



Developing precipitation- and groundwater-corrected stream temperature models to improve brook charr management amid climate change

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Abstract Conserving coldwater stream ecosystems in a warming world requires understanding how water temperature changes will affect the sustainability of coldwater fish populations such as brook charr (*Salvelinus fontinalis*). To date, many models for predicting stream temperature have either assumed spatially uniform (inaccurate) air-stream temperature relationships or required expensive measurement of hydrometeorological drivers (e.g., solar radiation, convection) in a manner impractical for fisheries management. Hence, we developed an accurate, cost-effective, management-relevant modeling approach for projecting how changes in air temperature, precipitation, and groundwater inputs will affect coldwater stream temperatures and brook charr survival and growth in Michigan, USA. Precipitation- and groundwater-corrected models predicted stream temperatures more accurately than air-stream temperature

models. Projected stream warming intensified in proportion to simulated air temperature warming and was most extreme in surface runoff-dominated streams with limited groundwater-driven thermal buffering. However, groundwater-dominated streams will not invariably provide sufficient coldwater habitats for brook charr survival and growth if groundwater temperatures increase or groundwater inputs decline due to reduced precipitation. Amid resource limitations, fisheries managers can use the stream temperature modeling approach described herein to predict effects of climate change on brook charr survival and growth and take actions to facilitate their sustainability in riverine systems.

Keywords Brook charr · Climate change · Coldwater streams · Groundwater · Growth · Precipitation · Survival

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Introduction

Streams provide important ecosystem services (e.g., recreation; water for municipal, industrial, and agricultural use; Loomis et al., 2000), but they are highly vulnerable to climate change (Woodward et al., 2010), human land use (LeBlanc et al., 1997; Kaushal et al., 2010), and associated thermal and physical habitat impairment for riverine organisms (Hershkovitz et al.,

2015; Kanno et al., 2015). Climate change has been projected to impact streams through numerous mechanisms, including increased water temperatures (including groundwater) and alterations to hydrological regimes (e.g., more frequent heavy precipitation, reduced snowpack), which alter habitat availability and quality for aquatic biota (Woodward et al., 2010; Snyder et al., 2015; Carlson et al., 2016). In addition, stream temperatures throughout the United States and the world have risen due to urbanization, agriculture, and other human land uses that create impervious surfaces, increase heated runoff, reduce riparian canopy cover and shading, and increase turbidity within streams (LeBlanc et al., 1997; Kaushal et al., 2010). Water temperature is a fundamental factor influencing the suitability and productivity of stream habitats for aquatic biota, especially thermally sensitive coldwater fishes. Hence, projected increases in stream temperatures resulting from short- and long-term changes in climate and land use are cause for concern among fisheries professionals, policy makers, and allied stakeholders (e.g., non-governmental organizations, general public), particularly those charged with conserving coldwater fishes.

As an example, brook charr *Salvelinus fontinalis* (Mitchill, 1814) are adapted to coldwater environments and have a relatively low thermal tolerance threshold (Raleigh, 1982) that makes them particularly sensitive to stream temperature warming. In addition, brook charr are valuable from ecological, economic, recreational, and cultural perspectives throughout their native and introduced ranges (Godby et al., 2007; USFWS, 2011; Karas, 2015). Hence, projecting effects of climatic and land use changes on stream temperatures, precipitation regimes, and ultimately brook charr population viability and productivity is needed to develop effective management strategies for conserving this species in a warming world.

Historically, regression models for predicting stream temperature have included air temperature as the only driver of water temperature because it is surrogate for solar radiation, the factor that most strongly influences stream temperature (Webb et al., 2008). Despite the importance of understanding how projected changes in air temperature affect stream temperature, air-stream temperature models do not account for other key thermal drivers—including groundwater input, precipitation dynamics (e.g., magnitude, intensity), watershed land cover, and riparian

shading—that have the potential to significantly affect stream temperature regimes (Constantz, 1998; Ebersole et al. 2003). Until recently, stream temperature models have largely ignored variability in groundwater dynamics (e.g., magnitude, temperature) among streams and stream reaches, thereby decreasing the accuracy of thermal forecasting in a changing climate, particularly in headwater areas where groundwater inputs tend to be relatively large (Snyder et al., 2015). By accounting for stream- and reach-level heterogeneity in groundwater dynamics, groundwater-corrected stream temperature models have the potential to provide a more realistic, reliable method for evaluating stream temperature warming than air-stream temperature models. In turn, groundwater-corrected stream temperature models can be used to inform land use planning and thermal habitat management actions needed to facilitate brook charr sustainability (e.g., forest canopy rehabilitation, riparian protection).

As a buffer to daily and seasonal temperature alterations, groundwater generally causes stream temperature to be cooler in summer and warmer in winter than in streams dominated by surface runoff, especially in headwater reaches (Webb et al., 2008). Thermal buffering is ecologically important because it has the potential to mitigate effects of climate change on coldwater fishes and their habitats. Despite the ecological significance of groundwater, its incorporation into stream temperature models can be confounded by the complexity of groundwater dynamics, especially heterogeneity in groundwater temperatures and input magnitudes among stream reaches (Snyder et al., 2015). Although stream heat budget models incorporate groundwater and other atmospheric, meteorological, and hydrological variables to predict water temperature (Leach & Moore, 2011; Westhoff et al., 2011), they are expensive, data-intensive, and generally impractical for use in fisheries management (Dunham et al., 2005; Snyder et al., 2015). Groundwater-corrected stream temperature regressions were recently developed to inform brook charr management in Virginia, USA (Snyder et al., 2015), but these models did not include other important thermal drivers (e.g., precipitation), nor was their applicability evaluated in other areas that have socio-ecologically valuable populations of brook charr and other coldwater fishes (e.g., Midwestern USA). Developing a methodology to integrate groundwater and precipitation dynamics into stream temperature modeling is

important because it can enhance stream management for thermal resilience using readily measureable temperature drivers. More broadly, such a methodology can support resilience-based management programs for coldwater streams that improve the ability of these ecosystems to absorb disturbances while retaining their ecological structure and function (Carlson et al., 2016, 2017; Paukert et al., 2016).

Compared to groundwater, effects of precipitation on stream temperature are infrequently studied. Precipitation is rarely included as an explanatory variable in stream temperature models (Snyder et al., 2015), perhaps because potential processes through which precipitation affects water temperature (e.g., changes in timing and magnitude of surface runoff delivered to channels, reduced relative influence of groundwater inputs on temperature, changes in turbidity) are indirect and difficult to measure. As such, the effects of climate change on precipitation, and resultant effects on stream temperature, have not been widely studied. In the Great Lakes region, climate change is expected to increase the frequency and intensity of precipitation events, particularly during winter and spring (Cherkauer & Sinha, 2010; Hayhoe et al., 2010), with potential effects on stream temperature. For example, precipitation may increase the discharge and volume of water exposed to solar radiation, causing stream temperature to decrease or rise at a slower rate. Alternatively, precipitation may increase sediment erosion, water turbidity, and absorption of solar radiation, causing stream temperature to rise (Merriam et al., 2017). However, the extent to which precipitation regimes in a changing climate will affect groundwater recharge and associated thermal buffering in coldwater streams, and the degree to which managers can influence these relationships via water and land use management practices to sustain coldwater fisheries, have not been thoroughly investigated in the Great Lakes region.

The State of Michigan, USA, has a diversity of coldwater stream ecosystems that experience different air temperature patterns and hydrological regimes (i.e., groundwater/surface runoff dominance) and currently support productive brook charr fisheries that are recreationally and culturally renowned (Godby et al., 2007; USFWS, 2011). Hence, Michigan was an ideal study area for addressing our goal: to develop an accurate, cost-effective, management-relevant approach for modeling coldwater stream temperatures

and brook charr survival and growth to assist fisheries professionals in sustainably managing brook charr amid climate change. Our objectives were to: (1) create stream-specific regression models that account for the influence of air temperature, precipitation patterns, and groundwater input on coldwater stream temperatures in Michigan; (2) compare precipitation- and groundwater-corrected models to air-stream temperature models in terms of accuracy (i.e., exactness of temperature projection); and, (3) use precipitation- and groundwater-corrected models to predict effects of climate change on stream temperature and thermal habitat suitability for brook charr survival and growth until 2056.

