

## Climate Change: Implications for Fish Growth Performance in the Great Lakes

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**Abstract.**—Climate change will alter the thermal regime in the Great Lakes, including the onset, duration, and structure of thermal stratification. Such changes may, in turn, affect spatial distributions of planktivores, rates of food web interactions, and growth rate potential of fishes. We use predicted changes in water temperatures for the years 2030 and 2090 to evaluate growth rate potential of lake trout *Salvelinus namaycush*, chinook salmon *Oncorhynchus tshawytscha*, and striped bass *Morone saxatilis* in Lake Michigan. Changes in the timing and extent of thermal stratification changed the predicted distributions of prey fish and the spatio-temporal patterns of growth potential. Overall, growth rate potential of all piscivores increased under climate warming simulations. For chinook salmon, an assumed 15% reduction of prey abundances reduced mean growth rate potential by 9%. A comparison of measured temperatures for 1996 and 1998 showed that current warm years (1998) are similar to mean conditions predicted between years 2030 and 2090. We suggest that studies of interannual variations in food web dynamics may provide insights into the potential impact of climate on fishes.

### Introduction

The Laurentian Great Lakes of North America support a thriving salmonine sports fishery that depends mainly on sustained stocking programs of chinook salmon *Oncorhynchus tshawytscha* and lake trout *Salvelinus namaycush*. As adults, these fishes feed primarily on pelagic alewife *Alosa pseudoharengus*, bloater *Coregonus hoyi*, and rainbow smelt *Osmerus mordax* (Brandt 1986; Rand et al. 1995). Previous work on how climate warming may affect the Great Lakes and their fisheries has focused primarily on water temperature (Magnuson et al. 1979, 1990). Questions of how climate warming might affect Great Lakes fishes in ways other than simply altering the extent of the thermal habitat have largely gone unaddressed. Here, we use climate, fish bioenergetic, and fish foraging models to consider multiple effects of how climate warming might affect Great Lakes fishes.

Water temperature strongly affects physiological rates of fish (e.g., metabolism, consumption, growth [Kitchell et al. 1977]), fish behavior, habitat selection (Brandt 1993), swimming (Facey and Grossman 1990), foraging (Persson

1986), and predator-prey interactions. Climate change may affect large predators that comprise the bulk of the Great Lakes fisheries by altering their thermal habitat. If given the opportunity and sufficient food resources, pelagic fishes will occupy a narrow range ( $\pm 2^\circ\text{C}$ ) of temperatures near their preferred temperature (Magnuson et al. 1979). Magnuson et al. (1990) suggested that climate warming might actually expand the thermal habitat of coolwater fishes in the Great Lakes because the earlier warming and later cooling of the mid-lake region would lengthen the time that preferred temperatures were available. Hill and Magnuson (1990) examined some of the growth responses of yearling lake trout, yellow perch *Perca flavescens* and largemouth bass *Micropterus salmoides* and concluded that these species would grow better (if prey consumption increased) because of the overall lengthening of the season in which optimal temperatures for growth were available.

Our objective here is to expand on the work of Magnuson et al. (1990) and Hill and Magnuson (1990) and quantify how climate changes might affect fish habitat quality as defined by growth rate potential (Brandt et

al. 1992). Growth rate potential is defined as the expected growth rate of a fish if placed in a volume of water with known environmental conditions such as water temperature, light levels and prey type, size, and density. Previous work has shown that growth rate potential provides a good measure of habitat quality (Tyler and Brandt 2001) and effectively incorporates biotic and abiotic characteristics of the environment in a metric that directly relates to the fitness of fish (Brandt and Kirsch 1993; Mason et al. 1995). Spatially-explicit models have been widely used in the Great Lakes (Goyke and Brandt 1993; Mason et al. 1995; Horne et al. 1996; Tyler and Rose 1997), estuarine (Hartman and Brandt 1995a, 1995b; Giske and Fiksen 1998; Demers et al. 2000), and other freshwater (Luecke et al. 1999) environments. To explore the effects of climate warming, we compare the growth rate potential of resident piscivores in Lake Michigan (chinook salmon, lake trout) and a nonresident warmer water striped bass *Morone saxatilis* under base (1954–1995) conditions, conditions predicted for years 2030 and 2090 made by the Canadian Climate Center climate change model, and conditions of reduced light intensity and lake productivity.

## Methods

### General Approach

We took a multi-tiered approach to determine how climate change may affect the quality of the Lake Michigan pelagic habitat for chinook salmon, lake trout, and striped bass. We chose to model the environment for these three species because chinook salmon and lake trout comprise the bulk of the Lake Michigan recreational fishery and striped bass are a commonly found warmwater fish that we use here as an example of how climate warming might affect warmwater fish. The striped bass was selected because this species had previously been proposed to be introduced into the Great Lakes (e.g., Magnuson et al. 1990) and a bioenergetics model for this species has been well developed (Hartman and Brandt 1995a, 1995b). We constructed climate change scenarios that include the change in water temperature in the lake, the spatial distribution of the pelagic prey base for the three piscivore species, and a foraging-bioenergetics model that quantifies changes in the quality of the pelagic environment over an annual cycle. We also evaluated the potential effects of reduced light intensity and primary production on habitat quality for chinook salmon. Reductions in light intensity and primary production may result from climate change (Brooks and Zastrow, in press).

### Climate Change Scenarios and Changes in Great Lakes Thermal Structure

We calculated the daily thermal profile over a one-year period for the years 2030 and 2090 and for base (1954–1995) conditions. Daily values of observed meteorological conditions from the years 1954–1995 were used to drive a model of the thermodynamics of the southern basin of Lake Michigan, treated as a 1-dimensional model with a depth of 150 m, as in Croley (1989). Meteorological inputs included daily minimum and maximum surface air temperature, precipitation, relative humidity, cloud cover, and wind speed. Alternative future scenarios were developed by adjusting these observed meteorological data to account for the mean departures of future climate in periods centered around 2030 and 2090 relative to the recent past, as predicted by multiple runs of the Coupled General Circulation Model version 1 of the Canadian Center for Climate Modeling and Analysis (Boer et al. 2000). The lake thermodynamics model was run again using these adjusted inputs, creating scenarios of climates of 2030 and 2090 for comparison to the base case with unadjusted input data. The procedure is described in detail in Lofgren et al. (in press).

