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The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries

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The Laurentian Great Lakes Basin provides an ecological system to evaluate the potential effect of climate change on dynamics of fish populations and the management of their fisheries. This review describes the physical and biological mechanisms by which fish populations will be affected by changes in timing and duration of ice cover, precipitation events and temperature regimes associated with projected climate change in the Great Lakes Basin with a principal focus on the fish communities in shallower regions of the basin. Lake whitefish *Coregonus clupeaformis*, walleye *Sander vitreus* and smallmouth bass *Micropterus dolomieu* were examined to assess the potential effects of climate change on guilds of Great Lakes cold, cool and warm-water fishes, respectively. Overall, the projections for these fishes are for the increased thermally suitable habitat within the lakes, though in different regions than they currently inhabit. Colder-water fishes will seek refuge further north and deeper in the water column and warmer-water fishes will fill the vacated habitat space in the warmer regions of the lakes. While these projections can be modified by a number of other habitat elements (e.g. anoxia, ice cover, dispersal ability and trophic productivity), it is clear that climate-change drivers will challenge the nature, flexibility and public perception of current fisheries management programmes. Fisheries agencies should develop decision support tools to provide a systematic method for incorporating ecological responses to climate change and moderating public interests to ensure a sustainable future for Great Lakes fishes and fisheries.

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A CHANGING GLOBAL CLIMATE

Scientific evidence suggests that global air and ocean temperatures are rising at a relatively rapid pace with increased melting of snow and ice and rising sea levels (IPCC, 2007). While some climatic variability is expected and cooler years have occurred, temperature increases over the past 50 years (1955–2005) have been nearly twice what they were in the 100 years preceding and are anthropogenically induced (IPCC, 2007).

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The effects of climatic warming are predicted to be significant on the distribution and abundance of freshwater fishes as water temperature, quantity and quality are all factors influenced by the atmosphere with direct implications for the structure of fish communities (Regier & Meisner, 1990). In particular, measures of sustained fish yields in North America have been empirically related to water temperature with increased yields at lower latitudes and in warmer-water systems (Schlesinger & Regier, 1982; Meisner *et al.*, 1987). In the Laurentian Great Lakes region, climate change is estimated to alter the hydrographic and geographic distributions of freshwater fishes (Regier & Meisner, 1990), their year-class strength (Casselman, 2002), growth and bioenergetics (Brandt *et al.*, 2002), and trophic dynamics (Jackson & Mandrak, 2002). For example, Regier & Meisner (1990) suggest that cold-water habitat for lake trout *Salvelinus namaycush* (Walbaum) and lake whitefish *Coregonus clupeaformis* (Mitchill) will be shifted deeper within each lake, particularly during the warmer summer months.

Climate change will challenge the current practices and tenets of fisheries management within the basin. It is important for fisheries managers to understand the implications for fish communities and their productivity within these lakes in order to implement strategies that accommodate climate change (*i.e.* focus conservation efforts on populations capable of persisting in a changing climate). This paper reviews the climate change literature pertinent to Great Lakes fisheries, with focused assessments on three key species from different thermal guilds, cold: *C. clupeaformis*, cool: walleye *Sander vitreus* (Mitchill) and warm: smallmouth bass *Micropterus dolomieu* (Lacépède). In addition, this paper suggests models for managing Great Lakes fisheries in a dynamic, adaptive manner based on lessons learned *via* aquatic invasive species management to ameliorate the effect of climate change on Great Lakes fishes.

CLIMATIC PROJECTIONS FOR THE LAURENTIAN GREAT LAKES BASIN

The regional climate of the Laurentian Great Lakes Basin is predicted to be warmer with increased precipitation and less ice cover by the end of the 21st century (Table I). Air temperatures in the Great Lakes region are projected to increase by 0–11°C in the summer and 0.5–9.1°C in the winter (Mortsch & Quinn, 1996; Sousounis & Albercook, 2000; Sousounis & Grover, 2002; Kling *et al.*, 2003; Wuebbles & Hayhoe, 2004).

Concurrent with temperature increases, Sousounis & Albercook (2000) estimate a 15 to 25% increase in summer precipitation across much of the region. This increase in precipitation, however, will not necessarily result in higher lake levels because higher temperature and evaporation rates will occur with less ice cover during the winter months (Smith, 1991); Angel & Kunkel (2010) modeled a range of –3 to +1.5 m changes in lake level, depending on emission conditions. These changes will contribute to an increase in water temperature and changes in Great Lake morphometry, which will influence resident fish distribution and production.

