

Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States

Allison A. Pease¹, Craig P. Paukert²

¹Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR Building, Columbia, MO 65211, USA

²U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR Building, Columbia, MO 65211, USA

Accepted for publication June 17, 2013

Abstract – Smallmouth bass (*Micropterus dolomieu*, SMB) is a broadly distributed, economically important species in the USA and Canada. Although previous research has suggested that projected climate warming may allow SMB to thrive beyond their current northern distribution, little research has been devoted to the population-level effects of climate change on warm-water fishes, including SMB. We modelled the impacts of projected climate change on growth of stream-dwelling SMB along a north–south gradient in the central USA. Using downscaled regional projections from three global climate models, we generated scenarios for thermal habitat change for four populations (in Oklahoma, Missouri, Iowa and Minnesota) and used bioenergetics simulations to estimate prey consumption and growth under future projections. Bioenergetics simulations showed that prey consumption is expected to increase in all populations with moderate stream warming (2–3 °C). Growth potential is predicted to increase by 3–17% if not limited by food availability with stream warming by 2060 and was most pronounced for southern populations. For each 1 °C increase in stream temperature, SMB consumption would be expected to increase by about 27% and growth would increase by about 6%. Due to implications for species interactions, population performance and regulation of local fisheries, a better understanding of how SMB populations will respond to climate change is recommended for effective management and conservation.

Key words: climate change; bioenergetics; growth; smallmouth bass; food-web effects

Introduction

Much of the research on potential impacts of climate change on stream fish populations has focused on cold-water species with narrow temperature tolerances (e.g., Keleher & Rahel 1996; Clark et al. 2001; Riemann et al. 2007). Potential impacts on broadly distributed, cool- and warm-water stream species have received less attention, although these stream species are very common and often play a vital role in shaping fish communities as competitors, predators or invaders in some cases. Smallmouth bass, *Micropterus dolomieu* (SMB), is a warm-water species broadly distributed throughout central and eastern North America (across 15 states and in two Canadian

provinces) with introduced populations in many regions beyond its native range. Smallmouth bass in lotic systems consume fish, crayfish and other invertebrates, and they occupy an important ecological position as top predators in stream food webs (e.g., Rabeni 1992; Johnson et al. 2008). Abundance of SMB in streams has been linked to habitat characteristics at multiple scales (e.g., Dauwalter et al. 2007; Brewer & Rabeni 2011), and stream temperature has been identified as an important local habitat influence (Sowa & Rabeni 1995). Smallmouth bass distribution in lakes is expected to shift with a warming climate (Shuter & Post 1990; Sharma et al. 2007; Sharma & Jackson 2008), but little is known about how predicted changes in stream temperatures will mecha-

Correspondence: A. A. Pease, Department of Natural Resources Management, Texas Tech University, Mail Stop 2125, Lubbock, TX 79409-2125, USA. E-mail: allison.pease@ttu.edu

nistically affect the performance of populations. Relationships between thermal habitat and growth of SMB are well studied (e.g., Beamesderfer & North 1995; King et al. 1999; Dunlop & Shuter 2006) and suggest that somatic growth is generally higher in warmer climates, but considerable geographical variation has been observed. Previous research suggests that warming temperatures might enhance SMB growth and over-winter survival in northern populations, allowing them to persist in areas beyond their current northern distributional limit (Shuter & Post 1990). Warming at the southern end of the SMB native range may lead to decreased growth potential as predicted for unusually warm summers in Missouri Ozark streams (Whitledge et al. 2006).

The impacts of predicted climate change on growth of SMB populations are important for management and conservation due to implications for species interactions, population performance and regulation of local fisheries. Fish growth is highly plastic and is influenced by temperature and other habitat conditions such as substrate characteristics and instream cover (e.g., McClendon & Rabeni 1987; Putman et al. 1995). Because environmental change often impacts fish populations via effects on growth (e.g., King et al. 1999), fish growth has been used as an indicator of habitat quality. For example, Munkittrick & Dixon (1989) suggested that white sucker (*Catostomus commersoni*) growth was an indicator of contamination stress in aquatic ecosystems. Changes in growth rates of fishes may result in alteration of key demographic parameters such as fecundity, age to reach maturity and survival of early life stages (Roff 1984; Shuter & Meisner 1992). Life-history theory predicts that populations with slower individual growth will display delayed maturation and reduced reproductive investment (Pianka 1970), which have been observed in fish populations (e.g., Trippel 1993; Shuter et al. 2005). Shuter et al. (1980) found that over-winter mortality of age 0 SMB was strongly size dependent and suggested that shorter growing seasons in colder climates limit SMB distribution. Because SMB are popular sport fish, changes in growth and population performance could have significant social and economic implications.

Growth changes also affect predator-prey relationships (e.g., Olson 1996) and could alter the impacts of SMB on local stream food webs. Strong interactions between SMB and their prey species have been documented in stream communities. A predator-prey model revealed that in the Missouri Ozarks, SMB and rock bass (*Ambloplites rupestris*) consume nearly one-third of total crayfish production (Rabeni 1992). Non-native populations of SMB have reduced the diversity of small-bodied native fish assemblages through predation (Jackson 2002), and SMB have

been shown to be a greater predatory threat to native fishes than other introduced piscivores (Johnson et al. 2008). Reduced abundance of SMB prey items has caused trophic shifts and altered food-web structure following SMB introduction (Vander Zanden et al. 1999). Changes in climate have been shown to influence consumption rates in other fish species, with important impacts on population performance (e.g., Biro et al. 2007; McCarthy et al. 2009). Johnson et al. (2008) suggested that warming in the Yampa River, Colorado, might lead to increased consumptive demand for non-native SMB, and higher predation rates would exacerbate negative impacts on native prey species. Therefore, changes in SMB consumption rates due to climate change may strongly affect fish assemblage structure and trophic interactions.

