



Synthesis

Eutrophication, water quality, and fisheries: a wicked management problem with insights from a century of change in Lake Erie

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ABSTRACT. Human-driven nutrient inputs into aquatic ecosystems must be managed to preserve biodiversity and to ensure that valued fishery and water quality services are not compromised by hypoxia and harmful algal blooms. Aiming for nutrient inputs that achieve an intermediate level of ecosystem productivity is expected to provide both high fish yield and good water quality. However, we argue that such an intermediate “optimum” may not exist for many aquatic ecosystems that support multiple fisheries with differing tolerances to eutrophication and that must provide multiple water quality services. We further support this argument with an empirical case study of nearly a century (1915–2011) of change in the productivity of Lake Erie and its lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*) fisheries. We discuss and show how the harvest of each fishery has been historically maximized at different levels of ecosystem productivity. Additionally, we examine how anticipated management efforts to improve water quality by reducing nutrient inputs (i.e., oligotrophication) may favor certain fisheries over others, resulting in no single optimal range of nutrient inputs that achieves all valued fishery and water quality objectives. Our synthesis and case study illustrate how the need to balance multiple services in aquatic ecosystems can create a wicked management problem with inevitable trade-offs. To navigate these trade-offs, we recommend the use of ecosystem-based management approaches, which can help decision makers identify and resolve complex trade-offs by facilitating cooperative research and communication among water quality regulators, fisheries managers, and end users.

Key Words: *ecosystem approach; ecosystem-based management; eutrophication; fisheries; Great Lakes; oligotrophication; socio-environmental system; social-ecological system; trade-off; water quality*

INTRODUCTION

Eutrophication, water quality, and fisheries

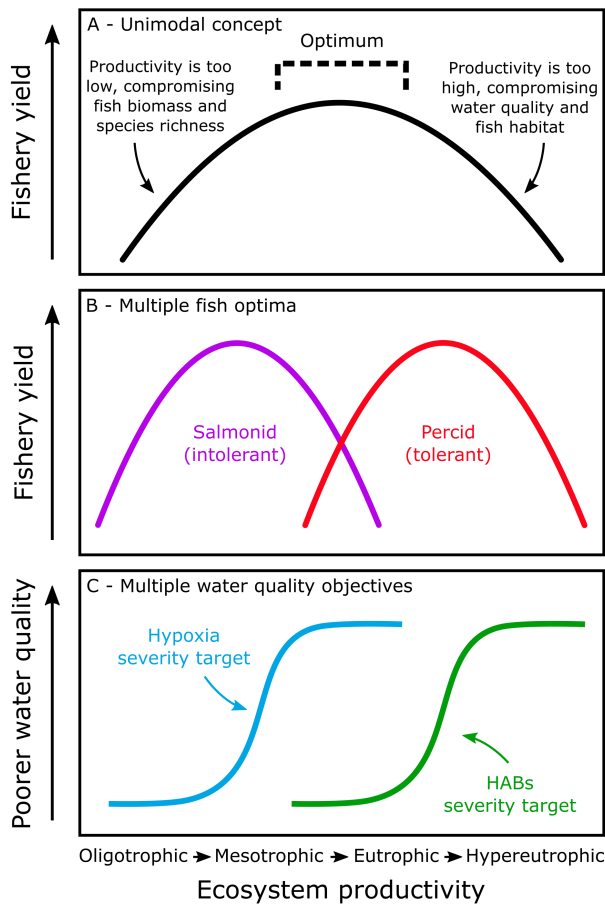
Eutrophication from anthropogenic nutrient inputs is increasingly impacting many aquatic ecosystems (Glibert and Burford 2017, Maúre et al. 2021, Fang et al. 2022), with associated hypoxia and harmful algal blooms (HABs) compromising a variety of ecological and ecosystem services, such as biodiversity, water potability, and recreational opportunities (Smith and Schindler 2009, MacDonald et al. 2016, St-Gelais et al. 2020). However, eutrophication can also provide some benefits through enhanced primary production. This added ecosystem productivity can drive bottom-up increases in the abundance and growth of secondary consumers (Lindeman 1942), such as fishes (Ludsin et al. 2001, Nixon and Buckley 2002, Müller et al. 2007, Saarinen and Candolin 2020), which can benefit different sectors of society by increasing total fishery yields (Pauly and Christensen 1995, Ware and Thomson 2005, Capuzzo et al. 2018, Marshak and Link 2021). These differing effects of eutrophication create a problem for management. Specifically, reducing nutrient inputs to mitigate water quality impairments via better water treatment and/or agricultural conservation practices can result in a trade-off of reduced fishery yields. Such trade-offs are exemplified by ecosystems in which fish biomass or fishery yield declined following nutrient abatement efforts (Baer et al. 2017, Capuzzo et al. 2018, Hossain et al. 2019). Therefore, as suggested elsewhere (Ludsin et al. 2001, Nixon and Buckley 2002, Breitburg et al. 2009, O’Higgins and Gilbert 2014, MacDonald et al. 2016), a better understanding of how best to navigate these trade-offs is critical to the effective management of multi-service aquatic ecosystems.

Trade-offs between eutrophication’s water quality detriments versus fishery benefits can be represented using a unimodal “subsidy-stress” curve (sensu Odum et al. 1979; Fig. 1A). Eutrophication initially subsidizes fisheries yield through bottom-up effects, but as enrichment intensifies these subsidies become outweighed by the stresses of degraded water quality, driving declines in fishery yield via declines in fish survival, growth, and reproduction (Breitburg 2002, Ludsin et al. 2009, Taipale et al. 2018, Jeppesen et al. 2018). This unimodal concept has been thoroughly detailed elsewhere (Ryder 1982, Caddy 1993, Stockner et al. 2000) and has been observed in marine (e.g., Oczkowski and Nixon 2008, O’Higgins and Gilbert 2014), estuarine (e.g., Breitburg et al. 2009), and freshwater ecosystems (e.g., Oglesby et al. 1987, Jonsson et al. 2011). Based on this relationship, total fisheries yield and water quality can be hypothesized to be optimized at intermediate levels of ecosystem productivity where yield is maximized and water quality is not yet severely compromised. The exact range that constitutes “intermediate” productivity likely varies among ecosystems, but the overall concept provides a useful starting point for managers and researchers.

Here, we argue that although it is conceptually intuitive that some eutrophication can be good but too much is bad, applying this concept to real-world ecosystems is more complicated than simply aiming for an optimal range of intermediate productivity. This complexity stems from the fact that many productive aquatic ecosystems support multiple fish populations of recreational, commercial, and/or cultural importance, each of which can require different habitat conditions associated with different levels

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Fig. 1. Fishery yields are expected to be (A) optimized at an intermediate level of ecosystem productivity (e.g., mesotrophic to eutrophic; Caddy 1993, Stockner et al. 2000), where yield is not constrained by low energy inputs nor poor water quality (e.g., harmful algal blooms [HABs] and bottom hypoxia). However, in ecosystems with (B) multiple valued fisheries, the yield of each may be optimized at different levels of ecosystem productivity owing to taxon-specific tolerances to enriched conditions (compare eutrophication-intolerant salmonids in purple to eutrophication-tolerant percids in red). Managing for intermediate productivity may therefore benefit only one species or cause both species to perform poorly. Similar trade-offs could emerge when managing for multiple water quality objectives that are achieved at different levels of ecosystem productivity (C). For instance, targeting low productivity (e.g., oligotrophy) might achieve all water quality objectives, but the ecosystem may no longer support fisheries that require higher productivities. Conversely, managing for eutrophication-tolerant species (percids) may suppress eutrophication-intolerant species (salmonids) and leave some water quality impairments unaddressed (bottom hypoxia). Collectively, these theorized relationships illustrate an ecosystem in which no single level of ecosystem productivity achieves all management objectives, resulting in trade-offs.



of ecosystem productivity (Oglesby et al. 1987, Ludsin et al. 2001, Hondorp et al. 2010, Jacobson et al. 2017, Sundblad et al. 2020). Thus, no single target level of nutrient inputs may exist that achieves the desired harvests of every fishery (Fig. 1B). Similarly, “water quality” also encompasses multiple services, including those related to ecology, human health, recreation, agriculture, and fisheries, and the most valued service can differ among the different agencies and end users involved (Anders and Ashley 2007, MacDonald et al. 2016, St-Gelais et al. 2020). Some may prioritize services achieved with the cleanest water possible, whereas others may prioritize services that necessitate less-clean water, such as total fishery yield or agricultural expansion. Thus, there may be no single target range for nutrient inputs that can address the water quality needs and interests of every group (Fig. 1C).

Ecosystems with multiple optima for fishery yield and nutrient inputs could create a “wicked” (sensu DeFries and Nagendra 2017) management problem of inevitable trade-offs in which one or more services must be sacrificed in pursuit of others. This issue has been partly acknowledged elsewhere (Hondorp et al. 2010, Sundblad et al. 2020, Link and Marshak 2022), but a better understanding of how these trade-offs play out across both multiple fishery and multiple water quality objectives is still needed. This understanding is essential to making management decisions and selecting nutrient management targets that account for different agency and end-user valuations of ecosystem services (Levin et al. 2009, Granek et al. 2010). To explore such trade-offs and to support our argument, we use Lake Erie (US–Canada) as an empirical case study. We begin by describing the relevant social-ecological features of the lake, with emphasis on its history of anthropogenic eutrophication, current policy objectives for water quality, and changes in three fisheries: lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*). Based on the best available data, we then provide an analysis of how these fisheries, as well as their combined yield, may exhibit trade-offs across the different water quality objectives. This case study supports the notion that, for multi-service ecosystems, no single target range for ecosystem productivity may exist that satisfies all fisheries and water quality objectives, resulting in inevitable trade-offs. We further argue that these trade-offs are best resolved through an ecosystem-based management approach (Slocombe 1993, Berkes 2012, Link and Marshak 2022) that facilitates open discussion of different agency and end-user values before setting management targets, that supports interdisciplinary research and monitoring, and that employs cooperative management decision making.

