Accepted: 6 September 2016
DOI: 10.1111/eff.12320

ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

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

Christopher R. Middaugh[1] | **Brin Kessinger**[2] | **Daniel D. Magoulick**[3]

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

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

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

Correspondence
Christopher R. Middaugh, Arkansas Cooperative Fish & Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, AR, USA.
Email: cmiddau@uark.edu

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^{-1} day^{-1} in runoff streams and 0.002 g g^{-1} day^{-1} in groundwater streams by the 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^{-1} day^{-1} in runoff and 0.0014 g g^{-1} day^{-1} 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.

KEYWORDS
bioenergetics, climate change, growth rate potential, smallmouth bass, water temperature

1 | 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 (Christie & Regier, 1988; Magnuson, Crowder, & Medvick, 1979). Water temperatures are also critical to structuring the distribution of organisms, for example, by limiting salmonids to high elevations in some regions (Flebbe, 1994) and limiting the latitudinal distribution of smallmouth bass (*Micropterus dolomieu*) (Shuter, MacLean, Fry, & Regier, 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 colonisation (e.g., smallmouth bass range expanding farther north; Vander Zanden, Olden, Thorne, & Mandrak, 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, Magoulick, & Longing, 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, Rabeni, Annis, & Sowa, 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, Taylor, Schlee, Zorn, & Infante, 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 characterised (Brewer & Orth, 2015) including bioenergetics parameters (Whitledge, Hayward, Zweifel, & Rabeni, 2003). Although 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, Hayward, & Rabeni, 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 range due to climate change (Dunlop & Shuter, 2006; Vander Zanden et al., 2004), 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, Stefan, & Eaton, 2003). In a comparison of smallmouth bass growth rate in four streams across a latitudinal gradient, Pease and Paukert (2014) 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, for example, 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 favours 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 versus 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 ten 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 characterised 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.

2 | MATERIALS AND METHODS

2.1 | Air and water temperatures

We selected fourteen streams in the Ozark–Ouachita Interior Highlands of Arkansas, Missouri and Oklahoma that contained smallmouth bass and had United States Geological Survey (USGS) river gages that collected water temperature data (Figure 1; Appendix 1). All temperature data for each site were downloaded (range 1–11 years; Appendix 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