Methods

Study area

This study included coldwater streams ($n = 15$) containing brook charr populations located throughout the State of Michigan (Fig. 1). These streams were distributed across most of Michigan from north to south (46.41°N to 42.64°N) to encompass latitudinal variation in air temperatures and thus stream thermal regimes. In addition, study streams exhibited differences in groundwater versus surface runoff dominance, which was evaluated according to base flow index, the proportion of streamflow represented by groundwater. Base flow index was calculated using a digital filter hydrograph separation method described by Neff et al. (2005). Streams were partitioned according to base flow index as: groundwater-dominated (base flow index > 0.60); surface runoff dominated (hereafter “runoff-dominated”; base flow index < 0.60); and intermediate groundwater input (base flow index = 0.60; McKergow et al., 2005; Dukić & Mihailović, 2012). Classifying streams in this manner is a relatively straightforward, scientifically valid way to characterize streams’ predominant hydrological drivers and is thus commonly used by Michigan coldwater fisheries managers and researchers (Carlson et al., 2016, 2017). Moreover, all streams studied were important for Michigan fisheries management because they contained viable, productive populations of brook charr, a thermally sensitive fish and indicator species for predicting how warmer water temperatures will affect stream fishes in both

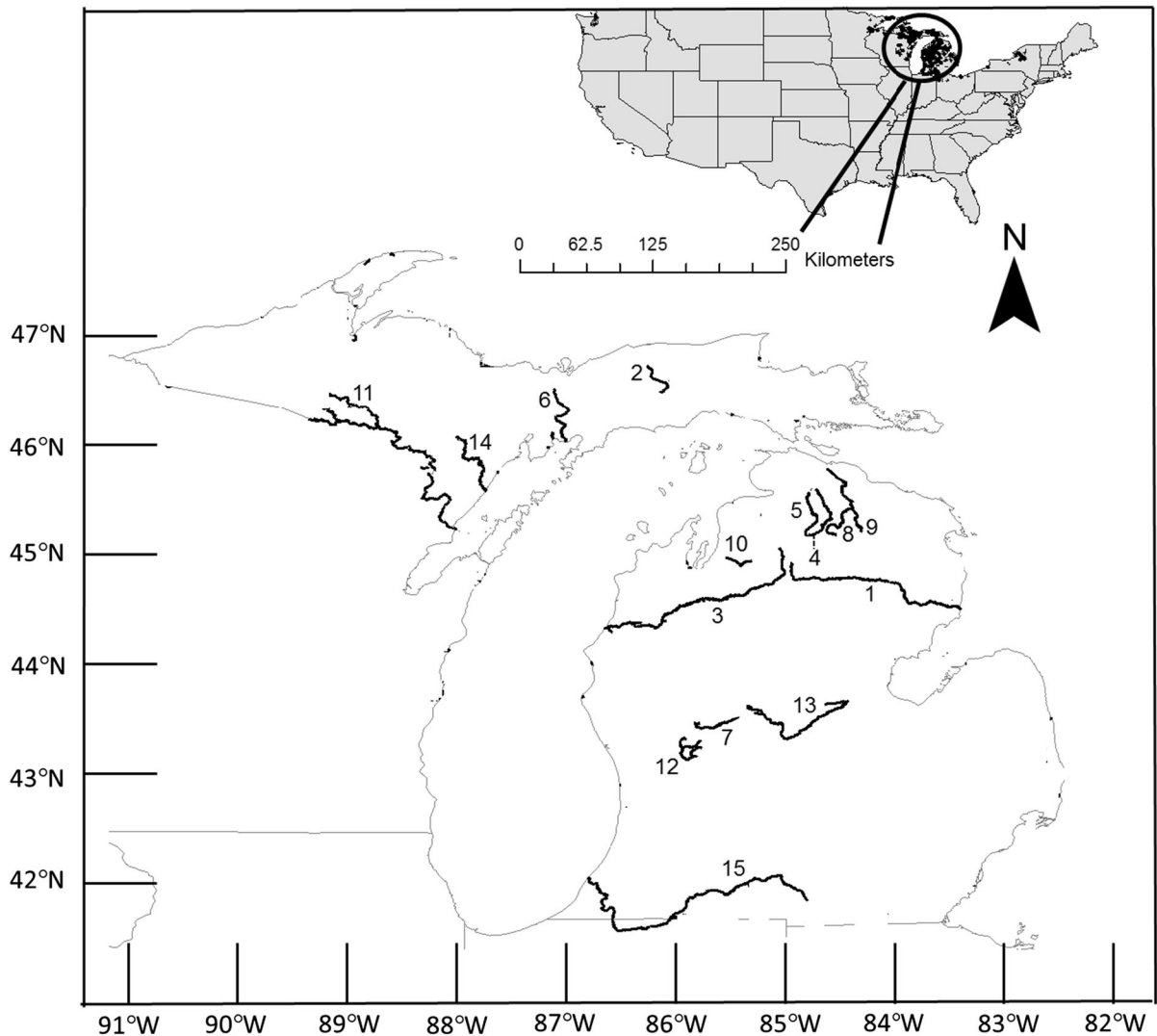


Fig. 1 Map of 15 brook charr streams used for water temperature modeling in Michigan. Streams and corresponding identification numbers are listed in Table 1

groundwater-dominated and runoff-dominated systems (Waco & Taylor, 2010; Carlson et al., 2016).

Temperature and precipitation measurements

Water temperature was measured hourly throughout July and August 2016 and 2017 in headwater portions of all 15 streams. These months were selected because they are generally the warmest and most thermally stressful for Michigan brook charr (Zorn et al., 2011) and would likely encompass the period during which predicted climatic changes would most strongly affect thermal habitat quality and quantity in the state.

Moreover, headwater reaches were selected because they typically receive relatively large groundwater inputs compared to downstream reaches that make them thermally optimal habitats for brook charr during warm summer months in Michigan (Hayes et al., 1998). As a result, headwaters are key habitats for brook charr conservation and management and ideal locations to conduct groundwater-focused stream temperature modeling. Moreover, if headwaters become warmer, temperatures in downstream reaches will also typically increase (given their lower groundwater inputs), making headwaters general predictors of downstream thermal conditions for brook charr

Table 1 Michigan stream information and model parameters

Stream	Map	BFI	Year	Int	MDAT	ADD	PR	<i>P</i>	AICc	Adj <i>R</i> ²	MDAT Adj <i>R</i> ²
Au Sable R.	1	0.67	2016	15.91	0.14	− 0.06	−	< 0.01	43.80	0.79	0.60
			2017	14.45	0.18	− 0.05	−	< 0.01	38.67	0.84	0.70
E. Branch Fox R.	2	0.61	2016	11.13	0.12	− 0.04	−	< 0.01	19.29	0.75	0.46
			2017	10.64	0.02	− 0.03	−	< 0.01	36.87	0.75	0.10
Manistee R.	3	0.61	2016	14.38	0.20	− 0.08	−	< 0.01	51.55	0.80	0.62
			2017	15.53	0.09	− 0.06	−	< 0.01	41.25	0.77	0.71
Pigeon R.	4	0.60	2016	10.52	0.14	−	−	< 0.01	47.04	0.56	−
			2017	9.08	0.21	−	−	< 0.01	77.94	0.58	−
W. Br Sturgeon R.	5	0.60	2016	9.86	0.18	−	−	< 0.01	57.76	0.45	−
			2017	9.45	0.19	−	−	< 0.01	87.34	0.52	−
Sturgeon R.	6	0.59	2016	14.04	0.40	−	− 0.64	< 0.01	75.86	0.89	0.64
			2017	13.35	0.35	−	− 0.55	< 0.01	100.93	0.86	0.65
Tamarack Creek	7	0.55	2016	15.23	0.47	−	− 0.52	< 0.01	40.23	0.90	0.55
			2017	11.37	0.37	−	− 0.31	< 0.01	54.86	0.88	0.80
Black R.	8	0.51	2016	11.98	0.22	−	− 0.40	< 0.01	33.69	0.83	0.77
			2017	11.43	0.22	−	− 0.60	< 0.01	51.52	0.85	0.72
Canada Creek	9	0.51	2016	15.72	0.11	−	− 0.71	< 0.01	49.40	0.78	0.55
			2017	14.22	0.21	−	− 0.60	< 0.01	59.42	0.75	0.62
Rapid R.	10	0.50	2016	11.55	0.08	−	− 1.44	< 0.01	25.72	0.85	0.47
			2017	11.76	0.04	−	− 2.51	< 0.01	69.46	0.84	0.49
Paint R.	11	0.49	2016	18.50	0.32	−	− 0.76	< 0.01	46.37	0.95	0.72
			2017	21.00	0.18	−	− 1.09	< 0.01	67.65	0.81	0.06
Rogue R.	12	0.47	2016	20.28	0.14	−	− 0.46	< 0.01	77.50	0.83	0.57
			2017	16.83	0.22	−	− 1.57	< 0.01	69.38	0.84	0.66
Pine R.	13	0.44	2016	15.58	0.08	−	− 0.20	< 0.01	37.06	0.75	0.50
			2017	13.18	0.06	−	− 0.93	< 0.01	31.03	0.79	0.43
Cedar R.	14	0.38	2016	14.60	0.27	−	− 0.68	< 0.01	51.24	0.77	0.57
			2017	12.76	0.35	−	− 0.63	< 0.01	74.87	0.87	0.74
St Joe R.	15	0.35	2016	17.56	0.23	−	− 0.62	< 0.01	19.65	0.86	0.71
			2017	15.96	0.28	−	− 1.20	< 0.01	62.32	0.89	0.76