Bioenergetics modelling provides a useful method for estimating the effects of a changing thermal regime on food consumption and the energy balance which ultimately result in changes in growth (Hanson et al. 1997). These models use species-specific functional relationships between temperature, energy density of prey items and growth and can be used to predict effects of changes in temperature on growth and consumption. Bioenergetics simulations are thus very useful for examining potential population-level impacts of climate change. They have been used to predict changes in somatic growth for salmonid populations (e.g., McCarthy et al. 2009; Beer & Anderson 2011) and changes in consumption for piscivorous fishes in the western USA (Petersen & Kitchell 2001; Johnson et al. 2008) due to climate change. Unlike correlative approaches, such as species distribution modelling, bioenergetics modelling provides a mechanistic way of examining changes in individual physiological performance in response to environmental change (McCarthy et al. 2009).

The availability of extensive data on populations across North America makes SMB an ideal species for examining population-level impacts of climate change. Four focal populations were chosen for this study to provide a broad latitudinal gradient for comparing impacts of climate change. Examining potential impacts across the native range of SMB allowed us to investigate whether northern and southern populations may respond differently to changes in climate. Our objectives were to (i) estimate potential changes in SMB prey consumption and growth based on recently developed regional climate change models and (ii) examine how these projected changes differ across the broad latitudinal gradient of the SMB native range. Due to implications for species interactions, population performance and regulation of local fisheries, a better understanding of how SMB populations will respond to climate change across a broad geographical range is vital for management and conservation.

Materials and methods

We chose four focal populations for this study: Upper Mississippi River, Minnesota; Maquoketa River, Iowa; Jacks Fork River, Missouri; and Glover River, Oklahoma (Fig. 1). For all four populations, data were available on growth, diet and daily stream temperatures. Descriptions of the study streams can be found in Stewig (2009), Paragamian & Wiley (1987), Rabeni (1992) and Balkenbush & Fisher (1999).

Climate projections

We used downscaled regional climate projections for predicted changes in air temperature across the four study areas from three global climate models. The downscaled regional climate projections provided simulated temperatures at much finer resolutions than are yielded from global, general circulation models (GCMs). The downscaling was performed by Hostetler et al. (2011) using the GENMOM (combination of the GENESIS version 3.0 atmospheric GCM and the MOM version 2.0 oceanic GCM), ECHAM5 (from the Max Planck Institute for Meteorology, Hamburg, Germany) and Global Fluid Dynamics Laboratory (GFDL) GCMs for present and future climates (all under the A2 ‘business as usual’ future emissions scenario) at high resolution (15-km). Details of the downscaling methods are described by Hostetler et al. (2011), and details of the three global climate models are given in Roeckner et al. (2003), Delworth et al. (2006) and Alder et al. (2010).

Projected changes in mean daily air temperature were used to predict changes in stream temperature based on relationships between air and stream temperature for each study area. We obtained data on daily stream temperatures from US Geological Survey stream temperature gauges nearest to each study area (on the same stream or nearest stream of the same order with a temperature gauge). Correlations between current daily air temperatures (from the nearest National Weather Service weather station) and stream temperatures were calculated using data for 5 years based on availability of stream temperature gauge data (Minnesota: 1995–1999, Iowa: 2000–2004, Missouri: 2006–2010, Oklahoma: 2000–2004). Periods of ice cover were not included in these analyses. These correlations were then applied to the projected air temperatures (following Pilgrim et al. 1999) to estimate average daily stream temperatures for 1995, 2040 and 2060 for all three GCMs. Projected daily temperatures at each time step were averaged across a 5-year period (i.e., temperatures for the 2040 time step were an average of 2040–2044 temperatures).

Bioenergetics simulations

We used a bioenergetics approach to predict potential effects of changes in stream temperature on SMB prey consumption and growth for each of the four populations (Hanson et al. 1997). We used the Wisconsin bioenergetics model (Fish Bioenergetics 3.0; Hanson et al. 1997), which has been widely applied to SMB populations, including studies examining impacts of nesting behaviour (Cooke et al. 2002),



Fig. 1. Map of locations of the four stream-dwelling SMB study populations in the central United States.

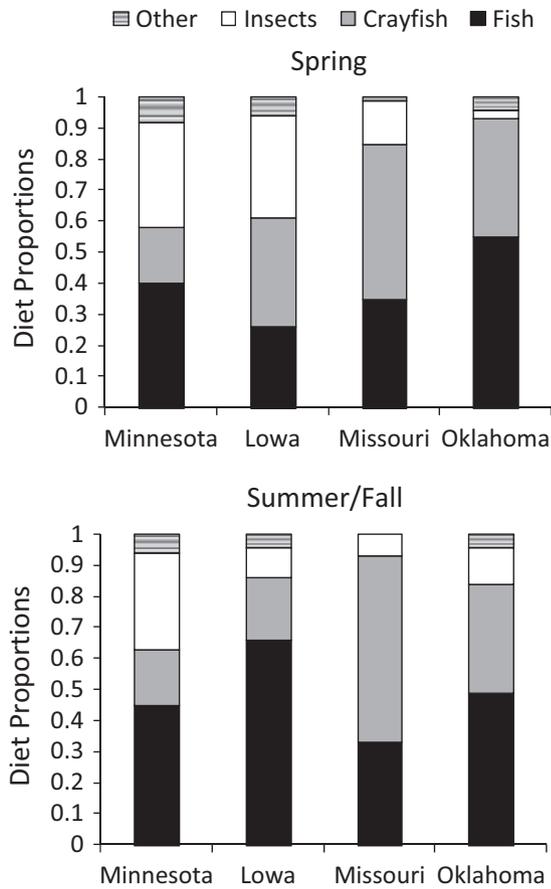


Fig. 2. Proportional composition of diets (by weight) of SMB in the four study areas based on published reports (see text for citations).

winter duration (Lyons 1997) and projected changes in reservoir temperatures and prey availability (Wuellner et al. 2010) on growth. Parameters for SMB consumption, respiration, and egestion and excretion were obtained from Shuter & Post (1990) and Whitley et al. (2003).