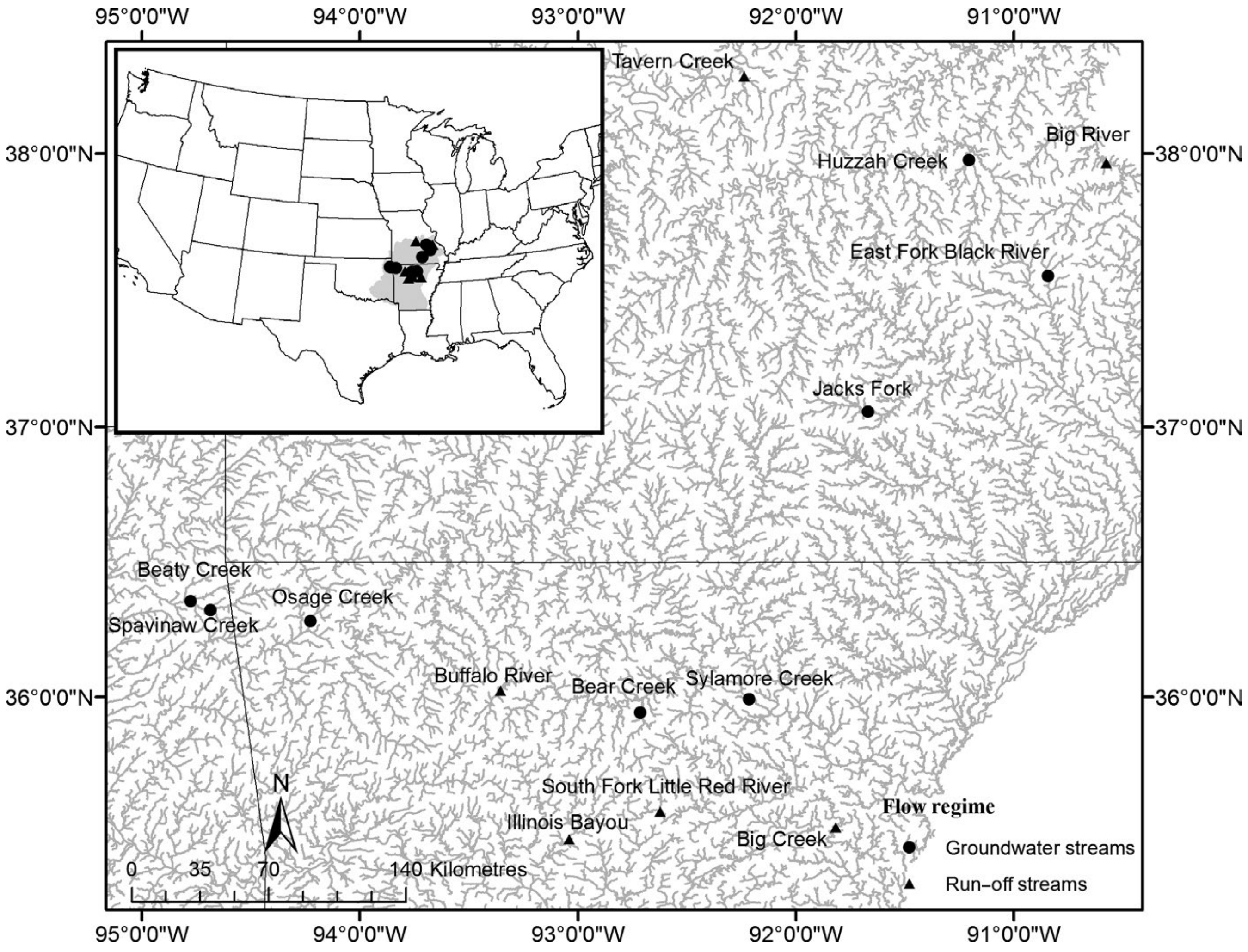

FIGURE 1 Location of sites across the Ozark–Ouachita Interior Highlands of Arkansas, Oklahoma and Missouri (shaded in grey). Each site corresponds to a USGS river gage which collects stream temperature data. Sites from runoff streams are designated with a triangle, and sites from groundwater streams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

TABLE 1 Linear regression results relating air and water temperatures from each site. Air temperature data were 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	.37	.79	Groundwater
Beaty Creek	6.23	.65	.92	Groundwater
East Fork Black River	2.66	.84	.96	Groundwater
Huzzah Creek	5.56	.97	.98	Groundwater
Jacks Fork	4.16	.88	.97	Groundwater
Osage Creek	10.00	.49	.79	Groundwater
Spavinaw Creek	8.66	.49	.88	Groundwater
Sylamore Creek	4.03	.76	.97	Groundwater
Big Creek	3.22	.82	.98	Runoff
Big River	1.80	.96	.99	Runoff
Buffalo River	4.67	.77	.96	Runoff
Illinois Bayou	1.85	.92	.96	Runoff
South Fork Little Red	2.34	.88	.97	Runoff
Tavern Creek	2.41	.95	.99	Runoff

(Alder & Hostetler, 2013) to determine modelled historical air temperatures (1950–2005) and future air temperatures under climate change for two decades (2040s and 2090s). 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.

2.2 | Bioenergetics modelling

We created a bioenergetics simulation based on the Wisconsin bioenergetics model (Hansen, Johnson, Kitchell, & Schindler, 1997) but coded in program R (R Development Core Team 2008) and parameterised for smallmouth bass (Shuter & Post, 1990; Whitledge et al., 2003, 2006; Wrenn, 1980; Zweifel et al., 1999). All simulations were run for a 300-g fish (275 mm (Kolander, Willis, & Murphy, 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 (Dauwalter & Fisher, 2008; Rabeni, 1992). Energy density of prey was set at 3,063 J/g for crayfish (*Procambarus* crayfish; Eggleton & Schramm, 2002), 3,853 J/g for fish prey (fathead minnow (*Pimephales promelas*); Whitledge et al., 2003) and 3,421 J/g 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

