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Potential Direct and Indirect Effects of Climate Change on a Shallow Natural Lake Fish Assemblage

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ECOLOGY OF
FRESHWATER FISH

Potential direct and indirect effects of climate change on a shallow natural lake fish assemblage

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Abstract – Much uncertainty exists around how fish communities in shallow lakes will respond to climate change. In this study, we modelled the effects of increased water temperatures on consumption and growth rates of two piscivores (northern pike [*Esox lucius*] and largemouth bass [*Micropterus salmoides*]) and examined relative effects of consumption by these predators on two prey species (bluegill [*Lepomis macrochirus*] and yellow perch [*Perca flavescens*]). Bioenergetics models were used to simulate the effects of climate change on growth and food consumption using predicted 2040 and 2060 temperatures in a shallow Nebraska Sandhill lake, USA. The patterns and magnitude of daily and cumulative consumption during the growing season (April–October) were generally similar between the two predators. However, growth of northern pike was always reduced (−3 to −45% change) compared to largemouth bass that experienced subtle changes (4 to −6% change) in weight by the end of the growing season. Assuming similar population size structure and numbers of predators in 2040–2060, future consumption of bluegill and yellow perch by northern pike and largemouth bass will likely increase (range: 3–24%), necessitating greater prey biomass to meet future energy demands. The timing of increased predator consumption will likely shift towards spring and fall (compared to summer), when prey species may not be available in the quantities required. Our findings suggest that increased water temperatures may affect species at the edge of their native range (i.e. northern pike) and a potential mismatch between predator and prey could exist.

Key words: shallow lakes; temperature; climate change; predation; growth; predator–prey dynamics; bioenergetics; consumption

Introduction

The onset of climate change will likely affect most ecological processes and functions as well as influence living organisms both directly and indirectly by affecting their physiology, growth and behaviour (Petersen & Kitchell 2001; Winder & Schindler 2004 Pörtner & Peck 2010); however, many uncertainties remain about the direction and/or magnitude of these alterations. For ectotherms such as fish, temperature shifts may have substantial impacts on the timing of reproduction, development, growth, mortality, recruitment and metabolism (Magnuson et al. 1979; Shuter & Post 1990; Tonn 1990; Brandt et al. 2002; Casselman 2002). Increased temperatures can affect fish metabolism by elevating metabolic demand to maintain cardiac function and respiration (Brown et al. 2004). Increased metabolism can lead to increased consumption rates that directly affect individual growth and survival rates (Christie & Regier 1988) and can indirectly affect the fish assemblage structure through mechanisms such as competition and predation (Biro et al. 2007; McCarthy et al. 2009; Wuellner et al. 2010).

Despite the growing wealth of information on climate change and subsequent effects on fish populations in lotic cold-water systems, information is

lacking on how fish communities will respond to climate change in warm-water ecosystems. Many changes will likely occur within these systems as well, with temperature having arguably one of the largest impacts (Walther et al. 2002). More attention has been given to individual species and how they might respond to changes in climate, while fewer studies have examined species interactions such as predator–prey dynamics. At higher temperatures, increased metabolic demands of predators must be met by similar increases in prey production to maintain balanced predatory–prey populations (Hill & Magnuson 1990; Johnson et al. 2008; Wuellner et al. 2010). Gaining insight into the effects of climate change on fish communities is important for future conservation efforts and management decisions (Tonn 1990).

Modelling provides a valuable tool to explore the potential impacts of increased temperature on fish physiology and understanding how those changes affect piscivores and their prey base. Changes in seasonal water temperature could affect species interactions, food consumption and fish production. The changes in fish physiology and assemblage structure will likely be most substantial where fish species are at the edge of their native range and thus examining how predators respond to changes in temperatures may provide the most insight into assemblage level effects (Magnuson 2001; Casselman 2002). Specifically, bioenergetics modelling (Hanson 1997) provides a robust method to explore the temperature effects on individual physiology that has been applied to a wide variety of systems and species (e.g. Chipps & Wahl 2008; Johnson et al. 2008; McCarthy et al. 2009). By accounting for temperature-dependence of fundamental energy budget components, bioenergetics modelling also offers insight to other processes that could be indirectly influenced by climate change (e.g. spawning phenology, recruitment, mortality and behaviour).

The objectives of this study were to model: (i) the direct effects of increased temperatures on consumption and growth rates of northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) populations and (ii) the potential indirect effects of consumption by northern pike and largemouth bass predators on bluegill (*Lepomis macrochirus*) and yellow perch (*Perca flavescens*) prey populations. Future consumption by largemouth bass and northern pike may require a larger prey base to meet these demands (e.g. compensatory response) based on climate change projections. Primarily, we were interested in the magnitude (substantial or minimal) and direction (lower or higher) of change related to temperature rather than specific estimates of growth, consumption and predation effects because of future population dynamics uncertainties for these species (i.e. recruitment, mortality).

We focused our study on a shallow lake ecosystem that contained two dominant predators common in many systems in the USA (largemouth bass and northern pike) and two common prey species (bluegill and yellow perch) within the Sandhills region of north-central Nebraska. These systems were ideal for studying the effect of changing water temperatures. First, most lakes are very shallow (i.e. 2.9 m average maximum depth; McCarraher 1977; Paukert & Willis 2000) and will respond much quicker to fluctuating temperatures than deeper lentic systems (Murdoch & Power 2013). Second, fish assemblages are relatively simple (Paukert et al. 2002b), enabling more accurate interpretations of potential future effects because complex food webs and species interactions are minimized. Third, northern pike are at the southern edge of their native range in the Sandhills while largemouth bass are not (Page & Burr 1991), offering an opportunity to compare two species with different thermal tolerances. Thus, we hypothesized that northern pike in these lakes will be most affected by water temperature increases that may exceed their optimal upper thermal limit and ultimately result in increased consumption to meet their metabolic demands (Casselman & Lewis 1996). Alternatively, largemouth bass will likely be less affected by increases in temperature as water temperatures may increase towards their optimal growth temperature (Niimi & Beamish 1974), followed by a slight increase in consumption and metabolism. We also expected greater predation pressure to be exerted on prey populations following these elevated changes in predator consumption rates, especially by northern pike.