LAKE ERIE: A HISTORY OF EUTROPHICATION

Lake Erie is the 11th largest freshwater lake globally and is divided into three basins—western, central, and eastern—with productivity tending to decline from the warmer, shallower western basin to the colder, deeper central and eastern basins (Sly 1976, Ludsin et al. 2001, Bunnell et al. 2014). During the early 1900s, Lake Erie was typically mesotrophic in the western basin and oligotrophic in the central and eastern basins (Sgro and Reavie 2018), with seasonal periods of more eutrophic conditions. Anthropogenic eutrophication likely first began during the late 1800s owing to expanded human settlement and deforestation in the lake’s watershed (Schelske et al. 1983). Eutrophication then intensified during the 1930s (Sgro and Reavie 2018), driven by

industrial, urban, and agricultural development. Conditions consistent with hyper-eutrophy occurred during the late 1950s through 1960s, characterized by extensive and widely publicized HABs and bottom hypoxia (Makarewicz and Bertram 1991, Watson et al. 2016). These conditions abated somewhat during the 1970s through 1980s owing to better management of primarily point-source phosphorus inputs, resulting in a period of “oligotrophication” in which productivity declined (Makarewicz and Bertram 1991, Ludsin et al. 2001). However, nutrient-driven water quality impairments have consistently occurred throughout the last four decades (Scavia et al. 2014, Watson et al. 2016). The lake has also undergone a recent period of anthropogenic “re-eutrophication” during the 2000s and 2010s (Kane et al. 2014, Scavia et al. 2014, Watson et al. 2016) driven by increased non-point-source inputs of more bioavailable forms of phosphorus from agriculture (Scavia et al. 2016, Baker et al. 2019). This history of eutrophication in Lake Erie, including its recent re-eutrophication, prompted action to reduce nutrient inputs to improve water quality, which we discuss in the next subsection.

Current water quality objectives

Initially, to mitigate water quality impairments from anthropogenic eutrophication during the 1950s through 1970s, the U.S. and Canadian governments signed the Great Lakes Water Quality Agreement in 1972 (with an amendment in 1978; IJC 2015). Associated abatement programs targeted and successfully reduced point-source phosphorus inputs from > 20,000 metric tons per annum (MTA) to 11,000 MTA (Dolan and McGunagle 2005). During the recent period of re-eutrophication, non-point-source inputs (particularly from agricultural runoff) became the focus of water quality management efforts (Scavia et al. 2016, Baker et al. 2019, GLWQA NAS 2019). The principal water quality objectives of these contemporary abatement efforts are to: (1) reduce HAB severity; (2) minimize bottom hypoxia; and (3) return the overall productivity of the lake to oligotrophic/mesotrophic conditions (Dove and Chapra 2015, GLWQA NAS 2019). The level of nutrient reductions required to reduce HABs are expected to be the least severe, with more severe reductions required to reduce hypoxia (IJC 2015, Scavia et al. 2016). Additionally, given that oligotrophic/mesotrophic conditions have not consistently occurred since before the 1930s (Sgro and Reavie 2018), the trophic status target likely requires even further reductions compared to the HABs and hypoxia targets.

Lake whitefish, walleye, and yellow perch

Lake Erie supports multi-billion dollar commercial, recreational, and sustenance freshwater fisheries. Two percids, walleye and yellow perch, currently supply much of these fisheries, but less-abundant salmonids like lake whitefish are also focal targets for fishing, management, and re-introduction. Salmonids used to be harvested extensively but these fisheries collapsed during the late 1800s to mid-1900s owing to a variety of anthropogenic pressures (Applegate and Van Meter 1970). In the case of the lake whitefish fishery, which collapsed during the mid-1900s, eutrophication was a principal driver in addition to overexploitation and invasive species (Regier et al. 1969, Hartman 1972). As salmonids and other species declined, yields of walleye and yellow perch increased (Applegate and Van Meter 1970). This shift was partly driven by exploitation as people adjusted to which species were available, but bottom-up effects from eutrophication also contributed (Regier et al. 1969, Parsons 1970) as did the higher

tolerance of walleye and yellow perch to nutrient pollution (Ludsin et al. 2001, Jacobson et al. 2017). Eventually the walleye fishery also collapsed during the late 1960s, coinciding with both a sharp rise in exploitation and severe eutrophication, the latter of which negatively affects walleye’s ability to forage (Nieman and Gray 2019) and the survival of its invertebrate prey that require oxygenated sediments (Parsons 1970, Bridgeman et al. 2006). The walleye fishery has since recovered owing to a combination of better fishery and nutrient management (Vandergoot et al. 2019). Conversely, the yellow perch fishery never collapsed because this species can persist and even proliferate under extremely eutrophic conditions (Reichert et al. 2010, Carreon-Martinez et al. 2014, Marcek et al. 2021). These historical patterns in the lake whitefish, walleye, and yellow perch fisheries indicate three example species with differing tolerances to eutrophication. Lake whitefish is the least tolerant of the three followed by walleye and then yellow perch.

Quantifying productivity, water quality objectives, and fisheries

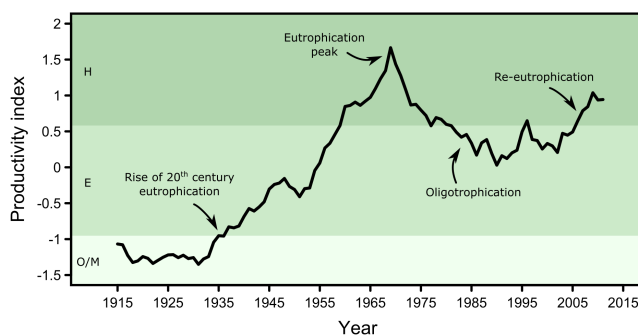
This brief history of Lake Erie illustrates why it is an excellent case study for examining water-quality-fisheries trade-offs. Lake Erie’s productivity has varied widely (across oligotrophic, mesotrophic, eutrophic, and hyper-eutrophic conditions), it is being managed for multiple water quality objectives that are achieved at different levels of ecosystem productivity, and it supports multiple fisheries that differ in their tolerance to eutrophication. This combination of factors allows us to examine potential productivity-driven trade-offs across multiple water quality and fishery services. Evaluating these trade-offs requires quantifying how productivity has changed, where the different water quality objectives fall along this gradient, and what level of productivity has historically maximized the yield of the different fisheries. No available metrics do any of this perfectly given that changes have been occurring since the early 1900s and most long-term monitoring programs only began (at best) around the 1970s (Fraker et al. 2022). However, we can develop proxy measures and we can verify the veracity of these proxies by comparing them to the known historical changes in the lake detailed above.

To quantify productivity, we developed a multi-metric index of annual lake-wide productivity during 1915–2011 (see Appendix 1 for methods). In brief, we collected and estimated annual data on five metrics representing non-point-source phosphorus inputs, sediment phosphorus and carbon concentrations, aqueous phosphorus, and the phytoplankton community across the different basins of the lake. We scaled these five metrics relative to their respective means and standard deviations and then averaged these values, with this average hereafter referred to as the “productivity index” (Fig. 2). The index therefore measures how the overall productivity of Lake Erie has varied through time in units of standard deviations from the long-term mean. Other metrics could be incorporated, but the current index acceptably represents nutrient-driven changes in Lake Erie’s productivity given that it closely matches the known patterns and timings of anthropogenic eutrophication (Fig. 2).

To link each water quality objective to our productivity index, we calculated target ranges for non-point-source phosphorus inputs that would potentially achieve the three water quality objectives for HABs, bottom hypoxia, and trophic status in Lake Erie (see Appendix 2 for methods). We used non-point phosphorus inputs

as a common currency because they are a known driver of recent eutrophication and are thus the focal target for recent management action aimed at achieving each water quality objective (Scavia et al. 2016, Baker et al. 2019, GLWQA NAS 2019). In addition, non-point-source inputs can be directly related to our productivity index because they are incorporated in its calculation. The results also match our expectations for these targets, specifically that more severe reductions are required to reduce hypoxia compared to HAB severity, with the most severe reductions required to achieve consistently oligotrophic/mesotrophic conditions.

Fig. 2. Time-series of Lake Erie productivity (1915–2011) based on a multi-metric index. The index begins the time series at its lowest values (representing oligotrophic to mesotrophic conditions; “O/M”) and then increases during the 1930s as the lake becomes consistently eutrophic (“E”). The index peaks during the late 1950s through 1960s (a period of hyper-eutrophy; “H”), declines somewhat during the 1970s through the 1980s, then increases again. These various changes in the index all match the history of changing productivity in Lake Erie that we have discussed. Trophic demarcations for O/M, E, and H are based on minimum and maximum nutrient index values during, respectively, 1915–1934, 1935–1958, and 1959–1969, which were selected based on threshold years of change in Lake Erie’s productivity from Sgro and Reavie 2018.



Lastly, to relate fish yields to the productivity index, we obtained data on the total U.S. and Canadian commercial harvest (kg) of lake whitefish, walleye, and yellow perch in Lake Erie during 1915–2011 from the Great Lakes Fishery Commission (<http://www.glfsc.org>). This dataset is the only one that goes back far enough to address our questions, but it is imperfect because the harvest of each species is not necessarily related to its population size. However, some extenuating factors allow us to broadly make this connection in Lake Erie across the last century. First, lake whitefish was only harvested in sufficient numbers before its decline during the mid-1900s, then harvest declined as the population declined (Hartman 1972). Thus, harvest broadly tracked the historical highs then lows of this population during the past century (note that we corrected lake whitefish harvests by 1.17 times up to 1977 to account for a switch in Lake Erie from primarily dressed to round weights in 1978). Second, like lake whitefish, yellow perch is a species of medium economic value that has been consistently harvested since the early 1900s. Thus, yellow perch harvest has tended to track broad population trends in contrast to lower-valued species in which harvest is more driven

by fluctuating market prices (Regier et al. 1969, Hartman 1972). Finally, the history of walleye harvest is more complex but can still be linked to population size. The U.S. commercial harvest of walleye broadly followed population trends up to the late 1960s, whereas the Canadian harvest did not because it was more influenced by changes in gear and effort (Regier et al. 1969, Parsons 1970). Both the U.S. and Canadian harvests then declined when the walleye population collapsed during late 1960s (Regier et al. 1969, Parsons 1970, Hartman 1972). The U.S. fishery permanently closed in 1970 owing to human health concerns over mercury bioaccumulation and so the U.S. harvest does not track the subsequent walleye recovery during this period. However, Canadian harvests do track this recovery because the Canadian fishery never closed and became more sustainably managed. Therefore, the best solution was to use U.S. harvests up to 1969 to reflect the increase and then collapse of the walleye population, then Canadian harvests thereafter to reflect its subsequent recovery. To summarize, we feel confident that our fisheries data sufficiently track the known historical responses of each species to eutrophication. We also conducted some follow-up analyses that confirmed that our results using the harvest data were robust to variability in the productivity index and variability in the relationship between harvest and the population size of each species (see Appendix 3).

