

Temperature effects induced by climate change on the growth and consumption by salmonines in Lakes Michigan and Huron

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Received: 10 August 2013 / Accepted: 25 August 2014 / Published online: 4 October 2014
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Abstract We used bioenergetics models to investigate temperature effects induced by climate change on the growth and consumption by Chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, and steelhead *O. mykiss* in Lakes Michigan and Huron. We updated biological inputs to account for recent changes in the food webs and used temperature inputs in response to regional climate observed in the baseline period (1964–1993) and projected

in the future period (2043–2070). Bioenergetics simulations were run across multiple age-classes and across all four seasons in different scenarios of prey availability. Due to the increased capacity of prey consumption, future growth and consumption by these salmonines were projected to increase substantially when prey availability was not limited. When prey consumption remained constant, future growth of these salmonines was projected to decrease in most cases but increase in some cases where the increase in metabolic cost can be compensated by the decrease in waste (egestion and excretion) loss. Consumption by these salmonines was projected to increase the most during spring and fall when prey energy densities are relatively high. Such seasonality benefits their future growth through increasing annual gross energy intake. Our results indicated that lake trout and steelhead would be better adapted to the warming climate than Chinook salmon. To maintain baseline growth into the future, an increase of 10 % in baseline prey consumption was required for Chinook salmon but considerably smaller increases, or no increases, in prey consumption were needed by lake trout and steelhead.

Electronic supplementary material The online version of this article (doi:10.1007/s10641-014-0352-6) contains supplementary material, which is available to authorized users.

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Keywords Climate change · Bioenergetics models ·
Salmonines · Lake michigan · Lake huron

Introduction

Following the global trend of changing climate, air temperatures in the Great Lakes region have increased

by an average of 0.28 °C per decade since 1970 (NCDC 2013). The increased air temperature has resulted in several changes in aquatic habitats of the Great Lakes including increased water temperatures (McCormick and Fahnenstiel 1999; Dobiesz and Lester 2009), shortened ice-covered periods, and consequently prolonged summer stratification periods (Assel 2005). Based on current projections of global greenhouse gas emissions, air temperatures in the Great Lakes region will increase by 3–5 °C by the end of this century (Hayhoe et al. 2010). Hence further changes in aquatic habitats of the Great Lakes along observed trends are expected.

Climate change may affect the growth and consumption by fish in the Great Lakes directly through effects of warming water temperature on fish physiology and indirectly through effects of changes in aquatic environment on prey availability. Being poikilothermic organisms, fish may behaviorally thermoregulate by moving to preferred thermal habitats in which temperatures are closer to their optima for growth (Coutant 1987). In cold and deep parts of the Great Lakes, Magnuson et al. (1990) predicted that the availability of fish thermal habitats will increase in a warming climate. Correspondingly, the growth and consumption by fish in the Great Lakes may both increase in a warming climate if prey availability is not limited (Hill and Magnuson 1990; Brandt et al. 2002). However, changes in aquatic environment induced by climate change may result in limited prey availability to fish in the Great Lakes (Magnuson et al. 1997; Kling et al. 2003). If prey consumption remains constant over time, the growth of fish in the Great Lakes may decrease in a warming climate because of the increase in metabolic rates (Hill and Magnuson 1990).

Among Great Lakes, salmonines (salmon and trout in the subfamily Salmoninae) are economically important as favorite targets in recreational fisheries in Lakes Michigan and Huron (Crawford 2001; Thayer and Loftus 2012). As salmonine populations are artificially maintained or supplemented by hatchery stocking, the potential for predator–prey imbalance in Lakes Michigan and Huron has long been a concern for researchers and resource managers (Brown et al. 1999). Such an imbalance could have occurred in Lake Huron where prey fish abundance decreased sharply after 2004 (Riley et al. 2008). Climate change may increase the potential of predator–prey imbalance because an increase in prey consumption is required for salmonine

predators to offset the increase in metabolic costs in a warming water temperature.

In this study, we used bioenergetics models (Kitchell et al. 1977; Hanson et al. 1997) to investigate temperature effects induced by climate change on the growth and consumption by three salmonine species representing the bulk of recreational harvests in Lakes Michigan and Huron: Chinook salmon *Oncorhynchus tshawytscha*, lake trout *Salvelinus namaycush*, and steelhead *O. mykiss*. To our knowledge, only two studies used bioenergetics models to explore effects of climate change on growth and consumption by fish in the Great Lakes (Hill and Magnuson 1990; Brandt et al. 2002) but both studies were limited in scope and consequently applicability to fisheries management. These researchers investigated climate change effects on annual growth and prey consumption by a fish at a specific age or with a specific weight, but not the growth and consumption by a fish across multiple age-classes. In addition, these researchers did not consider seasonal variation in diet composition, which has an important effect on attained growth and prey consumption by salmonines (Stewart 1980; Stewart et al. 1983).

We followed the scenario-simulation approach in Hill and Magnuson (1990) but made several major modifications to generate more informative results for fisheries management. Specifically, we (1) ran bioenergetics simulations, across multiple age-classes and across all four seasons, in a baseline scenario and different future scenarios of prey availability; (2) estimated prey consumption required to maintain baseline growth; and (3) assessed changes in growth, prey consumption, and seasonal and annual energy budgets under the future climate regime for salmonines in Lakes Michigan and Huron.

Methods

Bioenergetics models

The master equation of bioenergetics models (Stewart et al. 1983; Stewart and Ibarra 1991; Rand et al. 1993) used in this study represents the daily energy budget of a fish as:

$$C = P_{max}C_{max} = M + W + G \quad (1)$$

where C is the prey consumption in terms of the gross energy intake, P_{max} is the proportion of maximum

consumption that is realized, C_{max} is the maximum (prey) consumption, M is the metabolic cost, W is the waste loss or the total of egestion and excretion, and G is the net energy for growth (including reproduction). Following the approach by Kitchell et al. (1977), submodels for consumption, metabolic cost, and waste loss were expressed as a series of species-specific functions of fish weight and temperature together with predetermined parameters, as detailed in the Online Resource. With required biological inputs, temperature inputs, and simulation parameters, fish growth and energy budget can be simulated in these bioenergetics models on a daily basis.

We coded and ran these bioenergetics models in R (version 2.8.1, R Develop Core Team 2008) instead of using the software package Fish Bioenergetics 3.0 (Hanson et al. 1997) for better computational efficiency. In addition, Madenjian et al. (2012) reported an error in algorithms for balancing daily fish energy budget in Fish Bioenergetics 3.0. To ensure our R scripts are free from error, we validated outputs from these scripts multiple times with outputs from the corrected Fish Bioenergetics 3.0 software package used in Madenjian et al. (2012).

