1-2017

Interactive Effects of Flow Regime, Climate Change, and Angler Harvest on Smallmouth Bass at the Southern Range Extent

Christopher Middaugh
University of Arkansas, Fayetteville

Interactive Effects of Flow Regime, Climate Change, and Angler Harvest on Smallmouth Bass at the Southern Range Extent

A dissertation in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

Christopher Robert Middaugh
Lyon College
Bachelor of Science in Biology, 2009
Purdue University
Master of Science in Fisheries Science, 2011

August 2017
University of Arkansas

This dissertation is approved for recommendation to the Graduate Council

____
Dr. Daniel D. Magoulick
Dissertation Director

____
Dr. Jack Cothren
Committee Member

____
Dr. John David Wilson
Committee Member

____
Dr. Kusum Naithani
Committee Member

Abstract

The Ozark-Ouachita Interior Highlands of Arkansas, Oklahoma, and Missouri are the southern extent of native Smallmouth Bass *Micropterus dolomieu* range. Smallmouth Bass are an important species economically and ecologically, but it is unknown how climate change may affect them in this region and in particular how Smallmouth Bass may be affected differently across streams from various flow regimes. Here I present three projects investigating how climate change, flow regime, and angler harvest may interact to affect Smallmouth Bass over the coming century. I first modeled present and future water temperatures and calculated growth rate potential for Smallmouth Bass from streams within both groundwater and runoff flow regimes. Currently, water temperatures in runoff streams warm past optimal conditions for Smallmouth Bass during summer months and this is expected to be exacerbated by climate change. By the end of the century, my results predict that Smallmouth Bass growth could increase in winter, fall, and early spring in streams from both flow regimes, but will strongly decline during summer months in runoff streams. I next conducted an empirical study to examine differences in Smallmouth Bass body condition at present during summer months in both runoff and groundwater streams. I found in two out of three years of collections that Smallmouth Bass body condition declined during summer months in both groundwater and runoff streams with no significant difference between stream types. The final portion of my research examines population level effects of climate change on Smallmouth Bass from a runoff stream. I used empirical data to parameterize a simulation model where I simulated various climate scenarios such as increased flooding and drought probabilities. I found that increases in drought are likely to cause strong declines in adult Smallmouth Bass populations. Changes in harvest regulations could help protect Smallmouth Bass populations somewhat, but would likely not prevent

population declines in the coming century. The effects of climate change on Smallmouth Bass at the southern range extent will likely be complex, but groundwater streams may mitigate some of the negative effects of climate change on Smallmouth Bass.

Acknowledgments

There are many people that have helped me throughout my time here and without them this dissertation would not have been possible. First, I need to thank Dan Magoulick for taking me on as a student and allowing me the freedom to pursue my dream project. His advice and guidance along the way have been invaluable. My committee members, Kusum Naithani, J. D. Wilson, and Jack Cothren, have also provided me with many suggestions and helpful comments that have greatly improved this dissertation.

My lab mates have been a continual source of encouragement and have helped with talking through ideas and assisting with data collection and analyses. In particular I need to thank Robert Fournier, Doug Leasure, Dustin Lynch, Lindsey Bruckerhoff, Allyson Yarra, Nicky Graham, and Brittany Furtado. Other members of the Coop Unit and Biology department have also assisted with fieldwork, data analysis, and by being friends throughout this time, especially John Herbert, Joe Moore, Cari Sebright, Tyler Pitmann, Auriel Fournier, Philip Stephensen, Jake McClain, Allyn Dodd, and Brad Austin. This work would not have been possible without my three REU students: Tevin Douglas, Brin Kessinger, and Scott Koenigbauer. They provided invaluable assistance during summer months with fieldwork and with gathering data for modeling work.

I am grateful to the Arkansas Game and Fish Commission for providing me with data and in particular Jeff Quinn, Mark Oliver, Steve Filipek, and Stan Todd for providing feedback and ideas related to early versions of this project. I am also grateful to the USGS and NOAA for providing data.

Most people's families provide moral support, but mine went above and beyond by assisting with fieldwork. I am grateful to my Dad and my brothers for donating their time and fishing skills (such as they are) at various points to help me collect Smallmouth Bass. I am also grateful to my Mom for her support and encouragement throughout this time.

Finally, this work would not be possible without the support of my wife, Summer. You have allowed me to pursue my dreams and I could not have done this work without your love and encouragement. Thank you especially for your understanding of the long field hours, even just days after Andrew was born. I am lucky to have you.

Dedication

This dissertation is dedicated to my children. Your fascination and wonder at nature constantly remind me why I love my research. My prayer is that you develop a lifelong love and appreciation for the natural world and that my work will help us better understand and conserve natural resources for you and your children.

Table of Contents

Introduction……………………………………………………………………………………..1

Chapter 1: Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent………………………………………………………………………………...7

Abstract………………………………………………………………………………..…..8

Introduction…………………………………………………………………………..……9

Methods………………………………………………………………………………..….12

Results……………………………………………………………………………………14

Discussion………………………………………………………………………………..16

Acknowledgements………………………………………………………………………21

References……………………………………………………………………………...…...22

Tables, Figures, and Appendices…………………………………………………………...27

Chapter 2: Changes in body condition and diet of lotic Smallmouth Bass across two flow regimes during summer months at the southern extent of their native range……………………35

Abstract……………………………………………………………………………………..36

Introduction………………………………………………………………………………37

Methods……………………………………………………………………………………..40

Results……………………………………………………………………………………45

Discussion………………………………………………………………………………..47

Acknowledgements………………………………………………………………………52

References……………………………………………………………………………...……...54

Tables and Figures………………………………………………………………………….58

IACUC Approval Letters……………………………………………………….………..66

Chapter 3: Forecasting effects of angler harvest and climate change on smallmouth bass abundance at the southern edge of their range……………………………………………...68

Abstract……………………………………………………………………………………..69

Introduction…………………………………………………………………………………71

Methods……………………………………………………………………………………..73

Results………………………………………………………………………………………80

Discussion…………………………………………………………………………………..81

Acknowledgements…………………………………………………………………………86

References…………………………………………………………………………...…...87

Tables, Figures, and Appendices…………………………………………………………...91

Conclusion……………………………………………………………………………...…102

List of Published Papers

Chapter 1
Middaugh, C. R., B. Kessinger, and D. D. Magoulick. 2016. Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent. Ecology of Freshwater Fish. DOI: 10.1111/eff.12320. Published.

Chapter 2
Middaugh, C. R., and D. D. Magoulick. Changes in body condition and diet of lotic Smallmouth Bass across two flow regimes during summer months at the southern extent of their native range. American Fisheries Society Symposium Publication: Managing Centrarchid Fisheries in Rivers and Streams. Under Review.

Introduction

A recent report by the National Climate Assessment describes the "increasingly disruptive" effects of climate change already observed in the United States and predicts these effects to be exacerbated going into the future (Melillo et al. 2014). As such, it is critical to assess current population status and trends for species that may be affected by climate change especially in some of the most vulnerable systems such as streams and rivers. Climate change has already warmed streams across the United States (Kaushal et al. 2010) and has affected flow regimes through increased flooding and drought conditions (Groisman et al. 2001). Anthropogenic alterations to streams and watersheds exacerbate these alterations to stream systems (Hundecha and Bárdossy 2004), further disrupting the historic conditions that aquatic biota are adapted to.

Smallmouth bass are a popular sport fish species in Arkansas, Oklahoma, and Missouri and are distributed across much of the Ozark-Ouachita Interior Highlands. There are many threats that face smallmouth bass in the Ozark-Ouachita Interior Highlands in future years. These include warming temperatures (Alder & Hostetler 2013), changing hydrologic patterns (Ficke et al. 2007), stocking of non-native strain smallmouth bass (Malloy 2001; Brewer and Long 2015), and introduction of nonnative prey species such as crayfish (Magoulick and DiStefano 2007). Threats such as these could lead to smallmouth bass being outcompeted by largemouth bass *Micropterus salmoides* and spotted bass *Micropterus punctulatus* which are adapted to warmer water temperatures (Zweifel et al. 1999; Shepherd and Maceina 2009) and coexist with smallmouth bass in lotic systems in the region. Largemouth bass are replacing smallmouth bass in Ozark border streams in Missouri (Sowa and Rabeni 1995). This has been attributed to anthropogenic alteration of habitat (Sowa and Rabeni 1995) and these effects could be exacerbated by climate change.

Increases in water temperature could affect smallmouth bass. The upper lethal temperature limit for smallmouth bass is 35°C (Scott and Crossman 1973), but summer stream temperatures exceeding 27°C are predicted to result in loss of mass for smallmouth bass (Whitledge et al. 2006) and smallmouth bass scope for growth decreases as temperatures surpass 22°C (Zweifel et al. 1999). Largemouth bass scope for growth scope does not decrease until about 26°C which may give them a competitive advantage in warmer temperatures (Zweifel et al. 1999). It is unknown how spotted bass growth may be related to temperature, but they likely are energetically similar to largemouth bass (Shepherd and Maceina 2009). Smallmouth bass annual growth could increase in some streams in our region in the coming century, if prey are available in high enough abundances to allow increased consumption rates (Pease and Paukert 2014). However, summer water temperatures likely exceed levels of optimal growth for smallmouth bass during summer months presently and climate change could push conditions further past optimal, potentially to the point where growth is not bioenergetically possible.

Previous studies have predicted the expanding distribution of smallmouth bass in Canadian lakes under climate changes where they are an invasive species (Vander Zanden et al. 2004; Chu et al 2005; Sharma et al 2007; Sharma and Jackson 2008). However, climate change could also lead to a reduction of smallmouth bass range towards the southern portion of the United States. Eaton and Scheller (1996) took water measurements from over 1,300 USGS river gages and indicated that at 37.5% of sites smallmouth bass may be extirpated due to climate change. Niche models have been created to examine restriction of range of other lotic species (e.g., brown trout; Filipe et al. 2013) due to climate change and even to examine how competitive interactions may influence range shifts under climate change (e.g., salmonids, Wenger et al. 2011). No work has been conducted explicitly examining range shifts of smallmouth bass at the southern range extent and it is important to better understand the mechanisms by which climate change could affect smallmouth bass in this region.

Hydrologic regime is also an important structuring component for smallmouth bass. Many regions of the United States have had streams classified according to their flow regime (e.g., intermittent, groundwater, and runoff dominated; Leasure et al. 2016). Conditions across stream types are very different. For example, groundwater streams typically maintain a much more stable flow during summer months and cooler water temperatures during summer months (Whitledge et al. 2006). Differences across hydrologic regimes could affect the way streams change in response to changing climate and in turn how fishes within are affected. For example, streams with a high groundwater influence may not warm in response to warming air temperatures to the same extent as intermittent or runoff dominated streams (Carlson et al. 2015).

My dissertation investigates how climate change may affect smallmouth bass and how this may be different across stream flow regimes. I also investigate how angler harvest could interact with climate effects. I conducted three studies to examine these topics. My first question was whether growth may differ across stream type and if smallmouth bass could be affected differently by climate change between groundwater and runoff streams. To answer this, I determined growth rate potential of smallmouth bass at both present and forecasted stream temperatures in both groundwater and runoff streams. My second question was whether smallmouth bass currently are negatively affected by summer conditions in the Ozark-Ouachita Interior Highlands (i.e., high temperatures and drought) and if this differs between runoff and groundwater streams. I collected smallmouth bass from both groundwater and runoff streams for three years during summer months and examined trends in body condition and diets in both streams types. My final question was how climate change might affect a smallmouth bass population and how influential was angler harvest relative to climate change effects for that population. This project utilized empirical data collected by the Arkansas Game and Fish Commission to parameterize a simulation model which allowed me to simulate various climate and harvest scenarios and then compare the resulting effects on forecasted smallmouth bass abundances. All three projects have implications on how southern range smallmouth bass should be managed in the face of climate change.

References

Alder, J.R., & Hostetler, S.W. 2013. USGS National Climate Change Viewer. US Geological Survey http://www.usgs.gov/climate_landuse/clu_rd/nccv.asp.

Brewer, S. K., and J. M. Long. 2015. Biology and ecology of Neosho smallmouth bass and the genetically distinct Ouachita lineage. Pages 281-296 *in* M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Carlson, A.K., Taylor, W.W., Schlee, K.M., Zorn, T.G., & Infante, D.M. 2015. Projected impacts of climate change on stream salmonids with implications for resilience-based management. Ecology of Freshwater Fish doi:10.1111/eff.12267.

Chu, C., N. E. Mandrak, and C. K. Minns. 2005. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. Diversity and Distributions 11:299-310.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109-1115.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Review in Fish Biology and Fisheries. 17:581-613.

Filipe, A. F., D. Markovic, F. Pletterbauer, C. Tisseuil, A. D. Wever, S. Schmutz, N. Bonada, and J. Freyhof. 2013. Forecasting fish distribution along stream networks: brown trout (*Salmo trutta*) in Europe. Diversity and Distributions 19:1059-1071.

Groisman, P. Y., R. W. Knight, and T. R. Karl. 2001. Heavy precipitation and high streamflow in the contiguous United States: Trends in the twentieth century. Bulletin of the American Meterological Society 82:219-246.

Hundecha, Y. and A. Bárdossy. 2004. Modeling the effect of land use changes on the runoff generation of a river basin through parameter regionalization of a watershed model. Journal of Hydrology 292:281-295.

Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. Frontiers in Ecology and the Environment 8:461-466.

Leasure, D.R., Magoulick, D.D., & Longing, S.D. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32: 18-35.

Magoulick, D. D., and R. J. DiStefano. 2007. Invasive crayfish Orconectes neglectus threatens native crayfish in the spring river drainage of Arkansas and Missouri. Southeastern Naturalist 6:141-150.

Malloy, T. P. 2001. Introgressive hybridization between native and non-native smallmouth bass in Oklahoma. Doctoral dissertation. Oklahoma State University, Stillwater.

Melillo, J. M., R. Richmond, and G. W. Yohe (eds.) Climate change impacts in the United States: The third national climate assessment. U.S. Global Change Research Program, 2014.

Pease, A. A., and C. P. Paukert. 2014. Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecology of Freshwater Fish 23:336-346.

Sharma, S. and D. A. Jackson. 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., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish be in hot water because of climate change? Global Change Biology 13:2052-2064.

Shepherd, M. D., and M. J. Maceina. 2009. Effects of striped bass stockin on largemouth bass and spotted bass in Lewis Smith Lake, Alabama. North American Journal of Fisheries Management 29:1232-1241.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14:132-148.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Nevill, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences 108:14175-14180.

Whitledge, G. W., C. F. Rabeni, G. Annis, and S. P. Sowa. 2006. Riparian shading and groundwater enhance growth potential for smallmouth bass in Ozark streams. Ecological Applications 16:1461-1473.

Zweifel, R. D., R. S. Hayward, and C. F. Rabeni. 1999. Bioenergetics insight into black bass distribution shifts in Ozark border region streams. North American Journal of Fisheries Management 19:192-197.

Chapter 1

Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent

Christopher R. Middaugh[1], Brin Kessinger[2], and Daniel D. Magoulick[3]

[1]Arkansas Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, Fayetteville, Arkansas 72701

[2]Evolution, Ecology, and Organismal Biology Department, Ohio State University, Columbus, Ohio 43210

[3]U.S. Geological Survey, AR Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701

Abstract

Temperature increases due to climate change over the coming century will likely affect smallmouth bass (*Micropterus dolomieu*) growth in lotic systems at the southern extent of their native range. However, the thermal response of a stream to warming climate conditions could be affected by the flow regime of each stream, mitigating the effects on smallmouth bass populations. We developed bioenergetics models to compare change in smallmouth bass growth rate potential (GRP) from present to future projected monthly stream temperatures across two flow regimes, runoff and groundwater dominated. Seasonal differences in GRP between stream types were then compared. The models were developed for fourteen streams within the Ozark-Ouachita Interior Highlands in Arkansas, Oklahoma, and Missouri, USA which contain smallmouth bass. In our simulations, smallmouth bass mean GRP during summer months decreased by 0.005 g/g/day in runoff streams and 0.002 g/g/day in groundwater streams by end of century. Mean GRP during winter, fall, and early spring increased under future climate conditions within both stream types (e.g., 0.00019 g/g/day in runoff and 0.0014 g/g/day in groundwater streams in spring months). We found significant differences in change in GRP between runoff and groundwater streams in three seasons in end of century simulations (spring, summer, and fall). Potential differences in stream temperature across flow regimes could be an important habitat component to consider when investigating effects of climate change as fishes from various flow regimes that are relatively close geographically could be affected differently by warming climate conditions.

Introduction

Water temperature is one of the most important abiotic conditions affecting lotic systems. Water temperature influences metabolic rates, growth rates, and development of many different organisms (Naiman & Turner 2000) and it can help determine growth and survival of fishes (Magnuson et al. 1979; Christie & Regier 1988). Water temperatures are also critical to structuring the distribution of organisms, e.g., by limiting salmonids to high elevations in some regions (Flebbe 1994) and limiting the latitudinal distribution of smallmouth bass (*Micropterus dolomieu*) (Shuter et al. 1980). However, climate change is expected to increase lotic temperatures over the coming century and many lotic systems in the United States are already warming (Kaushal et al. 2010). This change in thermal habitat could alter current distributions of organisms by opening new habitats to colonization (e.g., smallmouth bass expanding farther north; Vander Zanden et al. 2004) and restricting the range of species adapted to cooler water (e.g., Bull trout (*Salvelinus confluentus*); Isaak et al. 2010).

In addition to thermal patterns, hydrologic regime is also a critical structuring component of stream ecosystems (Poff et al. 2010). Accordingly, many regions across the United States have had streams classified by flow regimes, such as groundwater and runoff (e.g., Leasure et al. 2016). These classification regimes provide clear, easily interpreted, and ecologically relevant methods of relating stream hydrologic regime to ecological data (Poff et al. 2010). Groundwater dominated streams are expected to exhibit very different thermal patterns than runoff dominated streams, with cooler water temperatures during summer months, and warmer temperatures during winter months (Whitledge et al. 2006). In addition, streams with more groundwater input are likely to be less sensitive to changes in warming air temperatures which could affect how fishes respond to climate change (Carlson et al. 2015).

Smallmouth bass is a warm-water riverine species broadly distributed throughout North America. Because of their ecological importance as apex predators in many lotic systems (Rabeni 1992), smallmouth bass is a commonly studied species with many of their life history traits characterized (Brewer and Orth 2015) including bioenergetics parameters (Whitledge et al. 2003). Though smallmouth bass are locally abundant in streams in the Ozark-Ouachita Interior Highlands, this region is at the southern extent of smallmouth bass native range and seasonal water temperatures exceed optimal growth levels (22°C; Zweifel et al. 1999) in many systems during a typical year. Air temperatures are expected to increase in the Ozark-Ouachita Interior Highlands due to climate change over the coming century (Alder & Hostetler 2013), potentially raising some stream temperatures past habitable conditions for smallmouth bass.

Although previous work has examined a potential northward expansion of smallmouth bass due to climate change (Vander Zanden et al. 2004; Dunlop & Shuter 2006), little work has examined how smallmouth bass could be affected by climate change at the southern portion of their range. Some fishes are expected to have truncated ranges due to climate change (e.g., brook trout (*Salvelinus fontinalis*); Meisner 1990), but some previous work has not indicated this for smallmouth bass (Mohseni et al. 2003). In a comparison of smallmouth bass growth rate in four streams across a latitudinal gradient, Pease and Paukert (2013) indicated a potential increase in smallmouth bass prey consumption and growth due to climate change across their range. However, they did not take into account variation among stream types or factors other than temperature which could affect growth.

Other research indicates that high water temperatures at the southern extent of smallmouth bass range can be detrimental to their growth and abundance. In the Ozark border region of Missouri, smallmouth bass have shown declines with replacement by their competitor, largemouth bass (*Micropterus salmoides*) (Sowa & Rabeni 1995). In particular, streams with higher maximum summer temperatures and more pool area had a stronger displacement (Sowa & Rabeni 1995). This is likely due in part to higher thermal optima of largemouth bass leading to a competitive advantage in warmer streams (26°C; Zweifel et al. 1999). However, certain aspects of the flow regime, e.g., the amount of groundwater influence, could influence competitive interactions and benefit smallmouth bass populations. Streams with large amounts of groundwater input could provide thermal habitat that favors growth of smallmouth bass (Westhoff & Paukert 2014). In addition, streams with high levels of groundwater input could increase recruitment of smallmouth bass relative to non-spring fed streams (Brewer 2013). No previous work has compared smallmouth bass growth in groundwater dominated vs. runoff dominated streams.

We examined how climate change could alter stream water temperatures in the Ozark-Ouachita Interior Highlands and how this could affect the growth rate potential (GRP) of smallmouth bass. Flow regimes have recently been predicted for every stream in the Ozark-Ouachita Interior Highlands region of Arkansas, Oklahoma, and Missouri (Leasure et al. 2016). These flow regime classifications were developed from 10 hydrologic variables and provide a classification of streams into three broad categories, groundwater, runoff, and intermittent with subcategories within each (Leasure et al. 2016). All of our study streams were classified as either groundwater or runoff. Groundwater streams are characterized by more flow stability and higher base flows than runoff streams (Leasure et al. 2016). Many runoff streams have multiple days of no flow each year in this region (Leasure et al. 2016). We did not include any intermittent streams as many of these do not support year-round smallmouth bass populations (Magoulick 2000). The flow classifications that we use are not based on the actual groundwater contribution to the system, but instead are based on a wide range of hydrologic variables (Leasure et al. 2016). We compared changes in seasonal GRP among streams from both flow classifications to determine how smallmouth bass growth could be affected differentially between flow regimes.

Materials and Methods

Air and water temperatures

We selected fifteen streams in the Ozark-Ouachita Interior Highlands of Arkansas, Missouri, and Oklahoma that contained smallmouth bass and had United States Geologic Survey (USGS) river gages that collected water temperature data (Fig. 1; App. 1). All temperature data for each site were downloaded (range 1-11 years; App. 1) and a monthly mean temperature for each month of data was calculated at each site. If a month had fewer than 20 days of temperature data collected, it was excluded from analyses. Next, we collected monthly mean air temperatures (from the National Oceanic and Atmospheric Agency National Center for Climate Data) for the county where each site was located for a corresponding time period to the water temperature data. We then calculated a least-squares linear regression for each site to predict stream temperature from air temperature data (Table 1).

After calculating a predictive relationship between air and water temperatures, we used the USGS National Climate Change Viewer (Alder & Hostetler 2013) to determine modeled historic air temperatures (1950-2005) and future air temperatures under climate change for two decades (2040's and 2090's). The National Climate Change Viewer provides monthly minimum and maximum temperatures downscaled to the county level for each year during the historical period, and projected monthly minimum and maximum temperatures for each year at the same resolution until the year 2099. We selected an emissions scenario of RCP 8.5 (highest CO_2

emissions) and used the ensemble average temperature predictions of 30 models. We chose to only model the highest climate scenario because of the exploratory nature of this analysis and because we focus on a comparison of two different future time periods which provides a contrast between a more and less severe change in air temperature. We calculated the mean minimum and maximum temperature of each month for the county corresponding to each of our streams during present and both future time periods. Monthly mean maximum and minimum temperatures were averaged to produce a monthly mean temperature for each time period. These monthly mean temperatures were then used to predict monthly mean water temperatures for each site at each time period using the previously calculated linear relationships. This approach assumes no changes in river conditions (e.g., hydrologic patterns) over the coming century other than temperature changes.

Bioenergetics modeling

We created a bioenergetics simulation based on the Wisconsin bioenergetics model (Hanson et al. 1997) but coded in program R (R Development Core Team 2008) and parameterized for smallmouth bass (Wrenn 1980; Shuter & Post 1990; Zweifel et al. 1999; Whitledge et al. 2003; Whiteledge et al. 2006). All simulations were run for a 300 g fish (275 mm (Kolander et al. 1993); approximately age 4 in the Buffalo River, AR (Whisenant & Maughan 1989)). We determined simulated diet based on diet samples collected using gastric lavage (Kamler & Pope 2001) from smallmouth bass captured in the Buffalo River, AR in May-September 2014 (n = 34; 73% crayfish, 24% fish, and 3% macroinvertebrate). These proportions are similar to what other researchers have found for smallmouth bass diets (Rabeni 1992; Dauwalter & Fisher 2008). Energy density of prey was set at 3 063 $J*g^{-1}$ for crayfish

(*Procambarus* crayfish; Eggleton & Schramm 2002), 3 853 $J*g^{-1}$for fish prey (fathead minnow (*Pimephales promelas*); Whitledge et al. 2003) and 3 421 $J*g^{-1}$ for aquatic insect larvae (average value of Chironomidae, Odonata, and Ephemeroptera; Cummins & Wuycheck 1971).

