

# **Interactive Effects of Nutrient Inputs and Climate Change on the Lake Erie Fish Community**

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## **Abstract**

Continued climate change holds great potential to alter Lake Erie's fish communities through its effects on in-lake physicochemical (habitat) conditions. To date, however, a general appreciation for how Lake Erie's fisheries are expected to respond to continued climate change is lacking, particularly with respect to processes that influence the delivery of subsidies (i.e., nutrients, sediments) from the watershed. Herein, we discuss four primary ways by which climate change might interact with the delivery of nutrients and sediments from the watershed to influence the fish community of Lake Erie. Specifically, we expect climate-driven water warming and increased precipitation during winter and spring to promote development of bottom hypoxic ("dead") zones, reduce water clarity, exacerbate harmful algal blooms, and alter invertebrate prey assemblages at the base of the food web. Each of these changes is expected to have a negative effect on Lake Erie fishes that are intolerant of eutrophic conditions (e.g., low water clarity and dissolved oxygen levels) when considered independently. However, these mechanisms have not been fully explored in the Lake Erie ecosystem, and understanding of their potential interactive effects with each and additional anthropogenic stressors (e.g., invasive dreissenid mussels) is lacking. Hence, more research is clearly needed to fully appreciate the potential for climate change to alter the dynamics of the fish communities of Lake Erie.

## General Introduction

Aquatic ecosystems are open and continuously subsidized by the delivery of atmospheric and terrestrial material. The magnitude of the effect of this delivery of materials on the recipient ecosystem can vary considerably through both space and time (Polis and Strong 1996, Polis et al. 1997, Flecker et al. 2010). In general, the more limiting a resource is to the recipient ecosystem, the greater its impact will be (Flecker et al. 2010). For this reason, allochthonous inputs of nitrogen and phosphorus (P)—typically limiting elements in marine and freshwater ecosystems—from both point and non-point sources can stimulate algal production at the base of these food webs (Schindler 1977, Howarth 1989, Elser et al. 1990, Vitousek and Howarth 1991, Smith 2003, Elser et al. 2007). Through stimulation of lower food web production, loading of limiting nutrients can drive the structure, function, and dynamics of coastal marine and freshwater ecosystems and modify the services that they provide through both direct and indirect pathways (Vitousek et al. 1997, Dauer et al. 2000, Cloern 2001, Ludsins et al. 2001, Dagg and Breed 2003, Kemp et al. 2005, Schmidt et al. 2012).

Because limiting nutrients are, by definition, low in availability, factors that influence the rate and magnitude of their delivery can potentially have an enormous effect on ecosystem processes. The strong influence of nutrient loading on aquatic ecosystem functioning has been demonstrated through both controlled and natural experiments (Schindler 1977, Nilsson et al. 1991, Worm et al. 2000, Cloern 2001, Gulati and van Donk 2002, Jeppesen et al. 2005a, Jeppesen et al. 2005c, Jeppesen et al. 2007). Moreover, studies have demonstrated that both the timing and frequency of resource delivery can influence the responsiveness of recipient ecosystems, with even short-lived (pulsed) events of low frequency demonstrating disproportionately large effects on population demographics and community structure and function (Nowlin et al. 2008, Yang et al. 2008, Yang and Naeem 2008, Flecker et al. 2010, Yang et al. 2010).

Numerous “natural” (i.e., non-human) factors can influence the magnitude, timing, and frequency of the delivery of limiting nutrients from a watershed to downstream receiving water bodies, including precipitation, temperature (e.g., via effects on snowmelt and evaporation), soil attributes, and above-ground surface properties (e.g., floral coverage) (Beckers et al. 2009). Similarly, the responsiveness of both abiotic (e.g., water clarity, dissolved oxygen levels) and biotic (e.g., producer and consumer production, food web interactions) components of the recipient aquatic system can be mediated by external and internal factors. For example, the system may respond differentially based on the quality of limiting nutrients delivered (e.g., dissolved reactive P can have a more immediate impact on downstream algal growth than particulate forms of P; Sonzogni et al. 1982, Correll 1998). Abiotic and biotic characteristics of the recipient ecosystem (e.g., depth, volume, and residence time that affect dilution of nutrients; bioavailability of the limiting nutrient to primary producers; water temperature that influences algal uptake rates; consumer abundance that determines rates of herbivory) may affect the sensitivity of the system as well.

Humans can greatly affect nutrient delivery and its impacts on downstream aquatic ecosystems through a number of pathways, including 1) land-use change in the watershed (e.g., agricultural, residential, and urban development; Allan et al. 1997, Carpenter et al. 1998a, Basnyat et al. 1999, Howarth et al. 2002), 2) the introduction of non-native species both in the watershed (e.g., wetland plant species; Gu 2006, Cuassolo et al. 2012) and receiving water body (e.g., zebra and

quagga mussels, *Dreissena polymorpha* and *D. bugensis*, respectively; Arnott and Vanni 1996, Hecky et al. 2004, Conroy et al. 2005), and 3) exploitation of consumer populations (e.g., planktivorous or piscivorous fishes; Meijer et al. 1999, Jeppesen et al. 2005b). In addition, climate change now could greatly affect the dynamics of aquatic ecosystems and their valued ecosystem services through a) precipitation- and temperature-driven mediation of the magnitude, timing, and frequency of delivery of limiting nutrients from the watershed (Bouraoui et al. 2004, Jeppesen et al. 2009, Ficklin et al. 2010, Riverson et al. 2013) and b) alteration of in-lake biological production (Maar and Hansen 2011, Winder et al. 2012), physicochemical properties (Gaiser et al. 2009, Sahoo et al. 2011, Carvalho et al. 2012), and food web interactions (Winder and Schindler 2004, Wagner and Benndorf 2007, Manca and DeMott 2009).

While much research has explored the impacts of climate change on aquatic ecosystems, both freshwater and marine (McGowan et al. 1998, Meyer et al. 1999, Edwards and Richardson 2004, Harley et al. 2006, Reist et al. 2006, Ficke et al. 2007, Sharma et al. 2007, Hobday and Lough 2011), its expected impact(s) on the fisheries of large freshwater ecosystems such as the Great Lakes of North America remains largely under-studied (but see: Magnuson et al. 1990, Shuter and Post 1990, Magnuson et al. 1997, King et al. 1999, Casselman 2002). This gap in knowledge is especially evident with respect to how climate change might indirectly influence Great Lakes fish populations and fisheries production through nutrient pathways. Towards filling this gap, we discuss several mechanisms by which climate change (including both warming and altered precipitation patterns) can modify nutrient loading patterns and in-lake factors to influence Great Lakes fishes, focusing on the Lake Erie ecosystem. As we describe more fully below, a focus on Lake Erie is well justified, given that it has a long history of responding rapidly to variation in nutrient inputs from the watershed; it supports a diversity of ecologically, recreationally, and economically important fish and fisheries that have different physical (e.g., temperature), chemical (e.g., dissolved oxygen), and biological (e.g., prey) requirements, and it has been experiencing warming trends and altered precipitation patterns that are typical of changes observed in other north-temperate ecosystems (including other North American Great Lakes basins).

At the outset we provide some pertinent background information on Lake Erie. First, we briefly describe historical patterns of nutrient loading and availability in Lake Erie and how the lower food web (phytoplankton, zooplankton) has responded. Second, we describe the Lake Erie fish community, including some of the major changes that occurred historically and their drivers. Third, we describe evidence of past and potential future climatic changes in the basin of the lake. Finally, we explore four mechanisms by which climate change and nutrient loading may interactively influence the fish community of Lake Erie through: 1) hypoxia; 2) changes in water clarity; 3) formation of harmful algal blooms; and 4) changes in invertebrate prey assemblages at the base of the food web.

### ***History of Nutrient Loading and Eutrophication in Lake Erie***

#### ***The Eutrophication Problem***

Of the numerous anthropogenic impairments experienced by freshwater ecosystems during this century, none has been more ubiquitous than cultural eutrophication (Carpenter et al. 1998b, Cloern 2001). In its worst form, excessive P inputs stimulate primary production in the water

column, especially of cyanobacteria that may be inedible for some consumers and potentially noxious for others (Schindler 1977, Correll 1998, Gulati and van Donk 2002, Smith 2003). In turn, excessive production of algae during late summer can reduce water clarity and increase bottom anoxia through enhanced bacterial respiration in bottom sediments (Carpenter et al. 1998a, Correll 1998, Ficke et al. 2007). Ultimately, degraded water quality can lead to alteration of other trophic levels, wherein species intolerant of eutrophic conditions are replaced by tolerant ones. Such shifts have been documented for zooplankton (Patalas 1972), benthic macroinvertebrates (Carr and Hiltunen 1965, Verdonschot 1996, Harman 1997) and fish communities (Colby et al. 1972, Leach and Nepszy 1976, Hartmann and Numann 1977, Leach et al. 1977, Oglesby 1977). These changes in fish community composition and water quality can cause economic damage by reducing commercial and recreational fishing opportunities (Carpenter et al. 1998a, Breitbart et al. 2001, Breitbart et al. 2009) and potentially lowering lake-side property values (Gibbs et al. 2002, Poor et al. 2007).

#### *Lake Erie's Eutrophication (Pre-1970s).*

Since the beginning of European settlement and especially during the last century, Lake Erie has experienced a broad suite of anthropogenic stressors, including overexploitation, habitat alteration, invasive species, heavy metal and organic contaminants, and land-use modification (Hartman 1972, Smith 1972, Regier and Hartman 1973, Makarewicz and Bertram 1991, Ludsin et al. 2001). No single perturbation, however, has influenced more components of the Lake Erie ecosystem than excessive P loading and resulting eutrophication (Laws 1981, Ludsin et al. 2001). Even today, Lake Erie lives in infamy, often cited as a (if not the) classic example of eutrophication. By enhancing phytoplankton and zooplankton production, excessive P inputs (> 20,000 tonnes annually) degraded water quality, reducing both water column transparency and hypolimnetic oxygen levels (Rosa and Burns 1987, Makarewicz and Bertram 1991, Bertram 1993, Ludsin et al. 2001) (Figure 1). Bottom anoxia, in turn, eliminated thermal habitat vital to cold-water organisms in the central basin of Lake Erie and contributed to the demise of important benthic macroinvertebrate prey species (e.g., the burrowing mayfly, *Hexagenia limbata*, a historically important prey item for fishes; Britt 1955, Krieger et al. 1996, Edsel et al. 1999, Schloesser and Nalepa 2001, Bridgeman et al. 2006).

#### *Lake Erie's Oligotrophication (Early 1970s to Early 1990s)*

In an effort to rehabilitate the Lake Erie ecosystem, P abatement programs were initiated in 1972 as part of the Great Lakes Water Quality Agreement (Dolan 1993). The Lake Erie ecosystem quickly responded to these efforts, with reduced P inputs driving reductions in water-column total P concentrations (Ludsin et al. 2001) and phytoplankton biomass (especially cyanobacteria; Makarewicz et al. 1989, Makarewicz and Bertram 1991, Makarewicz 1993b), as well as improved water quality and reduced bottom hypoxia lakewide (Makarewicz and Bertram 1991, Bertram 1993, Charlton et al. 1993, Ludsin et al. 2001) (Figure 1). However, due to physical differences, these water quality improvements varied between lake basins. For example, dramatic declines in total P concentrations in the shallow west basin caused its trophic status to shift from eutrophy to mesotrophy, whereas a less dramatic reduction in total P in the central basin caused it to become more oligotrophic (Makarewicz and Bertram 1991, Ludsin et al. 2001). Further, while the highly productive west basin experienced improved water clarity (Ludsin et al. 2001) following a two-thirds reduction in phytoplankton biomass (Makarewicz and Bertram 1991),

water clarity in the less productive central basin did not change markedly (Ludsin et al. 2001), even though phytoplankton biomass declined by more than one-third (Makarewicz et al. 1989, Makarewicz and Bertram 1991). Nonetheless, reduced bottom hypoxia allowed once-important benthic macroinvertebrates to recover in the lake (Krieger and Ross 1993, Krieger et al. 1996, Edsel et al. 1999, Bridgeman et al. 2006), most notably the burrowing mayfly. Although P abatement was primarily responsible for improvements in water clarity (Ludsin et al. 2001) and reductions in lake primary and secondary productivity through the mid-1980s (Makarewicz et al. 1989, Makarewicz and Bertram 1991, Makarewicz 1993a, Makarewicz 1993b), invasion of zebra and quagga mussels during the late 1980s likely magnified these changes (MacIsaac et al. 1992, Nicholls and Hopkins 1993, Holland et al. 1995) and may have contributed to the recovery of some benthic macroinvertebrate taxa (Botts et al. 1996, Ricciardi et al. 1997, Pillsbury et al. 2002).