Methods

Study site

West Long Lake is a 25-ha natural lake located on the Valentine National Wildlife Refuge in the Sandhills region of Cherry County, Nebraska, USA (Fig. 1). West Long Lake is a shallow eutrophic lake with a mean depth of 1.2 m and a maximum depth of 1.8 m; the lake is dominated by submerged vegetation (80% surface area coverage) in mid-summer (Paukert & Willis 2000) and is surrounded almost entirely by native grasslands (McCarraher 1977). The fish assemblage is relatively simple and includes largemouth bass, northern pike, bluegill, yellow perch and black bullhead (*Ameiurus melas*).

Field and laboratory methods

Largemouth bass ($N = 334$) and northern pike ($N = 21$) diets were assessed four times throughout the 2001 growing season (Table 1). Stomach contents
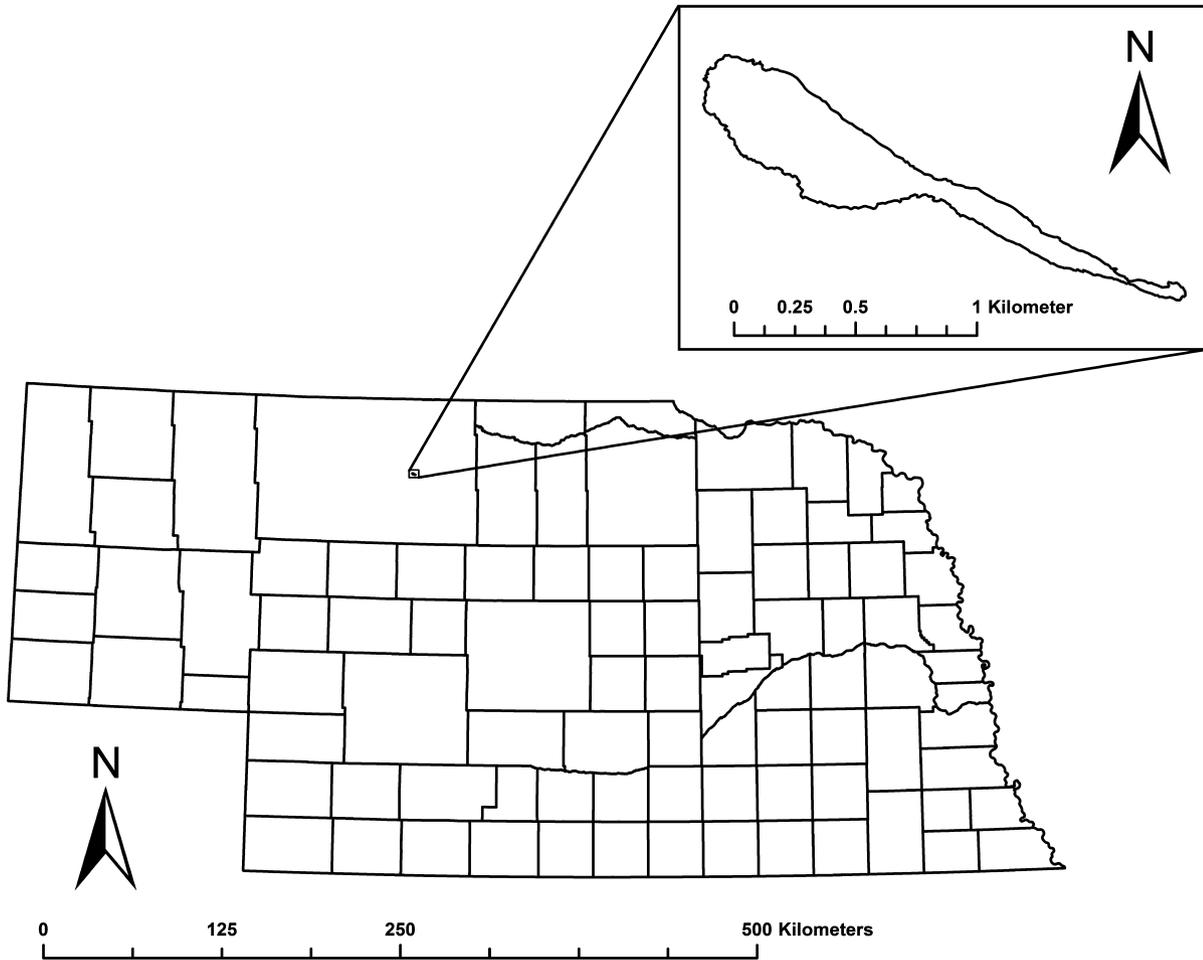
Fig. 1. State of Nebraska, USA (bottom left), and location of West Long Lake (upper right).

were collected April 18–24, June 19–21, August 5–6, and October 4, 7 and 15. Fish were collected using a combination of electrofishing and short-term gill net sets (Paukert et al. 2003). Stomach contents were extracted using acrylic tubes and gastric lavage (Light et al. 1983; Kamler & Pope 2001). Diets were collected from two length categories of largemouth bass (<300 mm and >300 mm, total length [TL]) and northern pike (<400 mm and >400 mm, TL). Diet items were identified to the lowest possible taxonomic resolution (e.g. family for macroinvertebrates and species for fish) and summarized as per cent of diet taxa by wet weight. Caloric values of prey items were obtained from published reports (Cummins & Wuycheck 1971; Kitchell et al. 1974; Craig 1977; Rice et al. 1983; Bevelheimer et al. 1985; Bryan et al. 1996).