The bioenergetics model was used to calculate GRP for smallmouth bass at each month for each time period. Calculating GRP allows assessment of the effects of water temperature on smallmouth bass growth with all other factors being held constant (e.g., Coulter et al. 2014). We conducted ten GRP models for each month, altering the proportion of maximum consumption (p value) from 0.1 to 1.0 at 0.1 increments and outputting growth in grams of growth per gram of fish per day ($g*g^{-1}*d^{-1}$). This range of consumption values is much wider than a fish likely experiences naturally, but we chose to model this wide range in order to examine effects of climate change even at unrealistically high consumption levels. This approach models all potential scenarios, from very low prey availability to assuming that prey availability will increase to compensate for increasing smallmouth bass consumption. This was repeated for each stream and for each time period (present, mid-century, and end of century). Next, mean growth rate potential for each month in each stream was calculated and a seasonal change in GRP from present to mid-century or end of century for each stream calculated (winter: January-March; spring: April-June; summer: July-September; fall: October-December). Changes in growth rate potential were compared between stream types using paired t-tests for each season at both time periods. All data analyses were conducted in program R.

Results

Air and water temperatures were significantly linearly related at all sites with all R^2 values greater than 0.78 (Table 1; Fig. 2). Groundwater streams typically showed less variation in temperature over the course of the year than runoff streams (Fig. 3). Climate simulations indicated that across our sites, future yearly mean air temperatures will increase by an average of 2.5°C by mid-century and increase by an average of 5.8°C by end of century. Future predicted water temperatures corresponded with predicted future air temperatures (Fig. 3).

Growth rate potential models indicated a general increase in GRP for smallmouth bass during most winter, early spring, and fall months and a general decrease in GRP during late spring and summer months relative to present water temperatures (Fig. 4). Runoff streams typically showed an increase in GRP during winter, spring, and fall months (e.g., 0.001 g/g/day increase in March GRP by mid-century; 0.003 g/g/day increase in March GRP by end of century), but a decrease in GRP during summer months (e.g., 0.001 g/g/day decrease in August GRP by mid-century, 0.006 g/g/day decrease in August GRP by end of century). Groundwater streams showed similar trends, but at a lower magnitude (e.g., 0.001 g/g/day and 0.003 g/g/day increase in March GRP for mid and end of century respectively; 0.001 g/g/day and 0.003 g/g/day decrease in August GRP for mid and end of century respectively).

In general, runoff streams demonstrated more extreme changes in temperature leading to larger changes in seasonal growth rate potential (Fig. 2, Fig. 5). Runoff streams had significantly more positive changes in growth rate potential than groundwater streams in both mid-century and end of century simulations during fall months (mid-century $t = -3.54$, $p = 0.007$; end of century $t = -3.18$, $p = 0.014$; Fig. 6). Groundwater streams had a more positive change in GRP than runoff streams in end of century simulations during spring months ($t = 2.80$, $p = 0.016$; Fig. 6). During late spring months, runoff streams were experiencing a decline in GRP leading to a lower change in GRP from present conditions than seen in groundwater streams (Fig. 5). Runoff streams had a significantly more negative change in growth rate potential than groundwater streams in end of century simulations during summer months ($t = 2.99$, $p = 0.012$; Fig. 6).

Discussion

Our models predict that an increase in stream warming across the Ozark-Ouachita Interior Highlands due to climate change will lead to an increase in GRP for smallmouth bass during winter, early spring, and fall months. However, late spring and summer months warmed past optimal temperature for smallmouth bass growth, resulting in a reduction in GRP for smallmouth bass in most of the modeled streams. Though the population level effects of reduced summer growth on smallmouth bass are unknown, it is possible that reduced GRP during these very warm months could lead to largemouth bass and spotted bass (*Micropterus punctulatus*) having a competitive advantage over smallmouth bass due to higher thermal optima (Zweifel et al. 1999), potentially leading to local declines or extirpation (Sowa & Rabeni 1995).

Smallmouth bass GRP was altered significantly differently between groundwater and runoff streams in multiple seasons. Previous work has indicated that spring-fed streams could have higher smallmouth bass growth relative to warmer, non-spring-fed streams (Whitledge et al. 2006). In addition, empirical work found that spring-fed streams have higher abundances of juvenile smallmouth bass, i.e., better reproduction (Brewer 2013) and lotic smallmouth bass abundance in Missouri is positively associated with higher spring-flow volumes (Brewer et al. 2006). Groundwater input may also provide thermal resistance to streams in Michigan, promoting the conservation of salmonids susceptible to the effects of climate change (Carlson et al. 2015). Our models predict that smallmouth bass in groundwater streams will not decline in growth rate potential during summer months to the extent of runoff streams, indicating the importance of these habitats for smallmouth bass populations during future temperature regimes.

Smallmouth bass have an upper mean weekly temperature threshold of 27°C for sustained positive growth and viable populations (Whitledge et al. 2006). Above this temperature, one would expect reduced annual growth, condition and fecundity (Bagenal 1967). Under present climate conditions, no streams that we modeled have a mean monthly temperature greater than 27°C at any point. By mid-century, this threshold is expected to be surpassed by one groundwater stream (Jack's Fork) for at least one month of the year, and in six runoff streams for at least one month of the year. By end of century this increases to four groundwater streams, and all seven runoff streams exceeding this threshold for at least one month out of the year. Similarly, Bouska et al. (2015) identified a threshold upper mean annual maximum air temperature of 31°C where smallmouth bass occurrence was not associated with streams across the central United States that experienced air temperatures exceeding this level. By the end of century, air temperatures associated with all of our modeled streams are predicted to exceed this level, but water temperatures are not likely to reach lethal limits for smallmouth bass (37°C; Wrenn 1980).

It is possible that adult smallmouth bass could behaviorally adapt to changing water temperatures. Adult smallmouth bass can migrate in order to regulate body temperature during winter months in Ozark streams with groundwater inputs (Peterson & Rabeni 1996; Westhoff et al. 2016). Therefore, it is plausible that smallmouth bass could regulate body temperature during summer months by utilizing spatial variations in thermal habitat, similar to salmonids (e.g., rainbow trout; Ebersole et al. 2001). Many streams in this region are thermally heterogeneous with cooler water patches due to stream stratification (Matthews 1998) and groundwater inputs

(Westhoff and Paukert 2014). Groundwater inputs into streams can range from large springs (e.g., Alley Spring on the Jack's Fork river; discharge = 2.7 m^3*s^{-1}; Mugel et al. 2009) with long downstream influence (Westhoff & Paukert 2014), to small seepages associated with channel curvature with localized influence (Dugdale et al. 2015). Smallmouth bass could migrate (Westhoff et al. 2016) or use other behavioral adaptations to utilize these temperature refuges. However, these refuges may be lacking in many runoff dominated streams and typical summer drought conditions lead to isolated pools in many runoff streams in this region (Magoulick 2000; Homan et al. 2005). This drying would prevent migrations of smallmouth bass in many runoff streams during summer months (Hafs et al. 2010). More data are needed on groundwater inputs into many of these systems to better understand available thermal refuges. The streams that we modeled encompass the range of several subspecies of smallmouth bass (Interior Highland intergrade and Neosho smallmouth bass (*Micropterus dolomieu velox*); Brewer and Orth 2015). We do not attempt to account for differences in bioenergetics parameters for these subspecies as no data exist; however, many of the parameters that we use were developed in the Ozarks of Missouri (Whitledge et al. 2003). Different subspecies could have different thermal tolerances affecting how fish adapt and respond to climate change.

There are several limitations to our study. For example, our water temperature predictions are relatively simplistic. Linear air and water temperature relationships are commonly used to examine the predicted effects of climate change on future stream water temperatures (e.g., Peterson & Kwak 1999; Almodóvar et al. 2012; Pease & Paukert 2014; Carlson et al. 2015). Predictive relationships between air and water temperatures generally improve at longer time scales (Morrill et al. 2005) and at the monthly scale are often strongly related (Erickson & Stefan 2000). However, these relationships are not as strong at temperature extremes and correlations tend to plateau at high temperatures (Erickson & Stefan 2000). We did not observe any leveling of stream temperatures at high air temperatures (Fig. 2) and our regressions were all significant and well fit. Although there may be a risk of over-predicting stream temperatures at the very warmest air temperatures, we believe our water temperature predictions were adequate for our modeling efforts because of our coarse time-scale and our strong regressions that we created specifically for each stream. Further, none of our streams were headwater streams (all either third or fourth order) which reduces variability associated with small streams. Linear relationships between air and water temperatures can strongly predict both groundwater dominated and runoff dominated streams, though groundwater streams typically have lower regression slopes (Erickson & Stefan 2000). Similar to our results, Whitledge et al. (2006) found strong predictive relationships between air and water temperature in both spring-fed and non-spring-fed streams in the Ozark Highlands of Missouri.

Another limitation to our study is that our temperature data are based solely on a single gage location for a river. In some cases this gage could be located very close to a spring and could be heavily influenced by groundwater (Westhoff & Paukert 2014). All of our streams have groundwater input to some extent, and the location of these inputs could have affected our temperature predictions. However, since we include at least six streams from each stream type, we assume that not all are affected in such a way. It is also possible that there may be thermal refuges present in both stream types that our models do not simulate. We model average stream temperatures and do not attempt to simulate the heterogeneous thermal environment that these streams likely contain. Another limitation is the limited amount of water temperature data that we have for each site. For example, temperature predictions from Tavern Creek are based on only one year of water temperature data. However, all air and water temperature linear regressions were highly significant and a good fit so we chose to include all sites to bolster our sample size.

Previous work has indicated some ways to mitigate the effects of increasing temperatures due to climate change. Stressors for smallmouth bass include destruction of riparian habitat leading to decreased shade and increased water temperatures (Whitledge et al. 2006), gravel mining (Brown et al. 1998), and other anthropogenic land use alterations (Allan 2004). Increasing riparian shading through restoration efforts can decrease the daily temperature fluctuations in streams, however, this is most pronounced in low order (narrow width) streams (Whitledge et al. 2006). Mitigation efforts can also focus on minimizing habitat degradation leading to the formation of pools and siltation of substrates (Waters 1995). Siltation and increased pool area can cause a reduction in preferred smallmouth bass prey and potentially increase risk of being outcompeted by largemouth bass (Sowa & Rabeni 1995). Protecting thermal habitat is of even higher importance as several species of native Ozark crayfish have similar optimal growth temperatures to smallmouth bass (22°C; Whitledge & Rabeni 2002). In general, groundwater streams are predicted to experience a much smaller reduction of GRP during summer months and could provide a thermal refuge for smallmouth bass and other species not adapted to warm temperatures. However, seasonal drying and drought conditions could prevent access to these refuges (Magoulick and Kobza 2003). Regulating flow levels and water withdrawal to preserve a minimum flow when possible could also facilitate access of smallmouth bass to potential thermal habitat from groundwater inputs. Excessive water withdrawals could lead to higher summer temperatures in groundwater streams, diminishing their refuge qualities for smallmouth bass.

In conclusion, we found that smallmouth bass will likely experience an increase in growth rate potential during cool months, but a decrease in growth rate potential during late spring and summer months over the course of the 21st century. We found that flow regime was a useful predictor of which streams may have the strongest temperature change, and in particular we suggest that monitoring and conservation efforts should be focused on runoff flow regimes as smallmouth bass in these streams will be subject to a greater change in temperature over the coming century. More work is needed to explore how these growth changes could affect smallmouth bass at the population level, but it is possible that elevated summer temperatures will leave them more at risk of being outcompeted by other *Micropterus* species, especially in runoff streams.

Acknowledgements

We thank the National Science Foundation for supporting B.K. through a Research Experience for Undergraduates fellowship. We also thank C. Paukert, J. Westhoff, and R. Fournier for providing comments that improved this manuscript. Two anonymous reviewers also provided helpful suggestions. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Alder, J.R., & Hostetler, S.W. 2013. USGS National Climate Change Viewer. US Geological Survey http://www.usgs.gov/climate_landuse/clu_rd/nccv.asp.

Allan, J.D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Evolution, Ecology, and Systematics 35: 257-284.

Almodóvar, A., Nicola, G.C., Ayllón, D., & Elvira, B. 2012. Global warming threatens the persistence of Mediterranean brown trout. Global Change Biology 18: 1549-1560.

Bagenal, T.B. 1967. A short review of fish fecundity. In: Gerking S.D. ed. The biological basis of freshwater fish production. Wiley and Sons, Inc., New York, NY, pp. 89-111

Bouska, K.L., Whitledge, G.W., & Lant, C. 2015. Development and evaluation of species distribution models for fourteen native central U.S. fish species. Hydrobiologia 747: 159-176.

Brewer, S.K. 2013. Groundwater influences on the distribution and abundance of riverine smallmouth bass, *Micropterus dolomieu*, in pasture landscapes of the Midwestern USA. River Research and Applications 29: 269-278.

Brewer, S.K., & Orth, D.J. 2015. Smallmouth bass *Micropterus dolomieu* Lacepéde, 1802. In: Tringali, M.D., Long, J.M., Birdsong, T.W. & Allen, M.S. eds. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, MD, pp. 9-26.

Brewer, S.K., Rabeni, C.F., Sowa, S.P., & Annis. G. 2007. Natural landscape and stream segment attributes influencing the distribution and relative abundance of riverine smallmouth bass in Missouri. North American Journal of Fisheries Management 27: 326-341.

Brown, A.B., Lyttle, M.M., & Brown, K.B. 1998. Impacts of gravel mining on gravel bed streams. Transactions of the American Fisheries Society 127: 979-994.

Carlson, A.K., Taylor, W.W., Schlee, K.M., Zorn, T.G., & Infante, D.M. 2015. Projected impacts of climate change on stream salmonids with implications for resilience-based management. Ecology of Freshwater Fish doi:10.1111/eff.12267.

Christie, G.C., & Regier, H.A. 1988. Measures of optimal thermal habitat and their relationship to yields for 4 commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45: 301-314.

Coulter, D.P., Sepúlveda, M.S., Troy, C.D., & Höök, T.O. 2014. Thermal habitat quality of aquatic organisms near power plant discharges: potential exacerbating effects of climate warming. Fisheries Management and Ecology 21: 196-210.

Cummins, K.W., & Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilung Internationale Vereinigung fuer Theorestische 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: 113-121.

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.

Dugdale, S.J., Bergeron, N.E., & St-Hilaire, A. 2015. Spatial distribution of thermal refuges analysed in relation to riverscape hydromorphology using airborne thermal infrared imagery. Remote Sensing of Environment 160: 43-55.

Ebersole, J.L., Liss, W.J., & Frissell, C.A. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10: 1-10.

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.

Erickson, T.R., & Stefan, H.G. 2000. Linear air/water temperature correlations for streams during open water periods. Journal of Hydrologic Engineering 5: 317-321.

Flebbe, P.A. 1994. A regional view of the margin: salmonid abundance and distribution in the southern Appalachian Mountains of North Carolina and Virginia. Transactions of the American Fisheries Society 123: 657-667.

Hafs, A.W., Gagen, C.J., & Whalen, J.K. 2010. Smallmouth bass summer habitat use, movement, and survival in response to low flow in the Illinois Bayou, Arkansas. North American Journal of Fisheries Management 30: 604-612.

Hansen, P., Johnson, T., Kitchell, J., & Schindler, D.E. 1997. Fish bioenergetics [version] 3.0. University of Wisconsin Sea Grant Institute, Madison, WI., USA.

Homan, J.M., Girondo, N.M., & Gagen, C.J. 2005. Quantification and prediction of stream dryness in the interior highlands. Journal of the Arkansas Academy of Sciences 59: 95-100.

Isaak, D.J., Luce, C.H., Rieman, B.E., Nagel, D.E., Peterson, E.E., Horan, D.L., Parkes, S., & Chandler, G.L. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20: 1350-1371.

Kamler, J.F., & Pope, K.L. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9: 1-11.

Kaushal, S.S., Likens, G.E., Jaworski, N.A., Pace, M.L., Sides, A.M., Seekell, D., Belt, K.T., Secor, D.H., & Wingate, R.L. 2010. Rising stream and river temperatures in the United States. Frontiers in Ecology and the Environment 8: 461-466.

Kolander, T.D., Willis, D.W., & Murphy, B.R. 1993. Proposed revision of the standard weight (Ws) equation for smallmouth bass. North American Journal of Fisheries Management 13: 398-400.

Leasure, D.R., Magoulick, D.D., & Longing, S.D. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32: 18-35.

Magnuson, J.J., Crowder, L.B., & Medvick, P.A. 1979. Temperature as an ecological resource. American Zoologist 19: 331-343.

Magoulick, D.D. 2000. Spatial and temporal variation in fish assemblages of drying stream pools: The role of abiotic and biotic factors. Aquatic Ecology 34: 29-41.

Magoulick, D.D & Kobza, R.M. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48: 1186-1198.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.

Meisner, J.D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 47: 1065-1070.

Mohseni, O., Stefan, H.G., & Eaton, J.G. Global warming and potential changes in fish habitat in U.S. streams. Climate Change 59: 389-409.

Morrill, J.C., Bales, R.C., & Conklin, M.H. 2005. Estimating stream temperature from air temperature: Implications for future water quality. Journal of Environmental Engineering 131: 139-146.

Mugel, D.M., Richards, J.M., & Schumacher, J.G. 2009. Geohydrologic investigations and landscape characteristics of areas contributing water to springs, the Current River, and Jacks Fork, Ozark National Scenic Riverways, Missouri. U.S. Geological Survey Scientific Investigations Report 2009-5138.

Naiman, R.J., & Turner, M.G. 2000. A future perspective on North America's freshwater ecosystems. Ecological Applications 10: 958-970.

Pease, A.A., & Paukert, C.P. 2014. Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecology of Freshwater Fish 23: 336-346.

Peterson, J.T., & Rabeni, C.F. 1996. Natural thermal refugia for temperate warmwater stream fishes. North American Journal of Fisheries Management 16: 738-746.

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.

Poff, N.L., Richter, B., Arthington, A.H., Bunn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse, C., Beldsoe, B.P., Freeman, M., Henriksen, J., Jacobson, R.B., Kenen, J., Merritt, D.M., O'Keefe, J., Olden, J., Rogers, K., Tharme, R.E., & Warner, A. 2010. The Ecological Limits of Hydrologic Alteration (ELOHA): A new framework for developing regional environmental flow standards. Freshwater Biology 55: 147-170.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Rabeni, C.F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. Canadian Journal of Fisheries and Aquatic Sciences 49: 1714-1721.

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., Minns, C.K., & Lestern, N.P. 2002. Climate change, freshwater fish, and fisheries: case studies from Ontario and their use in assessing potential impacts. In: McGinn, N.A. ed. American Fisheries Society Symposium 32: Fisheries in a changing climate, Phoenix, Arizona, USA, 20–21 August 2001. American Fisheries Society, Bethesda, Md, pp. 77–88.

Sowa, S., & Rabeni, C.F. 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.

Vander Zanden, M.J., Olden, J.D., Thorne, J.H., & Mandrak, N.E. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. Ecological Applications 14: 132-148.

Waters, T.F. 1995. Sediment in streams: sources, biological effects and control. American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, MD, USA.

Westhoff, J.T., & Paukert, C.P. 2014. Climate change simulations predict altered biotic response in a thermally heterogeneous stream system. PLoS. ONE 9(10): e111438.

Westhoff, J.T., Paukert, C., Ettinger-Dietzel, S., Dodd, H., & Siepker, M. 2016. Behavioural thermoregulation and bioenergetics of riverine smallmouth bass associated with ambient cold-period thermal refuge. Ecology of Freshwater Fish 25: 72-85.

Whisenant, K.A., & Maughan, E. 1989. Smallmouth bass and Ozark bass in Buffalo National River. Cooperative National Park Resources Studies Unit Technical Report No. 28.

Whitledge, G.W., & Rabeni, C.F. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. Canadian Journal of Fisheries and Aquatic Sciences 54: 2555-2563.

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.

Wrenn, W.B. 1980. Effects of elevated temperature on growth and survival of smallmouth bass. Transactions of the American Fisheries Society 109: 617-625.

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.

Table 1. Linear regression results relating air and water temperatures from each site. Air temperature data was collected from the NOAA National Climate and Data Center and water temperatures were collected from USGS water temperature gages. All regression models were significant at $p < 0.001$.

River	Intercept	Coefficient	R^2	Stream Type
Bear Creek	10.04	0.37	0.79	Groundwater
Beaty Creek	6.23	0.65	0.92	Groundwater
East Fork Black River	2.66	0.84	0.96	Groundwater
Huzzah Creek	5.56	0.97	0.98	Groundwater
Jacks Fork	4.16	0.88	0.97	Groundwater
Osage Creek	10.00	0.49	0.79	Groundwater
Spavinaw Creek	8.66	0.49	0.88	Groundwater
Sylamore Creek	4.03	0.76	0.97	Groundwater
Big Creek	3.22	0.82	0.98	Runoff
Big River	1.80	0.96	0.99	Runoff
Buffalo River	4.67	0.77	0.96	Runoff
Illinois Bayou	1.85	0.92	0.96	Runoff
South Fork Little Red	2.34	0.88	0.97	Runoff
Tavern Creek	2.41	0.95	0.99	Runoff

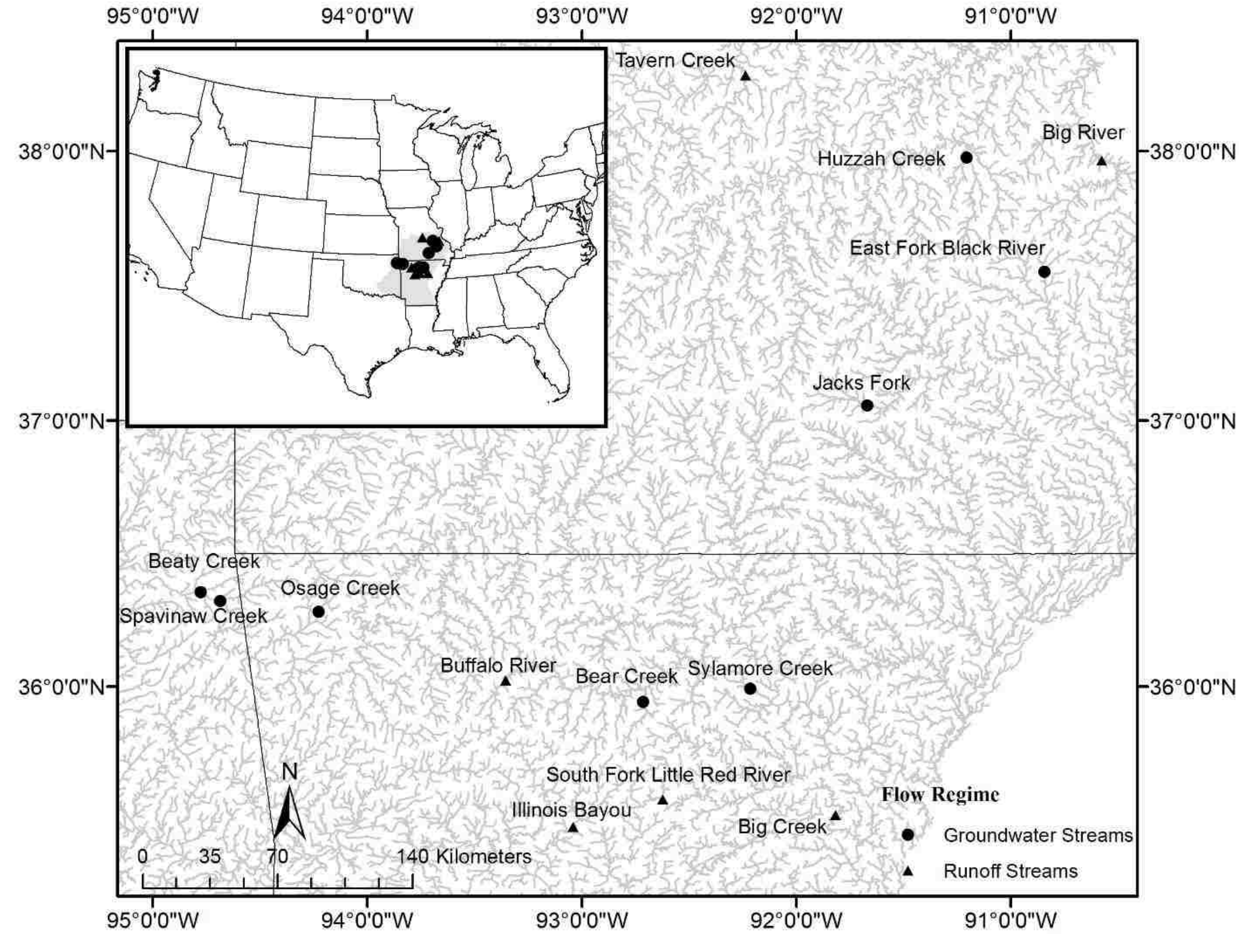


Fig. 1. Location of sites across the Ozark-Ouachita Interior Highlands of Arkansas, Oklahoma, and Missouri (shaded in grey). Each site corresponds to a USGS river gage which collects stream temperature data. Sites from runoff streams are designated with a triangle and sites from groundwater streams are designated with a circle.