EFFECTS ON GREAT LAKES FISH HABITAT

As one of the largest bodies of surface fresh water in the world, representing *c.* 20% of the world's supply (Lehman *et al.*, 2000), the Great Lakes provide a

TABLE I. Selected climate change projections grouped by feature class (air temperature, precipitation and water level, ice cover, wind speed, water temperature, stratification and dissolved oxygen, thermal habitat and bioenergetics) for the Laurentian Great Lakes region with ecological relevance to fisheries

Air temperature:		
4–11° C increase using three GCMs with 2× CO ₂		Croley (1990)
3–8° C increase (winter); 3–9° C increase (summer) by the end of the 21st century using two GCMs and three IPCC emission projections		Kling <i>et al.</i> (2003)
3.4–9.1° C increase (winter); 2.7–8.6° C increase (summer) with 2× CO ₂		Mortsch & Quinn (1996)
Minimum summer temperature increase by 1–2° C and maximum temperature increase by 0–1° C; minimum winter temperature increase by 0.5–6° C and maximum temperature increase by 0.5–3° C using two GCMs and steady CO ₂ increase for the period 2025–2034		Sousounis & Albercook (2000)
3–7° C increase (winter); 4–11° C increase (summer) by the end of the 21st century using two GCMs and four IPCC emission projections		Wuebbles & Hayhoe (2004)
Precipitation and water level:		
Declines from –3 m to increases of +1.5 m in lake level for all lakes using 23 GCMs and three IPCC emission scenarios		Angel & Kunkel (2010)
Reduction between 23 and 51% of water supply to the Great Lakes using three GCMs with 2× CO ₂		Croley (1990)
10–20% increase in precipitation by the end of the 21st century using two GCMs and three IPCC emission projections		Kling <i>et al.</i> (2003)
Significant decreases (1–1.5 m) or slight increases in Lakes Michigan, Huron and Erie water level using two GCMs with 2× CO ₂		Lofgren <i>et al.</i> (2002)
Declines by 0.06 to 0.94 m in water level for all lakes with a 3.2–4.8° C increase in average annual air temperatures for the Great Lakes Basin		Meisner <i>et al.</i> (1987)
Declines from –0.23 to –2.48 m in water level for all lakes with most scenarios using four GCMs and 2× CO ₂		Mortsch & Quinn (1996)
Precipitation increases throughout large portions of the basin but declines in south-western portion of the basin (Ohio and Indiana) using four GCMs and 2× CO ₂		Mortsch & Quinn (1996)

TABLE I. Continued

Precipitation and water level:	Mortsch & Quinn (1996)
Water supply decreases due to warmer air temperatures, higher evapotranspiration and evaporation and decreased run-off using four GCMs and 2 × CO ₂	Sousounis & Albercook (2000)
Summer precipitation increases by 15–25% using two GCMs and steady CO ₂ increase for the period 2025–2034	Assel (1991)
Ice cover:	Howe <i>et al.</i> (1986)
Ice cover virtually absent in Lake Erie's central and eastern basins and reduced from 4 months to 1 to 1.5 months in Lake Superior using three GCMs with 2 × CO ₂	Lofgren <i>et al.</i> (2002)
All but Lake Erie ice-free year round; Lake Erie with a 50% decline in ice cover using one GCM with 2 × CO ₂	Magnuson <i>et al.</i> (1997)
Substantially reduced ice cover duration in Lake Erie and Whitefish Bay, Lake Superior by the end of the 21st century using two GCMs with 2 × CO ₂	
Ice-free winters between 0 and 17% of simulated years for Lake Erie and between 7 and 43% of simulated years for Lake Superior using four GCMs and multiple emission projections	
Wind speed:	Sousounis & Grover (2002)
Average wind speed decline; more frequent easterly wind events using two GCMs and a gradual increase in CO ₂ concentrations	
Water temperature:	Lehman (2002)
As much as 5° C increase (bottom temperature) by the end of the 21st century using two GCMs with 2 × CO ₂	Trumpickas <i>et al.</i> (2009)
As much as 6° C increase (summer surface temperature) by the end of the 21st century using one GCM and two emission projections	
Stratification and dissolved oxygen:	Blumberg & Di Toro (1990)
Declines of 1 mg l ⁻¹ dissolved oxygen in upper layers and 1–2 mg l ⁻¹ in deeper layers of Lake Erie using three GCMs with 2 × CO ₂	Lehman (2002)
Increased duration of thermal stratification, stronger stability of stratification and deeper depth of daily mixing during peak thermal stratification using two GCMs with 2 × CO ₂	

