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Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron



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ABSTRACT

We used a bioenergetics modeling approach to investigate potential effects of climate change on the growth of two economically important native fishes: yellow perch (*Perca flavescens*), a cool-water fish, and lake whitefish (*Coregonus clupeaformis*), a cold-water fish, in deep and oligotrophic Lakes Michigan and Huron. For assessing potential changes in fish growth, we contrasted simulated fish growth in the projected future climate regime during the period 2043–2070 under different prey availability scenarios with the simulated growth during the baseline (historical reference) period 1964–1993. Results showed that effects of climate change on the growth of these two fishes are jointly controlled by behavioral thermoregulation and prey availability. With the ability of behavioral thermoregulation, temperatures experienced by yellow perch in the projected future climate regime increased more than for lake whitefish under scenarios where prey availability remains constant into the future. Under high prey availability scenarios, simulated future growth of these two fishes both increased but yellow perch could not maintain the baseline efficiency of converting prey consumption into body weight. We contended that thermal guild should not be the only factor used to predict effects of climate change on the growth of a fish, and that ecosystem responses to climate change should be also taken into account.

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Introduction

Freshwater fishes are especially vulnerable to environmental changes associated with climate change because they are ectothermic, their migration among water bodies is constrained by terrestrial and physical barriers, and many of them have been heavily exploited by humans (Woodward et al., 2010). As temperature is the most important abiotic factor controlling fish physiology (Brett, 1979), projected increases in water temperature resulting from climate change are expected to affect the growth of freshwater fishes, their population dynamics, and the ecology at community and ecosystem levels (Jeppesen et al., 2010, 2012; Portner and Farrell, 2008; Sheridan and Bickford, 2011). These increases in water temperature may also change geographical distributions of freshwater fishes (Comte et al., 2013) and the production of freshwater fisheries (Ficke et al., 2007; Portner and Peck, 2010).

Future fish growth may vary among species with different physiological thermal optima and among ecosystems with different responses to climate change. Increases in water temperature associated with climate change should benefit the growth of fishes with higher physiological thermal optima and stress the growth of those with lower (Graham and Harrod, 2009). However, changes in temperature experienced by a fish may not be as great as changes in the mean water temperature of its ecosystem because the fish may behaviorally thermoregulate by selecting thermal habitats in which temperatures are favorable to growth (Coutant, 1987). Hence, effects of climate change on fish growth may not be direct but may be mediated by availability of thermal habitat (Christie and Regier, 1988; King et al., 1999), which in turn largely depends on physical characteristics such as depth and trophic state of the ecosystem (Kling et al., 2003; Stefan et al., 2001). Climate change may also indirectly affect fish growth through altering prey availability (Durant et al., 2007; Woodward et al., 2010). Regardless of the physiological thermal optimum, the growth of fish may decrease with increases in metabolic costs in a warming climate if prey consumption remains constant over time (Sheridan and Bickford, 2011). Due to the wide diversity of freshwater ecosystems, availabilities of prey and thermal habitat for freshwater fish in the future climate regime may be more specific to the population and ecosystem than to the species.

In the Great Lakes of North America, responses of fish growth to climate change have rarely been investigated quantitatively using either empirical or theoretical approaches. Very few attempts (e.g., King

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et al., 1999; O'Brien et al., 2012) have been made to empirically link fish growth with changes in temperature associated with climate change, due to confounding effects of invasive species, exploitation, and nutrient loads that repeatedly caused abrupt and drastic changes in the ecosystem (Beeton, 2002). Even as water temperatures across the Great Lakes gradually increased over last three decades (Bai et al., 2013; Dobiesz and Lester, 2009), changes in fish growth in Lakes Michigan and Huron were mostly attributed to changes induced by invasive dreissenid mussels (Dreissena polymorpha and D. bugensis), which were associated with drastic reductions in prey availability over the same period (Madenjian et al., 2003; Pothoven and Madenjian, 2008; Rennie et al., 2009). To our knowledge, only three studies (Brandt et al., 2002; Hill and Magnuson, 1990; Ng and Gray, 2011) used a theoretical approach-bioenergetics modeling (Kitchell et al., 1977)-to explore potential effects of climate change on fish growth in the Great Lakes. Results from these studies consistently showed that the growth of fishes in the Great Lakes will increase with climate change if prey consumption also increases but will decrease if prey consumption remains constant. Nevertheless, these studies did not address seasonal and ontogenetic changes in fish growth in response to climate change as they primarily focused on general effects of temperature increases on fish growth on an annual basis (Brandt et al., 2002; Hill and Magnuson, 1990) or on bioaccumulation rates of contaminants (Ng and Gray, 2011).