### Comparison of Simulated to Measured Water Temperatures

We compared the simulated water temperature to actual water temperatures measured in the central southern basin of Lake Michigan during a cold and warm year. The data came from a monitoring site located in the central southern basin of Lake Michigan near the National Data Buoy Center's (NDBC) meteorological buoy. The site was established in 1990 to provide better estimates of the annual thermal cycle and offshore climatology (McCormick 1990; McCormick and Pazzdalski 1993). The interannual variability in the time of onset to full lakewide stratification has shown large variations with 1996 and 1998 representing the most extreme years since the study began. In 1996, the offshore waters of Lake Michigan did not stratify until late June, whereas 1998 was in stark contrast with stratification occurring in early April. Furthermore, analyses of surface water temperature anomalies over the past 20 years, from all NDBC Great Lakes buoys, suggest that all buoy sites experienced their coldest year in 1996 and their warmest in 1998. Thus, 1996 and 1998 were chosen to represent a "cold" and "warm" year, respectively.

The monitoring site consists of two moorings. The surface mooring is seasonal and is deployed during the ice-free season with nine self-recording temperature data loggers closely spaced to resolve the thermal structure of the upper 10 m of the water column. The subsurface mooring is maintained year round and has 11 temperature data loggers spaced over the remaining 140 m of the water column. The surface sensor records temperatures at

a 15-min time interval, while the sensors on the subsurface mooring record their data at hourly intervals. All of the sensors have an accuracy of  $\pm 0.1^\circ\text{C}$ . Because the moorings are serviced during the spring or summer months, the data used were taken from moorings deployed from 1995 through 1999. The data used for 1996, for example, were taken from the last portion of the 1995 mooring which was retrieved in early June 1996, and the rest of the 1996 data were obtained from the 1996 mooring. The same procedure was used for collating the 1998 yearlong data set. Typically, the sensor depths differ from one year to the next, so the individual data sets must be interpolated to the same depth grid before they can be added together.

The raw data from 1996 subsurface mooring were measured at 13.5, 23.5, 28.5, 33.5, 43.5, 63.5, 73.5, 83.5, 93.5, 103.5, and 133.5 m below the surface, while the surface mooring made subsurface measurements at 1.2, 3.5, 5.1, 6.7, 8.3, 9.1, 10.0, and 11.4 m. Correspondingly, the raw data from the 1998 mooring were measured at 17, 26.9, 32, 36.9, 46.9, 77.2, 87.2, 97.2, 107.2, and 152.3 m. The surface mooring in 1998 failed, and all data were lost. Surface water temperatures were, however, available from the NDBC weather buoy and were used.

Two assumptions were made in order to fill in spatial gaps in the data. First, during the winter months, when the weather buoy was absent, the upper water column was assumed to be isothermal and equal to the temperature recorded at the first sensor. Second, during the summer of 1998, when the upper water column had data only at 1 and 17 m, a linear temperature gradient was assumed to exist between the two depths. This assumption has little impact on the overall heat content of the water column and no impact on the timing and duration of the stratified season. None of these data were used in any of the model calculations and thus any small errors in temperature in the upper water column would be of no consequence to the modeling results. Once this was completed, the data were interpolated at 5-m intervals at 1, 5, 10 m on through to 130 m and were joined together to form continuous data sets for the entire calendar years of 1996 and 1998. The interpolated data sets were then contoured using Matlab routines.

#### *Prey Fish Distribution and Biomass*

Alewife (young of the year and adult), rainbow smelt, and bloaters were distributed in the climate change thermal scenarios based on their fundamental thermal niches (Magnuson et al. 1979). Fundamental thermal niche is where 66–70% of the total population occupies a  $4^\circ\text{C}$  thermal range (Magnuson et al. 1979). We assumed that fish would distribute themselves with respect to temperature according to a normal distribution (Figure 1), such

that about 70% of the fish will be found within  $\pm 2^\circ\text{C}$  of their preferred temperature and all fish would occupy their preferred temperatures  $\pm 5^\circ\text{C}$  (Magnuson et al. 1979). Food availability can affect temperature preferences in the field (e.g., Crowder and Magnuson 1983). We selected preferred temperatures based on field observations. These were young-of-the-year (YOY) alewife  $19^\circ\text{C}$  (Brandt 1980), adult alewife  $13^\circ\text{C}$  (Brandt 1980), rainbow smelt  $8^\circ\text{C}$  (Brandt et al. 1980), and bloater  $9^\circ\text{C}$  (Brandt et al. 1980; Crowder and Crawford 1984). The probability of occupying a given temperature at depth for a particular day was determined from the probability distribution (Figure 1). Biomass (B) for each species (kg/ha) was multiplied by the normalized probability of occupying a temperature for each day across the year. When preferred temperatures were unavailable, as in winter, prey fish were distributed consistent with the model and temperature preference theory. Fish would be distributed in the warmest water closest to their preferred temperature.

We used acoustic estimates of pelagic prey fish biomass averaged over a 6-year period, 1991–1996. Biomass estimates are from fall acoustical surveys performed by the U.S. Geological Survey Biological Resource Division (USGS-BRD). Total biomass density ( $B_t$ ) averaged  $121.9\text{ kg/ha}$  with densities of  $9.7\text{ kg/ha}$  for YOY alewife,  $11.1\text{ kg/ha}$  for adult alewife,  $14\text{ kg/ha}$  for smelt and  $87.1\text{ kg/ha}$  for bloaters (Argyle et al. 1998). We assumed that prey type and densities per square meter remained constant at 1991–1996 levels.

#### *Spatially-Explicit Models of Fish Growth Rate Potential*

Spatially-explicit models of fish growth rate potential describe the environment in terms of the amount of growth a fish will achieve which directly relates to individual fitness (Winemiller and Rose 1992). Here, we evaluate

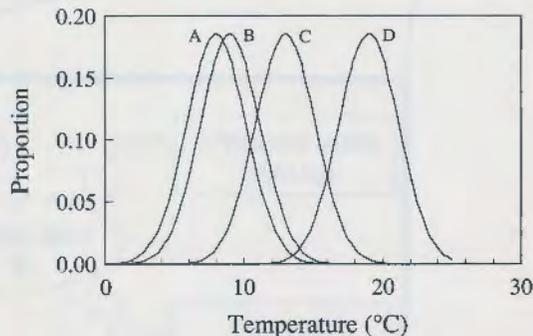


Figure 1. Thermal distributions of rainbow smelt (A), bloater (B), adult alewife (C), and young-of-the-year alewife (D) used to distribute prey across prevailing thermal habitats.

the growth rate potentials of chinook salmon, lake trout, and striped bass at daily intervals over the year, at one-meter intervals in the deep (150 m) portion of the southern basin of Lake Michigan. Thus, for each of the 54,750 cells of a year, we used water temperature from the climate change/hydrologic models and prey density for base conditions and for the years 2030 and 2090 (Figure 2). Brandt et al. (1992) and Tyler (1998) provide complete descriptions of spatially-explicit models of fish growth rate potential. The text below describes modifications to the earlier techniques that we used in this analysis.