TABLE I. Continued

Stratification and dissolved oxygen:	
Increased intensity and duration of summer stratification in Lake Michigan (by up to 2 months) using three GCMs with $2 \times \text{CO}_2$	McCormick (1990)
No thorough winter turnover in Lake Michigan using three GCMs with $2 \times \text{CO}_2$	McCormick (1990)
Thermal habitat:	
Habitat increases for all three thermal guilds in southern Lake Michigan and for cool and warm-water fishes in central Lake Erie with three GCMs and $2 \times \text{CO}_2$	Magnuson <i>et al.</i> (1990)
Increases in thermal habitat for all three thermal guilds in the deep, stratified lakes; decreases in thermal habitat for cold-water species in Lake Erie using four GCMs and multiple emission scenarios	Magnuson <i>et al.</i> (1997)
Twenty-seven of 58 fish species with high potential for expanding their range to the Great Lakes found to be likely invaders as a result of climatic warming using discriminate function and principal component analyses comparing ecological characteristics of potential invaders with recently established species	Mandrak (1989)
Bioenergetics:	
Year-class strength of <i>Micropterus dolomieu</i> increase by two to five times with a 1°C increase in temperature and six times with a 2°C increase in temperature at the northern boundary of the species' current distribution	Casselman (2002)
Increased growth of fishes if factors currently limiting growth also increase using three GCMs with $2 \times \text{CO}_2$	Hill & Magnuson (1990)
Increases in growth for species currently below their thermal optimum; decreases in growth for species at or above their thermal optimum using four GCMs and multiple emission projections	Magnuson <i>et al.</i> (1997)
Faster development and time to maturity with climate change	Regier <i>et al.</i> (1990)
GCMs, general circulation models; $2 \times \text{CO}_2$, $2 \times$ present CO_2 concentration; IPCC, Intergovernmental Panel on Climate Change.	

diverse set of fish habitats: wetlands, embayments, nearshore and open water. Climate change will alter the structure and dynamics of these habitats and affect the distributions of resident fishes. This will principally entail a northwards shift of colder-water species in the longitudinally oriented lakes (Michigan and Huron) and changing dominance in many assemblages towards warmer-water fishes in the southern and nearshore regions. For some species, the altered state will provide opportunities to extend their range, increase growth and reproductive rates and reduce overwinter mortality. For others, however, it will contract their niches. Because the shallower regions of these lakes will be the first to be affected by climatic warming, this review focuses principally on the effects within shallower areas of the basin. In long-term scenarios, though, these factors are also predicted to have significant influence on the deep, open-water regions of the lakes (Kling *et al.*, 2003).

TEMPERATURE

Temperature is an important abiotic factor governing the distribution (Shuter & Post, 1990), growth and survival of fishes in the Great Lakes and is directly linked to climate change (Christie & Regier, 1988; Brandt *et al.*, 2002). Because the northern and southern edges of the range for many species are largely influenced by temperature (Shuter & Post, 1990), there is greater variability in abundance and growth rates at the edges of their range than in the middle (Shuter *et al.*, 2002). Populations at these margins, consequently, show the most pronounced correlations with global climate signals (King *et al.*, 1999). For example, as climate warming shifts the southern limit of a species' range northwards in the Great Lakes Basin and deeper in the water column, previously stable populations may become more variable because they will no longer be in their optimal thermal habitat, which provides ideal conditions for maximal survival, growth and reproduction.

In the Great Lakes, fishes have been grouped into three broad thermal guilds according to their recorded approximate optimal temperatures (cold water: 15° C, cool water: 24° C and warm water: 28° C; Hokanson, 1977). Although it may appear counterintuitive, in a warmer climate, optimal thermal habitat is expected to expand volumetrically for all three thermal guilds in the Great Lakes. The reason for this is that fishes will have the opportunity to move both northwards (in the longitudinally oriented lakes) or deeper (in the deep lakes) to maintain their preferred temperature (Magnuson *et al.*, 1997). It is important to note, however, that while this analysis considered the deeper depth strata fairly depauperate of fish fauna (*i.e.* currently free habitat space), recent deep-water surveys have revealed higher than expected abundances of siscowet, the deep-water morphotype of *S. namaycush*, among other species, in depths exceeding 200 m (Sitar *et al.*, 2008).

Nonetheless, overall projections of warmer temperatures in the Great Lakes are predicted to increase growth and survival for most cold, cool and warm-water species (Shuter & Post, 1990). Additionally, fishes in the Great Lakes are often transition species, living at the edge of their thermal range. As such, they generally live in temperatures where their metabolic rate is not optimal; thus exhibiting lower growth and reproduction rates. Increased temperature, and consequently metabolic rates, will allow for greater growth, higher fecundity and generally better survival rates. This is particularly true for Great Lakes cool and warm-water species. Assuming

prey abundance is non-limiting, productivity of fishes increases with time spent at optimal temperature with optimal metabolic rates (Christie & Regier, 1988).

Increased optimal temperature alone, however, does not necessarily equate to increased optimal habitat space for all fishes. Lake morphometry also has a significant influence on the suitability of habitat available to fishes (Regier & Meisner, 1990). *Micropterus dolomieu*, for example, require sheltered environments to build nests. Although a habitat may have temperatures in their optimal range, if it is turbulent, it will not be suitable for high *M. dolomieu* nesting success (Goff, 1986).