In this study, our primary goal was to investigate potential effects of climate change on the growth of fishes from different thermal guilds (Magnuson et al., 1979) in Lakes Michigan and Huron. We focused on two native representatives of cool- and cold-water fishes: yellow perch (Perca flavescens) and lake whitefish (Coregonus clupeaformis) that have physiological thermal optima of 23 °C and 12 °C, respectively (Coutant, 1977). We did not focus on warm-water fishes such as centrarchids and channel catfish (*Ictalurus punctatus*) because they are in relatively low abundance in these lakes (Clapp et al., 2005; Schrouder et al., 1995). Additionally, we focused on yellow perch and lake whitefish because their populations support valuable fisheries (Brenden et al., 2012; Thayer and Loftus, 2012). Furthermore, yellow perch and lake whitefish are similar in their diets. Both are generalist feeders, relying mainly on zooplankton at young ages (Claramunt et al., 2010; Wu and Culver, 1992) and on benthic invertebrates as adults (Pothoven and Nalepa, 2006; Truemper et al., 2006).

The general approach in this study was adapted from that in Hill and Magnuson (1990), who explored how fish growth may respond to climate change using bioenergetics model simulations under different prey availability scenarios. We expanded the scope of the study carried out by Hill and Magnuson (1990) by conducting a detailed analysis of potential changes in both seasonal and ontogenetic energy budgets for fishes in response to climate change. Here we (1) predicted the growth under different scenarios of prey availability and (2) assessed age- and population-specific changes in seasonal and annual energy budgets under the projected future climate regime for yellow perch and lake whitefish in Lakes Michigan and Huron.

Material and methods

Bioenergetics models

We used the yellow perch bioenergetics model from Kitchell et al. (1977) and the lake whitefish bioenergetics model from Madenjian et al. (2013). The governing equation in these bioenergetics models represents the energy budget of an average individual from a fish population:

$$C = P_{Cmax}C_{max} = M + W + G \tag{1}$$

where *C* is the consumption or the gross energy intake, P_{Cmax} is the proportion of maximum consumption that can be realized, C_{max} is the

maximum consumption, *M* is the metabolic cost, *W* is the waste loss (the total of egestion and excretion), and *G* is the net energy for growth (including reproduction). In these bioenergetics models, C_{max} , *M*, and *W* are mathematically expressed as species-specific functions of temperature and body weight with pre-determined parameters. When using these models to run bioenergetics simulations, one of the three parameters of P_{Cmax} , growth (in terms of initial and final weights), or consumption (the weight of prey consumed) has to be specified so that the other two can be estimated in the simulation. The computational time step in these bioenergetics models is one day, which represents a compromise between computational accuracy and data availability.

Instead of using the program package Fish Bioenergetics 3.0 (Hanson et al., 1997), we coded these bioenergetics models and ran our bioenergetics simulations in R version 3.0.1 (R Development Core Team, 2013) as did in Hansen et al. (2013). Following the suggestion by Madenjian et al. (2012), we modified the algorithm for balancing daily fish energy budget. Outputs from our R scripts were validated with outputs from the modified Fish Bioenergetics 3.0 software package used in Madenjian et al. (2013) multiple times to ensure that our scripts are free from error.

Data

Inputs for the bioenergetics model can be categorized as biological inputs—including growth, reproduction, diet schedule, predator energy density, and prey energy densities for the modeled fish, and temperature inputs, which represent the ambient temperatures experienced by the modeled fish. The biological inputs were selected to represent average individuals from each yellow perch and lake whitefish population in Lakes Michigan and Huron. Values and data sources of these biological inputs are detailed in Electronic Supplementary Material (ESM) Appendix S1, ESM Tables S1–S5, and Figure S1.

Temperature inputs were derived using unpublished water temperature data from one of the authors (Lofgren), which were generated by a revised version of the Coupled Hydrosphere–Atmosphere Research Model (CHARM; Lofgren, 2004) in the baseline (historical reference) period (1964–1993) and in the future period (2043–2070). For the consistency in treatment, temperatures in the two periods were both modeled using CHARM. Water temperatures in the baseline period were modeled based on historically observed greenhouse gas concentrations. Water temperatures in the future period were modeled under the global development scenario A2 (IPCC, 2000), the "business as usual" scenario, in which greenhouse gas emissions and the mean global air temperature continue to increase throughout the 21st century. The water temperature profiles in each 40 \times 40 km² grid cells with up to 20 vertical layers across Lakes Michigan and Huron.

Study area and focal populations

We focused on yellow perch and lake whitefish populations in the main basin of Lake Michigan and in the main basin of Lake Huron (Fig. 1). These two fishes, especially yellow perch, are also abundant in the Green Bay of Lake Michigan and in the Saginaw Bay of Lake Huron. We chose to model populations in the main basin of each lake where water temperature predictions from the CHARM are more reliable. Water temperatures in the bays are strongly affected by land temperatures, surface runoff, and stream discharge. The spatial resolution in current version of CHARM is still not fine enough to model water temperatures in the bays accurately.

Main basins of Lakes Michigan and Huron are both deep and oligotrophic, with maximum depths greater than 200 m (Beeton et al., 1999) and primary production controlled by nutrient loads (Vollenweider et al., 1974). We modeled the growth for yellow perch from populations in nearshore waters of southern Lake Michigan and southern Lake Huron. These two populations are relatively large among yellow perch Download English Version:

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