Mark–recapture was used to estimate the number of largemouth bass and northern pike in West Long Lake. Schnabel multiple mark–recapture population estimates were used to estimate population size for both length categories of largemouth bass (May 22, 30, 31 and June 5–7, 2001) and northern pike (April

2–8, 2002). Northern pike were sampled and recaptured with modified fyke nets, and largemouth bass were collected and recaptured by night-time electrofishing. The left pectoral fin was clipped for both species, and lengths and weights were recorded for the first 100 fish of each species sampled to index size structure. For a more detailed description of the sampling methods used to estimate population size or biomass, see Paukert et al. (2002a) and DeBates (2003).

Direct effects on consumption and growth rates of predators

Potential effects of climate change on the fish assemblage in West Long Lake were assessed using bioenergetics models (Hanson 1997) to estimate largemouth bass and northern pike consumption and growth under observed and simulated temperature regimes. Water temperature was recorded every 2 h in 2001 for the duration of the study using a temperature logger placed at the centre of the lake 0.5 m below the surface. Because Sandhill lakes are

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Table 1. Sample sizes for bioenergetics modelling of largemouth bass (LMB) and northern pike (NOP) containing diet items by length categories during April, June, August and October 2001 (no samples '–' collected during May, July and September) in West Long Lake. Mean monthly predicted temperature changes (°C) in Cherry County, Nebraska, during the years 2040 and 2060 according to three regional climate models (i.e. MPI, USGS and GFDL; Hostetler et al. 2011).

| | Sample sizes | | | | Mean monthly predicted temperature changes | | | | | |
| | LMB | | NOP | | 2040 | | | 2060 | | |
Month	<300 mm	>300 mm	<400 mm	>400 mm	MPI	USGS	GFDL	MPI	USGS	GFDL
April	1	44	1	2	0.62	−0.18	−0.09	2.44	1.47	1.97
May	–	–	–	–	1.23	−0.10	1.34	3.03	1.31	3.06
June	22	39	1	0	0.96	0.28	2.32	2.40	1.09	2.96
July	–	–	–	–	0.96	0.94	2.07	2.34	2.84	3.36
August	31	35	7	1	0.94	1.33	2.17	2.84	2.99	3.14
September	–	–	–	–	1.73	0.77	1.96	2.50	2.10	1.73
October	28	27	5	1	2.01	1.30	0.98	2.65	2.93	3.51

polymictic, they do not typically stratify during summer months (Paukert & Willis 2000). We used predicted 2040–49 and 2060–69 (hereafter 2040 and 2060 respectively) air temperatures from three climate models coupled with regional climate downscaling for Cherry County, Nebraska (Hostetler et al. 2011; Table 1), to simulate effects of climate change on consumption and growth of fish predators (i.e. MPI ECHAM5 – Roeckner et al. 2003; USGS GENMOM – Alder et al. 2010; GFDL CM2.0 – Delworth et al. 2006). Downscaled regional models provided the accuracy required for the simulations used for this study compared to global general circulation models (GCMs) that are more generalized and coarse in resolution. Therefore, each of the bioenergetics simulations described below was run three separate times to accommodate each climate change model, using predicted 2040 and 2060 temperature changes.

Predicted air temperatures from each of the climate models were used to simulate water temperatures observed in West Long Lake. As in other studies, we adjusted water temperature to account for corresponding changes in air temperature (Pine & Allen 2001; Wuellner et al. 2010; Pease & Paukert 2014); for example, if mean air temperature increased by 1 °C, then we adjusted mean water temperature by +1 °C. Additionally, we examined empirical data from a nearby lake (i.e. Pelican Lake, NE, USA) with a similar morphometry and found a strong relationship between water temperatures and air temperatures during the 2010 and 2011 growing seasons (slope = 1.03; $F_{1, 414} = 1.64$, $P = 0.20$, $R^2 = 0.83$), thus providing additional support for our water temperature adjustments.

Diet information for largemouth bass and northern pike was used for bioenergetics simulations (Table 1). However, sample sizes were not sufficient to conduct bioenergetics simulations on age-specific cohorts, resulting in the use of two size categories per species. A natural break in length frequency distributions allowed for the separation of these length groups and minimized overlap (i.e. between size groups) in the modelling simulations (Paukert et al. 2002a; DeBates 2003). Bioenergetics modelling was used to evaluate two growth scenarios for each size group of fish predator; a 'no-growth' simulation based on maintenance consumption (i.e. no growth but metabolic demands were met) and a 'probable growth' simulation based on empirical growth data for northern pike and largemouth bass. Both simulations were conducted using observed water temperatures in 2001 (i.e. baseline models), and predicted water temperatures in 2040, and 2060 (Table 2). Daily consumption throughout the growing season (April–October, Northern Hemisphere) and cumulative food consumption at the end of the growing sea-

Table 2. Summary of the bioenergetics simulations used to assess (i) direct effects on consumption and growth rates of predators (top) and (ii) indirect effects of consumption by predators on prey populations (bottom). No-growth models did not allow for growth, and only metabolic demands were satisfied. Probable growth models used P-values generated from the 2001 baseline models. Multiple response metrics were generated and evaluated for each climate change model (i.e. MPI, USGS and GFDL) during three separate time periods (2001, 2040, 2060) where one variable in addition to temperature was manipulated (no growth, P-value) to assess climate change effects in West Long Lake.

Simulation	Time period	Variable manipulated	Response metric
Predator consumption and growth rates			
No growth	2001 (baseline); 2040; 2060	No growth	Daily consumption, cumulative consumption
Probable growth	2001 (baseline); 2040; 2060	P-value	Growth or final end weight
Consumption of prey populations by predators			
No growth	2001 (baseline); 2040; 2060	No growth	Cumulative consumption, per cent standing stock consumed
Probable growth	2001 (baseline); 2040; 2060	P-value	Cumulative consumption, per cent standing stock consumed

son were assessed under the no-growth models. Furthermore, final weights at the end of the growing season were also recorded for the probable growth models (Table 2).