To examine potential nutrient-driven trade-offs across multiple water quality and fishery services in Lake Erie, we related each species’ commercial harvest to our productivity index using quantile regression (via the “quantreg” package in R; Koener 2021, R Core Team 2022). These models also included a quadratic term for the index to allow for non-linear relationships. We chose this approach to model harvest as a range of highs and lows, which more closely follow the historical highs and lows of each species’ population. Modeling harvest as a range also allows for inter-annual fluctuations within this range owing to other factors, such as changes in fishing effort or demographic and environmental variation. After modeling harvest in relation to productivity, we then plotted these relationships alongside the different target ranges for nutrient inputs to examine which fisheries might be optimized for each water quality objective.

FISHERY AND WATER QUALITY TRADE-OFFS IN LAKE ERIE

Each fishery’s maximum harvest occurred at a different level of ecosystem productivity (Fig. 3) and the highest total maximum harvests of our focal species have historically occurred at the highest productivities (Fig. 4), rather than at intermediate levels. The maximum harvests of lake whitefish occurred at low levels of ecosystem productivity (about -0.5 standard deviations below the long-term mean; Fig. 3A), in contrast to harvests of walleye and yellow perch which were highest at, respectively, intermediate (+0.15 standard deviations; Fig. 3B) and high productivities (+1.7 standard deviations; Fig. 3C). These relationships matched the known historical responses of these species to eutrophication in Lake Erie and agreed with the known lower tolerances of salmonids to the impacts of nutrient pollution versus the higher tolerances of percids.

The unique productivity relationships for lake whitefish, walleye, and yellow perch suggested that achieving each of the different water quality objectives (i.e., HABs, hypoxia, and trophic status)

Fig. 3. Relationship between the commercial harvest of (A) lake whitefish (*Coregonus clupeaformis*), (B) walleye (*Sander vitreus*), and (C) yellow perch (*Perca flavescens*) and an index of productivity in Lake Erie during 1915–2011. The productivity index is reported in standard deviations relative to the long-term mean. Dashed lines indicate the respective lower 5% and upper 95% quantiles of harvest for each taxon based on quantile regression. Successive years are indicated by numbers across an orange to blue color gradient (red and purple represent intermediate years). Color bands indicate the estimated target ranges of non-point phosphorus inputs required to reduce harmful algal blooms (HABs) in western Lake Erie (green band), reduce bottom hypoxia in central Lake Erie (“Hypoxia”; blue band), and return the lake to desirable oligotrophic/mesotrophic conditions (“Oli/Meso”; orange band). The vertical red line (“15-19 mean”) indicates mean non-point-source phosphorus inputs into Lake Erie during 2015–2019, providing a comparison of recent nutrient inputs to the different water quality targets.

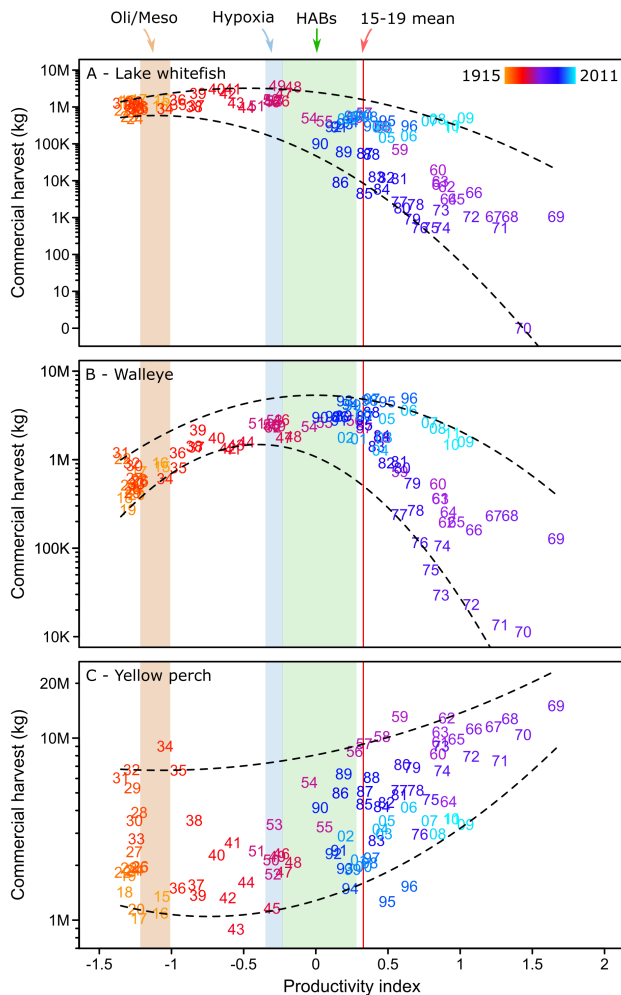
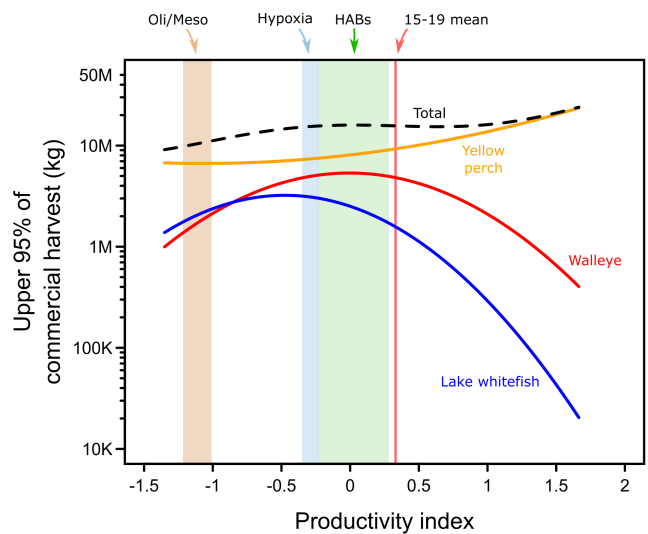


Fig. 4. Predicted upper 95% quantiles of lake whitefish (*Coregonus clupeaformis*; blue line), walleye (*Sander vitreus*; red line), yellow perch (*Perca flavescens*; yellow line), and total fishery harvest (all taxa summed; black dashed line) across an index of productivity in Lake Erie. Color bands indicate the estimated target ranges of non-point phosphorus inputs required to reduce harmful algal blooms (“HABs”) in western Lake Erie (green band), reduce bottom hypoxia in central Lake Erie (“Hypoxia”; blue band), and return the lake to desirable oligotrophic/mesotrophic conditions (“Oli/Meso”; orange band). The vertical red line (“15-19 mean”) indicates mean non-point-source phosphorus inputs into Lake Erie during 2015–2019, providing a comparison of recent nutrient inputs to the different water quality targets.



could create trade-offs in fishery yields. If non-point inputs are successfully reduced into the range of the HAB target, then walleye harvests may remain high as yellow fish harvests decline and lake whitefish harvests increase. If nutrient inputs are further reduced to meet the hypoxia and then lake trophic-status targets, then walleye harvests are likely to decline with further reductions in yellow perch, and even lake whitefish harvests may decline at the lowest extremes of ecosystem productivity (as has occurred in other North American Great Lakes; Rook et al. 2022).

Collectively, our case study portrays an ecosystem in which no single range of productivity likely exists that optimizes all fishery and water quality management objectives, creating a wicked management problem of inevitable trade-offs. For example, aiming to maximize total yields may allow for higher nutrient inputs, but this goal would compromise water quality and create a fish community dominated by only eutrophication-tolerant species (also see Ludsins et al. 2001). Alternatively, reducing nutrient inputs to reduce HAB severity would benefit water quality, and somewhat balance the harvests of all three fisheries, but would leave other water quality objectives unaddressed, such as minimizing hypoxia (Scavia et al. 2016). Further abatements

of nutrient inputs to reach the hypoxia and then trophic-status targets would further benefit water quality and potentially lake whitefish, but may substantially reduce percid harvests. Managing anthropogenic nutrient inputs into Lake Erie may therefore be expected to induce trade-offs across its multiple fishery and water quality services regardless of which target range for nutrient inputs is selected.

Furthermore, the socioeconomic reality of the above trade-offs is undoubtedly more complex than what we have shown and will depend upon agency and end-user valuation of numerous other ecosystem services, including human health concerns for safe drinking water and safe beaches, and suitable habitat for different fish species other than those we examined. For example, we only focused on three key species with available data and known linkages to eutrophication, however Lake Erie supports many fish species valued for a range of commercial, recreational, cultural, and/or sustenance purposes (e.g., white bass, *Morone chrysops*; lake trout, *Salvelinus namaycush*). Further research is therefore needed to quantify trade-offs across a wide variety of fish species, other types of water quality services, and varying economic, social, and cultural values, all of which may be optimized at different levels of productivity.

Do these trade-offs apply beyond Lake Erie?

The extent to which other ecosystems follow the example we have shown depends on several factors. First, productivity-driven trade-offs across the yields of different fisheries can only occur when the taxa supporting these fisheries have differing tolerances to eutrophication and its discontents (e.g., water clarity, dissolved oxygen availability, prey availability, etc.). This condition applies to many large and small freshwater ecosystems (Jeppesen et al. 2000, Maceina and Bayne 2001, Hossain et al. 2019, Sinclair et al. 2021), as well as marine ecosystems (Townsend 2014). However, it would not apply to ecosystems in which a single species is the focus of management (e.g., marine cod fisheries; Nguyen et al. 2016) nor fisheries supported by different species with similar tolerances to eutrophication (e.g., Lake Victoria; Taabu-Munyaho et al. 2016). In such instances, a single optimal range for productivity may exist that achieves the desired objectives for multiple ecosystem services.

