RESEARCH PAPER



Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America

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Abstract The Laurentian Great Lakes of North America provide valuable ecosystem services, including fisheries, to the surrounding population. Given the prevalence of other anthropogenic stressors that have historically affected the fisheries of the Great Lakes (e.g., eutrophication, invasive species, overfishing), climate change is often viewed as a long-term stressor and, subsequently, may not always be prioritized by managers and researchers. However, climate change has the potential to negatively affect fish and fisheries

in the Great Lakes through its influence on habitat. In this paper, we (1) summarize projected changes in climate and fish habitat in the Great Lakes; (2) summarize fish responses to climate change in the Great Lakes; (3) describe key interactions between climate change and other stressors relevant to Great Lakes fish, and (4) summarize how climate change can be incorporated into fisheries management. In general, fish habitat is projected to be characterized by warmer temperatures throughout the water column, less ice

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cover, longer periods of stratification, and more frequent and widespread periods of bottom hypoxia in productive areas of the Great Lakes. Based solely on thermal habitat, fish populations theoretically could experience prolonged optimal growth environment within a changing climate, however, models that assess physical habitat influences at specific life stages convey a more complex picture. Looking at specific interactions with other stressors, climate change may exacerbate the negative impacts of both eutrophication and invasive species for fish habitat in the Great Lakes. Although expanding monitoring and research to consider climate change interactions with currently studied stressors, may offer managers the best opportunity to keep the valuable Great Lakes fisheries sustainable, this expansion is globally applicable for large lake ecosystem dealing with multiple stressors in the face of continued human-driven changes.

Keywords Great Lakes · Climate change · Fisheries · Habitat · Management

Introduction

Large lakes are important ecosystems that contain the majority of the planet's surface freshwater and provide services valued by surrounding communities, including drinking water, hydropower, recreational opportunities, and fisheries (Beeton 2002). Historically, fish populations in large lakes have been adversely affected by the same diverse anthropogenic stressors that are impacting aquatic ecosystems across the globe, e.g., habitat degradation (Smith 2003), overexploitation (Pauly et al. 2002), and invasive species (Strayer and Dudgeon 2010). More recently, climate change has emerged as an additional stressor to fish populations and fisheries in these large lakes. Projected climate change is expected to cause increased temperature and changes in precipitation patterns, resulting in altered thermal regimes and nutrient loadings, and consequently bringing about changes in individual growth, population dynamics, community structure and ultimately, fisheries production in large lake fisheries (Jeppesen et al. 2010; Portner and Farrell 2008; Sheridan and Bickford 2011). These direct climate impacts coupled with other existing stressors may ultimately have strong effects on fisheries production in large lakes (Ficke et al. 2007; Portner and Peck 2010).

The Laurentian Great Lakes of North America form the largest group of freshwater ecosystems on Earth and contain nearly 20% of the planet's surface freshwater. The watershed of the Great Lakes basin (Fig. 1) generally ranges from more forested and less developed areas in the north to more agricultural and urban development in the southern portion of the basin (Hayes 1999). The lakes provide important ecosystem services, including fisheries, to one-tenth of the population of the United States and one-quarter of the population of Canada (Beeton et al. 1999). Historically, two main types of fish assemblages existed across the Great Lakes. In deeper and less productive open waters of lakes Superior, Michigan, Huron, and Ontario and eastern Lake Erie, the fish assemblage mainly consisted of salmonines and coregonids and main fishery species included lake trout (Salvelinus namaycush), lake whitefish (Coregonus clupeaformis), cisco (shallow water, or formerly lake herring, Coregonus artedi), and deepwater chubs (Coregonus spp.) (Eshenroder and Burnham-Curtis 1999). In the shallow and more productive western basin of Lake Erie and embayments such as Green Bay (Lake Michigan), Saginaw Bay (Lake Huron), and Bay of Quinte (Lake Ontario), the fish assemblage mainly consisted of percids, cyprinids, and centrarchids and the main fishery species included blue pike (Sander vitreus glaucus), walleye (Sander vitreus), and yellow perch (Perca flavescens) (Eshenroder and Burnham-Curtis 1999).

These historical fish communities of the Great Lakes have been reshaped by habitat alterations, overfishing, stocking, invasive species, and excessive nutrients and sediment loadings (Hayes 1999; Gaden et al. 2012). Because climate change has the potential to stress fish communities in the Great Lakes by further altering fish habitat and through its interactions with existing stressors, fish responses to climate change are best understood within an ecosystem context. Herein, we aim to improve our understanding of the potential responses of Great Lakes fisheries to climate change, both in isolation and in combination with other human-driven stressors. Such knowledge could enhance the ability of agencies to manage their fisheries, as well as the expectations of their constituents. Toward this end, our review paper seeks to, (1) summarize projected changes in climate and fish



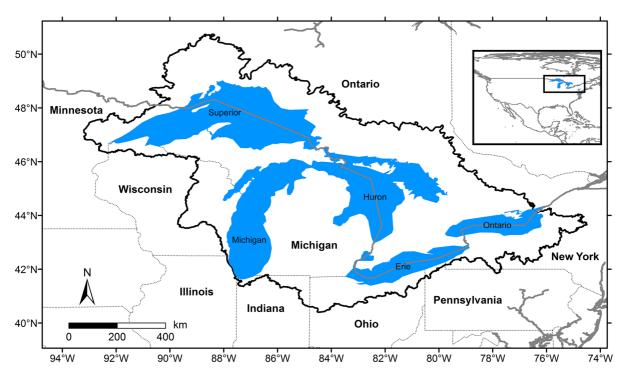


Fig. 1 Great Lakes watershed map

habitat in the Great Lakes; (2) summarize fish responses to climate change in the Great Lakes; (3) describe key interactions between climate change and other stressors relevant to Great Lakes fish populations, and (4) summarize how climate change can be incorporated into fisheries management. Below, we present a brief overview of the history both of humandriven stressors on Great Lakes fish and fisheries and relevant management actions as a way of providing some historical context to the issues currently facing fisheries management in this system.

Overview of non-climate anthropogenic stressors on Great Lakes fishes

Habitat destruction

Fish in the Great Lakes have been stressed by habitat alterations since the early eighteenth century when dams were first built in the drainage basin (Beeton et al. 1999). These dams not only blocked spawning migrations for potamodromous fishes but also altered flow regimes and habitat structures in tributaries (Hayes 1999). During the early twentieth century, fish

habitats were further degraded by human activities related to natural resource extraction in the watershed such as timber harvesting and mining and converting forests and wetlands into agricultural and other developed areas, which led to increased transport of sediments and decreased water clarity in nearshore areas (Beeton et al. 1999). Coastal wetlands in particular are important breeding or nursery habitats for many Great Lakes fish species (Jude and Pappas 1992; Trebitz and Hoffman 2015), and physical disturbances (e.g., drainage, diking, shoreline hardening) have led to loss of these services in many areas (Trebitz et al. 2009; Wilcox and Whillans 1999). For example, over 97% of the coastal wetland acreage surrounding the Detroit River (a major tributary in western Lake Erie) has been lost owing to development since the early 19th century (Manny 2007).

Invasive species

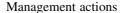
The proliferation of nonnative sea lamprey (*Petromyzon marinus*) and alewives (*Alosa pseudoharengus*), which reached the upper Great Lakes from the Atlantic Ocean through the Welland Canal, was one of the dominant stressors in the first half of the twentieth



century (Eshenroder and Burnham-Curtis 1999). Mortality imposed by parasitic sea lamprey contributed substantially to the collapse of lake trout populations already stressed from fishing pressure before the 1950s in Lakes Michigan, Huron, and Ontario. Later, fishing and sea lamprey predation shifted to smaller deepwater fishes and caused severe declines in lake whitefish populations and the extinction of three deepwater ciscoes (Coregonus nigripinnis, C. johannae, and C. reighardi). With severe declines in predatory lake trout and planktivorous ciscoes, planktivorous alewife populations exploded across the lakes by the late 1950s (Miller 1957). Alewife predation on larvae further stressed native fish populations such as lake trout, yellow perch, and walleye (Madenjian et al. 2008). Since the mid-1980s, a series of invasions by nonnative species from the Ponto-Caspian region have caused major changes in the Great Lakes. In particular, the dreissenid (zebra and quagga mussels, Dreissena polymorpha and D. bugensis) colonization of the Great Lakes has dramatically altered the fate of particulate nutrient inputs and the lake ecosystem. When dreissenids reach large population sizes, they sequester primary production in nearshore benthic habitats, which acts to constrain nutrients that would otherwise be available to higher trophic levels in offshore areas (Hecky et al. 2004; Higgins and Vander Zanden 2010).