To run preliminary simulations based on present-day conditions, we gathered existing data on growth, diet and stream temperatures for the four study SMB populations. Data on annual growth (as indexed from mean total length-at-age) and seasonal trophic resource use came from state agency reports and published studies of the focal populations or closest (distance < 100 km) stream-dwelling SMB populations with data available (Minnesota: Waters et al. 1993; Stewig 2009; Iowa: Paragamian 1984; Paragamian & Wiley 1987; Jansen et al. 2008; Missouri: Covington et al. 1983; Probst et al. 1984; Rabeni 1992; Meneau 2009; Roell & DiStefano 2010; Oklahoma: Orth et al. 1983; Stark & Zale 1991; Balkenbush & Fisher 1999; Dauwalter & Fisher 2008). Published length-at-age data were converted to weight (g) as needed for input in the bioenergetics simulations using the equation for SMB developed

by Kolander et al. (1993). Reported length-at-age varied among the four focal SMB populations along the latitudinal gradient. For example, SMB in the Maquoketa River, Iowa, were reported to have an average length of 366 mm at age 5 (Paragamian 1984; Jansen et al. 2008), whereas SMB in the Upper Mississippi, the Missouri Ozarks and eastern Oklahoma reached average lengths of 354, 296 and 330 mm, respectively, at the same age (Covington et al. 1983; Orth et al. 1983; Balkenbush & Fisher 1999; Meneau 2009; Stewig 2009). Diets of SMB also vary among the four populations (Fig. 2). In all four areas, SMB consume fish, crayfish and aquatic insects, but the relative proportions of each prey category differ. For example, SMB in the Missouri Ozarks were reported to consume a greater proportion of crayfish (Rabeni 1992), and SMB in the Upper Mississippi consumed more aquatic insects than the other three populations (unpublished data, Minnesota Department of Natural Resources). Within populations, SMB diets are also reported to vary across seasons. For example, in SMB populations near the Glover River, Oklahoma, Dauwalter & Fisher (2008) found that fish were more likely to be consumed by SMB in spring and crayfish were a more important component of the diet in the summer. Caloric density (Joule per gram wet weight) of the three categories of prey items (fish, crayfish and aquatic insects) was estimated from published values for cyprinid fishes ($3853 \text{ J}\cdot\text{g}^{-1}$ determined for fathead minnows, Whitley et al. 2003), *Procambarus* crayfish ($3063 \text{ J}\cdot\text{g}^{-1}$, Eggleton & Schramm 2002) and aquatic insect larvae ($3421 \text{ J}\cdot\text{g}^{-1}$, average of values for Chironomidae, Odonata, and Ephemeroptera; Cummins & Wuycheck 1971).

The empirical length-at-age, diet and stream temperature data for the four SMB populations were used to run initial bioenergetics simulations representing present-day conditions. We chose to begin the simulation year with a 300-g SMB (within the observed size range for age-4 adult SMB in these populations) for a 214-day growing season (April 1–October 31), and we used the published length-at-age data and length–weight conversions to establish the weight of an average age-4 individual at the end of one growing season. Using currently observed stream temperatures, growth rates and diet composition, the initial bioenergetics simulations provided an estimation of current consumption rates (P -value—the proportion of maximum consumption rate) for the four populations. To determine the effects of predicted changes in thermal habitat on prey consumption and growth, we then used the projected stream temperatures to run bioenergetics simulations [using P -values obtained from the initial simulations (0.7–0.8) and assuming that prey availability and energy density

remain constant] for the 1995, 2040 and 2060 time steps from climate projections from the three global climate models.

Results

Regional climate projections revealed that average air temperatures in all four study areas are expected to increase through 2060, with an average of 2–3 °C increase in the two southern areas and more modest (approximately 1 °C) warming for the northern sites. Projections based on the three global climate models differed in the extent of warming predicted. In the Minnesota and Iowa study areas, the GENMOM climate model indicated that air temperatures would increase slightly in 2040, but decrease slightly in 2060 (–1.0 and –1.9 °C, respectively), whereas the EH5 and GFDL model projected increases for both future time steps in the northern sites with a net increase of approximately 2 °C for both sites by 2060. Projections from all three models indicated that the Missouri and Oklahoma sites are expected to experience net air temperature increases of 2–4 °C. Based on correlations between daily air temperatures and stream temperatures for each study area, the stream temperature projections we generated reflected these patterns (Fig. 3). Air and stream temperatures correlated strongly in the four study areas (MN $r = 0.93$, IA $r = 0.92$, MO $r = 0.93$, OK $r = 0.87$), and on average, an increase in 1 °C air temperature resulted in a 0.8 °C projected increase in stream temperature. Projected net increases in stream temperature based on air temperature projections through 2060 were 0.6–1.7 °C for the northern sites with increases up to 2.5 °C in summer months (GFDL) and 1.6–3.4 °C for the two southern streams with summer temperatures up to 4.2 °C warmer (GFDL).

The bioenergetics model simulations based on the stream temperature projections from all three climate models indicated that SMB prey consumption and growth are expected to increase (compared with present-day conditions) with the warming predicted, if proportion of maximum consumption (P -values of 0.7–0.8) remains unchanged, prey availability is not limiting and prey energy densities do not change (Fig. 4; Tables 1 and 2). The extent of potential increases in consumption by 2060 differed along the latitudinal gradient, with greatest increases expected in the southern populations (Minnesota: 18.3%, Iowa: 14.6%, Missouri: 48.8%, Oklahoma: 63.9%). As with the projected changes in consumption, simulations showed greater increases in growth for the southern populations. Minnesota and Iowa SMB populations showed an increase in growth by 2060 of 4.3% and 3.2%, respectively, based on the mean of the simulations for the three global climate models. In the Mis-

souri and Oklahoma populations, simulations with 2060 temperature projections from the three models resulted in mean growth increases of 9.0% and 17.0%, respectively. With these projected increases in growth by 2060, annual growth of SMB (starting the growing season at 300 g) would increase by 15, 11, 31 and 61 g compared with present-day rates in the Minnesota, Iowa, Missouri and Oklahoma populations, respectively. For all four populations, more pronounced increases in growth rates corresponded with the relatively higher increases in temperature in summer months compared with present conditions. Across all simulations and populations, a 1 °C increase in stream temperature would result in a 6.3% increase in growth and a 27.4% increase in consumption (Fig. 5).