Focal populations and biological inputs

We focused on Chinook salmon, lake trout, and steelhead populations in the main basin of Lake Michigan and in the main basin of Lake Huron (Fig. 1). Following

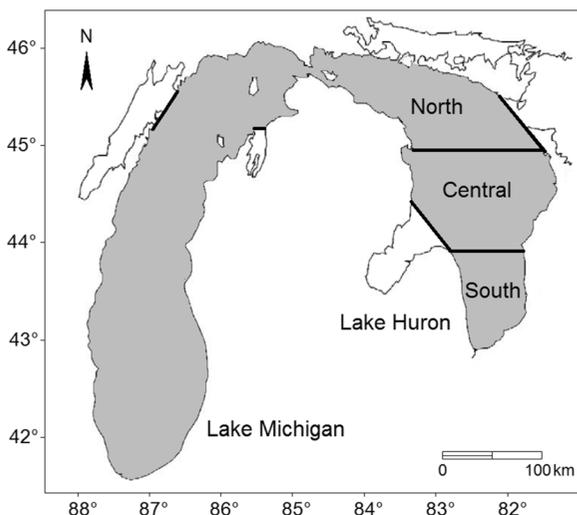


Fig. 1 Map of Lakes Michigan and Huron. The main basin of each lake was shaded. The Lake Huron main basin was divided into three lake regions using the 45 °N and 44 °N latitude lines

Eshenroder et al. (1995), we further divided Lake Huron lake trout into three populations: North, Central, and South Lake Huron lake trout.

Required biological inputs including growth (as initial and final weights of a bioenergetics simulation), reproduction, diet schedules, predator energy densities, and prey energy densities were selected to represent an average individual in each salmonine population. These inputs were updated to reflect changes resulted from invasive species and nutrient loads the food webs during past 20 years (Vanderploeg et al. 2002; Riley et al. 2008; Dolan and Chapra 2012). Values and data sources of these inputs were detailed in the Online Resource.

Temperature inputs

Temperature inputs were calculated using spatially explicit temperature profiles in Lakes Michigan and Huron from one of the co-authors (Lofgren, unpubl.) for the baseline period (1964–1993) and for the future period (2043–2070). These temperature profiles were outputs from a revised version of the Coupled Hydrosphere-Atmosphere Research Model (CHARM; Lofgren 2004) based on climate conditions in the Great Lake region observed in the baseline period and projected under the global development scenario A2 (IPCC 2000), the business as usual scenario, in the future period. The baseline period was selected as a historical reference and the future period was selected to represent the condition when climate change has made a substantial increase in the water temperature.

The temperature input in the bioenergetics model represents mean daily temperature experienced by the modeled fish. Following the approach used by Stewart et al. (1983), the temperature experienced by the modeled fish was set to the preferred temperature when it is available (Table 1). This approach was based on the assumption of behavioral thermoregulation that the modeled fish would move to a preferred thermal habitat when it becomes available in order to optimize the growth. Based on obtained water temperature profiles in Lakes Michigan and Huron, these preferred temperatures were only available during part of summer when water temperature is highest near the surface and decreased with depth until 4 °C in both of the baseline and future periods. Therefore when water temperature in the surface layer was higher than the preferred temperature, we set temperature experienced by the modeled fish to

Table 1 Preferred temperatures (T_{pre}) for salmonines in Lakes Michigan and Huron

	T_{pre} (°C)	Reference
Chinook salmon (age 0)	18	Stewart and Ibarra (1991)
Chinook salmon (age 1 and older)	13	Bergstedt ^a (unpublished)
Lake trout (age 1 and older)	9	Bergstedt et al. (2012)
Steelhead (lake-age 0)	19	Rand et al. (1993)
Steelhead (lake-age 1 and older)	15	Rand et al. (1993)

^a R. Bergstedt, U.S. Geological Survey, Hammond Bay, Michigan, USA

the preferred temperature. When the preferred temperature is not available (spring, part of summer, fall, and winter), we used water temperature in the surface layer to approximate surrounding temperature of the modeled fish because Lakes Michigan and Huron would be completely homothermous or homothermous to a great depth.

Specifically, temperature inputs (Fig. 2) were calculated as:

$$T(t) = \min[T_{pre}, T_{sur}(t)] \quad (2)$$

where $T(t)$ is the temperature input at time t , T_{pre} is the preferred temperature of the modeled fish, and $T_{sur}(t)$ is water temperature in the surface layer. $T_{sur}(t)$ was calculated by averaging obtained water temperature profiles of surface cells (up to 1.5-m depth) in the geographical range of each salmonine population (Fig. 1). We did not allow daily temperature input to drop below 0.1 °C because these bioenergetics models would not generate reliable predictions of consumption and growth below this level. Recent studies that investigated thermal habits of salmonines in the Great Lakes showed that this approximation is generally reliable and that these salmonines did not seek for the warmest temperature (about 4 °C) in the deep parts of the lakes during winter (Bergstedt et al. 2003; Stewart and Bowlby 2009; Bergstedt et al. 2012). The study from Bergstedt et al. (2012) also showed the lower limit 0.1 °C for our temperature input is very close to the minimum temperature occupied by Lake Huron lake trout in February and March.

Simulation parameters

Required simulation parameters in these bioenergetics models include initial weight (g), simulation length (number of days), and one of the three parameters of P_{max} , final weight (g), and total prey consumed (g). Of these three parameters, one parameter is selected as a model input while the other two parameters represent outputs from the bioenergetics simulation.

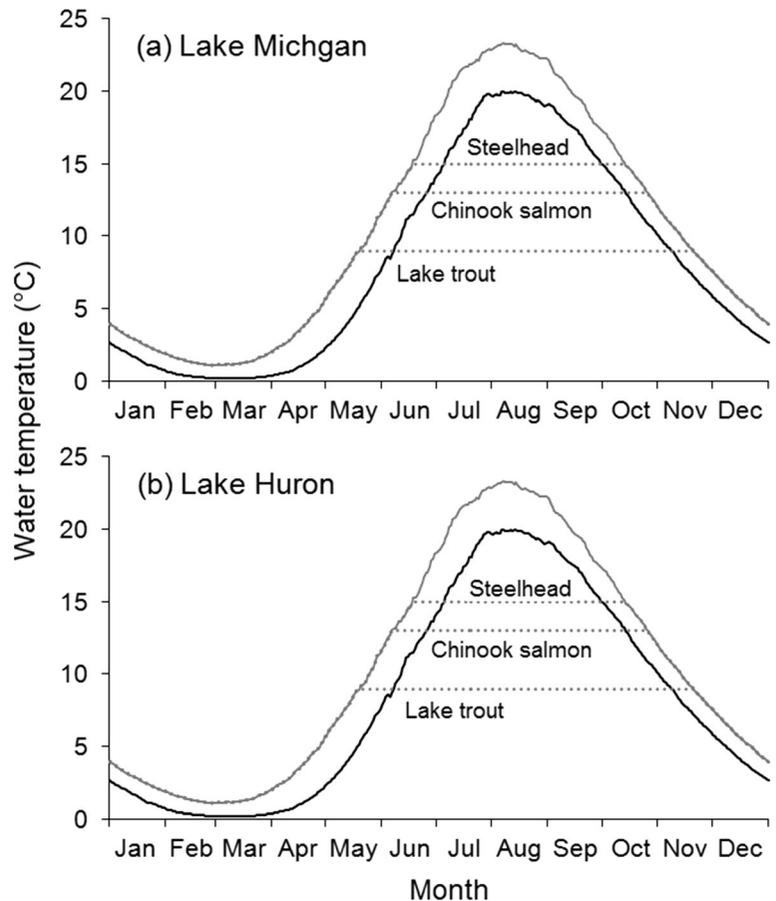
In this study we ran bioenergetics simulations by age and population for each salmonine species. We set the initial weight as the weight at a given age on the first day of simulation (Table 2) and ran bioenergetics simulations over a course of year (365 days). Thus the P_{max} and total prey consumption were on an annual basis and the final weight was the weight at the next older age on the first day of simulation. This bioenergetics modeling approach assumed that the P_{max} remained constant during each year-long simulation. This is an assumption to which the bioenergetics model estimates of consumption and growth appeared to be robust. Field evaluations of both the Chinook salmon bioenergetics model and the lake trout bioenergetics model indicated that model estimates of food consumption and growth were reliable (Brodeur et al. 1992; Madenjian et al. 2000). Further, results from laboratory evaluations of both models revealed little to no bias in model predictions of food consumption and growth (Madenjian et al. 2004, 2012, 2013).

