes, but this positive result was offset by the fact that many of the species experiencing increased growth were less desirable or valued, and their increased abundance further negatively impacted desirable species. The critical role of maintaining oligotrophy to sustain salmonid communities was implicit in the title of the symposium, even though the symposium per se did not suggest target TP concentrations to maintain oligotrophy. The targets established by the GLWQA (1978) which were meant to restore and maintain the upper Great Lakes in an oligotrophic condition were certainly in line with fishery research and agency views at the time. The GLWQA setting of meso-oligotrophic targets for Lake Ontario and the eastern basin of Lake Erie would also have been supportive of managing these two systems towards lower algal productivity to maintain healthy salmonid populations.

The Salmonid Communities in Oligotrophic Lakes symposium had thorough reviews of the state of fisheries in all five Great Lakes (Berst and Spangler, 1972; Christie 1972; Hartman 1972; Lawrie and Rahrer, 1972; Wells and McLain, 1972), and the reviews were discouragingly consistent in their view that the fisheries in all five lakes were highly degraded, including extirpations of native species, as a result of the sequential effects of overexploitation, sea lamprey (*Petromyzon marinus*) predation and pollution. Yields from traditional fisheries had collapsed. The only way to go was up, and recovery would be long and difficult and would require reversal of eutrophic trends in the lakes (Smith 1972). The only bright light in these reviews was the mention of a recently (late 1960s) burgeoning sport fishery on Lake Michigan because of successful stocking of introduced Pacific salmon (Chinook, *Oncorhynchus tshawytscha,* and coho, *Oncorhynchus kisutch*), which fed on the then abundant supply of invasive alewife, *Alosa pseudoharengus*. The reviews of the European lakes highlighted their experience with early overexploitation, which was addressed through subsequent regulation and the impact of pollution, especially eutrophication (Laurent 1972), on the fisheries. Nascent efforts to reduce phosphorus loading (Numman 1972) to restore the fisheries were also reported. In European lakes, top predators had not been decimated by sea lamprey and overexploitation, as had occurred in the Great Lakes. Therefore, native fish stocks persisted in most of the deep, oligotrophic or formerly oligotrophic European lakes, despite frequent introductions of nonindigenous fishes. The maintenance of native top predators had stabilized food webs in the lakes, even during eutrophication. The large and active top predatory fish are also usually the most highly valued commercial and sport fisheries, and their sustainability is a primary goal of managers.

2.3 Fisheries and re-oligotrophication

The relative integrity of the fauna of the European lakes over time enables their study, since control of nutrient loading was applied, to inform how fisheries respond to re-oligotrophication (recovery from eutrophic conditions by nutrient load reduction). By the late 1970s, there was a general acceptance that TP loadings needed to be reduced and controlled to prevent or reverse eutrophication in freshwater systems, and lakes around the world began to recover. A large survey of 35 European lakes found that phosphorus load reductions led to lower TP concentrations, lower chlorophyll concentrations (surrogate for phytoplankton abundance and productivity), higher transparency and increases in zooplankton relative to phytoplankton abundances. Fish biomass declined along with TP in 80 percent of the lakes with species shifts toward top predator characteristic of less eutrophic waters (Jeppesen et al. 2005). Many of the lakes in this study were quite shallow and small and did not stratify in summer, but in the 13 deeper lakes that did stratify the above trends were even more strongly correlated with TP than in the shallow lakes. The relevance of these results to the Great Lakes may be questioned because of the small size and different food webs, but the trends do follow a general expectation for the recovery and re-oligotrophication of lakes. However, nearly all the lakes in the study had higher TP concentrations even after recovery than the Great Lakes have today.

Another study of re-oligotrophication in 11 peri-alpine lakes in France and Switzerland (Gerdeaux et al. 2006) is more relevant to the Great Lakes, as several of the lakes are as deep as the Great Lakes (9 of 11 greater than 100 meters deep), have comparable food webs and current TP concentrations covering the range experienced by the Great Lakes in their recovery. The period covered in their analysis was 1970 to 2000 when TP was declining in all the lakes over this period. According to the authors, the common species of high economic value in these lakes are salmon, coregonids, trout, pike, perch and burbot (*Lota lota*), quite similar to the dominant large fishes in the Great Lakes. In the five most oligotrophic lakes in the survey, TP concentrations declined from 10-20 µg/L to 5-6 µg/L over the 30-year record (**Figure 3**).

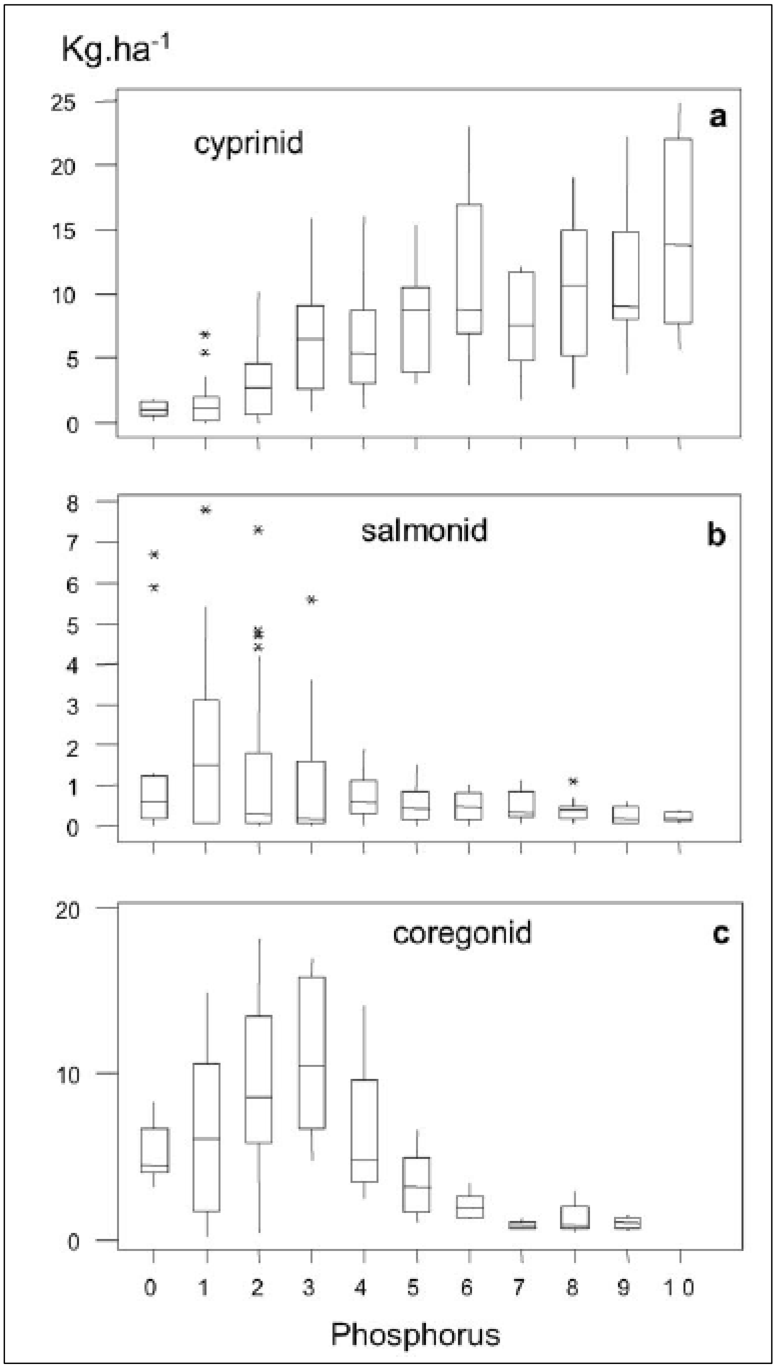

Figure 3: Relation of yields of different fish taxa to total P concentrations in 10 µg/L increments; 0=0-10, 1=10-20 µg/L TP etc. (Gerdeaux et al., 2006).

The authors found that total fish yield for all valued species fell continuously with TP concentrations below 40 µg/L, but with different contributions to total yield by different species. Coregonine yields were maximal in the TP range of 30-40 µg/L and fell as TP increased above or decreased below this range. Yields of salmonids peaked at 10-20 µg/L and fell at lower and higher concentrations in these lakes. The conclusion of the authors was:

> During re-oligotrophication, the total yield (of all fishes) remains nearly the same while coregonids become dominant. In very oligotrophic lakes, when the TP was below 5 µg/L, the total yield decreased rapidly, and fish production was low.

The current offshore TP levels in all the Great Lakes (with the exception of Lake Erie) are at or below 6 µg/L in 2010 (Dove and Chapra, 2015), which would suggest that potential yields would decline for coregonids and lake trout if TP concentrations fall lower in the Great Lakes, based on the European experience.

2.4 Experimental eutrophication and oligotrophication

Monitoring data, such as that available for the European lakes cited above or for the Great Lakes, although compelling and intuitively satisfying, cannot confirm causation for observed trends. Fortunately, the concern about the impact of nutrient enrichment on fish abundance and productivity led to whole lake experiments to test the hypothesis that phosphorus enrichment results in increased fish abundance and productivity in oligotrophic lakes. There is strong evidence from at least two whole-lake nutrient addition experiments at the Experimental Lakes Area (now operated by the International Institute for Sustainable Development and known as IISD-ELA) that have demonstrated that fish production and abundance is primarily limited by nutrients/primary production.

The ELA is a collection of 58 lakes reserved for study and experimentation established in 1968 in northwestern Ontario in order to inform nutrient management strategies on the Great Lakes (Johnson and Vallentyne, 1971). In a keystone experiment that supported the decision to control TP under the GLWQA, oligotrophic Lake 226 was divided with a curtain, with only carbon (C as sucrose) and nitrogen (inorganic fixed N) added to one side of the lake and C, N and phosphorus (P) added to the other for 7 years (1973 to 1980). Total phosphorus (TP) in the epilimnetic waters of the lake doubled from approximately 10 µg/L to around 20 µg/L. The aerial image of the result of the experiment is now a classic in many limnology and ecology textbooks; the side with P added turned green because of algal growth while the C- and N-only side remained relatively clear.

Of relevance here was how the fish population responded. Lake 226 supports a simple fish community, with the only large-bodied species being lake whitefish (*Coregonus clupeaformis*). Production and abundance of lake whitefish increased on the side of the lake receiving C, N and P additions, and then declined once nutrient additions ceased (Mills and Chalanchuk, 1987).

Lake whitefish production and abundance remained relatively stable on the side receiving only C and N. As a result, a strong dependence of lake whitefish production and abundance on mean annual TP concentrations in the lake was observed (**Figure 4**; Production, Pearson correlation coefficient ($\boldsymbol{\rho}$) = 0.90, t_{12}=7.4, P<0.0001; Abundance, $\boldsymbol{\rho}$ = 0.75, t_{20}=5.1, P<0.0001). Without P additions, the basin receiving only C and N remained relatively stable and at similar fish densities to the P addition basin prior to P addition, both before and after the addition of C and N.

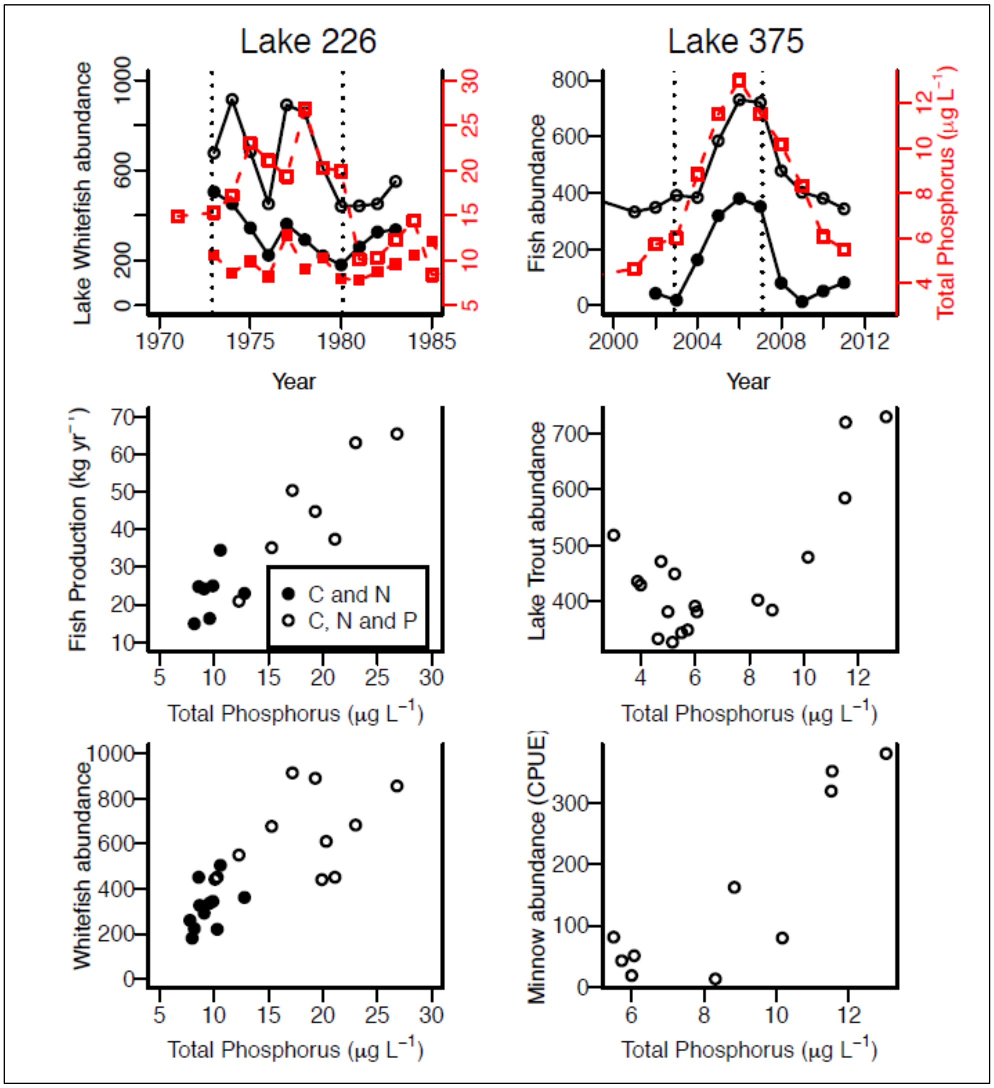

Figure 4: Changes in fish abundance and surface layer Total Phosphorus concentrations (TP, µg L-1) and significant correlations between them from whole-lake experiments at the IISD-ELA associated with nutrient additions. Dotted lines show start and end of whole-lake manipulations. ***Top left:*** Changes in abundance of Lake Whitefish (open circles) and TP (open squares) in the northeast basin of Lake 226 which received carbon, nitrogen and phosphorus additions, 1973 to 1980. Closed symbols show lake whitefish abundance (circles) and TP (squares) from the southwest basin, receiving only C and N. ***Top right:*** Changes in the abundance of Lake Trout (open circles), minnows (closed circles) and TP (squares) in Lake 375 during enrichment by an aquaculture enclosure, 2003 to 2007. ***Middle left:*** Significant correlation between lake whitefish production and TP in Lake 226; open circles, Northeast Basin, closed circles, Southwest basin. ***Middle right:*** Significant correlation between Lake Trout abundance and TP in Lake 375. ***Bottom left:*** Significant correlation between lake whitefish abundance and TP in Lake 226, symbols as in panel C. ***Bottom right:*** Significant correlation between minnow relative abundance and TP in Lake 375. Figure courtesy of Michael Rennie, IISD-ELA.