Discussion

In all four study populations, stream temperatures are expected to warm through 2060, and SMB growth and prey consumption are expected to increase if the increased demand for prey items can be satisfied. The extent of these changes differed along the latitudinal gradient, however, with greater increases in temperatures, growth and consumption predicted for the southern populations. Growth of SMB has been shown to be significantly influenced by temperature (e.g., Dunlop & Shuter 2006), and other studies have indicated that SMB growth may be expected to increase with warming for lake populations in the northern parts of their range, potentially allowing for range expansion (Shuter & Post 1990; King et al. 1999). Wuellner et al. (2010) also found that for SMB in a Missouri River reservoir, growth was predicted to increase with projected warming temperatures due to climate change. Our predictions of increased growth suggest that the projected moderate warming of stream temperatures in the central USA through 2060 will not exceed the limits of thermal conditions capable of supporting SMB growth even for the southern study populations of this warm-water species. Whitley et al. (2006) demonstrated with bioenergetics simulations that SMB performance would be expected to decline, however, with continued warming if stream temperatures more frequently exceed 27 °C. Under these conditions, growth potential would decrease.

The bioenergetics modelling technique yielded simulated impacts on SMB growth and consumption across a latitudinal gradient based on population-specific data on growth, feeding and temperature regime. Results of the simulations, however, should be interpreted with caution because there is uncertainty in model parameters (Chipps & Wahl 2008). We used the commonly applied parameters for SMB consump-

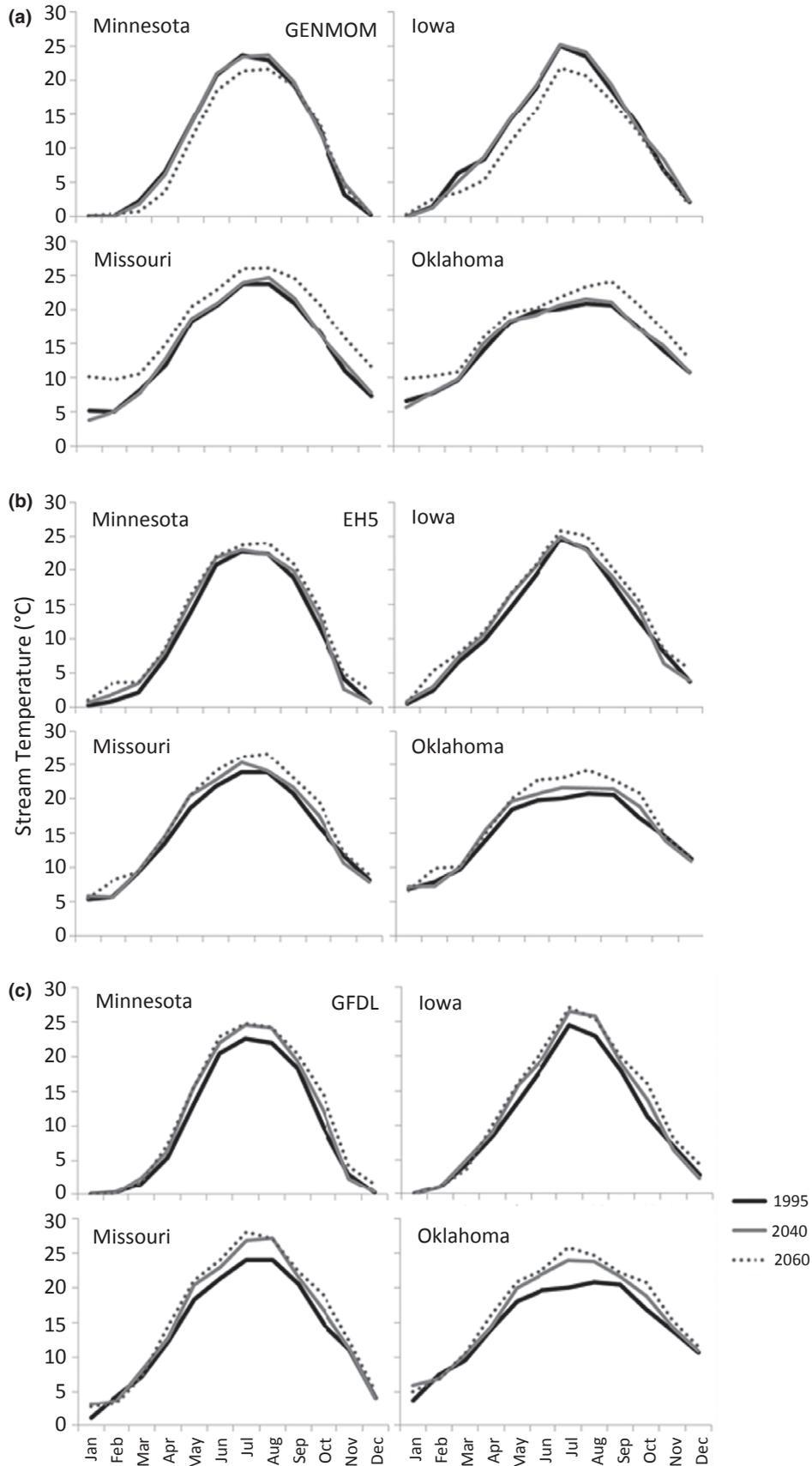


Fig. 3. Mean monthly stream temperatures at present (based on 1995 data) and for 2040 and 2060 climate change projections for the four study areas based on the GENMOM (A), EH5 (B) and GFDL (C) climate models. Stream temperatures were modelled based on correlations between air temperature and stream temperature for each location (MN $r = 0.93$, IA $r = 0.92$, MO $r = 0.93$, OK $r = 0.87$).