Second, the impacts of increasing or decreasing productivity depend on the environmental context. Lake Erie has exhibited comparatively little change in total harvests at the extreme ends of its productivity gradient across the three focal species (see Fig. 4), but other systems may exhibit more substantial declines and so may not exhibit multiple productivity optima. For example, Lake Erie is large and heterogeneous, which offers spatial refuges when conditions are unfavorable (Roberts et al. 2009, Stone et al. 2020). Ecosystems with no similar refuges, such as smaller lakes or marshes, may experience more severe declines in fishery yield in response to nutrient pollution. Furthermore, although our analysis and previous research in Lake Erie (e.g., Ludsin et al. 2001) suggest that total harvests are resilient to changes in productivity, the effects of declining productivity may be more pronounced in less-productive ecosystems. Lake Erie is naturally more productive relative to the other North American Great Lakes because it is warmer, shallower, and has a naturally nutrient-rich watershed (Dove and Chapra 2015). Consequently, even its lowest levels of productivity can support high fishery

yields. By contrast, in more oligotrophic ecosystems, reductions in nutrient inputs can have much stronger negative impacts on total fishery yields (e.g., Rellstab et al. 2007, Bunnell et al. 2014, Baer et al. 2017, Rook et al. 2021). Nutrient abatement efforts in these lower productivity ecosystems may therefore have a greater potential to harm fisheries than what we have shown here for Lake Erie.

Additionally, the presence of other anthropogenic stressors could alter expected yield-productivity relationships. For example, lake whitefish and other similar salmonids require both well-oxygenated and cold-water habitat (Hartman 1972, Ludsin et al. 2001, Müller and Stadelmann 2004), thus their survival depends on optimal productivity and temperature. Progressing climate change may therefore inhibit the recovery of these cold-water taxa even if nutrient inputs are reduced (Jeppesen et al. 2012, Collingsworth et al. 2017). Invasive species could also disrupt expected responses by suppressing yields through negative inter-specific interactions (e.g., invasive parasites; Brant 2019) or by disrupting the transfer of primary productivity to higher trophic levels (e.g., invasive omnivores; Sinclair and Arnott 2015, Kao et al. 2018). These complexities highlight the need to consider the unique context of each ecosystem to forecast whether planned nutrient abatement efforts will induce trade-offs against different fisheries.

NEED FOR ECOSYSTEM-BASED MANAGEMENT

Managing anthropogenic nutrient inputs in multi-service aquatic ecosystems requires continued movement toward ecosystem-based management. This approach seeks to identify linkages among the important components of an ecosystem, quantify trade-offs across different management objectives, and facilitate transparent discussions among agencies and end users to balance multiple ecosystem services (Berkes 2012, Link and Marshak 2022). Adopting such a holistic management approach is complicated, however, because the various natural- and human-related sectors of aquatic ecosystems (e.g., water quality, fisheries, tourism, agriculture, industry, etc.) are often managed by different agencies. The mandates of these agencies do not necessarily overlap, such as those mandated to maintain water potability and beach safety (e.g., U.S. Environmental Protection Agency) versus those mandated to sustain the commercial or recreational yields of individual fish species (e.g., fishery management agencies). This more traditional, sectorial approach to aquatic ecosystem management can prevent agencies from cooperating, communicating, and sharing information, which is necessary to identify and resolve trade-offs. Sectorial approaches can even create conflicts and inter-agency competition that is detrimental to effective management (Granek et al. 2010, Alexander and Haward 2019). Such issues can only be overcome by creating governance structures that require agencies with different mandates to communicate and collaborate to identify solutions to their shared problems (Rosenberg and McLeod 2005, Alexander and Haward 2019). If implemented well, these collaborations would consider the needs of multiple end users from the outset, including water and fishery managers, lake users, anglers, commercial fishers, and Indigenous peoples (Lapointe et al. 2014). Ideally these collaborations would also support research identifying linkages between nutrient abatement efforts and fishery yields (e.g., via food web modeling; Heymans et al. 2016) and would establish cooperative long-term monitoring programs

to collect the data necessary to inform these linkages (e.g., by directly measuring productivity; Hecky and DePinto 2020). Additionally, cooperative approaches to ecosystem management help to ensure that unanticipated outcomes or “ecological surprises” (Paine et al. 1998) that can disenfranchise end-user groups are kept to a minimum or avoided completely.

An additional complication to navigating trade-offs, which are always value-based, is that these values are changing through time owing to changing environmental contexts (e.g., climate change; Glibert 2020, Meerhoff et al. 2022) and societal expectations (e.g., “shifting” or “sliding” baselines; Pauly 1995, Dayton et al. 1998). Ecosystem-based management efforts should therefore also periodically re-assess the value of different ecosystem services. Such value shifts have already occurred in many anthropogenically impacted aquatic ecosystems. For instance, much of Lake Erie’s regional culture, livelihoods, and economies now depend on eutrophication-tolerant walleye and yellow perch. However, these species only became important after other fisheries were decimated by multiple anthropogenic stressors, including eutrophication, overexploitation, and invasive species. This modern social-ecological system, combined with our case study of potential fishery-water quality trade-offs, raises critical questions: (1) Does an optimal level of productivity that achieves all management objectives exist? If not, (2) do we prioritize currently valuable eutrophication-tolerant taxa over other species, while deprioritizing water quality objectives that may harm these fisheries? Or, (3) do we manage for the cleanest water possible, rehabilitate eutrophication-intolerant taxa (e.g., stocking salmonids like *Coregonus* spp.; Schmitt et al. 2020), and accept potential reductions in currently valued fisheries? These questions are difficult to answer and, combined with historical and ongoing temporal shifts in the value of different aquatic ecosystem services, further highlight the wickedness of trying to simultaneously balance multiple fisheries and water quality objectives. Continued movement toward ecosystem-based management that considers different end-user values, that better aligns different agency mandates and governance structures, and that helps base management decision making on a scientific understanding of ecosystem trade-offs will be key to navigating through such wicked management problems.

Author Contributions:

JSS wrote the majority of the manuscript with input and editing from all authors. EDR provided diatom and chlorophyll *a* productivity data for Lake Erie. MEF and SAL provided funding and supervision.

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We dedicate this work to the memory of our co-author, Dr. Michael Fraker. He was a great collaborator and friend who cared deeply about this research. We will miss you.

Data Availability:

All data is publicly available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.0gb5mkm6t>.

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APPENDIX 1

Productivity index

We developed an annual (1915-2011) multi-metric index of ecosystem productivity to relate to annual (1915–2011) lake-wide commercial fish harvest data. We needed to create this index because no long-term, lakewide dataset on Lake Erie productivity currently exists. For example, annual estimates of phosphorus inputs into each lake basin are available (Maccoux et al. 2016), but these inputs do not necessarily reflect actual lake productivity and estimates only begin in 1967, which would limit the historical perspective. By contrast, paleolimnological studies of sediment records have quantified long-term changes in phosphorus concentrations and phytoplankton since the 1900s (e.g., Schelske and Hodell 1995, Lu et al. 2010, Sgro and Reavie 2018, Yuan et al. 2020). These datasets reflect long-term changes in lake productivity, but their measurements are not on an annual timescale and are typically collected from sampling sites in a single basin. Thus, by themselves, none of the existing datasets can comprehensively represent shifts in lakewide productivity.

To produce a single, lakewide, annual metric of ecosystem productivity, we combined five datasets, each of which reflects different aspects of Lake Erie's productivity during 1915–2011. Our first metric represented lakewide, annual, non-point-source phosphorus inputs (Fig. A1.1). To derive this metric, we started with estimates of total phosphorus (TP) loads (metric tonnes annually) during 1967–2013 (Maccoux et al. 2016; Fig. A1.1a). We then extended these estimates back to 1913 based on a strong, positive relationship between TP loads and TP concentrations (mg g^{-1}) in the sediments of eastern Lake Erie ($R^2 = 0.78$; Fig. A1.2; extracted from Schelske and Hodell 1995). The resulting values accurately represent past changes in lake productivity, but they do not capture the fact that eutrophication has intensified in recent decades owing to increases in more bioavailable, non-point-source phosphorous inputs primarily from agriculture in the Maumee River watershed (Scavia et al. 2014, Watson et al. 2016, Baker et al. 2019; Fig. A1.1b). A more accurate representation of how phosphorus inputs have altered Lake Erie productivity would thus combine TP inputs from the early to mid-1900s with data on non-point-source inputs after this period. To produce this dataset, we converted TP loads during 1913–1973 into a rough approximation of non-point-source inputs then used annual monitoring data of non-point-source inputs up to 2013. For the 1913–1973 data, we assumed that non-point-source phosphorus inputs constituted 47% of TP loads based on the average percent of TP loads that were non-point-source phosphorus inputs during 1974–1978 (the first five years of data). This proportion does change through time, evidenced by its increase in recent decades as point-source phosphorus inputs declined (Fig. A1.3). Therefore, we are assuming that the proportion of point-source versus non-point-source phosphorus inputs was consistent prior to the decline in point-source phosphorus inputs during the late 1970s and early 1980s started by the implementation of the Great Lakes Water Quality Agreement (GLWQA 2015). The final metric of non-point phosphorus inputs from 1913–2013 therefore follows historic trends in TP inputs (predicted from sediment records) up to 1973, then follows trends in non-point-source inputs thereafter (Fig. A1.1c). Lastly, we converted the non-point-source phosphorus input metric into a

5-year moving average from 1915–2011 (Fig. A1.1c). We used a moving average because the older age classes of walleye (age 3+), yellow perch (age 2+), and lake whitefish (age 3+), which are generally targeted by Lake Erie’s fisheries, would be responding to changes in lake productivity across multi-year rather than annual timescales.