We modeled the growth rate potential of a 5-kg chinook salmon, a 4-kg lake trout, and a 1.9-kg striped bass using the Wisconsin bioenergetics model of fish growth (Kitchell et al. 1977; Hanson et al. 1997). The bioenergetics model is a species-specific, energy-balance approach that describes the flow of energy through an individual fish and how that energy is partitioned among consumption, growth (somatic and reproductive), and losses (respiration, egestion, excretion, and specific dynamic action). Energy per unit time is related to weight per unit time by a specific energy density (calories per unit weight) for predator and prey. The basic form of the

bioenergetics model in terms of weight specific growth rate ( $g\ g^{-1}\ d^{-1}$ ) is

$$\frac{1}{W} \cdot \frac{dW}{dt} = \phi - (R_{resp} + SDA + F + U),$$

where  $W$  is weight (g) of the individual predator,  $t$  is time in days,  $\phi$  is feeding rate ( $g\ g^{-1}\ d^{-1}$ ),  $R_{resp}$  is respiration ( $g\ g^{-1}\ d^{-1}$ ),  $SDA$  is specific dynamic action ( $g\ g^{-1}\ d^{-1}$ ),  $F$  is egestion ( $g\ g^{-1}\ d^{-1}$ ), and  $U$  is excretion ( $g\ g^{-1}\ d^{-1}$ ).

Feeding rate ( $f$ ) for chinook salmon, lake trout, and striped bass was modeled using type II functional response model (Figure 3) developed for lake trout (Eby et al. 1995)

$$\phi = \frac{C_{max} B}{0.865 + B},$$

where  $C_{max}$  ( $g\ g^{-1}\ d^{-1}$ ) is maximum daily consumption, and  $B$  is biomass density (kg/ha of prey).  $C_{max}$  is a function of water temperature and fish weight and defines the species-specific asymptote for the functional response

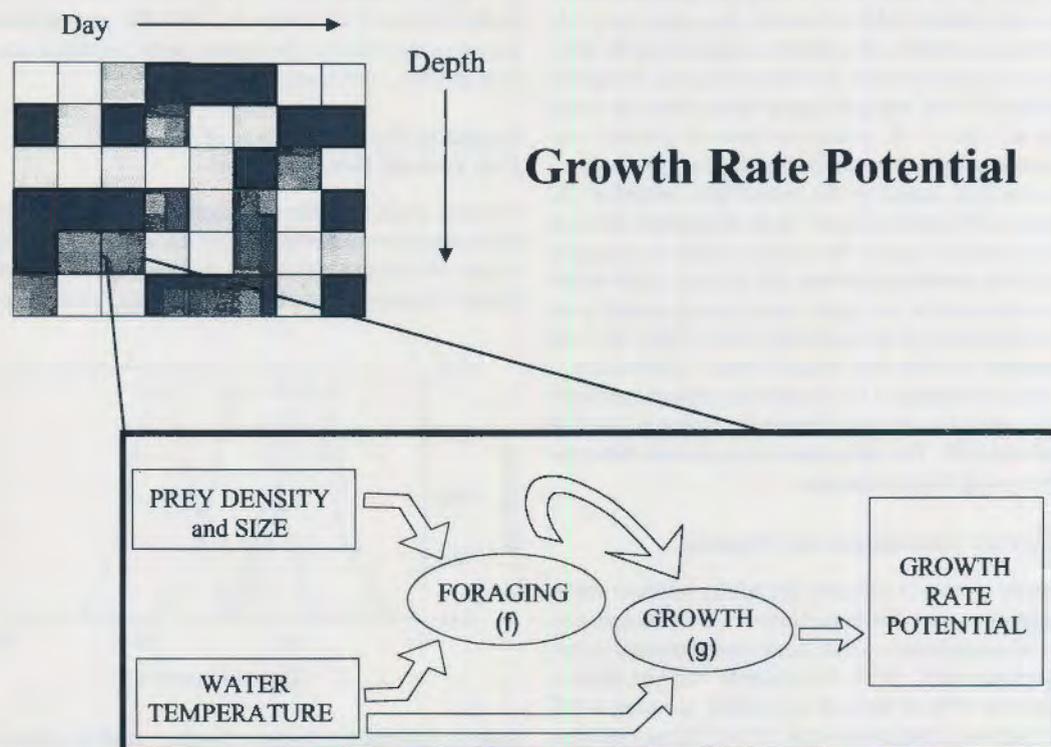


Figure 2. Diagrammatic view of the spatially-explicit modeling of fish growth rate potential.

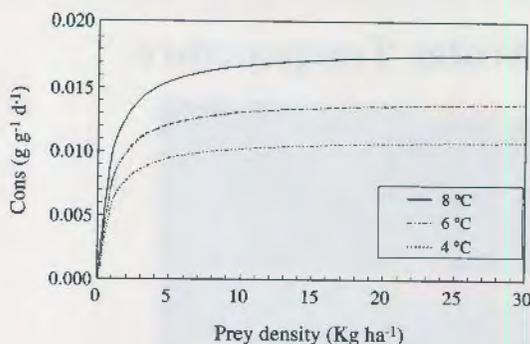


Figure 3. The predator-prey functional response showing the relationship of predator consumption rate ( $\text{g g}^{-1} \text{d}^{-1}$ ) versus prey density at different water temperatures.

curve. The functional response model was made species-specific by modifying the asymptote in  $C_{\max}$  as a function of water temperature. Species-specific maximum consumption is described by the equation

$$C_{\max} = aW^b \cdot f(T),$$

where  $a$  and  $b$  are the parameters of the weight dependence of consumption, and  $f(T)$  is the species-specific, temperature-dependent function of consumption (Hanson et al. 1997).

In a separate simulation, we further modified the foraging model for visually foraging chinook salmon by incorporating depth-dependent light levels. Light level was incorporated into the model by calculating a multiplier  $M$  (range: 0–1.0) that declined to zero at a light intensity of 0.01 lux (Blaxter 1965; Aksnes and Giske 1993; Petersen and Gadomski 1994), such that actual feeding rate was calculated as

$$C_{\max} \cdot M,$$

where  $M = 1 - e^{-b(I_x - I_0)}$ ,  $b$  is the slope (0.7),  $I_x$  is the ambient light intensity at depth  $x$  (m), and  $I_0$  is the threshold light intensity where reaction distance becomes zero (0.01 lux). Light level at depth  $I_x$  was determined as an exponential decay  $I_x = I_s e^{-ax}$ , where  $I_s$  is the light intensity at the surface during dawn and dusk assumed to be 1,000 lux, and 'a' is the extinction coefficient (0.3).

Complete equations describing the bioenergetics model (R, SDA, F, and U) can be found in Kitchell et al. (1977) and Beauchamp et al. (1989), and the values for the physiological parameters for chinook salmon, lake trout, and striped bass, can be found in Kitchell et al. (1977), Stewart et al. (1983), Beauchamp et al. (1989), Stewart and Ibarra (1991), Brandt and Kirsch (1993), Hartman and Brandt (1995 a, 1995b), and Tyler (1998). For a summary of bioenergetics model applications, model performance, and model assumptions and sensi-

ivities, see Bartell et al. (1986), Ney (1990, 1993), Brandt et al. (1992), and Madenjian et al. (2000).