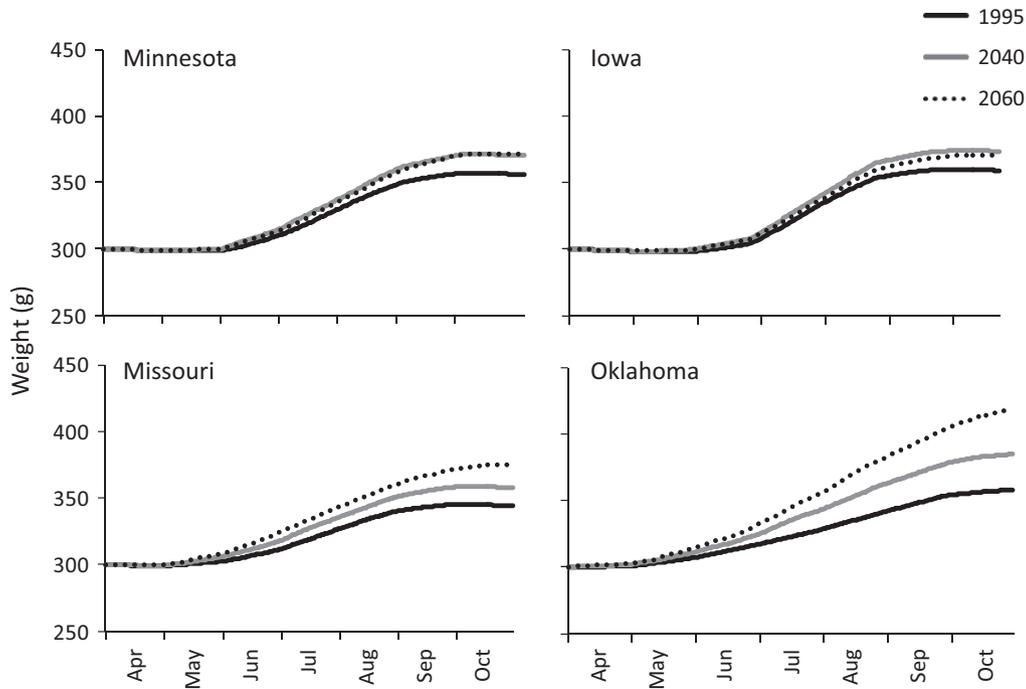


Fig. 4. Mean growth (g) projections for 300-g SMB in the four study areas from bioenergetics simulations based on present (1995), 2040 and 2060 stream temperature projections from the GENMOM, GFDL and EH5 GCMs. Projections for future growth are based on the assumption that current feeding rates remain the same and that prey availability is not limiting.

Table 1. End weights (g) of 300-g SMB after bioenergetics simulations (over 214-day growing season) using projected stream temperatures and present-day consumption rates for the three global climate models.

Population	Simulation end weight (g)						
	Present	GENMOM		EH5		GFDL	
		2040	2060	2040	2060	2040	2060
Minnesota	356.3	360.4	338.2	365.6	381.0	384.9	394.4
Iowa	359.3	365.6	329.3	368.9	386.8	386.1	395.4
Missouri	344.4	349.9	380.1	358.2	372.7	365.1	372.0
Oklahoma	358.1	363.8	403.3	381.0	418.0	410.2	435.1

Table 2. Total prey consumption (g) by SMB at the end of growing season bioenergetics simulations (over 214 days) using projected stream temperatures and present-day consumption rates (assuming prey availability is not limiting) for three global climate models.

Population	Simulated growing season total consumption (g)						
	Present	GENMOM		EH5		GFDL	
		2040	2060	2040	2060	2040	2060
Minnesota	733.4	810.4	609.5	824.2	956.7	940.6	1028.4
Iowa	757.8	836.3	502.4	867.0	1023.7	980.0	1073.8
Missouri	958.6	1022.8	1422.8	1164.7	1386.5	1280.7	1418.9
Oklahoma	788.3	843.8	1171.8	981.8	1283.2	1203.1	1431.4

tion, respiration and egestion–excretion from Shuter & Post (1990) with adjustments for adult, stream-dwelling SMB proposed by Whitlege et al. (2003)

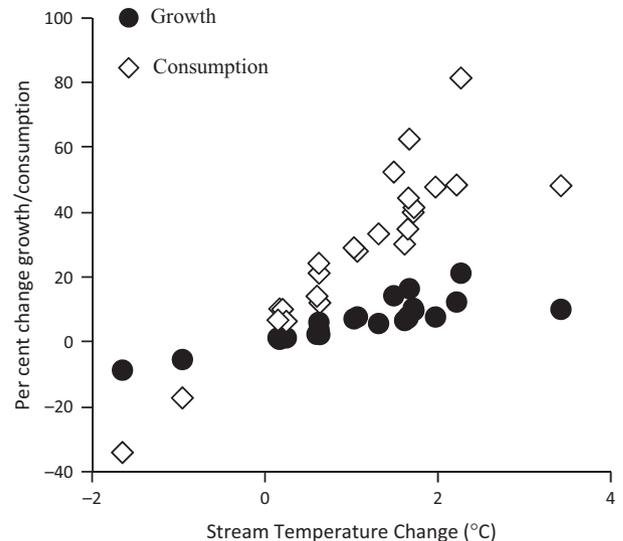


Fig. 5. Projected per cent changes in growth (g) and total consumption (g) of SMB at the end of a simulation growing season versus projected net change in temperature (°C). Each point represents projected change for one of the populations for either time step (2040 or 2060) from one of the GCMs (GENMOM, EH5 or GFDL).

to perform all simulations. This does not account for interpopulation differences in these parameters that may exist along the latitudinal gradient of the SMB range. For example, fishes often display plasticity in physiological tolerances as they adapt to the surrounding environments (e.g., Schaefer & Ryan 2006)

and this may occur in smallmouth bass. For some widespread fish species, however, variation in environmental tolerance is low among populations across broad latitudinal gradients (e.g., Matthews 1986). Future research on multiple stream SMB populations examining feeding, growth and metabolism as related to temperature in the laboratory and the field may be needed to improve the accuracy of these simulations. The assumption that SMB were able to feed at present-day proportions of maximum consumption also had a substantial influence on results of our simulations. Had we simulated growth with current consumption rates (e.g., g per day of prey items) instead, growth may have decreased if consumption could not meet metabolic demands with warming temperatures. Further, the air–stream temperature relationships used to convert air temperature projections from the GCMs to daily stream temperatures ignore other nonlinear influences on stream thermal regimes such as groundwater input, which provides thermal refugia for stream-dwelling SMB (Brewer & Rabeni 2011) particularly in the southern sites. The role of groundwater in tempering the impacts of warming air temperatures is an important area for future research.