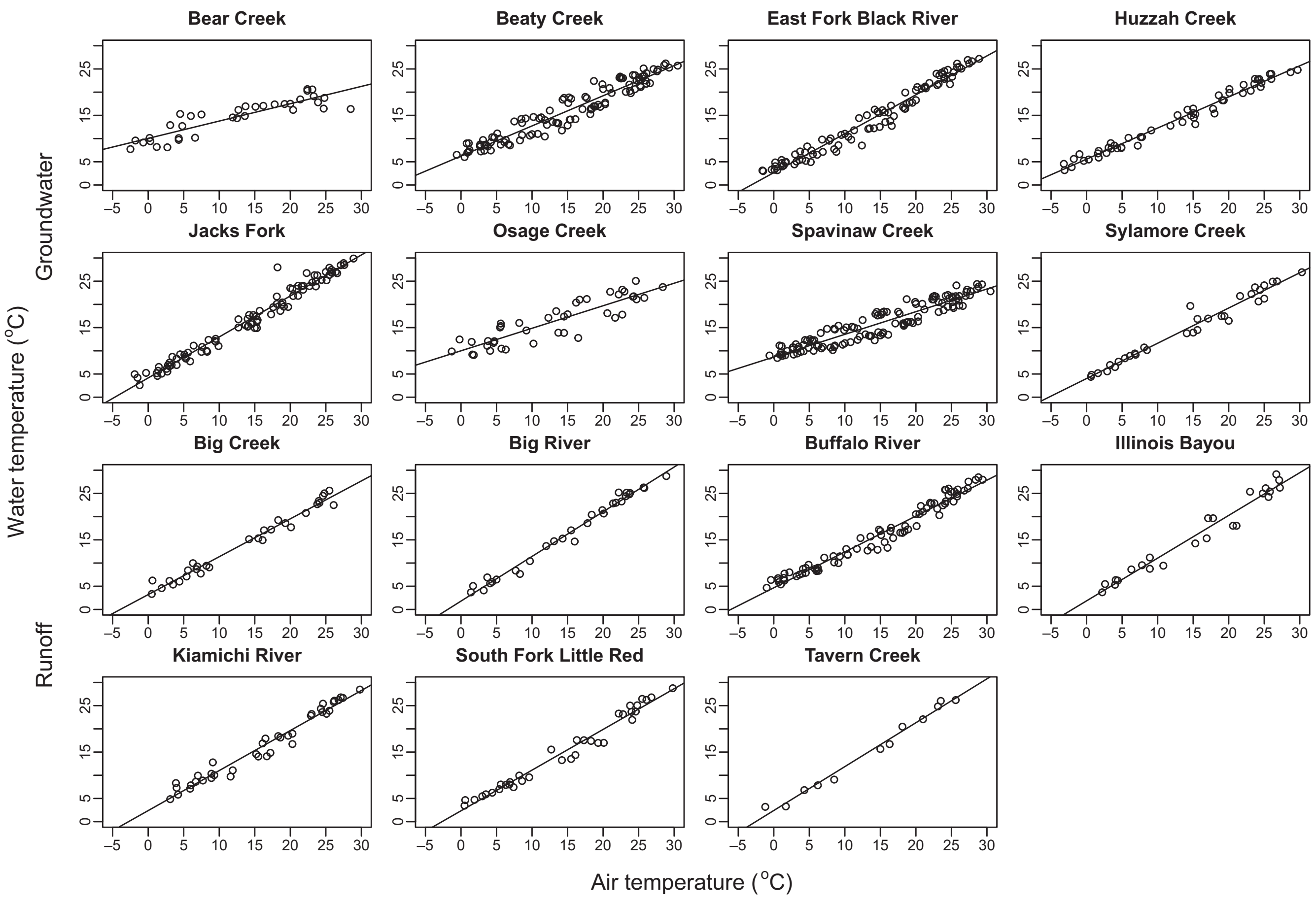

FIGURE 2 Linear regression models for each site relating mean monthly air temperature (from NOAA National Climate Data Center) and mean monthly water temperature (from USGS river gage specific to each site). Model results for each site are shown in Table 1

bass growth with all other factors being held constant (e.g., Coulter, Sepúlveda, Troy, & Höök, 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} day^{-1}). This range of consumption values is much wider than a fish likely experiences naturally, but we chose to model this wide range 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.