#### *Lake Erie's Re-eutrophication (Early 1990s to Present)*

Following a return to more historical lake productivity levels by the early 1990s, the Lake Erie ecosystem now appears to be moving back towards a more eutrophic state (Murphy et al. 2003, EPA 2010) (Figure 1). Indicators of this trend include dramatic increases in cyanobacteria populations (e.g., *Microcystis* spp., *Lyngbia wollei*) (Budd et al. 2002, Vincent et al. 2004, Rinta-Kanto et al. 2005, Ouellette et al. 2006, Rinta-Kanto and Wilhelm 2006, Millie et al. 2009), the return of frequent and extensive bottom hypoxia in the west and central basins (Burns et al. 2005, Hawley et al. 2006, Rucinski et al. 2010), and the resurgence of benthic algae such as *Cladophora* (Higgins et al. 2008, Stewart and Lowe 2008, Depew et al. 2011), which was highly abundant during the previous height of eutrophication. While the exact mechanisms underlying these changes remain debatable, evidence is accruing that increased inputs of dissolved reactive P from tributaries due to high precipitation during spring and changes in agricultural practices (e.g., type of fertilizer being applied, tillage practices) are contributing to Lake Erie's re-eutrophication (EPA 2010, Richards et al. 2010).

#### *Lake Erie Fish Community*

The Lake Erie ecosystem supports a species-rich and diverse fish assemblage, with more than 130 species being documented. In addition to many of these species playing important ecological roles, several species also support large recreational and commercial fisheries. For example, walleye (*Sander vitreus*) supports the lake's most valued recreational fishery and yellow perch (*Perca flavescens*), walleye and several other species support large commercial fisheries. Owing to the economic, ecological, and cultural import of fishes in the Lake Erie basin, fisheries management agencies have been working closely with the Great Lakes Fishery Commission to both protect—and when appropriate—rehabilitate native fish populations in the basin (Ryan et al. 2003).

Lake Erie consists of three geomorphologically distinct lake basins (western, central, eastern) that vary in terms of a) water volume and depth (both increase from west to east), b) temperature and lower food web biomass and production (both decrease west to east), and c) fish community structure (Leach and Nepszy 1976, Sly 1976, Ludsin et al. 2001, Ryan et al. 2003). In general, the shallow, warm, and productive western basin is dominated by species that are tolerant of high turbidity (i.e., low light levels) and warm temperatures, including temperate basses (*Morone*

spp.), ictalurids, centrarchids, and cyprinids, with cool-water species such as yellow perch and walleye also being high in abundance during most of the year. By contrast, the eastern basin, which is the deepest, coldest and least biologically productive basin, is typified by a deepwater fish community (e.g., salmonines, coregonines, and smelt) that prefers cold temperatures, high dissolved oxygen levels, and non-turbid waters. The central basin, which falls intermediate in terms of temperature, productivity, and depth, correspondingly is dominated by cool-water species such as yellow perch and walleye, with both warm-water and cold-water species also present to a lesser degree.

### *Drivers of Fish Community Change*

The Lake Erie fish community has been highly dynamic during the past century. While natural variation in recruitment that is associated with fluctuating weather patterns, population cycles, and biological interactions (e.g., predation, competition) underlies some of the shifts in fish community structure, function, and dynamics, human influences appear to have played a large role during the past half century (Regier and Hartman 1973, Leach and Nepszy 1976, Ludsin et al. 2001, Ryan et al. 2003). During the first half of the 20<sup>th</sup> century, several native, long-lived fish species were extirpated or driven to commercial extinction through overexploitation (e.g., blue pike *S. vitreus glaucus*, lake trout *Salvelinius namaycush*, lake sturgeon *Acipenser fulvescens*, lake herring *Coregonus artedii*), which was probably magnified by other stressors, such as invasive species (e.g., sea lamprey *Petromyzon marinus*, rainbow smelt *Osmerus mordax*, and alewife *Alosa pseudoharengus*), destruction of spawning and nursery habitat, heavy metal contamination, and nutrient pollution. Owing to a strong international (Canada-United States), inter-agency (state, provincial, and federal governments) partnership that led to the formation of the Great Lakes Fishery Commission, overexploitation has been less of an issue in recent decades. Instead, more recently humans have seemingly driven fish community change through other means, most notably the introduction of new invasive species (e.g., zebra and quagga mussels, round gobies *Apollonia melanostomus*) and the alteration of nutrient inputs (reviewed below).

### *Climate Change in the Lake Erie Basin*

Similar to other aquatic ecosystems throughout temperate regions of the world, historical data show that climate has been changing in the Great Lakes Basin. During 1895-1999, atmospheric temperatures within the basin increased 0.7°C, almost double the national rate (Mortsch et al. 2000). Furthermore, in Lake Superior, water temperatures actually have increased 2-fold faster than air temperatures (Austin and Colman 2007). Likewise, the frequency of both short (1 to 7 d) and long (> 7 d) precipitation events has increased during the past century in the Great Lakes region (Kunkel et al. 1999). Similar trends have been found in the Lake Erie basin (Jones et al. 2006). For example, the cumulative annual days with atmospheric temperatures below 0°C decreased linearly by 0.54 d/year during 1956-2007 and the mean minimum air temperature increased linearly by 0.23°C/year during 1977-2007 (T. Farmer and S. Ludsin, unpub. data). The frequency of rain events also has nearly doubled (from 2.8 to 5.3 d/year) since the early 1900s in this region, as has the number of prolonged wet periods (Mortsch et al. 2000). Numerous climate models predict that these temperature and precipitation trends will continue during this century (Kling et al. 2003, Hayhoe et al. 2010).

These changes in temperature and precipitation, possibly enhanced by land-use change, likely underlie observed increases in river discharge in the Great Lakes Basin (DeMarchi et al. 2009). For example, river inflows into Lake Erie increased by 22.3% (range = 2-55%) during 1999-2006 (DeMarchi et al. 2011). Because 60-75% of P inputs are delivered during precipitation-driven river discharge events (Richards et al. 2001, Baker and Richards 2002, Dolan and McGunagle 2005), increased storms due to climate change will likely further increase P inputs to the lake. This hypothesis is supported by a preliminary study of the impact of climate change on Maumee River sediment loads, which indicates a 10-30% increase, depending on the Global Circulation Model and greenhouse gas emission scenario employed (DeMarchi et al. 2011).

### *Interactive Impacts of Nutrient Alteration and Climate Change on Lake Erie Fishes*

While temporal trends of nutrient loading and Lake Erie fish communities have been co-described (see above), and some mechanistic impacts of eutrophication on Lake Erie fishes have been documented (reviewed below), many population-level consequences of eutrophication in Lake Erie are under-described or unknown. Moreover, it is largely an open question as to how fish assemblages of Lake Erie (and in particular, economically important exploited fish stocks) will respond in the future as continued nutrient loading may interact with a changing climate to alter eutrophication dynamics. Below, we explore four mechanisms by which climate change and nutrient loading may interactively influence the Lake Erie fish community through changes in: 1) hypoxia; 2) water clarity; 3) harmful algal blooms; and 4) the invertebrate food web.

#### *I: Hypoxia*

Bottom hypoxia (oxygen concentrations < 4 mg/l) is a global phenomenon (e.g., Diaz and Rosenberg 2008) that recurs in a diversity of freshwater, brackish, and marine ecosystems. In brief, within a thermally or chemically stratified water body, low photosynthetic activity in the bottom layer, coupled with low, density-impeded oxygen replenishment from the oxygenated top layer, can lead to bottom hypoxia. While bottom hypoxia is a natural occurrence in many systems, the rate of oxygen depletion in bottom layers can be exacerbated by anthropogenic nutrient loading. If excessive, nutrient inputs can lead to elevated phytoplankton production and biomass, which eventually settles in the bottom layer where its decomposition by bacteria can lead to severe hypoxia. In dimictic systems, this phenomenon is generally seasonal, with hypoxia developing after an extended period of stratification and ceasing with water-column turnover.

In Lake Erie, seasonal hypoxia is a natural event, with evidence to suggest that it has occurred in bottom waters of the central basin for hundreds, if not thousands, of years (Delorme 1982). In fact, the recurrence of seasonal hypoxic events in the central basin subsequent to significant nutrient reductions suggests that these low-oxygen events are not due solely to human-induced eutrophication (Charlton et al. 1993). A major reason for hypoxia formation in central Lake Erie relates to its bathymetry (Charlton 1980, Rosa and Burns 1987). Because central Lake Erie is deep enough to stratify (average depth = 18.3 m), but shallow enough that the thermocline can set up relatively close to the lake bottom (typically < 6 m from the bottom; Rosa and Burns 1987), the volume of hypolimnetic water that is cut off from surface replenishment is small. In turn, dissolved oxygen can be depleted before fall turnover, thus leading to bottom hypoxia. By contrast, hypolimnetic volume of the deeper east basin (average depth = 24.4 m) is relatively

large and does not become hypoxic before fall re-mixing (turnover), whereas the shallow (average depth = 7.3 m) west basin typically does not become hypoxic, owing to wind-driven circulation and storm events that keep the west basin well mixed during summer (Bridgeman et al. 2006).

While hypoxia is a natural phenomenon in central Lake Erie, research has indicated that the rate of oxygen depletion, as well as the extent of hypoxia, can be modified by human activities (Rosa and Burns 1987, Bertram 1993). Specifically, owing to excessive P inputs from both point- and non-point sources that stimulated pelagic and benthic algal production, oxygen depletion rates during summer increased during the mid-1900s, thus leading to a hypoxic area as large as 11,000 km<sup>2</sup> (Beeton 1963). While hypoxic conditions in the central basin of Lake Erie were first detected in the late 1950s (Charlton 1987), anthropogenic nutrient loading likely contributed to hypoxia much earlier. In addition, during the height of cultural eutrophication, even the shallow western basin of Lake Erie could become hypoxic during windless periods in summer (Hartman 1972). In fact, by 1963, even a 5-d period of hot, calm weather could cause 50% of the west basin to become hypoxic (Hartman 1972).

In an effort to mitigate bottom hypoxia, as well as other water quality impairments (e.g., reduced water clarity), P abatement programs were initiated as part of the Great Lakes Water Quality Agreement of 1972 (Dolan 1993). These programs are thought to have led to an observed decline in bottom anoxia and hypoxia in both western and central Lake Erie through the early 1990s (Makarewicz and Bertram 1991, Bertram 1993, Charlton et al. 1993). Since the late 1990s, however, the extent of bottom hypoxia has increased to levels on par with those during the height of cultural eutrophication (Hawley et al. 2006; U.S. EPA and Environment Canada, unpub. data). The exact causal mechanisms for this increase are not fully understood, although the recent increase in hypoxia does coincide with altered precipitation patterns, increased nutrient inputs from non-point sources (R. Peter Richards, Heidelberg College, unpub. data), and warmer water temperatures.