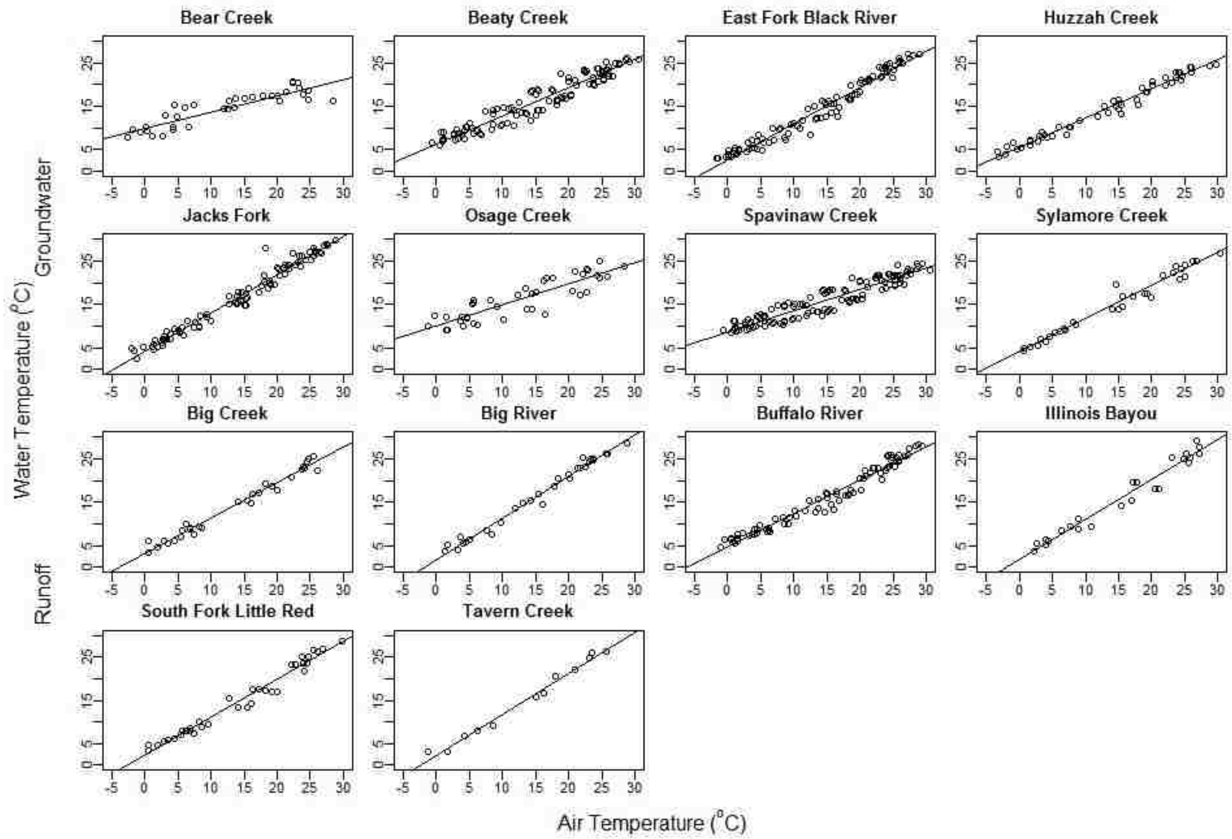


Fig. 2. Linear regression models for each site relating mean monthly air temperature (from NOAA National Climate Data Center) and mean monthly water temperature (from USGS river gage specific to each site). Model results for each site are shown in Table 1.

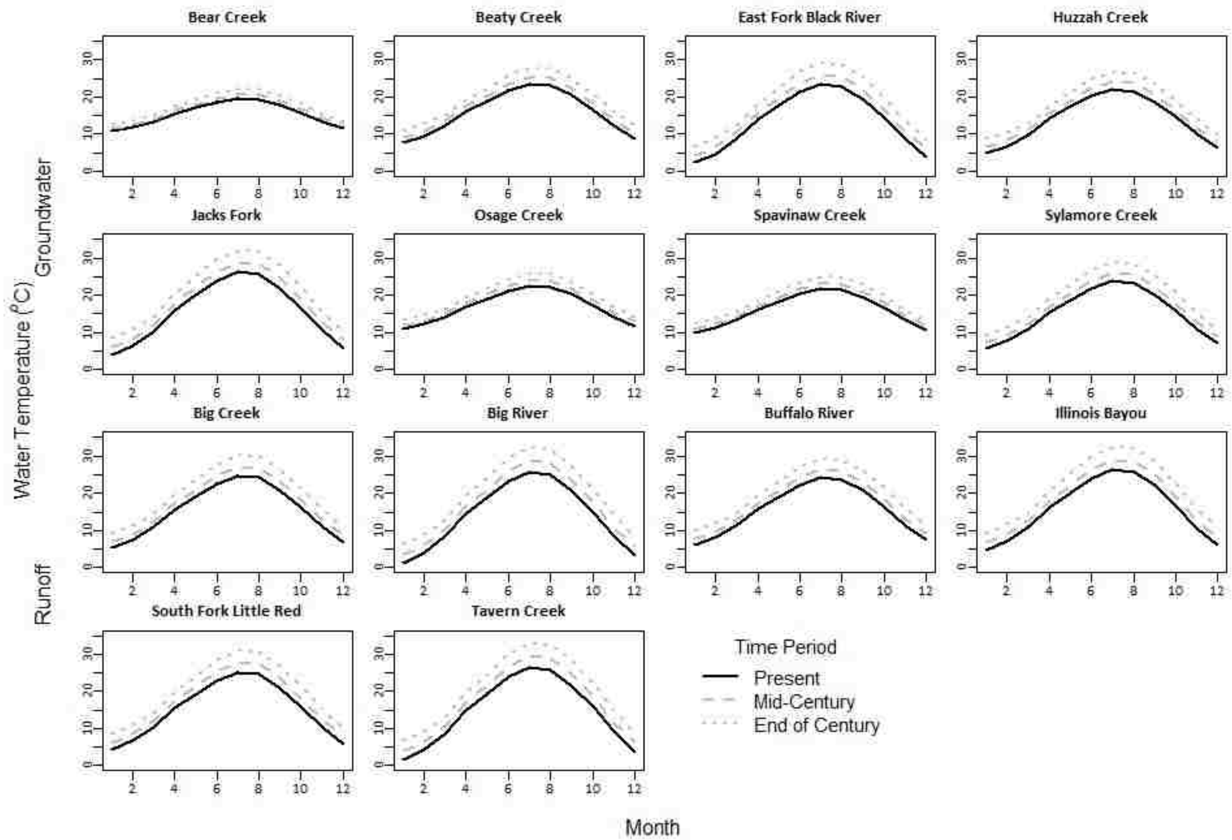


Fig. 3. Predicted historical (1950-2005; solid line), mid-century (2040-2049; long dash), and end of century (2090-2099; short dash) mean monthly stream temperatures calculated using linear regression predictive models for each stream and air temperature data from the USGS Climate Change Viewer ensemble average of all models. The top two rows are groundwater streams and the bottom two rows are runoff streams.

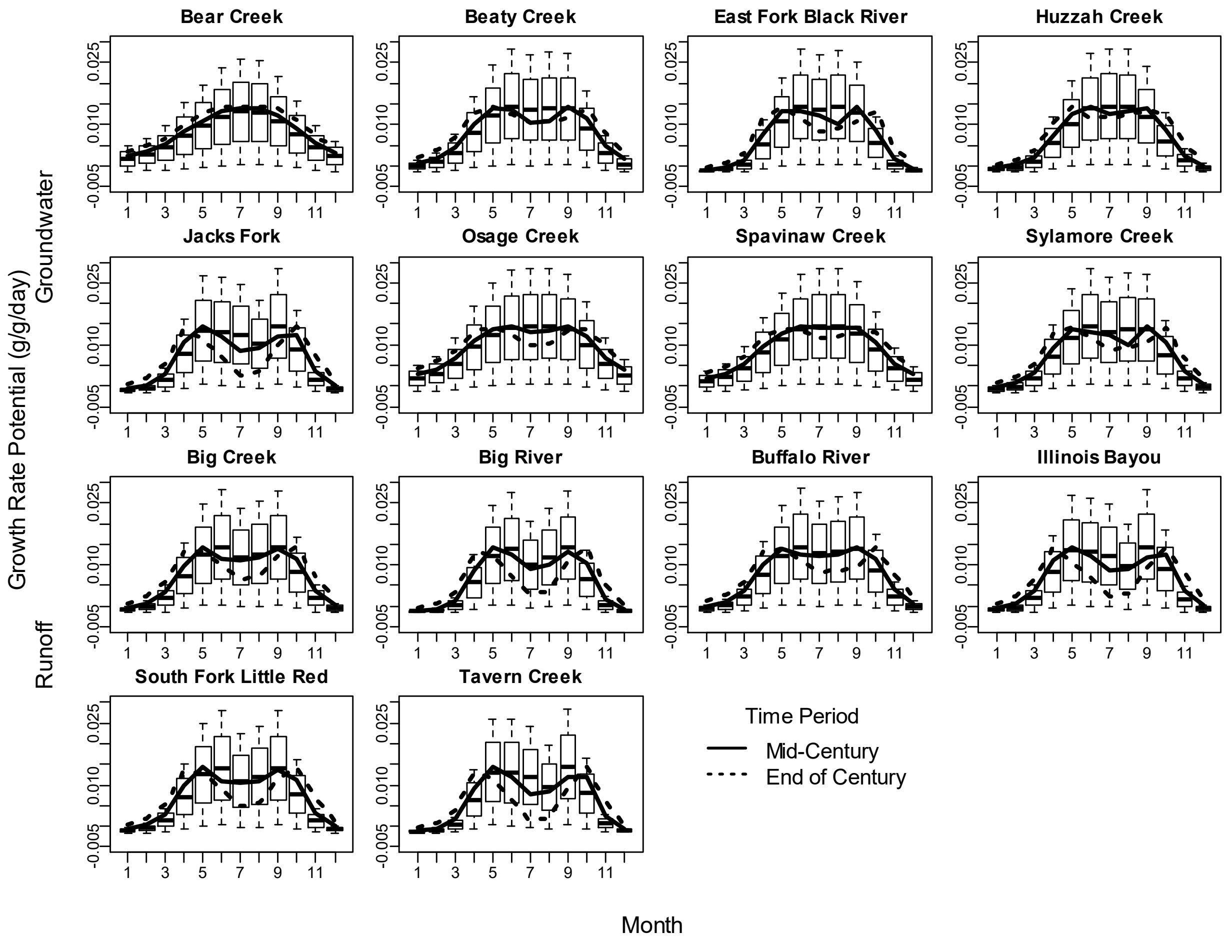


Fig. 4. Results of all growth rate potential models for adult smallmouth bass (p value range = 0.1-1) for present climate conditions (box plots), and mean of all growth rate potential models at mid-century (solid line) and end of century (dashed line). The top two rows are groundwater streams and the bottom two rows are runoff streams.

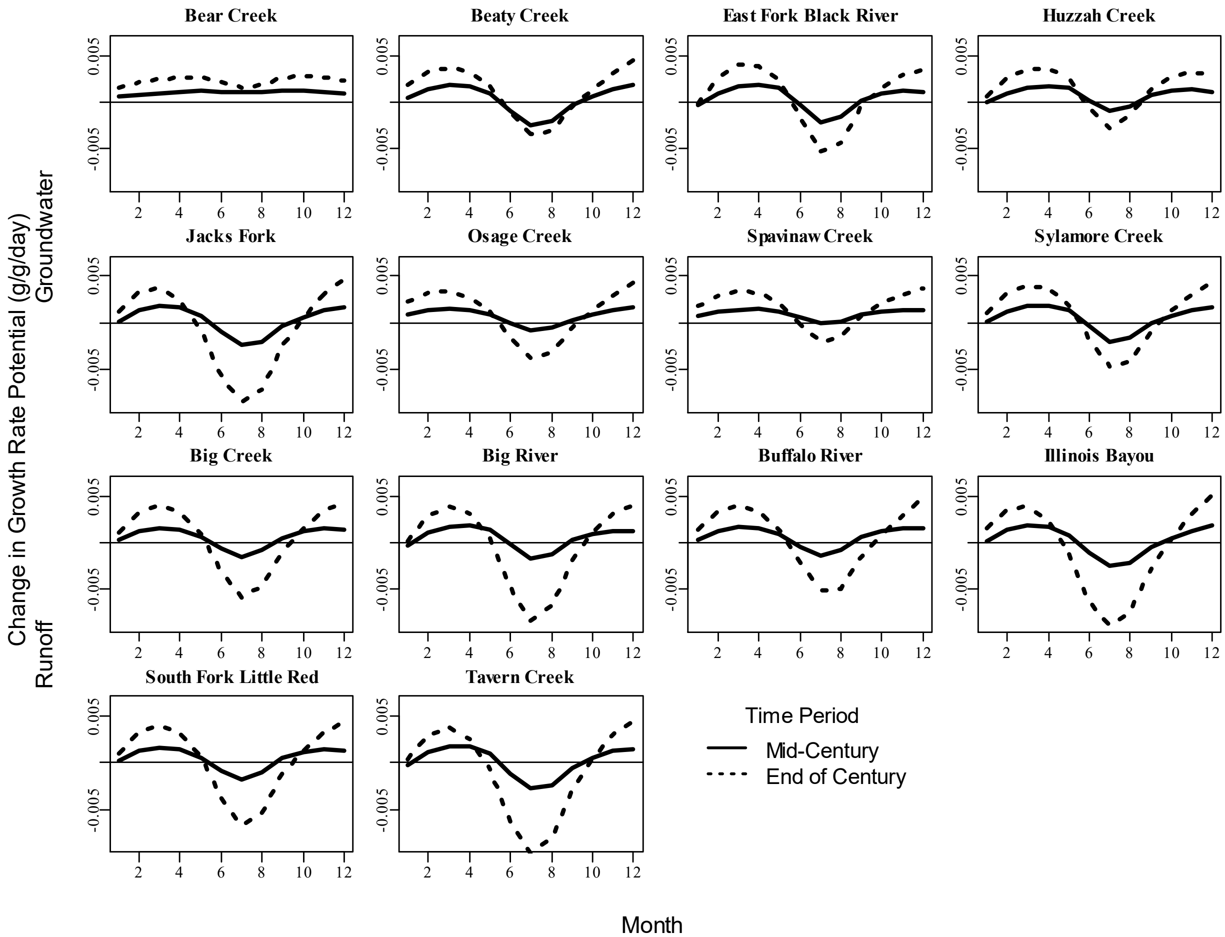


Fig. 5. Change in growth rate potential from present for each stream at both time periods. The solid horizontal line indicates no change from present. The top two rows are groundwater streams and the bottom two rows are runoff streams.

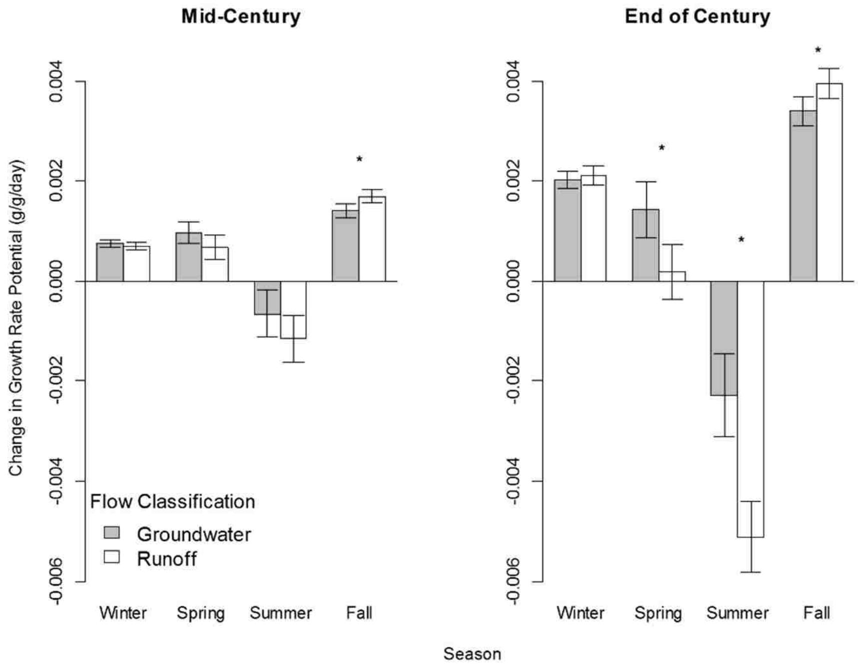


Fig. 6. Mean seasonal change in growth rate potential from present for both flow classifications at both time periods. Asterisks indicate a significant difference ($p < 0.05$) in the mean value of the change in growth rate potential between groundwater and runoff streams based on a paired t-test. Error bars show standard error.

Appendix 1. Location data, flow classification, and period of water temperature record for each USGS gage site used.

River	State	Latitude	Longitude	Flow Classification	Period of Record
Bear Creek	Arkansas	35.94	-92.71333	Groundwater	7/2012-5/2015
Beaty Creek	Oklahoma	36.35528	-94.776111	Groundwater	3/2005 - 10/2014
East Fork Black River	Missouri	37.55256	-90.842444	Groundwater	10/2007 - 5/2015
Huzzah Creek	Missouri	37.97472	-91.204444	Groundwater	12/2010 - 5/2015
Jacks Fork	Missouri	37.05611	-91.668056	Groundwater	1/2003 - 8/2005; 5/2010 –5/2015
Osage Creek	Arkansas	36.28139	-94.227778	Groundwater	11/2011 - 5/2015
Spavinaw Creek	Oklahoma	36.3225	-94.685	Groundwater	12/2004 - 4/2015
Sylamore Creek	Arkansas	35.99167	-92.213889	Groundwater	7/2012 - 5/2015
Big Creek	Arkansas	35.51	-91.817472	Runoff	12/2012 - 5/2015
Big River	Missouri	37.96553	-90.574417	Runoff	11/2011 - 5/2015
Buffalo River	Arkansas	36.0225	-93.354722	Runoff	5/2008 - 12/2014
Illinois Bayou	Arkansas	35.46639	-93.041111	Runoff	6/2013 - 5/2015
South Fork Little Red	Arkansas	35.56972	-92.621944	Runoff	7/2012 - 5/2015
Tavern Creek	Missouri	38.27778	-92.236111	Runoff	6/2014 - 5/2015

Chapter 2

Changes in body condition and diet of lotic Smallmouth Bass across two flow regimes during summer months at the southern extent of their native range

Christopher R. Middaugh[1*] and Daniel D. Magoulick[2]

[1]Arkansas Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, Fayetteville, Arkansas 72701

[2]U.S. Geological Survey, AR Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701

*Corresponding author: cmiddau@uark.edu

Abstract

The Ozark Plateau is located at the southern extent of native Smallmouth Bass *Micropterus dolomieu* range and water temperature and drought conditions during summer months may potentially affect growth of Smallmouth Bass in this region. Groundwater streams in the region do not warm to the same extent as runoff streams during summer months and could provide a thermal refuge habitat for Smallmouth Bass from high summer temperatures and drought conditions. Our study objective was to examine differences in body condition and diet of Smallmouth Bass through summer months between groundwater and runoff streams. We sampled Smallmouth Bass from eight streams across two flow regimes monthly from June-September 2014-2016 in the Ozark Plateau of Arkansas and Missouri. Relative weights were calculated and diet contents were examined for each fish. Linear mixed model analyses indicated that relative weights declined in both stream types in 2014 and 2015, but not in 2016. There was no significant difference in change in relative weights between runoff and groundwater streams in any year. No diet shifts over the course of the summer were noted in any year, and no diet differences were seen between stream types. Our results suggest that further work should investigate the refuge qualities of groundwater streams for Smallmouth Bass in this region as Smallmouth Bass from both stream types may currently respond similarly to summer conditions.

Flow regime, a measure of hydrologic classification, is a critical determinant of ecological processes within a stream (Olden et al. 2012). It can structure the fish assemblages present (Marchetti and Moyle 2001) and species abundances (Jowett et al. 2005). Flow regime could also affect the response of fish populations to climate change (Wenger et al. 2011). Because of the ecological importance of the flow regime, many streams across the United States have been classified according to their flow regimes. For example, in the Ozark-Ouachita Interior Highlands streams have been classified into three broad groups, groundwater, runoff, and intermittent (Leasure et al. 2016). Groundwater streams typically are more thermally regulated than runoff and intermittent streams with warmer temperatures in the winter and cooler temperatures during summer months (Whitledge et al. 2006; Middaugh et al. 2016). In the Ozark Plateau (hereafter Ozarks), many runoff and intermittent streams dry to a series of isolated pools during summer months (Homan et al. 2005; Dauwalter and Fisher 2008b; Hafs et al. 2010), whereas groundwater streams typically maintain a more stable baseflow. These differences in physical habitat conditions could lead to seasonal effects on fishes within the streams.

Water temperature and flow variability differ among flow regimes and both structure many aspects of lotic systems. Water temperature affects growth and survival of fishes (Magnuson et al. 1979; Christie and Regier 1988) as well as structuring distributions (e.g., Smallmouth Bass *Micropterus dolomieu*, Shuter et al. 1980). Similarly, flow related disturbance events, such as drought, can affect assemblage composition (Resh et al. 1988). Pool isolation caused by drought could potentially lead to increased competition (Zaret and Rand 1971) and increased susceptibility to predation (Harvey and Stewart 1991) for fishes as biotic and abiotic conditions can be severe in these pools (Magoulick and Kobza 2003). In a review, Walters

(2016) found that 65% of studies on lotic fish body condition response to low flow events showed a decline in body condition (Walters 2016).

Smallmouth Bass are an economically and ecologically important species and are locally abundant throughout the Ozarks (Robison and Buchanan 1988). However, this region is located at the southern extent of Smallmouth Bass native range and growth may be reduced in some systems during summer months as water temperatures exceed optimal levels (Zweifel et al. 1999; Middaugh et al. 2016). Climate change could further affect growth as air temperatures warm through the coming century, and many lotic systems in the United States are already warming above historical temperatures (Kaushal et al. 2010). In addition to increased water temperatures, climate change could affect drought conditions by prolonging the duration and increasing the severity of seasonal droughts (Girvetz et al. 2009). Changing temperatures and discharge patterns could favor competitor species such as Largemouth Bass *Micropterus salmoides* populations over Smallmouth Bass in this region (Sowa and Rabeni 1995), but groundwater streams could provide a thermal refuge to Smallmouth Bass if temperatures in runoff streams warm past habitable conditions. Similarly, streams with high groundwater influence will likely provide a thermal refuge for salmonids in Michigan streams (Carlson et al. 2017).