Nutrient pollution

Excessive nutrient loading and eutrophication was of major concern in the Great Lakes by the 1960s (Beeton 1965). Although open waters remained mostly oligotrophic, eutrophication became common in shallower waters with large tributary inflows such as the western basin of Lake Erie, and embayments such as Saginaw Bay and Green Bay (Vollenweider et al. 1974). Eutrophication was manifested through algal blooms (including harmful algal blooms, in the western basin of Lake Erie) and bottom hypoxia (in particular in the central basin of Lake Erie) (Bierman and Dolan 1981; Ludsin et al. 2001). Given the recognition that phosphorus typically limits primary production in freshwater, limits on total phosphorus loads were established in the 1972 Great Lakes Water Quality Amendment, which restricted phosphorus from point sources in particular (Dolan and Chapra 2012).



In the Great Lakes, policies and laws governing fisheries were developed in the states and Ontario during the nineteenth century (Brenden et al. 2012), and fish population declines throughout the first half of the twentieth century led to additional management actions (e.g., Smith 1968). However, the development of effective policies was slow (Regier et al. 1999). Commercial fisheries in the Great Lakes were well established by the 1880s and exploitation gradually increased due to increases in fishing effort and improvements in technology (Brenden et al. 2012). Through time, overfishing led to reductions in total harvests across all five Great Lakes, including sharp declines in once-abundant ciscoes, and extinctions of several valuable fishes such as blue pike (Eshenroder and Burnham-Curtis 1999). In response to the threats from sea lamprey, the Convention on Great Lakes Fisheries was signed by the U.S. and Canada in 1954 and the newly formed Great Lakes Fishery Commission was tasked with developing a sea lamprey management program that began during the late 1950s (Gaden et al. 2012). The sea lamprey control program eventually focused on the effective application of chemical lampricides targeting sedentary larval stages in streams (Smith and Tibbles 1980). To make use of the burgeoning populations of nonnative alewives and exploit the reduction in sea lamprey, salmonine stocking programs were initiated in 1966 and enjoyed tremendous success (Tody and Tanner 1966). The introduction of Coho (Oncorhynchus kisutch) and Chinook salmon (O. tshawytscha) resulted in profitable recreational and charter fisheries (Thayer and Loftus 2012) and reduced alewife abundance at levels far below those observed during earlier decades (Madenjian et al. 2008).

Projected changes in climate and fish habitat in the Laurentian Great Lakes

Temperature and precipitation are two notable external climate drivers predicted to change over this century in the Great Lakes region (see Fig. 2; Hayhoe et al. 2010; McDermid et al. 2015 for a summary of how climate has already been changing). Downscaled forecasts consistently predict warmer temperatures and increasing total precipitation, but with considerable



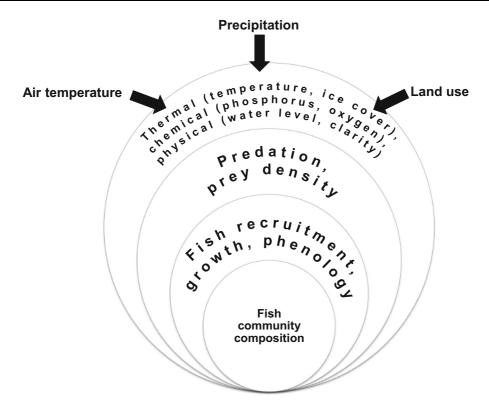


Fig. 2 Conceptual framework describing the complex, hierarchical linkages between external drivers (air temperature, precipitation, land use) and ultimate fish responses in the Great Lakes. The external drivers directly influence the abiotic variables associated with fish habitat (thermal, chemical, physical). These abiotic variables, in turn, can affect predation rates on fishes, as well as the densities of prey available to fishes.

spatiotemporal variation that is driven, in part, by which general circulation model (GCM) and emission scenario is used and the specific microclimate drivers affecting the Great Lakes region (Pryor et al. 2014). By the mid-twenty first century, air temperatures are generally projected to increase by 2–3 °C and precipitation by 5–10% (Kling et al. 2003; Hayhoe et al. 2010; Wang et al. 2016). Near the end of the twenty first century, those increases will rise to about 2–8 °C and 6-14%, respectively (Kling et al. 2003; Hayhoe et al. 2010; Wang et al. 2016). For both periods, large seasonal variation is predicted, with summer predicted to have the largest increase in temperature, whereas winter and spring are predicted to have the largest increase in precipitation (Kling et al. 2003; Hayhoe et al. 2010). Even within a season, the precipitation patterns may be variable, with the frequency of high rainfall events potentially doubling by 2100 (Kling In the Great Lakes, many of these biotic factors that influence fish populations are heavily influenced by nonindigenous species. Within this ecosystem perspective, these abiotic and biotic factors influence fish population demographics (e.g., recruitment, growth, phenology) which, in turn, shape community composition of fishes

et al. 2003). Atmospheric climate change can affect fish habitat by influencing aspects of the thermal environment (e.g., water temperature, ice cover), the chemical environment (e.g., nutrient concentrations, oxygen concentrations), and physical habitat (e.g., water levels, nearshore spawning habitat). In addition to affecting fish habitat, these changes can also affect the densities of prey available to fish (see Fig. 2). Below, we describe these potential effects in greater detail.

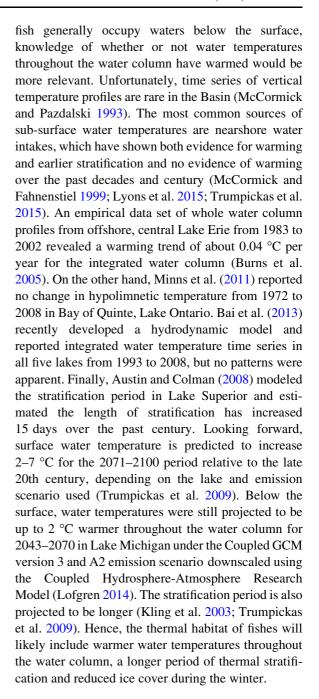
Thermal habitat

Warming air temperatures and increased downward longwave radiation can influence both water temperatures and ice cover in the Great Lakes. The spatial extent of ice coverage declined 71%, on average, in the Laurentian Great Lakes between 1973 and 2010



(Wang et al. 2012) and declined by 5 days per decade in 65 lakes during 1975-2004 in the Great Lakes region (Jensen et al. 2007). Ice cover can influence the physical conditions for fishes whose eggs incubate during the winter by ameliorating wave action in shallow areas (e.g., lake whitefish; Brown et al. 1993). Despite these observations, predicting exactly how ice cover will change with continued warming is difficult because of high, unexplained variation in the past (Wang et al. 2012), as exemplified by the recent near record-high ice coverage during 2013-2014 (Gronewold et al. 2015). Recognizing the potential for unusual years of high ice cover, most models project less ice cover for the Great Lakes by the middle and end of the twenty first century (Lofgren et al. 2002; Notaro et al. 2015b). For example, Lofgren et al. (2002) concluded that the duration of ice cover in Whitefish Bay (eastern Lake Superior) will decline by a factor of 3 by the late twenty first century, and by a factor of 8 in eastern Lake Erie, under the Canadian Global Coupled Model 1 business as usual scenario. Similarly, the frequency of ice-free winters in Whitefish Bay were predicted to increase from 0% in the late twentieth century to 36% in the late twenty first century, while in eastern Lake Erie, the increase was from 2 to 96%. Ice coverage, or lack thereof, can even have impacts on water temperature that carry over to subsequent seasons, leading to unseasonably cold or warm temperatures in the summer and fall, respectively (Austin and Colman 2007; Gronewold et al. 2015). Winter temperature variability could play an important role in future Great Lakes climates. Research has proposed that the preferential heating of high-latitude regions by greenhouse gases, greater than at low latitudes, can lead to greater and more persistent variability in temperatures at mid-latitudes, especially during winter. A general discussion is provided by Shepherd (2016), stemming in part from Francis and Vavrus (2012); however, these findings have been seriously called into question by Wallace et al. (2014). If this enhanced variability is borne out, it could lead to high contrast among winters in terms of air and water temperature and ice cover, as illustrated by the difference between the low ice-cover winter of 2011–12 and the high ice-cover winter of 2013–14.

Increased air temperature also has been associated with warming of the surface water temperatures in the Great Lakes during recent decades (Fig. 3; Austin and Colman 2007; Dobiesz and Lester 2009). Given that



Chemical habitat

One key aspect of the chemical habitat for fishes (see Fig. 2) is phosphorus concentrations, which generally limits primary production in freshwater ecosystems (Vollenweider et al. 1974). Projected changes in precipitation and air temperature can influence the delivery of phosphorus from the watershed to the lakes



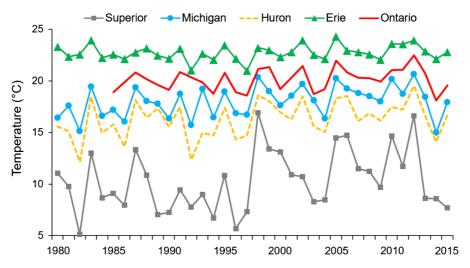


Fig. 3 Mean summer (July–September) water temperatures (°C) across the Great Lakes between 1980 and 2015, based on data from NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/) and Sharma et al. (2015). During this period, water

temperatures increased at rates of 0.08 °C/year in Lake Superior, 0.05 °C/year in Lakes Michigan and Huron, 0.02 °C/year in Lake Ontario, and 0.01 °C/year in Lake Erie. Note that data for Lake Ontario became available after 1985

by affecting tributary flow. Incorporating climate seasonality is especially important for determining tributary flow (LaBeau et al. 2015). In general, increased precipitation will increase flow, but this can be offset by increased evapotranspiration both on the lakes and the land of the drainage basin.