### Model Simulations

We simulated growth rate potential for the three piscivores under the three climatic conditions. In two separate simulations, we also examined the effect of changes in prey abundances and light conditions on the fishes' growth rate potentials. The initial climate change simulations include changes in water temperatures and in the distribution of prey populations in Lake Michigan, as described above.

Recently, Brooks and Zastrow (in press) have shown that changes in climate conditions can change primary production levels by changing light conditions (increased cloud cover) and the timing of the set up and breakdown of thermal stratification. In particular, earlier stratification reduced the amount of time for winter-spring mixing and stratification capped the nutrient supply. Primary production was reduced under most modeling simulations but by less than 15% during any one simulation. To examine the effect of reduced primary production on fish habitat quality, we assumed that prey densities were reduced by 15% throughout the year and ran the simulation for chinook salmon using water temperature and prey distribution data for the year 2030.

Climate models also predict an increase in cloudiness that could reduce light levels. Reduced light levels could reduce the ability of the predator to see prey. To test the potential magnitude of this effect, we ran a simulation that reduced light levels and evaluated the chinook salmon growth rate potential for the year 2030.

## Results

### Water Temperatures

The annual cycles of water temperature for base conditions and for the years 2030 and 2090 are shown in Figure 4. Climate warming produced 1) slightly warmer winter temperatures; 2) warmer summer surface temperatures; and 3) changes in the thermal structure of the environment, including a thermocline that formed earlier in the spring, broke-down later in the fall, and lay at greater depths during the summer. Overall mean seasonal temperature (averaged across depth and time) was 4.33°C under base conditions, 5.16°C in 2030 and 7.01°C in 2090.

### Prey Distribution

The climate induced similar changes in the distributions of smelt, bloater, adult alewife (Figure 5), and all prey combined (Figure 6). These three species have tempera-

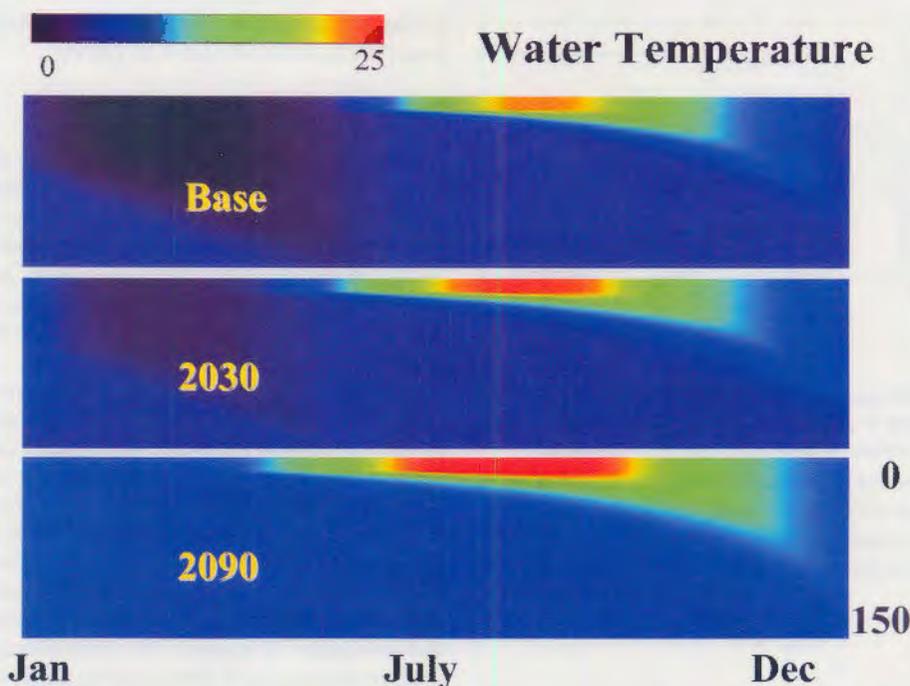


Figure 4. Temperature ( $^{\circ}\text{C}$ ) distributions for each day of the year at a 150 m deep location in southern Lake Michigan under base conditions and climate warming simulations for the years 2030 and 2090.

ture preferences that usually encompass the seasonal thermocline. Under base conditions, the fish were dispersed during winter but concentrated at or near the base of the thermocline during thermal stratification. These predicted midwater distributions are similar to those normally observed in the field (Brandt et al. 1980). Fish dispersed more throughout the water column after the breakdown of thermal stratification. Climate warming simulations show two main effects. First, the earlier formation and later breakdown of thermal stratification causes an earlier formation and later dispersal of fish midwater concentrations. Second, the depth of the thermocline increased slightly during years 2030 and 2090, and the thermocline was spread over a larger depth range under climate warming simulations. Fish vertical distributions followed the thermal structure. The spreading of the isotherms caused fish to disperse and deepen slightly. Fish densities were lower during 2030 and 2090.

The distributions of YOY alewife responded differently to the climate change simulations. Under base conditions, YOY alewife were largely spread from the top of the thermocline to the surface of the water column (Figure 5). Under climate warming simulations, the summer near-surface temperature increased, causing a concentration of YOY alewife in the thermocline. Thus, in contrast to smelt, bloaters, and adult alewife, the computed densities of YOY alewife increased during ther-

mal stratification with climate warming. This is a direct consequence of the higher temperature preferences for YOY alewife.

#### *Fish Growth Rate Potential*

Climate warming increased the duration of the period with positive growth rate potential and thereby the habitat quality for chinook salmon, lake trout, and striped bass (Figure 7). The vertical distribution in the pattern of good conditions for fish growth rate potential also followed that of the changes in thermal structure. The growth rate potential of chinook salmon increased from an annual mean of  $0.0156 \text{ g g}^{-1}\text{d}^{-1}$  under base conditions to  $0.0189 \text{ g g}^{-1}\text{d}^{-1}$  in 2030 and  $0.027 \text{ g g}^{-1}\text{d}^{-1}$  in 2090. Overall, mean growth rate potential increased by 73% in 2090 over base conditions. Despite the overall increase in mean growth rate potential under climate warming, the near surface conditions became more unsuitable for growth.