We utilize a measure of body condition, relative weight, to evaluate differences in Smallmouth Bass among streams. Relative weight is commonly used by fisheries biologists as it is relatively easy to measure and useful in describing population condition (Blackwell et al. 2000). Relative weights have been used to evaluate prey abundance, to make management decisions, and to compare condition across populations (Blackwell et al. 2000). Relative weights and other condition factors have been used to effectively measure seasonal and inter-annual change in body condition for a variety of fishes (e.g., Atlantic Cod *Gadus morhua*, Lambert and

Dutil 1997; Barbel *Barbus sclateri*, Encina and Granado-Lorencio 1997; Striped Bass *Morone saxatilis*, Smith 2012; Yellow Perch *Perca flavescens*, Staton et al. 2014). Lotic Smallmouth Bass relative weight can vary by season (Orth et al. 1983; Austen and Orth 1988; Dauwalter and Fisher 2008b). Two studies from Oklahoma found that relative weights were highest in the summer compared to other seasons (Austen and Orth 1988; Dauwalter and Fisher 2008b). In contrast, another Oklahoma based study found low relative weights during late summer and early fall (Orth et al. 1983). None of these studies incorporated multiple streams across flow regimes into investigations of Smallmouth Bass body condition.

In a review of North American inland fish climate change literature, Lynch et al. (2016) recommend investigating sources of resilience for fishes. Our study compares Smallmouth Bass body condition and diets across streams from two flow regimes in order to examine whether groundwater streams show greater refuge potential than runoff streams. We hypothesized 1) that Smallmouth Bass body condition would decline in runoff streams but not groundwater streams over the course of summer and 2) that Smallmouth Bass diet would shift in runoff streams but not groundwater streams over the course of summer. We expected to find differences between stream types because of differing hydrologic patterns over the course of summer and differing thermal conditions within both stream types. Groundwater streams have a more stable flow and typically a higher base flow than runoff streams (Leasure et al. 2016). In this region, many runoff streams have no flow during late summer and fall each year (Leasure et al. 2016). Low flow conditions could lead to sub-optimal conditions and higher competition in pool habitats affecting available prey density and type (Zaret and Rand 1971; Magoulick and Kobza 2003).Runoff streams typically warm to higher temperatures than groundwater streams, often exceeding optimal growth conditions for Smallmouth Bass whereas groundwater streams stay much closer to optimal temperatures for growth (22°C, Zweifel et al. 1999; Middaugh et al. 2016). We expected these flow and temperature differences between stream types to lead to differences in body condition over the course of the summer.

Methods

Study Site

During June-September 2014, 2015, and 2016 we collected Smallmouth Bass from streams in the Ozarks of northern Arkansas and southern Missouri (Figure 1) that had previously been classified into runoff and groundwater flow regimes (Leasure et al. 2016). These flow regime classifications were developed from 10 hydrologic variables and provide a classification of streams into three broad categories, groundwater, runoff, and intermittent with subcategories within each (Leasure et al. 2016).

We selected stream sites from each stream type based on preliminary sampling where we were able to effectively capture adequate numbers of adult Smallmouth Bass. Though Crooked Creek is classified as groundwater flashy by Leasure et al. (2016), many of the characteristics (summer drying, relatively large daily fluctuations in water temperature) are more similar to runoff streams and thus we grouped it into the runoff category. Two sites were on the same stream (Osage Creek-1 and Osage Creek-2) but were located ~13 km apart. Another site (Spring Creek) was located on a tributary of Osage Creek-1, and was located ~5.6 km away. All sites were either third or fourth Strahler stream order (Strahler 1957; third order: Buffalo River, Little Mulberry River, Osage River, and Spring Creek; fourth order: Crooked Creek, Big Sugar Creek, Osage Creek-1, Osage Creek-2 and Little Sugar Creek). Groundwater sites were located within two distinct hydrologic unit code (HUC) 8-digit watersheds and runoff sites were spread across four HUC-8 watersheds. We attempted to spread sample sites apart as much as possible, but were limited by the availability of regional groundwater sites where we were able to effectively capture Smallmouth Bass.

Fish Collection and Sample Processing

Our stream sites were too deep to effectively backpack electroshock or seine and too shallow for a motorized boat which restricted our sampling options. We determined that the most effective way to capture fish was through hook and line sampling. At each collection event, we used hook and line sampling to capture Smallmouth Bass using soft-plastic baits fished with spinning rods. We captured a small minority of fish on minnow imitation artificial baits or crayfish imitation patterns fished with a fly-rod. We collected Smallmouth Bass twice in June 2014, and monthly thereafter, typically collecting fish in the first two weeks of each month. Upon arriving at a site, we typically sampled upstream, fishing in all habitat units (i.e., pool, riffle, and run). We attempted to capture approximately ten fish on each sampling occasion and the stream distance sampled depended on the rate of capture of fish, but ranged from approximately 0.4 km to 2.4 km. Sites where samples were not taken in either August or September were excluded from all analyses. We excluded several samples from relative weight analyses due to few fish collected (< 6) and several samples were missed due to high water or other logistical constraints (Table 1). One site was sampled in 2014-2015 (Osage Creek-2) but not in 2016 because of access limitation, and so we added an additional site (Big Sugar Creek) in 2016 (Table 1).

After each fish was captured, we recorded total length (to the nearest mm) and wet weight (to the nearest 0.1 g). We used these measurements to calculate relative weight (Wr) for each fish based on the equation proposed by Kolander et al. (1993). The relationship is valid for fish >150 mm total length and we excluded any fish shorter than this length. After measuring weight and length, we collected the diet contents of each fish using gastric lavage (Kamler and Pope 2001). We performed gastric lavage by inserting a flexible plastic tube of varying diameter based on fish size through the mouth and into the stomach of the fish. We used a 1 L laboratory wash bottle with a long nozzle to flush water into the stomach. We caught diet contents in a fine mesh (1 mm) net as they exited the stomach. After washing the stomach, we checked the fish's stomach by inserting a finger through the mouth into the stomach to feel for additional contents which would subsequently be washed out with the wash bottle. In the event of difficulty washing a diet item out of the stomach (e.g., large crayfish), we used long forceps to remove the diet item. We chose to use this simplistic form of gastric lavage rather than a more complicated washing mechanism (e.g., Light 1983; Van Den Avyl 1980) due to our need for light-weight and non-bulky sampling equipment. After collecting the diet, fish were returned alive to the stream.

Diet contents were stored in 70% ethanol in the field and then examined later in the laboratory. We classified diet contents of each fish into the broad categories of crayfish, fish, invertebrate, and an "other" category because the heavily digested state of many samples prevented species level identification and our limited sample size prevented fine-scale analysis of the data. We measured wet weight to the nearest 0.001 gram of each category of diet item for each fish and noted the number of individual diet items (e.g., number of crayfish). Diet contents were then dried in a 70ºC oven for 48 hours and dry weight to the nearest 0.001 g was measured for each category of diet item for each fish. For each site, we calculated the mean proportional dry mass for each broad prey category for subsequent analyses.

Discharge and Temperature Data Collection

We collected data on historic discharge levels (1950-present) and air temperatures (1950-present) within our study region in order to compare our study time period to average conditions. We plotted discharge in the King's river (USGS gage number 07050500) as a representative runoff stream for the region because none of our runoff sites had historic gage data and this stream is in close proximity to our sample sites and is similar in terms of characteristics and magnitude. We used site Osage Creek-1 (USGS gage number 07195000) as a representative groundwater stream for the region in terms of discharge. We collected air temperature data from current and historic NOAA NCDC climate data for Drake Air Field (GHCND:USW00093993) in Fayetteville, Arkansas as this was relatively centrally located to all sample sites. We visually compared mean monthly historic high air temperatures and number of days with air temperature hotter than an upper thermal climate threshold previously identified as limiting the presence of Smallmouth Bass (> 31 ºC; Bouska et al. 2015) with air temperatures collected by the same weather station during the study period.

Data Analyses

We assessed change in relative weight over time using linear mixed effects models with the program lme4 (Bates et al. 2015) in program R (R Core Team 2015). This type of analysis has been previously used to examine change in relative weight over time (e.g., Dauwalter and Fisher 2008). We first created three mixed models (one for each year) to test for a change in relative weight by month. The response variable was relative weight and we used the variable month and the interaction between month and stream type as fixed effects. We included the month effect of site as a random effect with random slopes and intercepts for each site. The random slopes and intercepts for each site accounted for variation among sites and allowed each site to vary indepedent of other sites. We calculated p-values to test for a significant effect of month using likelihood ratio tests of the full model against reduced models. We next used the same mixed models as described above to test for an effect of stream type by calculating p-values of the full model against reduced models.

We created one additional mixed model to test for a significant difference in change in relative weight among years. Using all three years of combined data, the response variable was relative weight and we used month as a fixed effect. We included the month effect of site and the month effect of year as random effects with random slopes and intercepts used for each random effect to account for variation among sites and years. We calculated a p-value to test for a significant effect of year using likelihood ratio tests of the full model against a reduced model. Residual plots were examined for all models and no deviations from normality or homoscedasticity were noted.

Smallmouth Bass diets were analzed in two ways. First, we tested for differences in diets among months using a permutational multivariate analysis of variance (PERMANOVA) for each year. The response variables were the proportion of each prey group by dry weight, and the predictor variables were month, stream type, and the interaction of month and stream type. We included site as a stratifying variable to account for nestedness of sites within stream type. This causes randomizations in the PERMANOVA calculations to occur within each site and not across all sites (Oksanen et al. 2006). We used Bray-Curtis distance measures and 999 permutations for each test. We used the VEGAN package in R to conduct these analyses (Oksanen et al. 2017). We next examined whether the proportion of fish with empty stomach contents was related to month using logistic regression. Six logistic regression models were created, one for each stream type within each year. Chi square ANOVA tables were used to determine overall significance of final logistic regression models. All analyses were conducted in program R.

Results

We collected a total of 828 Smallmouth Bass over the course of three years across eight sites. We collected 218 Smallmouth Bass in 2014, 288 in 2015, and 322 in 2016 (Table 1). Mean total length of fish did not vary greatly among months or among sites (mean = 264.9 mm, range = 154 – 448 mm runoff streams; mean = 268.6, range = 152-403 mm groundwater streams). We found significant declines in Smallmouth Bass relative weight over the course of summer in 2014 and 2015, but not in 2016 (2014 $X^2 = 13.23$, $p < 0.001$; 2015 $X^2 = 27.15$, $p < 0.001$; 2016 $X^2 = 1.25$, $p = 0.26$). These analyses examine changes in all streams combined within each year. When differences between stream types were analyzed, no significant differences were found between runoff and groundwater streams in any year (2014 $X^2 = 0.29$, $p = 0.59$; 2015 $X^2 = 3.56$, $p = 0.06$; 2016 $X^2 = 0.57$, $p = 0.45$). This indicates that in 2014 and 2015 both groundwater and runoff streams declined in relative weight similarly, but in 2016 neither stream type declined significantly in relative weight (Figure 2). Two runoff streams, the Buffalo River and the Little Mulberry River, were consistent in showing declining relative weights over summer in all three years, though other sites did not decline in relative weight in 2016. Though we found a signifcant decline in relative weights from smallmouth bass collected in 2014 and 2015 but not in 2016, when data from all years were combined there were no significant differences in change in relative weight over the course of summer among years ($X^2 = 6.78$, $p = 0.08$).

We collected diets from 137 fish in 2014, 188 fish in 2015, and 207 fish in 2016 (Table 1). Logistic regression model results indicated no signficant effect of month on proportion of empty stomachs for all but one year and stream type (Chi square: 2014 groundwater $p = 0.63$; 2015 groundwater $p = 0.37$; 2015 runoff $p = 0.62$; 2016 groundwater $p = 0.41$; 2016 runoff $p = 0.40$). The only significant model was 2014 runoff (Chi square $p = 0.008$). The only significant month coeffecient within that model was September ($z = -2.85$, $p = 0.004$) and the proportion of empty stomachs was higher in this month than in previous months (Figure 3).

No significant effects of month on diet composition were found in any year (PERMANOVA: 2014 $F_4 = 0.58$, $p = 0.82$, 2015 $F_3 = 0.85$, $p = 0.49$; 2016 $F_3 = 1.04$, $p = 0.40$). Similarly, no significant effects of stream type were found in any year (PERMANOVA: 2014 $F_1 = 0.47$, $p = 0.80$; 2015 $F_1 = 2.90$, $p = 0.30$; 2016 $F_1 = 1.35$, $p = 0.38$). Smallmouth Bass consumed mostly crayfish and fish prey during the majority of months across both stream types (Figure 4). Crayfish prey was often the highest proportion of the diet by weight. Invertebrate and other prey were typically a small part of the diet, but in a few months invertebrate prey substantially contributed to the total proportion of fish diets (Figure 4).

About half of the months in the three years that we sampled fell within typical ranges for mean monthly discharge levels in both groundwater and runoff streams in this region (Figure 5). After comparing our sample period to historical averages, we found that the King's River had above average discharge levels in June and July 2015, but in August and September discharge fell to near normal levels. Similary, 2014 had high discharge in June, but more typical levels in later months. In contrast, 2016 had low- to average discharge levels in early summer, but then above average levels in August and September. Discharge at Osage Creek-1 was typically above average, but much less variable among years than in the runoff stream. Air temperatures were typically within expected values based on historical data (Figure 6). In general, 2016 was slighty warmer and had lower discharge levels in early summer compared to 2014 and 2015, but both 2014 and 2015 had lower discharge levels later in the summer.

Discussion

We found a significant decline in relative weight of Smallmouth Bass over the course of the summer for two out of three years and no differences in relative weight change over the course of the summer between groundwater and runoff streams in any year. Our results were suprising as we expected to see a decline in relative weight within runoff streams, but not in groundwater streams. Dauwalter and Fisher (2008b) examined relative weights in a runoff and groundwater stream in Oklahoma across a range of orders (order 3-5; upstream to downstream) and found differences in relative weights at the third order portion of the stream (with the groundwater stream having higher mean relative weights), but not in higher order (order 4-5) locations. Our streams were all either third or fourth order. Though we did not monitor water temperatures at each site, we assume that there were differences in water temperatures between groundwater and runoff streams as is commonly the case in this region (Whitledge et al. 2006; Middaugh et al. 2016). However, it is possible that high water levels during some months could prevent differences in temperatures between stream types from occuring (e.g., June and July 2015). Although within long-term average temperature and discharge levels, these three study years were all relatively mild compared to other recent years. We anticipate if a year of more severe drought or warmer temperatures were experienced, it could lead to differences in relative weight between flow regimes. Further research will be required to address this issue.

Our relative weight values were similar to those seen for lotic Smallmouth Bass from a range of locations (Oklahoma, Orth et al. 1983; Dauwalter and Fisher 2008b; Arkansas, Johnson et al. 2009; Iowa, Jansen et al. 2008). Orth et al. (1983) sampled Glover Creek, a runoff flashy creek in Oklahoma and found a decline in relative weight over the course of the summer during one year. Temperatures during that study were typically within optimal levels for Smallmouth Bass growth, so the authors postulated that the change may be due to food limitations. Dauwalter and Fisher (2008b) sampled a groundwater stream and a runoff stream in Oklahoma. They found that survival in both was lowest from summer to fall and they postulated that this could either be due to high temperatures or low water conditions, among other factors such as high angling pressure. They found lowest relative weights shortly before the spring spawn. Relative weight was higher during the summer sample and stayed at nearly the same level for the fall sample. Their results could be due to the coarse resolution that they used (seasonal rather than monthly sampling).

Our relative weight results could have a number of management implications. A decline in relative weight of Smallmouth Bass during summer months could reduce size-at-age and limit the number of trophy fish produced. These population changes could affect angler satisfaction, an important consideration in the region as many Ozark streams are popular fisheries for Smallmouth Bass. Type of water body can affect the relative weights of fish (Neuman et al. 2012) and in Ozark stream systems Smallmouth Bass populations typically have lower Wr values than lentic and more northern populations, consistent with our results (Orth et al. 1983; Dauwalter and Fisher 2008b, Johnson et al. 2009). Two of our streams (Buffalo River and Crooked Creek) are designated “Blue Ribbon Smallmouth Bass Streams” in Arkansas and are considered to be some of the best Smallmouth Bass fisheries in the state (Quinn et al. 2004). We were surprised to find that relative weights of Smallmouth Bass in these two sites were about the same as the other populations we sampled, and even lower than some groundwater streams in early summer samples (Figure 2).

Diet composition did not change over the course of the summer in any year of our study. Similarly, proportion of fish with empty stomachs also did not significantly change over the course of summer, except in runoff streams in 2014. We hypothesized that Smallmouth Bass from runoff streams would shift diets in response to low flow conditions as we expected high competition in refuge pool habitats (Magoulick and Kobza 2003) that would affect prey availability (Zaret and Rand 1971). However, we did not observe pool isolation lasting throughout the summer in any of our study years, likely preventing high levels of competition from occuring. Overall, diets were dominated by crayfish and fish prey, with a few months having higher contributions of invertebrate prey. Invertebrates seemed to be site dependent with several sites (Crooked Creek and Little Mulberry) having invertebrate prey items more commonly found in diets of fish. It is possible that our coarse resolution of data prevented us from observing fine scale shifts of prey use within diet categories. Our diet results were similar to other Smallmouth Bass diets collected in Arkansas. Johnson et al. (2009) found 39% of Smallmouth Bass had empty stomachs, and crayfish and fish were consumed in approximately equal numbers, followed distantly by insect prey. Similar to relative weights, diet patterns of Smallmouth Bass can vary seasonally. In an Oklahoma Ozark stream, Dauwalter and Fisher (2008a) found adult and sub-adult Smallmouth Bass diets varied seasonally, though they primarily consumed a mixture of fish and crayfish.

Capturing fish by angling could have introduced bias into our results. Vulnerability to angling is a heritable trait in some fishes (e.g., Largemouth Bass, Cooke et al. 2007; Philipp et al. 2009). Various factors can affect fish vulnerability to angling including fish size (Lennox et al.

2017), activity level (Alós et al. 2012), and metabolism (Cooke et al. 2007). However, factors affecting vulnerability can be species specific (Lennox et al. 2017) and no research has been conducted on this topic for Smallmouth Bass. In order to minimize bias in the fish captured, we typically used the same type of bait at each site and among time periods. Smallmouth Bass are an aggressive and opportunistic feeder and we often captured fish that had very full stomachs. Our diet results are similar to other studies of lotic Smallmouth Bass diets (Dauwalter and Fisher 2008a; Johnson et al. 2009), indicating that our choice of bait and method of sampling likely did not influence our diet results. Though a subset of the populations that we sampled may not have been vulnerable to capture by angling, we believe our sampling efforts provide a reasonably diverse sample over time.

Classifying our streams in a categorical way ignores the continuous nature of the differences in various flow characteristics in streams. One reason that our results may have been similar between stream types is that the streams selected may not have been as different as the categorical classification suggests. The base flow index, a measure of long-term baseflow relative to stream flow (Leasure et al. 2016; Figure 1), was lower in all of our runoff sites compared to groundwater sites, but there is a relatively wide range of values in base flow index among sites, indicating that our sites were varied in their relative classications. Interestingly, the two sites that were most consistent in declining relative weight all three summers (Buffalo River and Little Mulberry River) had the lowest base flow index value.

There is a chance that our repeated sampling could have affected our results, either because we recaptured individual fish multiple times each summer, or by causing increased mortality or other behavioral effects within a population. We did not mark individuals in any way and therefore do not know whether any fish were resampled. However, we were likely capturing a very small number of fish from the total population at each given time. We typically sampled a large section of stream, spreading the relatively few captures over a large area, reducing the likelehood of recaptures. It is also unlikely that we had an effect on the population as a whole as we observed very little capture mortality (e.g., from "gut hooking"; < 5%) and previous work with Largemouth Bass indicates that catch-and-release angling likely does not significantly affect growth (Pope and Wilde 2004).

Our results were surpising in that groundwater and runoff streams appeared to show very similar trends in body condition during summer months. Water temperatures in many runoff streams in the Ozarks currently exceed optimal levels for growth of Smallmouth Bass which could result in declines in growth and seasonal decreases in body weight (Middaugh et al. 2016). Under future climate conditions, Smallmouth Bass growth during summer months is predicted to strongly decline in runoff streams as temperatures increase, and decline only moderately in groundwater streams, providing a thermal refuge for Smallmouth Bass (Middaugh et al. 2016). However, our results indicate that groundwater streams may not provide as much of a growth refuge during summer months as predicted by Middaugh et al. (2016). Smallmouth Bass have been observed using large groundwater springs as a refuge from cold winter water temperatures (Westhoff et al. 2014) and could potentially use these refuge habitats during summer months. Smaller groundwater seepages could also provide smaller scale refuges within streams (Dauwalter and Fisher 2008b).

Our lack of differences between stream types could be due to the specific streams selected or other factors we do not take into account. For example, our groundwater streams were only located within two HUC-8 watersheds whereas runoff streams were spread throughout four HUC-8 watersheds, potentially increasing the variability among streams. The streams we selected all had robust populations of Smallmouth Bass which could have affected our results. We did not attempt to quantify the abundance of Smallmouth Bass in our streams and our results may not apply directly to streams with marginal habitat and limited Smallmouth Bass populations. We also did not take into account differences among years in seasonal conditions before summer months. This could affect relative weights of fish in initial June sampling each year. These differences could have led to the lack of a decline in relative weight in Smallmouth Bass from groundwater streams in 2016, however, initial relative weights of Smallmouth Bass in runoff stream samples were very consistant among years.

In conclusion, we found that Smallmouth Bass relative weights declined in both groundwater and runoff streams in two years of our study, and in all three years for select runoff sites. We did not observe any trends in diet composition over the course of summer months or any differences in diets of Smallmouth Bass between stream types. It is possible that years with higher temperatures and stronger seasonal drying, similar to conditions expected under climate change, could lead to differences in seasonal change in relative weight and diet between stream types. Future work could attempt to examine body condition and diet of Smallmouth Bass during strong drought years and focus on how isolated pool habitats in runoff streams could affect diet and body condition. Further work should also be conducted to determine refuge potential of groundwater streams in the region by comparing habitat conditions such as water temperature between runoff and groundwater streams during summer months.

Acknowledgements

We thank the numerous people who assisted with fieldwork, including T. Douglas, B. Kessinger, S. Koenigbauer, T. Pittman, R. Middaugh, J. Middaugh, and M. Middaugh. We would also like to thank M. Siepker, A. Hafs, and two anonymous reviewers for providing comments that improved this manuscript. This work was conducted under IACUC protocol # 14046. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Alós, J., M. Palmer, and R. Arlinghaus. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS ONE 7:e48030.

Austen, D. J., and D. J. Orth. 1988. Evaluation of a 305-mm minimum-length limit for smallmouth bass in the New Rive, Virginia and West Virginia. North American Journal of Fisheries Management 8:231-239.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (Wr) status and current use in fisheries assessment and management. Reviews in Fisheries Science 8:1-44.

Bouska, K.L., G.W. Whitledge, and C. Lant. 2015. Development and evaluation of species distribution models for fourteen native central U.S. fish species. Hydrobiologia 747:159-176.

Carlson, A. K., W. W. Taylor, K. M. Schlee, T. G. Zorn, and D. M. Infante. 2017. Projected impacts of climate change on stream salmonids with implications for resilience-based management. Ecology of Freshwater Fish 26:190-204.

Cooke, S. J., C. D. Suski, K. G. Ostrand, D. H. Wahl, and D. P. Phillip. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiological and Biochemical Zoology 80:480-490.

Dauwalter, D. C., and W. L. Fisher. 2008. Ontogenetic and seasonal diet shifts of Smallmouth Bass in an Ozark stream. Journal of Freshwater Ecology 23:113-121.

Dauwalter, D. C., and W. L. Fisher. 2008b. Spatial and temporal patterns in stream habitat and smallmouth bass populations in Eastern Oklahoma. Transactions of the American Fisheries Society 137:1072-1088.

Encina, L., and C. Granado-Lorencio. 1997. Seasonal changes in condition, nutrition, gonad maturation and energy content in barbell, Barbus sclateri, inhabiting a fluctuating river. Environmental Biology of Fishes 50:75-84.

Girvetz, E. H., C. Zganjar, G. T. Raber, E. P. Maurer, P. Kareiva, and J. J. Lawler. 2009. Applied climate-change analysis: the climate wizard tool. PLoS ONE 4:e8320.

Hafs, A. W., C. J. Gagen, and J. K. Whalen. 2010. Smallmouth bass summer habitat use, movement, and survival in response to low flow in the Illinois Bayou, Arkansas. North American Journal of Fisheries Management 30:604-612.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87:336-342.

Homan, J. M., N. M. Girondo, and C. J. Gagen. 2005. Quantification and prediction of stream dryness in the interior highlands. Journal of the Arkansas Academy of Sciences 59:95-100.