The last four metrics of productivity were extracted from four paleolimnological studies (Lu et al. 2010, Sgro and Reavie 2018, Yuan et al. 2020, Reavie et al. 2021). We chose these studies because they were conducted in different basins or involved different metrics, thus providing a more comprehensive overview of ecosystem productivity changes throughout the lake. We used data on sediment TP concentrations (mg g^{-1}) in the western basin during 1915–2008 (Yuan et al. 2020; Fig. A1.4b) to support the eastern basin records we used above to estimate non-point-source inputs. We also included data on sediment total organic carbon concentration (TOC; wt%) in the eastern basin during 1915–2003 (Lu et al. 2010; Fig. A1.4c) to provide a metric of productivity that was not based on TP. Additionally, we included data on aqueous TP concentrations ($\mu\text{g L}^{-1}$) in the central basin during 1915–2011, inferred from sediment records of the diatom community (Sgro and Reavie 2018; Fig. A1.4d), and data on sediment chlorophyll *a* concentrations ($\mu\text{g g}^{-1}$ dry weight) in the central basin during 1918–2011 (Reavie et al. 2021; Fig. A1.4e). These two metrics provided productivity values from the central basin to support our other eastern and western basin records, and provided productivity data derived from the biotic community as an added contrast to our TP- and TOC-based data. To produce annual values from non-annual sediment records, we predicted the value for a given year based on the linear relationship between the most recent previous and subsequent observations. For example, if observations from two parts of a sediment core were dated to 1972.5 and 1978.7 (i.e., a temporal resolution of about 6 years), then annual values for 1973–1978 were predicted based on the linear relationship between these values and time.

All five productivity metrics were then converted to *z*-scores, i.e., centered based on their respective means and standard deviations, then all metrics were averaged within each year from 1915–2011 to produce a single annual metric of Lake Erie productivity (termed the ‘productivity index’; Fig. A1.4f). We selected 1915 as the starting year because that is the first year of available fish harvest data. We chose 2011 as the end year because that is the last year for which we have data from more than one productivity metric. Given that the final productivity index is derived from an average of *z*-scores, it provides a proxy measurement of how the overall productivity of Lake Erie has changed through time based on where each year falls in terms of standard deviations from the long-term average.

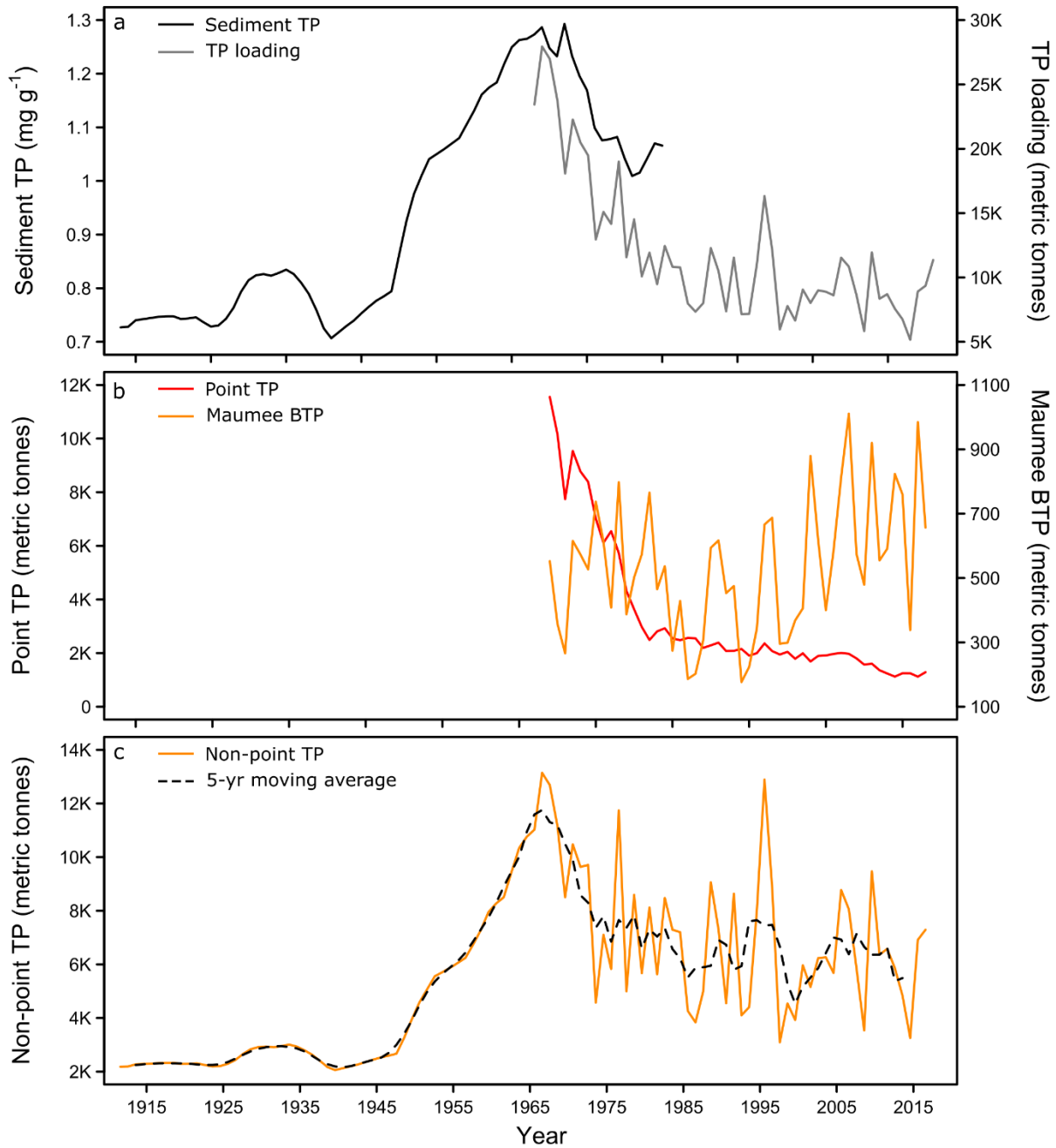


Fig. A1.1. Metrics used to produce our estimate of non-point-source phosphorus inputs during 1915–2011. In (a), sediment records of total phosphorus (TP) concentrations (mg g^{-1} ; black line) indicate eutrophication began around the 1930s, peaked in the 1960s, then declined into the 1980s (reproduced from (Schelske and Hodell 1995)). Monitored TP inputs (metric tonnes; grey line) during 1967–2018 also strongly correlate to the later sediment trends (see Fig. A1.2). However, (b) although TP inputs have declined owing to efforts to abate point-source phosphorus inputs (red line), non-point-source phosphorus inputs and subsequent eutrophication have increased during recent decades primarily driven by increases in more bioavailable forms of

total phosphorus (BTP) from the Maumee River (orange line; calculated following methods in Stumpf et al. 2016). To produce an (c) annual time-series for non-point-source inputs, we assumed that these inputs were 47% of TP inputs prior to 1974, with annual monitored loads used thereafter (orange line). We then converted the annual non-point-source phosphorus inputs into a 5-year moving average (dashed black line) for use in our analyses (Fig. A1.4a). This approach ensures that temporal changes in Lake Erie productivity are represented by changes in TP prior to 1974, and then by monitored non-point-source inputs thereafter to better capture recent re-eutrophication.

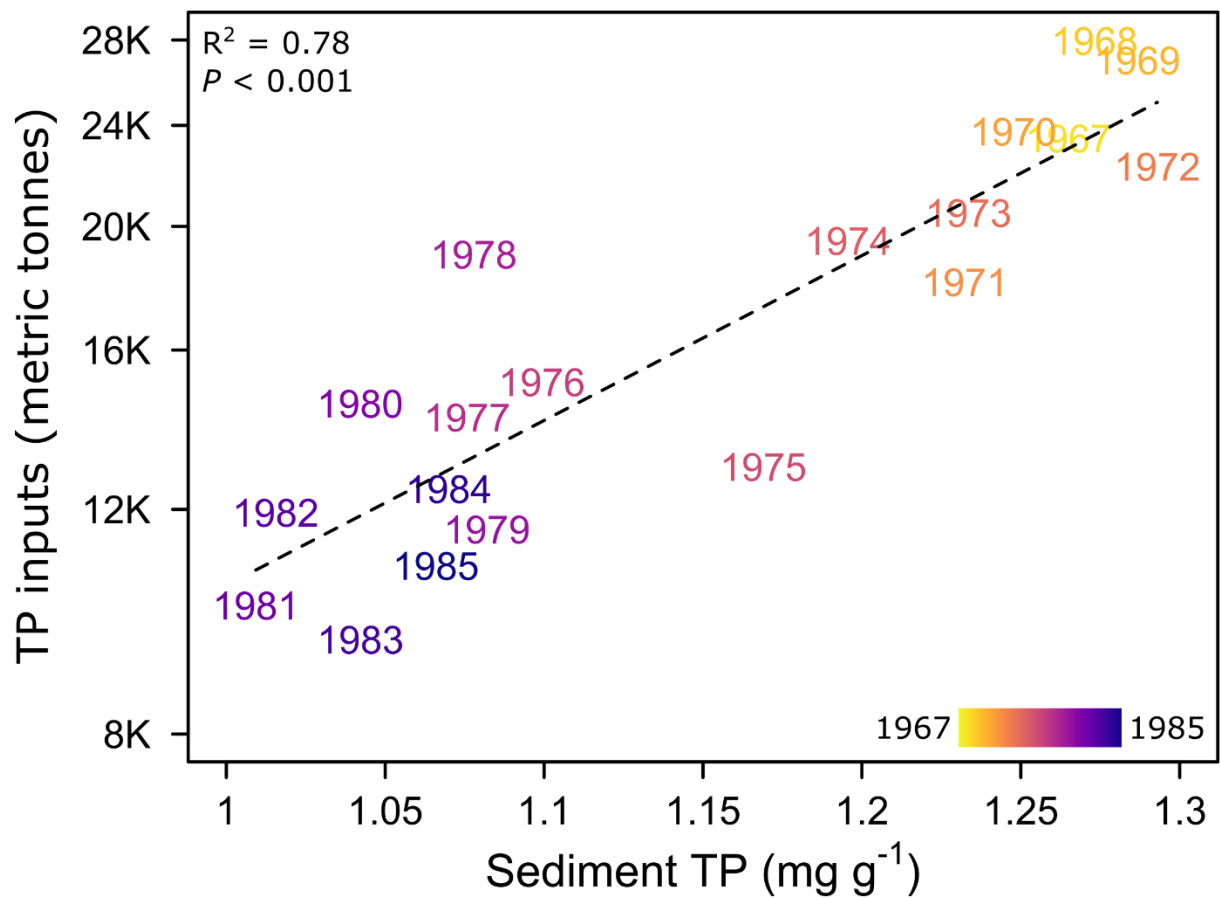


Fig. A1.2. Relationship between lakewide total phosphorus (TP) inputs (metric tonnes) into Lake Erie (from Maccoux et al. 2016) and sediment TP concentrations from the LE47-87 core in Lake Erie's eastern basin (from Schelske and Hodell 1995) during 1967–1985. Note the log-scale on the y-axis.