We ran bioenergetics simulations across all age classes when the model fish resided in the lake. For Chinook salmon, we ran bioenergetics simulations from age 0 when they were stocked to ages when they left the lake for spawning run (Table 2) (Fenske and Shouder 1992; Hay 1992). For lake trout, we ran bioenergetics simulations from age 1 when they were stocked to age 10 as most fish were younger than this age (He et al. 2012). Steelhead are known to have different life history forms in the Great Lakes region (Rand et al. 1993). We ran bioenergetics simulations for steelhead using the most common life history form, which entered the lake at lake age 0 as a smolt and lived another four years.

Bioenergetics simulations

We ran bioenergetics simulations by age and population in a baseline scenario and three future scenarios of prey availability for salmonines in Lakes Michigan and Huron. In each scenario, we kept biological inputs the

Fig. 2 Mean water temperatures in Lakes Michigan and Huron projected by the Coupled Hydrosphere–Atmosphere Research Model (CHARM) for the baseline period (1964–1993) and for the future period (2043–2070). Horizontal lines represented preferred temperatures for age-1 (or lake-age-1) and older salmonines



same and ran bioenergetics simulations year-by-year using temperature inputs from the baseline period (29 years) or the future period (27 years).

The baseline (Base) scenario is a historical reference, in which we used baseline growth inputs (Table 2) of the modeled fish to estimate its P_{max} and consumption by age in the baseline period. We averaged model-estimated P_{max} and consumption across years by age (baseline P_{max} and baseline consumption) and used them to present different prey availabilities in the future scenarios.

The first future scenario is a high consumption (HC) scenario, in which we used the baseline P_{max} of the modeled fish to simulate its growth and estimate its consumption by age in the future period. As the C_{max} increases with temperature, consumption by the modeled fish ($P_{max}C_{max}$) would increase in this scenario. This scenario implied that future prey availability is not limited so that consumption by the modeled fish can increase.

The second and third future scenarios are the constant consumption (CC) scenario and the reduced consumption (RC) scenario. In the CC scenario, we used the baseline consumption by the modeled fish to simulate its growth and estimate its P_{max} by age in the future period. The RC scenario was the same as the CC scenario but the input consumption was 90 % of the baseline consumption. These two scenarios implied future prey availability will be limited so that consumption by the modeled fish would be equal to or less than the baseline level.

In addition to scenario simulations, we estimated prey consumption required for the modeled fish to maintain the baseline growth in the future period. To do so, we ran bioenergetics simulations using baseline growth inputs and future temperature inputs. We also quantified the change in prey consumption by age, expressed as the percentage of baseline value.

To assess changes in growth and consumption by the modeled fish under the future climate regime, we

Table 2 Baseline growth inputs used in bioenergetics simulations

Age/lake age	Chinook salmon (5/1)		Lake trout (6/1)				Steelhead (5/1)	
	LM	LH	LM	LHN	LHC	LHS	LM	LH
0	4.54	4.54					50	50
1	586	458	40	40	40	40	932	970
2	2,557	2,160	128	128	128	128	2,664	2,258
3	5,463	4,865	443	443	443	443	3,700	3,203
4		6,324	1,009	829	858	1,123	4,434	3,958
5			1,721	1,225	1,233	1,409		
6			2,804	1,729	1,689	1,785		
7			3,474	2,299	2,194	2,167		
8			3,785	2,756	2,603	2,595		
9			4,519	3,061	2,862	2,822		
10			5,393	3,400	3,147	3,056		

Each value represented the initial weight (g) of the modeled fish at age on the first simulation day, the date (in parentheses) of which was determined based on the source(s) of growth data as detailed in the Online Resource. For age-3 Lake Michigan Chinook salmon and age-4 Lake Huron Chinook salmon that were set to leave the lake for spawning on simulation day 214, final weights were set to 7,865 g and 7,136 g, respectively

LM Lake Michigan; LH Lake Huron; LHN North Lake Huron; LHC Central Lake Huron; LHS South Lake Huron

quantified changes in the following three measures by age in the three future scenarios: weight, prey consumption, and gross conversion efficiency (GCE). The GCE is a measure of the efficiency to convert ingested food into body weight. In this study, we calculated it as the percent change in fish weight relative to consumption in the simulation period. Changes in these three measures were expressed as the percentage of baseline value.

To assess changes in seasonal and annual energy budgets of the model fish under the future climate regime, we quantified changes in energy budgets in the HC and CC scenarios. We divided a year into four seasons based on the temperature experienced by these salmonines in the baseline period: summer (when the lake was thermally stratified, June–October), fall (November–December), winter (when surface water temperature was lower than 4 °C, January–March), and spring (April and May). We quantified changes in quantities of prey consumption (C), metabolic cost (M), waste loss (W), and net energy for growth (G) in a relative manner, expressed as the percentage of baseline value; and quantified changes in proportions of M/C ,

W/C , and G/C in an absolute manner, expressed as the difference from the baseline value.

Results

Temperature effects in general

Our results showed the control by prey availability on responses in the growth and consumption by salmonines in Lakes Michigan and Huron to temperature effects induced by climate change. The growth of Chinook salmon, lake trout, and steelhead all increased substantially in the HC scenario where prey availability is not limited but generally decreased in the HC and RC scenarios where prey availability is limited (Fig. 3). Prey consumption of these salmonines also increased substantially in the HC scenario so that their gross conversion efficiencies (GCEs) generally increased or maintained at baseline levels. In the CC and RC scenarios, the GCEs generally decreased.