Map number refers to stream identifiers in Fig. 1. BFI represents base flow index, the mean rate of base flow divided by the corresponding mean rate of total streamflow (Neff et al., 2005). Year denotes the baseline year and corresponding weather conditions (2016: warm, dry; 2017: cool, wet) from which the model was developed. Other abbreviations denote model intercepts (Int); coefficients for mean daily air temperature (MDAT), accumulated degree-days above mean summer air temperature (ADD, a measure of groundwater input), and cumulative daily precipitation since July 1 (PR); *P* values; bias-corrected Akaike's information criterion scores (AICc); adjusted *R*² values (Adj *R*²) for groundwater- and precipitation-corrected models; and adjusted *R*² values for MDAT-only models (MDAT Adj *R*²)

survival and growth. Water temperature was measured using HOBO Pro v2 data loggers that are accurate within 0.2°C and have a drift of < 0.1°C every year (Onset Computer Corporation, 2009). Data loggers were installed in habitats of intermediate velocity and depth, and were shielded from debris and direct

sunlight using white polyvinyl chloride (PVC) pipes. Water was allowed to flow into the PVC pipes through a series of drilled holes. In all 15 streams, hourly water temperatures were used to calculate the mean daily stream temperature (MDST) as a 24-h average.

Hourly air temperatures and daily precipitation measurements were collected throughout the study period using the Michigan State University Enviro-weather Automated Weather Station Network (EAWSN, 2018) at stations within each stream's watershed. Hourly air temperature data were summarized as mean daily air temperatures (MDAT) for each stream reach. Likewise, precipitation measurements were summarized as cumulative daily precipitation for each reach.

Temperature projections

Three coupled climate models were used to project current and future (i.e., 2036, 2056) July and August air temperatures in each stream reach studied. These models included the Third Generation Coupled Global Climate Model (CGCM3, Canadian Centre for Climate Modelling and Analysis), the CM2 Global Coupled Climate Model (CM2, Geophysical Fluid Dynamics Laboratory at the National Oceanic and Atmospheric Administration), and the Hadley Centre Coupled Model version 3 (HadCM3, Met Office, United Kingdom's National Weather Service). These models were selected because they differ in their thermal input parameters (e.g., solar radiation, trace gases, sulfate aerosols), thereby encompassing a range of climatic conditions that Michigan streams could experience in the future. All coupled climate models were based on the World Climate Research Programme (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel dataset. The spatial resolution of climate models ($\sim 200 \times 200 \text{ km}^2$) was downscaled to a level appropriate for Michigan streams ($12 \times 12 \text{ km}^2$; Maurer et al., 2007) using the Bias-Correction Spatial Disaggregation approach. Current and future projected air temperatures based on the climate models were supplied by the United States Forest Service Eastern Forest Environmental Threat Assessment Center in North Carolina, USA, and calculated using the A2 (820 ppm atmospheric CO_2 by 2100) and B1 (550 ppm atmospheric CO_2 by 2100) climate forcing scenarios from the Special Report of Emission Scenarios (IPCC, 2007). Modeling air temperatures under A2 and B1 conditions represented upper and lower CO_2 emission thresholds for stream temperature prediction.

Coupled climate models produced a range of air temperature predictions that were used to define modeled air temperature warming (MATW) increments for projecting future MDST in each stream. This increment-based approach has been successfully used in previous research to represent wide-ranging scenarios of projected air temperature warming and produce accurate, straightforward (i.e., not overly parameterized) stream temperature models conducive for brook charr management (Snyder et al., 2015). Hence, an air temperature increment-based approach to modeling future stream temperatures was ideal for the purposes of the present study. The MATW increments used herein ($+1.7^\circ\text{C}$, $+3.4^\circ\text{C}$, $+5.1^\circ\text{C}$) reflected the range of differences between current and future air temperatures projected by the coupled climate models and thereby encompassed the climate scenarios predicted for Michigan over the next 40 years (Carlson et al., 2016, 2017). Stream temperatures were also projected under different prevailing weather conditions by applying MATW increments to both 2016 (relatively warm, dry) and 2017 (relatively cool, wet) air temperatures (EAWSN, 2018). These conditions were useful for forecasting future stream thermal regimes because they represented weather extremes for Michigan streams under predicted changes in climate (i.e., temperature, precipitation; Primack, 2000; Parry et al., 2007; Stoner et al., 2013).

Stream temperature models and projections

Least-squares linear regression was used to model MDST as a function of MDAT, groundwater, and precipitation. Initial modeling focused on stream-specific relationships between MDST and MDAT. Streams generally warmed throughout summer but varied in the degree to which MDST was correlated with MDAT, indicating stream-specific variability in how groundwater and precipitation affected stream temperature. Hence, in addition to MDAT, thermal effects of groundwater input and precipitation were modeled in each stream.

In groundwater-dominated streams, the thermal influence of groundwater was calculated as accumulated degree-days above mean summer air temperature (ADD) because it is directly related to summer ground surface temperature, the driver of groundwater temperature during this time of year (Kurylyk et al., 2013). Previous researchers have successfully used ADD to

incorporate groundwater dynamics into stream temperature modeling in Virginia, USA (Snyder et al., 2015). The ADD approach is readily applicable in groundwater-dominated Michigan streams and offers benefits for resource managers (e.g., accuracy, ease of use, inexpensive data collection) compared to complex heat budget models that require detailed atmospheric, meteorological, and hydrological data for each site studied (Webb et al., 2008). Stream temperatures in groundwater-dominated streams were thus modeled as:

$$\text{MDST}_i = m_1 \text{MDAT}_i + m_2 \text{ADD}_i + b_0 \quad (1)$$

where MDST_i is projected MDST ($^{\circ}\text{C}$) on day i , MDAT_i is projected MDAT ($^{\circ}\text{C}$) on day i , ADD_i is the ADD (degree-days) on day i , m_1 and m_2 are regression coefficients, and b_0 is the model intercept.

In runoff-dominated streams, MDST was modeled as a function of MDAT and precipitation using the following equation:

$$\text{MDST}_i = m_1 \text{MDAT}_i + m_2 \text{PR}_i + b_0 \quad (2)$$

where PR_i is the cumulative precipitation (since July 1) on day i and other model components are the same as above. Models including ADD were applied to runoff-dominated streams and those including precip-

had relatively high AICc scores (i.e., low parsimony) compared to MDAT-only models and thus were not considered further.

Groundwater inputs and precipitation may affect stream temperatures under projected climate change scenarios in different ways than they currently do (Kurylyk et al., 2013; Menberg et al., 2014). For example, although the amount of precipitation may remain relatively stable in summer, as predicted for Michigan under both high and low CO_2 emissions scenarios (Hayhoe et al., 2010), the temperature of precipitation (or groundwater) may change significantly in a warming climate. Hence, it was important to model effects of changes in thermal sensitivity of groundwater (TS_{gw} ; change in groundwater temperature per 1°C air temperature increase; Snyder et al., 2015) and precipitation (TS_{pr} ; change in precipitation temperature per 1°C air temperature increase) on future stream temperatures. In practice, this involved increasing model y-intercepts by the product of MATW and TS_{gw} (in groundwater-dominated streams) or TS_{pr} (in runoff-dominated streams). The stream-specific y-intercept increase is a function of TS_{gw} or TS_{pr} and the proportion of streamflow comprised of groundwater (R_{ADD}^2) or precipitation (R_{PR}^2), calculated as:

$$R_{\text{ADD}}^2 = \left[m_2 \left(\frac{S_{\text{ADD}}}{S_{\text{MDST}}} \right) \right] * \left[\left(\frac{1}{n-1} \right) \sum_{i=1}^n \left(\frac{\text{ADD}_i - \overline{\text{ADD}}}{S_{\text{ADD}}} \right) * \left(\frac{\text{MDST}_i - \overline{\text{MDST}}}{S_{\text{MDST}}} \right) \right] \quad (3)$$