Jansen, A. C., M. C. Quist, and J. Kopaska. 2008. Assessment of Smallmouth Bass populations in Iowa interior rivers. Journal of the Iowa Academy of Science 11:17-23.

Johnson, R. L., A. D. Christian, S. D. Henry, and S. W. Barkley. 2009. Distribution, population characteristics, and physical habitat associations of black bass (*Micropterus*) in the lower Eleven Point River, Arkansas. Southeastern Naturalist 8:653-670.

Jowett, I. G., J. Richardson, and M. L. Bonnett. 2005. Relationship between flow regime and fish abundances in a gravel-bed river, New Zealand. Journal of Fish Biology 66:1419-1436.

Kamler, J. F., and K. L. Pope. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9:1-11.

Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. Frontiers in Ecology and the Environment 8:461-466.

Kolander, T. D., D. W. Willis, and B. R. Murphy. 1993. Proposed revision of the standard weight (Ws) equation for smallmouth bass. North American Journal of Fisheries Management 13:398-400.

Lambert, Y., and J. D. Dutil. 1997. Condition and energy reserves of Atlantic cod (Gadus morhua) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences 54:2388-2400.

Leasure, D. R., D. D. Magoulick, & S. D. Longing. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32:18-35.

Lennox, R. J., J. Alós, R. Arlinghaus, A. Horodysky, T. Klefoth, C. T. Monk, and S. J. Cooke. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish and Fisheries DOI10.1111/faf.12219.

Light, R. W., P. H. Adler, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81-85.

Magoulick, D. D, and R. M. Kobza. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186-1198.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11:530-539.

Middaugh, C. R., B. Kessinger, and D. D. Magoulick. 2016. Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent. Ecology of Freshwater Fish DOI: 10.1111/eff.12320.

Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637-676 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Olden, J. D., M. J. Kennard, and B. J. Pusey. 2012. A framework for hydrologic classification with a review of methodologies and applications in ecohydrology. Ecohydrology 5:503-518.

Orth, D. J., D. D. Oakey, and O. E. Maughan. 1983. Population characteristics of smallmouth bass in Glover Creek, Southeastern Oklahoma. Proceedings of the Oklahoma Academy of Science 63:37-41.

Oskansen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, and H. Wagner. 2017. Vegan: Community ecology package. R package version 2.4-3.

Pease, A.A., and C. P. Paukert. 2014. Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecology of Freshwater Fish 23:336-346.

Philipp, D. P., S. J. Cooke, J. E. Claussen, J. B. Koppelman, C. D. Suski, and D. P. Burkett. 2009. Selection for vulnerability to angling in largemouth bass. Transactions of the American Fisheries Society 138:189-199.

Pope, K. L., and G. R. Wilde. 2004. Effect of catch-and-release angling on growth of Largemouth Bass, Micropterus salmoides. Fisheries Management and Ecology 11:39-44.

Quinn, J., B. Wagner, and S. Filipek. 2004. Characteristics of fish populations in the rivers and streams of Arkansas. Stream Fisheries Program Report STP2004-01.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Rabeni, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. Canadian Journal of Fisheries and Aquatic Sciences 49:1714-1721.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.

Robison, H. W., and T. M. Buchanan. 1988. Fishes of Arkansas. The University of Arkansas Press, Fayetteville.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Smith, N. G. 2012. Seasonal condition of adult striped bass relative to thermal habitat and forage availability. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 66:69-74.

Sowa, S. P. and C. F. Rabeni. 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.

Staton, J. M., C. R. Roswell, D. G. Fielder, M. V. Thomas, S. A. Pothoven, and T. O. Höök. 2014. Condition and diet of yellow perch in Saginaw Bay, Lake Huron (1970-2011). Journal of Great Lakes Research 40:139-147.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913-920.

Van Den Avyle, M. J. 1980. Evaluation of a simple method for removing food items from live black bass. The Progressive Fish-Culturist 42:222-223.

Walters, A. W. 2016. The importance of context dependence for understanding the effects of low-flow events on fish. Freshwater Science 35:216-228.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Nevill, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences 108:14175-14180.

Westhoff, J. T., C. Paukert, S. Ettinger-Dietzel, H. Dodd, and M. Siepker. 2014. Behavioural thermoregulation and bioenergetics of riverine smallmouth bass associated with ambient cold-period thermal refuge. Ecology of Freshwater Fish 25:72-85.

Whitledge, G. W., C. F. Rabeni, G. Annis, and S. P. Sowa. 2006. Riparian shading and groundwater enhance growth potential for smallmouth bass in Ozark streams. Ecological Applications 16:1461-1473.

Willard, A., S. Pomeroy, M. Lescaze, E. Beck, C. J. Bobbi, and L. A. Barmuta. 2004. Programmatic quality assurance plan for phase II stream geomorphic of the Browns River watershed, Vermont Agency of Natural Resources.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

Zweifel, R. D., R. S. Hayward, and C. F. Rabeni. 1999. Bioenergetics insight into black bass distribution shifts in Ozark border region streams. North American Journal of Fisheries Management 19:192-197.

Table 1. Numbers of Smallmouth Bass > 150 mm captured at each sampling event. Numbers in parenthesis are number of fish with diet contents. Values noted with a * indicate samples not included in relative weight analyses because of < 6 fish collected or failure to sample that site in late summer (August or September). Sampling events noted with n/a indicate missed samples due to high water, site access restriction, or other logistical failure to sample the site during that period.

	2014	2015	2016										
	June	Mid-June	July	Aug.	Sept.	June	July	Aug.	Sept.	June	July	Aug.	Sept.
Buffalo River	9 (8)	10 (6)	14 (9)	9 (9)	14 (2)	11 (7)	12 (5)	11 (8)	10 (9)	11 (7)	10 (7)	11 (4)	12 (8)
Crooked Creek	10 (8)	8 (6)	10 (9)	12 (9)	11 (2)	11 (7)	12 (11)	10 (9)	10 (2)	12 (7)	8 (5)	n/a	12 (8)
Little Mulberry	n/a	11 (9)	11 (6)	n/a	13 (9)	10 (9)	12 (9)	11 (8)	10 (5)	13 (10)	13 (3)	12 (5)	12 (6)
Osage River	13(10)*	n/a	11(6)*	n/a	n/a	n/a	12 (8)	10 (5)	12 (9)	10 (4)	8 (4)	11 (10)	10 (6)
Big Sugar Creek	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	12 (8)	12 (7)	11 (8)	10 (5)
Osage Creek-1	n/a	n/a	13 (8)*	n/a	4 (3)*	12 (6)	12 (6)	11 (8)	11 (8)	10 (9)	12 (8)	10 (8)	13 (9)
Osage Creek-2	8 (4)*	8 (6)*	7 (5)*	n/a	n/a	15 (13)	n/a	n/a	10 (6)	n/a	n/a	n/a	n/a
Spring Creek	10 (6)	6 (6)	14 (10)	7 (4)	n/a	9 (6)	12 (7)	10 (6)	n/a	11 (9)	n/a	11 (8)	10 (7)
Little Sugar Creek	8 (5)	9 (4)	13 (7)	9 (6)	n/a	n/a	10 (4)	12 (7)	n/a	11 (6)	10 (7)	10 (7)	10 (7)

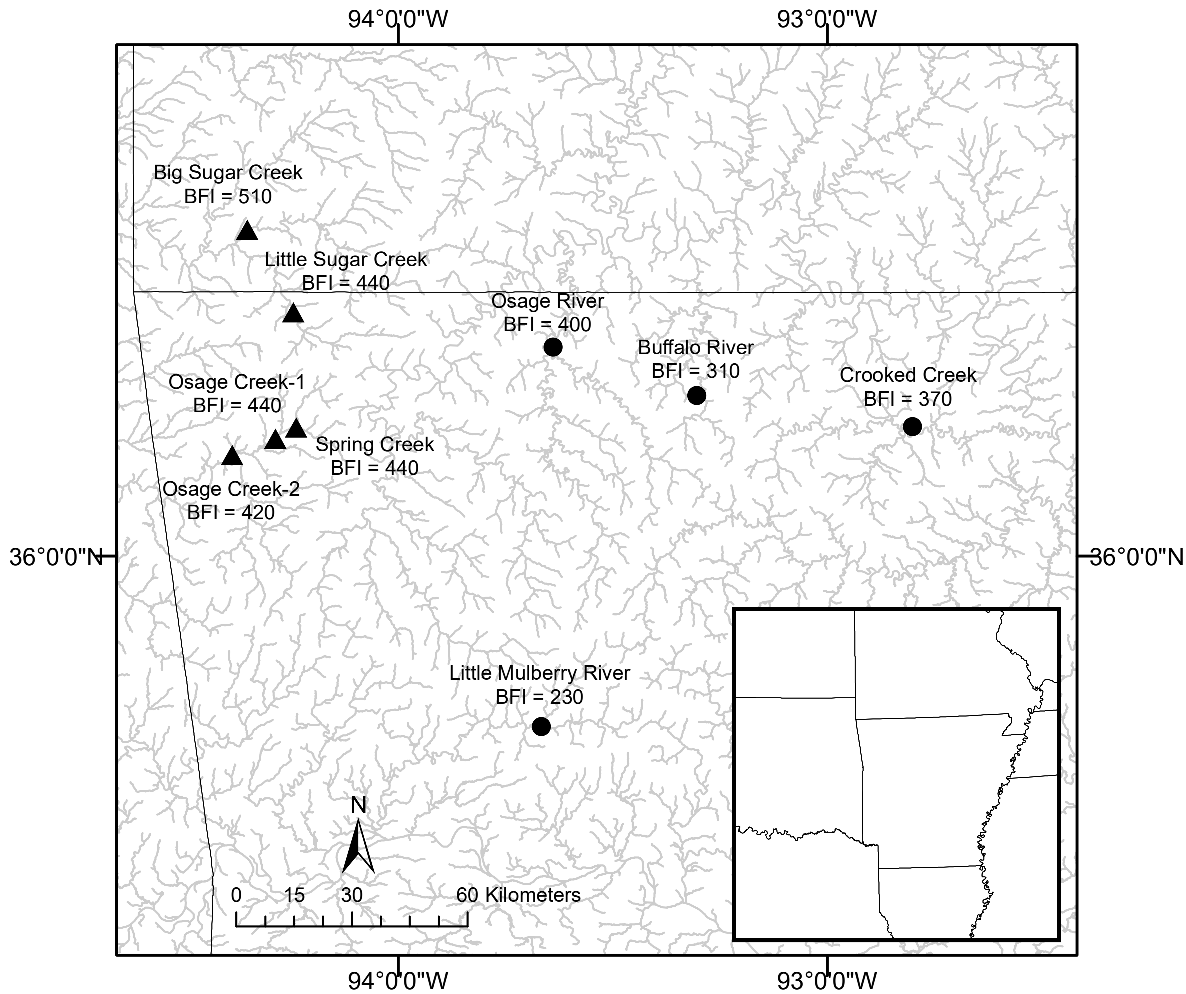
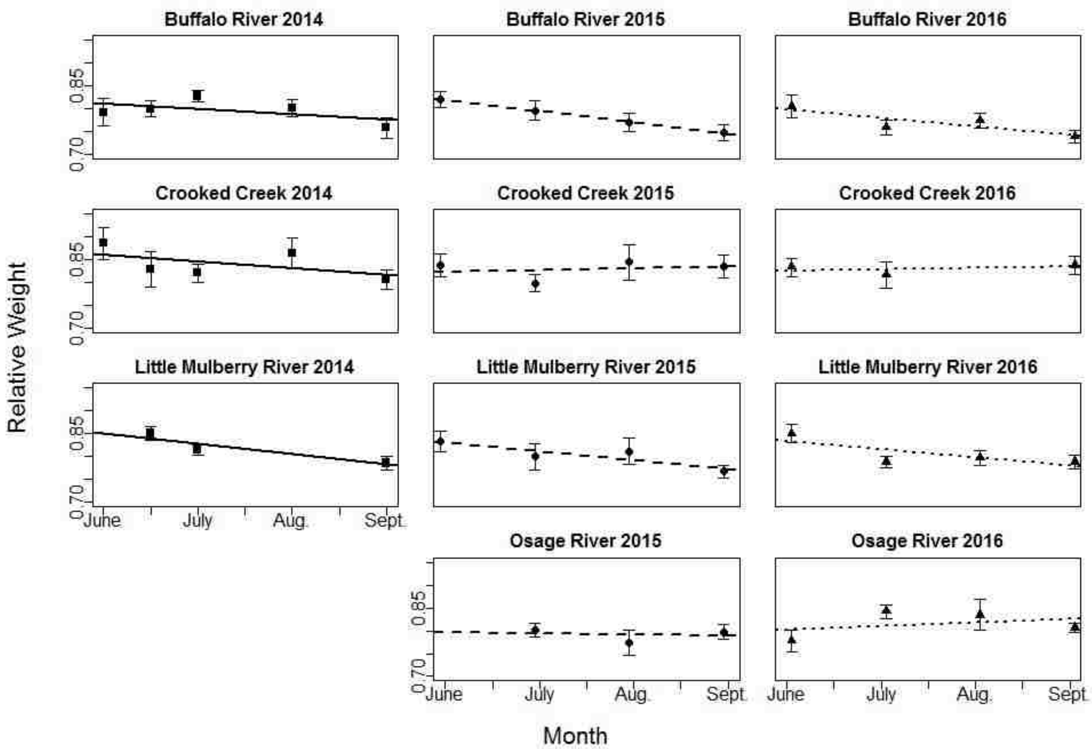


Figure 1. Map of study sites across the Ozarks region of Arkansas and Missouri. Triangles represent groundwater streams and circles represent runoff streams. Base flow index (BFI) values are show by stream names.

A)


Buffalo River 2014
Buffalo River 2015
Buffalo River 2016
Crooked Creek 2014
Crooked Creek 2015
Crooked Creek 2016
Little Mulberry River 2014
Little Mulberry River 2015
Little Mulberry River 2016
Osage River 2015
Osage River 2016
Relative Weight
0.70
0.85
June
July
Aug.
Sept.
Month

B)

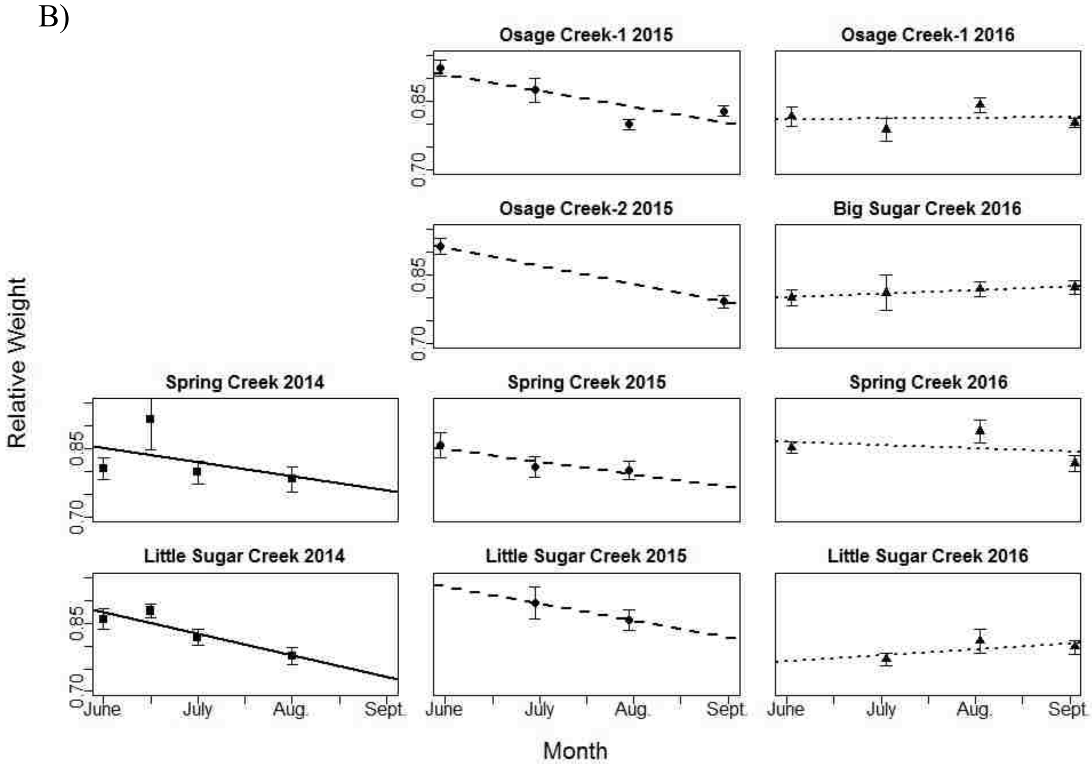

Osage Creek-1 2015
Osage Creek-1 2016
Osage Creek-2 2015
Big Sugar Creek 2016
Spring Creek 2014
Spring Creek 2015
Spring Creek 2016
Little Sugar Creek 2014
Little Sugar Creek 2015
Little Sugar Creek 2016
Relative Weight
0.70
0.85
June
July
Aug.
Sept.
Month

Figure 2. Change in mean monthly Smallmouth Bass relative weight over summer months for each study site in each year. Runoff streams are shown in A) and groundwater in B). Error bars show standard error.

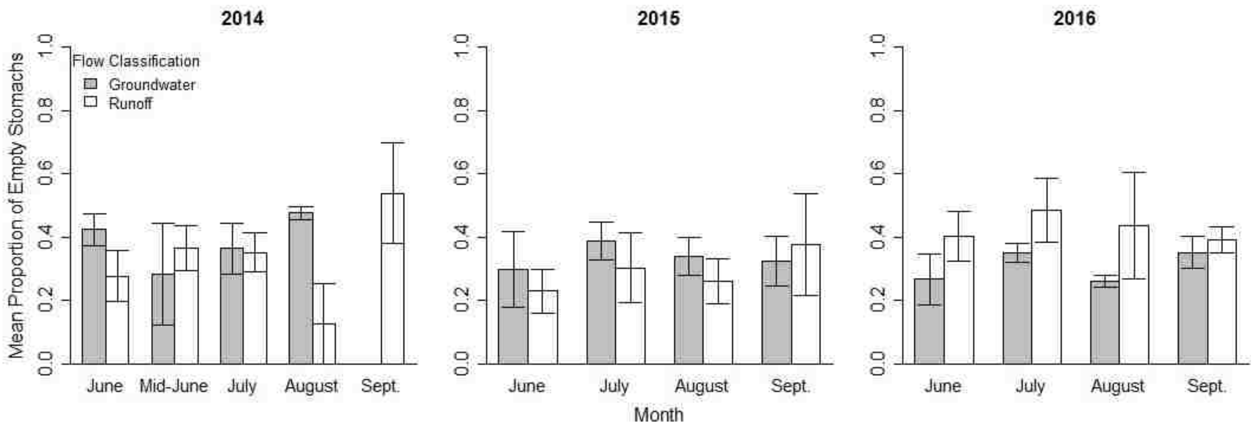


Figure 3. Proportion of collected Smallmouth Bass with no diet contents in both groundwater (dark bars) and runoff (white bars) sites in each study year. Error bars show standard error.

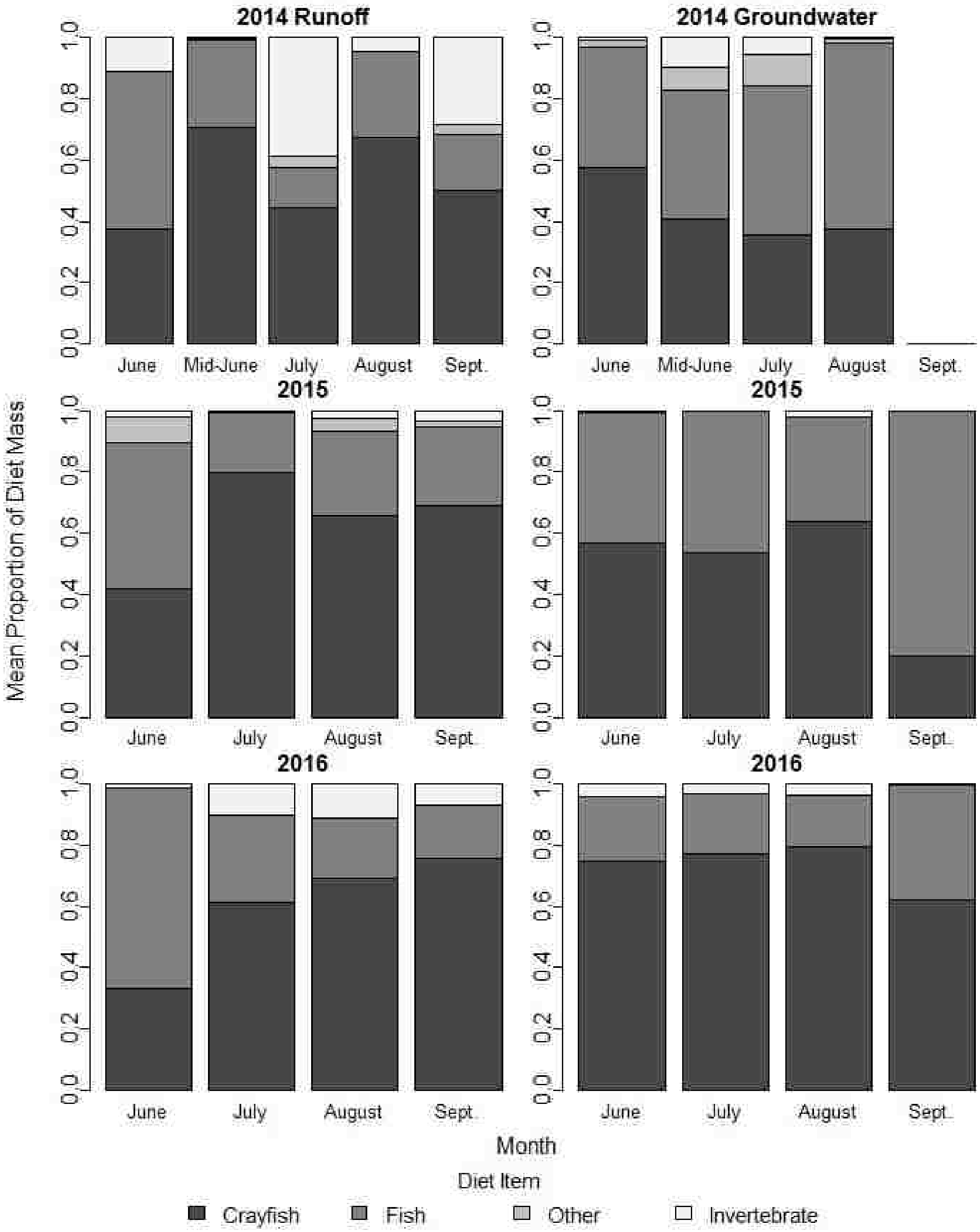


Figure 4. Monthly diet composition of Smallmouth Bass in runoff and groundwater streams each year. Diets are shown by prey type and are based on dry mass of prey. No significant trends were found for changes over the course of the summer or between stream types.