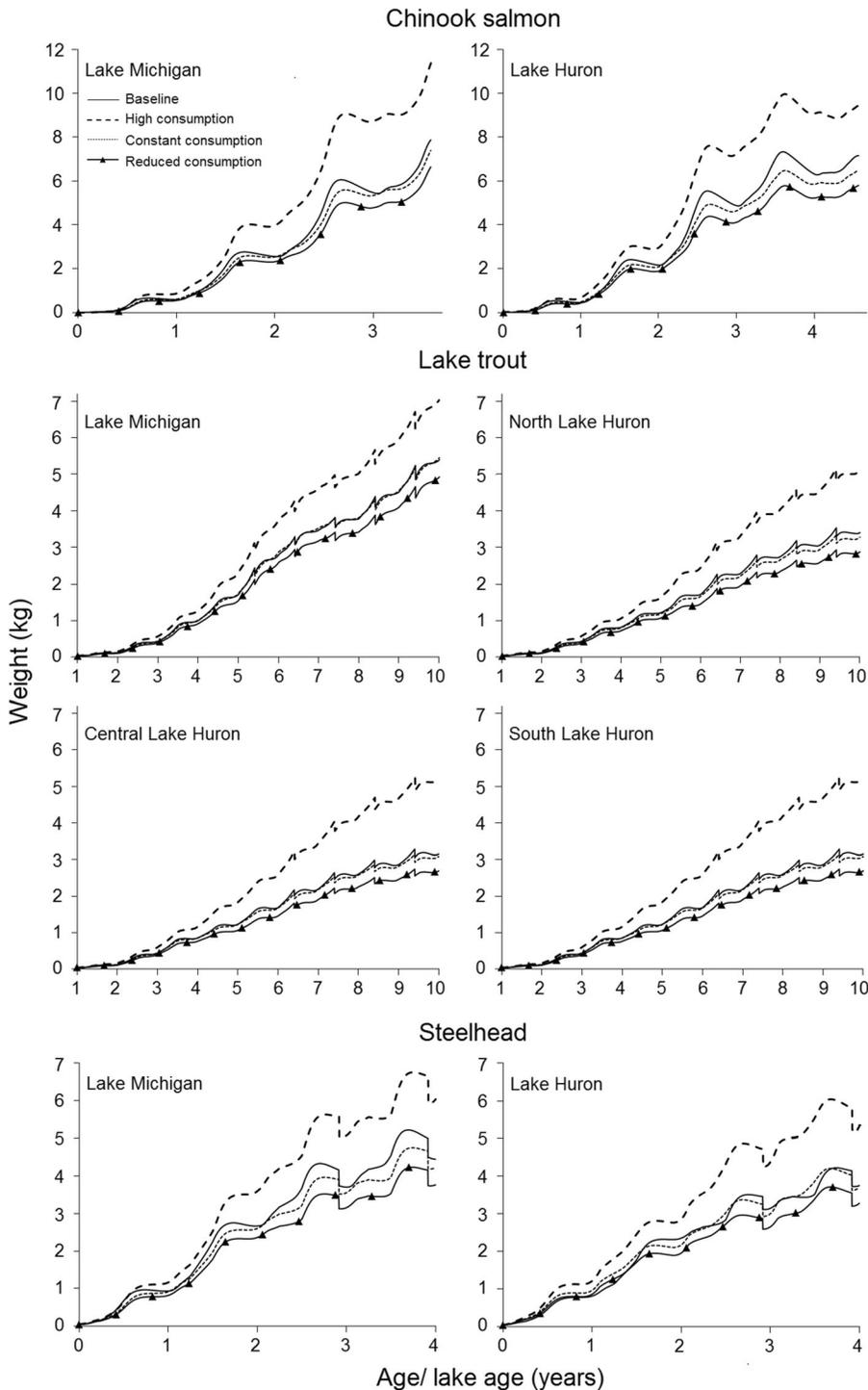


Fig. 3 Simulated growth trajectories of the salmonines in Lakes Michigan and Huron in a baseline (Base) scenario and three future scenarios of prey availability. Each growth trajectory represented an average across 29 years in the baseline period or across 27 years in

the future period. Relative to the baseline prey availability, future prey availability was assumed to increase in the high consumption (HC), to be limited in the constant consumption (CC) scenario, and to be reduced in the reduced consumption (RC) scenario

Our results suggested that temperature effects on growth and prey consumption are stronger for Chinook salmon than for lake trout and steelhead and are stronger for older fish than for younger fish from the same population. However, projected changes in growth and prey consumption under the future climate regime were similar in magnitudes among populations for a given species. We summarized results of our bioenergetics simulations by species in the following sections and reported model-estimated values for P_{max} in the Online Resource

Effects on Chinook salmon

The simulated growth of Chinook salmon in both Lakes Michigan and Huron increased substantially in the HC scenario, decreased in the RC scenario, and increased until age 1 but decreased thereafter in the CC scenario (Fig. 3). Mean weights at different ages increased by 32–60 % in the HC scenario and decreased by 4–19 % in the RC scenario (Fig. 4). In the CC scenario, mean weights increased by 4–7 % at age 1 but decreased by 0–9 % thereafter.

In both populations, mean consumption by Chinook salmon across age-classes in the HC scenario increased by 36–61 % (Table 3). We estimated that a 10 % increase in prey consumption is required for Chinook salmon in Lakes Michigan and Huron to maintain baseline growth in the future period (Table 3).

Table 3 Model-estimated consumption and gross conversion efficiency (GCE) for Chinook salmon

Age	Consumption (kg)			GCE (%)			
	Base	HC	MG	Base	HC	CC	RC
Lake Michigan							
0–1	1.7	2.5	1.7	33.4	34.5	34.7	34.6
1–2	9.1	13.9	9.1	21.6	22.2	21.2	21.6
2–3	17.6	28.3	18.0	16.5	16.8	15.9	15.4
3–3.6 ^a	18.5	27.7	19.9	13.0	9.6	11.1	11.1
Lake Huron							
0–1	1.7	2.3	1.6	26.6	28.7	28.6	28.4
1–2	8.1	11.7	8.4	21.1	19.3	19.8	20.0
2–3	17.3	26.1	18.1	15.7	16.3	14.7	14.3
3–4	19.7	29.9	21.3	7.4	6.3	6.2	6.3
4–4.6 ^a	15.6	21.7	17.2	5.2	1.7	4.1	4.1

Each value represented the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.7 for consumption and all less than 0.4 for GCEs

Base baseline scenario; *HC* high consumption scenario; *CC* constant consumption scenario; *RC* reduced consumption scenario; *MG* prey consumption required to maintain baseline growth under the projected future climate regime

^a Simulation ends on day 214

Mean GCEs of these Chinook salmon mostly increased before age 3 but decreased thereafter in the