itation were applied to groundwater-dominated streams, but these models were not sufficiently parsimonious (according to bias-corrected Akaike's information criterion [AICc], see Analyses section below) to warrant further consideration. In addition, both ADD and precipitation models were applied to streams with intermediate groundwater input, but they

where m_2 is regression coefficient for the ADD_i term in (1), S_{ADD} is the standard deviation of ADD, S_{MDST} is the standard deviation of MDST, n is the number of days, ADD_i is the ADD at day i , $\overline{\text{ADD}}$ is the mean ADD, MDST_i is the MDST at day i , and $\overline{\text{MDST}}$ is the mean MDST (Snyder et al., 2015). Similarly, R_{PR}^2 was calculated as:

$$R_{PR}^2 = \left[m_2 \left(\frac{S_{PR}}{S_{MDST}} \right) \right] * \left[\left(\frac{1}{n-1} \right) \sum_{i=1}^n \left(\frac{PR_i - \overline{PR}}{S_{PR}} \right) * \left(\frac{MDST_i - \overline{MDST}}{S_{MDST}} \right) \right] \quad (4)$$

where m_2 is the regression coefficient for PR_i (cumulative precipitation since July 1) in (2), S_{PR} is the standard deviation of PR , S_{MDST} is the standard deviation of $MDST$, n is the number of days, PR_i is the PR at day i , \overline{PR} is the mean PR , $MDST_i$ is the $MDST$ at day i , and \overline{MDST} is the mean $MDST$. To incorporate R_{ADD}^2 and R_{PR}^2 into stream temperature models, linear regressions were developed between model y -intercepts and R_{ADD}^2 (for groundwater-dominated streams) and y -intercepts and R_{PR}^2 values (for runoff-dominated streams):

$$b_0 = 8.20 + (10.03 * R_{ADD}^2) + e \quad (5)$$

$$b_0 = 4.29 + (14.75 * R_{PR}^2) + e \quad (6)$$

These models explained 68% and 72% of the variation in model y -intercepts, respectively, and residuals were uncorrelated and randomly distributed around zero. Hence, these models were considered suitable for use in stream temperature projection (Snyder et al., 2015). To model how changes in air temperature, TS_{gw} , and TS_{pr} would affect model y -intercepts, the following equations were used for groundwater-dominated and runoff-dominated streams, respectively:

$$B_{0adj} = 8.20 + [(10.03 + (MATW * TS_{gw})) * R_{ADD}^2] + e \quad (7)$$

$$B_{0adj} = 4.29 + [(14.75 + (MATW * TS_{pr})) * R_{PR}^2] + e \quad (8)$$

These adjusted model y -intercepts were used in place of those in model equations (1) and (2) to predict stream-specific $MDST$ as follows:

$$MDST_i = m_1 MDAT_i + m_2 ADD_i + B_{0adj} \quad (9)$$

$$MDST_i = m_1 MDAT_i + m_2 PR_i + B_{0adj} \quad (10)$$

Stream temperatures were modeled under three TS_{gw} and TS_{pr} conditions (0.0, 0.66, 1.0) that spanned a gradient from insensitive streams (i.e., groundwater and precipitation temperature do not change

substantially with air temperature) to highly sensitive streams (i.e., groundwater and precipitation temperature change in proportion to air temperature). The 0.0 condition was included as a reference point and is less realistic than 0.66 and 1.0, which entail groundwater warming in a changing climate (unlike 0.0) and encompass values reported or used in recent stream temperature research (Kurylyk et al., 2013; Snyder et al., 2015). Precipitation- and groundwater-corrected models (Eqs. 9, 10) were used to project $MDST$ in each stream reach in all climate change scenarios (i.e., combinations of $MATW$ [+ 1.7°C, + 3.4°C, + 5.1°C] and TS_{gw}/TS_{pr} [0.0, 0.66, 1.0]).

Stream thermal sensitivity—the increase in stream temperature (0.0 – 1.0°C) resulting from a 1.0°C air temperature increase (Snyder et al., 2015)—was also evaluated for each stream under the three TS_{gw} conditions. Stream thermal sensitivity measurements were derived by using model equations (9) and (10) to calculate $MDST$ for each stream using modeled present-day air temperatures. These temperatures were then subtracted from $MDST$ values calculated under 1.0°C air temperature warming (relative to modeled present-day temperatures). The difference between these two temperatures was treated as an empirical measurement of stream thermal sensitivity (Snyder et al., 2015).

Thermal habitat suitability predictions

Stream-specific temperature projections were compared with temperature ranges for brook charr survival and growth to assess future thermal habitat suitability for these fish under different combinations of $MATW$ and TS_{gw}/TS_{pr} . Temperature ranges for juvenile and adult brook charr survival and growth were obtained from a United States Fish and Wildlife Service Biological Report (Raleigh, 1982) and other peer-reviewed literature (Fry et al., 1946; Baldwin, 1957). In the present study, temperature thresholds (i.e., thermal minima, maxima) were defined in reference to juvenile brook charr (if they differed from those of

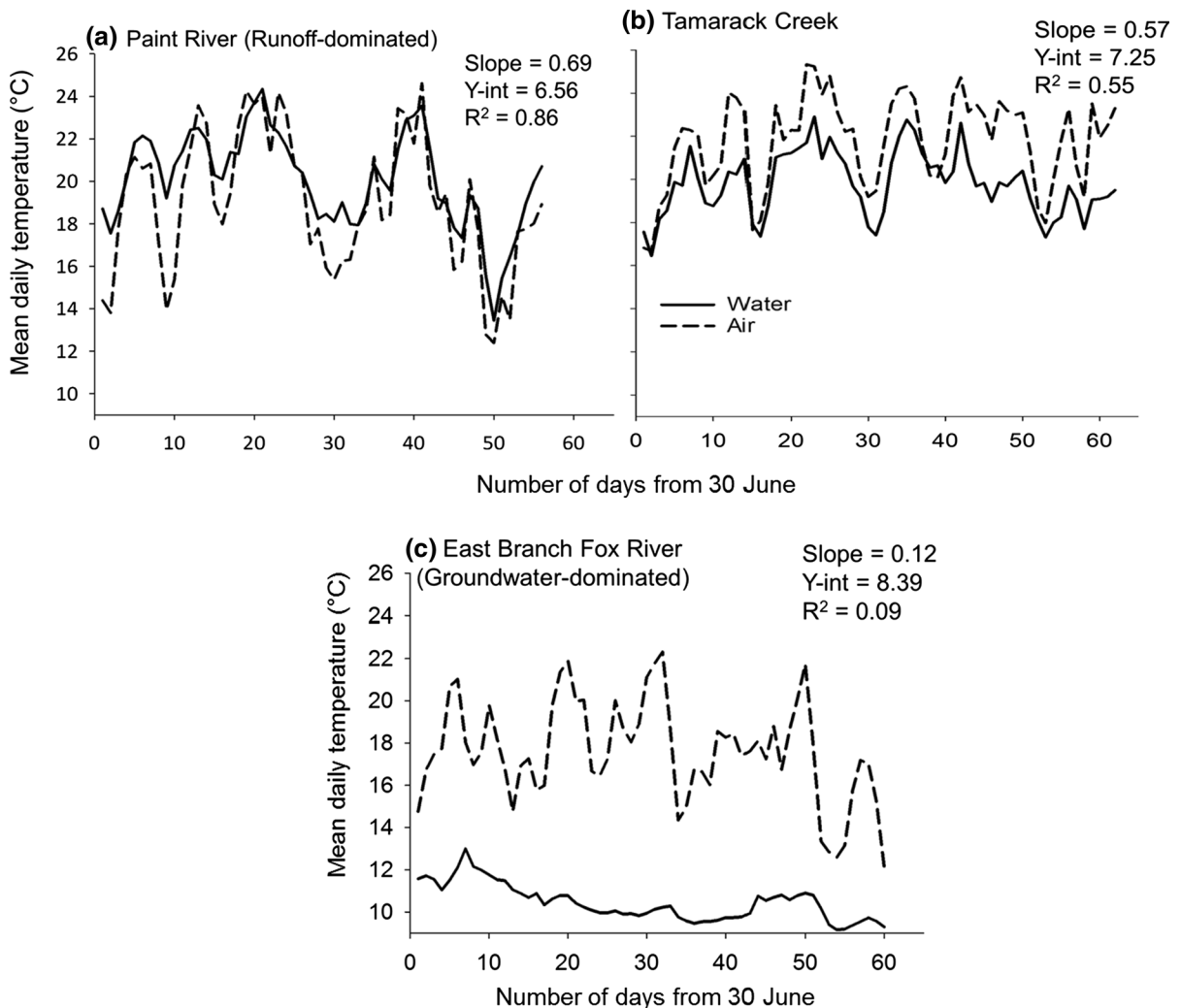


Fig. 2 Relationships between mean daily air temperature and mean daily water temperature in Michigan brook charr streams. Graphs **a**, **b**, and **c** display examples that span the range of air-

stream temperature relationships and corresponding regression statistics (including slope, y-intercept, adjusted R^2) observed in this study

adults) under the premise that resilient brook charr fisheries can only be conserved if young fish survive to adulthood. Streams with optimal brook charr growing conditions were those that had mean July–August temperatures ranging from 11.0 to 16.4°C (Raleigh, 1982). Streams with suitable (but not optimal) temperatures for brook charr growth ranged from 16.5 to 20.4°C (Raleigh, 1982). Streams that were too warm for brook charr growth in July–August had temperatures ranging from 20.5 to 25.3°C (Baldwin, 1957; Raleigh, 1982). Finally, streams that were too warm for brook charr survival in July–August had temperatures greater than 25.3°C (Fry et al., 1946; Raleigh

1982). These temperature ranges were used to calculate the proportion of streams that would remain suitable for brook charr survival and growth under alternative climate change scenarios.