Across the Great Lakes, phosphorus loading and the projected influence of climate change has received the most attention in western Lake Erie, where eutrophication and harmful algal blooms (HABs) continue to cause concern (Michalak et al. 2013; Kane et al. 2014; Bullerjahn et al. 2016). Although "best management practices (BMPs)" in agriculture would help reduce sediment and phosphorus runoff, recent simulations in western Lake Erie indicate that climate-driven changes in precipitation and air temperature, and the resultant effects on tributary flow would be even more influential (Bosch et al. 2014; Cousino et al. 2015). In the Lake Michigan basin, where phosphorus loading in the nearshore does not lead to HABs as commonly as in western Lake Erie, Robertson et al. (2016) modeled 24 different scenarios over the next century and predicted that a 5% average predicted increase in precipitation, coupled with a 2.6 °C average predicted increase in air temperature, would lead to reductions in annual tributary flow by an average of 1.8%. Although no simple consensus projection exists for future annual phosphorus loading in the Great Lakes basin, given the multiple climatic variables and potential for land use to influence stream flow, there is greater consensus about seasonal patterns (see Kunkel et al. 1999; Kling et al. 2003; LaBeau et al. 2015). Phosphorus loading will likely increase in the spring, when precipitation will be higher and the loading potential is higher, owing to agricultural fields being fallow or the crops not yet mature. Conversely, phosphorus loading will likely decrease in the summer when precipitation will be lower, evapotranspiration will be higher, and the crops will be active taking up phosphorus.

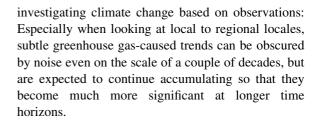
A second key aspect of chemical habitat for fishes is dissolved oxygen concentrations and the potential for hypoxia. Three main processes cause hypoxia in the Great Lakes and two of these processes are likely to lead to increased hypoxic conditions under future climate change. First, during summer stratification, hypolimnetic waters can become devoid of oxygen (e.g., central basin of Lake Erie, Scavia et al. 2014) when primary producers in the photic zone ultimately die and settle to the bottom of a lake and cause rapid oxygen depletion through decomposition. Due to vertical density differences and limited mixing, bottom oxygen is not adequately replenished and hypoxia develops. During this process, bottom oxygen depletion begins shortly after stratification and continues until fall turn-over. Warmer future temperatures are expected to lead to more intense stratification and a longer stratified period (earlier establishment and later turn-over, Kling et al. 2003; Trumpickas et al. 2009).



In addition, increased primary production could provide more biomass settling to the bottom, and, coupled with potentially slightly warmer bottom temperatures, will lead to increased and more rapid decomposition. In short, bottom hypoxia during the summer will likely develop earlier, last longer and cover a greater spatial extent. Second, shallow, productive areas of the Great Lakes, such as some coastal wetlands, can also experience hypoxia under diurnal cycles (e.g., Nelson et al. 2009). In this case, high photosynthetic activity during the daytime is replaced during nighttime by high respiration by both producers and consumers. Even under current conditions, this process can produce diurnal oxygen cycles, including nighttime hypoxia in highly productive ecosystems. Warmer temperatures will both decrease the solubility of oxygen in water and increase primary production which can potentially increase nighttime hypoxia. Finally, highly productive aquatic systems can become devoid of oxygen during extended periods of ice cover and winter stratification (e.g., Epstein et al. 1974; Madenjian et al. 2011). High respiration rates and limited photosynthetic activity under ice, coupled with lack of exchange with the atmosphere can contribute to hypoxia. While winter respiration is likely to increase in the future, we also previously noted that ice cover in the Great Lakes is projected to decline. As a consequence, the prevalence of winter, under-ice hypoxia is likely to cumulatively decrease in the Great Lakes.

Acidification

Not an impact of climate per se, but directly linked to increased atmospheric concentration of carbon dioxide, is the potential for acidification of water exposed to the atmosphere. This has been investigated extensively in the oceans, but on a much more limited basis in the Great Lakes. Phillips et al. (2015) showed that, although the various lakes have different baseline values of pH due to their geology, model simulations show a trend toward decreased pH over time for all of the lakes. At the same time, they call for more thorough and precise monitoring of lake pH, since they show that although existing measurements are consistent with their projected decrease in pH, their error bars are large enough that they don't actually preclude an increase in pH during 1990-2010. This is really a case in point of an issue that can cause difficulty in



Water levels

Another key habitat variable for many fishes that use the nearshore, coastal wetlands or tributaries during at least some portion of their life history is water level. Water levels in the Great Lakes are established through a balance of over-lake precipitation, overlake evaporation, runoff from the land portion of the lake's drainage basin (the net of these three items being termed "net basin supply"), inflow from any of the Great Lakes that are upstream, and outflow through the lake's outlet. While the impact of climate variability on Great Lakes water levels remained enigmatic during the twentieth century, the scientific community's understanding of climate change's influence on net basin supply and, ultimately, lake level has evolved considerably during recent years (Clites et al. 2014). The earlier studies almost exclusively projected lower lake levels (e.g., Croley 1990), whereas later studies using different methods (Manabe et al. 2004; MacKay and Seglenieks 2013; Notaro et al. 2015a) showed little change or even modest increases in lake levels. Lofgren et al. (2011) gave greater credence to the latter studies by demonstrating that studies that predicted lower water levels over-relied on nearsurface air temperature as a predictor of evapotranspiration from the land surrounding the Great Lakes, to the exclusion of factors such as the natural seasonal cycle of solar input. Lofgren and Rouhana (2016) expanded on this by using an ensemble of General Circulation Model inputs, and compared the earlier methods of Croley (1990) with three alternative methods deemed more physically plausible. The ensemble using the Croley (1990) method had a median drop in Lake Michigan-Huron levels of 0.66 m, whereas the alternative methods had a median drop of 0.14 m. This latter result appears more realistic, but at the same time, is only the central point of a large spread of possible results, and more studies are anticipated. Overall, a growing consensus is emerging that Great Lakes water levels will likely



not change as much in the twenty first century as was originally predicted.

Prey density

In this review, we consider the density of prey for fishes as an aspect of fish habitat (Fig. 2). Later in the manuscript, fish responses to these climate—driven changes in habitat will be further evaluated; because some fish are piscivores, they could be considered prey in this context. This section, however, will only focus on whether or not densities of invertebrates that feed planktivorous or benthivorous fishes could be influenced by climate—driven changes.

Depending on the lake, zooplankton densities in the Great Lakes have undergone varying degrees of change in density and community composition during recent decades (Conroy et al. 2005; Barbiero et al. 2012, 2014; Bunnell et al. 2014). One mechanism by which climate can influence zooplankton dynamics is by altering the timing of peak production. For example, in other temperate lakes earlier spring warming leads to earlier phytoplankton blooms, but not necessarily earlier peaks of herbivorous zooplankton (Winder and Schindler 2004; Shimoda et al. 2011). Only a few studies from the Great Lakes have reported a positive correlation between spring temperatures and total spring zooplankton biomass, but whether these relationships are causal was uncertain (Ludsin 2000; Vanderploeg et al. 2012). A second factor by which climate can influence zooplankton is by altering temperature-dependent growth and fecundity rates (e.g., Regier et al. 1990; Stockwell and Johannsson 1997). In this case, one would expect that a changing climate would influence the zooplankton community composition by favoring species that can maximize productivity in the new temperature regime. Despite these potential direct linkages between zooplankton and climate, we are unaware of any Great Lakes studies that have identified a linkage between zooplankton community changes or abundance and climate. Rather, most studies have concluded that the zooplankton community has been more regulated by bottom-up driven declines in phytoplankton biomass (Barbiero et al. 2011), non-consumptive predation effects (Pangle et al. 2007), or directly through predation (Lehman 1991; Stewart et al. 2010; Bunnell et al. 2011) than climate. Hence, future research should try to disentangle the effects of changing climate on Great Lakes zooplankton dynamics, given its potential direct (e.g., physiological, phenological) and indirect (e.g., chemical habitat) effects on zooplankton communities.