While predictive models of how climate change will influence hypoxia formation in the Lake Erie ecosystem have yet to be developed, predictions made for other temperate freshwater ecosystems indicate that we should expect continued climate change to exacerbate the magnitude, duration and frequency of hypoxia (Kling et al. 2003, Ficke et al. 2007, Fang and Stefan 2009, Jiang et al. 2012). Most directly, warmer future conditions should facilitate a longer stratified period during summer, with thermal stratification developing earlier in the year and turnover occurring later in the year. Thereby, bottom oxygen depletion will initiate earlier and hypoxic conditions are likely to be present over an extended time period (Fang and Stefan 2009). Expected reductions in water levels could further exacerbate bottom hypoxia. For example, lower water levels may interact with warmer temperatures and allow the thermocline to develop closer to the bottom (i.e., result in a thinner hypolimnion). Since a large proportion of hypolimnetic oxygen demand comes from the sediment (Rucinski et al. 2010), oxygen would be more rapidly depleted from a thinner hypolimnion. While uncertainty surrounding future regional precipitation patterns is greater than future regional temperatures, it is plausible that future precipitation patterns will be characterized by less frequent, but more intense, precipitation events (Kling et al. 2003, Kunkel et al. 1999). Such intense events could lead to high nutrient runoff from agricultural and urban lands, and in the absence of dramatic changes in land use, could lead to increased overall nutrient loads to Lake Erie. Depending on the timing of runoff,



future nutrient loading, coupled with warmer epilimnetic temperatures, could lead to greater overall phytoplankton production and ultimately exacerbate decomposition and oxygen depletion rates in the hypolimnion. Potential changes to future wind patterns have not received the same amount of attention as future temperature and precipitation patterns (e.g., Kling et al. 2003). However, by affecting limnetic stratification, wind events also have the potential to alter hypoxia patterns. Specifically, intense wind events could contribute to mass movement of water, including seiches and potential influx of hypoxic bottom waters into nearshore zones. Moreover, strong wind events could: a) facilitate vertical mixing and both delay stratification in the late spring and bring about earlier turnover in the fall (i.e., decrease the period of hypolimnetic oxygen depletion) and b) favor a deeper thermocline (i.e., lead to a shallower thermocline with rapid oxygen depletion). In short, while future wind patterns will likely impact hypoxia patterns, the magnitude (and even direction) of such effects is unclear.

### *Ecological Effects of Hypoxia*

Seasonal hypoxia may influence ecosystem structure and fishery production both directly and indirectly, at multiple temporal and spatial scales. There are direct physiological costs for aerobic organisms occupying hypoxic habitats. Further, organisms that can readily avoid hypoxic regions (through vertical or horizontal migrations) may be forced to occupy inferior thermal and optical habitats, immediately constraining growth. Such behavioral migrations may alter the spatiotemporal overlap, efficiencies, and vulnerabilities of predators and prey, leading to long-term changes to food-web structure and energy flow.

The most direct effect of hypoxia is mortality due to sudden or prolonged exposure to low ambient oxygen concentrations (Burnett and Stickle 2001). In addition, hypoxic events can trigger various sub-lethal behavioral and physiological responses, which can cause dramatic indirect effects on aquatic food webs (e.g., Prepas et al. 1997; Rabalais and Turner 2001; Taylor et al. 2007, Ludsins et al. 2009). For instance, several researchers have documented that fish (e.g., Aku et al. 1997) and zooplankton (e.g., Field and Prepas 1997; Qureshi and Rabalais 2001) adjust their vertical and horizontal distributions in response to low oxygen events. Such behavioral responses can impact the spatial overlap (and thus encounter rates) of predators and prey, and may lead individual organisms to concentrate in confined areas (i.e., leading to compensatory density-dependent effects; Eby and Crowder 2002) and/or occupy inferior thermal and optical habitats. Physiological responses to low oxygen (e.g., shift to anaerobic respiration, reduced activity levels, and decreased disease resistance) also can indirectly impact trophic interactions by affecting foraging abilities and prey vulnerabilities (Burnett and Stickle 2001). Ultimately, the combined direct and indirect effects of hypoxic events may have far-reaching trophic consequences, impacting the vital rates (growth and mortality) of multiple populations (both benthic and pelagic).

While the entire suite of hypoxic impacts on the biota of Lake Erie is unknown, various lines of evidence are suggestive of responses at individual, population, and community levels of biological organization. a) Coincident shifts in invertebrate/fish community composition coincide with historical patterns of hypoxia. b) Laboratory trials and field observations demonstrate that many species found in Lake Erie are directly affected by low oxygen concentrations and will adjust vertical/horizontal distributions and diets in the presence of

hypolimnetic hypoxia. c) Mechanistic models are suggestive that habitat quality, growth rates and population biomasses may all respond to hypolimnetic hypoxia in central Lake Erie.

*Historical patterns:* Historical changes in fish assemblages of Lake Erie are consistent with responses to long-term shifts in frequency and magnitude of bottom hypoxia. However, given that trends in bottom hypoxia have mirrored trends of other manifestations of eutrophication (e.g., algal blooms, water clarity, shifts in invertebrate assemblages), it is difficult to unequivocally identify hypoxia as the most influential driver of changes in fish assemblages. Nonetheless, declines in sensitive and benthivorous fish species occurring coincident with severe eutrophication (i.e., pre 1970s) and subsequent recoveries during oligotrophication (Ludsin et al. 2001) are suggestive of the strong controlling effect of bottom oxygen levels.

Prior to implementation of the Great Lakes Water Quality Agreement, P loading and resulting hypoxia in Lake Erie likely contributed to declines of important commercial and sport fishes (e.g., lake whitefish, burbot *Lota lota*; Hartman 1972, Leach and Nepszy 1976, Laws 1981). In turn, with P abatement and decreased hypoxia, these and other fish species (including smallmouth bass *Micropterus dolomieu* and silver chub *Macrhybopsis storeriana*) recovered (Ludsin et al. 2001). In total, from 1969 to 1996 there was an apparent increase in fish community richness in the central basin of Lake Erie (Ludsin et al. 2001). In particular, species sensitive or moderately tolerant of eutrophic conditions became more common during this period, while tolerant species declined (Ludsin et al. 2001). These general patterns are consistent with historic fish community responses to P abatement observed in other areas of the Great Lakes, e.g., Saginaw Bay (Ivan, Fielder, Thomas, Höök unpublished).

Nonetheless, historical changes in the fish community of Lake Erie have revealed some peculiarities. 1) Fish community responses to oligotrophication in the shallow western basin and deeper central basin have been somewhat inconsistent. Specifically, while Ludsin et al. (2001) demonstrated reduced tolerant species richness and increased sensitive species richness in the western basin, in the central basin sensitive species richness increased but tolerant species richness showed no trend. The mechanisms underlying these differential responses are unclear but may relate to depth, stratification patterns and the persistence of hypoxia in the central basin. 2) More recently, re-eutrophication of Lake Erie may be contributing to a reverse community shift, as evidenced by resurgence of certain mesotrophic fish species.

*Empirical patterns:* Field and laboratory observations collectively reveal that hypolimnetic hypoxia affects vertical and horizontal distributions of zooplankton, benthic invertebrates and fish in Lake Erie. In turn, shifts in distributions affect overlap of predators and prey, leading to altered diet patterns. However, it is less clear if altered distributions cascade to substantially impact individual growth rates and population-level survival and production rates. Moreover, while avoidance is a common response to hypoxic conditions, rapid changes in oxygen concentrations (e.g., Mobile Bay jubilees; Loesch 1960) may trap fish in hypoxic waters and lead to direct mortality. There is recent evidence of such events in nearshore Lake Erie, whereby wind-driven mass movement of hypoxic waters into nearshore zones appears to have led to localized fish mortalities (J. Casselman personal communication). It is unclear if the frequency and extent of such direct hypoxia mortality are sufficient to have population-level impacts in Lake Erie. We suspect that direct mortality is limited and the indirect effects of hypoxia on Lake

Erie fishes are more influential. However, climate change driven modifications to stratification and wind patterns may exacerbate such phenomena in the future.

Laboratory studies demonstrate that many Lake Erie zoobiota respond to direct exposure to low oxygen conditions. Survival capacity under hypoxia varies among species and life stages. For example, relatively tolerant fish species like yellow perch are able to survive at lower oxygen concentrations as compared to more sensitive species, like rainbow smelt. Similarly, while some Lake Erie zooplankton species experience poor survival under hypoxia (e.g., *Daphnia mendotae*; Goto et al. 2012), other taxa are seemingly able to survive under prolonged hypoxic conditions. Such taxa-specific direct effects of low oxygen are not limited to mortality. Casselman (1978) reviewed the environmental requirements of northern pike, a cool-water fish, and reported that any decrease in oxygen saturation had a direct negative effect on growth. Roberts et al. (2011) demonstrated that both consumption and growth rates of yellow perch decline in low oxygen conditions. In contrast, growth rates (as indexed by RNA:DNA ratios) of tolerant Chironomidae show no response to extremely low oxygen concentrations (Höök and Roberts unpublished data).

While direct hypoxia exposure has the potential to affect survival, consumption and growth rates of many Lake Erie zoobiotic taxa, for mobile species such effects may never manifest as species simply adjust their location to avoid hypoxia. Vanderploeg et al. (2009a) used an optical plankton counter and hydroacoustics to evaluate vertical and horizontal distributions of collective zooplankton and fish biomass in central Lake Erie before, during and after development of hypolimnetic hypoxia. While a fraction of mesozooplankton utilized hypoxic areas, the majority of zooplankton and fish biomasses appeared to entirely avoid hypoxic waters (Vanderploeg et al. 2009a). While taxa-specific spatial distributions are generally consistent with these patterns, certain fish and zooplankton utilize hypoxic waters. Vanderploeg et al. (2009b) used diel, depth-specific collections of zooplankton to evaluate taxa-specific vertical distributions and documented a diversity of responses: 1) some epilimnetic species remained in the epilimnion regardless of hypoxia and were unaffected (e.g., *Leptodora*); 2) some species migrated from the epilimnion to hypolimnion under normoxic conditions, but avoided the hypolimnion under hypoxia (e.g., *Bythotrephes*); and 3) some species continued to move into the hypolimnion even during hypoxia (e.g., *Bosmina*). Similarly, species-specific responses are evident for fishes. For example, some species, e.g., emerald shiners (*Notropis atherinoides*), primarily occupy the epilimnion before hypoxia development and remain in this top layer during the hypoxic period. In contrast, other species entirely avoid hypoxic waters. The obligate demersal round goby is present in the offshore bottom waters of central Lake Erie prior to hypoxia, but subsequently migrates horizontally and is entirely absent from this region once bottom hypoxia establishes (Höök, Pothoven and Ludsins unpublished data). Intolerant, cold-water rainbow smelt also entirely avoid hypoxic waters and respond by either a) moving up in the water column (to a thin metalimnetic zone with moderate temperatures and sufficient oxygen) or b) migrating horizontally to other regions of Lake Erie (e.g., eastern basin), where suitable thermal and oxygen conditions overlap. Finally, Lake Erie yellow perch display a complex response to hypoxia. While a portion of the yellow perch population appears to move horizontally away from the hypoxic region, many yellow perch remain in this region, but adjust their vertical distributions to zones above the hypoxic waters (e.g., Roberts et al. 2009 and 2012). Moreover, some of these yellow perch remaining in the hypoxic region undertake forays into the hypoxic zone; evidently diving into the hypoxic zone to feed on benthic invertebrates and then returning to the oxygenated epilimnion or metalimnion (Roberts et al. 2012).

