PERSPECTIVE / PERSPECTIVE

Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help[1]

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Abstract: Future changes to climate in the Great Lakes may have important consequences for fisheries. Evidence suggests that Great Lakes air and water temperatures have risen and the duration of ice cover has lessened during the past century. Global circulation models (GCMs) suggest future warming and increases in precipitation in the region. We present new evidence that water temperatures have risen in Lake Erie, particularly during summer and winter in the period 1965–2000. GCM forecasts coupled with physical models suggest lower annual runoff, less ice cover, and lower lake levels in the future, but the certainty of these forecasts is low. Assessment of the likely effects of climate change on fish stocks will require an integrative approach that considers several components of habitat rather than water temperature alone. We recommend using mechanistic models that couple habitat conditions to population demographics to explore integrated effects of climate-caused habitat change and illustrate this approach with a model for Lake Erie walleye (*Sander vitreum*). We show that the combined effect on walleye populations of plausible changes in temperature, river hydrology, lake levels, and light penetration can be quite different from that which would be expected based on consideration of only a single factor.

Résumé : Les changements climatiques futurs des Grands Lacs risquent d'avoir d'importantes conséquences sur les pêches commerciales. Les données indiquent qu'au cours du siècle dernier les températures de l'air et de l'eau dans les Grands Lacs ont augmenté et que la durée de la couverture de glace a diminué. Les modèles de circulation globale (GCM) laissent entrevoir la poursuite du réchauffement dans la région et une augmentation des précipitations. Nous présentons des données nouvelles qui indiquent que la température de l'eau a augmenté dans le lac Érié, particulièrement en été et en hiver, durant la période 1965–2000. Les prédictions des GCM associées à des modèles physiques laissent croire à des diminutions du ruissellement annuel, de la couverture de glace et des niveaux de l'eau du lac dans le futur, mais la certitude de ces prédictions est basse. L'évaluation des effets probables des changements climatiques sur les stocks de poissons nécessitera une approche intégrée qui tienne compte de plusieurs composantes de l'habitat et non de la seule température de l'eau. Nous recommandons l'utilisation de modèles mécanistes qui relient les conditions de l'habitat à la démographie des populations, afin d'explorer les effets intégrés des changements de l'habitat associés au climat. Un modèle sur le doré (*Sander vitreum*) du lac Érié nous sert à illustrer cette approche. Nous montrons que l'effet combiné sur les populations de dorés de changements vraisemblables de température, d'hydrologie fluviale, de niveau de l'eau du lac et de pénétration de la lumière est très différent de celui qu'on pourrait attendre de l'examen d'un seul facteur.

[Traduit par la Rédaction]

Received 18 October 2004. Accepted 20 September 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 19 January 2006.
J18365

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[1] This paper forms part of the proceedings of the Salmonid Communities in Oligotrophic Lakes II series of three workshops held during 2000–2003 at the University of Toronto at Mississauga, Ontario, the Harkness Laboratory for Fisheries Research, Ontario, and Le Manoir du Lac Delage, Quebec.

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doi:10.1139/F05-239

Introduction

At the 1971 symposium on Salmonid Communities in Oligotrophic Lakes (SCOL), the role of external stressors in shaping oligotrophic fish communities was a prominent theme (Loftus and Regier 1972). At that time, three stressors were considered prominent and pervasive: exploitation, eutrophication, and exotic species. Today, in the Laurentian Great Lakes, exploitation and eutrophication are not as frequently referenced as primary sources of stress (in fact, oligotrophication is perhaps a greater concern for fishers, particularly in Lake Erie), while concerns about exotic species have grown much greater (Mills et al. 1993; Ricciardi 2001). In addition, increased concern has been directed at stresses related to habitat, such as alterations to the physical environment of Great Lakes fishes that erode population and community productivity (Hartig et al. 1996; Kelso and Wooley 1996). Throughout the Great Lakes basin, human activities have led directly to drastic habitat alterations through activities such as shoreline modification, coastal wetland draining and filling, and channelization of tributary streams. Human activities also can have indirect effects on aquatic habitats. One example of this is human-caused changes to global climate. In this synthesis, we review the evidence that climate change is likely to be an important stressor for Great Lakes fishes, present new evidence that climate-driven habitat changes are already occurring in the Great Lakes, and discuss challenges associated with forecasting the consequences of alterations to future climate. We argue that mechanistic models that link plausible habitat change to fish population dynamics have an important, and underutilized, role in assessing potential climate-change effects on fishes and in guiding future research.

Evidence for climate change — present and future

Much scientific research and policy debate has occurred during the past decade on the topic of climate change. This debate has resulted in numerous recent synthetic publications and reports, including documents that address the issue globally (Intergovernmental Panel on Climate Change 2001) and that consider the Laurentian Great Lakes region in particular (Magnuson et al. 1997; Scheraga and Furlow 2002; Kling et al. 2003). Rather than attempt to summarize this evidence again, we will only briefly report on the key conclusions of these syntheses, emphasize the variety of possible effects on climate change on aquatic habitats, and supplement this with some new analyses of historical climate data for Lake Erie. We will emphasize variety because this is crucial to the central argument of this paper, and we will focus on Lake Erie because it is arguably the Great Lake most vulnerable to climate change and because our illustration of the mechanistic modeling approach that we advocate will be based on Lake Erie walleye (*Sander vitreum*) populations.

Recent changes in climate

The Intergovernmental Panel on Climate Change (IPCC) offered several relatively strong conclusions regarding global evidence for changes in climate, particularly air temperatures, during the 20th century (IPCC 2001). They reported that global average air temperatures have risen by 0.6 °C since 1900. They noted that the decade beginning in 1990 and the year 1998 were the warmest since adequate records have been kept, dating back to 1861, and considered that these years were likely the warmest in the Northern Hemisphere in the past 1000 years. They also documented evidence of milder winters in northern areas by noting that the average duration of the winter ice-cover period on lakes and rivers shortened by about 2 weeks during the 20th century. Finally, they concluded that small (<1% per decade) increases in precipitation and larger but less certain (2%–4%) increases in the frequency of heavy precipitation events occurred during the 20th century in mid- and high latitudes in the Northern Hemisphere. Magnuson et al. (1997) present similar evidence for the Laurentian Great Lakes region, although their analysis suggests slightly higher increases in long-term average precipitation (about 2% per decade).

The IPCC also concluded that "the warming over the past 100 years is very unlikely to be due to internal variability alone" (IPCC 2001, p. 56). Their conclusion was based on the observation that models attempting to explain recent warming trends are unsuccessful if they only include natural radiative forcing processes. In contrast, models that include the large increases in atmospheric greenhouse gas concentrations observed during the past century track past trends quite well. This evidence is also used to support the plausibility of model-based projections of future warming, discussed below.