The approach we used allowed us to predict how temperature changes would affect SMB growth, but it overlooks many other factors that may influence growth directly or indirectly (e.g., changes in habitat and flow regime) which may occur with climate change. Future changes in land use may be as important as changes in climate in terms of impacts on SMB populations. Peterson & Kwak (1999) found that with altered temperatures and flows predicted under climate change scenarios, SMB abundance would decline substantially in the Kankakee River, Illinois, if current land-use practices were maintained. In simulations with historical land use and predicted alterations in temperature and flow, SMB populations were predicted to increase, suggesting that land use may have an overriding influence on stream-dwelling SMB in the Central USA. Future research is needed to investigate potential impacts of land-use change on SMB populations across their native range. Nonetheless, our study does elucidate some of the potential impacts that climate change may have at the population level for this common warm-water species.

The potential changes in growth predicted here may have important implications for measures of SMB population performance, such as fecundity, over-winter survival of juveniles and time to reach quality length for harvest. For example, Shuter & Post (1990) found that SMB population viability depended upon the ability of young of year to complete a minimum amount of growth before winter in the northern USA and Canada. Changes in time to reach maturity

and desirable length associated with changes in growth have practical implication for fisheries management (Beamesderfer & North 1995), and managers may need to re-evaluate policies on length limits and seasonal closures in the face of climate change. Changes in population performance corresponding to enhanced growth may also lead to changes in SMB distribution. More favourable thermal habitat for SMB may allow SMB to persist beyond their current distribution following projected warming (Shuter & Post 1990; Sharma & Jackson 2008).

The predicted increases in consumption from the bioenergetics simulations indicate that impacts of future climate on SMB will have important effects on prey species. Indirect effects of stream temperature change through altered species interactions are expected to have substantial impacts on fish populations (e.g., Taniguchi et al. 1998; Rahel & Olden 2008). Rabeni (1992) showed that under current conditions in a Missouri Ozark stream, there is a strong trophic linkage between SMB and crayfish, with SMB consumption responsible for loss of a large proportion of crayfish biomass. Predation by SMB thus has a strong influence on crayfish population dynamics and general energy flow. Petersen and Kitchell (2001) showed that with an increase in stream temperatures in the Columbia River, per capita consumption of native salmonids by SMB and other non-native piscivores increased, suggesting that stream warming may cause declines in first-year salmonid survival rates due to predation. Increased SMB predation with predicted northern range expansion due to climate change may result in the loss of over 20,000 populations of native cyprinids in Ontario (Jackson & Mandrak 2002). In Canadian lakes, non-native SMB consumption altered food-web energy pathways by reducing the abundance and diversity of fish prey species, which led to a shift towards a more zooplankton-based diet in native lake trout (Vander Zanden et al. 1999). Predation by *Micropterus* species indirectly impacts lower trophic levels (i.e., small invertebrates, algae) negatively or positively (reviewed in Jackson 2002), and thus, stream ecosystems may experience cascading effects of changes in SMB consumption. With projected increases in growth rates, SMB may also experience earlier ontogenetic shifts from smaller invertebrate prey to crayfish and fish prey (Mittelbach & Persson 1998; Dauwalter & Fisher 2008), which would change the seasonality of trophic interactions and shorten the amount of time that some prey taxa are invulnerable due to SMB gape size constraints (Olson 1996). In addition to altered predator–prey interactions, climate change may also potentially impact competitive interactions between SMB and other species. Largemouth bass (*Micropterus salmoides*), for

example, are expected to benefit from warming stream temperatures and may increasingly compete with SMB for resources (Zweifel et al. 1999). In sum, impacts of projected climate change on SMB populations may have important implications for other species in North American streams, and climate responses of other species may also affect SMB populations.

Most of the prior research on potential impacts of climate change on stream fish populations has focused on salmonids and other species expected to be sensitive to warming temperatures. However, very few studies have examined impacts on species more tolerant to warming, or on populations in streams in the central USA. The distribution of some warm-water fish species is expected to increase with anticipated climate change scenarios (Eaton & Scheller 1996; Lyons et al. 2010), but studies examining population-level impacts on these species are scarce. We found that across a latitudinal gradient in the USA, stream populations of SMB are predicted to experience increased growth and consumption rates with projected temperature increases. These projections provide support for previous predictions that SMB will be a 'winner' species in climate change scenarios (Shuter & Post 1990; Sharma et al. 2007), and we provide population-specific information on impacts based on regionally downscaled climate models. The projected increase in growth rates relies on a key assumption that prey resource availability will not be limiting, and prior research shows that if warming continues beyond the extent projected through 2060, SMB growth may be inhibited (Whitledge et al. 2006). Our results show that predicted changes in stream temperature may affect the population performance of an economically important species, and that these changes may have substantial implications for species interactions and food-web dynamics. A better understanding of how SMB populations will respond to climate change across their broad native range is vital for management and conservation.

Acknowledgements

Funding for this research was provided by the US Geological Survey, National Climate Change and Wildlife Science Center. The authors thank Steve Hostetler and Jay Alder for providing and helping to interpret results from regionally downscaled climate projections, Jodi Whittier and Dan Wiefelich for assistance with data management, and the Minnesota Department of Natural Resources for providing additional diet data. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government. The Missouri Cooperative Fish and Wildlife Research Unit is jointly sponsored by the Missouri Department of Conservation, the University of Missouri, the US

Geological Survey, the US Fish and Wildlife Service and the Wildlife Management Institute.