Climate-driven changes in water temperature could also theoretically influence the productive capacity of benthic macroinvertebrates in the Great Lakes (Magnuson et al. 1997). Given the paucity of water temperature time series throughout the water column, it should not be surprising that no studies in the Great Lakes have argued that changes in the benthic invertebrate community are primarily the result of climate-driven temperature changes. In contrast, their dynamics are hypothesized to be regulated by interactions with invasive species (e.g., Nalepa et al. 2009) or changes in water quality (e.g., Krieger et al. 1996). However, hypoxia appears to negatively influence benthic macroinvertebrate production and recruitment in western Lake Erie. Once the water quality in western Lake Erie improved and mayfly (Hexagenia spp., a high-quality prey for fishes) populations recovered, recruitment of this species was higher between 1997 and 2002 during years with less summer stratification, and presumably less hypoxia (Bridgeman et al. 2006). Hence the benthic invertebrate community could be negatively affected by future increases in hypoxia, facilitated through warmer water temperatures.

Detecting and assessing fish responses to climate change

Habitat changes associated with climate change are expected to directly and indirectly affect fish and fisheries (Fig. 2). In the Great Lakes, however, few studies have explored the links between fish population abundance, habitat variables and climate change, likely because other human-driven stressors received more attention (e.g., nutrient inputs: Ludsin et al. 2001; invasive species: Steinhart et al. 2004.). Most studies examining fish responses to climate change have used empirical approaches that link observed growth or recruitment variables to habitat variables believed to be driven by climate change, either alone or with other biological variables. Fewer studies, however, have projected fish population and habitat responses to climate change, which require not only downscaled future climate projections, but also

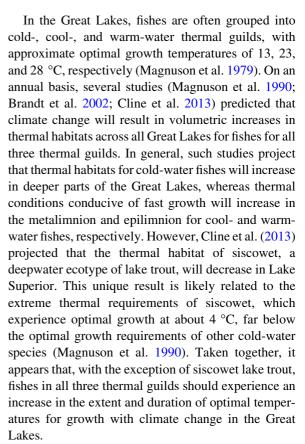


predictions for habitat variables driven by climate change in the Great Lakes. Most of these studies have been relatively limited in scope and fish responses were assessed under hypothetical changes in habitat variables (e.g., 1 °C increase in water temperature, Casselman 2002) or assumed scenarios of habitat changes (e.g., unchanged food availability, Hill and Magnuson 1990) rather than explicit predictions based on downscaled climate models. Although studies retrospectively detecting or projecting fish responses to climate change are small in number and limited in scope, they provide valuable insights into how climate change may affect fish growth, recruitment, phenology, and community composition in the Great Lakes.

Impacts on demographics

Growth

Climate change can affect fish growth directly through changes in thermal habitat and indirectly through effects on prey availability, as discussed above (Fig. 2). It is generally expected that climate-driven increases in water temperature would enhance the growth of fishes with higher physiological thermal optima (i.e., warmwater fishes) and reduce growth of those with lower thermal tolerances (i.e., cold water and perhaps coolwater fishes; e.g., Kling et al. 2003; Portner and Farrell 2008; Graham and Harrod 2009). However, the capacity of fish to maintain aerobic activity under increasing temperatures is related to temperature dependent oxygen limitation, which may be species-specific (Portner and Farrell 2008). In principle, increases in ambient temperature would be expected to enhance growth by increasing the capacity of fish to consume prey, at least until metabolic costs become too high to allow for normal, aerobic function or they surpass energy intake (Brett 1979). The net change in fish growth in response to climate change will be determined by how much of the increase in prey consumption capacity in a warmer environment can be realized to compensate for the increase in metabolic costs (Kao et al. 2014). The temperature at which growth is maximized, as well as the temperature at which growth becomes negative, will be speciesspecific and habitat-specific, depending ultimately on a variety of factors, including local habitat conditions (Stefan et al. 2001) and evolutionary history.



Responses of fish growth to climate change have been assessed using a theoretical approach—bioenergetics modeling-for cold-water salmonines (Chinook salmon, lake trout, and steelhead) and lake whitefish, cool-water yellow perch, and warm-water largemouth bass (Hill and Magnuson 1990; Brandt et al. 2002; Kao et al. 2015a, b). These studies projected that, because fish are able to behaviorally thermoregulate, their growth should increase with warmer thermal habitats, if prey does not become limiting. If prey was limiting, however, growth would be expected to decrease. Surprisingly, Hill and Magnuson (1990) and Kao et al. (2015a) both showed that growth of fishes in warmer thermal guilds may not always increase more than fishes in cooler thermal guilds when prey is unlimited. For example, during the period 2043-2070 under a global business as usual development scenario A2 (IPCC 2000), Kao et al.'s (2015a) model predicted a lower increase in growth for cool-water yellow perch (i.e., 7-12%) than for cold-water lake whitefish (13-34% increase) in southern Lake Michigan under an unlimited prey scenario, which is opposite than what one might expect with



warming water temperatures. The reasoning for this finding is related to the inability of many warm-water fishes to handle and consume sufficient prey to balance their larger metabolic costs (Kao et al. 2015a). Hill and Magnuson (1990) and Kao et al. (2015b) also showed that under a warming climate consumption will increase most in spring and fall when prey energy densities are relatively high (e.g., Madenjian et al. 2006). Such seasonality benifits fish growth because it increases gross energy intake on an annual basis (Kao et al. 2015b).

Collectively, the findings from these modeling studies suggest that changes in prey availability associated with climate change can be equally, if not more, important than changes in thermal habitats to fish growth. For example, under a global business as usual development scenario A2 (IPCC 2000), Kao et al. (2015b) showed that about a 10% increase in prey consumption is enough for Chinook salmon, lake trout, and steelhead in Lakes Michigan and Huron to maintain current growth in the projected warmer water temperatures of 2043-2070 even under less than ideal thermal conditions. Under unlimited prey conditions, however, their consumption could increase by 20-70%, and their growth could increase 23-69%. Because empirical studies also have shown that fish growth can be positively linked to the availability of thermal habitat (e.g., Coble 1966; King et al. 1999), prey availability (e.g., Headley and Lauer 2008; Lumb and Johnson 2012), or both (e.g., Kratzer et al. 2007; Rennie et al. 2009; Crane et al. 2015), the predicted response of fish species to climate change should not be made based on thermal guild alone. Consideration of prey and thermal habitat availability also are needed.

Recruitment

Climate change has the potential to influence fish recruitment (defined here as recruitment of adults to a fishery) directly by altering physical and thermal habitat during the spawning season, as well as during early development phases (Ludsin et al. 2014; Pritt et al. 2014). The direction and magnitude of direct climate change effects will ultimately be determined by the specific spawning behaviors of individual species and their thermal tolerances (Coutant 1987). Another, more indirect pathway for climate change to influence fish recruitment is through altering

population sizes of species that interact, either as prey, predators or competitors, with a particular species (i.e., through impacts on biotic interactions). Likely owing to the Great Lakes having long-term datasets on fish abundance, there is a long history of stock-specific recruitment studies and a full review of these studies is beyond the scope of this manuscript. Instead, the aim here is to review studies that directly addressed the role of climate on fish recruitment using various methods, including retrospective stock-recruitment, recruitment synchrony among multiple populations and assessment of recruitment success for fish during specific life stages.

Retrospective stock-recruitment analyses have long been used to identify how spawning stock size and climatic factors influence recruitment dynamics for a variety of fish species in the Great Lakes. More than any single factor, warm spring and summer water temperatures appear to promote recruitment and production of spring- and summer-spawning fishes across the basin (Madenjian et al. 1996; Fielder et al. 2007; O'Gorman and Burnett 2001; Redman et al. 2011; Madenjian et al. 2005; see Ludsin et al. 2014 for review of spawning times for economically and ecologically important Great Lakes species). Previous studies also have linked bloater recruitment to warmer water temperatures during egg incubation periods and early life stages (Rice et al. 1987), but a more recent study failed to find any consistent link between environmental conditions and bloater recruitment in lakes Michigan and Huron (Collingsworth et al. 2014). Recent evidence from Lake Erie suggests that precipitation-driven river discharge, brought on by climate change, could benefit yellow perch recruitment by influencing the formation of bigger, more prominent river plumes during the spring. In this system, larval yellow perch use turbid river plumes as a refuge from predators without compromising the ability of larvae to feed (Reichert et al. 2010; Pangle et al. 2012; Carreon-Martinez et al. 2015). However, the benefits of turbidity for fish recruitment are not universally experienced for fish across the Great Lakes. In Lake Superior, larval cisco survival may be impaired under turbid conditions because of increased predation by smelt, which are themselves freed from predation pressure and forage in surface waters during turbid conditions (Myers et al. 2014). Finally, several different climatic variables, including fall wind intensity, winter ice cover and



spring temperatures have been linked to whitefish recruitment in the Great Lakes (Lawler 1965; Freeberg et al. 1990), but these relationships are complicated by recent food-web changes brought about by the introduction of dreissenid mussels (Pothoven et al. 2001; Claramunt et al. 2010; Gobin et al. 2015). Lynch et al. (2015) directly assessed the impact of climate change on lake whitefish populations in the 1836 Treaty Waters of the upper Great Lakes, using traditional stock recruitment models and projected physical habitat conditions. They found that lake whitefish recruitment may increase in a majority of the management units of the 1836 Treat Waters, most likely due to calmer fall wind speeds and warmer spring temperatures as a result of climate change. However, the impact of climate change on lake whitefish recruitment was not uniform across the study area, with projected declines in recruitment for some management units (Lynch et al. 2015).