Similarly, during an experiment in Lake 375 which has a lake trout (*Salvelinus namaycush*) population and where a small aquaculture operation resulted in increased TP concentrations in the open lake between 2003 and 2007, fish abundance saw an increase during the operation, but then a decline once operations ceased. TP doubled from about 6 µg/L to 12 µg/L during the aquaculture operation (Bristow et al. 2008), but then declined once aquaculture operations were discontinued. A significant relation between mean annual TP with both the relative abundance (catch per unit effort) of fall-captured minnows (primarily fathead minnow, *Pimephales promelas*; $\boldsymbol{\rho} = 0.86$, t_8=4.84, P=0.0013) and with the abundance of lake trout ($\boldsymbol{\rho} = 0.70$, t_{16}=3.87, P=0.0014; Figure 4) was observed.

Both experiments conducted on naturally oligotrophic, pristine fish populations provide evidence for a 'ceiling' or upper bound on fish production in aquatic ecosystems based on the nutrients available in the system. When phosphorus inputs are increased, fish abundance and production also increase; when phosphorus inputs are lowered fish production is reduced. At some point, this relationship breaks down (i.e., excessive nutrients and algal growth causing deoxygenation and fish kills). Generally, reductions in phosphorus concentration (through management actions to limit loadings or ecosystem disturbances that re-route and increase sedimentation of phosphorus in lakes (i.e., the nearshore shunt (Hecky et al. 2004)) would be expected to reduce pelagic fish production. The responses of fish abundance to phosphorus levels in the European Lakes (**Figure 3**) and the experimental lakes (**Figure 4**) occurred over the same ranges of TP concentrations evident in the Great Lakes, suggesting that similar responses in fish abundance to changes in nutrients in the Laurentian Great Lakes could be expected.

2.5 Re-oligotrophication of the Great Lakes

The Gerdeaux et al. (2006) study of European peri-alpine lakes focused on yields of fish species to regulated commercial fishing, which was practiced on all the lakes with a relatively constant fishing effort over time. Such an analysis during the re-oligotrophication of the Great Lakes is difficult, if not impossible. Overexploitation in the first half of the last century—which overlapped with and then was followed by invasion and establishment of predatory sea lamprey—diminished important native fish populations nearly to extinction while removing the top predators from the food web and led to dominance of lower-valued prey species, such as alewife, in the lakes through the 1950s to the 1960s. Efforts to control sea lamprey by the Great Lakes Fishery Commission and stocking of top predator salmonids have led to recovery of piscivores in Lake Michigan (Bunnell et al. 2014; **Figure 5**) as well as in Lakes Huron and Ontario; but this recovery has been dominated by introduced and stocked Pacific salmon species. During the same period of piscivore recovery, the lower food web has also been impacted by highly successful invasive species which now dominate the lower food web (**Figure 5**) and modify trophic interactions and energy flow.

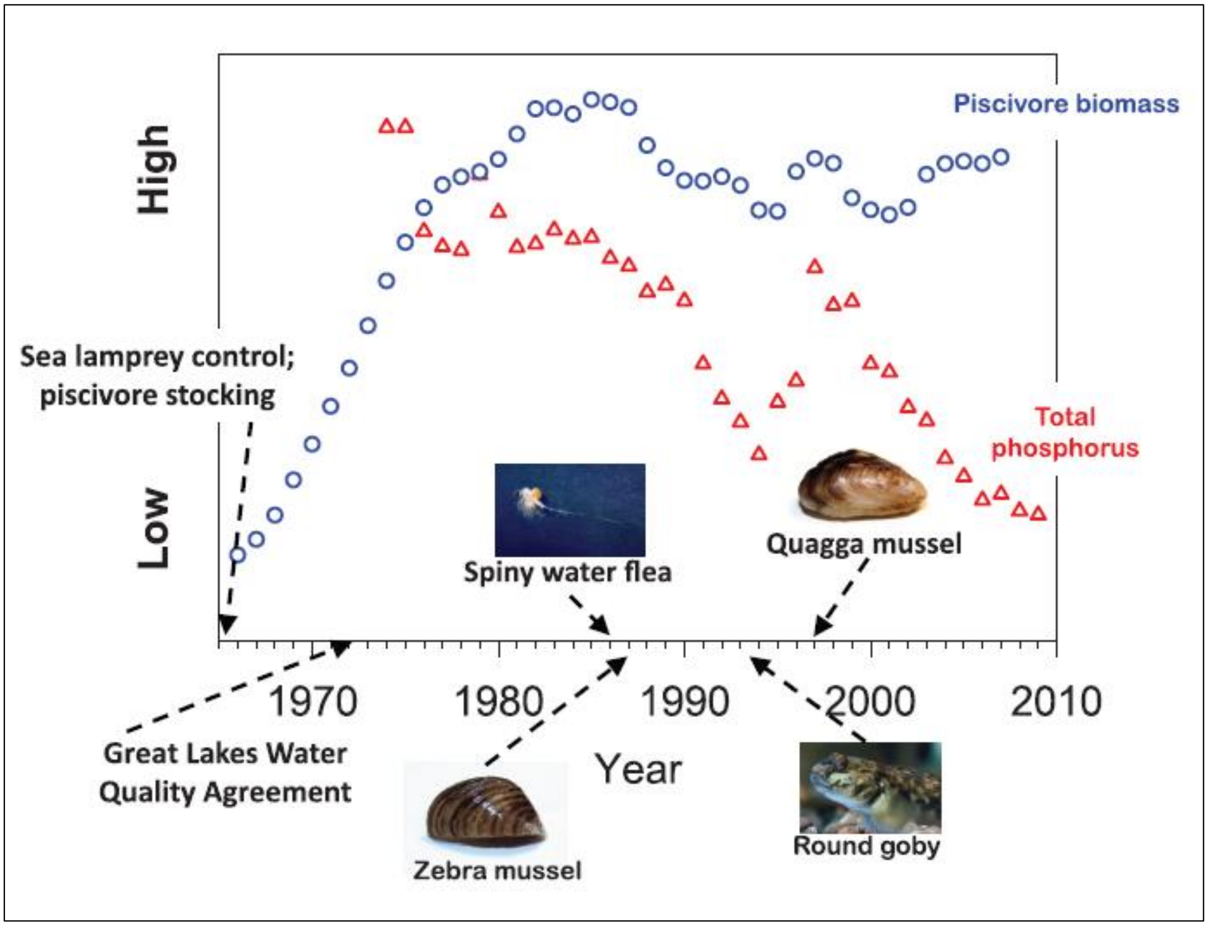

Figure 5: Trends in piscivore (top predator) biomass since 1965 and total P in Lake Michigan (both parameters normalized to maximum value achieved in the record and appearance of major impact Invasive species entering Lake Michigan. Sea lamprey control and salmonid stocking have enabled re-establishment of top predators in the food web but dominant lower food web organisms have also changed over time because of several successful invasions. Figure 2 of Bunnell et al (2014).

Lake Superior has also recovered the abundance of the native lake trout over the same period, but its food web has not been significantly altered by these invasive species. Lake Superior has been oligotrophic throughout this time period and is colder and more dilute (i.e., lower calcium levels may limit mussel growth) than the lower lakes, factors that provide resistance to invasive species. Lake Superior’s isolation and low population density also resulted in minimal nutrient impact on its trophic state. Consequently, Lake Superior has been oligotrophic throughout the period of recovery of the lower lakes, and so it is not possible to study it for re-oligotrophication impacts. In the lower lakes, Ludsin et al. (2001) reported the reduction of eutrophication tolerant species and an increase in species intolerant of eutrophication in Lake Erie during a period of declining TP concentrations, 1969 to 1996 (**Figure 6**), prior to recent eutrophication trend post-

2000. This study documented that controlling TP had had a positive effect on the fish community and favored species with higher value for sport and commercial fishing. However, in the lower lakes, clearly separating the response of top predator recovery to the multiple drivers of sea lamprey control, stocking, transformation of fishery to emphasis on sport fishing, phosphorus reduction (which began during the fishery recovery), and the alteration of food webs by invasive species is problematic. Sophisticated ecosystem models that can separate the possible impact of reduction in phosphorus loading on top predator recovery from other factors are just becoming applied for the Great Lakes (i.e., Kao et al. 2014; Kao et al. 2016; and see section below on modeling).

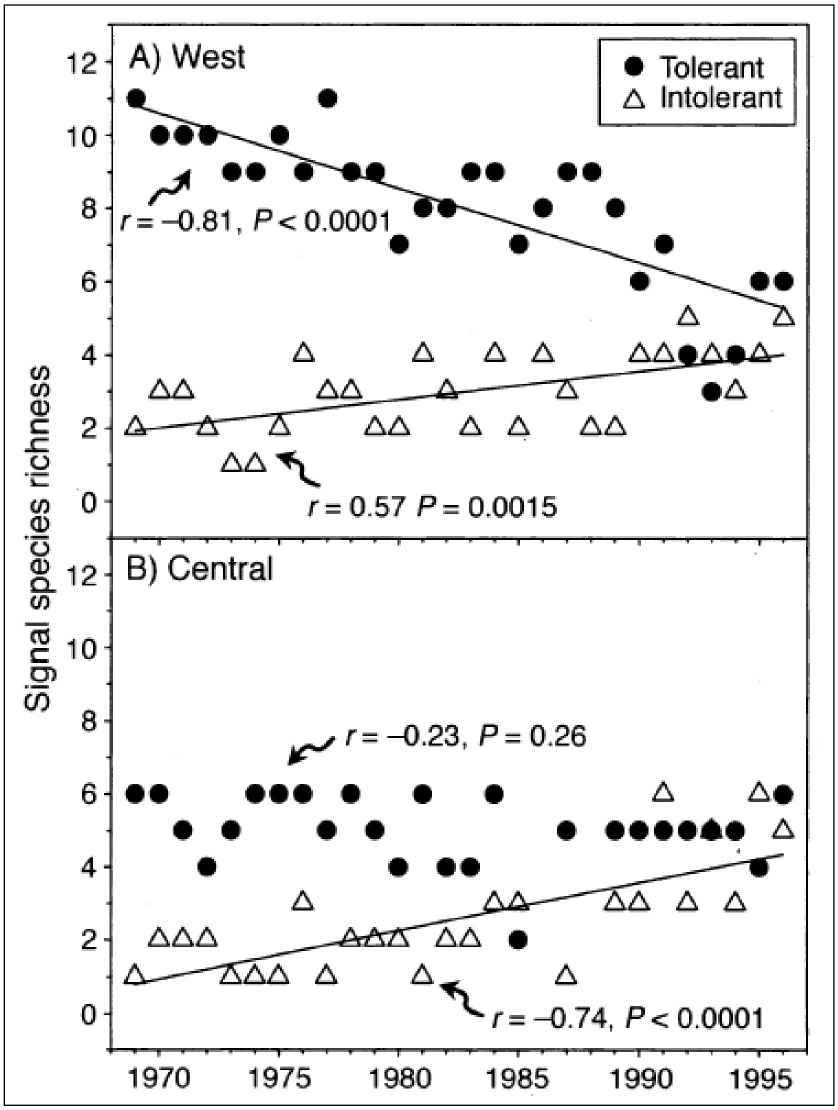

Figure 6: Total number of fish species tolerant and intolerant of eutrophy (i.e., anoxia or turbidity) captured in Lake Erie's (A) west and (B) central basins, 1969 to 1996. Correlation coefficients (r) and probability values (P) were included for all trends, whereas regression lines were included only for significant trends (α = 0.05). Figure 4 of Ludsin et al. (2001).

2.6 Prey fish and re-oligotrophication

Prey fish biomass has been measured with diurnal bottom trawls in all Great Lakes by various agencies since 1978 (**Figure 7**). In most of the Great Lakes (except Lake Erie), estimated prey fish biomass was highest prior to 1990 and has fallen since then to historically low levels. Trends in prey fish biomass were notably similar among Lakes Superior, Michigan and Huron, the three most oligotrophic Great Lakes (Gorman and Weidel, 2016).