Hypoxia-induced shifts in distributions lead to expected changes in diets of invertivorous fishes in central Lake Erie. While emerald shiners display differential prey consumption and selection patterns across months, they continue to consume almost entirely zooplankton throughout all months and there is limited evidence that seasonal diet patterns respond to hypoxia (Pothoven et al. 2009). In contrast, rainbow smelt display strong selection for Chironomidae pupae and larvae during normoxic periods, but avoid these prey and consume almost entirely zooplankton during hypoxia (Pothoven et al. 2009). While more tolerant fish species, e.g., white perch (*Morone americana*) and yellow perch, also alter their diets and consume more zooplankton (as compared to benthic invertebrates) in response to hypoxia (Roberts et al. 2009), these shifts are more nuanced. While perch may display a cessation of benthic feeding under extreme hypoxia (<1 mg/l), under moderate hypoxia they will continue to consume some benthic prey (Chironomidae larvae) through hypoxic foraging forays (Roberts et al. 2009 and 2012). Moreover, size of benthic prey consumed by perch may respond, with perch consuming larger Chironomidae larvae under hypoxia (Goto et al. in prep).

It is attractive to hypothesize that hypolimnetic hypoxia should lead to negative indirect effects on fish growth. Specifically, a) shifts in diets away from preferred prey, b) increased metabolic costs through occupation of higher, warmer zones in the water column, c) activity costs of long-distance horizontal migrations, and d) compensatory density-dependent effects through vertical and horizontal compression should collectively lead to reduced growth and population production rates. However, documenting such effects is not straightforward given that hypoxia in Lake Erie persists for a relatively short time period (i.e., 1 week to 2 months) and its effect on growth can be difficult to distinguish from a variety of other seasonal processes. Moreover, while nutrient additions can exacerbate hypoxia, such loadings can also increase system productivity, leading to greater prey densities and increasing growth and production rates. This positive effect may be most beneficial for epi- and meta-limnetic species that may feed at higher rates when their prey is concentrated into higher portions of the water column. For example, emerald shiners may benefit when zooplankters are forced up in the water column (Pothoven et al. 2009) and walleye may benefit when their piscine prey is concentrated in the metalimnion (Brandt et al. 2011). Further, these effects may not only increase prey vulnerabilities but also prey production rates, as many zooplankton taxa can express greater individual growth rates higher in the water column (i.e., where temperatures, light levels and phytoplankton are all greater; Goto et al. 2012).

Seasonal trends in condition (length-adjusted body mass and % dry mass) generally support the hypothesis that hypoxia leads to species-specific responses in growth. Most temperate fish species display an increase in condition from summer into fall; e.g., epilimnetic emerald shiners display such a pattern in central Lake Erie (Ludsin et al. unpublished). In contrast, mean condition of yellow perch does not increase as expected seasonally (Roberts et al. unpublished) and rainbow smelt condition declines during the hypoxic period (Ludsin et al. unpublished). These patterns are consistent with the hypothesis that emerald shiners are not affected, or perhaps benefit, from hypoxia, while yellow perch and rainbow smelt are moderately and severely negatively impacted, respectively. Nonetheless, other lines of evidence are less supportive of this hypothesis; e.g., RNA:DNA ratios of yellow perch (an index of short-term condition) do not reveal a strong negative response during the hypoxic period (Roberts et al. 2011). In short, while most indications point to a negative effect of hypoxia on fish growth and production in Lake Erie, the magnitude of this effect is an open question.

Any changes in growth rates may have important implications for individual and population-level growth, survival and reproduction success. For example, since energy stores are relatively low for small fish and mass-specific metabolic rates are negatively related to individual size, smaller, young fish are less likely to survive winter (a period of resource scarcity; Shuter and Post 1990). Hence, hypoxia may mediate survival rates of young fish and subsequent recruitment to adult populations. Moreover, since many Lake Erie fishes, e.g., walleye and yellow perch, are capital breeders that allocate energy reserves (lipids) accumulated during the summer and early fall to reproduction during late fall (Dabrowski et al. 1996), female condition entering the winter is likely to determine the amount of energy available for reproduction (Henderson et al. 1996). Thus, if hypoxia reduces female condition entering the winter, it could have a negative effect on reproductive output the following spring. Reduced growth prior to winter would only exacerbate this loss of reproductive potential, because fecundity increases with fish size for nearly all teleost fishes, including Great Lakes yellow perch (Lauer et al. 2005).

*Modeling analyses:* While disentangling the effect of hypoxia on fish growth and production from other seasonal effects is difficult through field surveys, quantitative models offer an alternative for exploring such potential impacts. For example, various bioenergetics growth rate potential (GRP) models have been applied to quantify impacts of hypoxia on species-specific habitat quality in Lake Erie. GRP models build from bioenergetics models to evaluate the consequences of spatiotemporal overlap of environmental conditions (e.g., temperature, oxygen, prey densities, light levels) on habitat quality. Brandt et al. (2011) used data collected during 2005 to apply a GRP model for walleye in central Lake Erie, and argued that hypoxia positively affected walleye habitat quality by forcing fish prey into areas with temperature, oxygen and light conditions favorable for walleye foraging and growth. Using output from retrospective 1-D hydrodynamics and limnological models, Arend et al. (2011) applied GRP models for yellow perch (juvenile and adults), rainbow smelt (juvenile and adults), emerald shiners and round goby for the period 1987-2005. These analyses demonstrated that habitat quality has generally responded to changes in P loading in Lake Erie; from the mid-1980s through mid-1990s, habitat quality improved coincident with reductions in P loading. However, habitat quality did not continue to improve from the mid-1990s through 2005 (and may even have decreased somewhat during this time period). Moreover, Arend et al. (2011) evaluated the impact of hypoxia on habitat quality for various taxa and suggested the most severe impacts for adult rainbow smelt and round goby and the least severe impact on adult and juvenile yellow perch. We applied the Arend et al. (2011) GRP model for two representative years: 1988, a relatively warm year with prolonged hypoxia extending far above the lake bottom, and 1994, a relatively cool year, with a thin hypoxic layer persisting for a short time (see Figure 3). As described above, we anticipate that with climate change, future habitat conditions in Lake Erie are more likely to mirror 1988, as compared to 1994.

While GRP models allow for consideration of spatiotemporal overlap of environmental conditions, they are static representations and do not incorporate many potential dynamic indirect impacts of hypoxia. For example, behavioral avoidance of hypoxia can lead to highly dynamic predator-prey interactions and various density-dependent effects. Moreover, hypoxia-induced changes in predator-prey interactions can cascade to not only effect a single predator-prey pair, but the entire food web. Other modeling approaches are being applied to incorporate and consider behavior-mediated (e.g., individual-based bioenergetics models; Goto et al. in prep) and food web (EcoPath with EcoSim [Zhang, Mason and Rutherford, unpublished] and

Comprehensive Aquatic Simulation Model [S. Bartell unpublished]) responses to hypoxia in Lake Erie.

These modeling approaches may also offer insights regarding how future physicochemical conditions in Lake Erie may impact habitat quality and population production. Previous modeling has indicated that warm-water, cool-water (including YP), and even some cold-water fishes could benefit from climate change in the Great Lakes basin, owing primarily to an increase in thermal habitat available for growth (Minns 1995; Stefan et al. 2001). Winter warming also would be expected to increase over-winter survival of juveniles of warm- and cool-water species such as smallmouth bass, white perch, and yellow perch (Johnson and Evans 1990; Shuter and Post 1990). The anticipated effects of climate on Great Lakes fishes are not all positive, however. As described above, climate warming scenarios also predict increased nutrient loading (via enhanced spring precipitation events), increased summer temperature, and reduced summer water levels (due to decreased summer precipitation and increased evapotranspiration) (Magnuson et al. 1997; Lofgren et al. 2002; Kling et al. 2003) that collectively are expected to lead to an increase in the intensity and duration of hypolimnetic hypoxia (Kling et al. 2003; Fang et al. 2004).

## **II: Water Clarity**

Increases in temperature and precipitation-driven inflows into Lake Erie that are expected to occur with continued climate change (Magnuson et al. 1997, Mortsch et al. 2000, Kling et al. 2003, DeMarchi et al. 2011) are likely to influence foraging and growth environments for fishes, especially those species that rely on vision to detect and capture prey (i.e., all commercially and recreationally important planktivores and piscivores). In general, water clarity will likely decrease in Lake Erie with continued climate change, owing to an increased frequency of precipitation-driven storm events during winter and spring that increase sediment and limiting nutrient (P) runoff from the watershed. These reductions in water clarity also are likely to be magnified by water warming and a longer growing season that stimulate phytoplankton production, especially positively buoyant, inedible species such as cyanobacteria (Paerl and Huisman 2008). Specifically, we expect that water clarity will decrease during spring primarily due to tributary loading of inorganic sediments from largely denuded agricultural landscapes, whereas during summer and fall, water clarity will be reduced primarily by biogenic turbidity such as noxious cyanobacteria (e.g., *Microcystis* spp.) that thrive under high temperatures and have the ability to store P for prolonged periods of time through luxury consumption (Elrifi and Turpin 1985, Paerl and Huisman 2008).

### *Ecological Effects of Water Clarity*

Water clarity is a highly dynamic habitat attribute of aquatic ecosystems that has been shown to modify fish species behavior (e.g., activity, foraging, mate selection; Gradall and Swenson 1982, Berg and Northcote 1985, Miner and Stein 1993, Järvenpää and Lindström 2004, Engström-Öst and Candolin 2007, Engstrom-Ost and Mattila 2008) and inter-species interactions (e.g., competition, predator-prey; Bergman 1991, Persson et al. 1991, Abrahams and Kattenfeld 1997, Pangle et al. 2012). Prominent studies have documented impacts of water clarity (or turbidity; i.e., suspended particles that cause “cloudiness” in water) on interactions involving visual foragers such as zooplanktivorous and piscivorous fishes. Reduced water clarity decreases prey

detection by visual predators through low ambient light intensity (Eiane et al. 1999) and diminished contrast between prey and its background (Lythgoe 1979). Thereby, in the absence of other factors, interactions between visual foragers and their prey are lessened when turbidity increases (see Pangle et al. 2012). Such an alteration of predator-prey interactions can influence the recruitment process of fishes by affecting early life growth and survival (e.g., turbidity can provide a refuge from predation; Boehlert and Morgan 1985, Reichert et al. 2010), mediate trophic interactions and energy flow through aquatic food webs (e.g., weaken trophic cascades, increase trait-mediated indirect interactions; Pangle et al. 2012), and cause shifts in community composition (e.g., from vertebrate to invertebrate planktivore assemblages, from piscivorous to planktivorous assemblages; Bergman 1991, Persson et al. 1991, Cuker 1993, Eiane et al. 1999, Aksnes et al. 2004, Horppila and Liljendahl-Nurminen 2005).

Spatiotemporal variability in water clarity is driven by multiple factors. Water clarity is primarily driven by the amount of suspended particles in the water column (i.e., turbidity), including both inorganic sediments and biogenic materials such as phytoplankton. Thus, those factors that influence turbidity hold great potential to indirectly affect fishes by altering their ability to consume prey and evade predators. Two such external factors include weather (e.g., precipitation) and watershed land use, which govern the timing, magnitude, and duration of sediment and nutrient inputs into downstream ecosystems through river inflow or overland runoff (Tong and Chen 2002, Lawler et al. 2006). Internal turbidity controls also exist, including biological controls (e.g., sessile filter-feeders such as invasive zebra and quagga mussels), whose water-filtering abilities have contributed to enhanced water clarity in lakes across the world (Mayer et al. in press), and physical controls (e.g., wind-driven upwelling and water-mixing events), which can reduce water clarity through the resuspension of nutrients and sediments from bottom waters (Davies-Colley and Smith 2007).