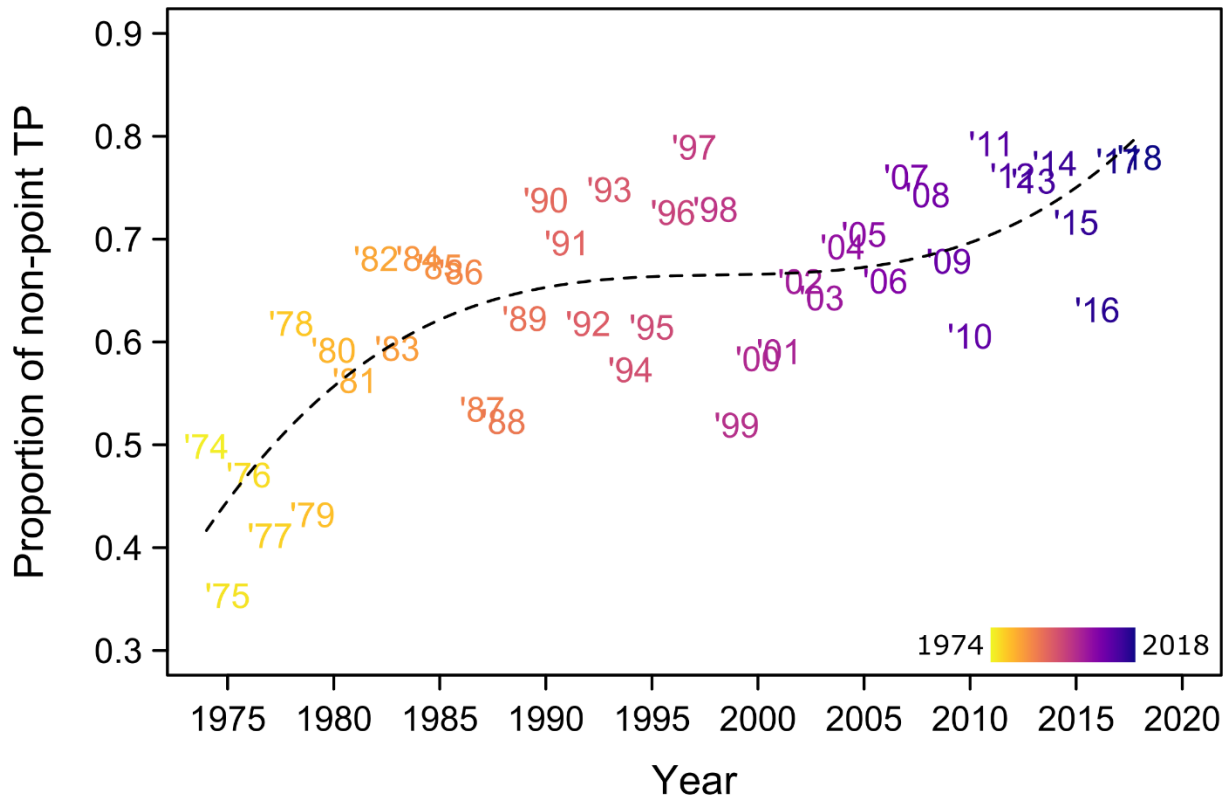


Fig. A1.3. Change in the proportion of total phosphorus (TP) inputs into Lake Erie that is comprised of non-point-source phosphorus inputs during 1974–2018 (data sourced from Maccoux et al. 2016). The increasing proportion of non-point-source inputs through time is driven by declines in point-source inputs during the 1980s through 1990s, and by increases in non-point-source inputs starting around the early 2000s (see Fig. A1.1b). Consequently, we used the average proportion across the first five years of data (1974–1978; 47%), prior to major declines in point-source inputs, to estimate non-point-source inputs based on estimated TP inputs during 1913–1973.

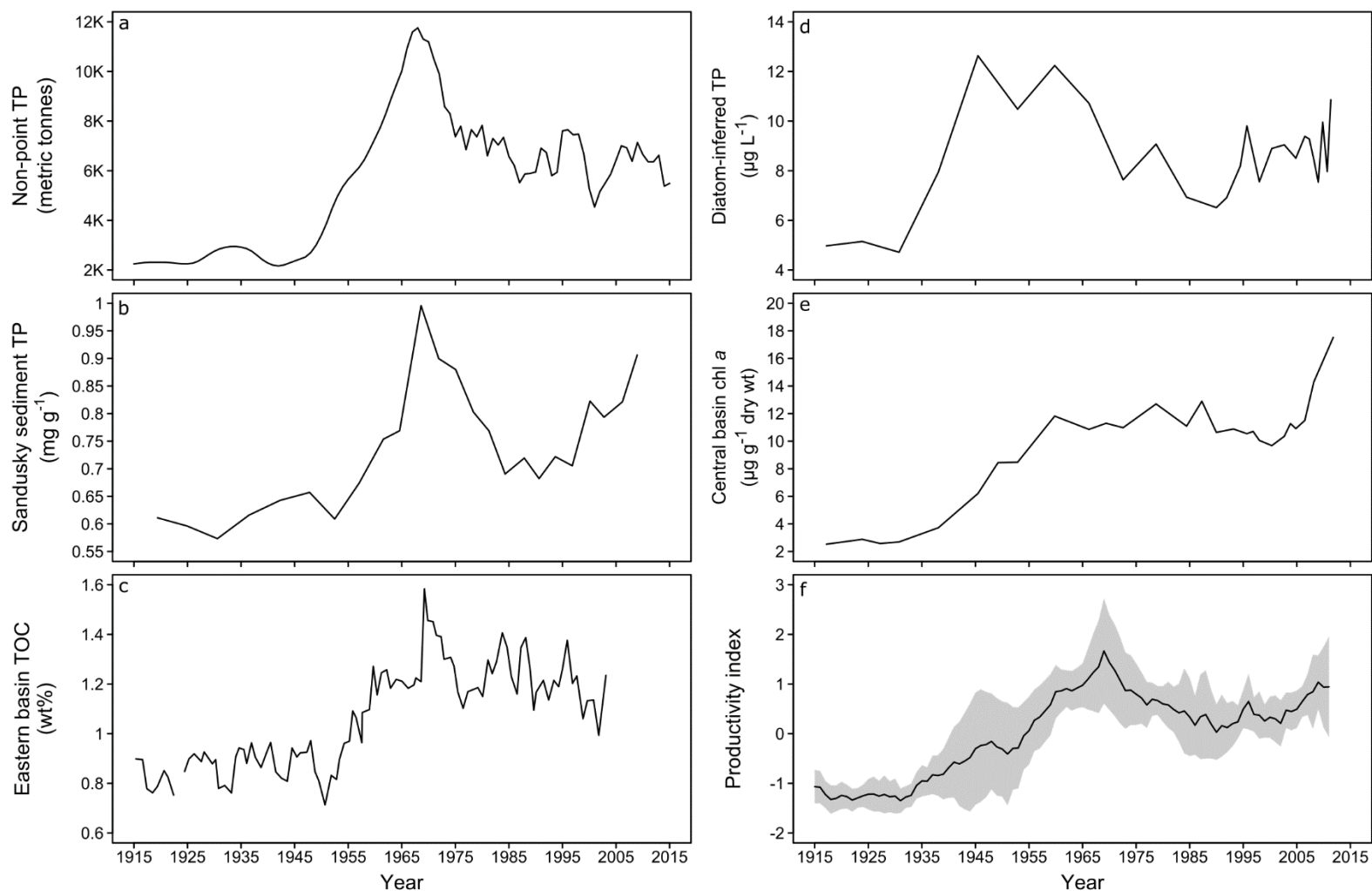


Fig. A1.4. Temporal changes in (a–e) the five metrics used to develop the (f) productivity index for Lake Erie during 1915–2011. Black lines in (a–e) are the annual values for each metric (methods and references detailed above), whereas in (f) it is the average across the scaled metrics for each year. Grey shading indicates the standard deviation of these averaged index values. The generation of the source data for (d) diatom-inferred phosphorus and (e) sediment chlorophyll *a* was supported by a grant to E. Reavie from the U.S. Environmental Protection Agency under Cooperative Agreement GL-00E23101-2.

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APPENDIX 2

Water quality objectives

We calculated the non-point-source phosphorus input targets using different methods for each Lake Erie water quality objective of: (1) mitigating harmful algal blooms (HABs); (2) reducing bottom hypoxia; and (3) achieving mesotrophic conditions in the western and central basins and oligotrophic conditions in the eastern basin (Dove and Chapra 2015, LEBPRS 2019). Recent non-point-source phosphorus inputs have averaged about $6,500 \pm 1,200$ (mean \pm SD) metric tonnes annually during the last five years of most recent data (2015–2019; from Maccoux et al. 2016 and <http://www.blueaccounting.org>). Conversely, point-source phosphorus inputs have been consistently lower, averaging about $1,300 \pm 160$ metric tonnes annually during the last 10 years (2010–2019). Point-source inputs are also unlikely to decline further given the already extensive efforts to reduce this source of nutrient pollution, such as via wastewater treatment (these efforts began with the Great Lakes Water Quality Agreement in 1972; (GLWQA 2015). Thus, further reductions of phosphorus inputs into Lake Erie are likely best accomplished through reductions in non-point-source inputs. We therefore converted each water quality objective into a potential range of targets for non-point-source phosphorus inputs.