Recent changes in aquatic habitats

What is the evidence that observed recent trends in global and regional climate have resulted in changes in aquatic habitats? McCormick and Fahnenstiel (1999) examined long-term (25–87 years) observations of water temperatures at seven locations throughout the Great Lakes (Sault Ste. Marie, Ontario; Green Bay, Wisconsin; St. Joseph, Michigan; Bay City, Michigan; Sandusky, Ohio; Put-in-Bay, Ohio; and Erie, Ohio). They found significant trends towards increasing temperature at two sites (Sault Ste Marie and Put-In-Bay) and weak trends at two other sites (Bay City and St. Joseph). They also documented significant increases at four sites in the duration of the period in each year for which temperatures exceeded 4 °C. Casselman (2002) presented evidence of increasing open-water water temperatures in the Bay of Quinte, Lake Ontario, from 1950 to the present and in winter temperatures from 1980 to the present. The only other evidence for recent climate-driven trends in aquatic habitats comes from Assel et al. (2003) in which they report recent (1983–2001 versus 1977–1982) declines in the annual maximum extent of ice cover in each of the five Great Lakes. Ice cover can affect aquatic habitat conditions by protecting shallow habitats from wave damage and reducing mixing and heat loss in winter-stratified waters.

Forecasted future global climate

Most experts agree that global climate will continue to change significantly during the next century. The IPCC (2001) concluded that it is "virtually certain" that fossil fuel burning will be the dominant influence on atmospheric CO_2 concentrations during the 21st century. By the end of the century, model projections of atmospheric CO_2 concentrations range from 490 to 1260 ppm, equivalent to between 75% and 350% above estimated levels in 1750. Projections for other greenhouse gases are less certain. Model projections of global air temperature increases during the 21st century range from 1.4 to 5.8 °C, relative to 1990 temperatures. According to the IPCC (2001) report, this projected increase is much larger than was observed during the 20th century and is very likely to exceed any century-long trend experienced during the past 10 000 years. The models also project a general increase in winter precipitation in northern mid- to high-latitude regions and larger interannual variation in precipitation.

Forecasted future Great Lakes climate

Forecasts of the future climate of the Great Lakes are less certain than global projections, principally because modeling regional-scale phenomena within the context of a global model is difficult. Most experts reporting on model-based forecasts of future conditions caution that forecasts should be viewed as plausible future conditions rather than confident forecasts. In the most recent synthesis available, Kling et al. (2003) concluded from a comparison of two global circulation models (GCMs) that air temperatures in the Great Lakes region are expected to increase by 3–8 °C in winter and 3–9 °C in summer by the end of the 21st century. Fall and spring increases will not be as large, and the overall magnitude of the projected increases was smaller in the center of the Great Lakes region (i.e., over the lakes) than to the northeast and southwest. They also concluded that annual precipitation is likely to increase by 10%–20% during this period, with relatively large increases in winter and spring and decreases in summer. Because of expected increases in evapotranspiration owing to warmer air temperatures, annual runoff is expected to decline moderately, with the largest declines occurring in summer and modest increases in spring and fall.

Sousounis and Grover (2002) examined two other GCMs and concluded that the future climate in the Great Lakes region will probably include fewer extremely cold days and more extremely warm days. They also noted that average wind speeds might decline somewhat and that easterly wind events may increase in frequency, although the two models yielded inconsistent results. Lofgren et al. (2002) used the same two models in their analysis of possible effects on future water levels and winter ice cover. The two models yielded contrasting forecasts of future lake levels, with one suggesting decreases as great as 1–1.5 m for Lakes Michigan, Huron, and Erie (the lakes without controlled outflows) and the other suggesting slight increases. Both models yielded predictions of substantially reduced ice-cover duration in Lake Erie and Whitefish Bay, Lake Superior, by the end of the 21st century. Finally, Mortsch and Quinn (1996) examined four GCMs and explored projected regional and seasonal variation in future climate and basin hydrology for the Great Lakes region. Their analysis suggests that temperatures will increase most and precipitation will decline most in the southwestern part of the basin (Ohio, Indiana). Conversely, temperatures are expected to increase somewhat less and precipitation to increase in more northerly areas. They also suggested that although annual runoff should decline overall, winter flows should increase, summer flows should decrease, and spring peak runoff events should occur earlier.

A critical appraisal of the evidence for future changes to Great Lakes climate and hydrology requires a far more thorough analysis than is possible here. Based on an examination of syntheses such as those of Kling et al. (2003) and Mortsch and Quinn (1996), our ability to predict future climate on relevant spatial scales for a Great Lakes assessment remains very limited. Nevertheless, this brief summary of relevant conclusions from other analyses provides a basis for assessing effects of plausible future physical conditions on Great Lakes fishes.

A new assessment of recent trends in the climate of the western basin of Lake Erie

We carried out parallel statistical analyses of air temperature data, from five rural sites along the southern shore of Lake Erie (source: National Aeronautics and Space Administration, www.giss.nasa.gov/data/update/gistemp/station data/), and water temperature data from two sites in the western basin of Lake Erie (McCormick 1997; McCormick and Fahnenstiel 1999). Our objectives were threefold: (*i*) to examine evidence for recent temporal trends consistent with climate warming; here we focused on the period 1965 through 2000, as there is strong evidence that the trends evident in global climate indices over this time period are due to greenhouse gas accumulation (Stott et al. 2000; IPCC 2001); (*ii*) to compare historical variation (1900 through 2000) in the local climate of Lake Erie with global variation, as characterized by the global air temperature index; and (*iii*) to use the results of these analyses to develop predictions of likely impacts of future global climate change on western basin water temperatures.