The impact of water clarity on biological interactions involving fishes also can be influenced by multiple factors, including attributes of both the forager and foraging environment. Each species has a unique ability to tolerate turbidity (Angermeier and Karr 1986, Leonard and Orth 1986, Minns et al. 1994, Lyons et al. 1996, Paller et al. 1996). In turn, these species-specific tolerances of turbidity have helped explain variation in fish community composition among ecosystems. For example, in Europe ruffe (*Gymnocephalus cernuus*) tend to dominate the fish biomass in highly productive, turbid lakes of low light penetration, owing to sensory organelles that allow it to continue to feed under dim light conditions (Bergman 1991, Persson et al. 1991). Conversely, European perch (*Perca fluviatilis*) out-compete ruffe for prey in low productivity (low turbidity) ecosystems, and hence, typically dominate there (Bergman 1991, Persson et al. 1991). The trophic position of the forager also can be important, with piscivores being more negatively impacted by turbidity than planktivores (Giske et al. 1994, De Robertis et al. 2003). This finding may help to explain why planktivore to piscivore ratios tend to increase in highly eutrophic, turbid ecosystems (De Robertis et al. 2003). With respect to the role of the foraging environment, Wellington et al. (2010) showed experimentally that the negative effect of biogenic (algal) turbidity on planktivory by intermediate consumers (i.e., larval and juvenile fishes) was greater than the effect of inorganic (sediment) turbidity, with biogenic turbidity impairing foraging of larvae and juveniles more than sediment turbidity, likely owing to the reflective properties of sediments increasing the contrast of prey relative to algae. As is explained more fully below, perceived predation risk by the intermediate consumer (e.g., planktivorous fishes) also can be important, with different foraging rate response curves in relation to turbidity expected under

conditions without predation risk (negative, linear) than in its presence (unimodal) (Pangle et al. 2012).

*Historical patterns:* While several long-term studies have evaluated fish community change in Lake Erie during the past half century, to our knowledge no study has explicitly investigated or clearly identified an impact of changing water clarity on fish population or community change. Ludsin et al. (2001) came closest to doing so, finding that a long-term (1969-1996) shift in the fish community of western Lake Erie from a species assemblage tolerant of eutrophic conditions (e.g., reduced water clarity) to one less tolerant of eutrophy coincided with a reduction in system productivity, including an increase in water clarity. Ludsin et al. (2001) speculated that reduced water clarity provided a foraging advantage to species intolerant of eutrophy that allowed them to out-compete more tolerant ones (sensu Bergman 1991, Persson et al. 1991). However, because other factors besides water clarity changed simultaneously with oligotrophication during this time period (e.g., P inputs declined, several invasive species established populations, bottom hypoxia declined), Ludsin et al. (2001) could not definitively identify the role of water clarity change. Thus, it remains an open question whether water clarity can affect fish community composition in Lake Erie.

*Theoretical and empirical studies:* Despite no definitive evidence to demonstrate that water clarity has driven long-term patterns in Lake Erie fish assemblages, two field investigations have demonstrated a true impact of water clarity on larval yellow perch foraging and recruitment to the juvenile stage. Reichert et al. (2010) and Ludsin et al. (2011) showed that turbid, open-lake plumes produced by the Maumee River in western Lake Erie during spring (2006-2009) provided a recruitment advantage to larvae residing inside the plume over those outside of it. In all years, Maumee River plume larvae recruited to the age-0 (juvenile) stage in August significantly better than expected, whereas recruitment of larvae residing outside the plume was significantly less than expected. Further, Ludsin et al. (2011) used field habitat (e.g., nutrients, turbidity, water clarity, temperature, zooplankton) data, larval yellow perch otolith growth information, predator abundance and diet data, and an individual-based model of larval yellow perch to clearly demonstrate that the positive effect of the Maumee River plume on larvae emanated more from low water transparency (high turbidity) that reduced predation risk than from bottom-up driven effects on zooplankton availability and larval yellow perch foraging and growth. The importance of turbid plume production in western Lake Erie is fully highlighted by Ludsin et al. (2010), who found a very strong correlation ( $r = 0.99$ ) between Maumee River plume size during spring and an index of juvenile yellow perch abundance in August, i.e., a strong predictor of the numbers of adults that recruit to the fishery at age-2 (Ludsin et al. 2001).

In addition to reducing predation risk and mortality for larval yellow perch in Lake Erie, water clarity (or the lack thereof) also may influence larval yellow perch foraging on zooplankton. Pangle et al. (2012) used larval yellow perch diet data and Secchi disk transparency measurements from nearshore waters of western and central Lake Erie to show that the relationship between water clarity and length-specific foraging rate (on zooplankton) is hump-shaped (unimodal), in the presence of predation risk. Specifically, Pangle et al. (2012) found that the foraging rate at an intermediate Secchi depth of 45 cm was more than 2-fold higher than at the highest level of water clarity (175 cm). These authors argued that moderate levels of turbidity are optimal for foraging, as they can provide larval yellow perch a refuge from abundant predators in Lake Erie (e.g., age-1+ white perch, white bass *M. chrysops*, and yellow



perch; Legler et al. 2010, Carreon-Martinez et al. 2011) without constraining their ability to recognize, capture, and handle prey (Pangle et al. 2012).

An important caveat to the above is that the type of particle causing turbidity can change the shape of the relationship between planktivore foraging rate and water clarity. For example, in a controlled laboratory setting, Wellington et al. (2010) showed that larval and juvenile yellow perch foraging rates on zooplankton did not vary across a wide turbidity gradient, a finding that has been previously demonstrated with a congener of yellow perch, the Eurasian perch (*Perca fluviatilis*) (Granqvist and Mattila 2004, Radke and Gaupisch 2005). However, Wellington et al. (2010) did find that phytoplanktonic turbidity negatively affected foraging abilities of both larval and juvenile yellow perch in the laboratory. These differences between turbidity types may emanate from the fact that light intensity was reduced more by phytoplankton turbidity than sediment turbidity (Thimijan and Heins 1983, Wellington et al. 2010). Given the far greater negative effects of phytoplanktonic turbidity relative to sediment turbidity, and the importance of foraging in the recruitment process of age-0 fish, we agree with Wellington et al. (2010) that watershed best management plans should focus their efforts on reducing nutrient inputs that can drive the production of phytoplankton blooms more than on sediment inputs.

Little other work has been conducted in Lake Erie *per se* with respect to the impact of water clarity on ecologically or economically important fish populations. However, a few experimental, theoretical, and habitat modeling studies have been conducted with walleye—the most abundant top predator and most economically important species in Lake Erie (Hatch et al. 1987)—which indicate that changes in water clarity can influence foraging habitat for walleye. Similar to yellow perch, foraging activity of walleye shows a hump-shaped (unimodal) relationship with light intensity (Ryder 1977, Lester et al. 2004). Likewise, walleye prefer to reside in and are most active at intermediate light intensities (~30 lux; Scherer 1976, Ryder 1977, Lester et al. 2004). Thus, as water clarity changes, availability of foraging habitat would be expected to also change, which could drive walleye spatial distributions and production potential (Ryder 1977, Lester et al. 2004). As an example, a thermal and optical niche model developed to quantify foraging habitat available to walleye predicted that enhanced water clarity emanating from nutrient abatement programs (Dolan 1993) and the establishment of dreissenid mussels in North American lakes (Mayer et al. in press) would reduce foraging habitat in the Laurentian Great Lakes basin (Lester et al. 2004). These authors, in fact, predicted a 50% reduction in foraging habitat in Lake St. Clair, owing to increases in water clarity, an ecosystem not too different from western Lake Erie in terms of depth, ecosystem productivity, and its optical properties. Further, Lester et al. (2004) found that observed walleye harvest levels across a wide range of Ontario lakes were positively correlated with predicted thermal-optical foraging habitat, highlighting the potential importance of water clarity changes to walleye production and harvest.

### ***III: Harmful Algal Blooms (HABs)***

As discussed previously, continued increases in temperature and precipitation-driven P inputs from the watershed are expected to increase phytoplankton production in downstream receiving water bodies around the world, including Lake Erie. Such increases could potentially benefit fish growth and survival through “bottom-up” effects that stimulate the production of herbivorous crustacean zooplankton taxa (e.g., cladocerans, copepods) important to fish consumers. However, the frequency, intensity, duration, and spatial extent of blooms of *non-*

edible phytoplankton taxa such as cyanophytes (formerly referred to as blue-green algae, cyanophytes, referred to hereafter as cyanobacteria) also have been predicted to increase with continued climate change in coastal marine and freshwater ecosystems (Paerl and Huisman 2008, Huber et al. 2012, Kosten et al. 2012, Paerl and Paul 2012, Reichwaldt and Ghadouani 2012); including Lake Erie (Conroy et al. 2007). Cyanobacteria are planktonic primary producers that are more related to bacteria than to plants, yet often are considered part of the phytoplankton community. The combination of higher temperatures for a longer period of time (i.e., an extended growing season due to early spring onset and delayed winter onset; Kling et al. 2003, Hayhoe et al. 2010), as well as increased runoff of limiting nutrients from the watershed, underscores the predicted dominance of cyanobacteria during summer and fall in freshwater and marine ecosystems alike (Paerl and Huisman 2008, Paerl and Scott 2010). Increases in cyanobacteria are expected to be particularly high in agricultural watersheds, where bioavailable (dissolved) forms of P that can be immediately used by cyanobacteria (and other algae) are a major component of fertilizers (Anderson et al. 2002, Paerl and Scott 2010). This concern is especially relevant for Lake Erie, as it drains the largest tributary in the Great Lakes basin, the Maumee River. This watershed is predominantly agricultural in nature (>85%; Karr et al. 1985, Richards et al. 2002) and has been experiencing increased inputs of dissolved reactive P (DRP) in recent decades. In fact, concentrations of DRP are on par with levels observed during the height of eutrophication during the 1970s (Ohio Lake Erie Phosphorus Task Force 2010, DeMarchi et al. 2011). As we explain below, these increases in cyanobacteria bloom formation are potentially problematic for the Lake Erie fish community, as they can indirectly and potentially directly influence fish health by altering prey availability and by exposing fish to a variety of toxins.

### *Ecological Effects of HABs*

Some zooplankton (Burns and Hegarty 1994, DeMott and Muller-Navarra 1997, Kurmayer 2001, Martin-Creuzburg et al. 2005, Tillmanns et al. 2008) and fish taxa (Kamjunke et al. 2002a, Perga et al. 2012) can derive energy from cyanobacteria. Likewise, experimental research has demonstrated that filamentous cyanobacteria blooms can benefit small-bodied fish by serving as a refuge from predators (Engstrom-Ost and Isaksson 2006, Engström-Öst et al. 2009). Even so, the negative impacts of an increase in cyanobacteria strains common to the genera *Anabaena*, *Aphanizomenon*, *Microcystis*, *Nostoc*, and *Oscillatoria* (*Planktothrix*) are expected to outweigh the positive ones. One reason for this assertion is that cyanobacteria are not considered a high-quality food resource for herbivorous zooplankton consumers important to fish (i.e., large-bodied crustacean zooplankters such as *Daphnia* spp.) because 1) their large cell sizes (e.g., filaments) and/or ability to form colonies can impede their efficient grazing (O'Brien and Denoyell 1974, DeMott et al. 2001, Nishibe et al. 2002) and 2) as a prokaryote, cyanobacteria lacks steroid alcohols and/or long-chain polyunsaturated fatty acids essential for growth and reproduction (Ravet et al. 2003, Martin-Creuzburg et al. 2008). For this reason, herbivorous zooplankton typically select for non-cyanobacteria taxa, feeding on cyanobacteria only when other phytoplankton taxa are less available (DeMott and Moxter 1991, Burns and Hegarty 1994, Pires et al. 2007). Further, by reducing grazing efficiency on other edible phytoplankton taxa (Gilwicz and Seidler 1980; Fulton and Paerl 1987; DeMott et al. 1991, Davis and Gobler 2011), high concentrations of cyanobacteria can impair crustacean zooplankton growth and production (Gliwicz 1990, Tillmanns et al. 2008), which in turn could reduce energy available to higher consumers such as planktivorous fish and their predators. In addition, cyanobacteria may

negatively affect zooplankton growth and production by altering their spatial distribution in the water column. For example, when the non-toxic, low-quality filamentous cyanobacteria *Synechococcus elongatus* was present in surface waters, *Daphnia pulicaria* avoided it by migrating into deeper and colder (hypolimnetic) waters (Reichwaldt and Abrusan 2007, Reichwaldt 2008), where food (high-quality algae) availability and growth (including reproductive) rates would be expected to be less due low-light conditions and cold temperatures (Orcutt and Porter 1983, 1984).