DISSOLVED OXYGEN

While temperature is generally predicted to expand the amount of optimal thermal fish habitat space in the Great Lakes with climatic warming, dissolved oxygen may well be a limiting factor to fish productivity, particularly in Lake Erie and warm nearshore bays such as Saginaw Bay (Lake Huron) and Green Bay (Lake Michigan) (Stefan *et al.*, 1996). With warmer water temperatures, the thermocline is expected to become more pronounced, the duration of stratification is predicted to increase and the timing, extent and duration of winter mixing are expected to decrease (Lehman, 2002). When light levels are too low in the hypolimnion to allow dissolved oxygen levels to be replenished *via* photosynthesis, oxygen consumed in respiratory activities of the biotic community, including fishes, zooplankton, phytoplankton and bacteria, cannot be readily replaced (Lehman *et al.*, 2000). This generally leads to hypoxic (*e.g.* ≤ 2 mg l⁻¹ dissolved oxygen) or even anoxic conditions. Some species and age classes of fish can avoid these harmful areas by being mobile and can relocate to suitable living conditions elsewhere. But as temperatures rise and fishes move deeper in the water column to maintain their optimal thermal habitat, loss of dissolved oxygen could become another factor reducing optimal habitat. Lower dissolved oxygen could also increase competition for food and space within the remaining livable habitat, further reducing overall fish production of the current assemblage of fishes.

Current summer oxygen levels in Lake Erie's central basin, for example, range between 8 and 9.5 mg l⁻¹ in the epilimnion and between 2 and 6 mg l⁻¹ in the hypolimnion (Rao *et al.*, 2008). Climate warming simulations for this location predict central basin summer oxygen declines by 1 mg l⁻¹ in the epilimnion and 1–2 mg l⁻¹ in the hypolimnion (Blumberg & Di Toro, 1990). These declines are expected to lead to increases in anoxic dead zones, or areas that do not contain sufficient oxygen levels to sustain aquatic organisms. Similarly, McCormick (1990) modelled an increase in summer stratification by up to 2 months and a permanent deep zone of isolated water below the thermocline because of minimal winter mixing in Lake Michigan. These studies suggest that climate-related reductions in dissolved oxygen will significantly limit the availability of suitable habitat for some cold-water fishes, including *C. clupeaformis* and *S. namaycush* (Magnuson *et al.*, 1990; Stefan *et al.*, 1996).

FOOD-WEB DYNAMICS

Plankton biomass is the foundation of the Great Lakes food chain. Phytoplankton supports the productivity of higher trophic levels, including bacteria, zooplankton and fishes (Lehman *et al.*, 2000). Although increasing temperatures are unlikely to increase the standing biomass of phytoplankton, annual productivity and diversity

are likely to increase with a longer ice-free season (Magnuson *et al.*, 1997). This is expected to occur because phytoplankton production depends principally upon water temperature, sunlight, oxygen and nutrients (*i.e.* nitrogen and phosphorus). Nutrients, rather than temperature, however, are the principal limiting factor for phytoplankton abundance in the Great Lakes (Hecky & Kilham, 1988). A shallower epilimnion is expected to affect the nutritional value of phytoplankton because of a reduced residence time of nutrients in the mixed layer where they can be incorporated into the phytoplankton and be transferred to higher trophic levels (Magnuson *et al.*, 1997).

Zooplankton species are also expected to be affected by climatic warming. Because temperature provides important cues for maturity stages of zooplankton, particularly overwintering stages (Magnuson *et al.*, 1997), some species of zooplankton may be physiologically more sensitive to warmer summer temperatures or lower oxygen levels (Stemberger *et al.*, 1996). The overall projection, however, is for zooplankton biomass to increase in the Great Lakes with warming (Regier *et al.*, 1990).

Climate change is projected to increase primary production and has the potential to translate through the intermediate zooplankton trophic levels to increase fish production in the Great Lakes overall. Rainbow smelt *Osmerus mordax* (Mitchill), as one example, are an important prey species for salmonids in the Great Lakes. With warmer spring water temperatures and greater plankton production, juvenile *O. mordax* abundances should increase (Bronte *et al.*, 2005), providing a larger forage base that could translate into increased salmonid production.

POTENTIAL CONSEQUENCES OF CLIMATE CHANGE ON FISH POPULATIONS

Overall, climate change projections for the Great Lakes fishes should result in an increase in optimal thermal habitat for cold, cool and warm-water species (Magnuson *et al.*, 1990). Habitat increases, however, will be largest for warmer-water species moving in to occupy the more southern and shallower habitat space vacated by the cool and cold-water species. Because the cool and cold-water fishes are expected to move to more northern and deeper offshore regions and not gain habitat, there should be a predominant shift of species types from the current colder-water dominated community towards a warmer-water assemblage (Mandrak, 1989). Further exacerbating this trend is the probable ecological consideration that cold-water species, such as *S. namaycush* and *C. clupeaformis*, may have difficulty competing with cooler-water adapted species at the warmer, southern edges of their current distributions.

Translation of this potential for greater optimal thermal habitat may not, however, directly transfer into greater overall fish production. A number of limiting habitat elements, namely anoxia, ice cover, dispersal ability and food-web dynamics need to be considered. For instance, while McLain *et al.* (1994) predicted that deep-water refuges over large latitudinal ranges for the Great Lakes would be maintained in the face of climate warming, they did not factor in effects from increases in anoxia that would be expected with warmer temperatures and higher phytoplankton production. These two factors will probably reduce suitable habitat. In open water, however, phytoplankton productivity is not expected to increase as much as in shallow areas and embayments because primary production in the open water is still heavily influenced by the establishment of the thermocline and nutrient availability (Lehman, 2002).