To examine changes in consumption related to climate change, a baseline model was constructed using temperatures recorded in 2001 and a no-growth estimate. Results from the baseline no-growth model were used to compare changes (%) in daily and cumulative consumption under the predicted 2040 and 2060 temperature regimes, again using a no-growth model. Mean monthly per cent change in daily consumption and per cent change in total cumulative consumption were calculated for largemouth bass and northern pike throughout the growing season (April–October). Growth rates were also estimated under probable growth scenarios for largemouth bass and northern pike. Probable growth increments of northern pike (149 g·y^{-1}: <400 mm; 1151 g·y^{-1}: >400 mm) were estimated from mean annual growth increments of eleven Sandhill northern pike populations during 1998 and 1999 (Paukert & Willis 2000). Probable growth increments for largemouth bass (177 g·y^{-1}: <300 mm; 466 g·y^{-1}: >300 mm) were estimated from annual growth increments from West Long Lake (Paukert & Willis 2000). Similar to the no-growth models, 2001 temperatures and the probable growth increments were used to develop baseline consumption models (Carey & Zimmerman 2014). P-values (per cent of maximum consumption) generated from baseline bioenergetics simulations (i.e. 2001 consumption) were held constant for largemouth bass and northern pike under the predicted 2040 and 2060 temperatures. Effects of warmer water temperature on growth of largemouth bass and northern pike were assessed by comparing the per cent change in final weight between 2001 and those predicted from the 2040 and 2060 temperature regimes.

Indirect effects of consumption by predators on prey populations

Bioenergetics simulations were used to examine the predatory effects of largemouth bass and northern pike on bluegill and yellow perch populations under different temperature scenarios in West Long Lake. Simulations were used to examine no growth and probable growth during the 2001 baseline, 2040 and 2060 temperature regimes (Table 2). For the 2040 and 2060 simulations, cumulative consumption of yellow perch and bluegill at the end of a growing season was used to calculate the per cent change in total consumption by the predator population (i.e. both size classes of northern pike and largemouth bass) compared to the 2001 baseline conditions (Table 2).

Results

Direct effects on consumption and growth rates of predators

Daily consumption by largemouth bass increased each month under the predicted 2040 and 2060 temperature models (Fig. 2). Average per cent change in daily consumption for both length categories of largemouth bass increased each month across the predicted 2040 and 2060 temperature models and ranged from 0.25 to 67.2% (Fig. 2). The greatest per cent increase in average daily consumption by largemouth bass typically occurred in the spring (April and May) and fall (September and October; Fig. 2). In contrast, estimates of average daily consumption by northern pike increased during April, May and June, decreased or remained nearly the same for July and August, and then increased again during September and October under the 2040 and 2060 temperature models (Fig. 2). Average per cent change in daily consumption by northern pike across the 2040 and 2060 temperature regimes ranged from −17.7 to 76.1% (Fig. 2).

Total food consumption by largemouth bass increased by approximately 5–15% under the predicted 2040 temperature models and approximately 20–30% under the predicted 2060 models (Fig. 3). Similarly, total consumption by northern pike increased by approximately 4–13% under the predicted 2040 temperature models and approximately 14–24% under the predicted 2060 models (Fig. 3). The per cent change in mean daily and total food consumption was greater under the predicted 2060 temperature models compared to the 2040 models for both largemouth bass and northern pike (Figs 2 and 3).

Bioenergetics simulations resulted in different growth outcomes for both length categories of largemouth bass under 2040 temperature models (MPI = gain weight; USGS and GFDL = lose weight; Fig. 4). However, changes in predicted final weights for both size categories of largemouth bass in 2040 were small compared to 2001 predicted final weights, ranging from a −1.3 to a 4.3% difference (Fig. 4). Furthermore, the 2060 temperature models predicted the small size category of largemouth bass to gain weight (1.7%) according to the MPI model but lose weight in both USGS (−5.1%) and GFDL (−6.4%) climate models (Fig. 4). The large size category of largemouth bass lost weight by the end of the growing season under all 2060 temperature models, with final weights ranging from −0.1 to −4.1% (Fig. 4). In contrast, northern pike had lower final weights by the end of the growing season under all the 2040 and 2060 temperature models (Fig. 4). The

per cent differences in final weights between the 2001 temperature model and the 2040 and 2060 temperature models ranged from −3.3 to −27.5% and −17.7 to −45.3%, respectively, for northern pike (Fig. 4).

Indirect effects of consumption by predators on prey populations

The largemouth bass population in West Long Lake in June 2001 was estimated at 2047 fish (95% confidence interval: 1670–2545); 22% (450 largemouth bass) were <300 mm and 78% (1597 largemouth bass) were >300 mm (TL range: 125–550 mm). The northern pike population in West Long Lake in April 2002 was estimated at 909 fish (95% confidence interval: 720–1180); 56% (509 northern pike) were <400 mm and 44% (400 northern pike) were >400 mm (TL range: 250–750 mm).

Using the no-growth scenario, total consumption of bluegill (kg·ha^{-1}) by all predators increased by approximately 8–18% under predicted 2040 temperature models and increased by 22–24% under predicted 2060 temperature models, compared to the 2001 baseline consumption model (Table 3). Under the probable growth scenario, largemouth bass and northern pike total consumption (kg·ha^{-1}) of bluegill increased by 7–13% under predicted 2040 temperature models and increased approximately 16–17% under predicted 2060 temperature models (Table 3).