3 | RESULTS

Air and water temperatures were significantly linearly related at all sites with all R^2 values >0.78 (Table 1; Figure 2). Groundwater streams typically showed less variation in temperature over the course of the year than runoff streams (Figure 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 the end of century. Future predicted water temperatures corresponded with predicted future air temperatures (Figure 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 (Figure 4). Runoff streams typically showed an increase in GRP during winter, spring and fall months (e.g., 0.001 g g^{-1} day^{-1} increase in March GRP by mid-century; 0.003 g g^{-1} day^{-1} increase in March GRP by the end of century), but a decrease in GRP during summer months (e.g., 0.001 g g^{-1} day^{-1} decrease in August GRP by mid-century, 0.006 g g^{-1} day^{-1} decrease in August GRP by the end of century).

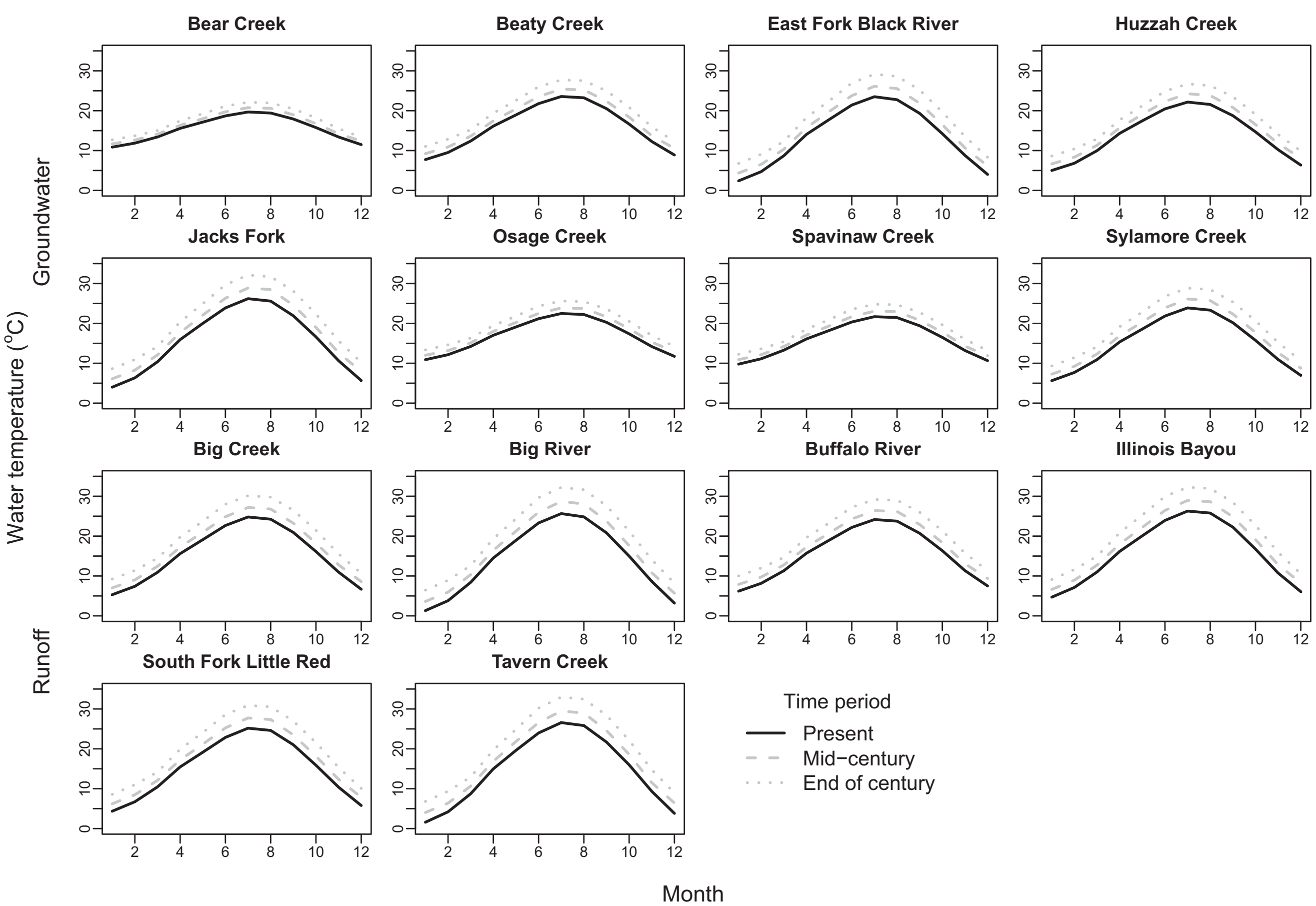

FIGURE 3 Predicted historical (1950–2005; solid line), mid-century (2040–2049; long dash) and end of century (2090–2099; short dash) mean monthly stream temperatures calculated using linear regression predictive models for each stream and air temperature data from the USGS Climate Change Viewer ensemble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