References

- Alder, J.R., Hostetler, S.W., Pollard, D. & Schmitter, A. 2010. Evaluation of a present-day climate simulation with a new atmosphere-ocean model GENMOM. *Geoscientific Model Development* 3: 69–83.
- Balkenbush, P.E. & Fisher, W.L. 1999. Population characteristics and management of black bass in eastern Oklahoma streams. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 53: 130–143.
- Beamesderfer, R.C.P. & North, J.A. 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. *North American Journal of Fisheries Management* 15: 688–704.
- Beer, W.N. & Anderson, J.J. 2011. Sensitivity of juvenile salmonid growth to future climate trends. *River Research and Applications* 27: 663–669.
- Biro, P.A., Post, J.R. & Booth, D.J. 2007. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proceedings of the National Academy of Sciences* 104: 9715–9719.
- Brewer, S.K. & Rabeni, C.F. 2011. Interactions between natural-occurring landscape conditions and land-use influencing the abundance of riverine smallmouth bass, *Micropterus dolomieu*. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1922–1933.
- Chippis, S.R. & Wahl, D.H. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society* 137: 298–313.
- Clark, M.E., Rose, K.A., Levine, D.A. & Hargrove, W.W. 2001. Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. *Ecological Applications* 11: 161–178.
- Cooke, S.J., Philipp, D.P. & Weatherhead, P.J. 2002. Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Canadian Journal of Zoology* 80: 756–770.
- Covington, W.G., Marteney, R.E. & Rabeni, C.F. 1983. Population characteristics of sympatric smallmouth bass and rock bass in the Jacks Fork and Current Rivers, Missouri. *Transactions of the Missouri Academy of Sciences* 17: 27–36.
- Cummins, K.W. & Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Mitteilung Internationale Vereinigung fuer Theoretische und Angewandte Limnologie* 18: 1–151.
- Dauwalter, D.C. & Fisher, W.L. 2008. Ontogenetic and seasonal diet shifts of smallmouth bass in an Ozark stream. *Journal of Freshwater Ecology* 23: 113–122.
- Dauwalter, D.C., Splinter, D.K., Fisher, W.L. & Marston, R.A. 2007. Geomorphology and stream habitat relationships with smallmouth bass (*Micropterus dolomieu*) abundance at multiple spatial scales in eastern Oklahoma. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1116–1129.

- Delworth, T.L., Broccoli, A.J., Rosati, A., Stouffer, R.J., Bala, V., Beesely, J.A., Cooke, W.F., Dixon, K.W., Dunne, J., Dunne, K.A., Durachta, J.W., Findell, K.L., Ginoux, P., Gnanadesikan, A., Gordon, C.T., Griffies, S.M., Gudgel, R., Harrison, M.J., Held, I.M., Hemler, R.S., Horowitz, L.W., Klein, S.A., Knutson, T.R., Kushner, P.J., Langenhorst, A.R., Lee, H., Lin, S., Lu, J., Malyshev, S.L., Milly, P.C.D., Ramaswamy, V., Russell, J., Schwarzkopf, M.D., Shevliakova, E., Sirutis, J.J., Spelman, M.J., Stern, W.F., Winton, M., Wittenberg, A.T., Wyman, B., Zeng, F. & Zhang, R. 2006. GFDL's CM2 global coupled climate models. Part 1: formulation and simulation characteristics. *Journal of Climate* 19: 643–674.
- Dunlop, E.S. & Shuter, B.J. 2006. Native and introduced populations of smallmouth bass differ in concordance between climate and somatic growth. *Transactions of the American Fisheries Society* 135: 1175–1190.
- Eaton, J.G. & Scheller, R.M. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41: 1109–1115.
- Eggleton, M.A. & Schramm, H.L. 2002. Caloric densities of selected fish prey organisms from the lower Mississippi River. *Journal of Freshwater Ecology* 17: 409–414.
- Hanson, P.C., Johnson, T.B., Schindler, D.E. & Kitchell, J.F. 1997. *Fish bioenergetics 3.0 for windows*. Madison: University of Wisconsin, Sea Grant Institute.
- Hostetler, S.W., Alder, J.R. & Allan, A.M. 2011. Dynamically downscaled climate simulations over North America: methods, evaluation, and supporting documentation for users. U.S. Geological Survey Open-File Report 2011-1238. Reston, Virginia: U.S. Geological Survey.
- Jackson, D.A. 2002. Ecological effects of *Micropterus* introductions: the dark side of black bass. In: Philipp, D.P. & Ridgway, M.S., eds. *Black bass: ecology, conservation, and management*. American Fisheries Society Symposium 31. Bethesda, Maryland: American Fisheries Society, pp. 221–232.
- Jackson, D.A. & Mandrak, N.E. 2002. Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. In: McGinn, N.A., ed. *Fisheries in a changing climate*. American Fisheries Society Symposium 32. Bethesda, Maryland: American Fisheries Society, pp. 89–98.
- Jansen, A.C., Quist, M.C. & Kopaska, J. 2008. Assessment of smallmouth bass populations in Iowa interior rivers. *Journal of the Iowa Academy of Science* 115: 17–23.
- Johnson, B.M., Martinez, P.J., Hawkins, J.A. & Bestgen, K.R. 2008. Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management* 28: 1941–1953.
- Keleher, C.J. & Rahel, F.J. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. *Transactions of the American Fisheries Society* 125: 1–13.
- King, J.R., Shuter, B.J. & Zimmerman, A.P. 1999. Empirical links between thermal habitat, fish growth, and climate change. *Transactions of the American Fisheries Society* 128: 656–665.
- Kolander, T.D., Willis, D.W. & Murphy, B.R. 1993. Proposed revision of the standard weight (W_s) equation for smallmouth bass. *North American Journal of Fisheries Management* 13: 398–400.
- Lyons, J. 1997. Influence of winter starvation on the distribution of smallmouth bass among Wisconsin streams: a bioenergetics modeling assessment. *Transactions of the American Fisheries Society* 126: 157–162.
- Lyons, J., Stewart, J.S. & Mitro, M. 2010. Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, USA. *Journal of Fish Biology* 77: 1867–1898.
- Matthews, W.J. 1986. Geographic variation in thermal tolerance of a widespread minnow *Notropis lutrensis* of the North American mid-west. *Journal of Fish Biology* 28: 407–417.
- McCarthy, S.G., Duda, J.J., Emlen, J.M., Hodgson, G.R. & Beauchamp, D.A. 2009. Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity watershed, California. *Transactions of the American Fisheries Society* 138: 506–521.
- McClendon, D.D. & Rabeni, C.F. 1987. Physical and biological variables useful for predicting population characteristics of smallmouth bass and rock bass in an Ozark stream. *North American Journal of Fisheries Management* 7: 46–56.
- Meneau, K.J. 2009. Stream black bass special management areas summary for smallmouth bass. Project and data summary report. Missouri Department of Conservation, Jefferson City, Missouri.
- Mittelbach, G.G. & Persson, L. 1998. The ontogeny of piscivory and its consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465.
- Munkittrick, K.R. & Dixon, D.G. 1989. Use of white sucker (*Catostomus commersoni*) populations to assess the health of aquatic ecosystems exposed to low-level contaminant stress. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1455–1462.
- Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology* 77: 179–190.
- Orth, D.J., Oakey, D.D. & Maughan, O.E. 1983. Population characteristics of smallmouth bass in Glover Creek, Southeast Oklahoma. *Proceedings of the Oklahoma Academy of Science* 63: 37–41.
- Paragamian, V.L. 1984. Population characteristics of smallmouth bass in five Iowa streams and management recommendations. *North American Journal of Fisheries Management* 4: 497–506.
- Paragamian, V.L. & Wiley, M.J. 1987. Effects of variable stream flows on growth of smallmouth bass in the Maquoketa River, Iowa. *North American Journal of Fisheries Management* 7: 357–362.
- Petersen, J.H. & Kitchell, J.F. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetics implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1831–1841.
- Peterson, J.T. & Kwak, T.J. 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecological Applications* 9: 1391–1404.
- Pianka, E.R. 1970. On r- and K- selection. *American Naturalist* 104: 592–597.
- Pilgrim, J.M., Fang, X. & Stefan, H.G. 1999. Stream temperature correlations with air temperatures in Minnesota: impli-