Again using the no-growth scenario, total consumption (kg·ha^{-1}) of yellow perch by largemouth bass and northern pike increased by approximately 5–14% under predicted 2040 temperature models and increased by about 17–23% under predicted 2060 temperature models, compared to the 2001 baseline model (Table 3). Under the probable growth scenario, largemouth bass and northern pike total
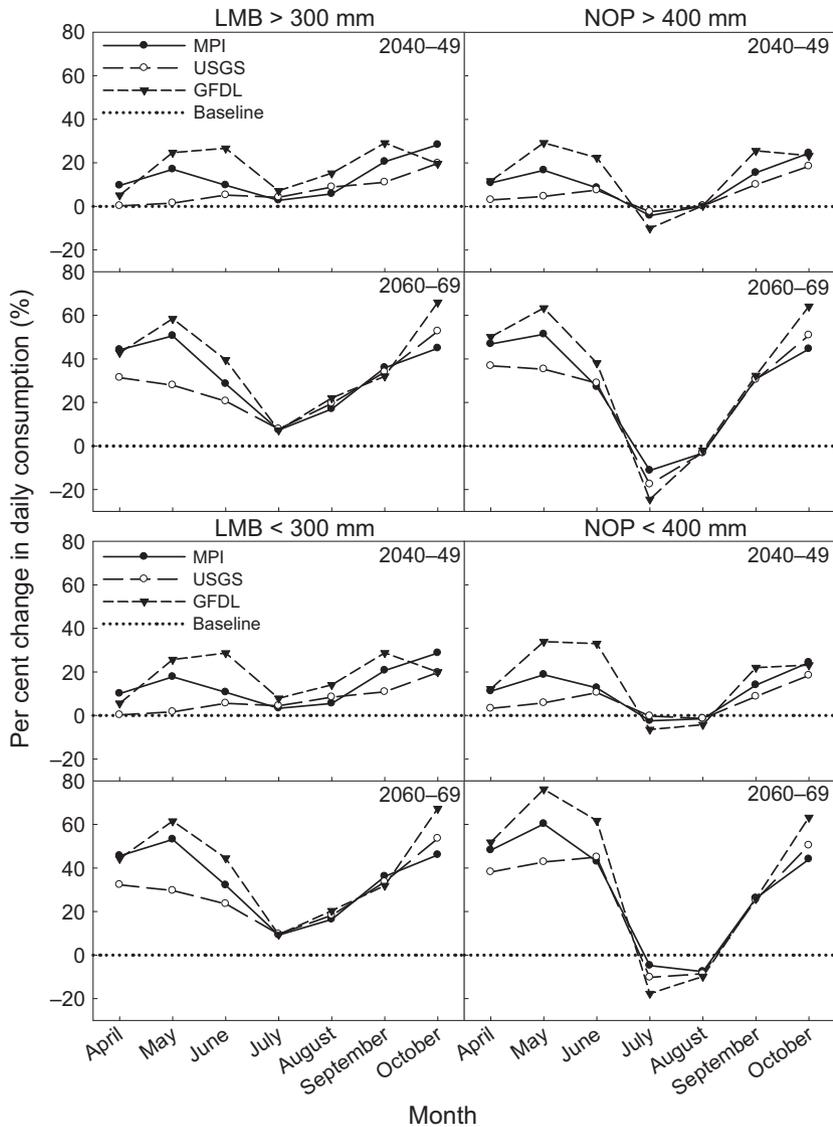

Fig. 2. Mean per cent change in daily consumption by month for two length categories of largemouth bass (LMB; >300 mm, upper left; <300 mm, lower left) and northern pike (NOP; >400 mm, upper right; <400 mm, lower right) modelled under projected 2040 and 2060 water temperatures from three different climate change models (i.e. MPI, USGS, and GFDL) compared to 2001 water temperatures (baseline) in West Long Lake, Nebraska.
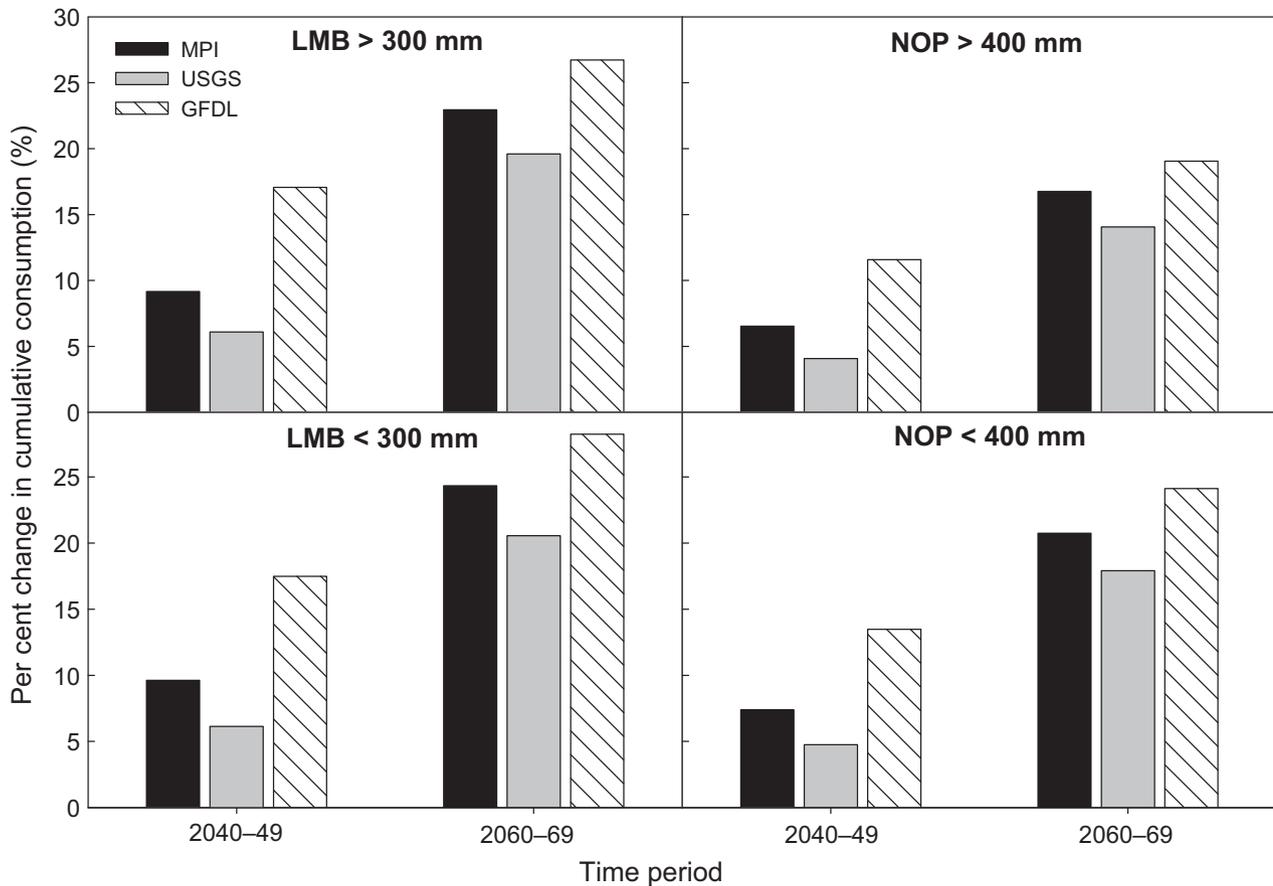
Fig. 3. Per cent change in cumulative consumption for two length categories of largemouth bass (LMB; >300 mm and <300 mm) and northern pike (NOP; >400 mm and <400 mm) modelled under projected 2040 and 2060 water temperatures from three different climate change models (i.e. MPI, USGS, and GFDL) compared to 2001 water temperatures (baseline) in West Long Lake, Nebraska.