Climate warming may also directly affect fish production through physiological means, particularly for fish species adapted to cold water. Some species, including yellow perch *Perca flavescens* (Mitchill), require cold temperatures for full gonadal development (Jones *et al.*, 1972). Others, like *C. clupeaformis*, need ice cover to protect overwintering eggs in marginal nursery habitat to increase year-class strength (Taylor *et al.*, 1987). While suitable habitat may exist in a theoretical context, actual habitat is only possible if a species can travel there, namely if eggs or larvae can physically reach suitable habitat (Sharma *et al.*, 2007). *Sander vitreus* larvae, for example, are passively transported long distances by surface currents. Their survival is dictated in part by drift into productive habitats that provide them with appropriate temperature and food for growth and survival (Roseman, 1997). Fish growth is also strongly dependent on biological factors, particularly production at lower trophic levels. Annual fish growth may decrease if prey availability is insufficient for the increased metabolic costs associated with living at higher temperatures (Hill & Magnuson, 1990).

Influx of new species is another extensive threat to current fish communities in the Great Lakes. Mandrak (1989) predicted that 19 warm-water fish species from Atlantic coastal basins and the Mississippi River may extend their range to Lakes Ontario, Erie and Michigan, and that eight warm-water species currently in these three lakes could expand to Lakes Huron and Superior. These 27 new species could additionally introduce up to 83 parasites that currently do not exist in the Great Lakes (Marcogliese, 2001).

To examine the potential effects of climate change on a smaller scale, three species were evaluated in this study as representatives of the three thermal guilds in the Great Lakes: *C. clupeaformis* (cold), *S. vitreus* (cool) and *M. dolomieu* (warm).

COLD WATER: *COREGONUS CLUPEAFORMIS*

Since 1980, populations of *C. clupeaformis* have supported the most economically valuable commercial fishery in the upper Great Lakes (Madenjian *et al.*, 2006). Commercial landings have fluctuated over the last half century with variation in population abundance caused by overfishing, habitat degradation, sea lamprey *Petromyzon marinus* L. parasitism and competition with exotic species (Taylor *et al.*, 1987). *Coregonus clupeaformis* populations have rebounded since the 1960s, with a 10 fold increase in Great Lakes commercial harvest between 1959 and 1995 (Ebener, 1997).

The *C. clupeaformis* recovery has been principally attributed to control of *P. marinus* (Ebener, 1997), but the species' recruitment variability has been linked with climatic influences, including water temperature, wind speed and ice cover (Miller, 1952; Christie, 1963; Lawler, 1965; Taylor *et al.*, 1987; Freeberg *et al.*, 1990). As a result, *C. clupeaformis* production varies with the amount of thermally suitable habitat (Christie & Regier, 1988), which is likely to be modified significantly by climate change. In particular, *C. clupeaformis* year-class strength has been found to be directly related to the timing and duration of ice cover (*i.e.* egg survival) and temperature of spring plankton blooms (*i.e.* larval growth and survival) (Taylor *et al.*, 1987; Freeberg *et al.*, 1990).

While climate warming should increase suitable thermal habitat volume for *C. clupeaformis* (Magnuson *et al.*, 1997) in most of the Great Lakes, predictions for actual habitat space are not entirely positive. There are projections for significant

reductions in ice cover (Marchand *et al.*, 1988) and higher mortalities at the southern boundary of the range (Meisner *et al.*, 1987) because of reduced egg and larval survival (Taylor *et al.*, 1987). In Lake Erie, for example, cold-water habitat will shrink between the thermocline and either the bottom of the lake or the anoxic dead zone (Magnuson *et al.*, 1990). In the deeper lakes, such as Lake Michigan, however, *C. clupeaformis* will not experience the same loss in potential habitat space because they can shift with the thermocline to deeper regions, which have suitable temperatures and oxygen levels (Regier & Meisner, 1990).

Additionally, the survival of eggs is largely contingent upon substratum size and the amount of ice cover during the winter (Taylor *et al.*, 1987). When winter ice cover is extensive, *C. clupeaformis* eggs are protected from wave and current damage and their survival is greater for all depths and substrata up to 6 m (Hayes *et al.*, 1996). With predictions for substantial reductions in annual lake ice cover (surface area and duration) (Lofgren *et al.*, 2002; Assel *et al.*, 2003), protection, and hence survival, for overwintering *C. clupeaformis* eggs will decline. This will particularly be the case in sub-optimal spawning habitat, which is essential for strong year classes.

On a basin-wide scale, abundance and distribution of *C. clupeaformis* adults are expected to shift northwards and deeper in the water column (Regier & Meisner, 1990). Although they may experience some decreases in habitat space at the southern edge of their range (Meisner *et al.*, 1987), mortality and reduced scope for growth will not be significant as the available deep habitat for these fish should increase. While distribution changes are likely, overall *C. clupeaformis* production in the Great Lakes is expected to remain stable, if not increase.