The frequency distribution of growth rate potential for chinook salmon changed in response to climate warming scenarios. With increased warming, the range in the frequency distribution was compressed, the mode for the minimum value in the range increased, and the mode for the maximum in the range decreased (Figures 8 and 9). In addition, the proportion of water on an annual basis that

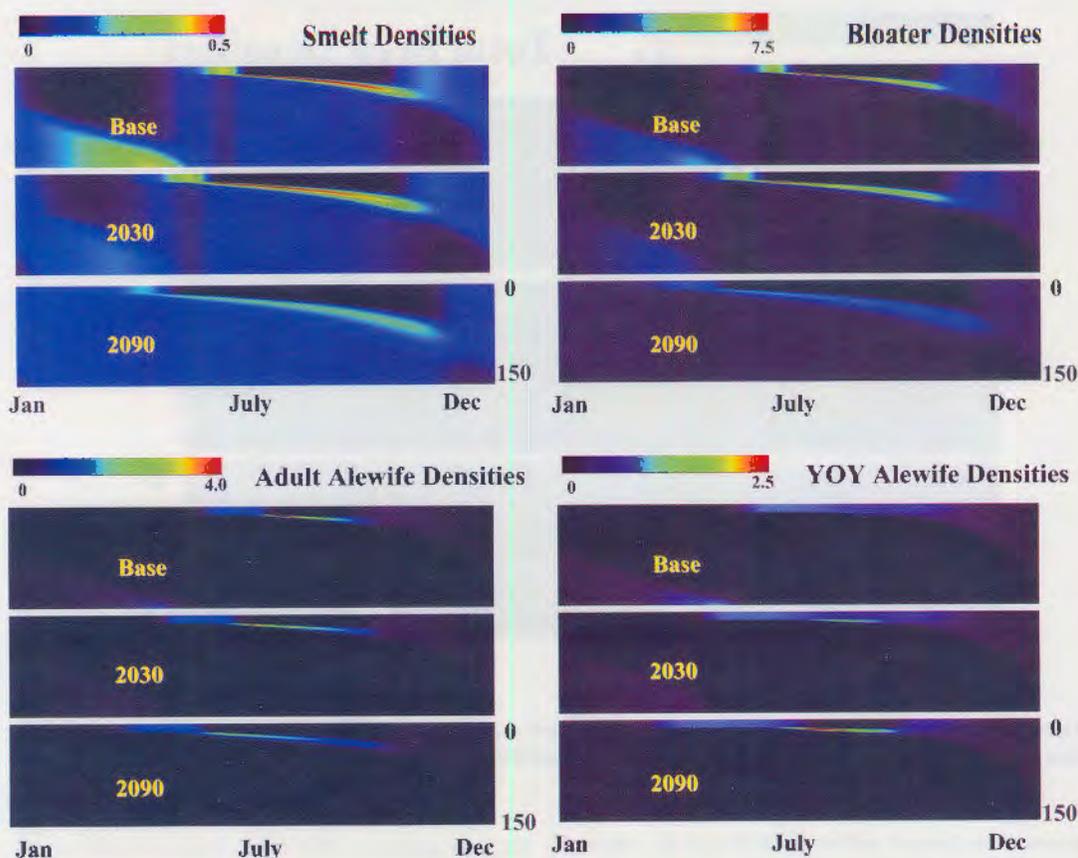


Figure 5. Density ( $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) of rainbow smelt, bloater, adult alewife, and YOY alewife for each day of the year at a 150 m deep location in southern Lake Michigan under base conditions and climate warming simulations for 2030 and 2090.

had poor growth conditions was reduced (Figure 8). This was caused by warmer temperatures in winter and early spring, as well as warmer temperatures and more prey in subthermocline waters during summer. In contrast, the very highest growth regions were present under base conditions but were reduced during climate warming (Figure 9). This reduction of the very high growth regions corresponds to the spreading out of the prey with the thermal expansion of their habitats.

The patterns of growth rate potential distributions for lake trout under all modeling simulations were similar to those of chinook salmon, although the annual scope for growth was smaller and more restricted in space than that of the chinook salmon during all climate simulations (Figure 7). As for chinook salmon, the regions of very low (Figure 8) and very high (Figure 9) growth rates were lost under climate warming. Overall mean growth rate increased by 72% from base conditions to 2090 conditions. Mean growth rate potential was  $0.0083 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  under base conditions,  $0.0105 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  in 2030, and

$0.0143 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  in 2090.

Mean growth rate potential for striped bass increased by about 114% between base conditions and conditions in year 2090. The distribution of growth rate potentials showed a similar trend to the two salmonine species, but the decrease in surface growth rate potentials for striped bass under climate warming conditions was much less than was observed in the chinook salmon and lake trout simulations. Mean growth rate potential was  $0.0100 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  under base conditions,  $0.0137 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  in 2030, and  $0.0213 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  in 2090. The seasonal duration of high growth conditions expanded under climate warming simulations (Figure 7).

#### *Reduced Prey Availability and Light Conditions*

Reducing prey densities 15% under the 2030 climate warming simulation resulted in a 9% reduction in mean growth rate potential for chinook salmon. The original 2030 climate warming simulation mean growth rate

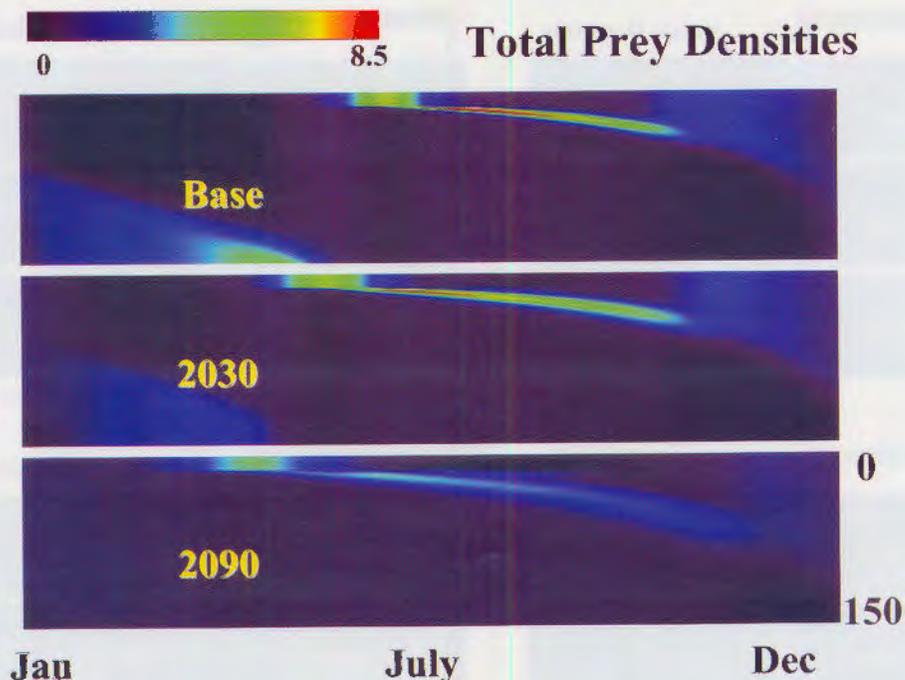


Figure 6. Density ( $\text{g g}^{-1} \text{d}^{-1}$ ) of total prey for each day of the year at a 150 m deep location in southern Lake Michigan under base conditions and climate warming simulations for 2030 and 2090.

potential for chinook salmon of  $0.0189 \text{ g g}^{-1} \text{d}^{-1}$ , whereas the mean growth rate potential under reduced prey densities was  $0.0173 \text{ g g}^{-1} \text{d}^{-1}$ . The overall spatial-temporal patterns under the two conditions are almost identical.