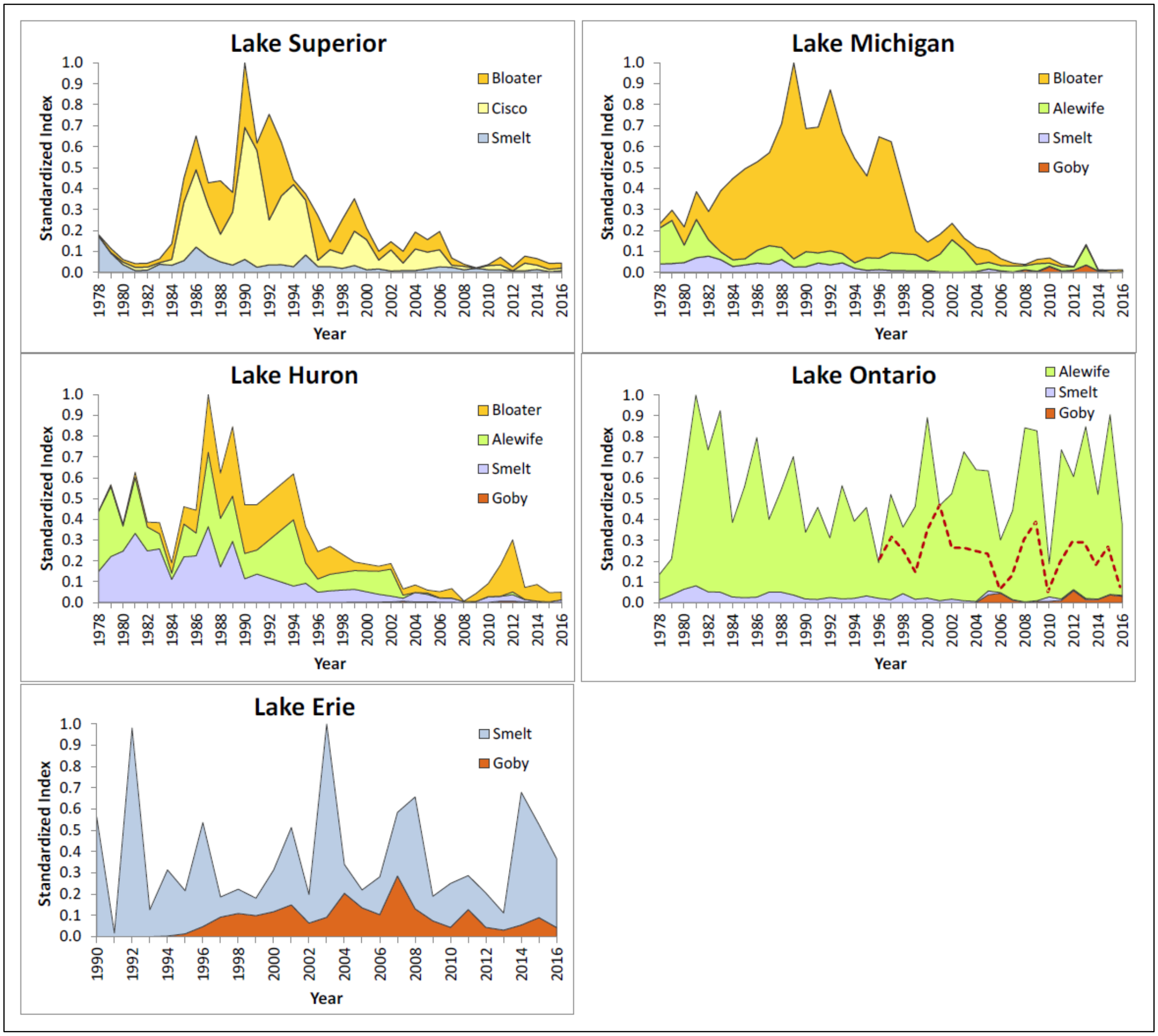

Figure 7: Lakewide standardized indices of pelagic prey fish biomass for selected species. The red dashed line on the Lake Ontario plot represents a continuing estimate of the adjusted values corrected to the historical sampling gear configuration, which was modified in 1997 and subsequent years (Gorman and Weidel, 2016). Figure 7 of LimnoTech (2018).

Dove and Chapra (2015) found significant downward trends in TP in these lakes since 1990, which may suggest a causative connection between TP and prey fish abundance. However, piscivores have substantially recovered in all three lakes from their low abundance of the 1960s, and their predation pressure on the prey fish likely contributed to the historically low prey fish biomass observed in recent years. In Lake Superior where there have been minimal lower food web disruptions by invasive species and the native fish fauna has remained intact throughout the available period of sampling (1978 to 2015), there is a remarkable correspondence in the time trend of prey fish biomass and predator (lake trout) biomass, consistent with bottom-up control on the predators (LimnoTech, 2018; **Figure 8**).

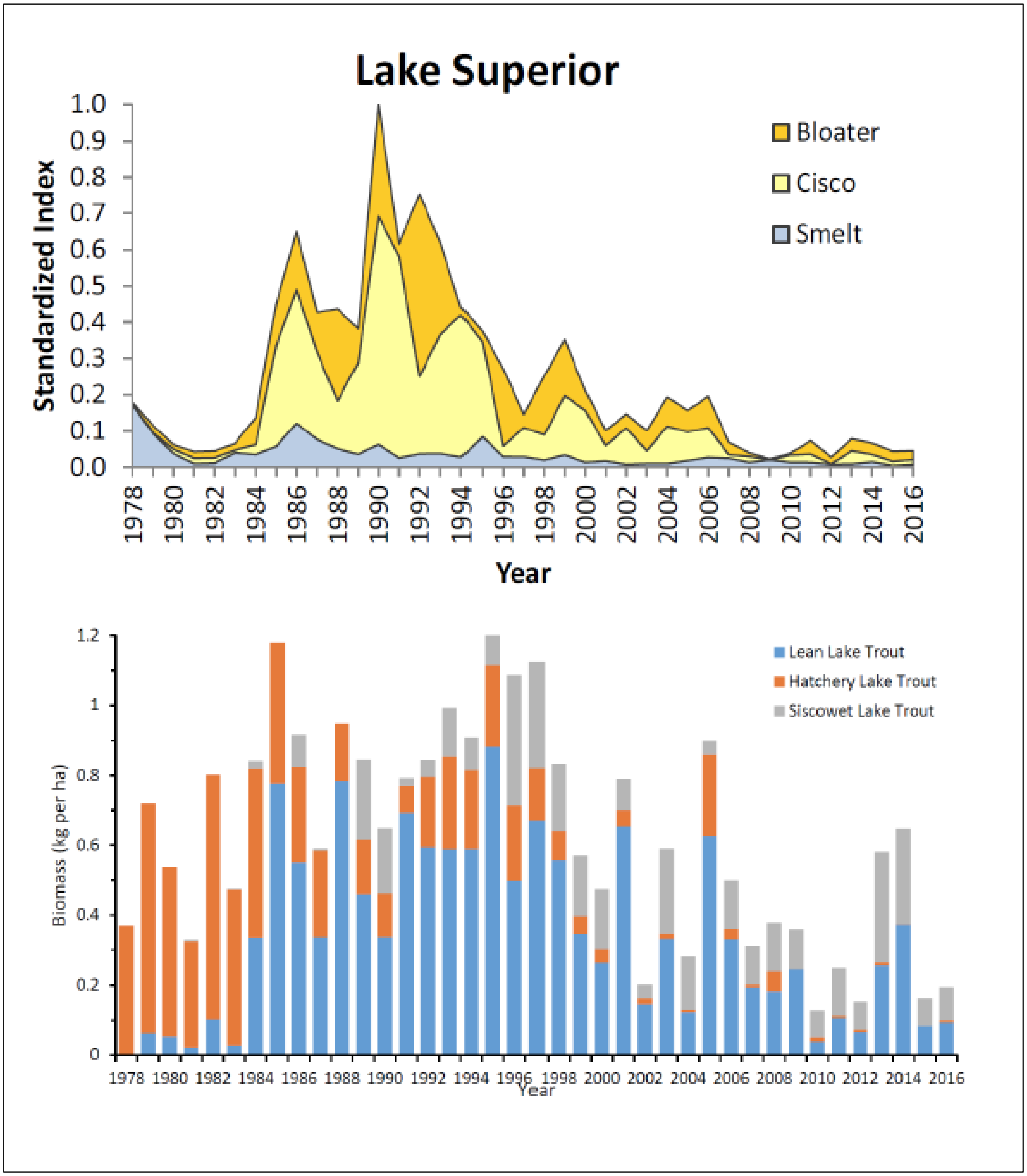

Figure 8: The top figure shows standardized prey fish biomass in Lake Superior (from **Figure 7** above) compared to nearshore lake trout biomass (bottom figure) (Figure 5 of Vinson et al. 2016). Similar temporal patters suggest bottom up control in the native food web (note rainbow smelt are not native but are minor portion of prey fish biomass).

In Michigan and Huron, the changes in the lower food web (i.e., Barbiero et al. 2018; Reavie et al. 2014) may also have contributed to the current low prey fish biomass, as quagga mussels and now round gobies (Figure 5) have been implicated in reducing and diverting pelagic phytoplankton production away from planktivorous fishes. Round goby, which invaded the Great Lakes during this period, is a benthic fish which is difficult to sample by the trawling techniques used in these surveys. Consequently, its abundance relative to other prey species is substantially underestimated. Because “top-down” impacts due to increased predator consumption and “bottom-up” effects due to declining TP concentrations over the period of record would have similar impacts on prey fish abundance (He et al. 2015; Tsehaye et al. 2014), it is not possible to interpret unequivocally the association between TP and prey fish abundance in the Great Lakes. Again, more sophisticated models linking TP, and ideally TP loading, to upper food web changes are necessary to parse the relative importance of the multiple factors potentially impacting pelagic fish production in these lakes. Correlations and associations do not have the predictive power required to evaluate future ecosystem states. This is especially true as continuous efforts using standard methods across the lakes to monitor the lower food web are only available since 1998. Consequently, the long term records back to the early 1970s for fisheries and water quality can only be suggestive of possible causative factors linking trends in TP and fish communities of the Great Lakes.

3.0 Recent Great Lakes Trends

Bunnell et al. (2014) compiled lake-specific trends for key physical-chemical parameters and multiple trophic levels across the Great Lakes Basin, with 2006 or 2010 or 2011 being the last year included in the study (year depending on the trophic level). The goals were:

1. To discern whether time series trends were present for each lake;
2. Whether observed trends were consistent with 'bottom-up' (nutrient controlled) or 'top-down' (predation pressure) regulation; and
3. To identify commonalities across the Great Lakes.

Common trends across at least three lakes (Michigan, Huron and Ontario) included increasing water clarity, and concomitant declines in phytoplankton, native invertebrates and prey fishes, with a caveat that the shallow nearshore regions of the lake were rarely represented in the time series. A correlation analysis indicated that the trends were more commonly consistent with bottom-up regulation (i.e., resource limitation), and Lake Huron was identified as the system with the strongest evidence for this effect. Further, using the USEPA Great Lakes National Program Office's long-term phytoplankton monitoring data, Reavie et al. (2014) noted the loss of pelagic phytoplankton biomass in lakes Huron and Michigan was largely due to the loss of heavy, filamentous diatoms. This loss suggested likely combined effects of filter feeding, lower nutrients and passive sinking of heavier cells. Bunnell et al. (2014) and Reavie et al. (2014) both speculated that long-term declines in phosphorus inputs and the proliferation of dreissenid mussels were an important causal factor for the declining biota. Moving forward, they recommended experimental and modeling work to bolster these correlative analyses and continued monitoring to extend the time series to enable future analyses.

The LimnoTech report (2018) provides an update to the time series and associated analyses for all the Great Lakes. The LimnoTech report is notable for its inclusion of lower trophic level data from Environment and Climate Change Canada (ECCC), especially chlorophyll and Secchi disk depth (transparency) which was not used in Bunnell et al. (2014). Below are highlighted some of the key findings from the LimnoTech report that updated these multitrophic level trends in the Great Lakes through 2016.

- Offshore TP in USEPA spring (April) surveys since 1998 (**Figure 9**): Updated analyses through 2016 revealed declining TP concentrations only for Lake Michigan (but not Lake Huron, as had been found through monitoring year 2010 by Bunnell et al. (2014)). Surprisingly, TP has significantly increased in Lake Superior between 1998 and 2016 in USEPA data but not in ECCC data, which showed a significant decline over this same time (Dove and Chapra, 2015). No significant time trends were found in any other lake or basin over the period 1998 to 2016. For Lake Huron, TP leveled out between 2010 and 2016. Ontario had been variable from 1998 to 2010 (no significant trend, but, since 2010, there has been a steady decline in TP). In Lake Erie, TP concentrations were relatively high and variable through time, with no evidence of declining TP in any basin.

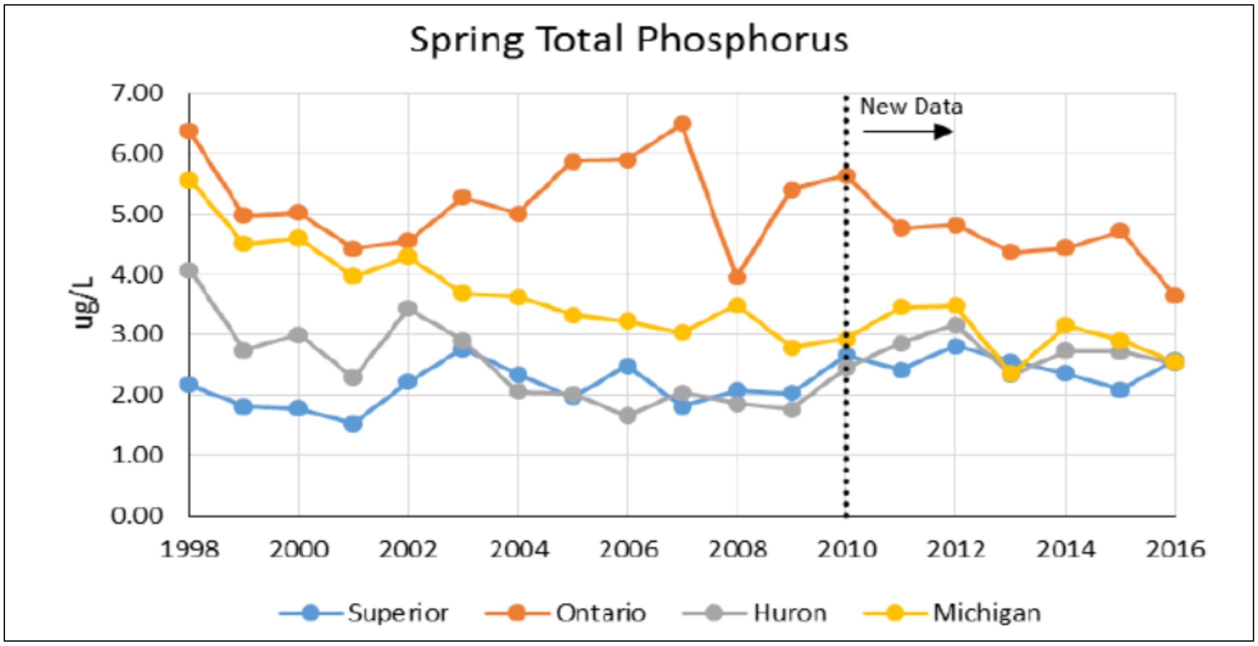

Figure 9: Spring TP during USEPA spring surveys. Lower food web sampling began in 1998. Bunnell et al. (2014) reported data from 1998 to 2010. LimnoTech report (2018) extended observational period to 2016 (new data).