To reduce HABs, the Great Lakes Water Quality Agreement (GLWQA 2015) provides two potential targets: the first is achieving below a 3 on an index of HAB severity (above 3 is considered a ‘severe bloom’) and another is to reduce total phosphorus (TP) inputs by 40% of the quantities recorded in 2008. The HAB severity index is strongly related to the amount of bioavailable total phosphorus (BTP) coming from the Maumee River during May through June (Stumpf et al. 2016; Fig. 2.1a), which is also weakly correlated to non-point-source phosphorus inputs (Fig. A2.1b). Based on these relationships, achieving a HAB severity index below 3 translates to getting BTP inputs from the Maumee River below about 235 metric tonnes annually, which is about 6,230 metric tonnes of non-point-source phosphorus inputs (Fig. A2.1). Regarding the target of 40% of 2008 TP inputs, non-point-source phosphorus inputs were 8,055 metric tonnes in 2008 (Maccoux et al. 2016), which corresponds to a target of 4,833 metric tonnes. Together, these two values provide a target range for non-point-source phosphorus inputs of between 4,833–6,230 metric tonnes. Achieving inputs within this range should reduce HAB severity.

To mitigate severe seasonal (summer through early fall) bottom hypoxia, a recommended target is 6,000 metric tonnes of TP loading across the western and central basins (Scavia et al. 2016). Given that reducing non-point-source phosphorus inputs is the primary method to hit this target, and that point-source phosphorus inputs have averaged about $1,300 \pm 160$ metric tonnes annually during 2010–2019, the 6,000 metric tonnes target translates to reducing non-point-source phosphorus inputs to between 4,500–4,800 metric tonnes. Note, however, that this range estimate is derived from lakewide loading values that include the eastern basin and is being compared to a target that excludes the eastern basin. This discrepancy is not too problematic because the majority of the lakewide loading comes from the western basin followed by the central basin.

Lastly, the objective to achieve mesotrophy in Lake Erie's western and central basins, and oligotrophy in the eastern basin, is not to our knowledge based on reaching any specific phosphorus input target. Therefore, we derived the non-point-source input targets for this objective from our own assessment of, and past research on, the trophic state of the lake. The last time the more productive basins of Lake Erie likely consistently experienced mesotrophic conditions was prior to cultural eutrophication that began around the mid-1930s (see Fig. 2 and (Sgro and Reavie 2018)). Thus, non-point-source phosphorus inputs would have to be reduced to their pre-1935 levels, which corresponds to a target of about $2,500 \pm 280$ metric tonnes based on average non-point-source phosphorus inputs during 1915–1934 (derived from our historical non-point-source input metric from Fig. A1.1).

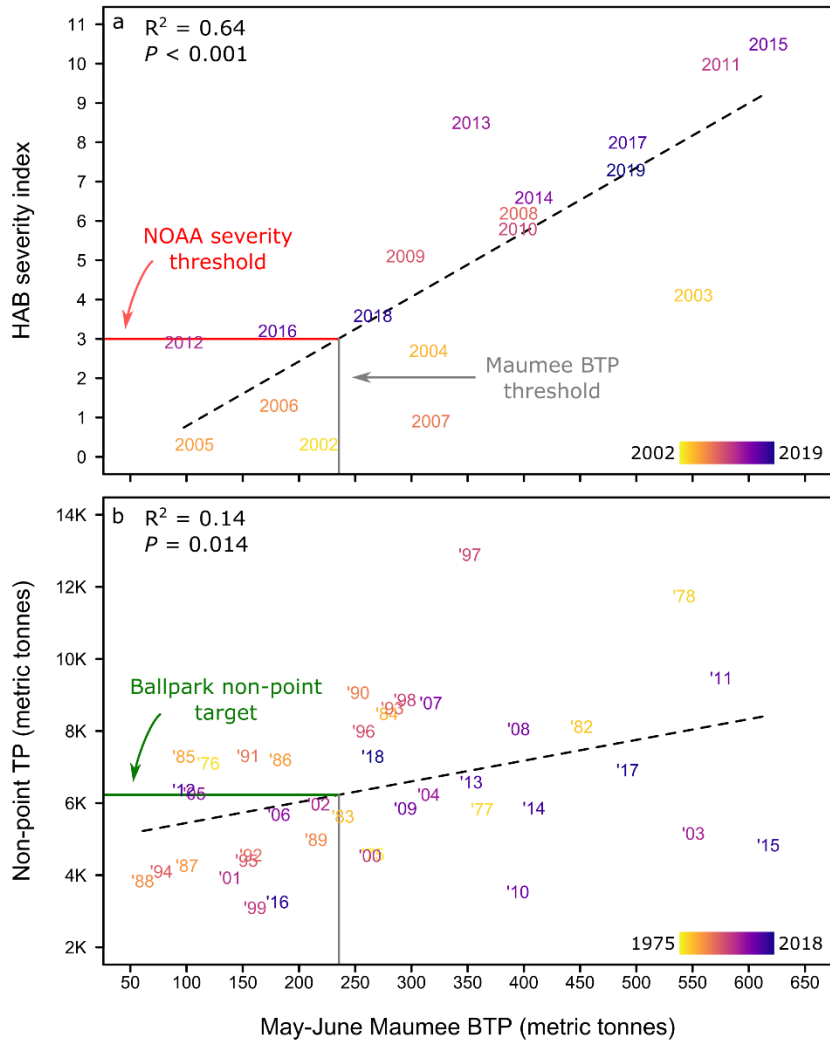


Fig. A2.1. Relationships between the amount of bioavailable total phosphorus (BTP; metric tonnes) from the Maume River (Ohio, USA) and (a) annual harmful algal bloom (HAB) severity (2002–2019), and (b) annual lake-wide non-point total phosphorus (TP) inputs (metric tonnes; 1975–2018) in Lake Erie. HAB severity data were obtained from the National Oceanic and Atmospheric Administration through <http://www.blueaccounting.org>. The red line in (a) indicates a HAB severity threshold of 3, which corresponds to ~235 metric tonnes of BTP (grey line). Based on its relationship to non-point-source inputs, (b) ~235 metric tonnes of BTP (grey line) corresponds to 6,230 metric tonnes of non-point-source phosphorus inputs (green line).

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APPENDIX 3

Bootstrapping of the productivity index and fish harvest

Both the productivity index and our harvest data have some additional complexity. The index broadly tracks known changes in the productivity of Lake Erie, but there is some potential variability in the exact values because the width of its standard deviation changes through time owing to interannual variability across its composite metrics. For example, its standard deviation is wider during the 1940s (Fig. A3.1) because sediment TP and TOC records indicate that productivity was generally low during this period, whereas the diatom community and chlorophyll *a* metrics suggest that productivity was higher. Similarly, harvest broadly tracks the historical highs and lows of each population, but the inter-annual relationship is much weaker. For example, using estimated population sizes for each species that are available for recent decades, we find a great deal of potential variability in their relationships to harvest (Fig. A3.2). While these issues are more concerned with shorter-term accuracy in individual year values rather than our focus on broad decadal historical changes, it would still help to confirm that our results are unchanged when this variability is considered.

To do so, we generated 1,000 new productivity indices and 1,000 estimates of the annual population size of each species (based on their relationship to harvest) and then related the estimated population sizes to the productivity indices to determine if the overall relationships remained unchanged. The new annual index values were randomly selected from a Gaussian distribution with a mean and standard deviation respectively equal to the productivity index value and its standard deviation in each year. We repeated this process 1,000 times to generate 1,000 indices. The relationship between population size and harvest was modeled using a Generalized Additive Model (GAM) with a smoothed term for harvest and a basis dimension (*k*) of five to ensure that relationships were not too wiggly. We then randomly selected the annual values for the population size of each species from a Gaussian distribution with a mean equal to the population size from the models predicted using the harvest value for each year and a standard deviation based on the standard error of the prediction. We repeated this process 1,000 times for each species. We then used linear models to relate the 1,000 population size estimates for each species to the 1,000 productivity indices. These models also included a quadratic term for the productivity index to allow for non-linear relationships.

The bootstrapped results generally exhibited the same relationships reported in our main results (i.e., in Fig. 3): (1) lake whitefish harvest tended to be negatively related to ecosystem productivity (Fig. A3.3a); (2) walleye harvest tended to be unimodally related to ecosystem productivity (Fig. A3.3b); and (3) yellow perch harvest tended to be positively related to ecosystem productivity (Fig. A3.3c). There is a high degree of uncertainty in the tails of all of these relationships because the models are limited to the last 30–50 years of data, whereas the harvest data used for the predictions comes from the last century. The historical harvest values therefore often fall outside the bounds of the modeled relationships. For example, lake whitefish harvests were close to zero during the 1970s when eutrophication was at its most severe, but

such low harvests have not occurred since population monitoring began in the 1990s. Consequently, when using the low harvests from the 1970s to predict population size, the resulting estimates are highly variable because the harvest values lay far outside the range of the modeled relationships.