The growth rate potential for chinook salmon for 2030 under reduced light conditions is shown in Figure 10. The reduced light conditions caused a dramatic decline in chinook salmon growth rate potential, as well as a change in the spatial-temporal pattern of growth rate potential. Overall mean growth rate was reduced by 49% to  $0.0057 \text{ g g}^{-1} \text{d}^{-1}$ . Reduced light decreased the amount of prey encountered by chinook salmon. Below a certain light level (and water depth), growth rate was reduced to zero.

#### *Comparison of Simulated and Observed Water Temperature*

We compared the simulated water temperature to actual water temperatures measured in the central basin of Lake Michigan during 1996 and 1998 (Figure 11). Water temperature ranges and spatial-temporal distribution during 1996 were very similar to those modeled under base conditions. Overall mean temperatures were  $4.33^\circ\text{C}$  under base conditions and  $4.30^\circ\text{C}$  in 1996. Water temperatures and spatial-temporal distributions dur-

ing the warm year, 1998, fell in between model simulations for 2030 and 2090. Overall mean water temperatures were  $5.16^\circ\text{C}$  in 2030,  $6.01^\circ\text{C}$  in 1998, and  $7.01^\circ\text{C}$  in 2090.

## Discussion

Our analysis of fish habitat quality, as measured by growth rate potential, suggests that climate warming will result in an overall increase in the habitat quality for Great Lakes fishes but that this increase is a balance of two important changes. Climate warming simulations, here and elsewhere (Meisner et al. 1987; Magnuson et al. 1990; Brooks and Zastrow, in press), suggest that the lake thermal structure will exhibit increased water temperatures and a longer period of thermal stratification. The change in lake thermal structure will also cause a change in the distribution of prey fish such that prey fish are more dispersed throughout the water column. A more dispersed prey field cause predator-prey encounter rates to decrease. The combined effects of these two factors could lead to an increased or decreased overall growth rate potential, depending on prey population sizes, piscivore foraging behavior, and piscivore bioenergetics. In the simulations performed here, the changes in water temperature

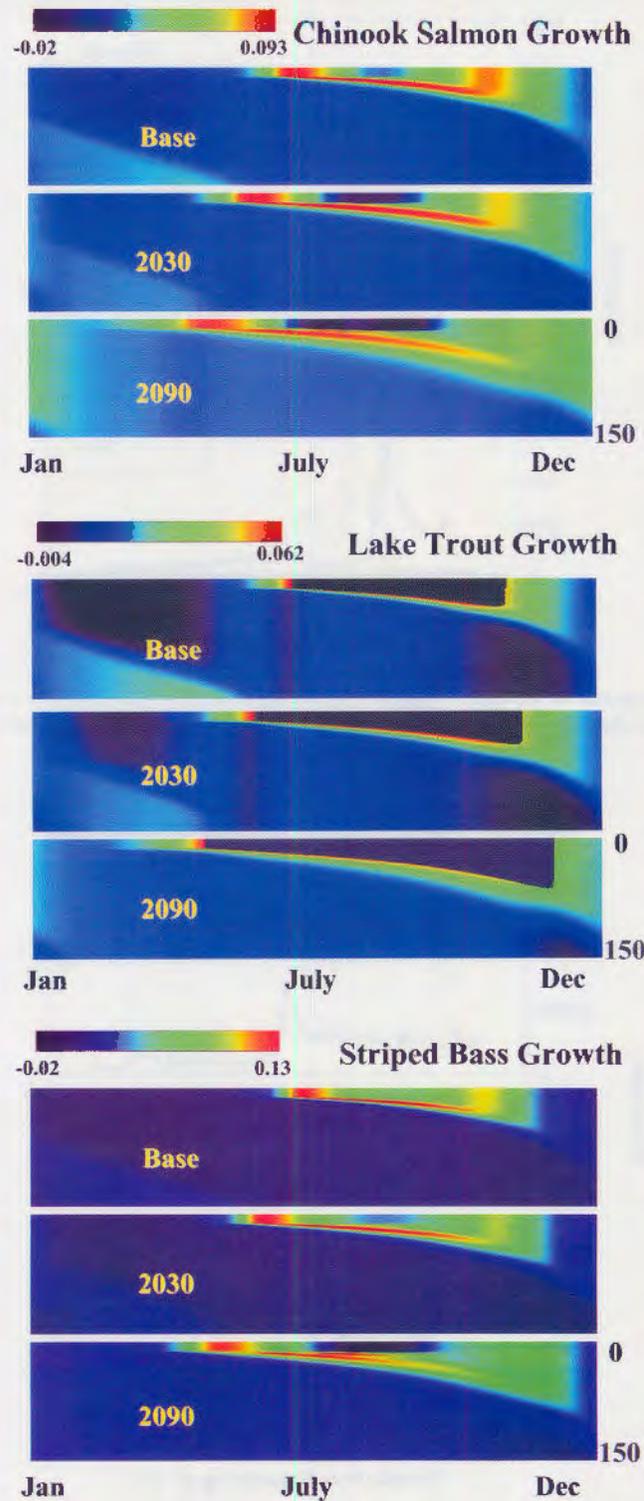


Figure 7. Growth rate potential ( $g \cdot g^{-1} \cdot d^{-1}$ ) of chinook salmon, lake trout, and striped bass for each day of the year at a 150 m deep location in southern Lake Michigan under base conditions and climate warming simulations for 2030 and 2090.