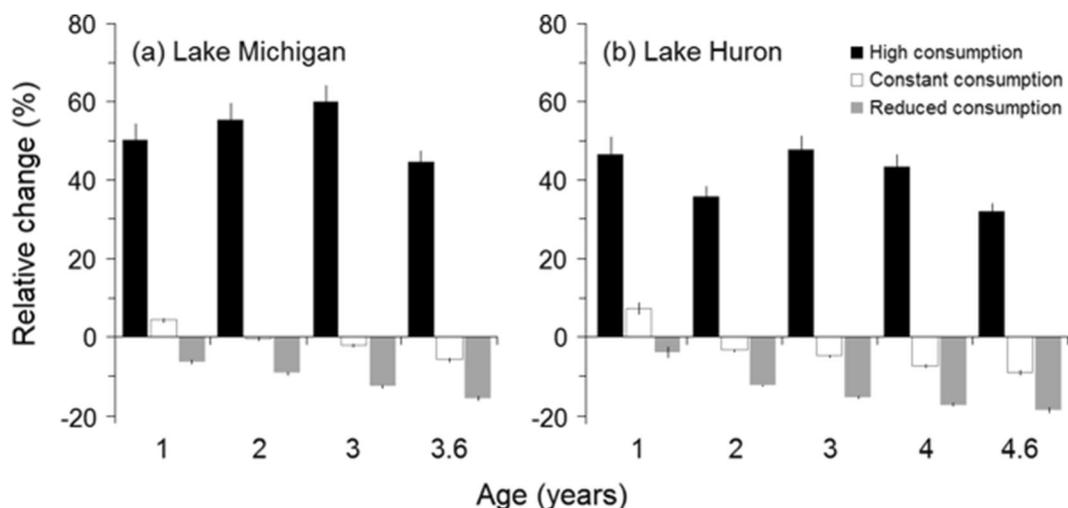


Fig. 4 Changes in model-estimated weights of Chinook salmon at different ages in the future scenarios. Each bar represents a mean change (\pm standard error) relative to the baseline weight at the same age across 27 years in the future period. Model-estimated

weights at age 3.6 or age 4.6 represent weights on simulation day 214 at age 3 or age 4, when bioenergetics simulations ended to represent that Chinook salmon leave the lake for spawning

HC scenario and increased at age 0–1 but decreased thereafter in the CC and RC scenarios. Changes in mean GCEs of Chinook salmon were less than 9 % (increase or decrease) before age 3 but drastic decreases by at least 14 % occurred thereafter in all future scenarios (Table 3).

Effects on lake trout

The simulated growth of lake trout increased substantially in the HC scenario and decreased in the RC scenario but maintained at baseline levels in the CC scenario (Fig. 3). In the HC scenario, mean weights of lake trout at different ages increased by 23–34 % in the Lake Michigan population (Fig. 5a) and by 27–69 % among Lake Huron populations (Fig. 5b–d). In the CC scenario, these changes ranged from an increase of 7 % to a decrease of 2 %. Mean weights of Lake Michigan lake trout increased slightly at all ages (Fig. 5a) but mean weights of Lake Huron lake trout increased at

ages before 5 and decreased thereafter (Fig. 5b–d). In the RC scenario, mean weights of lake trout at different ages decreased by 7–11 % in the Lake Michigan population (Fig. 5a) and by 6–14 % among Lake Huron populations (Fig. 5b–d).

Mean consumption by lake trout across age-classes in the HC scenario increased by 18–33 % in the Lake Michigan population and increased by 16–56 % among Lake Huron populations (Table 4). We estimated that a small increase of 2 % in prey consumption is enough for lake trout in Lakes Michigan and Huron to maintain baseline growth in the future period (Table 4).

Mean GCEs of these lake trout generally increased before age 3 by more than 3 % in the three future scenarios but changed differently across populations thereafter (Table 4). For Lake Michigan lake trout after age 3, mean GCEs at the same age-class varied little among the three future scenarios, ranging from a 10 % increase to a 14 % decrease among (Table 4). For Lake Huron lake trout at ages after 3, mean GCEs at different

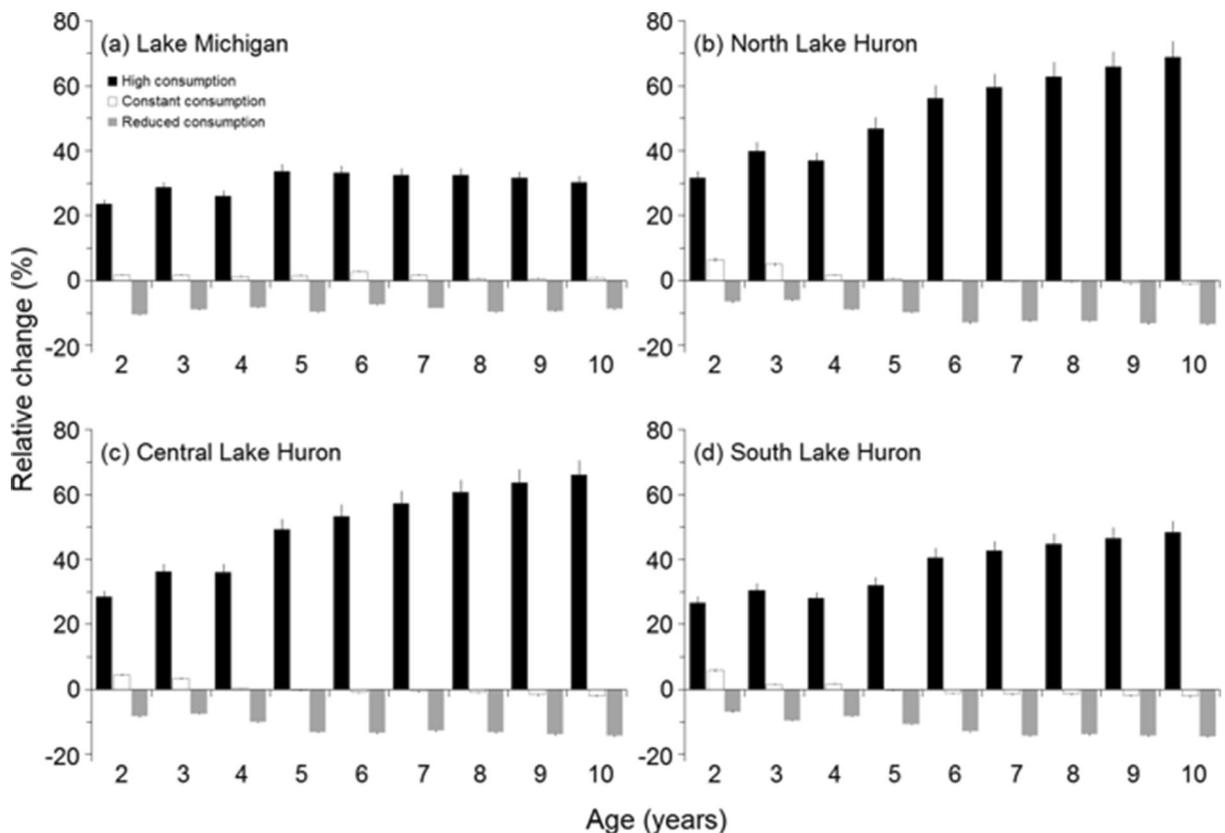


Fig. 5 Changes in model-estimated weights of lake trout at different ages in the future scenarios. Each bar represents a mean change (± standard error) relative to the baseline weight at the same age across 27 years in the future period

Table 4 Model-estimated consumption and gross conversion efficiency (GCE) for lake trout