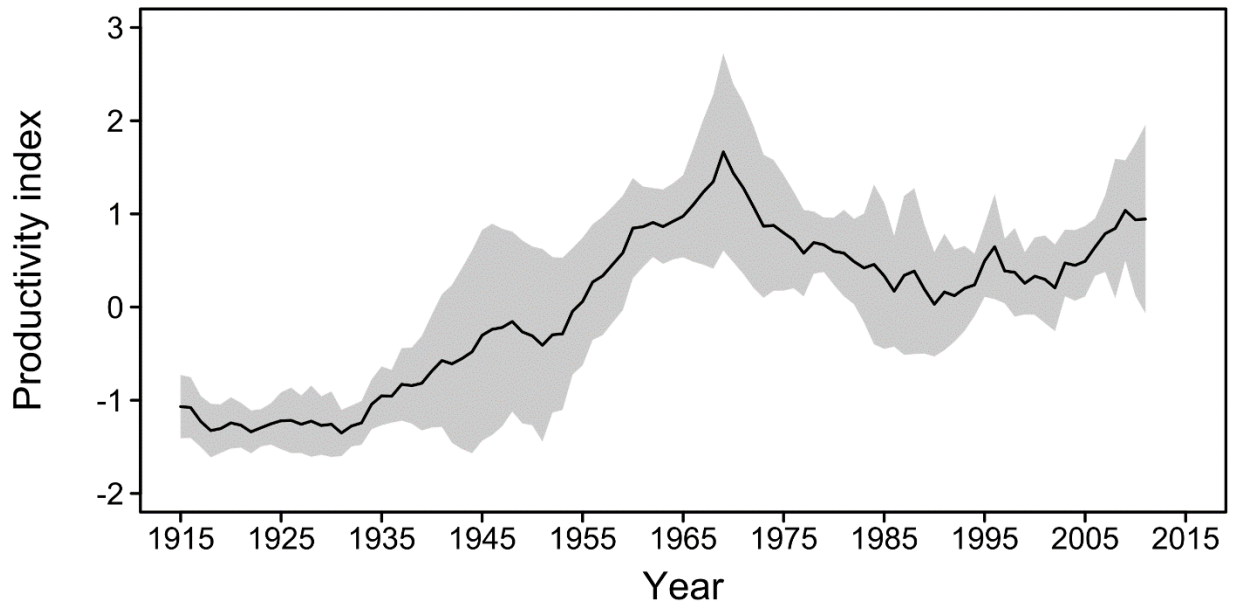


Fig. A3.1. Mean (black line) and standard deviation (grey shading) of the productivity index during 1915–2011.

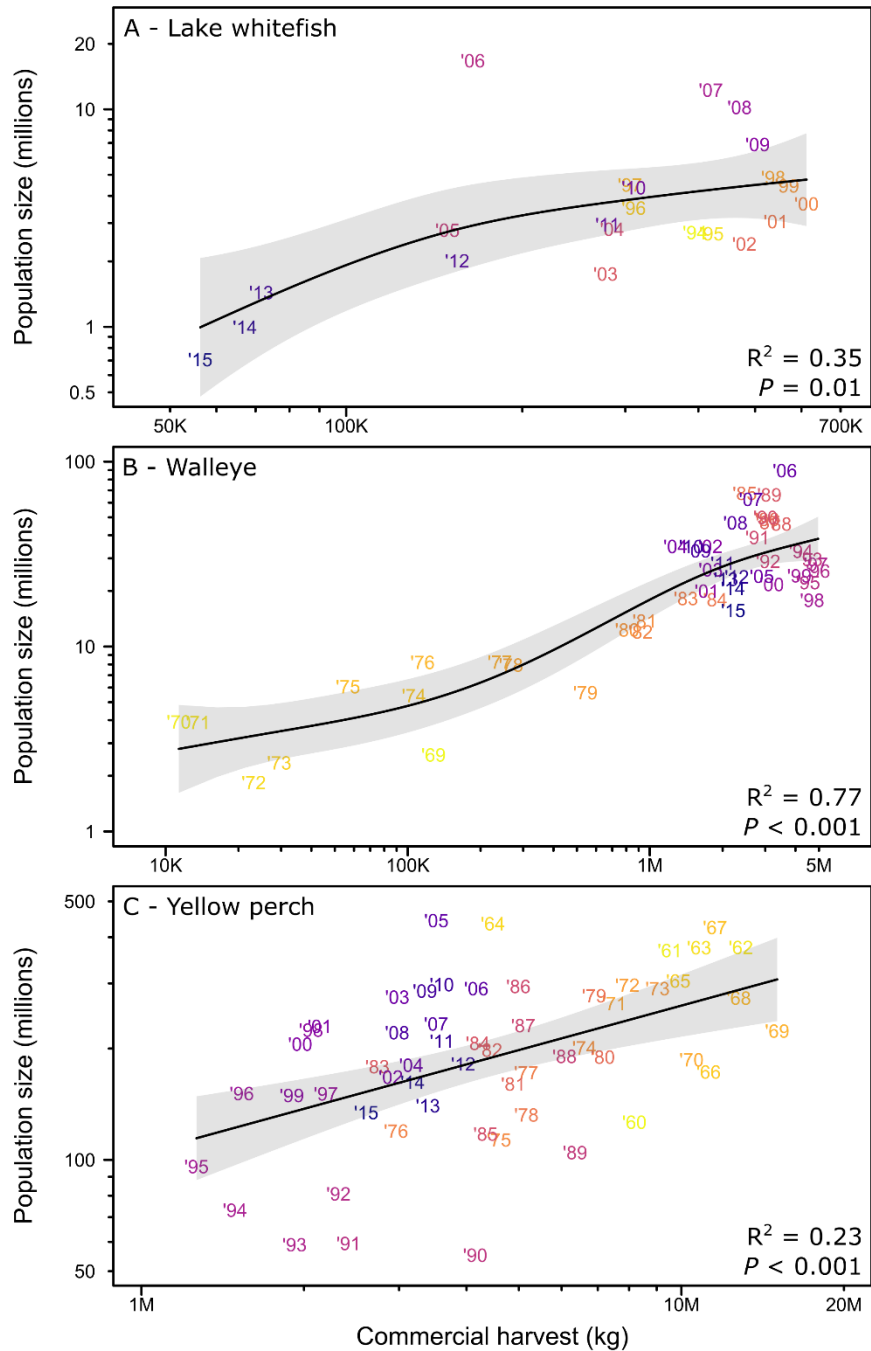


Fig. A3.2. Association between commercial harvest (kg) and the estimated size of the adult populations of (a) lake whitefish (age-3+ during 1994–2015), (b) walleye (age-3+ during 1969–2015), and (c) yellow perch (age-2+ during 1960–2015) in Lake Erie. Population sizes were estimated by the Lake Erie Management Unit of the Ontario Ministry of Natural Resources and Forestry (lake whitefish) and by the Ohio Department of Natural Resources-Division of Wildlife (walleye and yellow perch). These estimates were derived from statistical catch-at-age models

that include both fisheries-dependent commercial and sport harvest data, and fisheries-independent gill net assessment surveys.

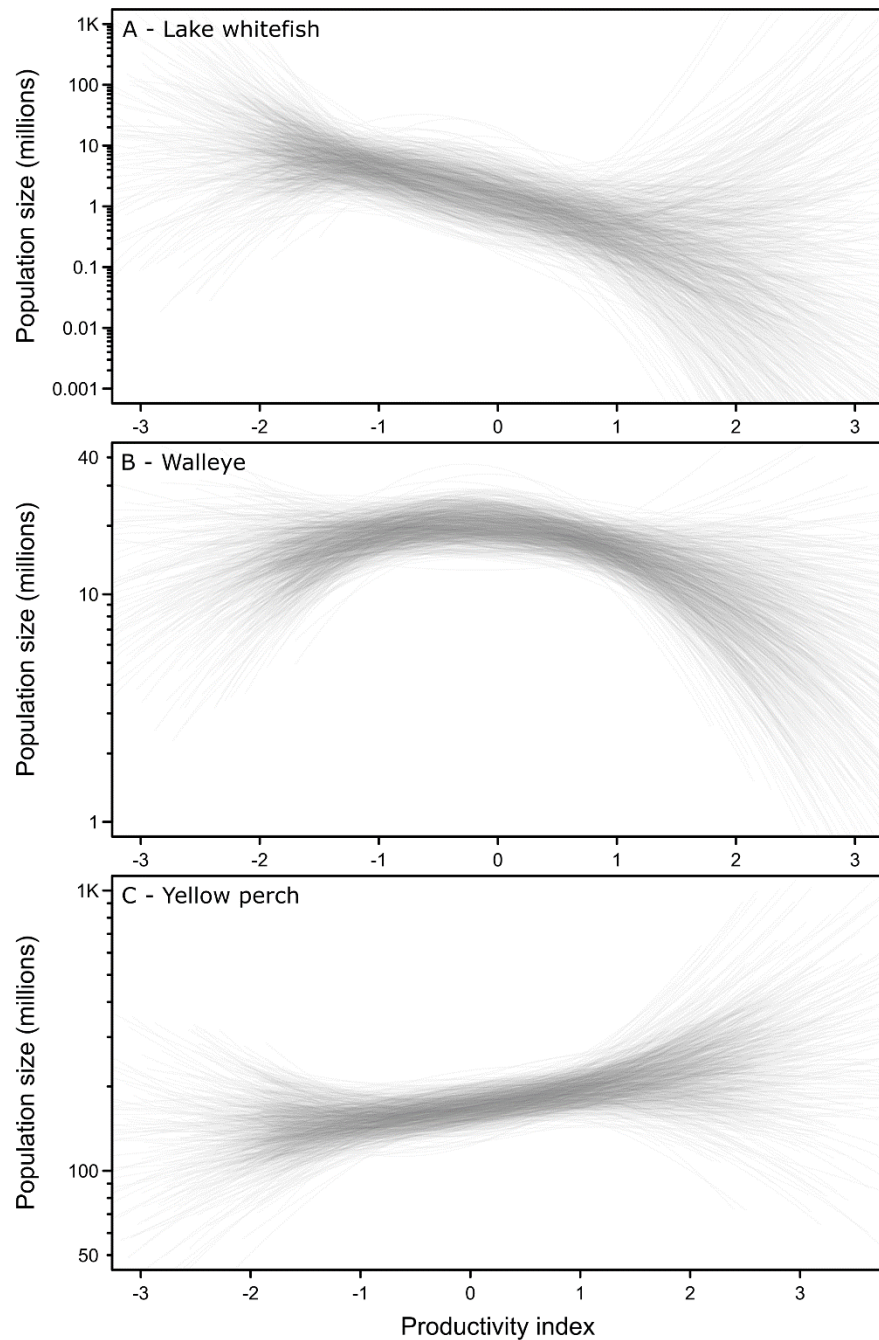


Fig. A3.3. Relationships between 1,000 sets of annual predicted values of the population size of (a) lake whitefish, (b) walleye, and (c) yellow perch (based on GAM models in Fig. A3.2) and 1,000 different productivity indices during 1915-2011. Lake whitefish are generally negatively correlated to productivity, whereas walleye generally exhibit a unimodal relationship and yellow perch tend to be positively related.