A second reason that enhanced cyanobacteria blooms are generally negative to fish populations is that many cyanobacteria species produce toxic compounds, such as anatoxin-a and saxitoxin, which are both neurotoxins, as well as the peptide hepatotoxin, microcystin (see reviews by Codd 1995, Ibelings and Chorus 2007, Kotak and Zurawell 2007). In general, the cyanotoxins anatoxin-a and saxitoxin are considered rare (or at least, less studied) in the Laurentian Great Lakes region, with microcystin-LR being the most common strain of the 70 known microcystin congeners (Ibelings and Chorus 2007, Kotak and Zurawell 2007). In addition to posing a threat to human health, by exposure through recreational activities (e.g., swimming) and consumption of fish flesh that has bioaccumulated microcystin (Ibelings and Chorus 2007, Poste et al. 2011), cyanotoxins such as microcystin pose a threat to aquatic animals. While it would be a gross overgeneralization to suggest that all strains of cyanobacteria are harmful to aquatic organisms (Wilson et al. 2006, Tillmanns et al. 2008), many studies have demonstrated that exposure to and consumption of toxic cyanobacteria (especially microcystin) can reduce the condition (health), growth, reproduction, survival, and long-term fitness of crustacean zooplankton that are important prey for Lake Erie fishes, including both small (but especially large) cladocerans (e.g., *Daphnia* spp.) and copepods (also see papers with meta-analysis studies by Wilson et al. 2006 and Tillmanns et al. 2008). Likewise, many negative effects of cyanotoxin exposure have been documented in fish, including impaired development and morphology, altered metabolic and other physiological rates, and reduced internal energy stores, growth rates, and survival (Kamjunke et al. 2002a,b Malbrouk and Kestemont 2006). Further, in their review of the effects of microcystins on fish, these authors concluded that the effects of microcystin exposure were generally greater in early life stages (egg, larval) than later ones, although there was little evidence to indicate that naturally occurring concentrations of microcystins would lead to acute mortality in fish. By contrast, however, Malbrouk and Kestemont (2006) concluded that even a few days of exposure to microcystins at naturally occurring concentrations during critical developmental windows in the embryonic or larval stage could reduce survival enough to influence fish population size. Given this suite of findings, the potential for climate change to negatively impact Lake Erie fishes through promotion of noxious cyanobacteria blooms is real.

*Historical patterns.* Similar to other ecosystems around the world, the Lake Erie ecosystem has seen an increase in the frequency, intensity, duration, and spatial extent of HABs since the last decade (Vincent et al. 2004, Stumpf et al. 2012), following a near 20-year period without such events (Figure 1). This increase coincides with a period of record-breaking temperatures and increased precipitation-driven inputs of dissolved forms of P, even surpassing levels typical of the 1970s during the height of eutrophication of Lake Erie (Richards et al. 2010). Further, strong predictive relationships have been developed between tributary inputs of P and the magnitude of HABs since the late 1990s (Wynne et al. 2011), with strong correlations among water-column total P concentrations, *Microcystis* spp., and microcystin levels in Lake Erie (Rinta-Kanto et al. 2009). Thus, potential exposure of Lake Erie fishes and their prey to microcystin is real.

Although we know that cyanotoxins such as microcystin have become prevalent in Lake Erie during recent years and can bioaccumulate in the tissue of fishes (e.g., smallmouth bass, lake whitefish, yellow perch, walleye; Wilson et al. 2008; Poste et al. 2011), no research has been conducted within the ecosystem to understand how HABs can affect Lake Erie fishes, either directly (i.e., via altered development, physiology, growth, reproduction, survival) or indirectly (i.e., via altered food web interactions, altered use of habitat). In fact, we only found one study (Davis et al. 2012) that looked at the impact of HABs on the ecology of the Lake Erie ecosystem. In that study, Davis et al. (2012) found that naturally occurring concentrations of cyanobacteria (primarily *Microcystis*) reduced grazing rates of *Daphnia pulex*, a common mesozooplankton species in Lake Erie. However, the effect of this reduction in grazing rate on population demographics was not studied. Given the multiple negative impacts that cyanobacteria have had on fish and zooplankton in other ecosystems (see above section), the fact that increasing temperature can magnify the negative effect of cyanobacteria on zooplankton grazing (Claska and Gilbert 2002), and the high likelihood that HABs will continue increase with continued climate change, we strongly encourage future research in this arena.

#### ***IV: Basal Invertebrate Prey***

##### *Ecological Effects of Basal Prey Production*

Food web structure and dynamics dictate the flow of energy through natural systems. Food web constituents are co-responsive such that alterations of a single component can cascade to affect divergent aspects of the network through both bottom-up and top-down processes. Therefore an appreciation of processes throughout the entire food web is necessary if one is to anticipate the consequences of stressors such as eutrophication. Over the past century, Lake Erie fish (see above) and invertebrate assemblages have shifted in response to eutrophication and other stressors. Future climate change (and resulting physical changes) will undoubtedly interact with existing stressors to further modify not only biotic composition and biomasses but also nutritional makeup of the prey base.

By affecting physicochemical, biomolecule and phytoplankton conditions, increased nutrient loading and resulting eutrophication can lead to a suite of impacts to lower trophic level consumers. Hypolimnetic hypoxia will favor benthic invertebrates that can tolerate low oxygen conditions (e.g., Oligochaeta and Chironomidae) over more sensitive organisms (e.g., *Hexagenia* spp.). Similarly, some zooplankters are able to survive under low oxygen and may even use a hypolimnetic hypoxic zone as a refuge from predators (e.g., Vanderploeg et al. 2009b) and thereby alter planktivore-zooplankton interactions (Pothoven et al. in press). Moreover, zooplankton taxa differ in their ability to feed under low light and to exploit various types of phytoplankton. Thus, low light and high cyanobacteria densities may lead to emergence of a eutrophic zooplankton assemblage (e.g., high biomass of cyclopoid copepods, cladocerans and low biomass of calanoid copepods; Gannon and Stemberger 1978).

*Historical patterns:* Historical patterns of lower trophic levels in Lake Erie are generally consistent with expected responses to eutrophication. For example, the elimination and subsequent recovery of sensitive burrowing mayflies (*H. limbata* and *H. rigida*) during the 1950s and 1980s, respectively (Britt 1955, Carr and Hiltunen 1965, Krieger and Ross 1993, Krieger et al. 1996), tracked changes in water quality conditions. In contrast, several tolerant benthic

invertebrate taxa declined with decreased nutrient loads from the 1970s to 2000s (Soster et al. 2011). Similar to benthic invertebrates, a variety of specific zooplankton taxa seem to have responded to changes in trophic conditions (Johansson et al. 1999, 2000; Barbiero et al. 2001). At a coarser taxonomic level, changes in zooplankton assemblages from the 1970s through the 1990s were consistent with a response to reduced eutrophic conditions: i.e., during this time period a zooplankton index of trophic status (ratio of calanoids to cyclopoids + cladocerans) increased in all three Lake Erie basins (Johansson et al. 1999; Barbiero et al. 2001).

In addition to shifts in taxonomic composition, nutrient loading affects system-wide production and lower trophic level biomass in Lake Erie. Such shifts in total biomass may ultimately have a stronger impact on fish stocks than shifts in taxa composition. In fact, despite dramatic temporal changes in zooplankton taxa composition, zooplankton size spectrum distributions in changed minimally from 1991 to 1997 (Sprules 2008); demonstrating that similar-sized prey were available notwithstanding taxonomic changes. Following reductions in nutrient loading, phytoplankton biomass in western Lake Erie declined by ~65% (Makarewicz and Bertram 1991, Makarewicz 1993b), and crustacean zooplankton biomass declined by as much as 60% (Makarewicz and Bertram 1991, Makarewicz 1993a). Such reductions in planktonic production may impact not only planktivorous fishes, but also detritivores, since reduced water column production will directly translate to reduced settlement of detritus to the bottom. In fact, benthic densities of several Lake Erie benthic invertebrates may have declined with reductions in nutrient loading (Soster et al. 2011; but see Johansson et al. 2000). Moreover, given that many eutrophic tolerant fish species are facultative detritivores, changes in abundance of such species may be linked to reduced detrital mass (availability) or its nutritional quality (Ludsin et al. 2001). Such reductions in detrital mass have been linked to reduced species diversity (e.g., species richness) in other systems (Gascon and Leggett 1977, Henderson and Crampton 1997).

While high nutrient loads can increase overall system productivity, this can also result in shifts in physicochemical conditions and alter the makeup of primary producers. Dense phytoplankton blooms can lead to hypoxic conditions, decreased water clarity and limited available nitrogen (relative to P). Such factors can contribute to phytoplankton assemblages dominated by taxa that can tolerate low light and compete under both nitrogen and P limitation, i.e., cyanobacteria. Diverse phytoplankton taxa differ not only in size, shape and buoyancy, but also chemical composition and nutritional value for consumers. For example, phytoplankton taxa differ in their ability and frequency of fatty acid synthesis (Dalsgaard et al. 2003). As consumers cannot synthesize many essential fatty acids and are dependent on primary producers for such macromolecules (Dalsgaard et al. 2003), shifts in phytoplankton assemblages will also lead to food web-wide shifts in fatty acid patterns. Ultimately, eutrophication-induced shifts in nutritional content of lower trophic levels can have important implications for fish growth, survival and reproductive success by affecting factors such as overwinter survival and offspring quality (e.g., Johnson and Evans 1990; Henderson et al. 1996).

*Recent Interactive Effects of Invasive Species:* More recently, lower trophic level patterns in Lake Erie and responses to nutrient loading have seemingly been mediated by effects of invasive species, most notably dreissenid mussels (zebra mussels and quagga mussels), but also invasive fishes (e.g., round goby, white perch) and predatory zooplankton (*Bythotrephes*). Filter-feeding dreissenids fill a novel trophic niche in Lake Erie and other Great Lakes. No native filter-feeders have been as abundant and voracious as dreissenids are currently. Throughout the Great Lakes,

reduced production and standing animal biomass in offshore and pelagic areas have been linked to dreissenid filtering and sequestering of nutrients in benthic and nearshore zones (Hecky et al. 2004).