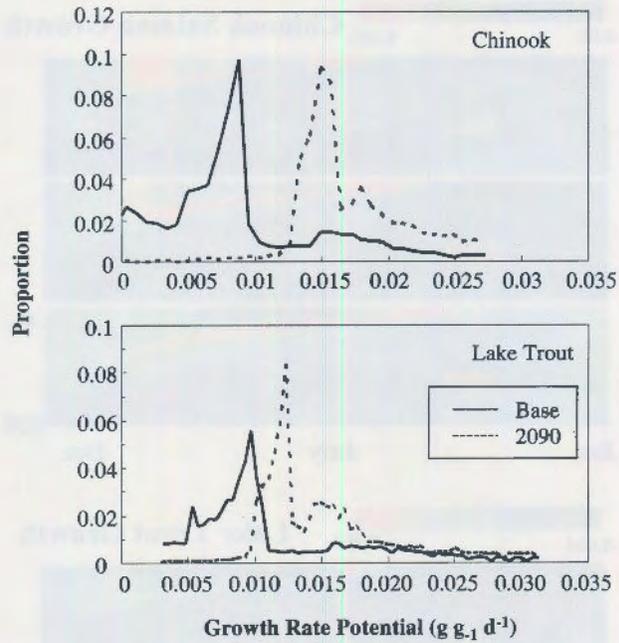


Figure 8. Frequency distribution of growth rate potential under base conditions and conditions in the year 2090 at the low end of the distribution for chinook salmon ( $0.001\text{--}0.027 \text{ g g}^{-1} \text{d}^{-1}$ ) and lake trout ( $0.003\text{--}0.03 \text{ g g}^{-1} \text{d}^{-1}$ ).

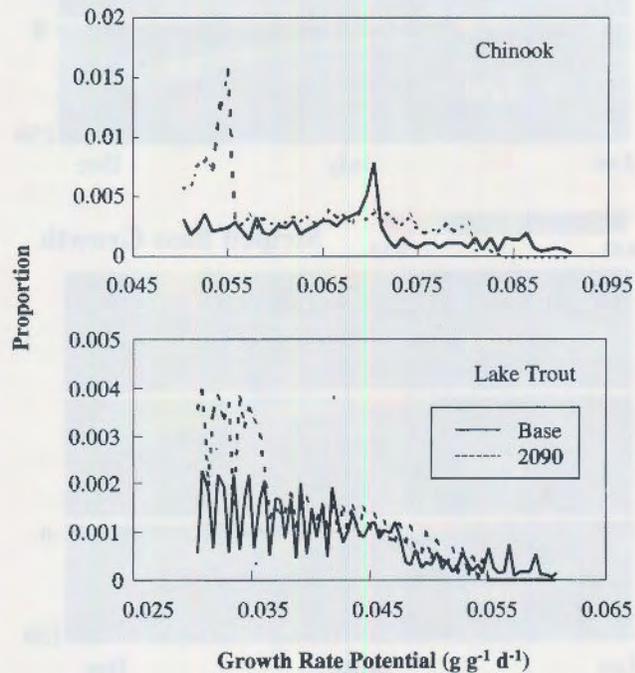


Figure 9. Frequency distribution of growth rate potential under base conditions and conditions in the year 2090 at the high end of the distribution for chinook salmon ( $0.05\text{--}0.093 \text{ g g}^{-1} \text{d}^{-1}$ ) and lake trout ( $0.03\text{--}0.062 \text{ g g}^{-1} \text{d}^{-1}$ ).

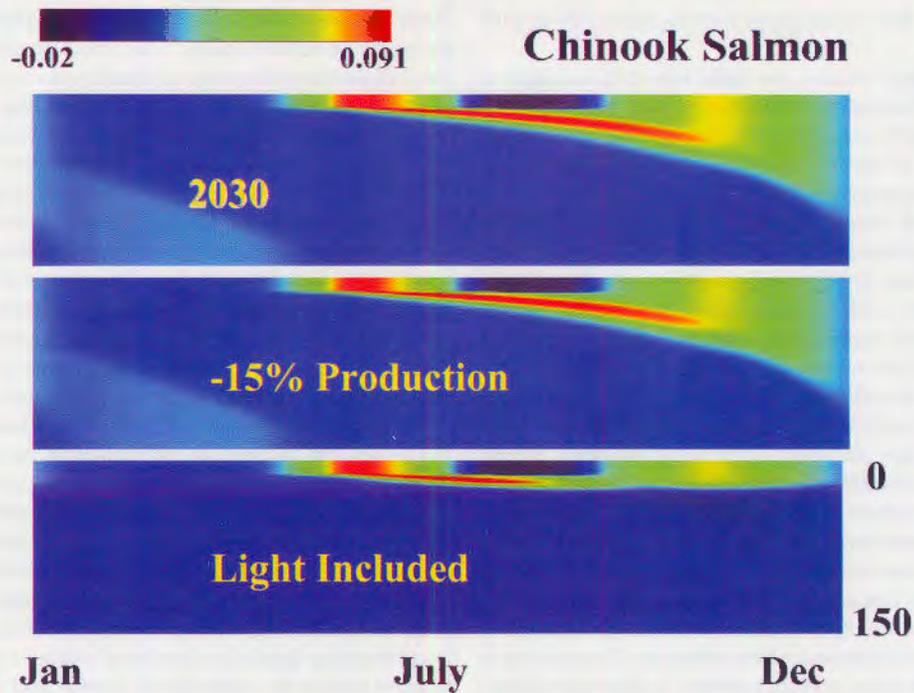


Figure 10. Growth rate potential of chinook salmon predicted for the year 2030 with and without a 15% reduction in prey densities and with light conditions included.

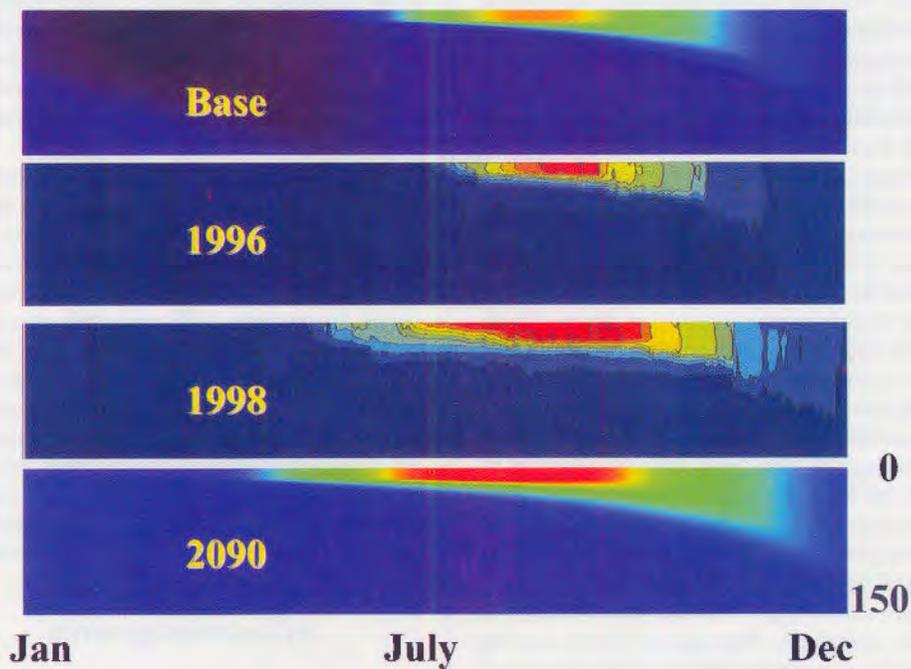


Figure 11. Comparison of water temperatures simulated for base conditions and the year 2090 and measured in the southern basin of Lake Michigan in the years 1996 and 1998.

and prey distribution results in an increase in habitat quality.