- Offshore chlorophyll *a* in May: These data (**Figure 10**) are based on satellite-derived estimates that can underestimate concentrations because the deep chlorophyll maximum below the mixed layer is not included. Nonetheless, chlorophyll *a* declined from 1998 to 2016 in Lakes Michigan, Huron, and Superior, that was the same result as found in Bunnell et al. (2014) over the shorter time period.

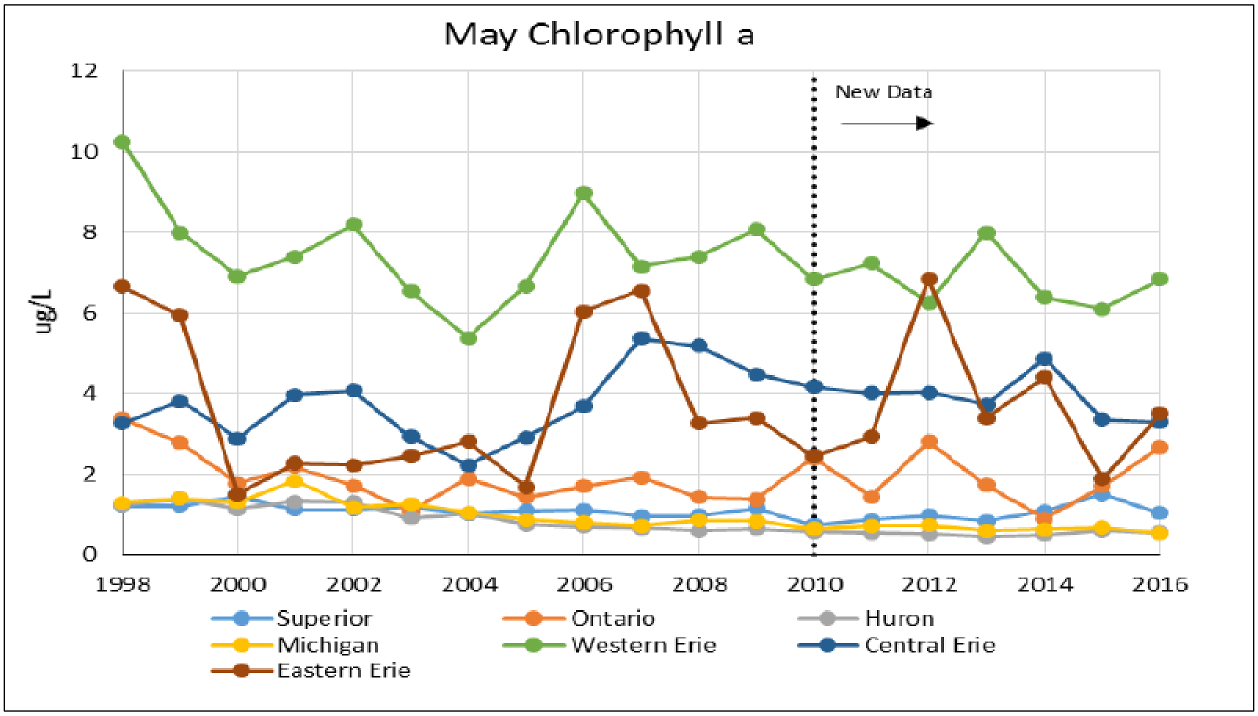

Figure 10: Spring chlorophyll *a* using satellite imagery and Great Lakes Fit algorithm.

- Offshore water clarity in April: Secchi disk depth (a measure of water clarity) increased in Lakes Michigan, Huron and Superior, following previously detected trends (Bunnell et al. 2014). Future research is required to understand how water clarity has increased in Lake Superior where dreissenid mussels have not successfully invaded. Such an increase is consistent with ECCC TP data for Lake Superior, but not with USEPA data, and warrants further research to resolve this apparent discrepancy in TP data.

- Offshore crustacean zooplankton: The length of the time series available for analysis more than doubled from Bunnell et al. (2014). Biomass declined in Lakes Michigan, Huron and Ontario from 1998 to 2016. A declining trend was not apparent in Lake Michigan where data were only available through 2006.

- Prey fish: Trends (**Figure 6**) were based only on bottom-trawl derived estimates of fish biomass; acoustic-derived estimates of fish biomass are also available in some lakes, but with shorter time series. From 1998 to 2016, prey fish biomass significantly declined in Lakes Michigan and Superior, and increased in western Lake Erie; no significant trends were present in the other lakes. These results differed from Bunnell et al. (2014) who reported declining prey fish biomass in Lake Huron, and no significant trend in any basin of Lake Erie.

- Piscivores: Biomass declined only in Lake Ontario and increased only in Lake Michigan, consistent with Bunnell et al. (2014). In 2018 Lake Erie walleye abundance was not increasing in Lake Erie, as was reported in Bunnell et al. (2014); however estimates have since changed and record high levels of adult fish are projected in 2020-2021 (Lake Erie Walleye Task Group 2020).

A summary of temporal trophic level trends over the expanded data series can be found in LimnoTech (2018, Table 4-1). TP concentrations did not trend downward over the past 20 or so years, with the exception of Lake Michigan. Water clarity continued to increase and chlorophyll *a* continued to decrease in the three upper Great Lakes. Crustacean zooplankton biomass declined in three of the lakes (Michigan, Huron and Ontario). Fewer trends were detected for fish. Prey fish declined in Lakes Michigan and Superior, but piscivores only decreased in Lake Ontario. The only positive trend for fish was increasing biomass of piscivores in Lake Michigan. Although not presented in the LimnoTech report, a recent summary of zoobenthos data for the Great Lakes from 1998 to 2014 (Burlakova et al. 2018; **Figure 11**) indicated major changes in the offshore benthos (greater than 70 meters) in lakes Michigan, Huron and Ontario characterized by the loss of *Diporeia* in these lakes and a significant increase in *Dreissena*. Similar trends, but of greater magnitude, also were dominant in shallower waters (less than 70 meters) of these three lakes. *Dreissenids* also exhibited a significant upward trend in Lake Erie over this time period. Bunnell et al. (2014) had noted that nondreissenid zoobenthos had significantly declined over the available period of record in Michigan, Huron and Ontario, but significantly increased in west and central Lake Erie. Burlakova et al. (2018) found there was no significant change in the zoobenthos community in either the nearshore or the pelagic depth zones in Lake Superior in agreement with Bunnell et al. (2014).

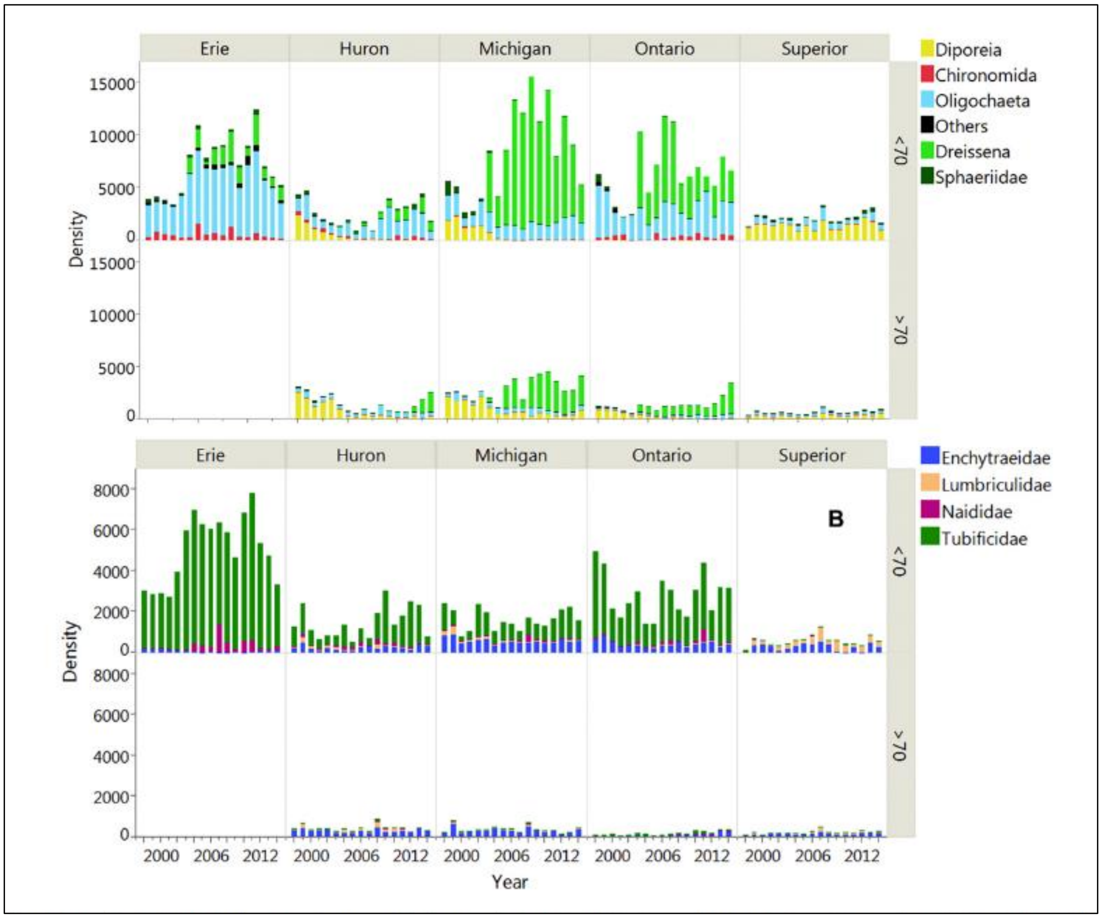

Figure 11: A) Trends in densities (ind./m^2) of major taxonomic groups and indicator species in the Great Lakes (averaged by lake, depth zone (greater than and < 70 m) and years (1998 to 2014), and **B)** separately for Oligochaeta. Bivalves, *Dreissena* and Sphaeriidae are shown separately since *Dreissena* species were not counted in 1998 to 2002. Figure 7 of Burlakova et al. (2018).

The LimnoTech report also revisited the correlational analyses of adjacent trophic levels to explore evidence for bottom-up or top-down regulation for each trophic level in each lake:

- Chlorophyll *a* concentrations were significantly correlated with TP in western and eastern Lake Erie, and Lake Michigan. Bunnell et al. (2014) also reported a similar correlation in Lake Huron but found no evidence of a significant correlation in any basin of Lake Erie in the shorter time series.

- Zooplankton biomass was positively and significantly correlated with chlorophyll (phytoplankton abundance) in Lakes Ontario, Michigan, and Huron consistent with bottom up regulation. Bunnell et al. (2014) only found evidence for bottom-up regulation of zooplankton in Lakes Michigan and Huron.

- Prey fish biomass was positively and significantly correlated with zooplankton abundance in Lakes Michigan and Huron consistent with bottom up regulation of prey fish abundance. Bunnell et al. (2014) reported this result for Huron and Superior.

- Piscivores exhibited no evidence of significant bottom-up limitation in the extended time series. There was evidence in Lake Michigan for top-down control of prey fish by piscivores, as reported previously (Bunnell et al. 2014). Bottom-up regulation was less evident in the long time series for Lakes Ontario and Huron (differing from Bunnell et al. 2014), but was still present in western Lake Erie.

A summary of a correlational analyses across trophic levels from expanded data series is given in LimnoTech (2018, Table 4-2). Bunnell et al. (2014) reported more (six-fold) instances of bottom-up regulation than top-down regulation. With the updated data, a similar dominance (eight-fold) of bottom-up regulation occurred. The strongest evidence for nutrient dependence occurred between phytoplankton and zooplankton. Although not reported in Bunnell et al. (2014) or in the LimnoTech report (2018), zoobenthos species richness and density have recently been reported to correlate with spring chlorophyll *a* both among and within the lakes, that would be consistent with bottom-up regulation as well (Burlakova et al. 2018).

The LimnoTech analyses reveal important new information regarding trends in the Great Lakes, including the stabilization of offshore TP concentration trends for most lakes and evidence of declining offshore zooplankton in more lakes than was previously observed. Lake Huron is an interesting case study because its trends were so consistently “negative” in Bunnell et al. (2014), yet phosphorus and prey fish no longer exhibit any trend when the time series were updated. From a process point of view, however, nutrient limitation of food web productivity remains a viable hypothesis for future food web research to test, given the predominance of correlations consistent with bottom-up regulation. For this reason, we agree with the assessment by LimnoTech that “overall, the trends from 1998 to 2016 remained similar to Bunnell et al. (2014) findings with respect to most time trends and trophic level relationships.”