Nutrient loading into Lake Erie may now not result in the same eutrophication responses as observed prior to dreissenid establishment. For example, due to their intense filtering, dreissenids have been linked to marked increases in water clarity in a variety of systems (e.g., Hecky et al. 2004; Binding et al. 2007; Higgins and Vander Zanden 2010); although a dreissenid – water clarity relationship in Lake Erie is inconsistent (Barbiero and Tuchman 2004). Moreover, dreissenid shells may provide appropriate substrate for various benthic taxa, both invertebrates and benthic algae, and dreissenid excretions (i.e., pseudo-feces) may serve to fertilize the benthic layer and facilitate benthic production and decomposition (e.g., Stewart et al. 1998; Hecky et al. 2004; Bridgeman and Penamon 2010). As a consequence, in a dreissenid-dominated system, increased nutrient loading may not result in dramatic increases in pelagic phytoplankton biomass or decreases in water clarity. Instead, high nutrient loading may result in increased benthic production, including increased benthic algal production; i.e., benefiting from increased a) hard substrate, b) benthic light level and c) benthic fertilization.

Dreissenids may also mediate hypoxia development in Lake Erie; however the cumulative mediating effects of dreissenids on oxygen patterns are unknown. On the one hand, sequestering of nutrients in the nearshore zone and lower pelagic phytoplankton biomass may be expected to contribute to decreased hypoxia. On the other hand, the collective effect of dreissenids may be to simply shunt productivity to the benthic zone. Dreissenid excretions could contribute to increased benthic production and decomposition, ultimately exacerbating benthic respiration and oxygen depletion rates. While dreissenid-facilitated hypoxia expansion seems plausible, such a phenomenon would include a spatial offset. That is, dreissenids cannot tolerate very low oxygen and old dreissenids are largely absent from the region of central Lake Erie which experiences seasonal hypoxia (i.e., dreissenid densities in this region are low and primarily include young, recent settling individuals; Höök unpublished data).

*Future Interactive Effects of Climate Change:* The impacts of climate change on lower trophic levels of Lake Erie will likely not be straightforward, and future climatic conditions will undoubtedly interact with nutrient loading and invasive species in structuring lower trophic level assemblages. As described above, warmer temperatures, lower lake levels and increased frequency of intense precipitation events all have the potential to enhance phytoplankton blooms, reduce water clarity and exacerbate future hypoxia. These expected responses would favor eutrophic tolerant invertebrate taxa. That is, zooplankton and benthic invertebrate taxa would likely increase in abundance if they can a) tolerate relatively warm temperatures, b) effectively consume cyanobacteria, c) feed under low light, and d) utilize a low oxygen zone as a refuge from predation. Moreover, with increased primary production and subsequent detrital deposition, total biomasses of both pelagic and benthic consumers could swell. On their own, expected climate change impacts could lead to invertebrate assemblages trending towards patterns observed during the 1950s and 1960s (i.e., at the height of eutrophication).

Some important caveats regarding climate change effects on Lake Erie invertebrate assemblages relate to the mediating effects of land use and invasive species. 1) Aggressive changes in land-use practices have the potential to dramatically reduce nutrient loads. 2) Dreissenid mussels

have contributed to system benthification, sequestering much carbon and production in benthic regions. Thereby, future increases in nutrient loads may not readily translate to higher planktonic production, lower water clarities and increased hypoxia. 3) Over the coming decades, additional non-indigenous species will undoubtedly establish in Lake Erie. In fact, several assessments speculate that changing climatic conditions will facilitate increased frequencies of invasion events worldwide (e.g., Dukes and Mooney 1999; Kling et al. 2003; Rahel and Olden 2008). While many taxa have been identified as having a high probability of invading the Laurentian Great Lakes (e.g., Ricciardi and Rasmussen 1998), the identity of future invaders and their impacts on the ecosystem are unknown. Nonetheless, several recent assessments have focused on potential invasion and impacts of Asian carp (silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*) on Great Lakes ecosystems; raising concerns that this large-bodied voracious planktivore could negatively affect the availability of lower trophic level prey for native fishes (Kolar et al. 2005; Cooke and Hill 2010; Hansen 2010). While all dire predicted future effects of Asian carp may not materialize, as evidenced by dreissenid mussels, invasive species have the potential to dramatically alter ecosystem processes and one or more future invasive species could dramatically affect how climatic changes mediate eutrophic conditions in Lake Erie.

### *Conclusions*

Over the past century, anthropogenic-mediated P loading has dramatically affected physicochemical characteristics and food web structure in Lake Erie. Before the 1970s, uncontrolled point and non-point additions of nutrients led to the emergence of prolonged hypoxic zones, nuisance algal blooms, high turbidity and declines of a large number of fish and invertebrate taxa. With subsequent abatement of P loads, these manifestations of eutrophication responded and abiotic and biotic conditions in Lake Erie began to resemble a pre-intense-eutrophication state. However, evidence over the past few years and projections into the future are suggestive that Lake Erie is returning to a more eutrophic state. Projections of warmer atmospheric temperatures and more intense precipitation events should lead to warmer water temperatures, a longer stratified period, and greater sediment and nutrient loading. In turn, these changes are expected to favor a more eutrophic state, with enhanced hypoxia, lower water clarity, frequent nuisance algal blooms and a less tolerant biotic community. Thus, we expect that in the absence of other changes, future climatic conditions and anthropogenic nutrient loading will promote a Lake Erie fish community resembling the community present during the height of eutrophication. That is, we expect cold-water species and species sensitive to low oxygen and reduced water clarity (e.g., salmonines, coregonines) to decline in abundance, while warm-water and tolerant species will expand.

In general, the interactive effects of climate change and nutrient loading are expected to promote a eutrophic-tolerant fish community; with visual feeding, cold-water and hypoxia-sensitive fish declining, and warm-water, tolerant detritivores increasing (i.e., trending towards the right in Figure 1). However, beyond such generalizations, species-specific, population-level responses may be more nuanced and difficult to predict. By influencing population vital rates (survival, growth rate, and reproduction), mechanisms such as hypoxia, reduced water clarity, harmful algal blooms and altered prey base have the potential to directly and indirectly mediate population trajectories. For example, while reduced water clarity may compromise foraging success, and hence growth rates, of visual planktivores, certain warm-water planktivores (e.g.,

emerald shiners) may actually benefit indirectly from bottom hypoxia forcing their zooplankton prey up into the meta- and epilimnion. Similarly, population-level reproductive success (recruitment) of several Great Lakes fish populations appears to respond positively to increased spring-summer annual temperatures and high river discharge; suggesting that warmer conditions and high spring precipitation will enhance recruitment. However, ovarian development for many fish species occurs over winter, and relatively short, warm winters may not allow for adequate gonadal development, thereby compromising recruitment potential. Consideration of such counteracting processes may be necessary to predict future population-specific responses.

We have focused explicitly on how climate change can influence the Lake Erie fish community through four mechanisms involving the alteration of nutrient (P) inputs. Each was discussed independently. However, the potential for non-additive or synergistic interactions among these changes exist. Further, other anthropogenic drivers will simultaneously influence the ecosystem and its fish communities, including invasive species, fisheries harvest, habitat alterations, and other aspects of climate change that don't involve nutrients (e.g., water warming). There is a plethora of potential interactions among these. While the realm of potential interactions is unfathomable, and hence greatly limits our ability to forecast the future, we acknowledge that there are several caveats to our general expectation regarding the future Lake Erie fish community. 1) Dramatic land-use changes have the potential to reduce nutrient loading in the face of climate change. 2) Dreissenid mussels have fundamentally changed the Lake Erie ecosystem in ways that are just beginning to be fully appreciated. In a dreissenid-dominated system, nutrient additions may not translate into the same manifestations of eutrophication as observed during an earlier time. 3) Unknown future invasive species have the potential to further modify the Lake Erie ecosystem, leading to ecological surprises.



## **Acknowledgements**

We thank John Casselman for providing useful suggestions which helped in developing this synthesis and Kimberly Winslow (Peters) for assistance with editing and literature review. In developing Figure 3, we acknowledge Kristin Arend for model code and Timothy Sesterhenn for model application and figure drafting.

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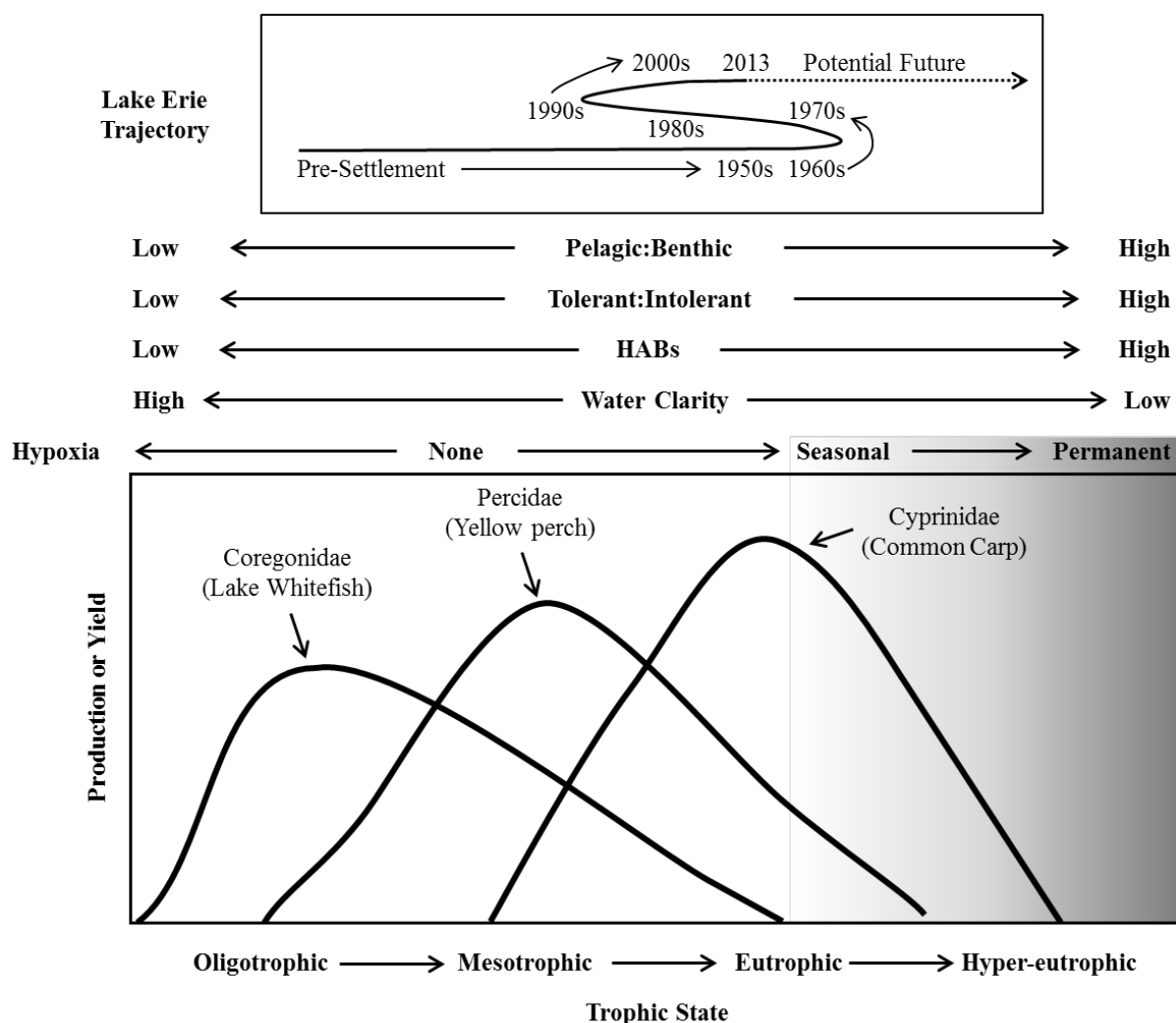


Figure 1. Conceptualization of how the trajectory of the Lake Erie ecosystem, including several of its habitat fish attributes, has varied in response to altered system productivity, and is expected to continue to vary with continued climate change (i.e., increased warming and precipitation). Increased nutrient and sediment runoff associated with continued climate change is expected to shift the trophic state of Lake Erie from mesotrophy to eutrophy (and possibly hyper-eutrophy), with an expected increase in harmful algal blooms (HABs) and decrease in water clarity. Such changes in habitat attributes are anticipated to drive shifts in community composition across all trophic levels (phytoplankton, zooplankton, and fish), from species intolerant of eutrophic conditions (e.g., hypoxia, low water clarity) to more tolerant species (i.e., increase ratios of tolerant:intolerant species abundance), as well as an increase in the ratio of pelagic to benthic fishes (via enhanced bottom hypoxia). Also depicted are hypothetical production (yield) curves for three common families of fish, which represent different tolerance, thermal, and feeding guilds: Coregonidae (e.g., lake whitefish; benthic-dwelling intolerant, cold-water invertivore); Percidae (e.g., yellow perch; benthic-dwelling moderately tolerant, cool-water omnivore); and Cyprinidae (e.g., common carp; benthic-dwelling tolerant, warm-water detritivore). Ideas herein were adapted from Oglesby (1977), Caddy (1993), and Diaz and Solow (1999).