Another way to discern the influence of climatic variables as a driver of recruitment variation is to examine patterns of recruitment synchrony for multiple populations over large spatial scales. Warm spring and summer temperatures have been shown to be positively related to yellow perch and walleye recruitment across the Great Lakes and have been implicated in the synchrony of strong yellow perch year-classes across the entire Great Lakes region over multiple decades (Honsey et al. 2016). Climate-induced synchrony has also been documented across multiple cool-water fish species in Lake Michigan, as strong alewife, yellow perch, and rainbow smelt year-classes were associated with warm spring and summer water temperatures as well as below-average wind speeds during this period (Bunnell et al. 2016). In a similar study, bloater population sizes and recruitment showed positive synchrony over multiple decades in Lakes Superior, Huron and Michigan, with climate being the most parsimonious explanation (although but no obvious climate signal was apparent; Bunnell et al. 2010). Although climate variables can explain some of the recruitment variability for these species, numerous examples can be found to show that nonclimate variables can be just as important recruitment drivers.

Successful recruitment depends, not only on the environmental conditions experienced by larval and juvenile fish, but also on different biotic and abiotic factors aligning at the appropriate place and time.

Therefore, studies that address climate impacts during specific life stages are particularly useful for detecting the influence of climate change on fish recruitment. For example, alewife (Madenjian et al. 2005; Collingsworth et al. 2014), yellow perch (Carreon-Martinez et al. 2015), and walleye (Fielder et al. 2007) recruitment has been shown to be negatively affected by predation at different times of their first years of life. Additionally, Jones et al. (2006) reviewed the available evidence for changing physical habitat conditions (e.g., increased water temperatures, altered hydrology, decreased ice cover and altered water transparency) in Lake Erie and evaluated how walleye recruitment could be affected. They used mechanistic models to simulate specific spawning behaviors for riverine and lake spawning populations, transport of larvae to nearby nursery habitats, and habitat supply for adults and juveniles. Not surprisingly, they concluded that effects of climate change on walleye recruitment are dependent on the specific spawning behavior (river spawning vs. lake spawning) and life stage (juvenile vs. adult) of walleye that was considered. Looking at another Percid species, climate warming may also have a negative impact on yellow perch recruitment by influencing egg development and, possibly, through altering the phenology of larval development and their preferred prey (see full description of phenology mechanism below). Many previous studies have suggested that warming would benefit yellow perch in the Great Lakes, however Farmer et al. (2015), using a combination of field-based recruitment estimates and controlled laboratory experiments, found that warm winters may reduce egg quality and hatching success for this cool-water, spring-spawning species. The above examples suggest that novel mechanisms for describing the effects of climate change on fish recruitment may be best uncovered by considering the effects of climate on survival during early life stages.

Taken collectively, the results from previous research show a complex relationship between climate and recruitment for fish populations in the Great Lakes. Fish recruitment is influenced by a complex suite of variables that govern the production and survival of early life stages (Houde 1994; Ludsin et al. 2014). In this regard, climate can be viewed as one of the many factors that regulate recruitment, but it may play a minor or interacting role when compared with other major drivers of recruitment success, such as



access to appropriate food resources and spawning habitat. When climate factors such as water temperatures or wind speeds are considered in isolation, models may not accurately project future recruitment success given the importance of other non-climate variables as drivers in Great Lakes fish species Most of the evidence for climate impacts on recruitment tends to come from traditional stock recruitment assessments using a single population, but few studies revisit these analyses when new data are collected and those that do are sometimes unable to reproduce their initial results when extrapolated to nearby populations (Myers 1998; Collingsworth et al. 2014). More complex models that take into account physical habitat influences on specific life stages (Jones et al. 2006) and models that project recruitment for multiple stocks using realistic climate change scenarios (Lynch et al. 2015) will help provide a realistic picture of the effects of climate change on fish recruitment in the Great Lakes, but climate remains but one of the many interacting factors regulating recruitment in these systems.

Phenology

Projected climate-driven changes that lead to altered thermal conditions (e.g., faster spring warming, longer stratification) can affect Great Lakes fish populations by altering their reproductive phenology. The direction and the magnitude of specific phenological shifts would be expected to vary among species, owing to variation in life-history strategies (e.g., spawning season), physiology (e.g., timing of and thermal requirements for ovarian development), and dependence on climate-driven environmental cues (e.g., water warming rate, river flows) relative to other cues that are less variable among years (e.g., photoperiod). These shifts in reproductive phenology can include spawning earlier in response to an early spring onset, as would be expected for most warm- and cool-water fishes (e.g., percids, clupeids, and moronids), or spawning later during the fall, which would be expected for most cold-water fishes, including lake trout, lake whitefish, bloater, and other introduced salmonines (Lyons et al. 2015). Such shifts in phenology have been documented in fish populations outside of the Great Lakes basin, including lake, riverine, estuarine, and oceanic environments (Taylor 2008; Genner et al. 2010; Schneider et al. 2010; Thackeray et al. 2010, 2013).

Few studies have explored the impact of climate change on reproductive phenology in the Great Lakes basin (e.g., Farmer et al. 2015; Lyons et al. 2015). However, those that have lend support to the notion that climate-induced warming can alter the timing of spawning. For example, Lyons et al. (2015) documented earlier spawning in Lake Michigan yellow perch in response to an earlier spring onset, with spawning advancing by 1.8 d to 6.8 d per decade since the 1980s. Similarly, Farmer et al. (2015) and May (2015) documented earlier spawning for Lake Erie yellow perch and walleye, respectively, following warm winters with an early spring onset relative to cold winters with a delayed spring onset. Lyons et al. (2015) also provided evidence to indicate that Lake Michigan lake trout spawned later during the fall during the past several decades, which matches theoretical expectations associated with a longer fall growing season (i.e., delayed winter onset). However, given that a corresponding increase in temperature was not detected, and no shift in spawning time was observed for a Lake Superior lake trout population despite warming there, the effects of climate change on the reproductive phenology of take trout and other fall spawners remains inconclusive (Lyons et al. 2015).

The lack of study on the impacts of climate change on reproductive phenology in the Great Lakes is concerning, given the many ways in which altered phenology can impact the recruitment process. Most notably, a climate-driven alteration of the spawning time can lead to mismatches between newly hatched larvae and their planktonic prey (Durant et al. 2007; Thackeray et al. 2010, 2013). This mechanism was posed as a possible reason for consistent failed yellow perch year-classes in Lake Erie following short, warm winters, in addition to the negative effects of a short winter duration on egg size and hatching success (Farmer et al. 2015). Specifically, Farmer et al. (2015) showed that, although yellow perch spawn earlier after a warm winter (and early spring onset), the shift was somewhat constrained (advanced by about 1 week) relative to the shift in the thermal regime (advanced by about 3 weeks). In turn, following a short, warm winter, yellow perch larvae may hatch too late after the peak in zooplankton production to allow for sufficient feeding to promote recruitment to the juvenile stage



(Farmer et al. 2015). Interestingly, mismatches between larval and zooplankton production may occur in the other direction, where a fish species spawns too early, and hence, misses the plankton peak on the other end. Lake Erie walleye appears to be a strong candidate for this mismatch, given that its spawning time appears less constrained than yellow perch (Schneider et al. 2010; May 2015). As an example, peak hatching of Lake Erie walleye larvae occurred two months earlier in response to an early spring onset (mid-March during 2012) relative to the prior year (mid-May peak), which had a thermal regime more typical of Lake Erie historically (May 2015). These differences between species reinforce the need to understand what physiological and evolutionary constraints affect the reproductive phenology of fish (Farmer et al. 2015; Lyons et al. 2015), as well as their prey and predators, to improve understanding and predictions of how climate change can alter fish populations through altered reproductive phenology.