COOL WATER: *SANDER VITREUS*

Sander vitreus is a very popular nearshore, shallower-water recreational species throughout the Great Lakes and is also currently a commercially captured species in Canada (Knight, 1997). Commercial landings increased steeply until catches collapsed around the basin in the first half of the 20th century due to overexploitation, pollution and degraded habitat (Roseman, 1997) but have since made significant recoveries. Although *S. vitreus* can disperse to open water in the summer, it is primarily restricted to the shallow waters and embayments of the Great Lakes and is prolific in Lake Erie and connecting waterways (*i.e.* Lake St Clair and Detroit River), Saginaw Bay (Lake Huron) and Green Bay (Lake Michigan). It is these shallower areas of the lakes that will be the first to experience significant effects from climate change. A number of key abiotic factors that influence *S. vitreus* recruitment will certainly be affected by climatic warming. The rate of spring warming and variability of May water temperature, for instance, both play important roles in structuring year-class strength during early life-history stages (Nate *et al.*, 2001). These abiotic factors serve principally as proxies for the presence and abundance of quality food sources for larval *S. vitreus* (Roseman, 1997). Additionally, adult *S. vitreus* need an extended period where temperatures are $<10^{\circ}\text{C}$ for initiation and successful completion of their gonadal maturation cycle (Hokanson, 1977). Given the forecast for warmer (*i.e.* when temperatures do not stay $<10^{\circ}\text{C}$ for extended periods of time) and shorter winters (Trumpickas *et al.*, 2009), *S. vitreus* reproductive success, and hence abundance, may be inhibited in the extreme southern edge of their range.

Nonetheless, populations of *S. vitreus* are expected to expand to more northern regions (Shuter *et al.*, 2002) and deeper depths throughout much of their present

range (Chu *et al.*, 2005). The resulting increase in fish production and change in distribution of *S. vitreus* will have major implications for fisheries management because recreational and commercial fisheries come principally from different jurisdictions (*i.e.* recreational from U.S.A. states and commercial from Ontario, Canada) (Roseman *et al.*, 2008). With climate warming, management authorities could be faced with potentially contentious policy issues because of a shift northwards in the abundance of *S. vitreus* populations, thus favouring stakeholders from some jurisdictions (*i.e.* Ontario) over others (*i.e.* U.S.A. states) (Roseman *et al.*, 2008).

WARM WATER: *MICROPTERUS DOLOMIEU*

Micropterus dolomieu is currently found in the southern regions of the Great Lakes Basin and inhabit warm-water habitats. Like *S. vitreus*, it is a particularly popular recreational species but, unlike *S. vitreus*, its commercial harvest is not permitted. As a result, there have been no large-scale surveys to monitor population distributions and abundances of this species within the Great Lakes. *Micropterus dolomieu* colonized the Great Lakes *via* multiple sequential dispersal events following Pleistocene glaciation (Borden & Krebs, 2009) and is expected to increase its range within the basin as a result of climate warming (Casselman, 2002).

Micropterus dolomieu is particularly sensitive to climatic events, particularly with respect to growth rates and nesting behaviour. Changes in growth rates, for example, are known to be associated with other global climate events, such as El Niño warming periods, (King *et al.*, 1999) and changes in nesting behaviour are related to storm events (Steinhart *et al.*, 2005). Warming periods are conducive to recruitment while high-intensity storms can hinder recruitment success. With climate change, warmer water temperatures and a longer growing season are predicted to lead to higher production of *M. dolomieu* because of a greater scope for growth (Shuter & Post, 1990). Casselman (2002) predicted that climatic warming would strongly favour *M. dolomieu* over pike *Esox lucius* L. by relating abundance indices to temperature variables for Lake Ontario populations of both species. Steinhart *et al.* (2005), however, found that storms reduce *M. dolomieu* reproductive (*i.e.* nesting) success. With greater numbers of extreme storm events predicted with climate change (Kling *et al.*, 2003), there is the potential for decreased *M. dolomieu* production due to this interference with successful nest recruitment.

The ability of this species to increase its range northwards will thus be limited by its ability to build and protect nests in a more turbulent, high-wave environment (Goff, 1986). If this does not become a major recruitment bottleneck, *M. dolomieu* is expected to extend its distribution northwards to inhabit shallow embayments and riverine systems. As its abundance increases in these areas, there is also the potential for the species to exert competitive and predatory pressure on the current fish communities in the nearshore zones of the Great Lakes (Vander Zanden *et al.*, 2004), which may be severe enough to further change the current fish community in these regions.