Analyses

Four stream temperature models (i.e., MDAT, MDAT + ADD, MDAT + precipitation, MDAT + ADD + precipitation) were developed and compared for each stream using information-theoretic model selection and bias-corrected AICc (Burnham & Anderson, 2002). Invariably,

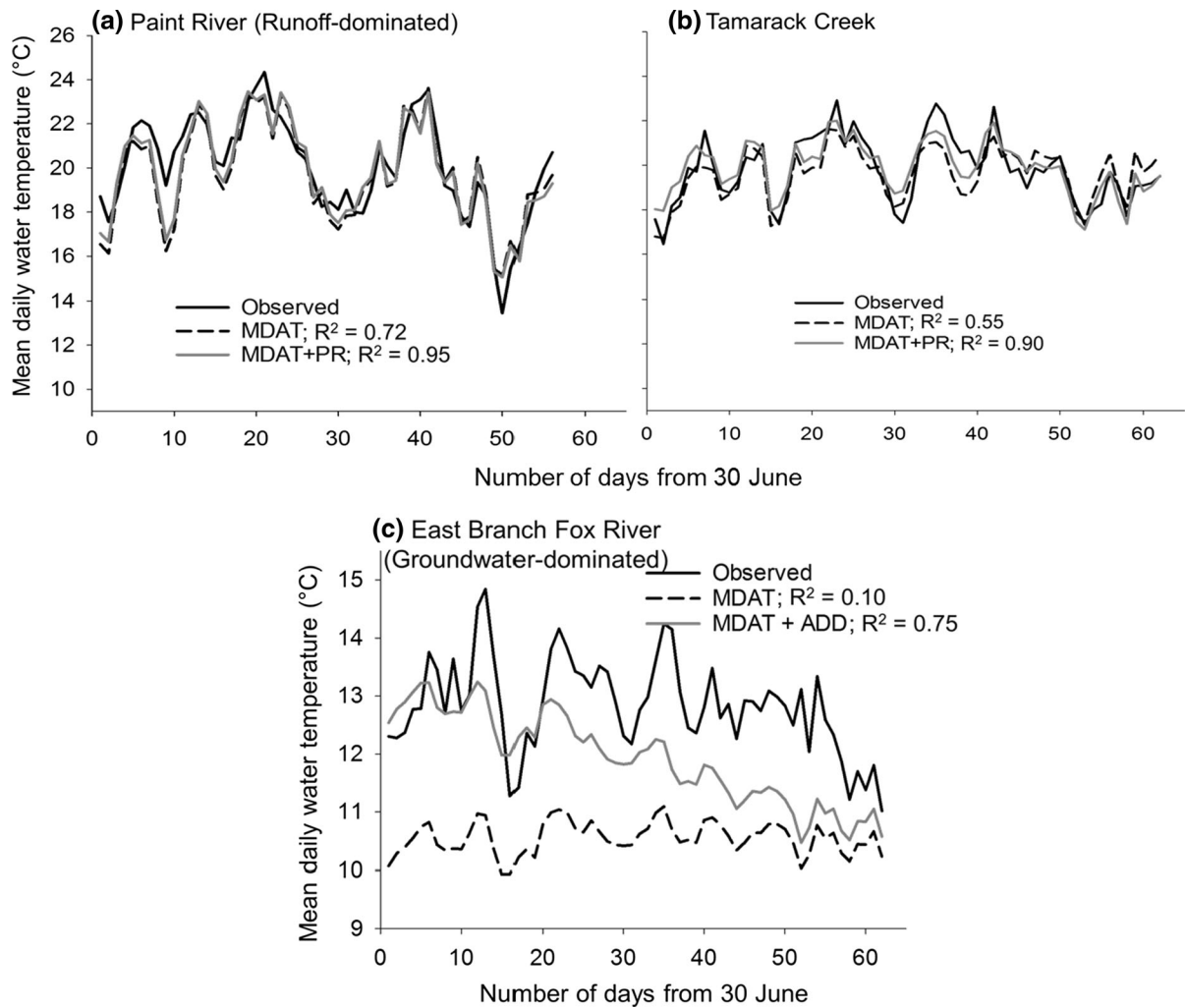


Fig. 3 Comparison of predictions of mean daily water temperature in Michigan streams between linear regressions that used only mean daily air temperature (MDAT) as an independent variable, and models that used both MDAT and an additional predictor (i.e., accumulated degree-days above mean summer air temperature [ADD], cumulative daily precipitation since

July 1 [PR]). Graphs **a**, **b**, and **c** show streams spanning a gradient of base flow from runoff-dominated to groundwater-dominated and encompassing the range of air-stream temperature relationships observed in this study. R^2 values are adjusted R^2

groundwater-dominated streams were modeled most accurately (i.e., lowest AICc scores, Δ AICc generally $\gg 2$) with the groundwater model (MDAT + ADD) and runoff-dominated streams with the precipitation model (MDAT + precipitation); thus, model equations (9) and (10) were applied to each of these stream types, respectively. Models including both ADD and precipitation were occasionally within two AICc units of top-supported models, wherein the additional parameter (relative to the top-performing model) was uninformative (i.e., did not reduce model

deviance) such that interpreting the extra parameter would have caused modeling bias (Burnham & Anderson, 2002; Arnold, 2010). Hence, by only including the top model for each stream, all models received substantial AICc support and only contained informative parameters (i.e., those that reduced model deviance). The predictive power of models was evaluated via temporal cross-validation in 12 of the 15 streams studied herein; necessary temperature data for cross-validation (i.e., pre-2016 or post-2017) were unavailable for the remaining three streams. In

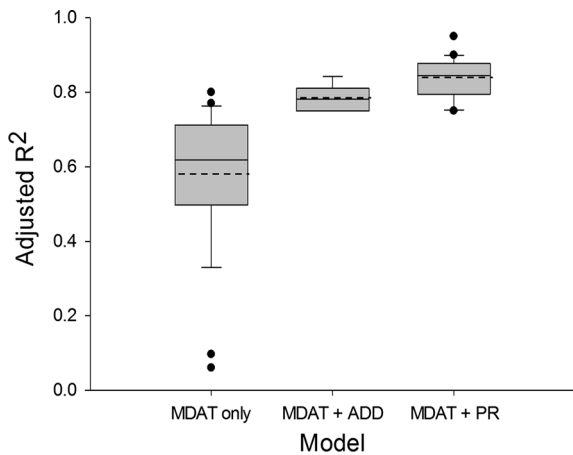


Fig. 4 Comparison of the distribution of adjusted R^2 values for Michigan stream temperature linear regressions that used only mean daily air temperature (MDAT only) as an independent variable, and models that used both MDAT and an additional predictor (i.e., accumulated degree-days above mean summer air temperature [ADD], cumulative daily precipitation since July 1 [PR]). Within each box plot, dashed lines are means and solid lines are medians

particular, models calibrated using 2016/2017 data (i.e., air temperature, stream temperature, ADD or precipitation) were used to predict stream temperatures in other years when water temperatures were measured (i.e., 2015 [$n = 1$ stream], 2018 [$n = 11$

streams]). Models used for temperature prediction were selected based on stream-specific prevailing weather conditions in 2015/2018 (i.e., 2016 model for warm, dry conditions; 2017 model for cool, wet conditions). Model performance was assessed by calculating the absolute and percentage difference between predicted and observed (i.e., field-measured) temperatures in 2015/2018, and determining whether those differences caused changes in projected thermal habitat suitability for brook charr survival and growth. All analyses were performed in RStudio Desktop version 1.1.423 (RStudio, 2015).