Impacts on community structure

Differences in fish growth and recruitment in response to climate change will result in changes in fish distribution and production and may, ultimately, change community structure (Fig. 2). The most common prediction for the effect of climate change on fish distribution is that warm-water fishes will expand northward and the southern boundary of cold-water fishes will retract (Magnuson et al. 1997). Studies have projected increases in thermal habitat for warm-water fishes in lakes Superior and Michigan where such thermal habitats currently exist only in some nearshore areas (Brandt et al. 1980; Magnuson et al. 1990; Cline et al. 2013). Hill and Magnuson (1990) and Brandt et al. (1980) showed that warm-water fishes may thrive in these new habitats so long as other environmental and biological conditions remain unchanged. Magnuson et al. (1990) suggested that thermal habitats for cold-water lake whitefish will increase with climate change in Lake Erie, the shallowest and southern-most Great Lake, which implies that increases in temperatures alone will not result in retraction of southern boundary of most cold-water species. One exception is siscowet, the deepwater ecotype of lake trout in Lake Superior, whose thermal habitats were predicted to decrease with climate change (Cline et al. 2013). Because of expected changes in fish distribution, the proportion of cool- and warm-water fishes may increase in fish communities of the Great Lakes, especially in the northern areas.

Fish community structure can change when predator-prey interactions are altered in food webs. In the Great Lakes, predator-prey interactions may change due to the northward expansion of warm-water predators (such as smallmouth bass Casselman 2002) and invasive fish species (Cline et al. 2013) in response to climate change. Predator-prey interaction may also be affected by species-specific differences in growth. For example, Kao et al. (2015b) showed that steelhead (Oncorhynchus mykiss) and lake trout may be better adapted to the future climate regime than Chinook salmon. These salmonines have different diet compositions and consumptive demands. Steelhead and lake trout have lower consumptive demands (Kao et al. 2015b) and feed heavily on warm-water round goby (Roseman et al. 2014) whereas Chinook salmon have higher consumptive demands (Kao et al. 2015b) and prefer feeding on cool-water alewives (Jacobs et al. 2013). In addition, Cline et al. (2014) showed that sea lamprey-induced mortality on lake trout may increase with water temperature. The findings from these studies demonstrate the complexity of climate change effects on fish community structure.

Interactions between climate change and other stressors

Climate change also can interact with other humandriven stressors to influence fish production, fish community composition, and fisheries management. Below, we discuss interactions between climate change and three other prominent anthropogenic stressors in the Great Lakes basin: invasive species; nutrient pollution; and alteration of top predator biomass via fish stocking and harvest. These discussions are highly speculative, as empirical investigations into the effect of these multiple stressors on fish populations are sparse (e.g., Moran et al. 2010), especially in the Great Lakes basin (no known studies).

Climate change and invasive species

Climate warming could facilitate the establishment of new invaders, both vertebrate and invertebrate, or



expand the potential range of existing invaders (see Mandrak 1989; Rahel and Olden 2008; Whitney et al. 2016). In Lake Superior, for example, white perch and alewife are relatively rare, but are expected to expand their distributions when with continued climate warming (Bronte et al. 2003), likely owing to reduced overwinter mortality (Johnson and Evans 1990; Hook et al. 2007). Invasive round goby is also another species that is expected to gain more physiologically beneficial habitat with continued warming across the Great Lakes (Kornis et al. 2012). Expanding populations of invasive species could in turn exacerbate the largely negative impacts that invasive species have had on Great Lakes ecosystems via both competitive and predatory interactions. For example, competition for zooplankton prey may increase due both to expanding invasive planktivore populations (e.g., white perch; Schaeffer and Margraf 1986) and continued reductions in pelagic productivity due to dreissenid mussels (Conroy et al. 2005). In turn, the largely negative impacts that invasive species have had on the ecosystems of the Great Lakes could be exacerbated. While increased competition for prey (e.g., zooplankton) may occur with expanded invasive species populations (Schaeffer and Margraf 1986), we expect that invasive species would have greater negative effects on native fishes through predatory effects. For example, expanded round goby, alewife, and white perch populations would be expected to negatively affect native fishes such as smallmouth bass Micropterus dolomieu (Steinhart et al. 2004) and yellow perch (Brandt et al. 1987; Carreon-Martinez et al. 2014) by preying on pre-recruited individuals during the egg and/or larval stage. Similarly, enhanced predation by invasive species on older, recruited life stages is conceivable. Bioenergetics modeling has demonstrated how sea lamprey have benefitted from a warming Lake Superior since 1979 by growing larger and more fecund (Cline et al. 2014). This is problematic because invasive sea lamprey have already had devastatingly negative effects on fisheries by parasitizing and killing recreationally important piscivores and commercially important lake whitefish as adults (Bence et al. 2003), and larger individuals likely could inflict a higher mortality rate on their hosts than smaller ones.

Interactions between climate change and non-fish invaders, which have proliferated across the Great Lakes basin during recent decades (see Vanderploeg et al. 2002) also may indirectly affect fish recruitment and production in the Great Lakes by altering food web interactions. These effects, however, can be both positive and negative. For example, the spiny water spiny water flea, (Bythotrephes longimanus), is a voracious carnivorous zooplankter that can compete with zooplanktivorous fishes (including larval fish) for smaller zooplankton prey (Bunnell et al. 2011). Bythotrephes individuals typically attain high densities in summer and fall in each of the five lakes, with their densities influenced by both temperature and predation by alewife and cisco (Keeler et al. 2015; Pothoven et al. 2007). Warmer surface temperatures can result in earlier peak densities (Manca and DeMott 2009) and higher consumption rates (Yurista et al. 2010). Together, these factors could lead to intensified competitive interactions between spiny water flea and planktivorous fishes in the Great Lakes. By contrast, climate warming could simultaneously increase prey availability to zooplanktivorous fishes (and larvae) by reducing the grazing potential of the quagga mussel (Dreissena bugensis), a sessile, benthic, filter-feeder that, in any given year, filters the largest amount of phytoplankton during non-stratified periods (e.g., spring), because plankton can settle down to the lake bed from anywhere in the water column (Barbiero et al. 2011). Spring is a period when the larvae of many ecologically and economically important obligate zooplanktivore fishes are in high abundance (Ludsin et al. 2014). Because thermal stratification is expected to start earlier and last longer in large lake ecosystems, including the Laurentian Great Lakes (Kling et al. 2003), the ability of quagga mussel grazing to suppress phytoplankton production during spring would be expected to decline. In turn, zooplankton availability to larval fish during the spring could increase, through bottom-up effects (Bunnell et al. 2014). However, we remain uncertain of how climate change will interact with invasive species in this context to affect fish community composition and fisheries production.

Another high profile invasive species threat in the Great Lakes is the risk of introduction and establishment of several species of Asian carps, with recent focus on bigheaded, silver, and grass carp (e.g., Cuddington et al. 2014; Anderson et al. 2015; Chapman et al. 2013; Grippo et al. 2017). Though there have been a number of risk assessments concerning Asian carps and the Great Lakes, we are not aware of major efforts addressing the threats in a



climate change context, though water temperature is a key parameter related to spawning and maturation of bighead carp (Cooke 2016).

A related issue is threats from fish diseases, which have been the subject of increasing research in the Great Lakes region, including some nonnative pathogens such as viral hemorraghic septicemia (VHS) and microsporidian parasites (e.g., Bain et al. 2010, 2011; Escobar et al. 2017). While research is increasing on implications of climate change on parasites and fish health generally (e.g., reviewed by Lohmus and Bjorklund 2015; Cornwell et al. 2015; Sheath et al. 2016; Bruneaux et al. 2017), it appears there has been limited research with particular focus on the Great Lakes region. A simple conceptual approach to such research would entail considering climate implications for the physical environment, fish, and pathogens of interest (Chiaramonte et al. 2016).

Climate change and eutrophication

Future climatic conditions in the Great Lakes region are expected to not only lead to warmer temperatures, but also increase the intensity and frequency of storm and precipitation events (Kunkel et al. 1999, 2002). As discussed above, such increases are expected to cause enhanced nutrient loading during some seasons (e.g., spring, winter), and in turn, shifts in the composition of primary producers (from edible to inedible species such as cyanobacteria; Haney 1987; Ghadouani et al. 2003; Litzow et al. 2006), reduced water clarity (with influences on predator-prey dynamics; Swenson 1977; Lester et al. 2004; Myers et al. 2014), and increased summertime hypoxia in some highly productive locations. As we discuss below, the effects of these changes on individual fish populations can be quite complex, depending in large part on attributes of the ecosystem.