consumption (hg·ha^{-1}) of yellow perch increased by approximately 3–10% under predicted 2040 temperature models and increased by about 12–16% under predicted 2060 temperature models (Table 3).

Discussion

The change in daily and total consumption between largemouth bass and northern pike was not as pronounced as expected. While both species generally consumed substantially more under warmer climate scenarios, the magnitude and patterns were quite similar despite different species-specific thermal tolerances and optimums (Coutant & Cox 1976; Casselman 1978; Pierce 2012), and despite the fact that northern pike are at the southern edge of their range and largemouth bass are not (Page & Burr 1991). One major difference was found during the summer months (i.e. July and August) when northern pike consumed less than they did in 2001 compared to largemouth bass; but overall, both species will likely require a greater annual supply of prey. Patterns in daily consumption also revealed a temporal

aspect that is equally as important as the magnitude and direction of overall consumption. Durant et al. (2007) explored this relationship in greater detail and exposed critical phenology mismatches between reproductive processes and predator–prey relationships that are unlikely to align with climate change. Our study suggested that much higher prey demands will be anticipated for largemouth bass and northern pike during the fall (September and October) and spring (April and May) compared to 2001 estimates. Not only will an increase in prey be required for these two predators but the timing of prey availability will be critical, particularly because predation pressure on bluegill and yellow perch populations is already high in these systems (Paukert et al. 2003). Increased recruitment and production of both prey species will be necessary to sustain largemouth bass and northern pike populations.

Feeding and growth of northern pike were predicted to respond to climate change to a greater extent than largemouth bass because Sandhill lakes are located near the southern edge of the northern pike's range (Page & Burr 1991). Largemouth bass
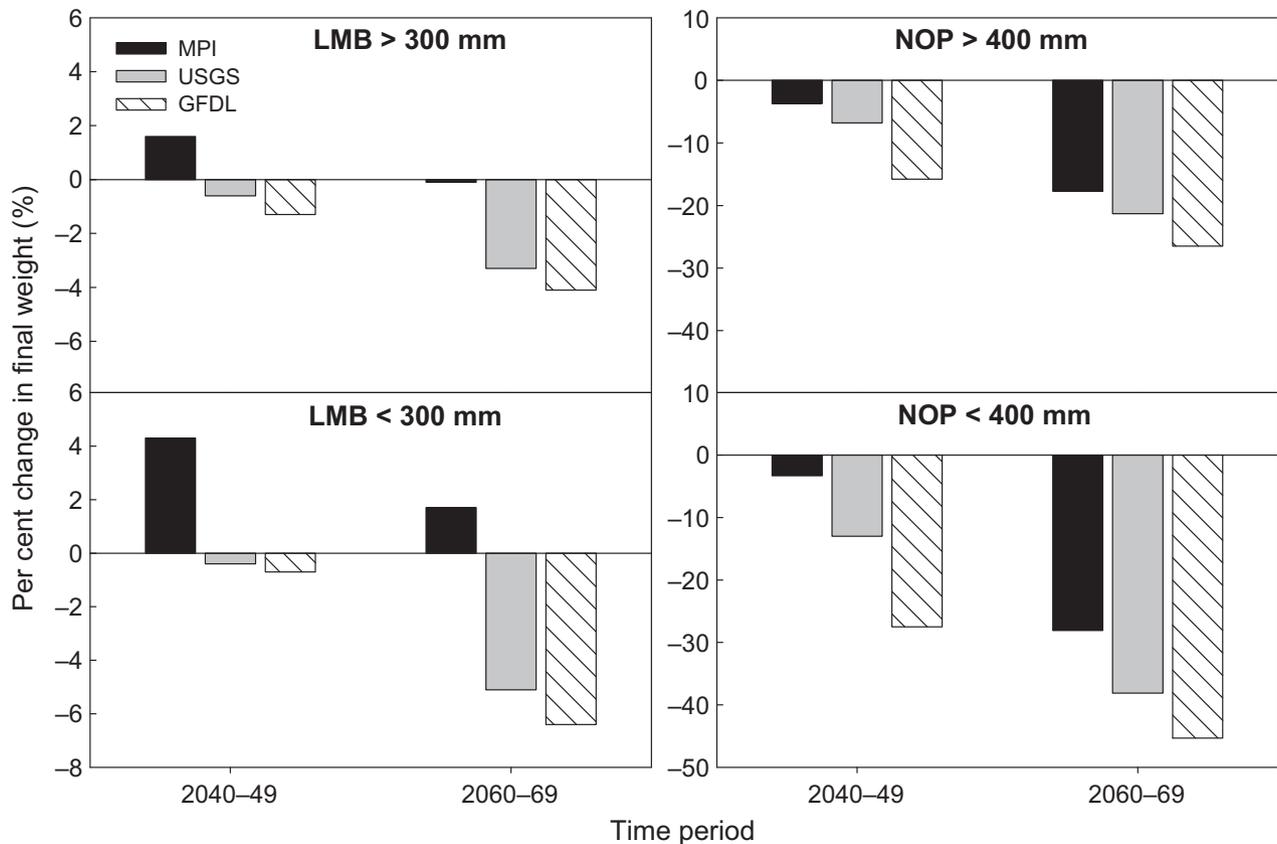
Fig. 4. Per cent change in final weight for two length categories of largemouth bass (LMB; >300 mm and <300 mm) and northern pike (NOP; >400 mm and <400 mm) modelled under projected 2040 and 2060 water temperatures from three different climate change models (i.e. MPI, USGS and GFDL) compared to 2001 water temperatures (baseline) in West Long Lake, Nebraska.