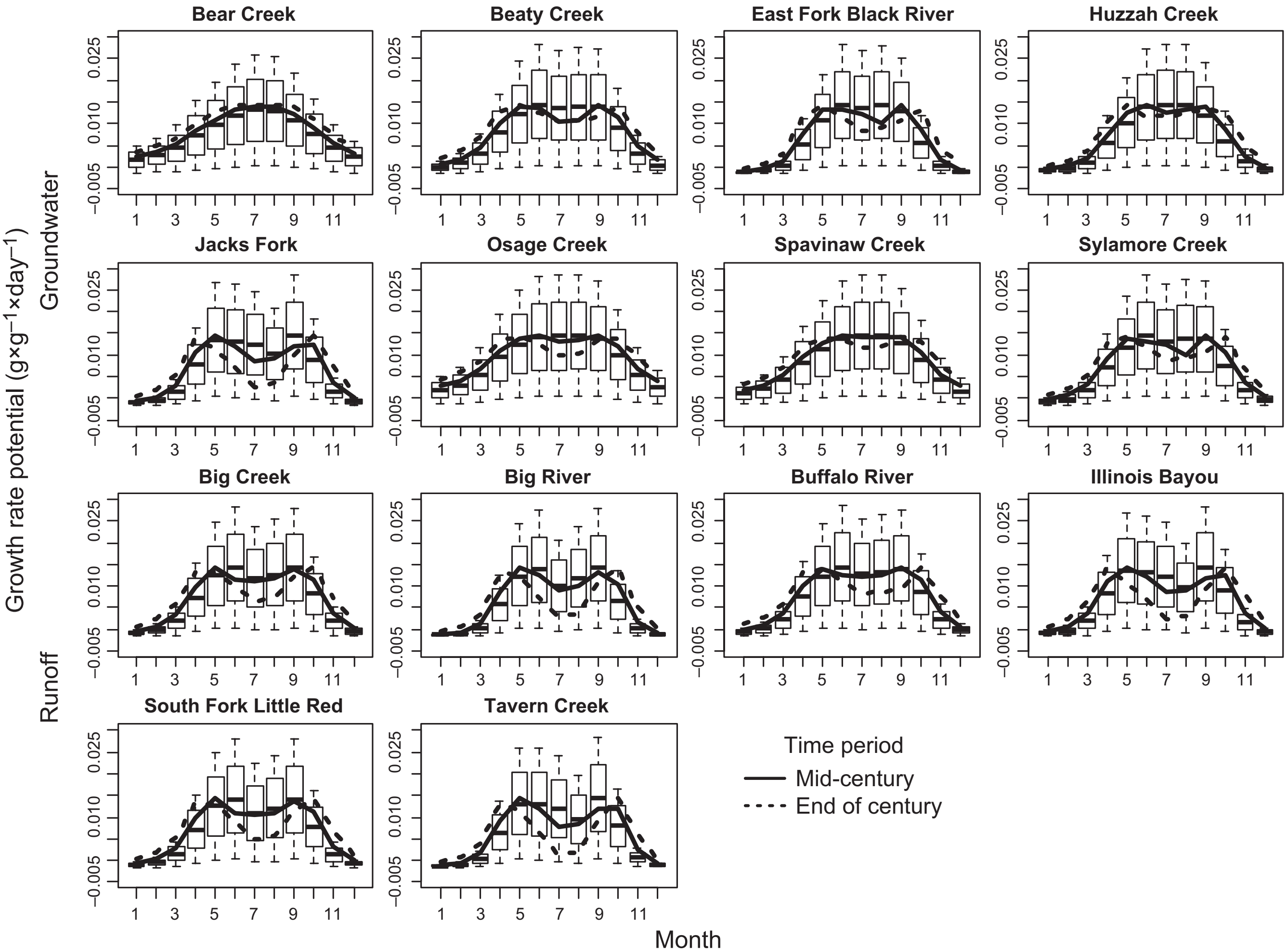

FIGURE 4 Results of all growth rate potential models for adult smallmouth bass (*p* value range = .1–1) for present climate conditions (box plots), and mean of all growth rate potential models at mid-century (solid line) and end of century (dashed line). The top two rows are groundwater streams, and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

Groundwater streams showed similar trends, but at a lower magnitude (e.g., 0.001 g g^{-1} day^{-1} and 0.003 g g^{-1} day^{-1} increase in March GRP for mid- and end of century respectively; 0.001 g g^{-1} day^{-1} and 0.003 g g^{-1} day^{-1} 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 (Figures 2 and 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 $t = -3.54$, $p = .007$; end of century $t = -3.18$, $p = .014$; Figure 6). Groundwater streams had a more positive change in GRP than runoff streams in end-of-century simulations during spring months ($t = 2.80$, $p = .016$; Figure 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 (Figure 5). Runoff streams had a significantly more negative change in growth rate potential than groundwater streams in end-of-century simulations during summer months ($t = 2.99$, $p = .012$; Figure 6).

4 | 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 modelled streams. Although 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