This report ultimately seeks to determine what linkages exist between phosphorus and fish productivity. Several meta-analyses have already clearly demonstrated that more phosphorus increases fish biomass (Deines et al. 2015; Downing et al. 1993; Oglesby 1977), although theory predicts that, at some high level of phosphorus, fish biomass will begin to decline owing to suboptimal fish habitat or failure to translate increased primary productivity up the food web to fish (i.e., diversion of energy from grazing food chain to detrital food chain). We have no reason to suspect that excessive phosphorus could be the cause of declining fish biomass anywhere in the Great Lakes, although historically high levels of phosphorus in western Lake Erie resulted in a fish community composition that was less desirable by fishery managers (Ludsin et al. 2001; Ryan et al. 2003). The analyses in this report did not directly relate phosphorus to fish in the Great Lakes, but the preponderance of evidence for bottom-up limitation is suggestive that decreasing phosphorus concentrations are contributing to declining fish biomass in some lakes. Also, the review of global experience of oligotrophication in the European lakes and in whole lake experiments is consistent with fish species composition and abundance being largely dependent on TP at the current concentrations in all the Great Lakes. At the same time, we note that several other factors influence fish biomass, including fishery management actions (i.e., stocking densities, harvest regulations), climate, quality of fish habitat, and the efficiency with which energy moves through the food web from primary producers up to fish. These factors (and others) cause the positive relationship between phosphorus concentrations and fish biomass to be variable and noisy in both time and space across the lakes.

In the Great Lakes, water quality and fishery managers would be assisted by an improved understanding of what factors influence the transfer of trophic energy up to fish biomass and, even more challenging, to particular high-valued species of management concern (Stewart et al. 2018). Many of the ecosystem modeling tools that are needed have already been developed and are described below. Those that can simulate the spatial complexity of the Great Lakes and link TP concentrations to fish will be most effective. Most of the trends described above were based on data collected in offshore waters, which comprise the bulk of volume and surface area of the Great Lakes and are relatively well monitored by federal agencies. The nearshore waters, however, have less standardized and spatially less frequent monitoring relative to the greater variability in nearshore conditions which are most directly impacted by coastal anthropogenic influences. This nearshore under-sampling occurs despite the nearshore areas providing key spawning and nursery habitat for many important prey and piscivorous fish species. In Lake Michigan for example, trends for nearshore phosphorus and zooplankton are much different than the trends revealed from offshore monitoring (Bunnell et al. 2018). Provincial and state programs also contribute to offshore monitoring and include some lower trophic level monitoring. The states and province also lead most fisheries monitoring programs. Therefore, existing ecosystem models would benefit from more comprehensive and coordinated monitoring and research of the nearshore waters in many of the lakes to validate existing models and to inform the necessity and calibration of new models. For example, recalling the nearshore shunt hypothesis from over a decade ago (i.e., Hecky et al. 2004), what is the fate of the nutrients that are delivered to the nearshore? How much of that phosphorus is sequestered into benthic organisms such as *Cladophora* or dreissenid mussels, instead of phytoplankton and zooplankton? With few exceptions, young fishes in the nearshore zone can directly access the zooplankton, but not the benthic algae or mussels. This is just one example of how the transfer of energy from the base of the food web up to invertebrates can have consequences for fish, and ultimately fisheries.

Jain and DePinto (1996) developed a simple food web model for Lake Ontario to examine how bottom-up (P load control) and top-down (stocking) interact to determine salmonid biomass. The model corroborated other studies by demonstrating that, under low P load and therefore low in-lake concentrations, additional salmonid stocking did not produce significant increases in salmonid production; while at high P loads (leading to higher carrying capacity for salmonids), additional stocking does indeed produce higher annual salmonid production (see Figure 12). This result indicates a strong relationship between TP and salmonid production at low TP concentrations, but a weak relationship between TP and salmonid production at high, plentiful, TP concentrations. Although instructive of the interaction of these processes on a lakewide basis, this model does not address the reorganizing of nutrient and energy flows within the lake that are the consequence of the successful invasion of dreissenid mussels in the lakes. This invasion has also altered the relationship between external P loading and the realized distribution of P concentrations (Cha et al. 2011; Hecky et al. 2004) in all the lakes except Superior. Models that are spatially explicit will be necessary to address this new reality.

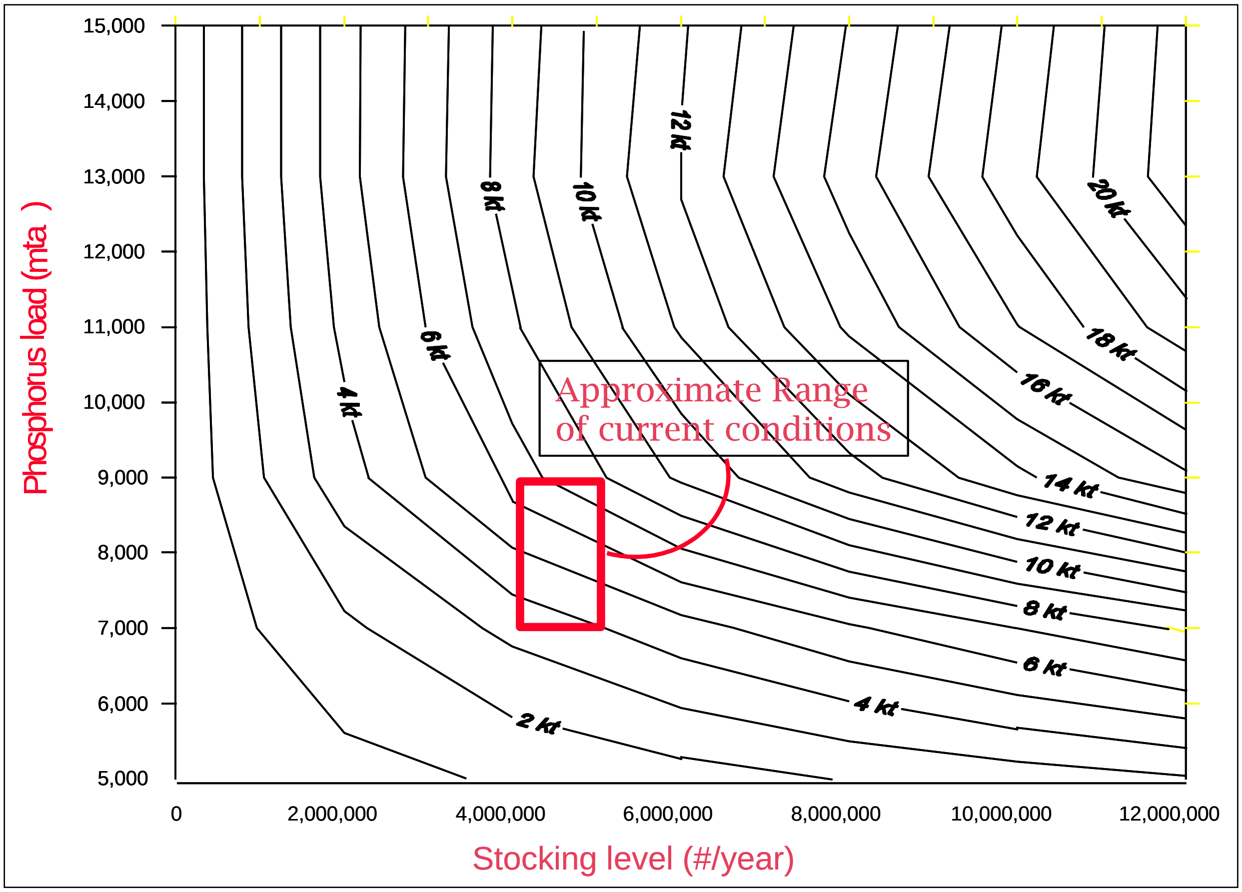

Figure 12: Predicted fifteen year average adult salmonid biomass (10^9 g W/W) in Lake Ontario as a function of TP load (mta) and salmonid stocking rate (#/year).

4.0 Present and Future Modeling of Lake Productivity

4.1 Modeling requirements

Models that can help provide a quantitative understanding of the current spatial and seasonal distribution of productivity in the Great Lakes and can project the future trends in response to natural and anthropogenic stressors must have the following capabilities:

- Computing fine-scale hydrodynamics to capture advection and dispersion fluxes in both nearshore and offshore zones of the lake;
- Computing the gradients of nutrients, primary production, and secondary production between nearshore regions and offshore regions;
- Partition primary production in nearshore zones between various phytoplankton functional groups, including cyanobacteria, and benthic algae such as *Cladophora*;
- Quantify the role of dreissenids and *Cladophora* in nutrient cycling and trapping of nutrients in the benthic and nearshore zones and determine their potential or realized trophic contribution to fish productivity;
- Represent a detailed structure and function of the whole food web from phytoplankton functional groups to top predator fish at the functional group or even species level for highly valued species;
- Compute the impact of fish stocking and harvesting on fish production in the lake;
- Incorporate the impacts of fish habitat quality and quantity on fish reproduction and survival;
- Incorporate the capacity to consider the impacts of invasive species (present and potential) and climate change; and
- Compute the relative impact and importance of bottom-up versus top-down control of the food web structure and function by accurately modeling the feedbacks between the upper and lower food web as mediated primarily at the zooplankton level in the deeper offshore regions. In the longer term, building on increasing sophistication of watershed models to estimate P loading to coastal areas, evaluate the modifying effect of terrestrial and coastal habitat management, i.e., land management practices, dam removal, wetland restoration, etc., on offshore fish production.

To accomplish these capabilities in a single modeling framework, we must develop a blending of two modeling domains currently being applied in the Great Lakes: nutrient - lower food web eutrophication models and fisheries models that focus on the upper food web structure and function. Below is a brief summary of the status of the latest iterations of these two modeling domains in the Great Lakes.

4.2 State of modeling in the Great Lakes

4.2.1 Ecosystem models that focus on the lower food web

Numerical ecosystem modeling in the Great Lakes was first applied to the management of eutrophication by applying a suite of models to establish phosphorus load targets for each of the lakes (Bierman 1980; Chapra and Robertson, 1977; DePinto et al. 1986). These models were focused on eutrophication symptoms (chlorophyll *a*, dissolved oxygen, water clarity and phosphorus concentrations) in the offshore waters of the lakes. With the invasion of dreissenids and the resurgence of *Cladophora*, these models were found to be insufficient to address the nearshore re-eutrophication occurring in the lakes (DePinto et al. 2006). Therefore, a new generation of eutrophication models was developed to address nearshore ecosystem impacts of dreissenids and *Cladophora* and fine-scale nutrient and production gradients that had resulted from the ecosystem structural and functional changes that had occurred. These models are part of the suite of models that have been applied to re-evaluate target phosphorus loads as requested in Annex 4 of the 2012 GLWQA Protocol (Scavia et al. 2016). However, the characteristics of some of these models also make them valuable in assessing and quantitatively understanding the offshore productivity decline that is the concern of this work group.

The nutrient cycling/lower food web models that meet one or more of the model requirements listed above include the Advanced Aquatic Ecosystem Model (A2EM), which was linked to Environmental Fluid Dynamics Code (EFDC) and applied recently to the assessment of phosphorus loading on harmful algal blooms in the western basin of Lake Erie (Western Lake Erie Ecosystem Model) (Verhamme et al. 2016). This model was also applied to assess the impacts of multiple stressors in Saginaw Bay, Green Bay, Sandusky Bay, Sodus Bay (Lake Ontario) and Missisquoi Bay (Lake Champlain). It contains all of the components and associated processes necessary to develop a quantitative understanding of the role of phytoplankton, *Cladophora* and dreissenids in nutrient cycling and productivity gradients in the Great Lakes. The phosphorus cycling process diagram for this model is shown in **Figure 13**. In fact, the EFDC-A2EM is currently being developed to support the Annex 4 process in Lake Ontario, where the concern is that the nutrient load reduction necessary to control nearshore *Cladophora* growth may further lower offshore TP concentration which may severely limit the lake’s carrying capacity for top predator fish, especially the sport fishery for introduced Pacific salmon.

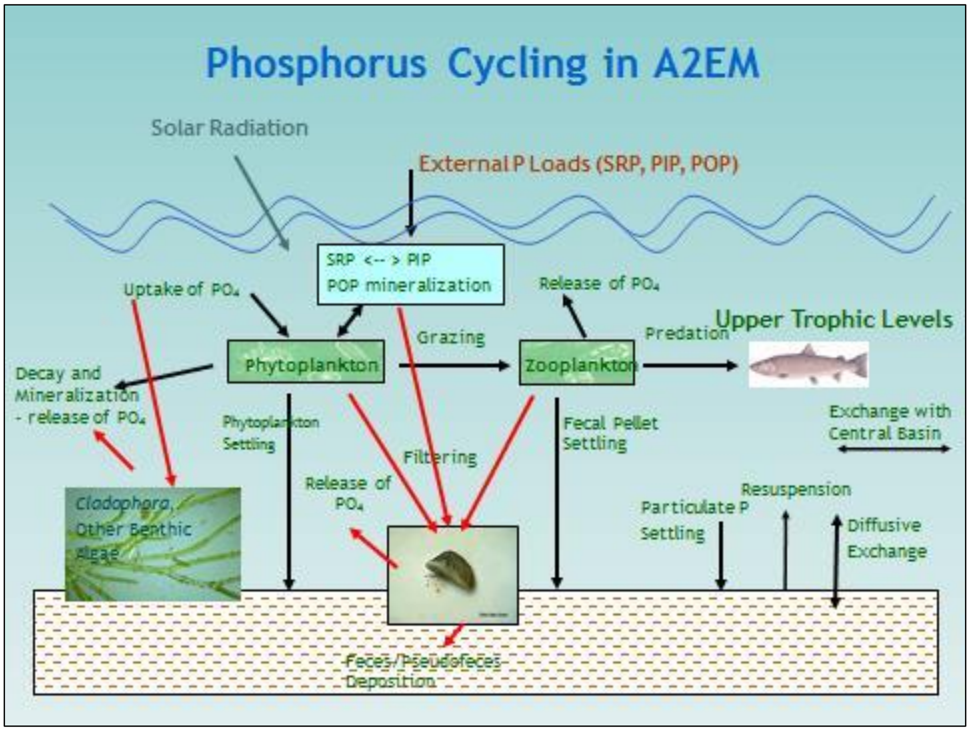

Figure 13: Diagram of phosphorus cycling pathways and associated processes represented in each spatial segment of A2EM. Simulating the flux rate of each of these pathways as a function of space and time will provide a quantitative understanding of nearshore - offshore productivity gradients in the lake being considered.