- cations for climate warming. *Journal of the American Water Resources Association* 34: 1109–1121.
- Probst, W.E., Rabeni, C.F., Covington, W.G. & Marteney, R.E. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. *Transactions of the American Fisheries Society* 113: 283–294.
- Putman, J.H., Pierce, C.L. & Day, D.M. 1995. Relationships between environmental variables and size-specific growth rates of Illinois stream fishes. *Transactions of the American Fisheries Society* 124: 252–261.
- Rabeni, C.F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1714–1721.
- Rahel, F.J. & Olden, J.D. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533.
- Rieman, B.E., Isaak, D., Adams, S., Horan, D., Nagel, D., Luce, C. & Myers, D. 2007. Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River Basin. *Transactions of the American Fisheries Society* 136: 1552–1565.
- Roeckner, E., Bäuml, G., Bonaventura, L., Brokopf, R., Esch, M., Giorgetta, M., Hagemann, S., Kirchner, I., Kornbluh, L., Manzini, E., Rhodin, A., Schlese, U., Schulzweida, U. & Tompkins, A. 2003. The atmospheric general circulation model ECHAM5. Part I: model description. Report 349. Hamburg, Germany: Max Planck Institute for Meteorology.
- Roell, M.J. & DiStefano, R.J. 2010. Effects of a conservative rock bass length limit on angler participation, sport fish populations, and crayfish prey in a Missouri Ozark stream. *North American Journal of Fisheries Management* 30: 552–564.
- Roff, D.A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 989–1000.
- Schaefer, J. & Ryan, A. 2006. Developmental plasticity in the thermal tolerance of zebrafish *Danio rerio*. *Journal of Fish Biology* 69: 722–734.
- Sharma, S. & Jackson, D.A. 2008. Predicting smallmouth bass (*Micropterus dolomieu*) occurrence across North America under climate change: a comparison of statistical approaches. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 471–481.
- Sharma, S., Jackson, D.A., Minnis, C.K. & Shuter, B.J. 2007. Will northern fish be in hot water because of climate change? *Global Change Biology* 13: 2052–2064.
- Shuter, B.J. & Meisner, J.D. 1992. Tools for assessing the impact of climate change on freshwater fish populations. *GeoJournal* 28: 7–20.
- Shuter, B.J. & Post, J.R. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119: 314–336.
- Shuter, B.J., MacLean, J.A., Fry, F.E.J. & Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109: 1–34.
- Shuter, B.J., Lester, N.P., LaRose, J., Purchase, C.F., Vascotto, K., Morgan, G., Collins, N.C. & Abrams, P.A. 2005. Optimal life histories and food web position: linkages among somatic growth, reproductive investment, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 738–746.
- Sowa, S.P. & Rabeni, C.G. 1995. Regional evaluation of the relation of habitat to distribution and abundance of smallmouth bass and largemouth bass in Missouri streams. *Transactions of the American Fisheries Society* 124: 240–251.
- Stark, W.J. & Zale, A.V. 1991. Status of smallmouth bass populations in eastern Oklahoma. Final report. Oklahoma City, Oklahoma: Oklahoma Department of Wildlife Conservation. Available from <http://digitalprairie.ok.gov/cdm/compoundobject/collection/stgovpub/id/10394/rec/44>. Last accessed 7 June 2013.
- Stewig, J.D. 2009. Mississippi River smallmouth bass regulation evaluation 2000–2008. Completion Report F-29-R(P)-27. St. Paul, Minnesota: Minnesota Department of Natural Resources. Available from http://files.dnr.state.mn.us/areas/fisheries/montrose/miss_river_smb_final_report_2008.pdf. Last accessed 7 June 2013.
- Taniguchi, Y., Rahel, F.J., Novinger, D.C. & Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1894–1901.
- Trippel, E.A. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario lakes. *North American Journal of Fisheries Management* 30: 64–72.
- Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401: 464–467.
- Waters, T.F., Kaehler, J.P., Polomis, T.J. & Kwak, T.J. 1993. Production dynamics of smallmouth bass in a Minnesota stream. *Transactions of the American Fisheries Society* 122: 588–598.
- Whitledge, G.W., Hayward, R.S., Zweifel, R.D. & Rabeni, C.F. 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Transactions of the American Fisheries Society* 132: 316–325.
- Whitledge, G.W., Rabeni, C.F., Annis, G. & Sowa, S.P. 2006. Riparian shading and groundwater enhance growth potential for smallmouth bass in Ozark streams. *Ecological Applications* 16: 1461–1473.
- Wuellner, M.R., Chipps, S.R., Willis, D.W. & Adams, W.E. 2010. Interactions between walleyes and smallmouth bass in a Missouri River reservoir with consideration of the influence of temperature and prey. *North American Journal of Fisheries Management* 30: 445–463.
- Zweifel, R.D., Hayward, R.S. & Rabeni, C.F. 1999. Bioenergetics insight into black bass distribution shifts in Ozark border region streams. *North American Journal of Fisheries Management* 19: 192–197.