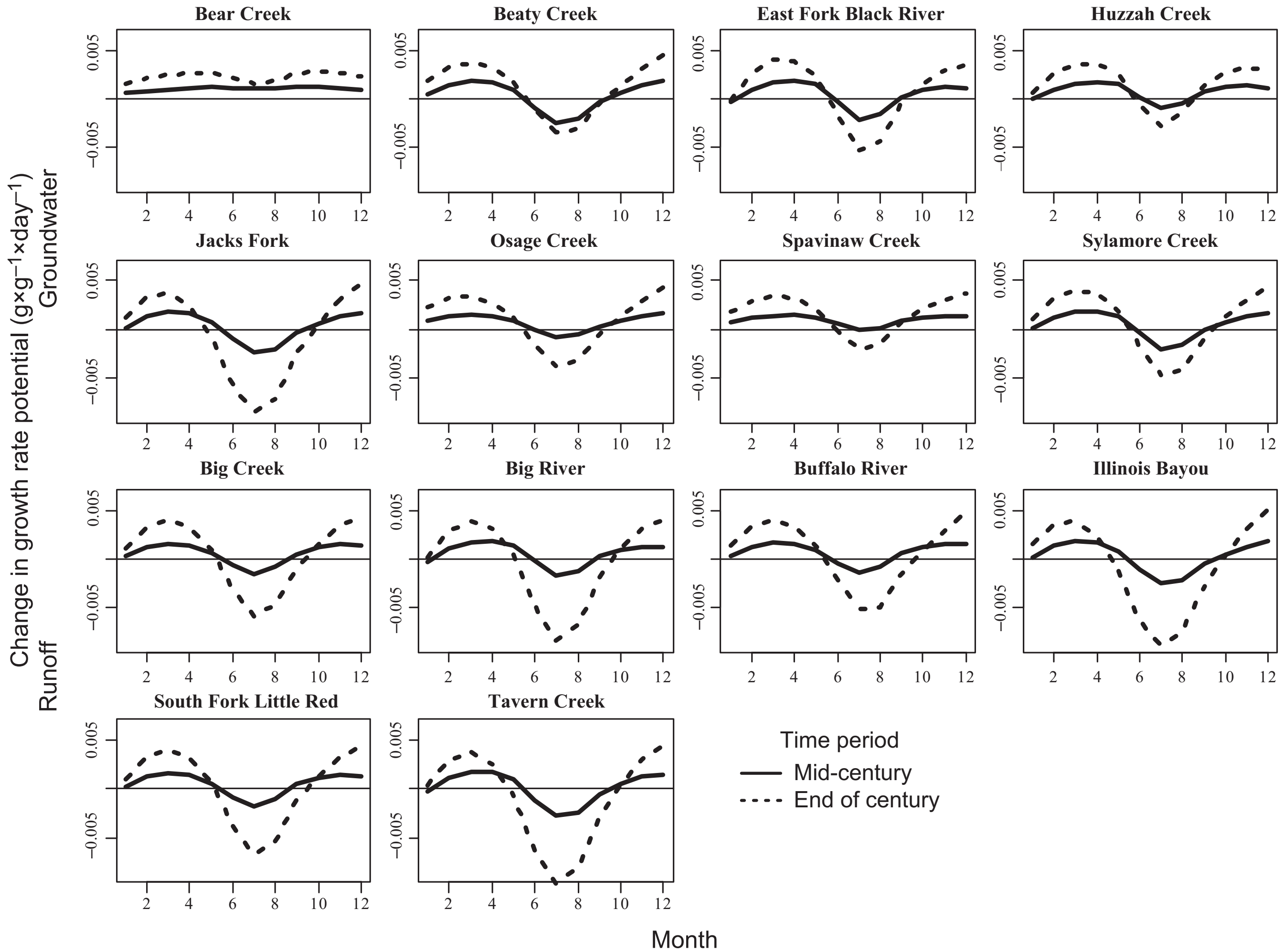

FIGURE 5 Change in growth rate potential from present for each stream at both time periods. The solid horizontal line indicates no change from present. The top two rows are groundwater streams, and the bottom two rows are runoff streams

have higher abundances of juvenile smallmouth bass, that is, better reproduction (Brewer, 2013) and lotic smallmouth bass abundance in Missouri are positively associated with higher spring-flow volumes (Brewer, Rabeni, Sowa, & Annis, 2007). 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 modelled have a mean monthly temperature >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 the end of century, this increases to four groundwater streams, and all seven runoff streams exceed this threshold for at least one month out of the year. Similarly, Bouska, Whitledge, and Lant (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 modelled 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 behaviourally adapt to changing water temperatures. Adult smallmouth bass can migrate to regulate body temperature during winter months in Ozark streams with groundwater inputs (Peterson & Rabeni, 1996; Westhoff, Paukert, Ettinger-Dietzel, Dodd, & Siepker, 2016). Therefore, it is plausible that smallmouth bass could regulate body temperature during summer months by utilising spatial variations in thermal habitat, similar to salmonids (e.g., rainbow trout; Ebersole, Liss, & Frissell, 2001). Many streams in this region are thermally heterogeneous with cooler water patches due to stream stratification (Matthews, 1998) and groundwater inputs (Westhoff & Paukert, 2014). Groundwater inputs into