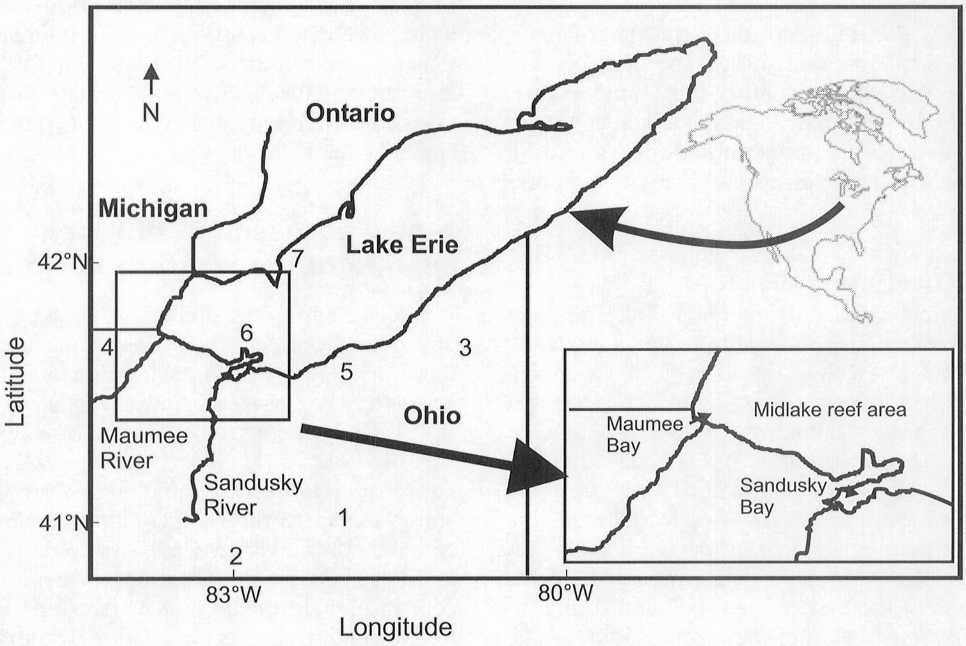
Methods

We based our analyses on the following data sources (Fig. 1): (*i*) annual mean monthly air temperature data for the period 1900 to 2001 from five rural sites (towns of Franklin, Fredonia, Hiram, Lockport, and Oberlin) along the southern shore of Lake Erie; and (*ii*) daily surface water temperature data from two sites in the western basin of Lake Erie: Put-In-Bay, Ohio, from 1918 to 1992, and Union Municipal Water Intake, Leamington, Ontario, from1960 to 2001.

For the period 1900–2001, annual estimates of monthly mean air temperatures were available for at least four of five air temperature sites. We assessed the consistency of the monthly values across sites and averaged the consistent values to obtain a single mean rural air temperature for each month of each year. We used these data to derive two indices to summarize the seasonal air temperature cycle for each year: (*i*) summer warmth index (mean temperature for July); and (*ii*) winter duration index (the number of days, beginning in the fall of each year, that the air temperature was continuously below 0 °C). The winter index was derived as follows: we assigned each monthly mean temperature to the middle day in each month; we then estimated daily temperatures for each month using linear interpolation between these mid-month values; from the autumn of year i to the spring of year $i + 1$, the number of days that these estimated daily temperatures were continuously <0 °C was determined; this value was set equal to the winter duration index for year i.

Similar indices of summer warmth and winter duration were derived from daily surface water temperature values: (*i*) summer warmth index (the median surface water temper-

Fig. 1. Map of Lake Erie showing the location of the air (denoted 1–5) and water (denoted 6 and 7) temperature monitoring stations, the Sandusky and Maumee Rivers, and the midlake reef area.



ature for the 30-day period centred on 7 August); and (*ii*) winter duration index (the number of days, beginning in the fall of each year, that the surface water temperature was continuously below 4 °C).

To develop the longest possible time series of comparable water temperature indices, we used the Union water temperature time series and the air temperature time series described above to extend the Put-In-Bay water temperature time series forward from 1992 (the year that Put-In-Bay data collection ceased) to 2000 and backward from 1918 (the year that Put-In-Bay data collection began) to 1900. The statistical bases for these extensions are outlined below.

The water temperature indices for the Put-In-Bay and Union sites were highly correlated (R^2 values > 0.54) during the period over which values for both sites were available (1960–1992). The summer indices for the two sites were linearly related, and the residuals from this regression equation were normally distributed with no sign of systematic bias or temporal trend. The winter indices were also linearly related, and the residuals from this regression equation were also normally distributed with no sign of systematic bias or temporal trend. We used these regression equations to estimate Put-In-Bay values from the Union values for the period 1993–2000.

Regression analysis demonstrated that there were strong associations (summer warmth, $R^2 = 0.48$, $n = 78$, $p < 0.0001$; winter duration, $R^2 = 0.75$, $n = 78$, $p < 0.0001$) between the Put-In-Bay water temperature time series and the Lake Erie air temperature time series for the period 1918–2000. This analysis also demonstrated a relatively small but systematic temporal shift in the intercept of the linear relation linking the Put-In-Bay summer index to the air temperature summer index — the intercept increased over time. The linear relation for the winter index also exhibited a systematic temporal shift — here the intercept decreased over time. With these temporal effects included, both the summer and winter regression equations had normally distributed residuals with no signs of systematic bias or temporal trend. We used these regression equations to estimate values for the Put-In-Bay water temperature indices from the Lake Erie air temperature indices for each year from 1900 to 1917 (temporal effect fixed at 1918 value) and for four missing years in the interval 1918 to 1959. Through this sequence of steps, we developed a complete set of annual air and water temperature indices for the period from 1900 to 2000. We then smoothed all our climate indices using 5-year running averages and assessed the presence or absence of temporal trends using these smoothed data.

Findings

We found statistically significant, temporal trends for most of our climate indices for the period 1965–2000 (Table 1). Only the autumn air temperature values do not exhibit a warming trend during this period. Values observed for the indices over the final decade of the time series are typically outside the range exhibited for the 90-year period before 1990 (Fig. 2). Over the entire period from 1900 to 2000, both of our Lake Erie water temperature indices were significantly correlated with the global air temperature anomaly index (winter duration, $r = -0.53$, $p < 0.0001$; summer warmth, $r = 0.29$, $p < 0.003$).

Our results demonstrate that (*i*) in recent years, the annual water temperature cycle of the western basin of Lake Erie has changed progressively in ways that are consistent with those expected from global warming, and (*ii*) over the last century, the annual Lake Erie water temperature cycle has varied in parallel with the global air temperature index. Therefore, we expect that future changes in the global index, such as are expected under various climate change scenarios, will be reflected in changes in the annual water temperature cycle of the western basin of Lake Erie. As noted earlier, this global index may increase from 1.4 to 5.8 °C in the next

Table 1. Temporal correlations for air and water climate indices (i.e., index versus year) for the period 1965–2000.

Average air temperatures		Annual indices	
Month	Correlation (r)	Index	Correlation (r)
January	**0.479**	Summer warmth	
February	**0.663**	Air[a]	**0.607**
March	**0.452**	Water[b]	**0.753**
April	**0.501**	Winter duration	
May	**0.402**	Air[c]	**–0.746**
June	**0.372**	Water[d]	**–0.705**
July	**0.607**		
August	**0.668**		
September	0.013		
October	–0.063		
November	–0.090		
December	**0.474**		

Note: Correlations were derived from annual values that were smoothed using a 5-year running average, with the average value assigned to the final year in each set of 5 years (n = 36). Values in bold type are statistically significant at the 0.02 level; most values are significant at the 0.001 level.

[a] The July mean air temperature.

[b] The median water temperature for 30 days centred on 7 August.

[c] The number of days that air temperatures remain below 0 °C.