There are two other modeling efforts that allow one to address the nearshore - offshore productivity gradient issues considered by this work group. The Estuary, Lake and Coastal Ocean Model-Computational Aquatic Ecosystem Dynamics Model 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. Also, Pilcher et al. (2017) and Rowe et al. (2017) simulated nutrient cycling in Lake Michigan, including mussel grazing impacts in three dimensions, using Nitrogen, Phytoplankton, Zooplankton, and Detritus models linked to Massachusetts Institute of Technology General Circulation Model and Finite-Volume Community Ocean Model circulation models, respectively. Shen et al. (2018) also looked at the regulation of plankton and nutrient dynamics by profundal quagga mussels in Lake Michigan using a one-dimensional model. This model suggested the potential for profundal mussels to significantly alter the distribution of energy and nutrients in the water column. Confidence in these models will build if they continue to develop and converge on similar results. Comparison of multiple models provides a basis for some quantitative statistical evaluation of future projections by these models.

4.2.2 Ecosystem models that focus on upper food web

Modeling the balance between fish stocking and fish harvest in the Great Lakes started during the late 1970s when piscivore stocks were recovering and concerns arose over a possible imbalance between piscivore consumptive demand and prey fish production. Early model development of the upper food web combined increasingly sophisticated accounting of piscivore population dynamics with bioenergetics models in an effort to quantify predator consumptive demand and prey production. For example, Stewart et al. (1981) analyzed the potential for prey fish biomass to support Salmonine predators in Lake Michigan (Chinook and coho salmon, steelhead, lake trout). Rand et al. (1995) estimated prey fish production and consumption in Lakes Ontario and Michigan, and Rand et al. (1993) analyzed steelhead population dynamics and consumptive demand in Lakes Ontario and Michigan. Stewart and Ibarra (1991) updated their estimates of piscivore production and consumption in Lake Michigan; and Jones et al. (1993), He et al. (2015) and Tsehaye et al. (2014) combined population estimates of piscivore biomass, harvest and bioenergetics consumptive demand with prey fish production estimates for lakes Ontario, Huron and Michigan, respectively. Most of these early models concluded that piscivore consumptive demand was higher than available prey production, and recommended cuts in stocking to better balance predator consumption levels with their prey biomass and reduce risk of fishery collapse (i.e., Jones et al. 1993). Missing from the He et al. (2015) and Tsehaye et al. (2014) models was an accounting of increased movements of Chinook salmon from Lake Huron to Lake Michigan after the population collapse of their primary prey, the alewife (Clark et al. 2016, 2017). Effects of increased water clarity on piscivore-prey relationships also may have complicated predictions of predator consumptive demand. Recent workshops on declines in offshore fish productivity in Lake Michigan (Bunnell et al. 2018) and throughout the Great Lakes (Stewart et al. 2018) suggest that piscivore foraging behavior may have changed given increased water clarity because of dreissenid mussel filtration, thus allowing piscivores to maintain high consumption rates as prey fish biomass declined, by increasing search volume. In an earlier study, Eby et al. (1995) demonstrated that lake trout in Lakes Superior, Michigan and Huron maintained similar prey fish consumption rates despite differences in prey fish biomass among lakes. They speculated that lake trout in Lake Superior may have maintained their consumption rate by increasing their search volume despite having lower prey fish biomass. Bence et al. (2008) suggested further cross-lake comparisons of piscivore growth relative to prey fish abundance may illustrate how piscivores respond to changing (prey) environments.

Simulation models linking phosphorus to upper food web dynamics in the Great Lakes have primarily used the Ecopath with Ecosim (EwE) software. EwE was initially developed to quantify effects of fishing on fish and their sustaining food webs (Christensen et al. 2005). Ecopath provides a mass-balanced snapshot of predator-prey dynamics among selected organisms or groups in the food web, while Ecosim allows time-dynamic simulation of the food web response to nutrients and other forcing variables (invasive species, fishing effort). Several EwE models have been developed for the Great Lakes to study invasive species effects in Lake Superior (Kitchell et al. 2000), Ontario (Stewart and Sprules, 2011), Huron (Kao et al. 2016; Langseth et al. 2014), Michigan (Kao et al. 2017; Rogers et al. 2014) and Erie (Zhang et al. 2016). Fewer models compared energy flow to upper trophic levels in Great Lakes embayments

(Blukacz-Richards and Koops, 2012, Kao et al. 2014). Kao et al. (2014, 2016, 2017) used EwE to conduct a set of factorial simulation experiments to identify the relative influence of nutrient loads, invasive species and piscivore consumptive demand on prey fish production in Saginaw Bay and in the main basins of Lake Huron and Lake Michigan. The results of these factorial simulation experiments indicated that bottom-up effects (nutrient declines and dreissenid mussel filtration) had a greater influence on prey fish production than did salmon consumption, a result consistent with the recent monitoring analysis of bottom-up dominance in these food webs. Kao et al. (2017) used the food web model to suggest optimal stocking strategies for salmonids in Lake Michigan (i.e., favoring lake trout over Chinook salmon) given the current depressed biomass of prey. These models may be improved by consideration of spatial heterogeneity in habitat use by predators and prey, and research on piscivore and prey fish foraging behavior given future predictions of a warmer, clearer environment (see Kao et al. 2015).

Recently, efforts have begun to compare effects of nutrients on fish production across the Great Lakes. Stewart et al. (2017) and others conducted a meta-analysis of all existing EwE models to quantify fish production and biomass relative to nutrient loads and lower trophic level production. These analyses identified the strong impacts of invasive dreissenid mussels on energy flow, trophic transfer and fish production. The meta-analysis also revealed differences in model topology and data collection that may have affected conclusions about energy flow and trophic transfer in some lakes. For example, conclusions about efficiency of energy flow across the Great Lakes may have been biased owing to differences in modelers’ objectives or the data available for each lake modeled. Some modelers neglected to include protozoans as part of the food web, although they are equal in biomass to crustacean zooplankton, are a major diet component for zooplankton and feed on picoplankton and bacteria as well as each other. As well, differences among lakes in timing of sampling for prey fish, and availability of population estimates and diet information for prey and predators have hindered meta-analysis of nutrient effects on fish. A new project led by Marten Koops (Department of Fisheries and Oceans Canada) and funded by the GLFC should improve cross-lake comparison of statistical and simulation models to quantify effects of nutrients on fish production.

To date, the EwE modeling efforts in the Great Lakes have primarily avoided consideration of spatial heterogeneity in habitat and treated the ecosystem as a homogeneous environment. Also early versions of the EwE software did not permit explicit simulation of environmental factors such as temperature or oxygen. Recent improvements to Ecospace, the spatial component of EwE software, may encourage modelers to use this software to simulate nutrient fluxes and organism movements between nearshore and offshore (Christensen et al. 2014).

Other modeling approaches that link nutrients to fish have incorporated effects of spatial heterogeneity in the physical environment on food web dynamics. Two specific examples include individual-based community models (Ivan et al. in prep) and the Atlantis ecosystem model, a whole ecosystem, biophysical model (Mason et al. 2016). In contrast to the EwE model, the Atlantis ecosystem model is spatially explicit across horizontal and vertical domains, and can simulate effects of nutrients, currents, water temperature and biogeochemistry on the entire food web. Difficulties with both models include a lack of data at the appropriate horizontal and vertical resolution for calibration, and for the Atlantis model, a considerable time period needed to understand and configure the model.

The upper trophic level models and whole ecosystem models discussed above may be used to provide data needed to inform lower trophic models, and vice versa. For example, A2EM requires estimates of mortality rates of zooplankton which could be provided by consumptive demand estimates output for planktivorous fish from an individual-based model or an EwE model. Similarly, the A2EM lower trophic model could refine or improve simulations of nutrient drivers of plankton and prey fish dynamics, and better inform fisheries managers of the implications of potential stocking decisions. Thus, having increased connectivity between lower and upper trophic level models could improve model predictions of effects of revised nutrient load targets on *Cladophora* growth and abundance in the nearshore zone or fishery production offshore.

4.3 Future modeling needs

Given the state of modeling in the Great Lakes relative to nutrient - upper food web conditions, the following needs have been identified:

- Effort to develop coupled hydrodynamic - lower food web - upper food web ecosystem models;
- Develop a coordinated program of enhanced nearshore monitoring and research to support fine-scale modeling efforts;
- Use Lake Ontario Annex 4 process as an opportunity to use modeling to help reconcile *Cladophora* control and offshore productivity impact of phosphorus load reductions;
- Use the Cooperative Science and Monitoring Initiative process to implement an interactive model – monitoring – research adaptive management process in the Great Lakes;
- Develop modeling work groups to compare and standardize data sources and topologies of models to improve meta-analysis of drivers and modifiers of offshore productivity;
- Include nearshore - offshore coupling of nutrient fluxes, and active and passive organism movements and receive increased data input from enhanced monitoring programs for these increasingly complex models especially in nearshore areas where spatial variance is high;
- Include weather and climate variability on short (days) and medium (season) time scales; and
- Explicitly consider and communicate uncertainty in model predictions.

5.0 Findings, Knowledge Gaps and Recommendation

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. These objectives were supported by an extensive data compilation (LimnoTech 2018) bringing together multiple data sets from nutrients to fish from the diverse agencies producing and holding these data. An overview and summary of the resulting findings, gaps and the report's recommendation follows.

5.1 Findings

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

1. Offshore total phosphorus concentrations have fallen across lakes Michigan, Huron and Ontario since the implementation of the GLWQA (1972) but have now fallen below targets at least in part due to the diversion of nutrient and energy flow into the nearshore and, in some cases, profundal areas of these lakes attributable to the impacts of invasive mussels. This is in contrast to the western and central basins of Lake Erie and embayments such as Green Bay, Saginaw Bay and the Bay of Quinte, which are suffering from a resurgence of eutrophication symptoms driven by changes in agricultural nutrient loads and in the shallow water ecological processing of those loads. There is uncertainty about the long-term trends in Lake Superior, which is now also below the GLWQA target concentration, where ECCC monitoring reports a significant continuing decline while USEPA monitoring suggests a recent increase in TP.

2. Fish populations, especially for large bodied top predators, were in a degraded condition because of overexploitation and invasive sea lamprey predation when the GLWQA was implemented. Several deep water dwelling coregonid species had been extirpated from all the lakes except Superior, and the top predator lake trout was in low abundance in all the lakes. Some of the Great Lakes (especially Michigan and Ontario) continue to have substantial stocking of valued species (primarily salmonids) in efforts to meet lake-based Fish Community Objectives. Several introduced salmonid species have also become naturalized in some of the Great Lakes, partially reducing the effectiveness of the stocking management for fishery managers. Salmonid stocking and piscivore restoration complicate simple interpretation of the prey fish population dynamics even though they have been monitored since the early 1970s by various agencies. Prey fish stocks have declined in all the lakes (except Erie) since historic highs in the 1980s and early 1990s to historic lows in recent

years. Although contemporaneous with declining TP in these lakes, the recovery of predation pressure by piscivores would also depress prey fish biomass. Therefore, a correlation between declining TP and prey fish biomass would be insufficient to infer causality over this post-GLWQA period. Further complicating the trends in prey fish abundance is the prominence in this category of nonnative invasives, i.e., rainbow smelt, alewife, and round goby (Figure 7), in all the lakes except Superior. The deep water coregonid fauna lost over the last century in several of the lakes may have left trophic niches vacant and contributed to successful invasions over the same period. The extent to which these invasives can replace the extirpated deepwater coregonids and maintain food web efficiencies in increasingly oligotrophic lakes is uncertain. Consequently, efforts are now underway to stock the extirpated native coregonids to stabilize or increase fish production in some of the lakes. Restoration of these deep water coregonids may enable increased food web efficiency to maintain or increase fish productivity in the increasingly oligotrophic offshore waters of the Great Lakes. Success in these restoration efforts may be critical to maintaining fish production in these oligotrophic lakes.

3. Round gobies have become well established in all Great Lakes, except Superior, since the turn of the century. They are not well sampled, with current monitoring methods and are underrepresented in prey fish biomass estimates, even though they are prominent in the diets of many large bodied predators. Round gobies in high abundance may compete with other prey fish for food and contribute to the observed decline in prey fish abundance recorded by standard monitoring. Alternatively, round gobies may be helping to recycle P and maintain current levels of food web productivity by consuming dreissenids. In any case, these possible round goby effects on prey fish complicate any simple relationship between prey fish abundance and TP.

4. Average spring total phosphorus concentrations and abundance of prey fish and predatory fish have shown continued variation but few strong trends in the most recent period of monitoring after 2005, including the most recent five additional years since the Bunnell et al. (2014) data compilation. This suggests that most lakes may be approaching a steady state with regard to TP concentrations and external and internal P loadings, mussel populations and their effects, along with other recent drivers of algal productivity change.

5. A review of the global literature on the impacts of re-oligotrophication of lakes indicates that the offshore TP concentrations in Lakes Superior, Michigan, Huron and Ontario are in a range where TP concentrations are likely limiting fish production, even for oligotrophic species such as coregonids and salmonids, the most valued and exploited species in these lakes. Future reductions in P loading, therefore, would be expected to result in further declines in these valued fisheries all other environmental factors being unchanged.

6. Monitoring of lower food web organisms (other than chlorophyll as a surrogate for phytoplankton) with standard stations and sampling protocols across all lakes only began in 1998 in the Great Lakes after the most substantial declines in TP had already occurred. However, over the relatively short period of record, multiple lines of evidence show a major decline in the productivity of the lower food web organisms in Lake Michigan and Lake

Huron and to a lesser extent in Lake Ontario. Impacts from the lower food web on the fish community and associated fisheries have varied among lakes and over years within lakes, and are difficult to discern from the effects of predation and recruitment on fisheries. A correlation analysis of the trophic levels indicates that the food webs of Lakes Michigan, Huron and Ontario appear to be dominated by bottom up regulation. This is consistent with very low TP concentrations in these lakes and the global experience with re-oligotrophication. Trapping of nutrients by dreissenids has increased benthic productivity and decreased pelagic primary productivity in lakes where dreissenids have become the dominant benthic fauna. The virtual disappearance of *Diporeia*, the primary benthic food source for fishes historically, from all lakes except Superior has compounded the effects of phosphorus shunting by mussels on offshore fish productivity.