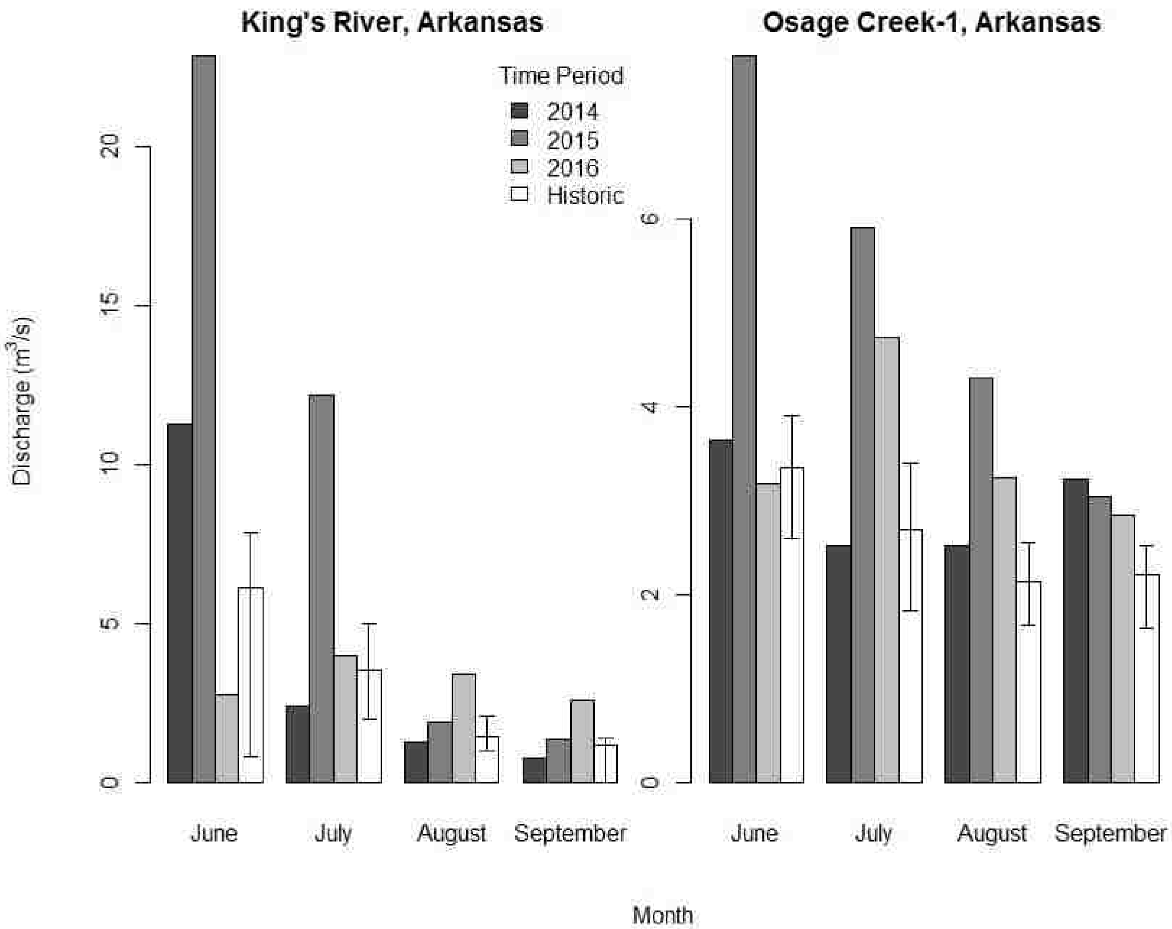


Figure 5. Observed and historical median monthly discharge values for a groundwater stream (Osage Creek-1, Arkansas; USGS gage number 07195000) and a runoff stream (King's River, Arkansas; USGS gage number 07050500) in the sample region. Historical values span from 1950-2016. Error bars show 95% confidence intervals of the median values calculated using a bootstrap procedure with 1,000 replicates.

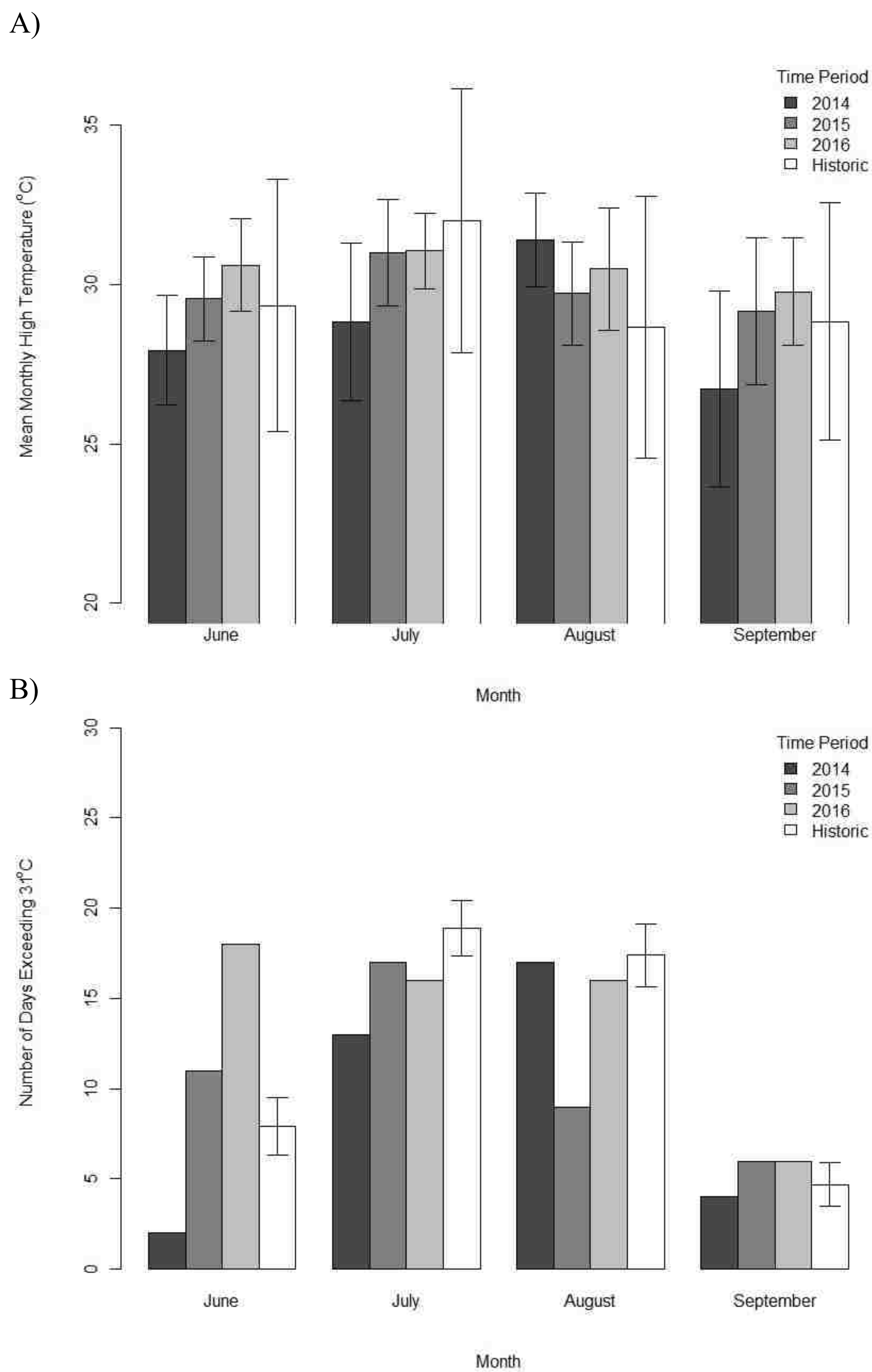


Figure 6. Observed and historical mean monthly high temperatures at Fayetteville, Arkansas at Drake Air Field (A) and observed and historical mean number of days exceeding 31 ºC during summer months (June-September; B). Historical values span from 1950-2016. Error bars show 95% confidence intervals.

UNIVERSITY OF ARKANSAS

Office of Research Compliance

MEMORANDUM

TO: Dr. Daniel Magoulick

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee

DATE: May 23, 2014

SUBJECT: IACUC APPROVAL
Expiration date: October 31, 2014

The Institutional Animal Care and Use Committee (IACUC) has APPROVED protocol 14046: "<u>Effect of Ozark Stream Pool Isolation on Smallmouth Bass Growth</u>". The scheduled start date is listed as May 27, 2014.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing(via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond October 31, 2014 you must submit a modification for extension. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

Administration Building 210 • 1 University of Arkansas • Fayetteville, AR 72701-1201 • 479-575-4572
[illegible]

UNIVERSITY OF ARKANSAS

Office of Research Compliance

MEMORANDUM

TO: Dr. Daniel Magoulick

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee (IACUC)

DATE: October 15, 2014

SUBJECT: IACUC APPROVAL
Expiration date: 10-31-16

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your modification (to extend study dates and add additional animals) to protocol 14046: <u>*'Effect of Ozark Stream Pool Isolation on Smallmouth Bass Growth'*</u>

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing(via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond October 31, 2016 you must submit a new protocol or protocol modification prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian

Administration Building 210 • 1 University of Arkansas • Fayetteville, AR [illegible]
Fax [illegible]
[illegible]

Chapter 3

Forecasting effects of angler harvest and climate change on smallmouth bass abundance at the southern edge of their range

Christopher R. Middaugh[1] and Daniel D. Magoulick[2]

[1]Arkansas Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, Fayetteville, Arkansas 72701

[2]U.S. Geological Survey, AR Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701

Abstract

Climate change will affect stream systems in numerous ways over the coming century. In particular, streams in the southern region of the United States will experience changes in temperature and flow regime. Previous work has indicated that these changes will likely affect fish distributions, but little work has been conducted examining population level effects of climate change on warmwater fish at the southern range extent. We model several potential climate change-related stressors and the resulting effects on smallmouth bass *Micropterus dolomieu* populations in the Buffalo National River, Arkansas. Smallmouth bass are a popular recreational fish in the region and angler harvest likely contributes substantially to annual mortality. We created a simulation model parameterized with data collected from the Buffalo National River to evaluate the relative importance of climate stressors and angler harvest on smallmouth bass populations. Our simulations suggest that increases in springtime temperature and reductions in river discharge during the spawning period could increase recruitment, resulting in increases in adult abundance (8% higher). However, when increased flooding and drought probabilities are considered, our model indicates the Buffalo River could experience large reductions in adult smallmouth bass abundance (≥50% decline) and increased probability of extinction compared to present levels. Simulations showed that harvest reduction could be a viable strategy to reduce the negative effects of climate change, but that even with complete closure of harvest, smallmouth bass population levels would still be well below present abundance (46% lower than present). Climate change is likely to affect smallmouth bass in complex ways. Our results indicate that smallmouth bass populations at the southern range extent could decline due to increased flooding and drought conditions, but changes in management

strategies and other efforts to reduce these effects could help mitigate population declines and reduce the probability of extinction.

Introduction

The anticipated effects of climate change on aquatic ecosystems in the central United States will be complex (Karl et al. 2009) and are likely to result in increased temperature, decreased dissolved oxygen, increased toxicity of pollutants, and changes in hydrologic regimes (Ficke et al. 2007). The southern region of the United States is projected to warm 3-4°C by the year 2050 (Alder & Hostetler 2013). Along with the temperature change is an expected change in precipitation, including more extreme events leading to higher stochasticity and potentially an increase in flooding frequency and severity (Novonty and Stefan 2007) even though average annual precipitation is projected to decrease slightly in parts of the southern region (Alder & Hostetler 2013). Precipitation patterns are likely to change seasonally and a decrease in precipitation is anticipated in the summer months (Karl et al. 2009), potentially leading to more severe and longer drought conditions (Strzepek et al. 2010).

Stream fishes may be particularly susceptible to the effects of climate change. For example, climate change could affect stream fishes through changes in stream discharge patterns such as increased flooding chances. Adult fish can become displaced and juveniles could be injured by flood events (Harvey 1987). Spring floods can lead to failed year classes of fishes in streams (e.g., smallmouth bass *Micropterus dolomieu*, Smith et al. 2005; Salmonids, Warren et al. 2009; Shoal Bass *Micropterus cataractae,* Woodside et al. 2015). Though chances of flooding could increase due to climate change, climate change is also expected to result in an overall reduction in precipitation which could lead to lower mean discharge levels (Alder & Hostetler 2013). Recruitment of fish in many stream systems can be positively affected by low discharge levels during the spawning and rearing period which often enhances year class strength (Peterson and Kwak 1999; Buynak and Mitchell 2002; Smith et al. 2005). Water temperature will also be affected by climate change and can influence growth and survival of stream fishes (Magnuson et al. 1979; Christie & Regier 1988). Changes in stream temperature could also lead to range restrictions or expansions (Eaton and Scheller 1996). Because of the many potential effects of climate change on stream systems, it can be difficult to anticipate how stream fishes will be affected.

Harvest is also an important factor structuring stream fish populations. For example, harvest of stream black bass is an important contributor to mortality in streams open to exploitation (e.g., Suwannee bass and largemouth bass, Middaugh et al. 2016b; smallmouth bass, Reed and Rabeni 1989, Williamson et al. 2015). Climate change will likely make managing harvested fisheries more complex and harvest regulations will need to be adapted as fish populations change (Walters and Parma 1996, Punt et al. 2014). High harvest levels, when combined with climate and anthropogenic related stressors, could lead to population declines (Bradford and Irvine 2000). As the world population grows, it is likely that fishing pressure will increase, potentially resulting in increased harvest levels that will need to be managed in conjunction with changing climate stressors.

Smallmouth bass are a warm-water riverine species broadly distributed throughout North America. The Ozark-Ouachita Interior Highlands of Arkansas lie at the southern extent of smallmouth bass native range. At this southern range extent, smallmouth bass populations may be vulnerable to population declines due to climate change as summer temperatures will likely reach levels that will affect growth and survivorship (Whitledge et al. 2006; Middaugh et al. 2016a), especially during summer drought conditions which are common in Arkansas streams and rivers (Hines 1975; Hafs et al. 2010). Smallmouth bass are at risk of being outcompeted in some lotic habitats by largemouth bass and spotted bass, which both have a competitive advantage over smallmouth bass at higher temperatures (Zweifel et al. 1999).

To investigate the relative effects of angler harvest and climate change on the smallmouth bass population in the Buffalo National River, Arkansas (hereafter, Buffalo River) we created an age-structured population model to simulate various climate and harvest scenarios. The structure for the model was based on previous work comparing land use and climate change effects on lotic smallmouth bass in an Illinois river (Peterson and Kwak 1999). We used empirical data collected in the Buffalo River to create a Ricker model modified with environmental parameters which was subsequently used to predict annual recruitment of age-0 smallmouth bass within a stage structured simulation model. Our objective was to compare the effects of climate change stressors (i.e., flooding and drought) and harvest mortality on smallmouth bass. We hypothesized that changing climate conditions would negatively affect smallmouth bass populations. In addition, we hypothesized that if current levels of harvest were maintained or increased in future climate scenarios, then smallmouth bass populations would further decline and extinction probability would increase.

Methods

Empirical Smallmouth Bass Data

The Buffalo River originates in the Boston Mountains region of Arkansas, USA and flows 238 km before entering the White River (Figure 1). The National Park Service protects approximately 90% of the river length. The Arkansas Game and Fish Commission sampled smallmouth bass in the Buffalo River twelve years between 1992 and 2012 using boat electroshocking. Sites were sampled a single time each year and during each sample fish were measured to the nearest millimeter and weighed to the nearest gram. We selected a subset of data from sites sampled at least three years in the month of October, and during nighttime boat electrofishing. This left 15 samples, collected from four different sites over the course of six years (Table 1). The sites were all located in the lower Buffalo River with approximately 24 miles between the most upstream (Rush) and the farthest downstream site (Elephant Head; Figure 1). We selected only sites sampled during October in order to reduce bias associated with small age-0 fish recruitment to the sampling gear and also because Autumn can be a reliable indicator of year-class strength for lotic smallmouth bass (Smith et al. 2005). We then removed any outliers by examining fish length and weight data. We did this by calculating relative weights (Wr) for each fish > 150 mm (Kolander et al. 1993) and removing any fish with an extreme Wr (Wr < 55 or > 145).

We next created length histograms for each site to estimate the length cutoff between age-0 and older fish in order to determine the number of age-0 fish collected during each sampling event. This length cutoff varied by site and by year (Table 1). We assume that fish age-3+ are mature based on previous work in the Buffalo River (Kilambi et al. 1977) and we determined the number of adults at each sampling event by counting the number of fish ≥ 225 mm based on Whisenant and Maughan (1989) estimates for age-3 smallmouth bass in the Buffalo River. Counts of age-0 and adult fish were then standardized by dividing by sampling effort (minutes of shocking time) for each sample. These standardized catch-per-unit-effort (CPUE) data were then used in subsequent analyses.

Environmental Data

Environmental data for monthly mean air temperature and monthly mean river discharge were obtained in order to relate to yearly CPUE of age-0 smallmouth bass. We selected these discharge and temperature variables to relate to age-0 fish abundances as similar environmental variables are related to age-0 smallmouth bass recruitment in other river systems (Lukas and Orth 1995; Peterson and Kwak 1999; Armour 2003; Smith et al. 2005) and we chose to include both temperature and discharge variables in the final model as both factors are important in structuring recruitment and can be interrelated (Swenson et al. 2002). We downloaded daily discharge data from USGS gage 07056000 on the Buffalo River near St. Joe, AR. We used these data to determine mean monthly discharge and standard deviation for the years 1940-2013. Air temperature data was downloaded from long-term climate data collected by a National Oceanic and Atmospheric Agency National Center for Climate Data weather station in nearby Harrison, AR (Station USW00013971). We related mean monthly air temperature and mean monthly discharge to CPUE of age-0 smallmouth bass for each month during the spawning/rearing period (March-July). The month with the strongest relationship based on least squares regression R^2 value for each environmental parameter was selected for use in subsequent analyses (Figure 2).

Model Overview

We created an age-structured smallmouth bass model with age-specific environmental effects, and harvest mortality (Figure 3). Fish age groups are set as age-0, age-1, age-2, age-3 and age-4+ to age-8 (we assume assume 100% mortality of age-8 fish as no fish older than this were collected by Whisenant and Maughan (1989)). All smallmouth bass abundances are reported in units of CPUE because these are the units our empirical data is based on. Final model output examines relative changes in predicted abundances of smallmouth bass in the Buffalo River rather than absolute changes in fish abundances. The model is programmed and run in R (R Core Team 2017).

Reproduction

Age-0 fish abundances in the model are determined using a Ricker stock-recruitment model with environmental terms incorporated (e.g., Peterson and Kwak 1999; Maceina and Pereira 2007). This type of model incorporates adult densities and assumes competition among juveniles in order to predict number of recruits. We incorporate May temperature and June discharge into the model as these were the best predictors of age-0 fish abundance from empirical data. The Ricker model was structured as:

$$CPUE(age0) = CPUE(adults) * \exp(a - (b * CPUE(adults)) + (c * May\ Temp) + (d * June\ Discharge))$$

We solved for the parameters a, b, c, and d using non-linear regression. The final model took eleven iterations to converge on a solution and had a residual standard error of 0.0916. We next performed leave-one-out cross validation to evaluate model fit and compute 95% confidence intervals for each parameter (Appendix 1). We then plotted predicted CPUE of age-0 fish and actual CPUE of age-0 fish (Figure 4) and calculated fit with a least squares linear regression.

To evaluate uncertainty within the model, we conducted a sensitivity analysis on each of the parameters predicted by the non-linear regression where all other values were held constant (May temperature, Adult CPUE, and June discharge were set at the mean values from collected data). We modified each parameter by ± 25% and recorded the values of predicted age-0 CPUE (Appendix 2). The parameter modifying adult CPUE (b) was the most influential in the model and so we next predicted age-0 CPUE based on a range of adult CPUE values. For each adult

CPUE value, we varied the parameter b ± 25% to demonstrate model uncertainty (Figure 4). All statistical analyses were conducted in R (R Core Team 2017).

Model parameters

Age-group mortality within the simulation model was assessed through two different mechanisms. First was natural mortality factors that varied among age groups in the simulation model (Table 2). Natural mortality values were based on previous work in the Buffalo River, but these studies only estimated survival for all ages combined and do not separate harvest mortality (Kilambi et al. 1977; Whisneant and Maughan 1989). We modified these estimates to reflect higher mortality of young age classes (Table 2). Age-0 fish mortality is set at a low level to reflect overwinter mortality as age-0 fish abundance is predicted for October. We assigned a standard deviation to every mortality value to create variation among simulation years and reflect the stochastic nature of stream systems. The second form of mortality that we assessed was harvest mortality. We applied harvest mortality to adult fish age-4+ as the Buffalo River currently has a 305 mm length limit and most age-4+ smallmouth bass in the river are above this length cutoff (Whisenant and Maughan 1989; AGFC unpublished age data). We estimated harvest mortality based on exploitation studies conducted by Missouri Department of Conservation in similar Ozark rivers (Williamson et al. 2015).

Simulations

The simulation model runs on an annual time step from October to October and each simulation was conducted over 100 years and replicated 1,000 times. We began each simulation with a very high abundance for each age group of fish (Table 2). A break-in period followed before the model settled into a relatively stable abundance of each age group of fish around year ten. Preliminary runs of our simulation model indicated an under prediction of adult abundance in present climate simulations compared to empirical data. Therefore, we modified the number of age-0 smallmouth bass predicted by the Ricker spawner-recruit model by multiplying by four in all simulations. This resulted in very similar predicted abundances in the present climate simulation to the mean CPUE of adult smallmouth bass collected in empirical data.

We conducted ten different simulations where we examined different climate and harvest related scenarios. The first simulation was based on present climate conditions where June discharge and May temperature were taken from historical values for the Buffalo River area. Using the NOAA climate station and USGS river gage described above, we calculated a mean value and standard deviations based on May temperature from the years 1948-2013, and a median value and standard deviation based on June discharge from the years 1940-2013. The remaining nine simulations were set at future climate conditions for June discharge and May temperature. We determined future mean monthly May temperature and mean monthly June discharge values based on climate simulation results from an ensemble average of 30 downscaled climate models for an RCP 8.5 emissions scenario at mid-century (2050-2074; USGS National Climate Change Viewer; Alder and Hostetler 2013). Mean minimum and maximum temperatures output by the models were averaged to calculate a future mean monthly May temperature and standard deviation. Because the Buffalo River is runoff dominated (Leasure et al. 2016), we determined future discharge by modifying historical median discharge proportionally to the change in future projected precipitation (about 8% lower in June and 19% more variable).

We modeled two different types of drought simulations based on current and future projected drought frequency in the region. Summer drought conditions are presently common in runoff dominated rivers like the Buffalo River in this region (Hines 1975; Hafs et al. 2010;

Leasure et al. 2016) and climate change could lead to prolonged and more severe drought conditions in the region (Strzepek et al. 2010). We modeled drought probabilistically where each simulated year had a chance of being a drought year (Table 2). We based present drought chances on long term discharge data from the Buffalo River during summer months (June-September) where we defined a moderate drought year as being lower than 50% of mean discharge during the period of record (1940-2013) and a strong drought year as being less than 25% of mean discharge. Natural mortality during moderate drought years was increased 50% above normal levels for all age groups and natural mortality during strong drought years was increased 75% above normal levels for all age groups. In future higher frequency drought simulations, we modeled expected future increases in drought in this region (moderate drought 5% more frequent and extreme drought 9% more frequent; Strzepek et al. 2010).

We modeled two different types of flood simulations based on current and future projected flood frequency in the region. We simulated flooding during the spawning and rearing period and the associated mortality of age-0 fish. Though floods likely affect older age groups as well, it is more difficult to quantify those effects. Similar to drought, we simulated flooding probabilistically where every year had a chance to be a flood year. We based present flood probability on discharge data from the Buffalo River (1940-2013) during June where we defined a flood event as an increase in mean June discharge of 100% above median discharge (about 10% of years from 1940-2013). If a flood year occurred, mortality of age-0 fish was set at 90%. We modeled some scenarios as having a higher flood chance to simulate an increase in extreme precipitation events due to climate change. Though increases in extreme precipitation events are expected in this region, there are no models projecting the associated effects on numbers of flood events with high confidence in this region (Kundzewicz et al. 2014). We chose to increase flood probability in a given year to 20% as an exploratory examination of future flooding potential.

We modeled two different harvest morality simulations. Though recent estimates of harvest of smallmouth bass in the Buffalo River are not available, we used harvest mortality estimates from similar Missouri Ozark rivers in our simulations (approximately 20% annual harvest mortality; Williamson et al. 2015). Use of the Buffalo River has increased in recent years (a 240% increase in visitors from 2000 to 2016; National Park Service 2016) and is likely to increase in the future, potentially leading to higher harvest of smallmouth bass. Assuming no change in regulations and an increase in river use, we modeled a future harvest scenario as 75% higher than present harvest mortality (35% annual harvest mortality). Finally, we modeled a scenario where harvest of smallmouth bass is closed to facilitate a comparison of the importance of harvest and other mortality factors in affecting population levels.

Results

Sensitivity analysis was performed on the four parameters within the Ricker Model equation (Appendix 2). These analyses indicated that parameter b, modifying adult abundance, was the most influential parameter in the model. A ± 25% change in b elicited a 39% decrease and a 29% increase in CPUE of age-0 fish predicted by the model when all other parameters were held at mean values. A ± 25% change in a resulted in a 13% decrease and a 15% increase in CPUE of age-0 fish. A ± 25% change in c resulted in a 10% decrease and a 12% increase in CPUE of age-0 fish. A ± 25% change in d resulted in a 16% decrease and a 19% increase in CPUE age-0 fish. Because of the indicated importance of adult abundance in structuring model results, we plotted predicted age-0 abundance by a range of adult abundance values to examine model behavior with the error ranges showing the range of results if b was varied ± 25% (Figure 5). The linear regression between predicted age-0 CPUE and observed age-0 CPUE indicated that our model adequately predicted the number of age-0 fish ($p=0.004$, $R^2=0.48$).