During summer, we might expect that changes in prey population distributions and lake thermal conditions might have more subtle or secondary effects, particularly for species that have cooler preferred temperatures. Preferred temperatures of coolwater piscivores such as chinook salmon and lake trout will still be available during summer and changes in prey distribution, and thermal structure will likely only cause a change in the depths of the lake with suitable habitat. In particular, surface waters will become unsuitable and deeper waters will become more suitable. During the spring and fall, however, the overall result will be that areas with high growth conditions will increase and the period of high growth rates for coolwater piscivores will noticeably increase. The effect on warmwater piscivores, such as striped bass, is similar but enhanced. These species adapted to warmer water temperatures have an even greater increased habitat quality under climate warming simulations than do the coolwater piscivores. Temperatures begin to warm earlier in the spring, and the onset of thermal stratification can begin a month or more earlier than under base conditions. This increase in the length of the thermal conditions for high growth rates was shown to be the main cause of increases in fish growth rate potential for all species under climate warming.

Clearly, any effect of climate warming on the top predators will depend on prey availability and prey fish populations. We made several assumptions concerning prey availability in our simulations: 1) that prey abundance/composition remained constant throughout the year as well as across the model simulations, 2) that the spatial distributions of planktivores were determined strictly on the basis of thermal preferenda, and 3) that climate changes on components of the food web below planktivores did not affect planktivore populations. Violations of these assumptions may affect our results. Prey populations in the Great Lakes have a long history of large variations in abundance and species composition from year to year or over longer time frames (Wells 1968; Rand et al. 1995). Unfortunately, there are no good predictors of abundances or year-class strength for any of these species. Indeed, there are no direct measures of seasonal availability of the total prey field in the Great Lakes, although this has been modeled (Rand et al. 1995). We felt that it was beyond the scope of this paper to evaluate seasonal changes in prey abundances because our focus was on 1) an instantaneous measure of growth rate potential (rather than annual growth), and 2) a comparison across three large scale time frames rather than within year differences. That said, we would note that our simulation showing the effect of a 15% reduction in prey abundance resulted in a 9% reduction in chinook salmon growth rate potential suggests that there may be

some mitigating effect of a decrease in prey populations on piscivore habitat quality. This effect resulted from the temperature preferences of planktivores overlapping with the temperature preferences of piscivores.

We feel quite confident about our second assumption that planktivore distributions closely follow species temperature preferenda. Thermal preferenda are solid species characteristics, and these species have been shown to follow temperatures in the Great Lakes (e.g., Brandt et al. 1980). This assumption does not take into account any changes that may occur in the lower trophic levels that may cause planktivores to change distributions in response to changes in their prey availabilities, which is why we make the third assumption, that climatic effects on the lower food webs had no impact on the planktivores. We do expect that the seasonal differences in the onset of thermal stratification will have direct effects on primary (e.g., Brooks and Zastrow, in press) and secondary production and thus on planktivores seasonal and interannual abundances. These effects are unpredictable at this time.

One of the more subtle effects of changes in the thermal structure was the impact on prey densities. Climate warming simulations produced a larger volume of thermal habitat for adult alewife, bloater, and smelt. If we distribute the same numbers of prey across this larger volume of habitat, prey densities encountered by a predator would be reduced. This is shown conceptually in Figure 12. Reduced prey densities would reduce the predator encounter rate with prey, which would reduce predator consumption rates. The highest chinook salmon and lake trout growth rate potential was thus lost under the climate-warming simulations (Figures 8 and 9). This would occur only if original prey densities were not at predator saturation levels.

Observed water temperatures in southern Lake Michigan occasionally reach levels that are predicted under climate warming simulations (Figure 11), which are often focused on mean conditions. We do not know how interannual variations in water temperatures, as observed for the years 1996 and 1998, affect growth rates of predators or food web dynamics in the Great Lakes. Clearly, a better understanding of production dynamics in the Great Lakes during a typical cold year, and a typical warm year might provide important clues to the potential impact of climate on fishes. We suggest that an integrated study of interannual variations in food web dynamics and productivity and their relationships to seasonal variations in water temperature is warranted.

### Acknowledgments

We thank Mason Thornburg for help with the computer programming and Cynthia Sellinger for helping in the preparation of the illustrations. This research was sup-

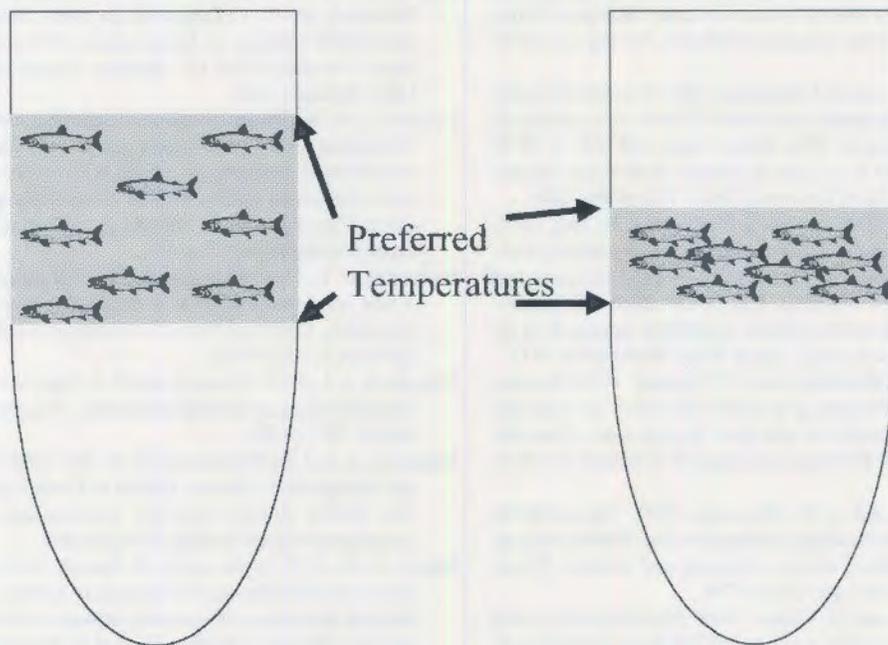


Figure 12. Conceptual demonstration of the effect of changes in the volume of thermal habitat on prey densities.

ported in part by NSF Grant OEC9417540 to S. B. Brandt, NSF Land Margin Ecosystem Research Program DEB-9412113, and the NOAA Coastal Ocean Program (COASTES). This is contribution #1244 of the NOAA Great Lakes Environmental Research Laboratory.

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