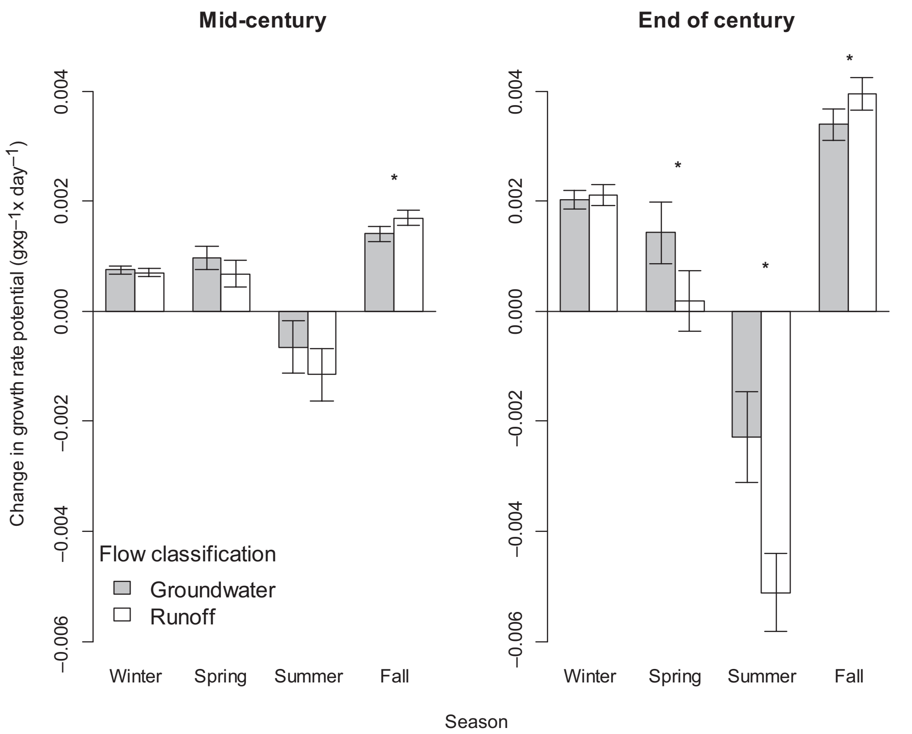

FIGURE 6 Mean seasonal change in growth rate potential from present for both flow classifications at both time periods. Asterisks indicate a significant difference ($p < .05$) in the mean value of the change in growth rate potential between groundwater and runoff streams based on a paired t-test. Error bars show standard error

streams can range from large springs (e.g., Alley Spring on the Jack's Fork river; discharge = 2.7 m^3/s; Mugel, Richards, & Schumacher, 2009) with long downstream influence (Westhoff & Paukert, 2014), to small seepages associated with channel curvature with localised influence (Dugdale, Bergeron, & St-Hilaire, 2015). Smallmouth bass could migrate (Westhoff et al., 2016) or use other behavioural adaptations to utilise 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 (Homan, Girondo, & Gagen, 2005; Magoulick, 2000). This drying would prevent migrations of smallmouth bass in many runoff streams during summer months (Hafs, Gagen, & Whalen, 2010). More data are needed on groundwater inputs into many of these systems to better understand available thermal refuges. The streams that we modelled encompass the range of several subspecies of smallmouth bass (Interior Highland intergrade and Neosho smallmouth bass (*Micropterus dolomieu velox*); Brewer & 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., Almodóvar, Nicola, Ayllón, & Elvira, 2012; Carlson et al., 2015; Pease & Paukert, 2014; Peterson & Kwak, 1999). Predictive relationships between air and water temperatures generally improve at longer timescales (Morrill, Bales, & Conklin, 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 levelling of stream temperatures at high air temperatures (Figure 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 modelling efforts because of our coarse timescale 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, although 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, as 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, Lyttle, & Brown, 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 minimising 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 in 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 & 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 Retrieved from 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 S. D. Gerking (Ed.), *The biological basis of freshwater fish production* (pp. 89–111). New York, NY: Wiley and Sons Inc.

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 M. D. Tringali, J. M. Long, T. W. Birdsong & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (pp. 9–26). Bethesda, MD: American Fisheries Society, Symposium 82.

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.

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.

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.

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*. Madison, WI: University of Wisconsin Sea Grant Institute.

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., … 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., … 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*. New York, NY: Chapman and Hall.

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. (2003). 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., & Kwak, T. J. (1999). Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecological Applications*, *9*, 1391–1404.

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

Poff, N. L., Richter, B., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, 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*. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Retrieved from 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., 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., & Post, J. R. (1990). Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society*, *119*, 314–336.

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. Bethesda, MD: American Fisheries Society.

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., 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. (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., & Rabeni, C. F. (2002). Maximum daily consumption and respiration rates at four temperatures for five species of crayfish from Missouri, U.S.A. (Decapoda, *Orconectes* spp.). *Crustaceana*, *75*, 1119–1132.

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.

How to cite this article: Middaugh CR, Kessinger B, Magoulick DD. Climate-induced seasonal changes in smallmouth bass growth rate potential at the southern range extent. *Ecol Freshw Fish*. 2018;27:19–29. https://doi.org/10.1111/eff.12320

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