The future climate simulation predicted a 15% increase in abundance of adult smallmouth bass compared to present conditions (Figure 6). This scenario only took into account changes in May temperature and June discharge, not increased flooding, drought, or harvest conditions. The only other scenario that predicted an increase in abundance of adult smallmouth bass from present conditions was the future high flood scenario (6% increase in adult CPUE; Figure 7). Simulations with increased drought chances predicted a large decline in adult abundance from present conditions (52% decline in adult CPUE for the high drought scenario; Figure 7) and the scenario with high drought, high flood, and high harvest had the greatest change from present conditions for any modeled scenario (71% reduction in adult CPUE; Figure 7). In the final scenario, harvest was eliminated in the model, resulting in a 46% decline in CPUE compared to the present climate simulation, less of a decline than any other scenario with high drought included (Figure 7). The only scenarios where extinction occurred were scenarios that included high probabilities of drought. Extinction probabilities ranged from 0 in present climate conditions to 0.08 in the scenario with high drought, flood, and harvest (Figure 8).

Discussion

Our simulation model predicted an increase in abundance of adult smallmouth bass under future May temperature and June discharge conditions, but this population increase could be offset by other expected climate related changes in the region such as increased drought and flooding. Temperature and discharge during the spawning and rearing period has been shown to affect year-class strength of lotic smallmouth bass in other streams (Armour 1993; Lukas and Orth 1995; Peterson and Kwak 1999; Swensen et al. 2002; Smith et al. 2005). Mean June discharge was found to be the best predictor of smallmouth bass recruitment in three Virginia Rivers and years with very high flows in June led to near year-class failures (Smith et al. 2005). Similarly, several sportfish species were negatively related to spring season discharge in four Florida rivers (Bonvechio and Allen 2005). Higher temperatures during spring and summer months can positively affect smallmouth bass recruitment through increased growth which can reduce predation risk and increase overwinter survival (Shuter et al. 1980). Climate change is likely to result in an increase in May temperature and a decline in June discharge, both of which should benefit smallmouth bass recruitment, leading to higher adult abundances.

Flooding during the spawning and rearing period can devastate year classes of lotic smallmouth bass (Smith et al. 2005) and other lotic black bass species (e.g., shoal bass *Micropterus cataractae*; Woodside et al. 2015). Heavy precipitation events have increased over the past century, leading to more frequent high flow events (Groisman et al. 2001). Climate change is likely to increase the frequency of severe storms that will affect short-term discharge variation (Groisman et al. 1999) and lead to more high flow events. Flooding can affect smallmouth bass year class strength through nest destruction and fry displacement (Winemiller and Taylor 1982; Harvey 1987; Simonson and Swenson 1990). Flooding can also lead to mortality through rapid changes in water temperature (Larimore 2002). Timing of flooding can be important as the size of the fry can determine the response to the flood event (Simonson and Swenson 1990). However, high flow during any period of spawning and rearing is likely to negatively affect smallmouth bass year class strength (Peterson and Kwak 1999). This corresponds to our empirical data where a single year had a very high June discharge level

($23.28\ m^3/s$) and almost no age-0 smallmouth bass were collected that year. Overwinter discharge can also be an important predictor of smallmouth bass recruitment (Peterson and Kwak 1999). We chose not to include overwinter discharge or temperature in the juvenile fish reproduction model because overwinter survival is less of a concern at southern latitude populations as spawning occurs relatively early in the year, allowing time for a long growing season before winter (Wrenn 1984; Orth and Newcomb 2002).

Our simulations indicate that increases in drought frequency could strongly affect abundance of smallmouth bass in the Buffalo River. Previous work has documented a decline in body condition of smallmouth bass during summer months in some streams in the Ozark region, including the upper Buffalo River (Middaugh unpublished data), and it is likely that increasing stream temperature due to climate change will decrease growth potential of smallmouth bass during summer months (Middaugh et al. 2016a). Drought conditions can stress fish and result in population declines (Matthews and Marsh-Matthews 2003). Drought in the Ozark-Ouachita Interior Highlands leads to pool isolation in runoff streams which can increase competition and predation risk (Zaret and Rand 1971; Harvey and Stewart 1991). Strong drought can cause severe abiotic conditions within pools (Magoulick and Kobza 2003) and can lead directly to mortality of smallmouth bass through complete drying of pools (Hafs et al. 2010). In our simulations, drought was the only stressor that affected every age class, leading to the strong effects we found.

Angler harvest is an important mortality component in exploited fish populations. Limited angler harvest data is available for the Buffalo River in the form of creel surveys collected between 1989 and 1995, but we do not have an estimate of current exploitation in the Buffalo River. Work conducted in six Ozark streams in Missouri found that exploitation ranged from 7-26% of the population with three rivers having exploitation rates over 20% (Williamson et al. 2015). The Buffalo River is heavily utilized (NPS 2016), and many of those users fish for smallmouth bass (Middaugh and Magoulick personal observations). Therefore, we modeled current exploitation near the high level found in Missouri streams, 20%. Missouri Ozark streams are closed to harvest for approximately three months in the spring, but there is no harvest closure in the Buffalo River, indicating that our present simulation harvest estimate is likely conservative. Our high exploitation scenario reflects increasing usage of the river in future years.

There are several limitations inherent in our modeling approach. We do not attempt to model some aspects of smallmouth bass population dynamics such as growth and intraspecific competition. Our modeling also only takes into account a few of the potential effects of climate change. For example, we do not simulate habitat or land use changes that could occur over the coming century. However, a riparian buffer around the Buffalo River is protected by the National Park Service which may limit effects of land use change on the river. We also assume that relationships between May temperature and June discharge and smallmouth bass recruitment will be the same in the future as during the period that data was collected. The Buffalo River is a runoff stream and other stream types, such as intermittent or groundwater dominated, could have different responses to climate change than runoff streams (e.g., temperature, Middaugh et al. 2016a). Another simplifying assumption occurs in the way we model harvest mortality. We do not take into account catch and release mortality that can be an important component of overall mortality (Bartholomew and Bohnsack 2005). In our closed harvest scenario in particular, catch and release mortality or sub-lethal effects would likely still occur, especially at high temperatures during summer months (Cooke et al. 2002), which could reduce the effectiveness of eliminating harvest through changing regulations. An additional assumption of our model is that variables such as age-specific mortality vary independently each year.

Our model has a number of management implications. Our results indicate that increases in drought prevalence could have the strongest effects on smallmouth bass abundance. Management actions designed to mitigate the effects of drought could reduce these effects. For example, management in this region could be directed towards reducing water withdrawals (Kanno and Vokoun 2010), preserving spring inputs into streams, and increasing riparian canopy to reduce water temperatures and evapotranspiration (Whitledge et al. 2006). Though we found that increases in flooding frequency had a much smaller effect on adult smallmouth bass abundance than drought, reducing flooding risk by decreasing channelization and protecting the riparian buffer could reduce the flashiness of streams (Naiman et al. 1993). The Buffalo River region is remote, reducing the risk of major land use changes over the coming century, but increases in development and agriculture usage in the watershed could further increase flooding chances and alter discharge during the spawning and rearing period, affecting fish populations (Peterson and Kwak 1999).

More restrictive harvest regulations could reduce the negative effects of climate change on smallmouth bass populations in the Buffalo River. Currently, the river has a twelve inch minimum length limit and a four fish bag limit. If harvest was eliminated, we found a 37% increase in adult smallmouth bass over a future climate, low harvest, high flood, and high drought scenario, and an 86% increase in adult smallmouth bass abundance over a future climate, high harvest, high flood, and high drought scenario. In addition, removing harvest almost eliminated the chance of smallmouth bass population extinction occurring. Managers could consider restricting or eliminating bag limits for smallmouth bass if noticeable declines in adult smallmouth bass abundance occur due to climate change.

In conclusion, we found that changes in May temperature and June discharge could benefit smallmouth bass recruitment, but increased flooding and increased drought conditions are likely to reduce adult smallmouth bass abundance below present levels in the Buffalo River. Reducing or eliminating harvest could prove a viable strategy to reduce the negative effects of climate change and lessen the risk of population extinction. Future work is needed to further understand the effects of climate change on smallmouth bass populations at the southern range extent, especially in streams from differing flow regimes.

Acknowledgements

We would like to acknowledge a number of people who assisted with this study. We thank the Arkansas Game and Fish Commission for providing data, especially S. Todd, J. Quinn, M. Oliver, and S. Filipek for providing constructive input on the project. J. Cothren, K. Naithani and J. D. Wilson provided useful suggestions and edits for this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Alder, J. R., and S. W. Hostetler. 2013. USGS National Climate Change Viewer. US Geological Survey http://www.usgs.gov/climate_landuse/clu_rd/nccv.asp.

Armour, C. L. 1993. Evaluating temperature regimes for protection of smallmouth bass. US Department of Interior Fish and Wildlife Service, Resource Publication 191, Washington.

Bartholomew, A. and J. A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Reviews in Fish Biology and Fisheries 15:129-154.

Bonvechio, T. F. and M. S. Allen. 2005. Relations between hydrological variables and year-class strength of sportfish in eight Florida waterbodies. Hydrobiologia 532:193-207.

Bradford, M. J., and J. R. Irvine. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. Canadian Journal of Fisheries and Aquatic Sciences 57:13-16.

Buynak, G. L., and B. Mitchell. 2002. Response of smallmouth bass to regulatory and environmental changes in Elkhorn Creek, Kentucky. North American Journal of Fisheries Management 22:500-508.

Christie, G. C., and H. A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for 4 commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45:301-314.

Cooke, S. J., J. F. Schreer, D. H. Wahl, and D. P. Philipp. 2002. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Pages 489-512 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109-1115.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Review in Fish Biology and Fisheries. 17:581-613.

Groisman, P. Y., R. W. Knight, and T. R. Karl. 2001. Heavy precipitation and high streamflow in the contiguous United States: Trends in the twentieth century. Bulletin of the American Meterological Society 82:219-246.

Groisman, P. Y., T. R. Karl, D. R. Easterling, R. W. Knight, P. F. Jamason, K. J. Hennessy, R. Suppiah, C. M. Page, J. Wibig, K. Fortuniak, V. N. Razuvaev, A. Douglas, E. Førland, and P. M. Zhai. 1999. Changes in the probability of heavy precipitation: important indicators of climatic change. Climatic Change 42:243-283.

Hafs, A. W., C. J. Gagen, and J. K. Whalen. 2010. Smallmouth bass summer habitat use, movement, and survival in response to low flow in the Illinois Bayou, Arkansas. North American Journal of Fisheries Management 30: 604-612.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851-855.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87:336-342.

Hines, H. S. 1975. Flow-duration and low-frequency determinatinos of selected Arkansas streams. USGS Water Resources Circular No. 12, Arkansas Geological Commission, Little Rock, AR, USA.

Kanno, Y., and J. C. Vokoun. 2010. Evaluating effects of water withdrawals and impoundments on fish assemblages in southern New England streams, USA. Fisheries Management and Ecology 17: 272-283.

Karl, T. R., J. M. Melillo, and T. C. Peterson (eds.) 2009. Global climate change impacts in the United States. Cambridge University Press.

Kilambi, R. V., W. R. Robison, and J. C. Adams. 1977. Growth, mortality, food habits, and fecundity of the Buffalo River smallmouth bass. Arkansas Academy of Science 31:62-65.

Kolander, T. D., D. W. Willis, and B. R. Murphy. 1993. Proposed revision of the standard weight (Ws) equation for smallmouth bass. North American Journal of Fisheries Management 13:398-400.

Kundzewicz, Z. W., S. Kanae, S. I. Seneviratne, J. Handmer, N. Nicholls, P. Peduzzi, R. Mechler, L. M. Bouwer, N. Arnell, K. Mach, R. Muir-Wood, G. R. Brakenridge, W. Kron, G. Benito, Y. Honda, K. Takahashi, and B. Sherstyukov. 2014. Flood risk and climate change: global and regional perspectives. Hydrological Sciences Journal 59:1-28.

Larimore, R. W. 2002. Temperature acclimation and survival of smallmouth bass fry in flooded warmwater streams. Pages 115-122 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Leasure, D.R., D. D. Magoulick, and S. D. Longing. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32:18-35.

Lukas, J. A. and D. J. Orth. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. Transactions of the American Fisheries Society 124:726-735.

Maceina, M. J. and D. L. Pereira. 2007. Recruitment. Pages 121-186 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19:331-343.

Magoulick, D. D, and R. M. Kobza. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186-1198.

Matthews, W. J., and E. Marsh-Matthews. 2003. Effects of drought on fish across axes of space, time and ecological complexity. Freshwater Biology 48:1232-1253.

Middaugh, C. R., B. Kessinger, and D. D. Magoulick. 2016. Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent. Ecology of Freshwater Fish DOI:10.1111/eff.12320.

Middaugh, C. R., T. A. Alfermann, P. A. Strickland, and P. Nguyen. 2016. A regional evaluation of Suwannee bass and largemouth bass exploitation in North Florida Rivers. North American Journal of Fisheries Management 36:958-963.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209-212.

National Park Service (NPS). 2016. Visitor use statistics. https://irma.nps.gov/Stats/SSRSReports/Park%20Specific%20Reports/Annual%20Park%20Recreation%20Visitation%20Graph%20(1904%20-%20Last%20Calendar%20Year)?Park=BUFF.

Novotny, E. V., and H. G. Stefan. 2007. Stream flow in Minnesota: Indicator of climate change. Journal of Hydrology 334:319-333.

Orth, D. J., and T. J. Newcomb. 2002. Certainties and uncertainties in defining essential habitats for riverine smallmouth bass. Pages 251-264 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Peterson, J. T., and T. J. Kwak. 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. Ecological Applications 9:1391-1404.

Punt, A. E., T. A'mar, N. A. Bond, D. S. Butterworth, C. L. de Moor, J. A. A. De Oliveira, M. A. Haltuch, A. B. Hollowed, and C. Szuwalski. 2014. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. ICES Journal of Marine Science 71:2208-2220.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reed, M. S., and C. F. Rabeni. 1989. Characteristics of an unexploited smallmouth bass population in a Missouri Ozark stream. North American Journal of Fisheries Management 9:420-426.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young of year smallmouth bass in relation to habitat use. Transactions of the American Fisheries Society. 119:902-909.

Smith, S. M., J. S. Odenkirk, and S. J. Reeser. 2005. Smallmouth bass recruitment variability and its relation to stream discharge in three Virginia rivers. North American Journal of Fisheries Management 25:1112-1121.

Strzepek, K., G. Yohe, J. Neumann, and B. Boehlert. 2010. Characterizing changes in drought risk for the United States from climate change. Environmental Research Letters 5:1-9.

Swenson, W. A., B. J. Shuter, D. J. Orr, and G. D. Heberling. 2002. The effects of stream temperature and velocity on first-year growth and year-class abundance of smallmouth bass in the Upper Mississippi River. Pages 101-114 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Walters, C. and A. M. Parma. 1996. Fixed exploitation rate strategies for coping with effects of climate change. Canadian Journal of Fisheries and Aquatic Sciences 53:148-158.

Warren, D. R., A. G. Ernst, and B. P. Baldigo. 2009. Influence of spring floods on year-class strength of fall and spring-spawning salmonids in Catskill mountain streams. Transactions of the American Fisheries Society 138:200-210.

Whisenant, K. A., and E. Maughan. 1989. Smallmouth bass and Ozark bass in Buffalo National River. Cooperative National Park Resources Studies Unit Technical Report No. 28.

Whitledge, G. W., C. F. Rabeni, G. Annis, and S. P. Sowa. 2006. Riparian shading and groundwater enhance growth potential for smallmouth bass in Ozark streams. Ecological Applications 16:1461-1473.

Williamson, C., N. Girondo, P. Cieslewicz, S. Peper, D. Knuth, M. Reed, J. Ackerson, A. J. Pratt, and J. Girondo. 2015. Harvest Evaluation of smallmouth bass from selected Ozark streams. Missouri Department of Conservation Final Report.

Winemiller, K. O., and D. H. Taylor. 1982. Smallmouth bass nesting behavior and nest site selection in a small Ohio stream. Ohio Journal of Science. 82:266-273.

Woodside, K. L., C. J. Paxton, and N. C. Kierl. 2015. Stock assessment of shoal bass in the Chipola River, Florida. Pages 139-156 *in* M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Wrenn, W. B. 1984. Smallmouth bass reproduction in elevated temperature regimes at the species' native southern limit. Transactions of the American Fisheries Society 113:295-303.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

Zweifel, R. D., R. S. Hayward, and C. F. Rabeni. 1999. Bioenergetics insight into black bass distribution shifts in Ozark border region streams. North American Journal of Fisheries Management 19:192-197.

Table 1. Data collected by the Arkansas Game and Fish Commission in the Buffalo River, AR. Number of age-0 and adult smallmouth bass columns show ranges of counts of fish designated as those age groups.

Site	Years sampled	Num. of Age-0 (<151-176 mm)	Num. of Adults (≥250 mm)
Rush	2008-2012	5-49	43-182
Middle Creek	2008-2010	4-32	40-116
Elephant Head	2006, 2008, 2012	6-40	13-73
Hudson Bend	2006, 2011, 2012	6-34	50-52

Table 2. Smallmouth bass age-structured model parameters. Each year in the simulations a random, normally distributed value for each parameter is selected based on the mean and standard deviation listed below.

Variable	Mean	SD
Environmental Parameters		
Present May Temperature	18.33 ºC	0.3
Future May Temperature	21.97 ºC	0.59
Present June Discharge	12.87 m^3/s	8.84
Future June Discharge	11.83 m^3/s	10.51
Minimum Discharge	0.5 m^3/s	
Flood chance low	10%	
Flood chance high	20%	
Moderate and strong drought chance (present drought frequency)	34%; 14%	
Moderate and strong drought chance (future high drought frequency)	39%; 23%	
Mortality Parameters		
Age-0 Flood Mortality	0.9	0.01
Age-0 Natural Mortality	0.1	0.1
Age-0 Mortality Moderate Drought	0.3	0.1
Age-0 Mortality High Drought	0.5	0.1
Age-1 Natural Mortality	0.4	0.1
Age-1 Mortality Moderate Drought	0.6	0.1
Age-1 Mortality High Drought	0.8	0.1
Age-2 Natural Mortality	0.3	0.1
Age-2 Mortality Moderate Drought	0.45	0.1
Age-2 Mortality High Drought	0.6	0.1
Adult Natural Mortality	0.3	0.1
Adult Mortality Moderate Drought	0.45	0.1
Adult Mortality High Drought	0.6	0.1
Adult Fishing Morality Low	0.2	0.05
Adult Fishing Morality High	0.35	0.05
Mortality Lower Limit (all ages)	0.05	
Mortality Upper Limit (all ages)	0.95	
Population Parameters		
Initial number of age-0 fish	1.2	0.2
Initial number of age-1+ fish	0.15	0.1

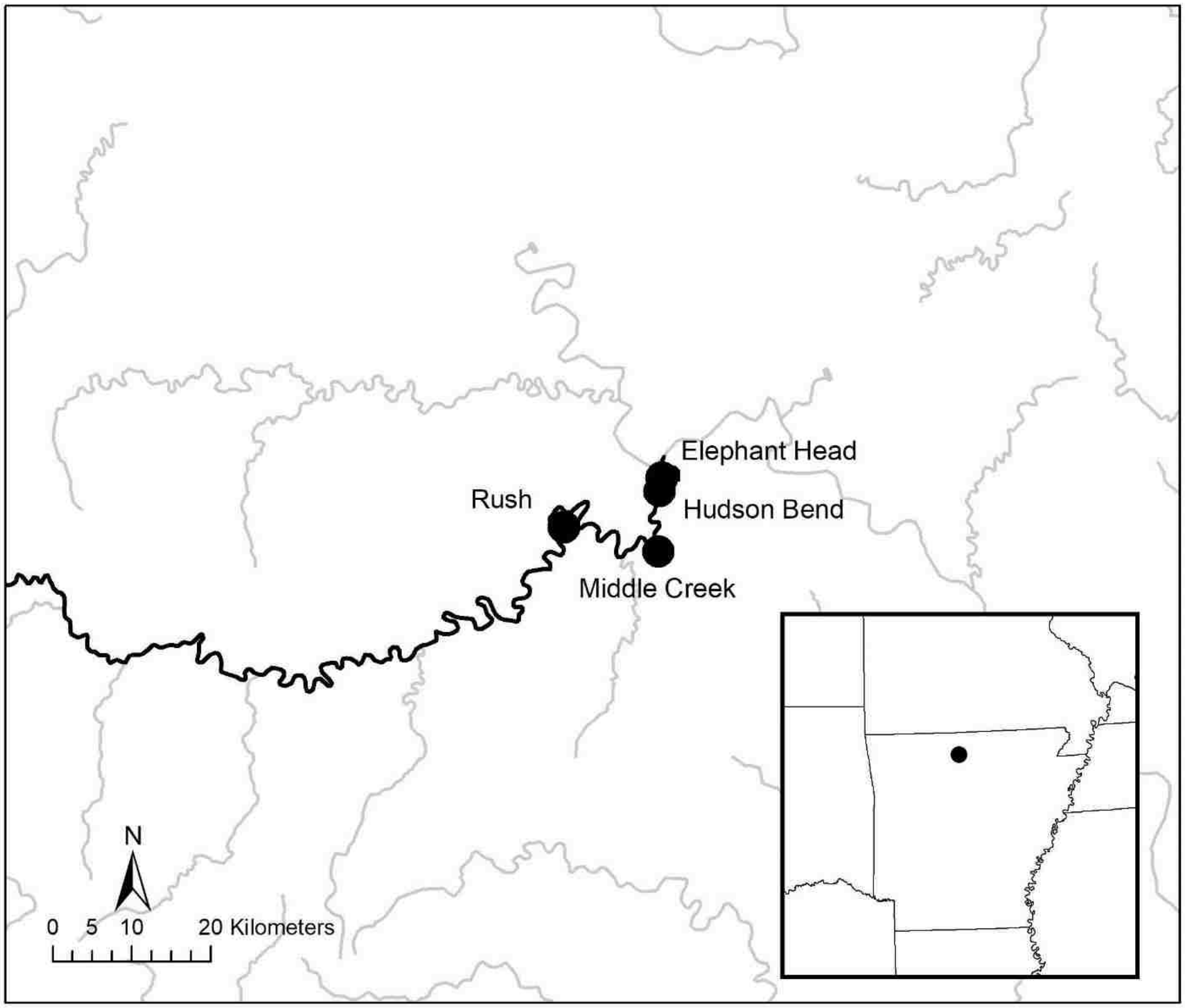


Figure 1. Map of the Buffalo River, Arkansas and locations sampled by the Arkansas Game and Fish Commission. The Buffalo River is highlighted in black.

A) B)

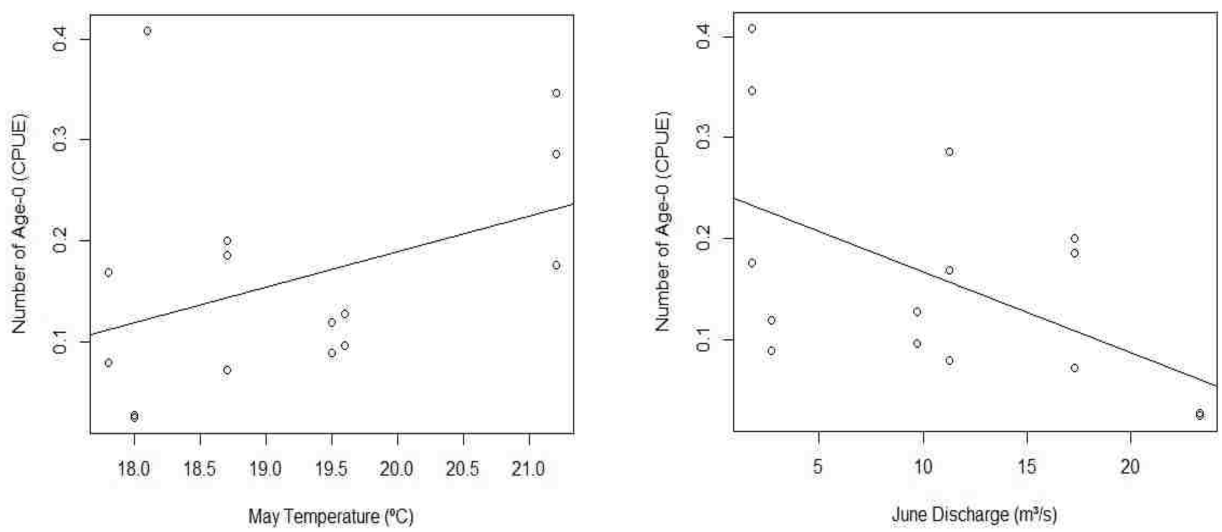


Figure 2. Relationship between May temperature (A) and June discharge (B) and number of age-0 smallmouth bass collected by the Arkansas Game and Fish Commission during October boat electrofishing samples. Best fit lines are shown in plots to demonstrate trends.