Age	Consumption (kg)			GCE (%)			
	Base	HC	MG	Base	HC	CC	RC
Lake Michigan							
1–2	0.63	0.75	0.62	13.9	15.8	14.3	13.1
2–3	1.8	2.3	1.7	17.8	18.2	18.1	18.1
3–4	3.4	4.3	3.3	16.8	16.2	16.9	17.2
4–5	5.5	7.1	5.4	13.1	14.4	13.3	12.8
5–6	9.2	12.2	8.9	11.8	11.7	12.3	12.5
6–7	8.2	10.9	8.1	8.2	8.0	8.0	8.0
7–8	7.7	10.3	7.8	4.0	4.0	3.6	3.5
8–9	10.8	14.3	10.7	6.8	6.5	6.9	7.0
9–10	13.2	17.3	13.0	6.6	6.3	6.8	6.9
North Lake Huron							
1–2	0.69	0.82	0.65	12.8	20.0	14.1	12.9
2–3	1.8	2.4	1.7	17.6	18.9	18.4	18.4
3–4	2.8	3.8	2.7	14.0	13.8	13.7	13.6
4–5	3.7	5.1	3.7	10.6	12.8	10.5	10.5
5–6	4.6	6.8	4.6	10.9	13.2	10.8	9.6
6–7	6.0	9.0	6.1	9.4	10.6	9.4	9.3
7–8	6.8	10.3	6.8	6.7	7.9	6.6	6.5
8–9	6.9	10.7	7.0	4.4	5.5	4.2	4.0
9–10	7.5	11.8	7.6	4.5	5.5	4.4	4.2
Central Lake Huron							
1–2	0.69	0.82	0.67	12.7	15.1	13.5	12.5
2–3	1.9	2.5	1.8	16.9	17.8	17.4	17.5
3–4	3.2	4.3	3.2	12.9	13.0	12.5	12.5
4–5	4.2	6.0	4.3	8.8	11.2	8.7	7.8
5–6	5.1	7.5	5.2	8.9	10.0	8.7	8.5
6–7	6.6	9.8	6.6	7.7	8.8	7.7	7.6
7–8	7.0	10.5	7.0	5.9	6.9	5.7	5.5
8–9	7.0	10.7	7.0	3.7	4.6	3.4	3.2
9–10	7.5	11.7	7.7	3.8	4.7	3.6	3.5
South Lake Huron							
1–2	0.63	0.73	0.60	13.9	16.6	15.1	13.9
2–3	1.6	2.1	1.6	19.5	20.2	19.5	19.4
3–4	4.0	5.1	3.9	17.1	16.9	17.4	17.6
4–5	3.6	4.6	3.6	8.0	9.1	7.3	7.0
5–6	4.4	5.9	4.4	8.6	11.1	8.3	7.5
6–7	5.2	7.1	5.2	7.4	8.2	7.2	6.6
7–8	6.1	8.4	6.2	7.0	7.9	6.9	6.9
8–9	6.0	8.3	6.1	3.8	4.6	3.6	3.5
9–10	6.3	8.9	6.4	3.7	4.4	3.5	3.4

Each value represented the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.3 for consumption and all less than 0.2 for GCEs

Base baseline scenario; *HC* high consumption scenario; *CC* constant consumption scenario; *RC* reduced consumption scenario; *MG* prey consumption required to maintain baseline growth under the projected future climate regime

age-classes mostly increased by 10–20 % in the HC scenario but mostly decreased by about 5 % in the CC scenario and by 10 % in the RC scenario (Table 4).

Effects on steelhead

The simulated growth of steelhead in both Lake Michigan and Lake Huron populations increased substantially in the HC scenario but decreased in the CC and RC scenarios (Fig. 3). In both steelhead populations, mean weights at different ages increased by 24–37 % in the HC scenario, decreased by 0–6 % in the CC scenario, and decreased by 11–17 % in the RC scenario (Fig. 6).

Mean consumption by steelhead across age-classes increased by 26–41 % in the HC scenario for both populations (Table 5). We estimated that an increase of 6 % in prey consumption is required for steelhead in Lakes Michigan and Huron to maintain baseline growth in the future period (Table 5).

Mean GCEs of steelhead in both populations increased in some age-classes but decreased in the others in the HC scenario but decreased across all age-classes in the CC and RC scenarios. Changes in mean GCE across age-classes ranged from a 4 % increase to a 7 % decrease for Lake Michigan steelhead and ranged from a 16 % increase to a 10 % decrease for Lake Huron steelhead (Table 5). In both populations, mean GCEs of steelhead across age classes decreased by 1–12 % in the CC scenario and by 1–18 % in the RC scenario.

Table 5 Model-estimated consumption and gross conversion efficiency (GCE) for steelhead

Lake age	Consumption (kg)			GCE (%)			
	Base	HC	MG	Base	HC	CC	RC
Lake Michigan							
0–1	4.2	5.4	4.3	20.8	20.6	20.3	20.1
1–2	12.4	16.7	12.8	14.0	14.6	13.6	13.8
2–3	18.2	25.6	19.0	5.7	5.8	5.2	4.8
3–4	21.2	29.8	22.3	3.5	3.2	3.1	3.2
Lake Huron							
0–1	5.1	6.4	5.1	18.0	18.1	17.9	17.8
1–2	10.7	14.4	11.2	12.0	11.4	11.2	11.3
2–3	16.0	22.3	16.8	5.9	6.8	5.2	4.8
3–4	18.7	26.4	19.9	4.0	3.6	3.8	3.7

Each value represented the mean of simulated values across 29 years in the baseline period or across 27 years in the future period. Corresponding standard errors were all less than 0.5 for consumption and all less than 0.2 for GCEs

Base baseline scenario; *HC* high consumption scenario; *CC* constant consumption scenario; *RC* reduced consumption scenario; *MG* prey consumption required to maintain baseline growth under the projected future climate regime

Effects on energy budgets

Simulated energy budgets of these salmonines changed the most during spring and fall in response to the increased water temperatures induced by climate change.