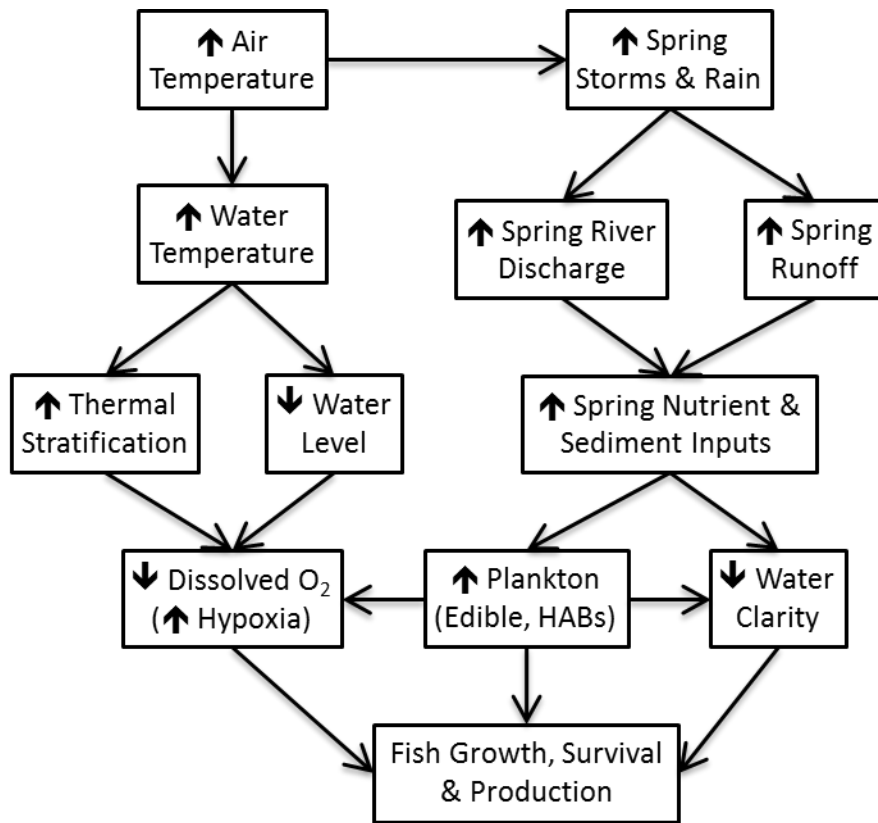
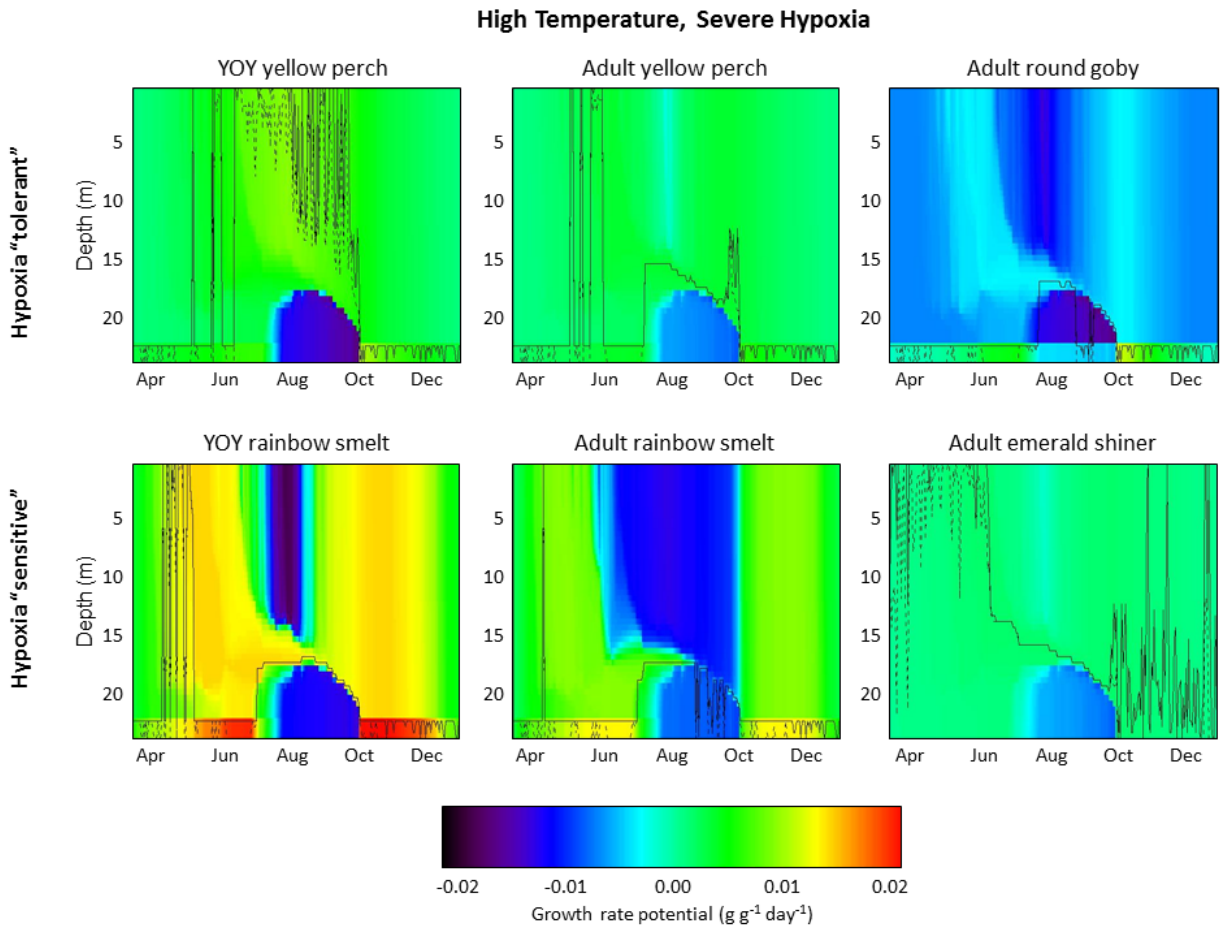


Figure 2 Potential pathways by which climate change (i.e., warming, increased precipitation events during spring) can influence fish communities through effects on nutrient availability that influence habitat quality for fishes, including dissolved oxygen availability, algal production (both edible and harmful), and water transparency.

a) 1988



b) 1994

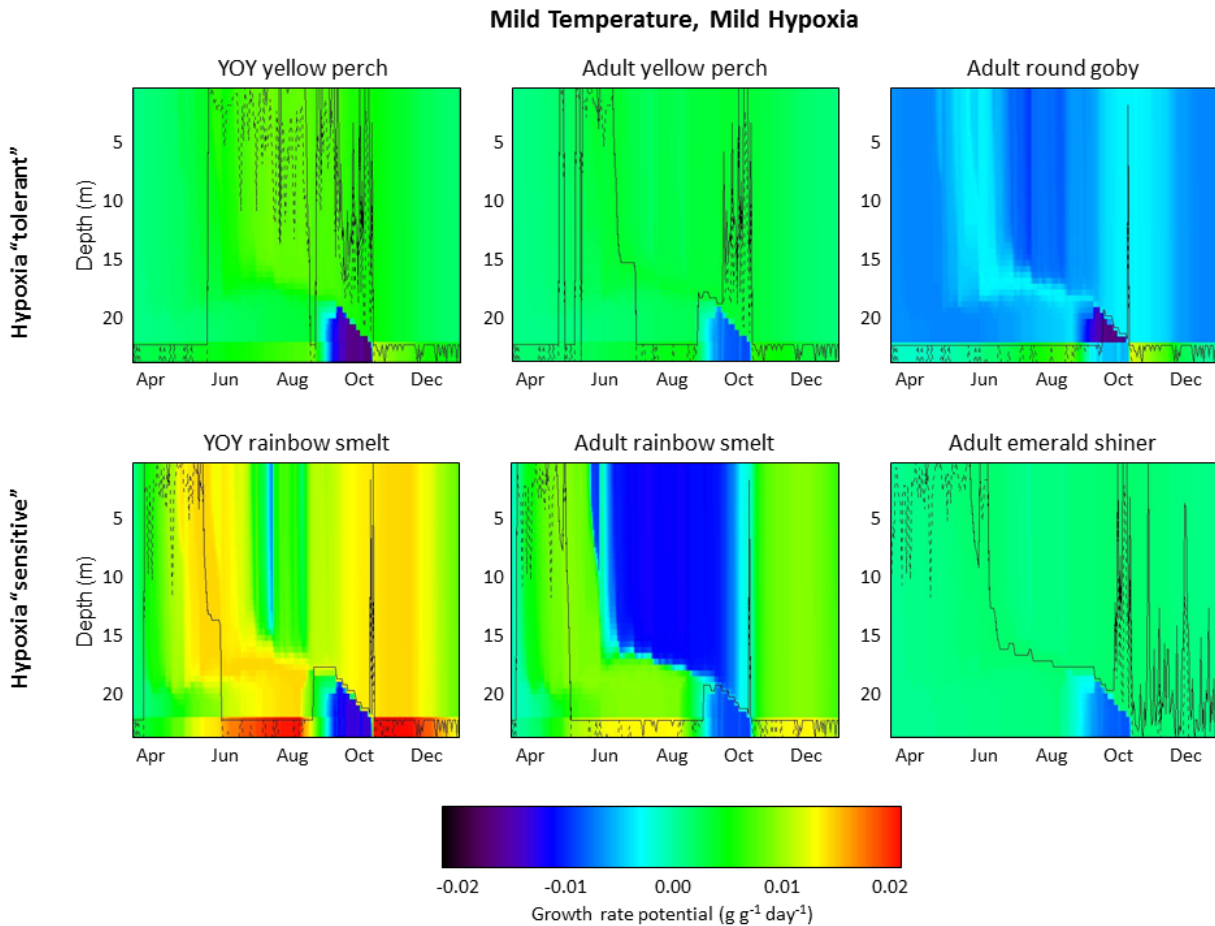


Figure 3. One-dimensional habitat quality for representative fishes in central Lake Erie as indexed by bioenergetic growth rate potential (GRP). This index of habitat quality is an integration of vertical temperature and oxygen daily hindcasts (from Rucinski et al. 2010), and is based on the assumption that fish feed at 50% of their maximum daily rate. “Hot” colors depict higher habitat quality and the black line tracks the vertical position of daily greatest habitat quality. Note the difference in habitat quality between a warm year with a long duration of hypoxia, 1988 (a), as compared to a cool year, with brief hypoxia, 1994, (b). Model details are presented in Arend et al. (2011).