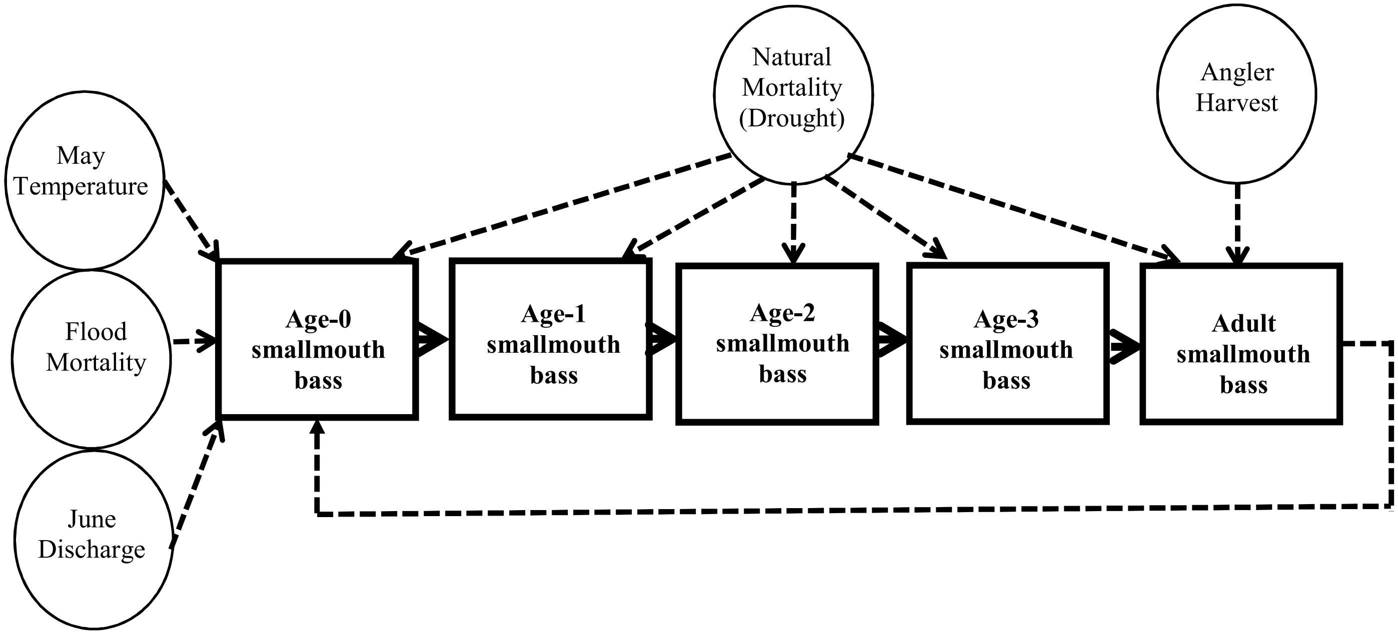


Figure 3. Conceptual diagram of the age-structured simulation model. Rectangles represent age-classes of fish and circles represent parameters affecting different age groups.

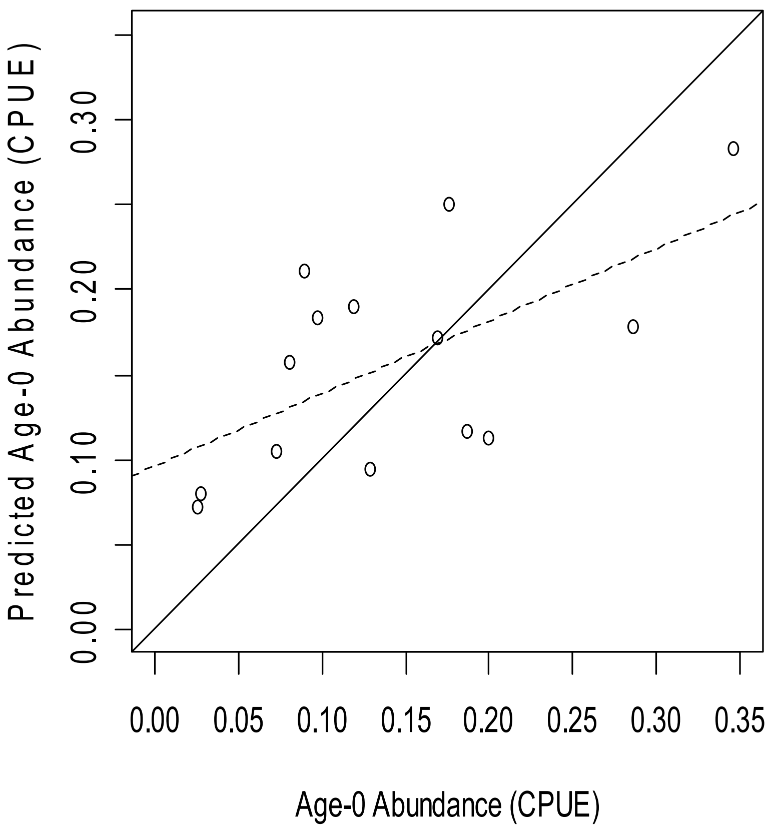


Figure 4. Plot of age-0 smallmouth bass for each sample predicted by the Ricker model plotted against the actual number of age-0 fish collected. The solid line shows a 1:1 fit and the dashed line shows the least squares linear regression of the plotted and observed data ($p=0.004$, $R^2=0.48$).

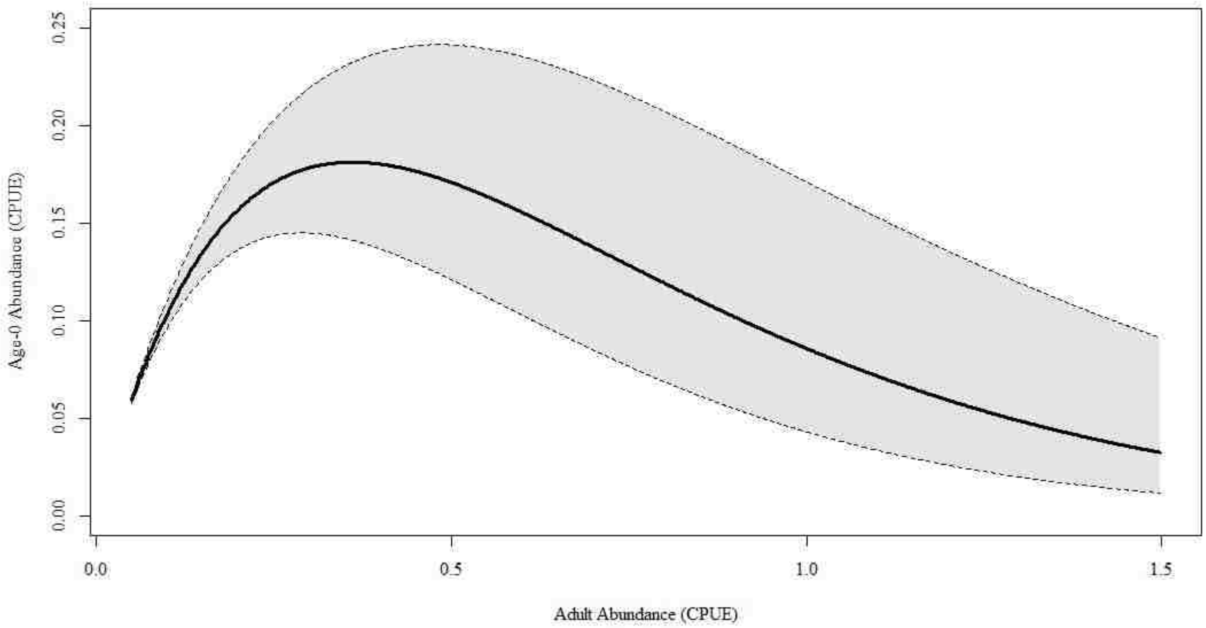


Figure 5. Ricker model with environmental parameters added. Here all parameters are held at a constant value except for adult abundance. Grey area shows the range of values for adult abundance as the parameter b is varied ±25%.

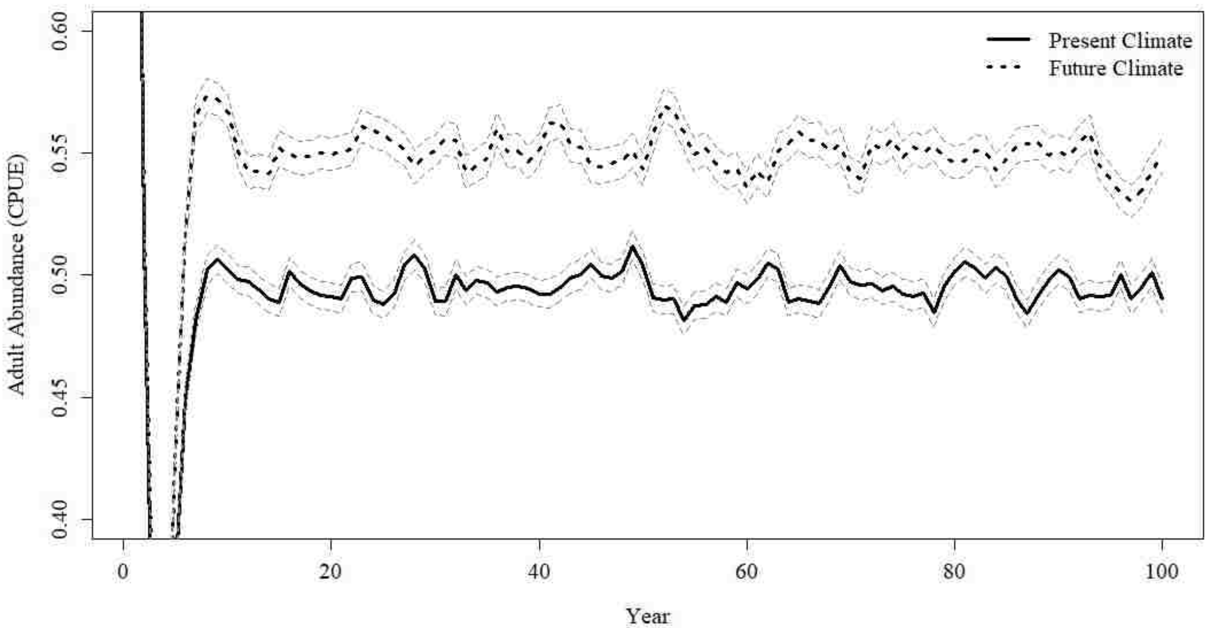
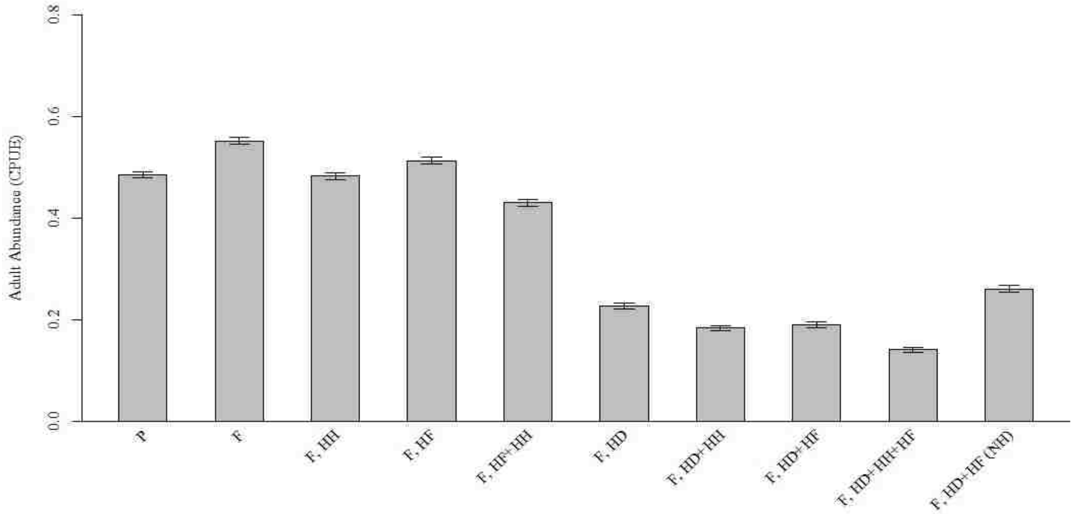


Figure 6. Mean adult abundances from the 1,000 replications of the present (solid black line) and future climate (dashed black line) simulations. Grey dashed lines represent standard error.

A)



B)

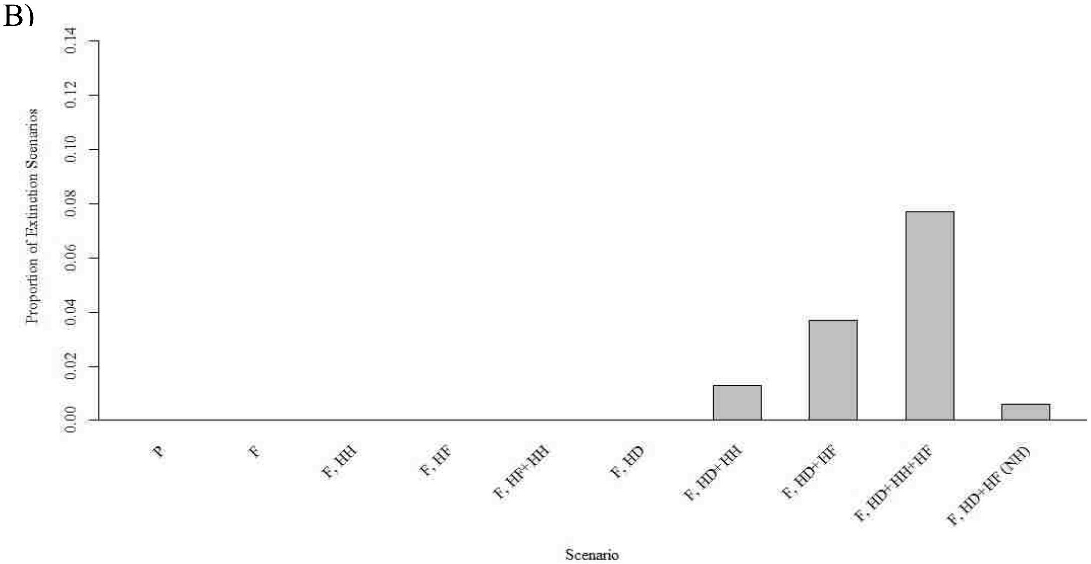
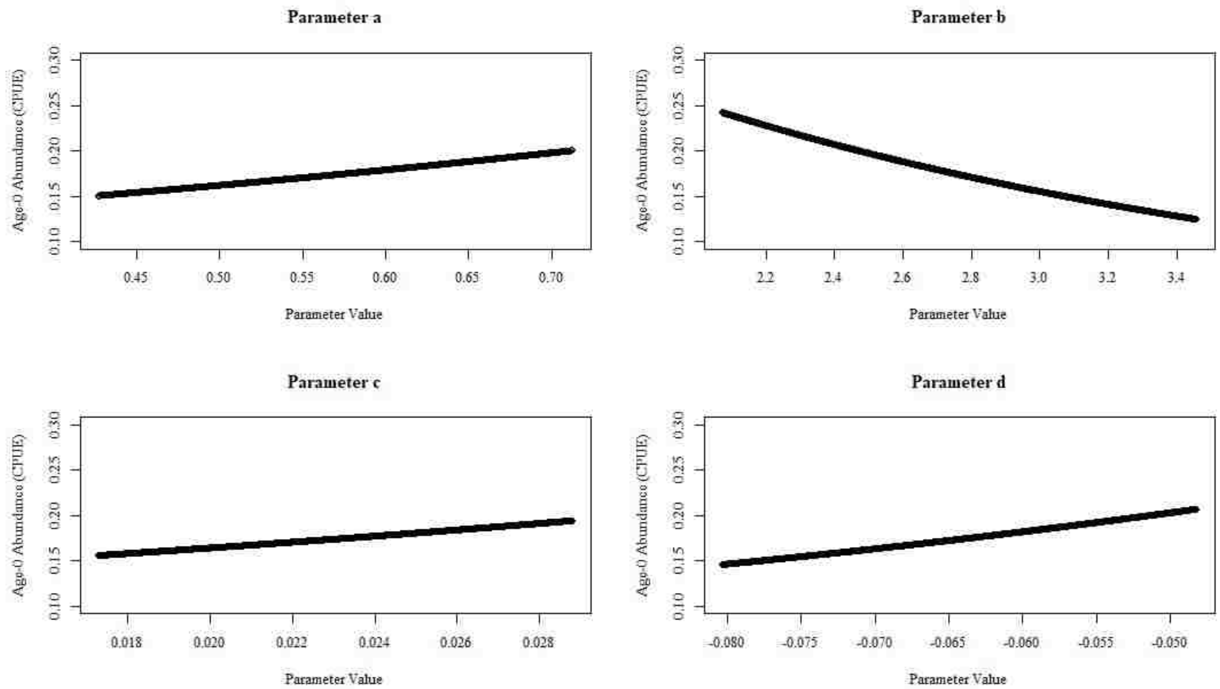


Figure 7. Mean adult abundances based on 1,000 replications for the final year (year 100) for each model simulation (A) and proportion of simulations where smallmouth bass population extinction occurred (B). P represents present climate conditions (May temperature and June discharge), F represents future climate conditions (May temperature and June discharge), HH represents high harvest, HF represents high flood, HD represents high drought, and NH represents no harvest. Error bars indicate standard error based on the 1,000 replications of each simulation.

Appendix 1. 95% Confidence intervals for parameters from the Ricker stock-recruit model.

Parameter	Value	Lower Bound	Upper Bound
a	0.570	-3.886	2.402
b	2.767	2.447	4.829
c	0.023	-0.069	0.238
d	-0.0642	-0.117	-0.0326

Appendix 2. Sensitivity analysis results. Each parameter was varied ±25% of the value solved for in the non-linear regression. As each parameter was tested, all others were held at the solved value and other model data (adult abundance, May temperature, June Discharge) were held at mean values based on the original data.



Conclusion

My results indicate that flow regime may be a critical factor affecting smallmouth bass *Micropterus dolomieu* at the southern range extent, and that flow regime should be taken into account when considering the effects of climate change. In particular, I found that temperatures differ among runoff and groundwater streams throughout the year. This can lead to differences in smallmouth bass growth among streams, especially in winter and summer months. I also found that runoff streams are likely to warm more than groundwater streams in all months of the year due to climate change. In addition to temperature, summer drought presently leads to differences in abiotic conditions among stream types as runoff streams are more susceptible to drought conditions. My simulation model suggests that increased drought conditions could strongly affect smallmouth abundances in the future, especially in runoff streams such as the Buffalo River. Groundwater streams are likely to be more resistant to increased frequency and intensity of drought conditions expected under climate change.

Though the streams I sampled did not experience prolonged drought conditions during any year of my field study, my empirical data supports my modeling results. I found that smallmouth bass body condition, an indicator of growth, was negatively affected by summer conditions in two runoff streams in all three years studied and in groundwater streams in two out of three years. I did not investigate the mechanism causing the decline in body condition, but stream temperature and partial drying in runoff streams likely contributed to these results. Though my modeling work suggests that groundwater streams may provide a thermal refuge for smallmouth bass under future climate conditions during summer months, my field study results indicate that smallmouth bass in many groundwater streams may respond to summer conditions more similarly to runoff streams than anticipated. There is a need for further research into the mechanisms by which climate change will affect smallmouth bass and whether differences can be expected between runoff and groundwater streams.

While we did not find any significant changes in smallmouth bass diet over the course of summer from either groundwater or runoff streams, it is possible that drought conditions could lead to summer diet shifts and these could be exacerbated by climate change. Stream drying causes fish to crowd into pool habitat where competition could be high which can lead to altered diets especially as largemouth bass *Micropterus salmoides* prefer pool habitat and have been shown to displace smallmouth bass from these habitats (Sowa and Rabeni 1995). Changing temperatures and hydrologic regime could also facilitate invasion by exotic species (Rahel and Olden 2008) which may outcompete native prey species. These changes could lead to different available prey and altered diets under future climates. More research is needed on this and whether groundwater and runoff streams may differ in changes in prey species and diets of smallmouth bass.

Though my smallmouth bass population model only simulated a single stream from a runoff flow regime, it has implications for management of smallmouth bass in the coming century across their southern-most range. My model results indicate that smallmouth bass populations could decline drastically in runoff streams such as the Buffalo River due to increased drought and flooding frequency and severity. However, smallmouth bass in streams from other flow regimes could have very different responses to climate change. For example, drought impacts are likely to be much lower in groundwater streams as they maintain a much more stable base flow than runoff streams during summer months. However, intermittent streams may be even more susceptible to the effects of increasing drought as they typically have much flashier flows (Leasure et al. 2016). Many intermittent streams do not currently maintain large populations of smallmouth bass (Magoulick 2000), and it is possible that these streams may be more susceptible to extinction than the population that I modeled. We were unable to model any additional streams to provide a comparison to the Buffalo River due to insufficient data in this region. Future work could be directed towards collecting empirical data in streams from different flow regimes in order to construct similar models for comparison.

Within the Ozark-Ouachita Interior Highlands, three subspecies of smallmouth bass exist, the Northern Smallmouth Bass, the Neosho smallmouth bass, and the Ouachita lineage smallmouth bass (Brewer and Orth 2015). These subspecies could be differentially adapted to stream systems and thus respond to climate change differently (Brewer and Long 2015). For example, it is unknown whether Neosho and Ouachita smallmouth bass could be better adapted to warm water temperatures than the northern strain, though they live at the very southern range extent of smallmouth bass (Brewer and Long 2015). It is important to for managers to consider the differences among strains and continue to preserve the unique genetic populations in the future. Future work should attempt to better identify differences among subspecies in terms of bioenergetics parameters and habitat requirements.

In conclusion, I found that climate change could affect smallmouth bass growth rate potential by increasing growth potential during winter months, and decreasing growth potential during summer months. The rate of change is dependent on stream type where groundwater streams are more moderated in temperature than runoff streams. I also found that smallmouth bass body condition declined during summer months in two of three years that I collected fish and that the rate of decline was independent of stream type. However, in the third year of study, smallmouth bass from two runoff streams declined in body condition while no other streams demonstrated trends. Finally, I found that climate change could negatively affect smallmouth bass abundance in Buffalo River, a runoff stream within the Ozark-Ouachita Interior Highlands. In particular, drought conditions could lead to large population reductions. Adjusting harvest regulations could help to mitigate some of these negative effects, but likely would not be enough to prevent population declines. Relatively little work has been conducted to examine the effects of climate change on warmwater species at the southern range extent. Smallmouth bass are an important species ecologically and economically in the region and it is imperative that we better understand how this species may be affected by climate change. These results could have implications for how smallmouth bass and similar species are managed into the coming century.

References

Brewer, S. K., and D. J. Orth 2015. Smallmouth bass *Micropterus dolomieu* Lacepéde, 1802. Pages 9-26 *in* M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Brewer, S. K., and J. M. Long. 2015. Biology and ecology of Neosho smallmouth bass and the genetically distinct Ouachita lineage. Pages 281-296 *in* M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Leasure, D.R., Magoulick, D.D., & Longing, S.D. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32: 18-35.

Magoulick, D.D. 2000. Spatial and temporal variation in fish assemblages of drying stream pools: The role of abiotic and biotic factors. Aquatic Ecology 34: 29-41.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521-533.

Sowa, S., C. F. Rabeni. 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.