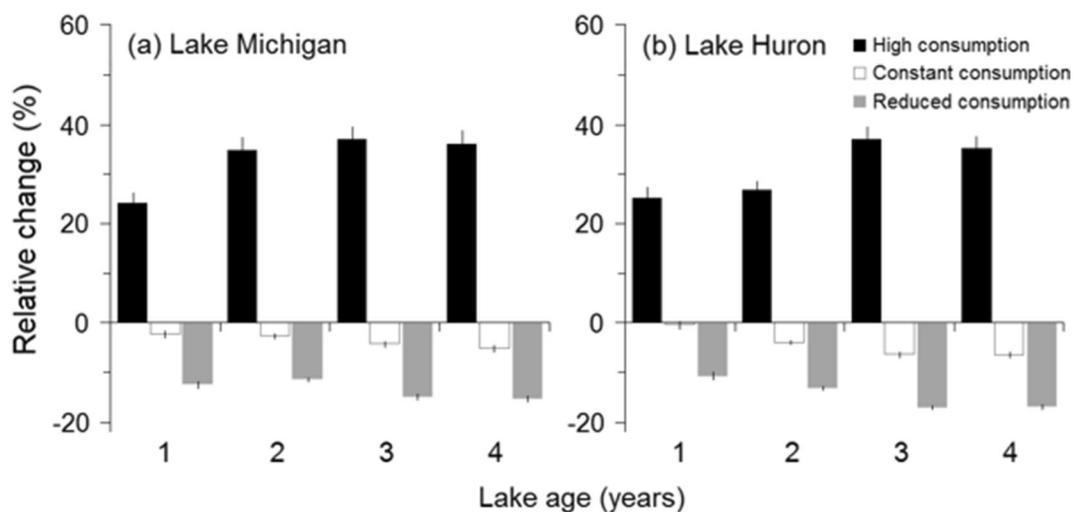


Fig. 6 Changes in model-estimated weights of steelhead at different ages in the future scenarios. Each bar represents a mean change (\pm standard error) relative to the baseline weight at the same age across 27 years in the future period

In the HC scenario, quantities of metabolic cost (M), waste loss (W), and net energy for growth (G) all increased with the increase in prey consumption (C) on an annual basis and in all four seasons (Table 6). The largest increases of these quantities occurred in spring and fall. In the CC scenario, the prey consumption and metabolic cost decreased in summer but increased during the rest of the year while the waste loss increased in spring but decreased during the rest of the year. As a result, the net energy for growth increased substantially in spring. On an annual basis, the increase in metabolic cost was generally larger than the decrease in waste loss, resulting in a decrease in net energy for growth. In both of the HC and CC scenarios, proportions of M/C , W/C , and G/C of these salmonines changed little on an annual basis and in all seasons except spring (Table 6). Simulated proportions of M/C and W/C both decreased in spring and consequently the proportion of G/C increased substantially.

Discussion

Processes underlying changes in growth and consumption

The increase in water temperatures induced by climate change would affect the growth and consumption by

salmonines in Lakes Michigan and Huron by increasing the capacity of prey consumption and by altering the energy budget. Our bioenergetics simulations showed how these processes may be controlled by behavioral thermoregulation and prey availability. Hence final changes in the growth and consumption by these salmonines would depend on future changes in the ecosystem under the future climate regime.

The projected increases in future water temperatures will increase the capacity of prey consumption for salmonines in Lakes Michigan and Huron and impart the potential for increased growth. Due to behavioral thermoregulation, temperatures experienced by these salmonines would never exceed their preferred temperatures under the projected future climate regime (Fig. 2). When the temperature approaches the preferred temperature from below, the maximum consumption by these salmonines increases with temperature more rapidly than the sum of metabolic cost and waste loss does. Hence changes in the growth and consumption by these salmonines under the future climate regime will depend on how much of the increased maximum consumption rates can be realized, which, in turn, depends on the prey availability. When prey availability was not limited, our simulations in the HC scenario showed that the growth and consumption by these salmonines will always substantially increase under the future climate regime, and this part of our results was in complete agreement with

Table 6 Simulated seasonal and annual changes in energy budgets for salmonines in Lakes Michigan and Huron in the high consumption (HC) scenario and in the constant (CC) consumption scenario

	HC				CC				M/C	W/C	G/C
	C	M	W	G	C	M	W	G			
Spring	↑↑	↑	↑	↑↑	↑↑	↑↑	↑↑	↑↑	↓	↓	↑↑
Summer	↓	–	↓	↓	↑	↑	↑	↑	↑	–	↓
Fall	↑	↑	–	↑	↑↑	↑↑	↑↑	↑↑	–	–	–
Winter	↑	↑	↓	↑ ^a	↑↑	↑↑	↑	↑ ^a	↓	↓	↑
Annual	–	↑	↓	↓	↑	↑↑	↑	↑↑	–	–	–

The prey consumption (C), in terms of gross energy intake, was partitioned into metabolic cost (M), waste loss (W), and growth (G), and M/C , W/C , and G/C were proportions of gross energy intake represented by metabolic cost, waste loss, and growth, respectively. For these proportions of consumption, the changes were similar in the HC and CC scenarios so results were pooled. Degrees of changes were divided into four levels based on the median of changes among ages and populations—substantial increase (↑↑): increase over the Base scenario value by more than 0.10 for the proportions of M/C , W/C , and G/C or by more than 40 % for the quantities of C , M , W , and G ; increase (↑): increase over the Base scenario value by between 0.02 and 0.10 for the proportions or by between 5 % and 40 % for the quantities; little change (–): change from the Base scenario by less than 0.02 for the proportions or by less than 5 % for the quantities; and decrease (↓): decrease from the Base scenario value by between 0.02 and 0.10 for the proportions or by between 5 % and 40 % for the quantities

^a In some simulations, this increase (↑) reflected a reduction in energy loss under the HC and CC scenarios compared with the Base scenario. Note that growth for these salmonines in the winter was predominately negative in the Base scenario

results and implications from previous studies (Hill and Magnuson 1990; Magnuson et al. 1990; Brandt et al. 2002). If prey availability was limited, our simulations in the CC scenario showed that the growth of these salmonines will mostly, but not always, decrease under the future climate regime. This part of our results did not fully agree with results from Hill and Magnuson (1990), who concluded that the growth of a fish in the Great Lakes will always decrease without an increase in prey consumption that compensates for the increased metabolic cost in the warming climate.

The disagreement between results from Hill and Magnuson (1990) and ours can be explained by examining the details of the energy budget. When prey consumption (C) is constant over time, future growth (G) of a fish will depend on changes in metabolic cost (M) and in waste loss (W). With the increase in temperature, the metabolic cost will surely increase but the waste loss may decrease. The proportion of W/C of these salmonines is jointly controlled by the parameter P_{max} and temperature (Stewart et al. 1983). Within the range of model-estimated P_{max} among our simulation scenarios, the proportion of W/C would decrease with the increase in water temperature when it is lower than 5 °C and would change little with water temperature when it increases from 5 °C to the preferred temperature. Hence the growth of fish will increase when prey consumption is limited if the waste loss decreases more than the increase in metabolic cost under the projected future climate regime.

This study and the study by Hill and Magnuson (1990) both simulated the growth of yearling lake trout under the same CC scenario but had opposite results: the simulated growth increased in this study but decreased in Hill and Magnuson (1990). This discrepancy results from a difference in winter water temperatures during baseline periods between these two sets of simulations. Hill and Magnuson (1990) ran baseline simulations using Lake Erie temperatures, which were less frequently below 5 °C on an annual basis than those for Lakes Michigan and Huron temperatures. Consequently, the decrease in the proportion of W/C in a warming climate for yearling lake trout in Lake Erie would be less pronounced than that in Lakes Michigan and Huron.

Seasonal effects

Our results also showed that temperature effects induced by climate change on the growth and consumption by

these salmonines vary by season. Due to behavioral thermoregulation, projected surrounding temperatures of these salmonines in the future period increased the most during spring and fall (Fig. 3). Thus simulated growth and consumption increased the most in spring and the second most in fall under both the HC and CC scenarios.