[d] The number of days that water temperatures remain below 4 °C.

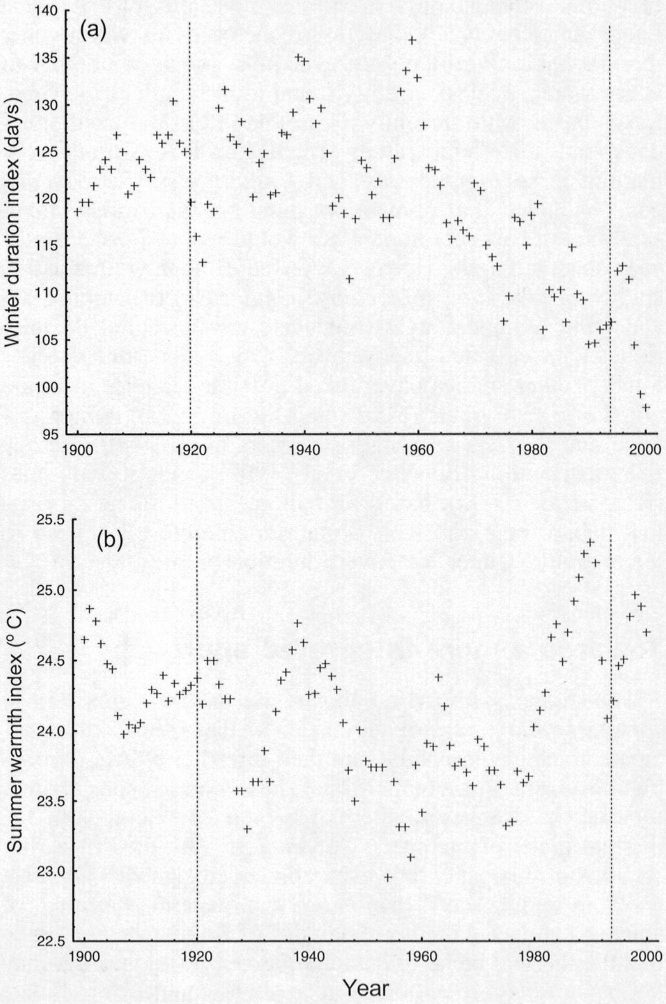
100 years, depending on the future rate of greenhouse gas accumulation in the atmosphere. The estimated impact of a change midway in this range (3.5 °C) on the western basin thermal climate, using the linear regression models that link our two annual indices to the global anomaly index, would be an increase in the summer temperature index from 24.8 °C (1991–2000 average) to 26.7 °C and a decline in the winter duration index to 33 days, which suggests that the western basin would be much warmer in summer and virtually ice free during winter. Changes of this magnitude would likely have significant effects on aquatic biota in western Lake Erie. Our results also suggest that autumn water temperature conditions may be relatively insensitive to these expected changes in climate, so that biological impacts may initially be driven by species with life stages that are most sensitive to winter, spring, and summer conditions.

Forecasted effects of climate change on Great Lakes fisheries

Climate change will affect fish populations and communities through its effect on fish habitat. For a particular species, the effect can operate directly on habitat important to that species or indirectly via effects on the habitat of another species (e.g., a competitor). In either case, predictions of the effect of climate change will depend on understanding (*i*) expected changes in physical conditions that comprise habitat for fishes and (*ii*) the link between changes to physical habitat and the demographic performance of the affected species (e.g., growth, survival, and reproduction). In the latter case, effects will also depend on the strength of interactions between species affected by the habitat change and the species of interest.

Nearly all analyses of the expected effect of climate change on Great Lakes fishes have focused on the effects of changes in thermal regime. Magnuson et al. (1990) projected changes in thermal habitat for cold-, cool-, and warm-water fish in southern Lake Michigan and central Lake Erie. They related the thermal niche of several Great Lakes fish species to forecasted changes in lake volume at different temperatures and concluded that habitat would increase for all thermal guilds in southern Lake Michigan and for cool- and

Fig. 2. Historical variation in indices of the annual water temperature cycle in the western basin of Lake Erie over the period 1900 to 2000. Five-year running averages of annual values are plotted. Each average is plotted against the most recent year included in the average. The values from 1920 through 1994 (between the vertical dotted lines on each panel) are derived primarily from the observed daily surface water temperature time series recorded at Put-In-Bay, Ohio; the earlier and later time periods are estimated Put-In-Bay values, derived from climate time series recorded at sites close to Put-In-Bay. (*a*) Variation in index of winter duration: the number of days between the last day in fall when the surface water temperature is above 4 °C and the last day in the following spring when the surface water temperature is below 4 °C. (*b*) Variation in index of summer warmth: the median surface water temperature for the 30-day period, centred on 7 August. The mid-1990s dip in the summer warmth index is due to a very low (22.5 °C) annual value for 1992; this low value is likely a result of the global cooling effect of the Mt. Pinatubo eruption (e.g., King et al. 1997, 1999*b*).



warm-water guilds in central Lake Erie. McLain et al. (1994) reached similar conclusions by modeling the effect on thermal habitat in an inland lake of varying climate along latitudinal and longitudinal gradients. Hill and Magnuson (1990) coupled temperature-change predictions with bioenergetics models and concluded that growth rates of young fish would increase as long as prey consumption increased but would decrease if prey consumption remained constant. Their results highlight the importance of considering interactions among effects (in this case, direct thermal effects on the energetics of a predator and indirect effects on the availability of its prey) when analyzing the overall effects of climate change on fish. Shuter and Post (1990) developed a more mechanistic model of the influence of seasonal temperature on the growth and resistance to winter starvation of yellow perch (*Perca flavescens*) and smallmouth bass (*Micropterus dolomieu*) and concluded that climate change would likely increase the northern range limit of both of these species. Mandrak (1989) analyzed the potential effect of climate change on fish species invasions of the Great Lakes and concluded that future increases in warm-water thermal habitat are likely to favor invasions by a number of warm-water species currently found to the south of the Great Lakes basin. More recently, Casselman (2002) related abundance indices to temperature variables for Lake Ontario populations of smallmouth bass and northern pike (*Esox lucius*) and concluded that climate warming would strongly favor smallmouth bass recruitment but would reduce northern pike year-class strength. He also inferred from egg incubation studies of lake trout (*Salvelinus namaycush*) that higher fall and winter temperatures would lead to substantial declines in hatch success and thus year-class strength of this species. Finally, other studies have linked possible changes in future climate to fish yields (Minns and Moore 1992), winter survival and year-class strength (Freeberg et al. 1990), riverine fish distribution (Scheller et al. 1999), and growth rates (King et al. 1999*a*), based on hypothesized effects on thermal habitat or a physical habitat variable closely related to temperature (winter ice cover, duration of stratification).