Results

Stream temperature models and thermal sensitivity

Relationships between MDAT and MDST were highly variable among the Michigan coldwater streams evaluated (Table 1). Air and stream temperatures were positively correlated in runoff-dominated systems (e.g., Paint River; $R^2 = 0.86$; Fig. 2a) and in streams with intermediate groundwater input (e.g., Tamarack Creek; $R^2 = 0.55$; Fig. 2b) but not significantly correlated in groundwater-dominated streams

Table 2 Results of stream temperature model cross-validation, including observed stream temperatures (Observed), predicted stream temperatures (Predicted), the difference between

predicted and observed temperatures ($\Delta (P-O)$), and the percent difference between predicted and observed temperatures (% difference)

Stream	Observed	Predicted	$\Delta (P-O)$	% Difference	THS	Data year	Model year
Au Sable R.	16.55	16.68	+ 0.13	0.79	Same	2018	2017
E. Branch Fox R.	12.76	12.72	- 0.04	0.31	Same	2018	2016
Manistee R.	16.08	16.17	+ 0.09	0.56	Same	2018	2017
Pigeon R.	13.49	13.39	- 0.10	0.74	Same	2018	2017
Sturgeon R.	22.32	21.78	- 0.54	2.42	Same	2018	2016
Tamarack Creek	19.36	18.61	- 0.75	3.87	Same	2018	2017
Black R.	14.53	14.60	+ 0.07	0.48	Same	2018	2017
Canada Creek	17.66	17.30	- 0.36	2.04	Same	2015	2017
Paint R.	23.33	23.99	+ 0.66	2.83	Same	2018	2017
Pine R.	16.97	16.91	- 0.06	0.35	Same	2018	2016
Cedar R.	17.54	17.62	+ 0.10	0.57	Same	2018	2017
St. Joe R.	20.27	20.09	- 0.18	0.89	Same	2018	2017

The table also includes the effects of predicted-observed temperature differences on brook charr thermal habitat suitability status (THS, “same” indicates no change) and the years for which temperatures were predicted (Data year) using a model for a particular year (Model year)

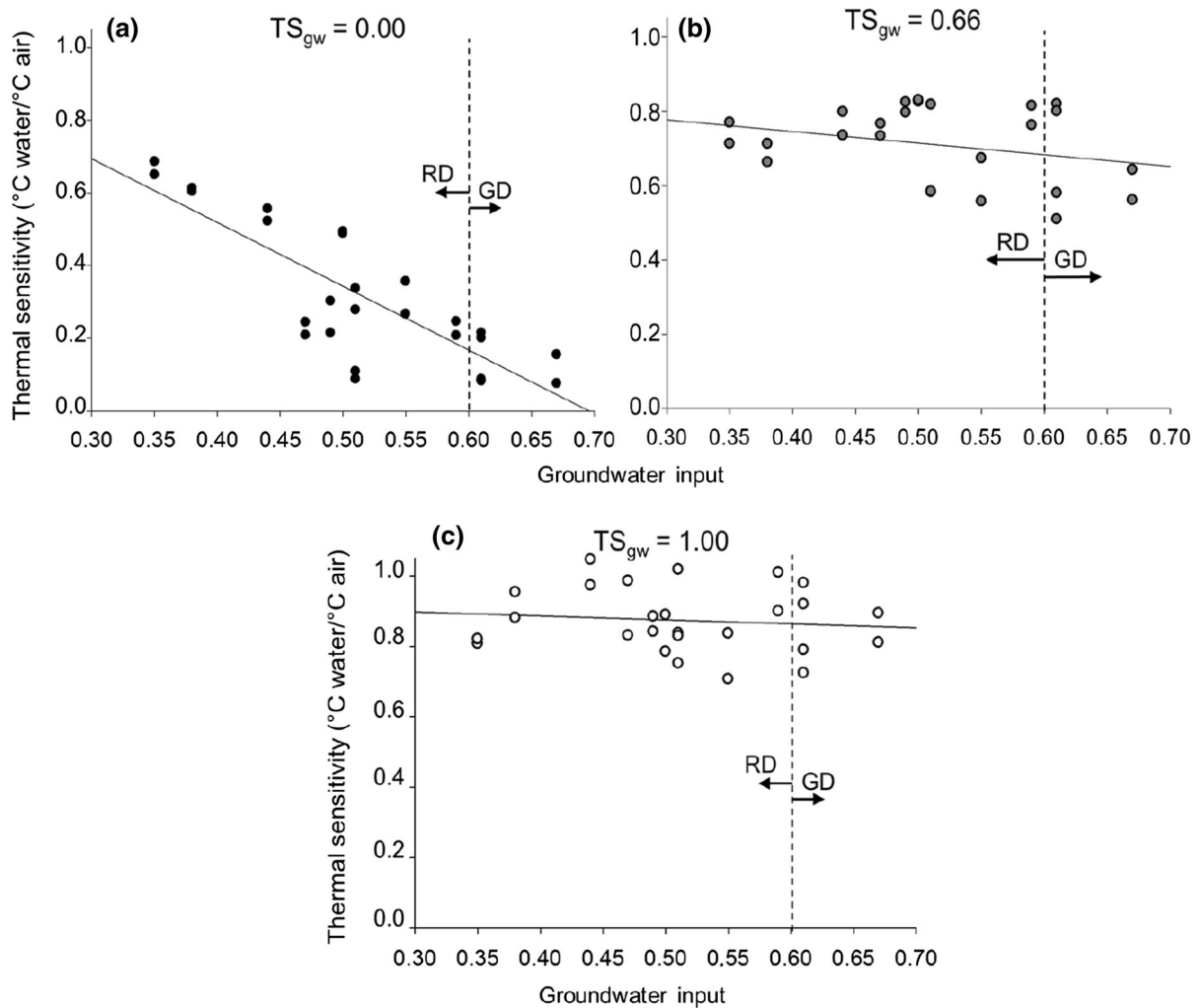


Fig. 5 Relationships between modeled stream thermal sensitivity ($^{\circ}\text{C water}/^{\circ}\text{C air}$) and groundwater input for the 13 Michigan streams best modeled with MDAT + PR (surface runoff-dominated [RD] streams) and MDAT + ADD (groundwater-dominated [GD] streams). Graphs (a), (b), and (c) display

stream thermal sensitivities for three conditions of increasing groundwater thermal sensitivity ($TS_{gw} = 0.0, 0.66, 1.0$). Dotted lines denote transitions between RD and GD streams

(e.g., East Branch Fox River; $R^2 = 0.09$; Fig. 2c). Temperatures in most streams (87%) were modeled most accurately (i.e., lowest AICc values) by combining ADD and MDAT in groundwater-dominated streams and precipitation and MDAT in runoff-dominated streams. Including ADD and precipitation improved model accuracy, with adjusted R^2 values increasing by 0.06 to 0.75 (Table 1, Fig. 3a–c). Models including ADD and precipitation had a mean adjusted R^2 of 0.83 (range 0.75–0.95), compared to 0.58 (range 0.06–0.80) for unadjusted models with only MDAT (Table 1, Fig. 4). Water temperatures in

streams with intermediate groundwater input (i.e., Pigeon River, West Branch Sturgeon River) were modeled most accurately with MDAT alone (Table 1). Model cross-validation showed that the deviation between predicted and observed stream temperatures in 2015/2018 was small (mean -0.08°C , SD 0.36°C , range -0.75 to 0.66°C), so thermal habitat suitability for brook charr survival and growth was projected accurately in all of the streams evaluated (Table 2).