FUTURE OF FISHERIES MANAGEMENT

Climate change compounds the uncertainty of Great Lakes fisheries management, making the already difficult task more complex. With climate change, fisheries

managers must consider potentially greater abundances of some fish populations, possible collapses of others, and probable expanded warm-water habitat in their decision-making process. These changes will, ultimately, affect opportunities for commercial and recreational fisheries in these lakes and affect the value they represent to the public. Management in a changing environment must be adaptive and decisive in the face of uncertainty. While improving data sets, ecological modelling and predictions will surely aid decision-makers with more precise planning (Smith, 1991), management initiatives often need to be implemented before such improvements to the predictions can be fully achieved. The question for managers is how to implement measures that effectively sustain Great Lakes fisheries using the available science.

Site-based management is, ultimately, ineffective and inappropriate, given the scale at which the threats from climate change act upon Great Lakes fisheries and their ecosystems. The application for this type of management paradigm, which has been used as the standard in addressing many 20th century concerns in fisheries management (*e.g.* overfishing in specific areas and point-source pollution), is clearly not adequate for broadscale threats such as climate change. Stabilizing a segment of shoreline on Lake Erie will not, for example, ensure that the habitat is suitable for *S. vitreus* if the winter temperature exceeds 10° C. To address issues, such as climate change, at a broad scale, management must shift from site-based to regional-based; higher levels of governance are needed to prioritize landscape-level actions for rehabilitation efforts (Liu & Taylor, 2002). By considering Great Lakes fisheries management from a basin-wide scale, managers can act strategically, comprehensively and in a coordinated fashion so as to better address key elements. This approach will increase the resilience of the fisheries for the entire basin.

The second issue that needs to be recognized for effective Great Lakes fisheries management in the face of a changing climate is that there are few realistic opportunities for mitigating its effects. If there is no change in greenhouse gas emissions, it is estimated that up to one-third of plant and animal species worldwide will be 'committed to extinction' by 2050 (IPCC, 2007). It is important to take responsibility for the consequences of anthropogenic changes to biodiversity; but, even if some remediating changes are implemented, chances are it will not be enough to protect all Great Lakes species. Thus, fisheries managers must gauge their ability to rehabilitate, maintain or enhance these ecosystems and the expense of such action in relation to its benefits and likelihood of success. As optimistic as fisheries managers might like to be, pragmatic management strategies will serve the resources and the public better. As management ethics have the goal of conserving natural resources for future generations, fisheries managers must focus their efforts on populations and species of fish that are capable of being conserved in the face of changing climate *in lieu* of those, such as the cold-water *C. clupearformis* in Lake Erie, that are not likely to persist.

LEARNING FROM AQUATIC INVASIVE-SPECIES MANAGEMENT

The spread of aquatic species beyond their native ranges, be it intentional or unintentional, is considered one of the most ubiquitous and detrimental processes to ecosystems (Ricciardi & Rasmussen, 1998). It can also serve as a model, of what should and should not be done, for designing management methods to address climate change. Despite the often devastating consequences of invasions, forecasting

invasions by aquatic species and taking precautionary measures are almost always difficult to implement because of tracking the potential paths of invasion (Cooney, 2005). Management of invasive species is often reactionary; a response to successfully established threats. This approach to management is inherently inefficient, expensive (Office of Technology Assessment, 1993) and almost always unsuccessful (*i.e.* does not eradicate the threat).

Because of its large-scale causes and implications, the effects of climate change may be orders of magnitude greater than the effects of aquatic invasive species observed to date. Reactionary management measures may have less potential to restore fish populations to pre-climate change conditions than is even possible when dealing strictly with aquatic invasive species. The Great Lakes will probably never return to a prior state, but the term 'restore' brings exactly that connotation to the public. Fisheries and ecosystems may be rehabilitated to some level of former state and function, such as a given spawning stock biomass or specific water quality variables; but ecosystems evolve and the managers and the public must be prepared to cope with that change.

Natural resource managers are increasingly aware of the importance of human values in the process of achieving management goals (Decker *et al.*, 1996). Jacobson & McDuff (1998) state that people must be considered 'the beginning, middle, and end of all management issues. Recognition of this central role will improve our ability to conserve.' The public can inform and improve sustainable strategies for managing effects on natural resources related to climate change in comparison with what has been used to manage effects of invasive species. Coping with change is difficult for the general public. Managers and researchers often struggle to prepare the public for inevitable changes that are bound to occur.

A prime example of this is the introduction of predatory Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) in Lake Huron to control invasive alewife *Alosa pseudoharengus* (Wilson). A by-product of this fishery management strategy has been the creation of a highly valued recreational fishery for *O. tshawytscha* (Wheilan, 2004). Subsequent decreases in biomass of *A. pseudoharengus*, a function of *O. tshawytscha* predation, climatic conditions and other invasive species (*i.e.* *Dreissena* spp. mussels), have caused the *O. tshawytscha* population and the recreational industry dependent upon it to crash in recent years (Johnson *et al.*, 2007).