Towards a more integrated approach

The studies summarized above have used the approach of comparing the general requirements of fish species with anticipated changes in habitat and then inferring effects on populations from this comparison. These comparisons mainly focused on changes to thermal habitat compared with the thermal niche of the species of interest. As noted in earlier sections of this paper, however, climate change will manifest itself in more ways than simply a general warming of aquatic habitats. For the remainder of this paper, we argue that the thermal niche or habitat approach, while useful, may not be sufficient to anticipate many consequences of climate change, suggest an alternative and complementary approach, and illustrate our argument with examples from models that we developed for walleye in Lake Erie.

The future climate of the Great Lakes is likely to be reflected in an altered distribution of thermal habitats throughout the basin. In addition, the water budget of the basin is expected to change, thereby resulting in altered hydrologic regimes in Great Lakes tributary streams and changes in Great Lakes water levels. Storm frequency and temporal pattern may change, and the extent and duration of winter ice cover is expected to be substantially less. Finally, climate change may lead to effects on other habitat features, such as altered water clarity or production at lower trophic levels, as an indirect consequence of altered thermal and hydrologic regimes (Magnuson et al. 1997). These considerations suggest that climate change could affect habitat in many different ways, and thus to infer the consequences for fish populations by examining only a single dimension of change may be misleading. We prefer to investigate the integrated effect of multiple, climate-induced changes on habitat. Our contention is that this can only be accomplished by constructing mechanistic models that explicitly link habitat to fish population dynamics and include the breadth of plausible changes to habitat that the climate change might cause.

Habitat affects fish populations through demographic parameters (rates of reproduction, recruitment, survival, and growth; Hayes et al. 1996) and the overall effect of habitat change on a population will thus ultimately depend on the integrated effect, throughout the life history of the population, of habitat-induced changes to demographic parameters on population dynamics. A mechanistic model allows consideration of how various changes to habitat, and other stresses such as exploitation or the establishment of an exotic competitor, might interact with one another and lead to effects on fish populations. Mechanistic ecological models tend to be complicated, parameter rich, and difficult to validate, so to suggest that models of this type are likely to yield accurate predictions of future consequences of climate change is not realistic. However, the strength of such models is that they allow scientists to recognize possibilities that might not be easily inferred from less integrated and more empirical approaches.

A model that allows assessment of the integrated effects of climate change has three components: (*i*) plausible descriptions of future habitat conditions that might result from climate change; (*ii*) submodels that link these habitat conditions to specific demographic parameters; and (*iii*) an overall model that integrates these submodels across habitat factors and life stages to forecast population dynamics. Plausible descriptions of future habitat conditions that are consistent with global-warming scenarios can be derived by using outputs of global circulation models as inputs to physical models of habitat, such as water-balance models. Alternatively, time series of historical data on habitat conditions such as stream temperatures or lake levels can be used to simulate altered future conditions by selecting only extreme periods (or artificially increasing their probability of occurrence) for simulations. A third option is to spatially transpose observed climate conditions from another region that might represent future climate in the region of interest and use these conditions as inputs to physical habitat models. All three of these approaches were used by Mortsch and Quinn (1996) to examine possible future environmental conditions in the Great Lakes region.

A large body of empirical research links habitat features to demographic parameters of fish populations, particularly for economically important and well-studied freshwater species such as salmonines and walleye (e.g., Johnson 1961; Chapman 1988; Scrivener and Brownlee 1989). These empirical observations can be used to define functional relationships between changes in habitat conditions and growth, survival, or recruitment of fish populations (Hayes et al. 1996). Surprisingly, however, relatively few published examples of models that forecast fish population dynamics explicitly include habitat (but see Minns et al. 1996; Clark and Rose 1997; Jones et al. 2003).

A working example — Lake Erie walleye

Context

Of all the Laurentian Great Lakes, Lake Erie is arguably the most vulnerable to the effects of future climate change. Lake Erie has by far the smallest volume, so its heat storage capacity is much less than that of the other lakes, which implies that thermal conditions, including the duration and extent of winter ice cover (Lofgren et al. 2002), are more sensitive to air temperature changes. Lake Erie's shallow mean depth, especially in the western and central basins, suggests greater vulnerability to the effects of water level changes. Further, Lake Erie's southerly position in the basin and the abundance of all types of thermal habitats (cold, cool, and warm) make this lake especially vulnerable to the northward expansion of exotic species with thermal tolerances that make the Great Lakes a marginal environment today.

Lake Erie walleye have been a focus for our research on linking habitat supply to population dynamics (Hayes et al. 2001). We developed models that link habitat conditions to indicators of population performance (e.g., stream flow and temperature to larval recruitment of river-spawning walleye (Jones et al. 2003); thermal and optical habitat volume to adult walleye yield (Lester et al. 2004)). Here, we use these models to examine plausible effects of future habitat change on Lake Erie walleye. Specifically, we address the question of whether consideration of the integrated effect of habitat change due to multiple factors and at different life stages leads to different conclusions about possible consequences of climate change than consideration of single factors alone.

Lake Erie walleye spawn in both riverine and lacustrine habitats. The largest walleye populations in Lake Erie originate in the western basin from spawning habitats in the Sandusky and Maumee rivers and from a series of reefs (midlake reef area) in the southern part of the western basin (Fig. 1). Adult walleye spawn in spring and larval walleye emerge about 2 weeks later. The initiation of spawning and the duration of egg development are both temperature-dependent. Egg survival depends on spawning habitat quality, with coarser substrates conferring a survival advantage (Johnson 1961; Corbett and Powles 1986), and eggs deposited at greater depth in lacustrine habitats are less vulnerable to catastrophic losses due to storm events during incubation (Roseman et al. 2001). Both riverine and lacustrine larval walleye must be transported to zooplankton-rich nursery areas to feed. In the Sandusky and Maumee rivers, walleye larvae are carried downstream from spawning areas by river currents to Sandusky and Maumee bays (Fig. 1; Mion et al. 1998). High discharge events transport walleye more rapidly to nursery habitats, thereby reducing the risk of starvation between emergence and arrival at nursery grounds, but such events are also associated with elevated mortality of larvae during downstream transport (Mion et al. 1998). Similarly, larvae from lake-spawned walleye depend on surface currents to be transported from the midlake reef complex to suitable nursery habitat along the southern shore of the western basin (Roseman 1997).

Once larval walleye reach suitable nursery grounds, their future growth and survival depend on the availability of food resources and suitable physical habitat in the lake. Growth rates of young walleye varied over time in Lake Erie (Hatch et al. 1987; Madenjian et al. 1996), with the greatest growth occurring during a period of low abundance (1960s), suggestive of a density dependence of growth rates. Larval walleye feed in zooplankton-rich inshore nursery habitats. Once they become piscivorous, however, walleye disperse more widely and show preference for habitats that are thermally and optically suitable (Lester et al. 2004). Evidence from other walleye populations suggests that overall population productivity is related to the abundance of these habitats (Christie and Regier 1987; Lester et al. 2004).