did not experience much difference in final weight, whereas northern pike suffered weight loss under elevated temperatures and in some cases (i.e. small size classes – 2060) over 30%. Northern pike are a cool-water fish with an optimum growth temperature range of 20–24 °C (Pierce 2012). In 2001, water temperatures in West Long Lake surpassed this range during July and August, as well as portions of June and September (Fig. 5). Additionally, West Long Lake is a shallow, polymictic lake that has no summer thermal stratification, and thus no thermal refuge for large northern pike (Paukert & Willis 2000). Growth rates and condition of northern pike in West Long Lake are already lower than their northern counterparts (Paukert & Willis 2003), and future increases in water temperature will likely exacerbate limitations on growth potential. Other studies have revealed range limitations and habitat shifts for several species due to temperature or climate change (Christie & Regier 1988; Perry et al. 2005). In contrast, large-mouth bass are a warmwater fish with an optimum growth temperature range of 26–28 °C (Coutant & Cox 1976). In 2001, water temperatures in West Long Lake reached this range for about a month from July to August (Fig. 5). However, the projected tem-

peratures for 2040 predict that water temperatures will enter this range about 2 weeks earlier, near the end of June (Fig. 5). Therefore, water temperatures in 2040 may be more optimal for largemouth bass growth resulting in the slight increase in growth observed during that decade. Increased growth rates have been predicted for other species that may experience elevated water temperatures compared to current conditions (King et al. 1999; Pease & Paukert 2014). Under projected 2060 temperatures, water temperatures will exceed optimal thermal largemouth bass conditions for about a month from July to August, resulting in reduced growth compared to 2001. The decrease in growth rates for largemouth bass during 2060 compared to the more recent time period was not nearly as extreme as it was for northern pike.

Largemouth bass growth was minimally influenced by changes in water temperature whereas northern pike were moderately influenced by 2040 modifications in temperature regimes and influenced even more by 2060 temperatures. Northern pike gained less weight in both time periods compared to the 2001 model. Decreased growth of northern pike could result in an alteration of maturation rates,

Table 3. Estimated consumption (kg·ha^{-1}) of bluegill and yellow perch by two length categories of largemouth bass (LMB) and northern pike (NOP) based on no growth (left) and probable growth (right) simulations in 2001 and predicted 2040 and 2060 water temperatures from three different climate change models (i.e. MPI, USGS, and GFDL) in West Long Lake, Nebraska. No bluegill were consumed by LMB <300 mm total length or NOP >400 mm total length. Total consumption (kg·ha^{-1}) and the per cent change in total consumption (i.e. consumption by all predators) under all predicted future temperature scenarios.

	No growth				Probable growth			
	2001	MPI	USGS	GFDL	2001	MPI	USGS	GFDL
Bluegill								
2040								
LMB <300 mm	4.9	5.5	5.4	5.8	8.6	9.3	9.2	9.7
NOP <400 mm	0.1	0.1	0.1	0.1	0.8	0.9	0.9	0.9
Total consumption	5.0	5.5	5.4	5.9	9.4	10.2	10.1	10.6
Change in consumption (%)	NA	10.0	8.0	18.0	NA	8.5	7.4	12.8
2060								
LMB <300 mm	4.9	6.1	6.1	6.1	8.6	9.9	10.1	10
NOP <400 mm	0.1	0.1	0.1	0.1	0.8	1.0	1.0	1.0
Total consumption	5.0	6.1	6.2	6.2	9.4	10.9	11.1	11.0
Change in consumption (%)	NA	22.0	24.0	24.0	NA	16.0	18.1	17.0
Yellow perch								
2040								
LMB <300 mm	1.5	1.6	1.6	1.8	3.8	4.0	4.0	4.1
LMB >300 mm	24.9	27.6	26.4	29.4	41.0	44.1	42.7	46.1
NOP <400 mm	0.7	0.7	0.7	0.8	4.7	4.8	4.7	4.9
NOP >400 mm	48.2	51.4	50.2	53.8	78.9	82.7	81.3	85.7
Total consumption	75.3	81.3	78.9	85.8	128.4	135.5	132.6	140.7
Change in consumption (%)	NA	8.0	4.8	13.9	NA	5.5	3.3	9.6
2060								
LMB <300 mm	1.5	1.8	1.8	1.8	3.8	4.2	4.2	4.2
LMB >300 mm	24.9	31.7	30.4	32.6	41.0	48.8	47.3	49.9
NOP <400 mm	0.7	0.9	0.8	0.9	4.7	5.1	5.0	5.1
NOP >400 mm	48.2	56.3	55.0	57.4	78.9	88.8	87.2	90.1
Total consumption	75.3	90.6	88.0	92.8	128.4	146.9	143.6	149.3
Change in consumption (%)	NA	20.3	16.9	23.2	NA	14.4	11.8	16.3