7. The collaborative and cooperative management of the offshore commercial and recreational fisheries has been proactive across fisheries agencies in response to the declining offshore fish productivity through review of stocking rates, informing fisheries managers on the possible impacts of disrupted food webs and supporting new modeling research to address the linkages between P and fish abundance and productivity. However, nutrient management lies outside the sole responsibility of the fisheries agencies and, going forward, even greater cooperation between water quality and fisheries agencies will be essential to maintaining a healthy and valuable fishery in the lakes.

8. 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 and spatial patterns remain to be worked out. At this time, models used to support fishery management decisions have been somewhat limited in favor of more direct measures of fish community and population condition (i.e., stock assessment data). Use of nutrient-based models within a framework that evaluates alternative fishery management actions (i.e., stocking, harvest and habitat remediation) and policies may enhance their usefulness and incorporation into formal management frameworks.

9. Ecosystem models that link biogeochemistry, lower food web productivity, nearshore ecology and offshore fish productivity are currently under development. These aquatic ecosystem models can best be attained by coupling nutrient – lower food web eutrophication models with upper food web fish production models at the zooplankton level of the food web. Optimized monitoring that supports adaptive management and modeling would benefit 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). Optimized monitoring data will require increased spatial and temporal resolution for external nutrient loading and primary productivity, including the seasonal DCL and winter seasons. Monitoring data generated and reported annually in an integrated format would enable rapid management response to ecosystem change. These complex ecosystem models will be an essential component of an integrated ecosystem adaptive management system.

10. Lake Ontario, for which nutrient targets are currently being reviewed under Annex 4 of the GLWQA, will be an important test case for such ecosystem modeling. Major reductions in upstream nutrient loading to Lake Erie together with stakeholder concerns about increased coastal, nuisance *Cladophora* growth and declining salmonid biomass (LimnoTech 2018) present a 'nearly-perfect storm' for both water quality and fisheries managers. Fisheries managers could team up with Annex 4 subcommittee members working on nutrient targets to avoid unintended consequences that may result from a focus on a single aspect of the ecosystem. Adopting a true ecosystem analysis approach and adaptive management can lead to an optimum balance between nutrient loads and offshore fishery production.

11. Although conditions in the offshore have been the primary focus of this report, it is recognized that enhancing nearshore monitoring of nutrients, chlorophyll *a*, zooplankton, larval fish and fisheries monitoring across the basins, and linking and coordinating the timing of data processing and reporting of all lower trophic level data to annual fishery stock assessment metrics, would improve our ability to connect and adapt nutrient-related actions to fishery production and conditions in following seasons.

5.2 Knowledge 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 includes, "Quantification of energy and nutrient dynamics in Great Lakes food webs, and the role of food web members in structuring resilient communities and ecosystems,"[1] and Stewart et al. (2018) illustrates growing concern among fishery managers around the issue of declining productivity across the lakes.

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

1. 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 deep water mussel grazing.

2. Combined effects of declining TP concentrations and mussel grazing have also led to an increase in water clarity especially for Superior, Michigan and Huron. Bunnell et al. (2014) also found a significant increase in clarity in Ontario, but this was not significant in the extended dataset (LimnoTech 2018). This increase in clarity would be expected to affect foraging by sight-feeding fishes allowing more efficient predation. Increased clarity may also

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[1] Accessible at: glfc.org/pubs/pdfs/research/FRP%20Theme%20Conceptual%20Diagram.pdf.

result in altered depth distribution of prey fish and their predators as well as photosensitive invertebrates. Possible impacts on trophic ecology, including a downward adjustment in light-dependent primary productivity and altered fish distributions, are not well defined. Possible increases in trophic efficiency of sight feeding fishes may in part offset declining abundances of prey caused by increasing nutrient scarcity. More research is required on the impact of clarification of the lakes on ecosystem processes. Future research is required to understand how water clarity has increased in Lake Superior where dreissenid mussels have not successfully invaded. Such an increase is consistent with ECCC TP data for Lake Superior, but not with USEPA data, and warrants further research to resolve this apparent discrepancy in TP data.

3. The relative impacts of predation on prey fish (top-down) versus decreased food supply (bottom-up) are still not well known in most lakes as piscivore stocks are still adjusting to historic disruptions as well as to food web structures modified by invasives. Increased temporal and spatial monitoring will be required to model and better understand the transition between nearshore and offshore areas.

4. 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. This is a limitation of the current report as only TP concentration data in the lakes are considered. The processes by which phosphorus loads, historically dominated by spring loading, are currently transformed into primary productivity in offshore areas are not clear, including the transformation of bioavailable phosphorus loading into algal productivity on seasonal and annual time scales.

5. Algal productivity is often discussed but only seldom measured due to logistical demands of classical methods such as radiocarbon uptake during prolonged incubations. Algal productivity is the critical transformation which links P concentrations to food web growth. Yet, there is only one long-term (1980s to 2000s) monitoring site for primary productivity on the Great Lakes (Lake Michigan off Muskegon) where declines of 70 percent in primary productivity have been observed (Fahnenstiel et al. 2010). The productivity of the DCL, which forms seasonally in all the lakes during the summer stratified season, is not monitored routinely and its capacity to compensate for declining primary productivity in the surface mixed layer is poorly defined. Increased transparency and longer stratified seasons should increase the importance of the DCL. Innovative technologies are needed to address this fundamental deficiency in our analysis of productivity trends and trophic efficiencies in the Great Lakes. Current reliance on total chlorophyll as our metric for productivity also hides important changes in algal species composition, and most worrying trends in cell sizes. Shifts in algal cell sizes may ramify through food webs as the efficiency of harvesting smaller sizes is often lower than harvesting larger algal cells. More research at the critical interface between algal productivity and zooplankton is required to determine if declining productivity may be accompanied by reduced trophic transfer to higher trophic levels including fish in offshore waters.

6. There is a need to better understand how changes in nearshore trophic ecology have translated into increased uncertainty in expected outcomes from management actions. These may include potential tradeoffs between water quality and fishery management objectives.

7. Lake Ontario receives a significant portion of its TP load from Lake Erie, 30 to 50 percent (Chapra and Dolan, 2011) which is a much higher proportion of total loading than Huron and Erie receive from their upstream Great Lakes. New loading objectives for Lake Erie call for a 40 percent reduction in nutrient loading to the western and central basins, where most loading enters Lake Erie, which in turn should impact the Lake Erie loading to Lake Ontario. Forecasting TP concentrations in Lake Ontario must recognize this inter-lake connectivity especially given evidence that TP concentration in Ontario are already in a range where nutrients can be limiting to fish production. If the committed TP reduction in nutrient loading were realized in Lake Erie, Lake Ontario may suffer declining fish productivity comparable to changes that have occurred in Michigan and Huron. The likelihood of such a decline would be increased if direct catchment loadings to Ontario were also reduced to control *Cladophora*. Lake Ontario poses some unique and difficult challenges for modeling to guide the Annex 4 review of nutrient loading. Those modeling efforts will need to include predictions of the impacts of nutrient loads on offshore fish productivity. Filling this gap would be a significant advance.

8. Modeling methods for determining the relative effectiveness and impact of alternative phosphorus reduction strategies on offshore fish productivity and species distribution are not well developed, so they need to be applied within an adaptive management framework that recognizes the importance of monitoring and continuous improvement. Incorporating nearshore processes into whole ecosystem models will require evolving and increasingly complex modeling approaches to address spatial and temporal variability in loading and subsequent impacts on offshore fisheries.

5.3 Recommendation

The Great Lakes Executive Committee (GLEC) should explore and implement opportunities and capacities for cooperative application of ecosystem forecasting science addressing nutrient and fisheries management in the Great Lakes. In order to address this recommendation, GLEC should engage and partner with state and provincial fisheries and environmental agencies as well as other national and binational agencies involved with monitoring and managing Great Lakes aquatic resources.

To initiate comprehensive engagement, the GLEC should form a multiagency Cooperative Ecosystem Monitoring and Modeling Advisory Committee ("Committee"). This Committee could be an *ad hoc* or standing committee focusing on:

- Reviewing ecosystem forecasting science and its potential application to current and emerging issues confronting environmental and fisheries managers in the Great Lakes;

- Identifying key data requirements for the effective use of ecosystem modeling and forecasting science by managers in the Great Lakes and fostering the exchange of such data, especially among fishery and water quality programs to support integrative decision support;

- Evaluating potential benefits from, as well as tradeoffs between, nutrient management and fisheries within and among the Great Lakes, especially for lakes Huron, Michigan, Ontario and the eastern basin of Erie where changes in fisheries could be induced by enhanced nutrient management under the Annex 4 process;

- Identifying and implementing strategies to enhance collaborative decision making and adaptive management of the Great Lakes ecosystems among water quality and fisheries managers through existing administrative structures or, if necessary, new collaborative structures;

- Enabling and promoting consistency and clarity of public communications from water quality and fisheries agencies regarding current and potential interactions between these resources and their management; and

- Other aspects that arise during discussions.

The Committee should be established within two years along with its terms of reference, multiagency composition, procedures and work plan (to be reviewed annually). The Committee should use the ongoing Annex 4 assessment on Lake Ontario as a test bed for integrating and instituting coordinated data/information management aimed at reducing eutrophic conditions nearshore while sustaining healthy fish populations offshore. Progress on measures, analysis and outcomes should be shared publicly at annual Lake Committee meetings hosted by the Great Lakes Fishery Commission. After the next two consecutive five-year Cooperative Monitoring and Science Initiative cycles, the Parties should report on their success in connecting and adapting nutrient-related actions to fishery management through effective information flow and decision support, modeling and forecasting.

Facing the dual challenge of improving offshore fisheries productivity while at the same time taking action to reduce nutrients loads to the nearshore to control the proliferation of cyanobacteria in shallow embayments and *Cladophora* growth in many coastal areas will require robust collaboration and inspired leadership. This complex challenge will require that we fully utilize our collective science capabilities and apply them directly to evaluating ecosystem services and the tradeoffs between them. Establishing a committee to foster active engagement between fisheries and water quality managers and institute an interdisciplinary adaptive ecosystem management approach will be a significant step forward to solve this complicated problem.

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7.0 Glossary

ADAPTIVE MANAGEMENT – A planning process that can provide a structured, iterative approach for improving actions through long-term monitoring, modeling and assessment. Through adaptive management, decisions can be reviewed, adjusted and revised as new information and knowledge becomes available or as conditions change.

ALGAE – Aquatic plants that survive through photosynthesis; they can range in size from microscopic organisms to large filamentous algae, like *Cladophora*.

ALGAL BLOOMS – An excessive and relatively rapid growth of algae on or near the surface of water.

ANNEX COMMITTEE – A committee appointed by the Great Lakes Executive Committee to implement actions to achieve the general and specific goals of an annex of the Great Lakes Water Quality Agreement.

AQUATIC INVASIVE SPECIES – As defined in the Great Lakes Water Quality Agreement, AIS refers to any nonindigenous species, including its seeds, eggs, spores or other biological material capable of propagating that species, that threatens or may threaten the diversity or abundance of aquatic native species, or the ecological stability, and thus water quality, or water quality of infested waters, or commercial, recreational, or other activities dependent on such waters.

BENTHIC COMMUNITY – Benthic means the bottom habitat of a water body, and can mean anything as shallow as a salt marsh or the intertidal zone, to areas of the bottom that are several miles deep in the ocean. Benthic community refers to those organisms that live in and on the bottom (in meaning they live within the substrate; i.e., within the sand or mud found on the bottom).

BENTHOS – Originating from the Greek word for “bottom,” is now nearly uniformly applied to animals associated with substrata.

BIOLOGICAL CARRYING CAPACITY - The number of organisms that an ecosystem can sustainably support.

BIOMASS – The total mass of living matter in a given unit area or the weight of a fish stock or portion thereof. Biomass can be listed for beginning of year (Jan-1), Mid-Year or mean (average during the entire year). In addition, biomass can be listed by age group (numbers at age * average weight at age) or summarized by groupings (i.e., age 1+ , ages 4+ 5, etc.).

BLUE-GREEN ALGAE – Though they are classified as bacteria, cyanobacteria—sometimes referred to as blue-green algae—exhibit characteristics of algae and are associated with harmful algal blooms (HABs).

BOTTOM-UP REGULATION – Control of the food web production through resource limitations (nutrients, base of the food web (food source/prey fish abundance)).

CLADOPHORA – A genus of green algae found growing attached to rocks or timbers submerged in lakes and streams. *Cladophora* grows in the form of a tuft or ball with filaments that may range up to 13 cm (5 inches) or greater in length.

CHLOROPHYLL *a* – Chlorophyll *a* is quite often used as a surrogate measure of the amount of phytoplankton in a water sample. Comparing water bodies on the basis of chlorophyll *a* content implicitly assumes the algae are composed of equivalent amounts of chlorophyll though. The chlorophyll content of algae is usually about 0.5-1.5 percent of the dry weight. But increased amounts, up to 6 percent have been recorded in algae culture in weak light. Chlorophylls are ‘tetrapyrrolic molecules with a central magnesium atom and two ester groups,’ hence the need for micronutrients by plants and animals. Chlorophyll *a* is the ‘master pigment’ in blue-green algae and higher plant photosynthesis (apparently some photosynthesizing bacteria can do it without chlorophyll *a*). It is chlorophyll *a* that ultimately captures energy from light (photons) and packages it as energy in chemical bonds for use by plants and eventually animals. There are other ‘accessory pigments’ (such as chlorophylls *b*, *c*, and *d*, carotenoids, phycoerythrins, phycocyanins and xanthophylls) which can trap light energy at shorter wave lengths and pass it along to chlorophyll *a* which absorbs at longer wavelengths. It is the unique combination of accessory pigments with chlorophyll *a* that help to distinguish certain groups of algae and higher plants from one another. For example, Euglenophyta are characterized by the presence of chlorophyll *a* and the accessory pigments b-carotene and the xanthophyll lutein.