These observations suggest that walleye population performance could be affected by changes to several physical habitat variables: river and lake temperatures, river discharge, lake winds and currents, lake water levels (through their effect on spawning habitat depths and thermal–optical habitat volume for juvenile and adult walleye), and lake thermal and light regimes. Each of these variables is subject to effects of global climate change. To explore possible effects of climate-induced changes in physical habitat for Lake Erie walleye, we developed models of riverine spawning and recruitment to nursery habitats, lacustrine spawning and recruitment to nursery habitats, and habitat supply for juvenile and adult walleye.

River-spawning model

This model was described in detail for the Sandusky River by Jones et al. (2003). We used the same model for the Maumee River. Briefly, walleye spawning in the Sandusky and Maumee rivers was assumed to occur in all available habitats, with the timing of spawning and incubation being driven by temperature. Upon emergence, walleye larvae are immediately transported downstream and survival during downstream transport was modeled as a function of both temperature (warmer temperatures leading to greater risk of mortality) and discharge (higher discharge leading to higher risks of poor transport survival). We obtained records of daily stream temperature and discharge for both rivers for 5 years in which complete data were available for both rivers and for western Lake Erie (1967, 1969, 1971, 1972, and 1973) and used these data to simulate typical historical patterns for these two habitat variables.

Mortsch and Quinn (1996) concluded that future conditions in the Lake Erie basin are likely to include warmer water temperatures, lower discharge, and earlier springs. To simulate these possible effects, we systematically adjusted the historical temperature and discharge data by increasing daily water temperatures by a fixed amount, reducing discharge by a fixed proportion, and shifting the timing of the discharge time series to earlier dates, again by a fixed amount. For the simulations presented here, we increased temperature by 4 °C, reduced discharge by 40%, and advanced the time series by 10 days. These adjustments are within the range of possible increases in temperature and reductions in discharge reported in Mortsch and Quinn (1996) and within the range in timing of peak discharge among the 5 years of historical data used in our analysis. We compared predicted recruitment to nursery habitats using the actual historical temperature and discharge data with predictions from simulations where all three adjustments were applied and where each adjustment was applied on its own. For these simulations, we fixed spawner abundance at a relatively low level to avoid having our results affected by saturation of the available spawning habitat.

Lake-spawning model

Large numbers of walleyes spawn in the midlake reef complex of western Lake Erie. We modeled spawning and recruitment to nursery grounds for these fish in a similar fashion to the river-spawning model described by Jones et al. (2003). Timing of spawning and duration of incubation was driven by temperature, and walleye were assumed to deposit eggs on all available habitats. Egg incubation success depended in part on the depth of egg deposition, with eggs deposited in shallower habitats experiencing a greater risk of catastrophic mortality due to storm events (Roseman et al. 2001). We specified the proportion of eggs deposited in deep (>5 m) and shallow habitats (0–5 m) to be equivalent to the relative area of reef habitat in these two depth ranges. To simulate the effect of catastrophic mortality, eggs deposited in shallow habitats were subject to a 10% chance of an additional 80% mortality (Roseman et al. 2001). Emerging walleye larvae were passively transported to nursery habitats by prevailing currents. Daily wind speed and direction data from Toledo airport were used to simulate currents by assuming that current speeds would be 2% of wind speed and that current direction would be 20° to the left of wind direction (Olson 1950). If larvae do not reach nursery habitat before their yolk reserves are depleted, a temperature-dependent process, they are assumed to suffer mortality. Thus, recruitment success will depend on the depth of spawning, water temperature, and current patterns during the period of larval emergence.

Future climate changes could affect lake-spawning walleye through elevated water temperatures, altered lake levels, and changes to the frequency, magnitude, and average direction of wind events. Mortsch and Quinn (1996) suggested that Lake Erie surface water temperatures could increase by 3–5 °C and that lake levels could fall by 1–2 m. We simulated scenarios with a 2 °C increase in lake temperatures, assuming that spring lake temperatures at all depths might not increase as much as average annual surface temperatures, and with both 1 and 2 m drops in lake levels. We used a digital bathymetric map of the midlake reef complex in western Lake Erie to estimate changes in the relative proportion of deep and shallow spawning habitat due to lower lake levels. Increased frequency and magnitude of storm events are also possible consequences of climate change, but no forecasts of such changes have been published, so we have not included this effect in our scenarios.

Juvenile and adult model

Juvenile and adult walleye prefer dim-light feeding conditions and water temperatures ranging from 18 to 22 °C. In this case, our objective was to model how the supply of preferred habitat for these life stages might change as either lake levels or water temperature, or both, change as a consequence of climate change. During their juvenile and adult life stages, walleye originating from western basin spawning stocks can occupy habitat throughout Lake Erie, so we needed to consider all three basins to assess potential changes in habitat supply. For each basin, we divided the entire volume into 1 m vertical layers based on basin bathymetry, estimated temperature and light intensity for each layer on an hourly basis from 1 May to 31 October, and used these estimates to calculate a time-integrated habitat suitability value for each basin. Finally, we compared the basin habitat suitability estimates among four scenarios of altered future climate.

Extensive data on light intensity, water temperature, and light extinction coefficients for all three basins of Lake Erie were available for 1998 from the Lake Erie Biomonitoring (LEB) program (MacDougall et al. 2001), so we used this year as our baseline. Using these data, we estimated hourly light and temperature values for each 1 m depth layer in each basin. Missing values were estimated by linear interpolation. We used habitat suitability curves (US Fish and Wildlife Service 1981; McMahon et al. 1984) to translate estimated light and temperature conditions in each 1 m depth layer into a measure of habitat quality for walleye (Fig. 3). The curves were derived from data on walleye light (Ryder 1977; Lester et al. 2004) and temperature (Hokanson 1977; Christie and Regier 1987) preferences. Then, we multiplied either the area of lake bottom or the volume associated with each layer by its suitability index value and summed this over all depths to obtain hourly estimates of weighted thermally or optically suitable habitat and the product of the two indices (weighted thermal–optical habitat). To obtain total basin-specific thermal, optical, or thermal–optical habitat areas or volumes, we summed the hourly weighted areas or volumes over the entire time interval (1 May – 31 October). Finally, we simulated five scenarios of climate change by (*i*) increasing average water temperature by 2 °C, (*ii*) decreasing water levels by 1 m, (*iii*) decreasing water levels by 2 m, (*iv*) combining (*i*) and (*ii*), and (*v*) combining (*i*) and (*iii*).