Stream thermal sensitivity tended to decline with increasing groundwater input but was highly influenced by TS_{gw} conditions. The decrease in stream

Table 3 Modeled present-day and future mean daily stream temperatures in three conditions of modeled air temperature warming (+ 1.7°C, + 3.4°C, + 5.1°C) and thermal sensitivity of groundwater/precipitation (0.0, 0.66, 0.1; in parentheses) based on 2016 weather conditions in Michigan (i.e., warm, dry)

Stream	Present	+ 1.7(0)	+ 1.7(0.66)	+ 1.7(1)	+ 3.4(0)	+ 3.4(0.66)	+ 3.4(1)	+ 5.1(0)	+ 5.1(0.66)	+ 5.1(1)
Au Sable R.	17.37	17.50	18.33	18.75	17.73	19.39	20.24	17.97	20.45	21.73
E. Branch Fox R.	12.75	13.14	13.48	13.66	13.35	14.04	14.40	13.56	14.60	15.14
Manistee R.	17.17	17.55	18.23	18.58	17.89	19.26	19.96	18.23	20.29	21.34
Pigeon R.	13.52	13.78	13.78	13.78	14.02	14.02	14.02	14.26	14.26	14.26
W. Br Sturgeon R.	13.71	13.95	13.95	13.95	14.25	14.25	14.25	14.55	14.55	14.55
Sturgeon R.	23.94	24.30	25.04	25.42	24.97	26.45	27.21	25.64	27.87	29.01
Tamarack Creek	19.95	20.87	21.82	22.31	21.67	23.57	24.55	22.48	25.32	26.79
Black R.	15.98	16.35	17.16	17.59	16.71	18.35	19.19	17.08	19.53	20.80
Canada Creek	17.07	17.26	18.10	18.53	17.44	19.12	19.99	17.62	20.15	21.45
Rapid R.	12.91	13.30	13.87	14.17	13.43	14.58	15.17	13.56	15.28	16.17
Paint R.	22.54	23.38	24.37	24.87	23.92	25.90	26.91	24.46	27.43	28.95
Rogue R.	22.14	22.38	23.26	23.72	22.61	24.39	25.29	22.85	25.51	26.88
Pine R.	16.79	17.24	18.03	18.43	17.38	18.95	19.76	17.51	19.87	21.08
Cedar R.	19.22	19.68	20.48	20.89	20.14	21.73	22.55	20.59	22.98	24.22
St. Joe R.	22.22	22.61	23.51	23.97	23.00	24.80	25.72	23.40	26.09	27.48

“W. Br” “West Branch”

thermal sensitivity with increasing groundwater input was most pronounced for $TS_{gw} = 0$ (Fig. 5a) and considerably weaker for $TS_{gw} = 0.66$ (Fig. 5b). For $TS_{gw} = 1.00$, thermal sensitivity remained stable regardless of groundwater input (Fig. 5c), indicating an absence of groundwater-driven temperature buffering and hence unfavorable thermal conditions for brook charr survival and growth.

Stream temperature projections

Projected future water temperatures in Michigan coldwater streams varied among climate change scenarios and between baseline weather conditions (i.e., warm/dry, cool/wet). In warm, dry conditions, projected stream temperatures warmed as both MATW and TS_{gw}/TS_{pr} increased (Table 3). In groundwater-dominated streams, projected mean stream temperatures across TS_{gw} categories were 16.58°C (MATW + 1.7°C), 17.36°C (MATW + 3.4°C), and 18.15°C (MATW + 5.1°C; Fig. 6). Within all

MATW categories, predicted mean groundwater-dominated stream temperatures warmed as TS_{gw} increased; the magnitude of stream warming increased as MATW intensified from + 1.7°C (0.94°C warming) to + 3.4°C (1.88°C) to + 5.1°C (2.82°C; Fig. 6).

In runoff-dominated streams under warm, dry weather conditions, projected water temperatures were appreciably higher than those in groundwater-dominated systems (Fig. 6) despite similar trajectories of thermal change (i.e., stream temperatures increased in proportion to MATW and TS_{pr} ; Table 3). In runoff-dominated streams, projected mean stream temperatures across TS_{pr} categories were 20.43°C (MATW + 1.7°C), 21.52°C (MATW + 3.4°C), and 22.60°C (MATW + 5.1°C; Fig. 6). Within all MATW categories, predicted mean runoff-dominated stream temperatures warmed in proportion to TS_{pr} ; the magnitude of stream warming became larger as MATW increased from + 1.7°C (1.25°C warming) to + 3.4°C (2.51°C) to + 5.1°C (3.76°C; Fig. 6).

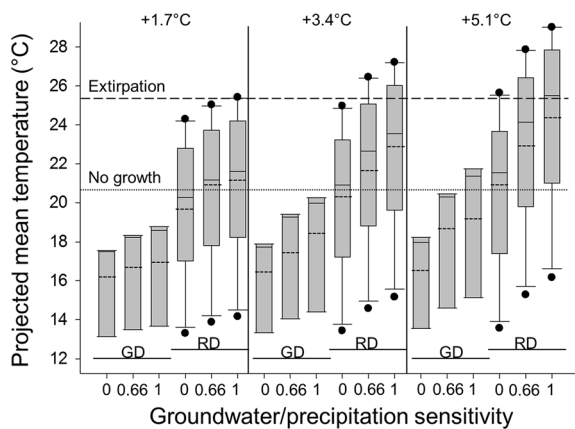


Fig. 6 Projected summer mean daily water temperatures based on 2016 weather (warm, dry) and three conditions of air temperature warming (modeled present-day temperatures + 1.7°C, + 3.4°C, and + 5.1°C) and thermal sensitivity of groundwater/precipitation (0.0, 0.66, 0.1) for the 13 Michigan streams best modeled with MDAT + PR and MDAT + ADD. Within each box plot, small dashed lines are means and solid lines are medians. The long dashed line spanning the entire panel represents an upper thermal threshold for brook charr survival (Fry et al., 1946; Raleigh, 1982), whereas the long dotted line denotes an upper threshold for brook charr growth (Baldwin, 1957; Raleigh, 1982)

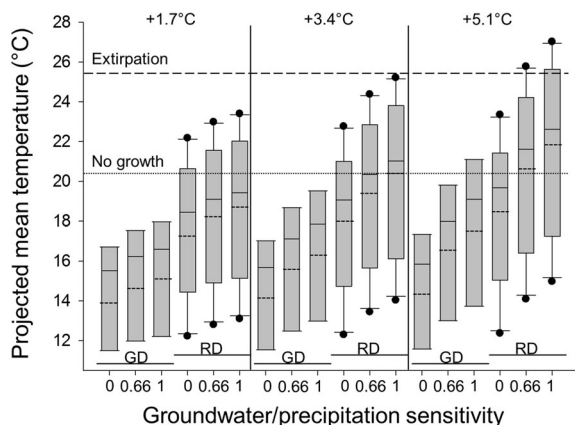


Fig. 7 Projected summer mean daily water temperatures based on 2017 weather (cool, wet) and three conditions of air temperature warming (modeled present-day temperatures + 1.7°C, + 3.4°C, and + 5.1°C) and thermal sensitivity of groundwater/precipitation (0.0, 0.66, 0.1) for the 13 Michigan streams best modeled with MDAT + PR and MDAT + ADD. Within each box plot, small dashed lines are means and solid lines are medians. The long dashed line spanning the entire panel represents an upper thermal threshold for brook charr survival (Fry et al., 1946; Raleigh, 1982), whereas the long dotted line denotes an upper threshold for brook charr growth (Baldwin, 1957; Raleigh, 1982)

In cool, wet weather conditions, projected stream temperatures were lower than those predicted in warm, dry conditions (Figs. 6, 7). However, temperatures warmed with increasing MATW and TS_{gw}/TS_{pr} (Table 4). In groundwater-dominated streams, projected mean stream temperatures across TS_{gw} categories were 15.15°C (MATW + 1.7°C), 15.88°C (MATW + 3.4°C), and 16.61°C (MATW + 5.1°C; Fig. 7). Within all MATW categories, predicted mean groundwater-dominated stream temperatures warmed as TS_{gw} increased; the magnitude of stream warming increased as MATW intensified from + 1.7°C (1.02°C warming) to + 3.4°C (2.03°C) to + 5.1°C (3.05°C; Fig. 7).

In runoff-dominated streams under cool, wet weather conditions, projected water temperatures were higher than those in groundwater-dominated systems (Fig. 7) notwithstanding similar trajectories of thermal change (i.e., stream temperatures increased in proportion to MATW and TS_{pr} ; Table 4). Projected mean stream temperatures across TS_{pr} categories in runoff-dominated streams were 18.50°C (MATW + 1.7°C), 19.50°C (MATW + 3.4°C), and 20.51°C (MATW + 5.1°C; Fig. 7). Within all MATW categories, predicted mean runoff-dominated stream temperatures warmed as TS_{pr} increased; the magnitude of stream warming became larger as MATW increased from + 1.7°C (1.12°C warming) to + 3.4°C (2.24°C) to + 5.1°C (3.36°C; Fig. 7).

Thermal habitat suitability predictions

In 2016, all streams evaluated in this study had a MDST that was suitable for brook charr survival (Table 3). Most streams (73%, $n = 11$) had temperatures that were optimal (33%, $n = 5$) or suitable (40%, $n = 6$) for summer brook charr growth, whereas four streams (Paint, Rogue, St. Joseph, and Sturgeon rivers) were unsuitable for summer growth (Table 3). Based on 2016 weather conditions (i.e., relatively warm, dry), thermal habitats in groundwater-dominated streams were predicted to be suitable for brook charr survival regardless of MATW/ TS_{gw} conditions (Table 5, Fig. 6). Projected groundwater-dominated stream temperatures were optimal or suitable for summer brook charr growth except when MATW = 5.1°C and $TS_{gw} = 1$ (Tables 3, 5, Fig. 6).