This seasonality in prey consumption will benefit the growth of these salmonines through increasing the annual mean prey energy density in diet. Mean prey energy densities in diets of these salmonines were primarily highest in fall and lowest in early summer because energy densities of the two most important prey fishes—Lake Michigan alewife *Alosa pseudoharengus* and Lake Huron rainbow smelt *Osmerus mordax*—had similar seasonal cycles, which peaked in fall, gradually decreased through winter until the early summer minimum, and increased again until the fall peak (Dobiesz 2003; Madenjian et al. 2006). In addition, mean prey energy densities were the highest in spring for Chinook salmon and steelhead in Lake Huron because emerald shiner *Notropis atherinoides* was important in their diets at that time (Madenjian et al. 2011).

The increases in prey consumption during spring and fall may lead to an increase in gross energy intake for these salmonines under the future climate regime, even when the prey consumption, in terms of weight, remains constant over time. Our simulations in the CC scenario showed the gross energy intake can increase as much as 1 % (as for lake-age-2 and older Lake Michigan steelhead), which compensated for nearly a 40 % of increase in metabolic cost.

Validity of behavioral thermoregulation

The validity of our results from bioenergetics simulations especially depends on the validity of the behavioral thermoregulation assumption, which was used to model the temperature actually experienced by these salmonines in the projected warming climate (Fig. 2). The assumption of behavioral thermoregulation depends on three components: (1) the existence of behavioral thermoregulation, (2) the unchanged temperature preference, and (3) the occupation of the best available thermal habitat (where the temperature that is closest to the preferred temperature) under the future climate regime.

There is little doubt about the existence of behavioral thermoregulation of these salmonines as field evidence

and bioenergetics model simulations both suggested current summer epilimnion temperatures in Lakes Michigan and Huron are too high for these salmonines to thrive. On an annual basis, many field studies (Spigarelli and Thommes 1979; Olson et al. 1988; Bergstedt et al. 2003; Stewart and Bowlby 2009; Bergstedt et al. 2012) have shown temperatures experienced by adult salmonines in the Great Lakes all plateaued at different temperatures between 8 °C and 15 °C regardless of how high the surface temperatures became. In addition, observed growth of these three salmonines could be accurately predicted by bioenergetics models when behavioral thermoregulation was assumed.

Preferred temperatures of these salmonines will probably change very little under the future climate regime. Two potential causes of changes in preferred temperatures are changes in the prey distribution and changes in environmental conditions. As salmonines' prey also behaviorally thermoregulate, their distributions are also controlled by water temperature profiles (Wells 1968; Brandt et al. 1980). For example, Brandt et al. (2002) projected that the thermal habitat of adult alewives that prefer 13 °C in Lake Michigan will increase with a warming climate. Thus their density within the thermal habitat will decrease if the population size remains unchanged. In such case, lake trout that prefer 9 °C may be forced to stay in temperatures higher than 9 °C in order to meet their consumptive demand. In contrast, environmental factors that can force these salmonines out of their preferred thermal habitats, such as dissolved oxygen (Stefan et al. 2001) and light penetration (Magnuson et al. 1997), are unlikely to change with the water temperature. The main control on these environmental factors is nutrient loading, which is well managed in watersheds of Lakes Michigan and Huron (Dolan and Chapra 2012). Even if changes in preferred temperatures of these salmonines occur, preferred temperatures in the future climate regime will not be too much different from the ones used in this study because of physiological constraints of these salmonines and of their prey (Olson et al. 1988).

The most questionable component in the assumption of behavioral thermoregulation is the occupation of the best available thermal habitat. Field studies have shown salmonines in the Great Lakes did not always occupy the best available thermal habitat probably because of competition and the limitation of prey availability. In Lake Ontario, Stewart and Bowlby (2009) found that

temperatures experienced by Chinook salmon were higher than those experienced by steelhead in June and July. Bergstedt et al. (2012) showed that temperatures experienced by Lake Huron lake trout during May and June were lower in 2002–2005 than in 1998–2001 after the change in prey base (Riley et al. 2008). The study also showed that Lake Huron lake trout did not occupy the preferred thermal habitat of 9 °C until July, a month later than when it became available.

These two studies (Stewart and Bowlby 2009; Bergstedt et al. 2012) indicated modest departure from behavioral thermoregulation for part of the year. For example, the input temperature for Lake Huron lake trout was about 1 °C higher than the occupied temperature from field observations in May and June but was similar to those observed during other months (Bergstedt et al. 2012). With this difference, results from our bioenergetics simulations would slightly underestimate the consumption required to maintain the observed the growth for Lake Huron lake trout in the Base scenario, resulting in the slight underestimation of growth and consumption in the future scenarios.

In summary, the assumption of behavioral thermoregulation in this study is not perfect but is not far from reality. The absolute growth and consumption by these salmonines estimated in our bioenergetics simulations might be biased (e.g., Lake Huron lake trout, as discussed above). Nevertheless, the changes in growth and consumption by these salmonines between the base and the future periods projected in our bioenergetics simulations are robust to the validity of the assumption of behavioral thermoregulation.

Message to fishery managers

Our bioenergetics simulations showed how the growth and consumption by salmonines in Lakes Michigan and Huron will change under the projected future climate regime for both high and low prey availability scenarios. However, future prey availability is unlikely to increase in Lakes Michigan and Huron because of the establishment of the quagga mussel (*Dreissena rostriformis bugensis*) population that has sequestered much of the primary production (Vanderploeg et al. 2002; Fahnenstiel et al. 2010) and the continued control of nutrient loads from the watershed (Dolan and Chapra 2012). In addition, preferred temperatures of these salmonines will occur in deeper parts of the lakes where prey availability may be lower in the future climate

regime (Brandt et al. 2002). Thus the projected changes in the growth and consumption by these salmonines in CC and RC scenarios, where the prey availability is limited, are more likely to occur in the future. Based on bioenergetics simulations in these two scenarios, we predicted that (1) lake trout and steelhead will be better adapted to the projected future climate regime than Chinook salmon and (2) within the same salmonine population, younger individuals will be less negatively affected by the warming climate than older individuals. In fact, simulated growth of age-0 and age-1 salmonines increased in many cases because of the warmer winter, during which the simulated growth is actually negative under the baseline climate regime. However, older individuals will be more affected by the warming climate because of the allometric increase in metabolic cost with body weight. Lastly, we estimated a 10 % increase in prey consumption would be sufficient for all of these salmonines to maintain current growth into the future climate regime.

Acknowledgments We thank Michael Wiley and James Breck for providing valuable comments on an early draft of manuscript. We also thank Roger Bergstedt, Jixiang He, Gregory Jacobs, Amber Peters, and Jeffery Schaeffer for sharing unpublished data. Simon Hsu and Yo-Jin Shiau provided technical support. This research was funded by the U.S. Geological National Climate Change and Wildlife Science Center. This article is Contribution 1864 of the U.S. Geological Survey Great Lakes Science Center.

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