Results

River-spawning model

Survival of larval walleye to the nursery grounds for both the river-spawning and lake-spawning models was simulated as a stochastic process, as described for the river-spawning model in Jones et al. (2003). Thus recruitment values reported in Tables 2 and 3 are means of 100 simulations. When all three changes were simulated simultaneously, recruitment of larval walleye to the nursery grounds was predicted to increase or remain the same in 9 of 10 cases (Table 2). The only exception was 1971 for the Sandusky River, when predicted recruitment based on historical conditions was by far the lowest. When only temperature was increased and discharge amount and timing were not modified, recruitment increased in only 4 of 10 cases. When discharge was reduced but not shifted earlier in the year and temperature was not changed, recruitment increased or remained the same in 8 of 10 cases, the only exceptions being 1971 in both rivers. When discharge was advanced by 10 days, all else being equal, recruitment increased in 7 of 10 cases. Furthermore, differences among scenarios depended on both

Fig. 3. Habitat suitability curves for (*a*) temperature and (*b*) light for juvenile and adult walleye (*Sander vitreum*).

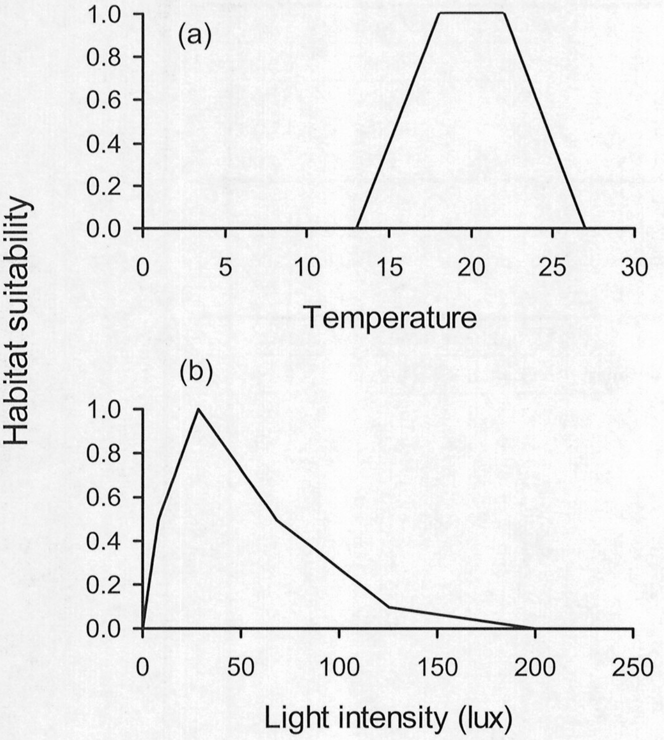


Table 2. Predicted larval walleye (*Sander vitreum*) recruitment (total numbers) to nursery grounds in the Sandusky and Maumee rivers for 5 years, based on historical temperature and discharge data (baseline) and percentage changes in predicted recruitment for four scenarios of modified temperature and (or) flow conditions.

			Scenario[a]			
River	Year	Baseline ($\times 10^6$)	1	2	3	4
Maumee	1967	52.1	53.4	−18.3	70.0	83.3
	1969	58.1	70.6	−17.3	10.8	155.6
	1971	86.7	66.5	74.5	−7.8	−9.2
	1972	45.9	14.7	79.1	14.8	13.3
	1973	57.8	0.3	−12.3	43.9	160.4
Sandusky	1967	4.0	26.7	−37.3	5.7	−34.7
	1969	1.8	81.3	60.2	0.1	50.0
	1971	0.2	-97.0	−96.8	−2.5	−79.5
	1972	1.3	36.1	142.3	16.0	183.6
	1973	3.2	20.5	−58.7	10.2	7.5

[a] Scenarios: 1, all changes, water temperature increased 4 °C, discharge reduced 40%, discharge timing shifted 10 days earlier; 2, increased water temperature only; 3, reduced discharge only; 4, earlier timing of discharge only.

Table 3. Predicted larval walleye (*Sander vitreum*) recruitment (total numbers) to nursery grounds in the western basin of Lake Erie for 5 years, based on historical temperature, wind and lake level data (baseline), and percentage changes in predicted recruitment for four scenarios of modified temperature and (or) lake level conditions.

		Scenario[a]			
Year	Baseline ($\times 10^6$)	1	2	3	4
1967	3053	−75.0	−54.3	−29.2	−50.9
1969	835	−14.3	88.2	−42.1	−50.9
1971	570	72.8	255.9	−30.5	−56.3
1972	2576	−47.7	−2.5	−21.2	−44.3
1973	166	421.1	1039.8	−39.3	−56.7

[a] Scenarios: 1, increase water temperature 2 °C and lower lake levels by 2 m; 2, increase water temperature 2 °C only; 3, lower lake levels by 1 m; 4, lower lake levels by 2 m.

year and river. For example, advanced discharge had an unusually large effect in the Maumee River in 1969 and 1973 but only in the Sandusky River in 1972. Increased temperature had a relatively large positive effect in the Maumee River in 1971 but a large negative effect in the Sandusky River in the same year.

Lake-spawning model

Reduced lake levels consistently resulted in reduced recruitment to the nursery grounds, with a 2 m drop in lake levels leading to declines of up to 56% in recruitment (Table 3, scenarios 3 and 4). This effect is a consequence of a large increase in the proportion of reef spawning habitat that would be at depths less than 5 m if lake levels fell by 2 m (from 40% to 90%). Warmer lake temperatures led to increased recruitment in 3 of 5 years and especially in 1973 when baseline recruitment was especially low (Table 3, scenario 2). In the model, temperature affects spawning by altering the timing of egg deposition and the duration of the incubation period. Large increases in predicted recruitment were observed when warmer temperatures altered the timing of larval emergence to coincide with favorable current conditions for transport of larvae to nursery habitats. Lower lake levels tended to reduce the effect of temperature increases (Table 3, scenario 1) when the latter effect was positive (1969, 1971, 1973) and increase the magnitude of the temperature effect when it was negative (1969, 1972).

Juvenile and adult model

Using 1998 data, we estimated that habitat areas and volumes were substantially larger for the central basin than for the other two basins (Table 4), regardless of the metric used (area versus volume, light versus temperature). Habitat areas were larger in the western basin, whereas habitat volumes were larger in the eastern basin, reflecting the far greater mean depth of the eastern basin. Optical habitat area and volume were consistently smaller than the corresponding thermal habitat area for all basins. Both optical and thermal habitat volumes were larger in the eastern basin than in the western basin, but their combination, thermal–optical habitat volume, was very similar for the two basins, which suggests a smaller spatial overlap between thermally and optically suitable habitats in the eastern basin.