Concurrently, populations of recreationally viable native species of fishes including *S. vitreus*, *S. namaycush*, *M. dolomieu* and *E. lucius* have rebounded (Johnson *et al.*, 2007). These species, however, are not perceived by the public to have the same value as *O. tshawytscha*. This is somewhat ironic as residents on Lake Huron three-quarters of a century ago did not have the productivity of native species that is present today and they would probably have found the recreational and commercial opportunities provided by the current fish communities in Lake Huron to be outstanding and highly valuable. This highlights the importance of perception of value in fisheries management. The recreational fishery for *O. tshawytscha* was non-existent mere decades ago. But, as the salmonid fishing industry grew and boomed, people came to rely upon its economic outputs and set expectations that were unrealistic for the Lake Huron fishery ecosystem.

Managers preparing strategies for climate change have an advantage over those dealing with aquatic invasive species, in that effects from climate change will probably be gradual. While people are resistant to change and the change associated

with aquatic invasive species is generally rapid and drastic, climate change will occur over a much longer period of biological time. As such, managers will have time to educate the public on predictions for ecosystems changes, mitigating the negative perceptions by giving the public time to adjust and accept the changes.

CLIMATE CHANGE DECISION SUPPORT

Forecasting the effects of climate change on Great Lakes fisheries, as with aquatic invasive species, will be a difficult task because the projections have high uncertainty and also because fisheries management needs to effectively integrate differing perspectives and competing objectives (Clemen & Reilly, 2001). Good decisions require good information, but in the absence of perfect knowledge about a fishery and its ecosystem, managers can use adaptive management practices in the decision-making process (Enck & Decker, 1997). In the context of Great Lakes fisheries management, climate change poses to have a significant, long-term effects on the biological, economic and social functioning of this system. By integrating these analyses into the management process, decision support tools can facilitate the communication of the most current scientific, economic and social data and management outcomes. An understanding of the interactions between these factors will improve the prospect for implementing appropriate conservation action that is feasible, cost-efficient and sustainable.

Jones *et al.* (2006) argued that mechanistic modelling of habitat changes, which incorporates the interactions of multiple climate-induced changes to thermal habitat with fish population dynamics, is a useful, though by no means perfect, approach to fisheries management. As a working example of this approach to decision support, Jones *et al.* (2006) developed a series of models linking habitat variables with population dynamics for *S. vitreus* in Lake Erie and applying five climate-change possibilities. This study found that warmer temperatures led to increased habitat space for *S. vitreus*, primarily in the central and eastern basins of Lake Erie, but that lower water levels counteracted that increase to produce a net decline in habitat space in the western and central basins. While high uncertainty limits the predictive powers of this and other modelling exercises, Jones *et al.* (2006) revealed potentially important interactions between *S. vitreus* habitat (*i.e.* basin hydrology and water levels) and population dynamics (*i.e.* larval recruitment) which can help inform management decisions.

For these large-scale changes, decision support tools can be particularly useful because ecosystem and regional-level issues are dynamic and operate at large spatial scales (Gavaris, 2009). Fisheries management also includes multiple considerations (*e.g.* biological, economic, social and political) involving many participants (Lane & Stephenson, 1998). In the context of the three thermal guild case studies, decision support tools can assist in defining policies that increase the resilience of fish populations in the Great Lakes to the effects of climate change. Building from the Jones *et al.* (2006) example, when setting harvest allocations for Lake Erie *S. vitreus*, managers could potentially take climate change into consideration by lowering catch quotas in the western and central basins while maintaining quotas in the eastern basin. In the case of *M. dolomieu*, a biological understanding of future habitat usage could allow for the management of extended seasons for recreational fisheries. With regard to *C. clupeaformis*, because it has a particularly important commercial

fishery, managers could use predicted habitat and population changes to allocate quotas appropriately among the multiple jurisdictional interests (*i.e.* state, provincial and tribal). With the integration of interdisciplinary considerations, decision support tools can assess multiple decision alternatives (Lane & Stephenson, 1998) and can help objectively compare potential policies and their outcomes for the fishes, their ecosystems and society (Azadivar *et al.*, 2009).

As helpful as it sounds to have a decision support tool simplify these complexities, it is important to note that these decision support tools are just that, *i.e.* decision support. They will not 'fix' the Great Lakes and the tools' limitations must be taken into account (Shim *et al.*, 2002). Models of ecological systems, for example, are rarely very precise or reliable; but, they can examine proposed management actions and suggest which options are the most feasible to carry forward through the policy process (Riley *et al.*, 2003). When carefully applied, they can assist with making better decisions (Azadivar *et al.*, 2009) but may not necessarily give a manager the 'correct' answer in an unpredictable environment. The managers and decision-makers cannot shirk the responsibility for the management of the resources to a support tool (Taylor & Dobson, 2008).

Climate change will surely challenge the flexibility of current Great Lakes fisheries management programmes and require enlisting public support to set realistic expectations. Learning from past experience and the public's perception of invasive-species management, a precautionary, adaptive approach to managing Great Lakes fisheries is essential. Decision support tools provide a platform for integrating the best and most current science with management needs to craft appropriate fisheries conservation action in the face of a changing climate.

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