fecundity and overall fitness (Roff 1984; Shuter & Meisner 1992). Climate change could also affect recruitment and egg development (Straile et al. 2007; Karjalainen et al. 2014). Provided that overall population dynamics become altered (recruitment, growth, and mortality; Dudgeon et al. 2006), consequences of increased temperatures for northern pike in the Nebraska Sandhills could extend to the entire fish assemblage because of their primary predatory role in these systems (Paukert & Willis 2003). Therefore, largemouth bass could become the primary predator in many of these systems if northern pike cannot tolerate expected temperatures or find thermal refuge. According to estimated consumption rates, this would benefit yellow perch populations as northern pike consumed nearly twice the amount of yellow perch compared to largemouth bass. Community-level impacts could be mediated through temperature shifts that directly affect predator consumption rates and growth but indirectly affect prey populations via changes in predation pressure (Jeppesen et al. 2010). Climate change may therefore lead to future Sandhill fish communities that are dominated by largemouth bass and smaller populations of bluegill (increased
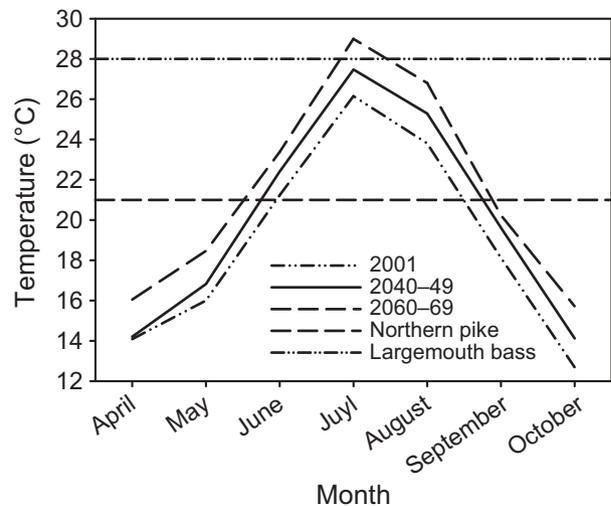

Fig. 5. Mean monthly water temperatures (°C) during 2001, and projected 2040 and 2060. Temperature averages across each climate change model (i.e. MPI, USGS and GFDL) are given for graphing simplicity and clarity, rather than depicting each model separately (as conducted in the analyses). Thermal optimum growth temperatures are also shown as horizontal reference lines for largemouth bass and northern pike (Coutant & Cox 1976; Pierce 2012).

predation by largemouth bass) and larger populations of yellow perch (predation release from northern pike – but see Discussion on temporal shifts in consumption and competitive interactions between prey species).

The potential for competition between northern pike and largemouth bass for available prey (e.g. yellow perch) could become an important factor to consider in the future (Lehtonen 1996). We postulate that largemouth bass would be favoured in this case as northern pike already exhibit poor condition and could experience shortages in preferred prey items (i.e. yellow perch) (Paukert & Willis 2003). Yellow perch and bluegill populations are critically important for largemouth bass and northern pike in the Nebraska Sandhills (Paukert et al. 2002b, 2003; DeBates et al. 2003; Jolley et al. 2008), as evident by the current and future contribution to overall consumption and growth. Other studies have identified the significance of yellow perch and bluegill as prey for both of these species across their geographic range and in more diverse fish assemblages that could offer other foraging options (Seaburg & Moyle 1964; Post & Prankevicius 1987; Olson 1996). Assuming predator populations remain similar, it is possible that prey fish biomass could meet the consumption demands of both predators so long as their populations show a congruent (i.e. compensatory) response to increased water temperature; in this case, combined biomass of bluegill and yellow perch would need to increase by up to 24% compared to observed conditions.

Recruitment dynamics and year-class strength can vary for both species in Sandhill lakes but are more consistent than other systems containing bluegill and yellow perch (Kaemingk et al. 2014a,b). Although annual consumption demands may not have increased substantially for either species (always <30%), a shift occurred in the timing of when prey is required to meet these consumptive demands, especially for northern pike. Subtle changes and shifts in timing of consumption for northern pike and largemouth bass may influence how much prey is available (e.g. spring vs. summer feeding) and the overall impact it has on prey populations. Elevated predation pressure during spring when yellow perch are spawning could affect yellow perch recruitment as juveniles are much smaller and more vulnerable to predation (Sogard 1997). Predation intensity could remain high well into the fall season for both species (i.e. focusing more on late-hatched bluegill populations), and this may create a unique scenario as most bluegill recruitment is generated from late hatching individuals in a Nebraska Sandhill lake (Kaemingk et al. 2014b), further impacting long-term bluegill population structure and dynamics, but may also provide a source of prey

in the fall for these predators. Future research is needed to examine how shifting predation pressure and consumption at different times of the year could alter fish assemblage dynamics. Additionally, accounting for potential growth and elevated consumption during other seasons (i.e. winter) should be explored as optimal temperatures could extend beyond typical growing seasons (i.e. spring, summer, and fall) for many species.

Our study highlighted several important aspects of how climate change may affect warm-water fish communities in shallow lakes. Growth of northern pike and largemouth bass varied among climate warming scenarios owing to differences in optimal metabolic temperatures between species. Because West Long Lake is near the southern extent of the northern pike's natural range, a warming climate had relatively larger impacts on growth rate of northern pike compared to largemouth bass. Thus, the effects of climate change on predator energy demands extend to predation on prey fishes resulting in increased and perhaps differential predation pressure on prey populations. Moreover, climate change may lead to a shift in the timing of predator–prey interactions which could lead to a shift in fish assemblage structure and dynamics within shallow lake ecosystems.

Acknowledgements

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