An increase in water temperature resulted in greater walleye habitat in the eastern and central basins but a decrease in thermal habitat and no change in thermal–optical habitat in the western basin (Table 5, scenario 1). Lower water levels reduced optical habitat in all three basins (Table 5, scenarios 2 and 3), with the greatest effect in the western basin. Thermal habitat also decreased in the central and western basins,

Table 4. Estimated hourly average weighted habitat area (ha) and volume (hm^3) for walleye (*Sander vitreum*) in three basins of Lake Erie from May to October 1998.

	Weighted habitat area			Weighted habitat volume		
Basins	Optical	Thermal	Combined	Optical	Thermal	Combined
Eastern	60 000	117 000	5 000	12 000	56 000	2 000
Central	262 000	1 041 000	175 000	25 000	213 000	17 000
Western	63 000	344 000	42 000	3 000	31 000	2 000

Table 5. Percentage changes from 1998 estimated values of hourly average weighted habitat area and volume for walleye (*Sander vitreum*) in three basins of Lake Erie for five climate change scenarios.

		Weighted habitat area			Weighted habitat volume		
Basins	Scenario[a]	Optical	Thermal	Combined	Optical	Thermal	Combined
Eastern	1	0	16	23	0	9	13
	2	–3	2	3	–5	–2	–2
	3	–5	5	8	–10	–4	–5
	4	–3	18	27	–5	7	10
	5	–5	22	32	–10	4	7
Central	1	0	9	14	0	1	6
	2	–4	0	–4	–10	–5	–10
	3	–9	–1	–7	–20	–10	–20
	4	–4	8	8	–10	–4	–6
	5	–9	8	3	–20	–9	–16
Western	1	0	–6	1	0	–6	0
	2	–14	–4	–14	–20	–11	–20
	3	–29	–8	–28	–38	–21	–37
	4	–14	–9	–12	–20	–16	–20
	5	–29	–13	–26	–38	–26	–38

[a] Scenarios: 1, water temperature increased 2 °C; 2, water level decreased 1 m; 3, water level decreased 2 m; 4, combine 1 and 2; 5, combine 1 and 3.

particularly habitat volume, but thermal habitat area actually increased in the eastern basin. Thermal–optical habitat also decreased in the central and western basins, with the strongest effect on volume in the western basin. Smaller changes were estimated for the eastern basin, with area increasing and volume decreasing moderately. When water temperature and lake level changes were combined (Table 5, scenarios 4 and 5), the eastern basin showed substantial increases in estimated thermal–optical area and volume, whereas the western basin showed sharp declines in all metrics. In the central basin, thermal–optical habitat area increased, but volume declined.

Discussion

The results from all three models demonstrated that consideration of a single factor alone (e.g., temperature) could lead to a different conclusion about the effect of future climate change than would consideration of multiple effects on habitat. For the river-spawning model, consideration of the effect of temperature alone would yield a much more pessimistic projection of effects on recruitment (declines in 6 of 10 cases) than would consideration of temperature change in combination with changes in discharge patterns (declines in only 1 of 10 cases). For the lake-spawning model, the forecasted effect of elevated temperature was more optimistic than was the case when the effect of lower lake levels was also considered. Furthermore, the predicted effects of elevated temperature in the lake-spawning model are a consequence of the interaction between emergence timing and wind and (or) current patterns. Adding plausible scenarios of altered future wind patterns would add further realism to this model. Our analysis of the effects of changes in water temperature and water level on juvenile and adult walleye habitat also illustrated the importance of considering multiple factors. In general, warmer lake temperatures led to increased habitat area and volume, particularly in the central and eastern basins, but reduced lake levels tended to offset these increases and lead to net declines in habitat area and volume in the western basin and in volume in the central basin.

Conclusions

We believe that the evidence for a recent global warming trend has become compelling and that continued warming can be expected in the next century. Analyses of trends in global and regional temperatures, as well as other indicators of warming such as the duration of winter ice cover, strongly suggest that we are already experiencing a warmer climate in the Great Lakes region. Our analysis of reconstructed century-long time series of air and water temperature data for western Lake Erie supported this conclusion. We conclude that water temperatures in the Great Lakes and its tributaries will likely rise substantially during the 21st century and that the duration and spatial extent of winter ice cover events will likely be substantially reduced.

Substantial changes in other climate-related physical habitat attributes are also likely. However, predictions of changes in precipitation, evapotranspiration, and winds, and thus in basin hydrology and water movement patterns, are far less certain, as are predictions of changes in the frequency and magnitude of storm events. Therefore, probable scenarios of future habitat conditions in the Great Lakes that include features other than average surface water temperatures are difficult to develop. Consequently, most published assessments of the probable effects of climate change on Great Lakes fishes have focused on the effects of changes to thermal habitat.

We have argued that although these assessments have provided valuable insight into the possible consequences of global warming for Great Lakes fishes, they are not enough. Even though future changes to physical habitat features other than temperature cannot be predicted with confidence, the consequences of plausible scenarios of future habitats that are consistent with global-warming scenarios are possible to examine. We believe that these plausible scenarios should be combined with mechanistic models that link physical habitat to fish population dynamics and used to consider the integrated effect of changes to multiple components of habitat. To illustrate this approach, we used descriptions of plausible changes to future basin hydrology and lake levels summarized in Mortsch and Quinn (1996) together with models of walleye reproduction and lacustrine habitat quality to examine the consequences for this species of changes to multiple habitat features.

We were able to show, using the Lake Erie walleye example, that consideration of multiple habitat components can lead to a different conclusion about the effect of climate change than would result from consideration of temperature effects alone. Our example illustrates the possibility of completing such an analysis. A more comprehensive analysis would link different life stages into a complete life-cycle model to determine whether effects predicted at a particular life stage would be offset by population bottlenecks at other life stages (Minns et al. 1996). Many uncertainties limit the predictive power of such models. Our quantitative understanding of the mechanistic linkages between habitat and population processes is remarkably limited — indeed, it is attempts to construct models such as this that enlighten researchers to the magnitude of these uncertainties. The great value of mechanistic models that link habitat supply to population dynamics will not lie in their power as predictive tools, but in their use as heuristic devices that expose potentially important interactions between the many dimensions of fish habitat and the dynamics of fish populations, especially in the context of globally significant issues such as climate change. The alternative is to remain ignorant of possibly important effects.

Acknowledgements

We thank all of the participants in the SCOL 2 workshops for their contributions to the ideas discussed in this paper and two anonymous reviewers for their helpful comments on an earlier draft. We are especially grateful to Michael Hansen and Steve Kerr, the leaders of the SCOL 2 process, for their guidance and patience with the rest of us. Wenjing Dai and John Netto assisted with the development and application of the walleye models and Li Wang assisted with the analysis of the Lake Erie climate data.

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