CLIMATE CHANGE – A change of climate that is attributed directly or indirectly to human activity, that alters the composition of the global atmosphere, and which is in addition to natural climate variability observed over comparable time periods.

CYANOTOXINS – Toxins which are produced and contained within cyanobacterial (blue-green algae) cells. Toxins are released during death or cellular rupture, including mechanical or chemical reactions. Cyanotoxins can be produced by a wide variety of cyanobacteria including *Microcystis, Anabaena and Planktothrix*. Definition derived from the USEPA.

DEAD ZONES – Dead zones are hypoxic (water with dissolved oxygen levels below 2 mg/l) or anoxic (water that does not contain dissolved oxygen) areas without enough dissolved oxygen to support fish and/or zooplankton.

DETRITUS – Living organisms constitute only a very small portion of the total organic matter of ecosystems. Most organic matter is nonliving and is collectively called detritus. Detritus consists of all dead particulate and dissolved organic matter. Dissolved organic matter is about 10 times more abundant than particulate organic matter. Much of the newly synthesized organic matter of photosynthesis is not consumed by animals, but instead enters the detrital pool and is decomposed.

DIATOMS – Small plants (algae) with silicified (silica, sand, quartz) skeletons. They are among the most abundant phytoplankton in cold waters, and an important part of the food chain.

DIPOREIA – A small energy-rich shrimp-like organism, *Diporeia* were the dominant benthic macroinvertebrate in offshore waters of the Great Lakes, however abundance has significantly decreased over the past 25 years and they have virtually disappeared in many areas. *Diporeia* feed on organic material settled from the water column, especially diatoms. In turn, *Diporeia* are eaten by most offshore fish species. (National Oceanic and Atmospheric Administration)

DREISSENIDS – Zebra mussels (*Dreissena polymorpha*) and Quagga mussels (*Dreissena bugensis*). Dreissenids are high impact aquatic invasive species. When established, these mussels can clog water intake and supply pipes, infest hydropower facilities, blanket boats and pilings, and foul recreational beaches. They compete with native mussels, disrupt food webs, bio accumulate toxins and alter the physical characteristics of the ecosystem by creating higher transparency in the water column and providing substrate for other invasive organisms (i.e., *Cladophora*) to attach to.

ECOSYSTEM – A biological community of interacting organisms and their physical environment, including the transfer and circulation of matter and energy.

ECOSYSTEM-BASED MANAGEMENT – A management approach that takes major ecosystem components and services—both structural and functional—into account, often with a multispecies or habitat perspective.

EUTROPHIC – A lake characterized by an abundant accumulation of nutrients that support a dense growth of algae and other organisms, the decay of which depletes dissolved oxygen in the summer.

EUTROPHICATION – The process whereby water bodies become over-nourished either naturally by processes of maturation or artificially by excessive nutrient enrichment. The term eutrophication is synonymous with increased growth of the biota of lakes, and that the rate of increasing productivity is accelerated over that rate which would have occurred in the absence of perturbations to the system. The measurable criterion of accelerated productivity is an increased quantity of carbon assimilated by algae and larger plants per given area. Under a large majority of lake conditions, the most important nutrient factors causing the shift from a lesser to a more productive state are phosphorus and nitrogen. If one of the three elements is limiting and all other elements are present in excess of physical needs, phosphorus can theoretically generate 500 times its weight in living algae, nitrogen 71 (500:7) times, and carbon 12 (500:40) times.

FISH COMMUNITY OBJECTIVES – Goals and objectives for a Great Lake fish community established by one of the Great Lakes Fishery Commission’s Lake Committees.

GREAT LAKES WATER QUALITY AGREEMENT – The Agreement expresses the commitment of Canada and the United States to restore and maintain the chemical, physical and biological integrity of the Great Lakes Basin Ecosystem. The most recent protocol amending the 1978 Agreement was signed in 2012.

HARMFUL ALGAL BLOOMS (HABs) – HABs result from the proliferation of blue-green algae (including cyanobacteria) in environmentally stressed systems, where conditions favor opportunistic growth of one or more noxious species, displacing more benign ones. The blooms are considered harmful because excessive growth can harm ecosystems and produce poisons (or toxins) that can cause illness in humans, pets, livestock and wildlife.

HYPOXIA – A condition of low or depleted oxygen in a water body, leading to regions where life cannot be sustained. Hypoxia occurs most often as a consequence of human-induced factors, especially nutrient pollution.

LOWER FOOD-WEB – Food chain of producers and primary consumers.

MESOTROPHIC – Mesotrophic lakes fall somewhere in between eutrophic and oligotrophic lakes.

MICROBIAL – Of or relating to microorganisms.

MICROCYSTIN – A naturally-occurring, potent liver toxin produced by the cyanobacteria Microcystis. Microcystin toxins are the most widespread cyanobacterial toxin and can bioaccumulate in common aquatic vertebrates and invertebrates such as fish, mussels and zooplankton. Definition derived from the USEPA.

NEARSHORE – As defined in IJC’s 15th Biennial Report on Great Lakes Water Quality, the nearshore includes the relatively warm shallow areas near the shores, coastal wetlands that are dependent on lake levels, the connecting channels and virtually all of the major embayments of the system. This area is estimated to include approximately 90 percent of shallow Lake Erie, 25 percent of each of lakes Michigan, Huron and Ontario, but only five percent of Lake Superior, which has deeper waters. The definition also describes the nearshore zone as including the land areas that are affected by the waves, wind, ice and temperature. In general, the nearshore zone extends about 16 kilometers (ten miles) into both land and water.

NITROGEN – A nutrient essential for plant and animal growth and nourishment which may exist in the forms of nitrate, nitrite or ammonium. Excess nitrogen can cause the rapid growth of aquatic plants and algae.

NUTRIENT – A food or any nourishing substance assimilated by an organism and required for growth, repair and normal metabolism. For example, phosphorus and nitrogen are nutrients for algae.

OLIGOTROPHIC – A lake with low nutrient concentrations.

PARTIES – The parties or signatories to the Great Lakes Water Quality Agreement. That is, the governments of Canada and the United States.

PELAGIC – Relating to open waters.

PHOSPHORUS – A nutrient essential for plant and animal growth and nourishment, which exists in particulate or soluble reactive forms. The element used in a wide range of agricultural, industrial and domestic products. It is a key nutrient limiting the amount of phytoplankton and attached algae in the Great Lakes and most freshwater bodies.

PHYTOPLANKTON – Assemblage of small, microscopic plants having no or very limited powers of locomotion; they are therefore more or less subject to distribution by water movements. Certain planktonic algae move by means of flagella, or possess various mechanisms that alter their buoyancy. However, most algae are slightly denser than water, and sink, or sediment from, the water.

PISCIVORE – A species feeding preferably on fish.

PLANKTIVORE – An animal that feeds on plankton.

PRODUCTION and PRODUCTIVITY– Production refers to new organic matter formed over a period of time plus losses to respiration, excretion, secretion, mortality, grazing and predation. All living organisms obtain the energy of life by combustion of organic matter. Autotrophs capture solar energy radiating through air or water and store (‘fix’) captured energy as environmental redox potential (Eh) between the photosynthetic products, oxygen and organic matter. Autotrophs essentially ‘make their own fuel’ in a process called synthesis or production. Productivity usually refers to an average rate of production over a distinct period of time (i.e., day, year). Primary productivity can be estimated from changes in oxygen production or rates of inorganic carbon assimilation.

RECRUITMENT – The amount of fish added to the fishery each year due to growth and/or migration into the fishing area. For example, the number of fish that grow to become vulnerable to fishing gear in one year would be the recruitment to the fishery. ‘Recruitment’ also refers to new year classes entering the population (prior to recruiting to the fishery).

SALMONID – A fish from the salmon family (*Salmonidae*), i.e., salmon, trout, chars, freshwater whitefishes and graylings.

SIGNAL SPECIES - A subset of the lake fish assemblage defined by general characteristics that were chosen to eliminate confounding factors of fish community change and reveal species richness trends. (Ludsin et al. 2001).

STOCK – A grouping of fish usually based on genetic relationship, geographic distribution and movement patterns. A region may have more than one stock of a species (for example, Gulf of

Maine cod and Georges Bank cod). A species, subspecies, geographical grouping or other category of fish capable of management as a unit.

TAXA – The plural of taxon. Taxon is a named group or organisms of any rank, such as a particular species, family or class.

THERMAL STRATIFICATION – Vertical layering of water within a lake or in the ocean. Warm water being less dense tends to form a layer above colder, denser water.

THERMOCLINE – A transition layer of water that separates the warm mixed surface layer of water from the cold deep water in the lake. The thermocline acts as a barrier to the mixing of water and nutrients.

TROPHIC STATUS – Trophic status is a means of classifying lakes in terms of their productivity. Eutrophication is the process by which lakes are enriched with nutrients, increasing the production of rooted aquatic plants and algae. The extent to which this process has occurred is reflected in a lake's trophic classification or state:

- Oligotrophic is nutrient poor
- Mesotrophic is moderately productive
- Eutrophic is very productive and fertile

TROPHIC LEVELS – Functionally similar organisms can be grouped into trophic levels based on similarities in patterns of food production and consumption. Energy is transferred and nutrients are cycled within an overall ecosystem trophic structure. With respect to zooplankton trophic abundance:

- In oligotrophic systems, concentrations of edible algae are lower, so zooplankton concentrations are also lower. Perhaps as important, there is a shift in dominance to copepods which have lower per capita filtering rates and excrete fecal pellets rather than dissolved nitrogen and phosphorus. All these factors contribute to reduced coupling at this interface.
- In mesotrophic systems, edible and nutritious algae are in higher concentrations than in more nutrient-poor waters, and the proportion of these algae is greater than in more eutrophic systems. In these intermediate systems there are also sufficient concentrations of cladoceran herbivores. A number of species in the genus *Daphnia* have particularly high per capita filtering rates. Cladocerans also regenerate nitrogen and phosphorus in the soluble available forms. This enhances phytoplankton productivity, speeds nutrient cycling and tightens coupling between these trophic levels.
- Ciliated protozoans and rotifers become more important in the zooplankton among eutrophic, subtropical lakes. As lakes become more eutrophic, a greater proportion of the phytoplankton biomass and productivity often results from large algae (mostly colonial or filamentous). The larger algae interfere with food collection to a greater extent in larger cladocerans causing reduced growth and fecundity than in smaller cladoceran species that feed on small particles.

- Predation by fishes and size selectivity: Planktivorous fish can be important in regulating the abundance and size structure of zooplankton populations. Prey are visually selected in most cases, on an individual basis, although the gill rakers of certain fish collect some zooplankton as water passes through the mouth and across the gills. Planktivorous fish select large zooplankters and can eliminate large cladocerans from lakes. When size selection by fish is not in effect, and when large zooplankters are present, smaller-sized zooplankton are generally not found to co-occur with the larger forms. The cause is likely a result of size-selective predation of smaller zooplankton by invertebrates (copepods, phantom midge larvae and predaceous Cladocera).

TOP-DOWN REGULATION – Control of the food web production through fish predation and harvest.

ZEBRA MUSSEL – The zebra mussel (*Dreissena polymorpha*) is a small, nonnative mussel originally found in Russia. In 1985, the zebra mussel was introduced into the Great Lakes most likely via the ballast water of one or more transoceanic ships. In less than 10 years zebra mussels spread to all five Great Lakes. They are voracious ‘filter feeders,’ processing up to 1 gallon of water per day per mussel. This filter feeding process depletes critical microscopic organisms necessary for a healthy food web. Zebra mussels also destroy native mussels, greatly reducing their populations.

ZOOPLANKTON– Small, often microscopic animals that drift in currents; they feed on detritus, phytoplankton, and other zooplankton. They are preyed upon by fish, shellfish, whales and other zooplankton. Animals of fresh waters are extremely diverse, and include representatives of nearly all phyla. The zooplankton include animals suspended in water with limited powers of locomotion. Like phytoplankton, they are usually denser than water, and constantly sink by gravity to lower depths. The distinction between suspended zooplankton having limited powers of locomotion, and animals capable of swimming independently of turbulence-the latter referred to as nekton-is often diffuse. Freshwater zooplankton are dominated by four major groups of animals: protozoa, rotifers, and two subclasses of the Crustacea, the cladocerans and copepods.

- Protozoa: have limited locomotion, but the rotifers, cladoceran and copepod microcrustaceans and certain immature insect larvae often move extensively in quiescent water. Many pelagial protozoa (5-300 µm) are meroplanktonic, in that only a portion, usually in the summer, of their life cycle is planktonic. These forms spend the rest of their life cycle in the sediments, often encysted throughout the winter period. Many protozoans feed on bacteria-sized particles (most cells < 2 µm), and thereby utilize a size class of bacteria and detritus generally not utilized by large zooplankton.
- Rotifers: Although most rotifers (150 µm - 1 mm) are sessile and are associated with the littoral zone, some are completely planktonic; these species can form major components of the zooplankton. Most rotifers are nonpredatory, and omnivorously feed on bacteria, small algae, and detrital particulate organic matter. Most food particles eaten are small (< 12 µm in diameter).

- Cladocerans: Most cladoceran zooplankton are small (0.2 to 3.0 mm) and have a distinct head; the body is covered by a bivalve carapace. Locomotion is accomplished mainly by means of the large second antennae.
- Copepods: Planktonic copepods (2 - 4 mm) consist of two major groups, the calanoids and the cyclopoids. These two groups are separated on the basis of body structure, length of antennae, and legs.

Glossary Sources: National Oceanic and Atmospheric Administration Fisheries Glossary - https://www.st.nmfs.noaa.gov/st4/documents/FishGlossary.pdf

Michigan Sea Grant – teaching Great Lakes Science – Glossary - https://www.michiganseagrant.org/lessons/teacher-tools/glossary/

New England Fishery Management Council, Glossary of Fisheries Management and Science Terms -https://www.nefmc.org/files/Glossary.pdf

Soil & Water Conservation Society of Metro Halifax, Limnological terms, definitions, acronyms and concepts, http://lakes.chebucto.org/glossary.html#autotrophy