One key factor that will determine whether the expected increases in precipitation-driven nutrient and sediment loading positively or negatively affect fish production is current ecosystem productivity. In more oligotrophic systems where bottom-up regulation of higher consumers appears to be occurring and water transparency tends to be high (e.g., lakes Huron and Michigan; (Bunnell et al. 2014; Barbiero et al. 2011b), moderate, climate-driven increases in nutrient runoff may have primarily positive effects on fish production by promoting zooplankton production. Likewise,

enhanced precipitation-driven sediment runoff could benefit fish recruitment in these systems by creating sediment plumes in the open lake that can offer a refuge to native species (e.g., yellow perch) from invasive predatory fishes without compromising feeding (Reichert et al. 2010; Pangle et al. 2012; Carreon-Martinez et al. 2014). By contrast, in highly eutrophic ecosystems, climate-driven increases in nutrient loading could hamper fish production by reducing the availability of preferred thermal habitat and prey to benthic fishes during periods of extended bottom hypoxia (Arend et al. 2010; Ludsin et al. 2001; Brandt et al. 2011), or by promoting the production of cyanobacteria at the base of the food web that are largely inedible, toxic to crustacean zooplankton, and of low nutritional value (Haney 1987; Ghadouani et al. 2003; Litzow et al. 2006). In this way, the relationship between nutrient loading (or lake trophic status) and species-specific fish production in the Great Lakes is likely to follow a dome-shaped curve with greatest fish production at some moderate nutrient loading (mesotrophy) and various deleterious effects leading to decreased fish production at high nutrient loading (Oglesby et al. 1987; Caddy 2000).

Given that water clarity is highly influenced by nutrient and sediment runoff, water clarity is likely to be highly influenced by changing precipitation patterns. With expected increases in precipitation and storm events during spring that will cause more nutrient and sediment runoff, as well as higher temperatures during the summer that will promote cyanobacteria production, we should expect water clarity to decrease with continued climate change. In addition, changes in turbidity have the potential to alter lake warming and stratification, depending on factors such as lake depth and trends in water turbidity (Rose et al. 2016). Such a shift holds great potential to indirectly affect fish growth and recruitment by influencing thermal habitat quality, foraging success and predation risk (Fiksen et al. 2002; Pangle et al. 2012). However, whether reduced water clarity will benefit or harm fish recruitment and fisheries production is difficult to predict, as it will depend on many factors, including the nature of the turbidity (sediment or phytoplankton; Wellington et al. 2010) and the level of predation risk in the system (Pangle et al. 2012). For example, previous research has suggested that phytoplankton turbidity can greatly reduce foraging success of all life stages of fish relative to sediment turbidity



whereas sediment turbidity only seems to negatively affect older life stages of fish (Wellington et al. 2010). Thus, in systems such as Lake Erie that are highly eutrophic and plagued by cyanobacteria blooms during the summer, fish foraging success might be expected to decline with continued nutrient loading, at least during part of the year (Manning et al. 2014). By contrast, in systems with abundant predators, climatedriven reductions in water clarity could benefit fish foraging by serving as a refuge from predation from predators (Miner and Stein 1996; Abrahams and Kattenfeld 1997; Reichert et al. 2010; Pangle et al. 2012; Carreon-Martinez et al. 2014), although shifts in spatial overlap between larval fish and their predators may result in increased mortality in some cases (Swenson 1977; Myers et al. 2014). Similar to the relationship between lake trophic status and fish production, we expect that the foraging success, and subsequent growth and recruitment of most species, will show a unimodal (hump-shaped) relationship with water clarity (Pangle et al. 2012), similar to the relationship between Secchi depth and walleye yield observed by Lester et al. (2004) in Ontario inland lakes. Ultimately, this expectation points to the need to model water clarity, and potential interacting effects of temperature, in the face of future climate and landuse change, which has yet to be conducted for any lake ecosystem.

Climate change and fish stocking

Although models indicate that the primary piscivorous species that are stocked in the Great Lakes (lean form of lake trout, Chinook salmon, rainbow trout (Oncorhynchus mykiss), brown trout (Salmo trutta), coho salmon) could theoretically experience a more optimal growth environment based on a warming climate, these populations could also experience even lower growth rates in the future if prey densities are limiting (see Kao et al. 2015b). These salmonine species, in particular, are largely reliant on alewife as prey, and climate alone suggests that alewife recruitment could increase with increasingly frequent warm springs and summers (Madenjian et al. 2005). At the same time, salmonine predation will likely increase under warming water temperatures, potentially leading to conditions similar to those preceding the decline of the Chinook salmon fishery in Lake Huron in the early 2000s and creating complex management decisions in the other lakes (Dettmers et al. 2012; Claramunt and Clapp 2014). In the future, managers will have to recognize the lake-specific impacts from climate change and alter stocking policies to better balance salmonine physiology and life history with the prey dynamics and environmental conditions within each Great Lake (Kao et al. 2015b).

Climate change effects on thermal habitat availability, forage fish populations, and consumptive demand have the potential to dramatically influence future management of both introduced salmonid populations and future protection and restoration of important native species. Recent collapses of pelagic prey fish populations (Riley et al. 2008) and increasingly intense predation pressure on these populations by naturalized and stocked Pacific salmonids (Jacobs et al. 2013; Johnson et al. 2010) have led to declines in the condition and abundance of these popular game fish and a substantial debate about their future management in the Great Lakes (Dettmers et al. 2012; Claramunt and Clapp 2014). Although the primary mechanism for the decline in prey fish biomass and production is thought to be from factors other than climate change (e.g., increased piscivory, declining nutrient inputs, invasive species; Bunnell et al. 2014), climate change could further complicate managers' ability to mitigate such declines through either stocking or harvest policies.

As part of providing sustainable and diverse fisheries throughout the Great Lakes, native species conservation and rehabilitation has been one of the primary goals of Great Lakes fisheries managers for several decades (Christie 1963; Stockwell et al. 2009). Recently, there has been increased interest in reintroducing ciscoes or deepwater ciscoes to areas where they have previously been extirpated (Zimmerman and Krueger 2009). Given that the success of many species reintroductions generally depends on the availability of quality habitat (Cochran-Biederman et al. 2015), changes in the thermal suitability and resource availability in proposed reintroduction areas should be considered in future restocking efforts. Although no models have forecasted potential changes in cisco or deepwater cisco thermal habitat, we can assume that thermal conditions may actually increase given that other studies have projected increases for cold-water species (Magnuson et al. 1990; Brandt et al. 2002; Cline et al. 2013). However, climate change may also alter the depth distributions of



coregonid complexes in the Great Lakes, as increasing epi- and metalimnetic temperatures may force shallower-dwelling species to thermal refugia at deeper depths, while hypolimnetic processes like hypoxia may limit the extent of deepwater habitats (Lynch et al. 2016), thus potentially altering niche differentiation or causing novel trophic interactions between species. Given that the success of many species reintroductions generally depends on the availability of quality habitat (Cochran-Biederman et al. 2015), and considering the successful reintroduction of important forage species like ciscoes may also form the basis for further rehabilitation of native predators like lake trout, changes in the thermal suitability and resource availability in proposed reintroduction areas could be beneficial to future restocking efforts.

Incorporation of climate change into fisheries management

Climate change adaptation in natural resource management is a relatively young field, though with a rapidly expanding literature (e.g., Staudinger et al. 2013; Stein et al. 2013). Stein et al. (2013) reiterated five adaptation principles, including embracing forward-looking goals, linking actions to climate impacts (while considering non-climate stressors), considering the broader landscape context, selecting strategies robust to an uncertain future, and having agile and informed management (including, but not limited to, adaptive management). Adaptation can be targeted at different levels of biological organization (e.g., species, habitats, ecosystems), and ecosystem-based adaptation is a framework of increasing interest (Stein et al. 2013), an approach consistent with longstanding interest in an "ecosystem approach" to fisheries management in the Great Lakes (Gaden et al. 2012). A key approach in climate change adaptation is reducing vulnerability by addressing exposure (i.e., change in a climate-related threat), sensitivity (of a species or system to those changes), and adaptive capacity (enhancing the capacity of the species or system to accommodate changes) (Stein et al. 2013).

Approaches to considering climate change implications for Great Lakes fisheries must take into account the complicated nature of fisheries management in the Great Lakes region, involving eight states, a Canadian province, and several tribal entities (including two U.S. inter-tribal organizations), two federal governments, and the binational Great Lakes Fishery Commission (GLFC) (Gaden et al. 2008). Though most management occurs at the state, provincial, and tribal levels, the GLFC has key roles: (1) coordinating research to inform management allowing for maximum sustainable production of particular fish stocks of concern; and (2) controlling sea lamprey populations (GLFC 2007). The guiding document for management coordination is *A Joint Strategic Plan for Management of Great Lakes Fisheries*, and in the most recent revision climate change was recognized as a new emerging issue, though no specific research or management actions were identified in the plan (GLFC 2007).

The extent of consideration of climate change in Great Lakes fisheries management planning among the states, province, and tribes appears to vary, at least based on public management documents (see Table 1). For example, Ontario's provincial fish strategy references multiple potential impacts from climate change, including its role as an interactor with other stresses such as invasive species (Forestry 2015); the Ohio Department of Natural Resources-Division of Wildlife's fisheries tactical plan recognizes climate change as an unmanageable threat to Lake Erie fisheries and seeks ways to understand its impact (Hale et al. 2013); and the Great Lakes Indian Fish and Wildlife Commission has multiple projects addressing climate change and fisheries (Commission 2016). Michigan's general fisheries planning document also references the need for developing decision-support tools to help in broader scale planning that account for climate change (Resources 2013). We recognized that other agency research projects may also be considering climate-effects on fisheries. For example, the Michigan Department of Natural Resources carried out a recent climate change vulnerability assessment of 400 fish and wildlife species of greatest conservation need (and game species), and identified 25 fish species that would be at least "highly vulnerable" to climate change in the state (Hoving et al. 2013).

Several broader agreements, strategies and programs with relevance to Great Lakes fisheries have begun to address climate change in various ways. The recently revised Great Lakes Water Quality Agreement has annexes addressing habitat, species, climate change and other components relevant to fisheries



(including Lakewide Management Plans) that can incorporate climate change considerations (see Table 1). The major program in the United States addressing multiple aspects of Great Lakes restoration and protection, the Great Lakes Restoration Initiative, has in recent years been considering climate resiliency as part of project review criteria (Agency 2014). There are multiple references to climate change in Ontario's Great Lakes Strategy, including a call for further research on climate change impacts to fisheries.

In summary, incorporation of climate change considerations into fisheries management planning in the Great Lakes region varies but is generally in early stages. Given that research seeking to understand the risk of climate change to Great Lakes fisheries dates back to the late 1980s (e.g., Meisner et al. 1987; Mandrak 1989; Magnuson et al. 1990), this undeveloped management response may be, in part, explained by more immediate threats to the sustainability of Great Lakes fisheries, including invasive species and habitat degradation, as ranked by decision and policy

Table 1 List of public management documents and their relevance climate change

Program/agreement/plan	Lead agency	Climate component	References
A Joint Strategic Plan for Management of Great Lakes Fisheries	Great Lakes Fishery Commission (GLFC)	Climate change identified as "new emerging issue" in 1997 plan; no specific research or management actions identified, though climate change has arisen in research priorities	GLFC (Great Lakes Fishery Commission 2007)
Environmental Principles for Sustainable Fisheries in the Great Lakes Basin	Council of Lake Committees (GLFC)	No principle emphasizing climate change; however example includes reference to "climate changes" and uses of habitat, and Principle 3 references adaptive approaches to protection and improvement of functional habitats	Council of Lake Committees (2016)
Charting the Course: Fisheries Division's Framework for Managing Aquatic Resources	Michigan DNR	Objective on decision support tools references need to address climate change in landscape/ waterscape-level decision-making	Resources (2013)
Fisheries Management Plan for the Minnesota Waters of Lake Superior	Minnesota DNR	Includes brief section on climate change, and reference to supporting LaMP document on climate change and Lake Superior (Huff and Thomas 2014)	Huff and Thomas (2014)
Lake Michigan Integrated Fisheries Management Plan, 2003–2013	Wisconsin DNR	No reference to climate change	Team (2004)
Ohio's Lake Erie Fisheries, 2015	Ohio Division of Wildlife	Multiple references to climate change, including improving understand of fisherie impacts	Hale et al. (2013)
Lake Erie 2015 Annual Report; Lake Ontario 2015 Annual Report	New York State DEC	No reference to climate change	Conservation (2016a) and Conservation (2016b)
Ontario's Provincial Fish Strategy: Fish for the Future	Ontario MNRF	References climate change and multiple potential impacts (shifting ranges, interaction with other stresses, etc.)	Forestry (2015)
Great Lakes Water Quality Agreement	USEPA, ECCC	Includes annexes on habitat and species (Annex 7) and climate change (Annex 9); Lakewide Management Plans (Annex 2) also addressing climate change	States (2012)
Climate Change Program	GLIFWC	Multiple projects examining impacts of climate change on fisheries	Commission (2016)
Great Lakes Restoration Initiative	USEPA	Action Plan II notes consideration of climate resiliency criteria in project review	Agency (2014)
Ontario's Great Lakes Strategy	Government of Ontario	Multiple references to climate change, including improving understanding of fisheries impacts	Ontario (2012)

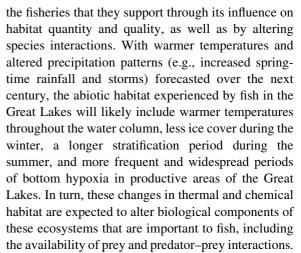


makers as well as fishery researchers (Mulvaney et al. 2014). In their survey of fisheries managers, climate change was recognized as a threat concerning "long-term stability" (Mulvaney et al. 2014). Given that managers can be judged by fisheries sustainability and production in the present day and expectations for the near term, it may not be surprising that those surveyed also favored modeling exercises that provided predictions for the nearest time scale (2030–2039) as opposed to decadal periods later in the century.

Other recent reviews have identified a number of issues that should be addressed in understanding and managing freshwater fisheries more broadly in a changing world, with several common themes identified, including the value in a broader ecosystem perspective and accounting for multiple interacting stresses, the importance of adequate monitoring programs, and involvement/consideration of perspectives of diverse stakeholders/users (e.g., Poesch et al. 2016; Paukert et al. 2016; Hunt et al. 2016). Poesch et al. (2016) highlighted the importance of adaptive management, and noted several adaptation plans have been developed for eastern Canada. In a similar vein, the importance of both managing for ecological resilience as well as developing resilient management systems (given factors such as interacting stresses and broader uncertainties going forward) has been recognized (Paukert et al. 2016). For example challenges with cisco in inland lakes in Minnesota (perceived as related to climate) led to research and consideration of management responses in a broader landscape context (Paukert et al. 2016), and such an approach will be needed to address similar challenges to Great Lakes fisheries. The importance of considering broad linkages between ecological and social systems should also be considered, including, for example, the implications of ecological (e.g., warming waters, changed fish assemblages) or social changes (e.g., anglers' behaviors in response to policy changes) on broader fisheries management challenges (Hunt et al. 2016). A number of these themes are also identified in a recent review as part of general recommendations on Great Lakes fisheries management (Minns 2014).

Conclusions

Climate change shows great potential to directly and indirectly influence Great Lakes fish populations and



Unfortunately, few climate change studies have been conducted in the Great Lakes basin to explore the effects of these expected changes on fish populations. The majority of such studies have been bioenergeticsbased modeling studies that are laden with assumptions about prey availability, foraging rates, and intraand inter-species interactions. Further, nearly all of these studies have only focused on the impact of warming on thermal habitat, with little (if any) consideration of expected simultaneous changes in precipitation. Acknowledging these limitations, however, these studies have shown general agreement, suggesting that climate warming will positively influence most species—especially coolwater warmwater species—by creating more habitat for positive growth, with exception of coldwater species living in ecosystems at the extremes of their distributions in the basin (e.g., Lake Erie lake trout, burbot, and whitefish; Lake Superior siscowet lake trout).

Given the dearth of climate-related fisheries investigations in the Great Lakes, reliable predictions of the future of fish population demographics, fish community composition, and fisheries production are speculative at best. Compounding this uncertainty is a lack of understanding as to how other anthropogenic stressors, both planned (e.g., harvest, stocking) and unplanned (e.g., invasive species, eutrophication), will interact with climate change to affect the ecosystems of the Great Lakes and the fisheries that they support. This collective lack of understanding should be recognized and rectified, as numerous examples from marine ecosystems have shown that climate change has already begun to cause population declines (e.g., Portner and Knust 2007), shifts in species distributions



(e.g., Perry et al. 2005), and fluctuations in fisheries production (e.g., Southward et al. 1988). We suspect that Great Lakes fish populations also have begun to respond to climate change, given the many documented changes in temperature, precipitation, and aquatic habitat in the Great Lakes, as well as the likelihood that climate-induced change would be faster in the smaller Great Lakes than in large marine environments (Adrian et al. 2009; Schindler 2009; Williamson et al. 2009). In support of this notion, Farmer et al. (2015) used long-term agency assessment data, field-based sampling, and a controlled laboratory experiment to show how winter warming may have contributed to failed yellow perch recruitment events in Lake Erie during the past four years, through effects on reproduction. Because of the high degree of climate-driven synchrony that has been demonstrated in Great Lakes yellow perch (Honsey et al. 2016) and bloater (Bunnell et al. 2010) populations, and even synchrony across multiple fish species in Lake Michigan (Bunnell et al. 2016), we strongly support the call by others (e.g., Ludsin et al. 2014; DeVanna-Fussell et al. 2016) for expanding long-term monitoring of these ecosystems, as well as for additional modeling and experimental research investigations that test effects of climate change in combination with other anthropogenic stressors.

While most Great Lakes fishery management agencies acknowledge that climate change is a threat, the published research indicates that most of the funded research and monitoring has largely ignored human-driven stresses (excepting harvest and stocking) or has focused on other human-driven stressors, such as invasive species and eutrophication. Expansion of monitoring and research to consider the stresses of climate change, along with these better-studied stressors, should offer managers the best opportunity to keep the valuable Great Lakes fisheries sustainable in the face of continued human-driven changes.

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