In warm, dry weather conditions, runoff-dominated streams became progressively less suitable for brook

Table 4 Modeled present-day and future mean daily stream temperatures in three conditions of modeled air temperature warming (+ 1.7°C, + 3.4°C, + 5.1°C) and thermal sensitivity of groundwater/precipitation (0.0, 0.66, 0.1; in parentheses) based on 2017 weather conditions in Michigan (i.e., cool, wet)

Stream	2017	+ 1.7(0)	+ 1.7(0.66)	+ 1.7(1)	+ 3.4(0)	+ 3.4(0.66)	+ 3.4(1)	+ 5.1(0)	+ 5.1(0.66)	+ 5.1(1)
Au Sable R.	16.41	16.72	17.55	17.97	17.03	18.68	19.53	17.34	19.82	21.09
E. Branch Fox R.	10.96	11.51	11.98	12.22	11.55	12.49	12.98	11.59	13.00	13.73
Manistee R.	15.36	15.52	16.24	16.61	15.68	17.12	17.86	15.84	18.00	19.11
Pigeon R.	12.89	13.18	13.18	13.18	13.53	13.53	13.53	13.88	13.88	13.88
W. Br Sturgeon R.	12.73	13.10	13.10	13.10	13.43	13.43	13.43	13.75	13.75	13.75
Sturgeon R.	21.59	22.17	22.98	23.40	22.76	24.38	25.21	23.35	25.77	27.02
Tamarack Creek	17.76	18.59	19.09	19.35	19.23	20.23	20.75	19.86	21.36	22.14
Black R.	14.42	14.79	15.12	15.29	15.15	15.82	16.16	15.52	16.52	17.03
Canada Creek	16.82	17.17	17.97	18.39	17.52	19.13	19.96	17.86	20.29	21.54
Rapid R.	11.99	12.23	12.80	13.10	12.30	13.44	14.03	12.37	14.09	14.97
Paint R.	20.90	21.65	22.53	22.99	21.96	23.73	24.64	22.27	24.93	26.30
Rogue R.	19.61	20.32	21.24	21.71	20.69	22.53	23.48	21.06	23.82	25.24
Pine R.	13.07	13.40	14.22	14.64	13.50	15.13	15.98	13.59	16.05	17.32
Cedar R.	17.70	18.30	19.09	19.50	18.89	20.49	21.31	19.49	21.88	23.11
St. Joe R.	19.73	20.20	21.15	21.63	20.67	22.56	23.53	21.15	23.97	25.43

“W. Br” “West Branch”

charr survival and growth as MATW and TS_{pr} increased (Table 5, Fig. 6). As MATW increased from + 1.7 to + 5.1°C, the mean percentage of runoff-dominated streams suitable for brook charr survival and growth declined from 93% (survival) and 60% (growth) to 67% (survival) and 47% (growth). Streams with intermediate groundwater input were projected to be suitable for brook charr survival and growth in all MATW/ TS_{pr} conditions (Table 5, Fig. 6).

In the relatively cool, wet weather conditions of 2017, streams were generally more suitable for brook charr survival and growth than in 2016 (i.e., warm, dry). All streams were suitable for brook charr survival in 2017 (Table 4), and most streams (87%, $n = 13$) had observed temperatures that were optimal (47%, $n = 7$) or suitable (40%, $n = 6$) for summer brook charr growth. Only two streams (Paint and Sturgeon rivers) were unsuitably warm for summer growth (Table 4). Based on 2017 weather conditions, thermal habitats in groundwater-dominated streams were predicted to be suitable for brook charr survival regardless of MATW/ TS_{gw} conditions (Table 5, Fig. 7).

Projected groundwater-dominated stream temperatures were optimal or suitable for summer brook charr growth except when MATW = 5.1°C and $TS_{gw} = 1$ (Tables 4, 5, Fig. 7).

In cool, wet weather conditions, runoff-dominated streams became less suitable for brook charr survival and growth as MATW and TS_{pr} increased, but to a lesser extent than in warm, dry conditions (Table 5, Figs. 6, 7). As MATW increased from + 1.7 to + 5.1°C in cool, wet conditions, the mean percentage of runoff-dominated streams suitable for brook charr survival and growth declined from 100% (survival) and 67% (growth) to 80% (survival) and 53% (growth). Streams with intermediate groundwater input were projected to be suitable for brook charr survival and growth regardless of MATW/ TS_{pr} conditions (Table 5, Fig. 7).

Discussion

Overall, coldwater stream temperatures in Michigan, USA, were projected to increase in proportion to the

Table 5 Modeled present-day and future thermal habitat suitability for brook charr survival and growth in Michigan streams. “Present” denotes the present-day (i.e., 2016 or 2017) proportion of streams that are suitable for brook charr survival (numerator) and growth (denominator)

Year (weather)	Stream	Present	+ 1.7(0)	+ 1.7(0.66)	+ 1.7(1)	+ 3.4(0)	+ 3.4(0.66)	+ 3.4(1)	+ 5.1(0)	+ 5.1(0.66)	+ 5.1(1)
2016 (warm, dry)	GD	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/0.33
	RD	1/0.6	1/0.5	1/0.5	0.9/0.4	1/0.5	0.9/0.4	0.7/0.4	0.9/0.4	0.5/0.4	0.5/0.1
	Int	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
2017 (cool, wet)	GD	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/0.67
	RD	1/0.8	1/0.8	1/0.6	1/0.6	1/0.6	1/0.6	1/0.4	1/0.6	0.9/0.4	0.7/0.3
	Int	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1

Other table entries report the future proportion of streams that are projected to be suitable for brook charr survival/growth in distinct prevailing weather conditions (i.e., warm and dry, based on 2016 data; cool and wet, based on 2017 data) and three conditions of modeled air temperature warming (+ 1.7°C, + 3.4°C, + 5.1°C) and thermal sensitivity of groundwater/precipitation (0.0, 0.66, 0.1; in parentheses). Streams are classified as groundwater-dominated (GD; base flow index > 0.60), runoff-dominated (RD; base flow index < 0.60), or systems with intermediate groundwater input (Int; base flow index = 0.60; Neff et al., 2005)

magnitude of air temperature warming and groundwater/precipitation thermal sensitivity. Stream temperature warming was predicted to be more severe under warm, dry future weather conditions than cool, wet conditions. However, regardless of weather, groundwater-dominated stream temperatures were projected to increase by a smaller magnitude than runoff-dominated stream temperatures such that brook charr will continue to survive and generally maintain summer growth in all of the groundwater-dominated systems studied herein. In contrast, brook charr survival and growth will likely decline in runoff-dominated streams with continued air temperature warming and increased stream thermal sensitivity, particularly in warm, dry future weather conditions.

Projected declines in thermal habitat suitability for summer brook charr growth—and, to a lesser extent, survival—will likely be manifested by changes in thermal habitat availability and connectivity. For instance, reduced overall availability of thermal habitats suitable for brook charr survival/growth will likely reduce brook charr movement between such habitats, with possible effects on brook charr population distribution in Michigan (Carlson et al., 2016), where dam-induced habitat fragmentation is already extensive (Cooper et al., 2016). By isolating coldwater habitats in particular locations (e.g., headwaters), climate change could contribute to fragmentation of brook charr populations and further reduce survival (Steen et al., 2010). For instance, in Wisconsin, USA, the length of streams suitable for brook charr was projected to decline by 44, 94, and 100%, respectively, under climate change classified as limited (summer air temperatures increase 1.0°C and water 0.8°C), moderate (air +3.0°C, water +2.4°C), and major (air +5.0°C, water +4.0°C; Lyons et al., 2010). Although annual (and perhaps summer) brook charr growth could stabilize or increase in particularly cold streams amid climate warming due to a lengthened growing season and potentially greater prey availability, fisheries and aquatic resource professionals should anticipate reductions in brook charr survival and growth in Michigan streams during the warmest period of the year.

Our results indicate that basic modifications to air-stream temperature models greatly improved model fit while incorporating stream-specific groundwater and precipitation dynamics and accurately projecting brook charr thermal habitat suitability in a changing

climate. Applicable across the spectrum of groundwater to surface runoff dominance, these models expand the scope of previous research focused on groundwater-dominated systems (Snyder et al., 2015). As observed herein and in previous research (Westhoff & Paukert, 2014), parity between a stream's most accurate temperature model and its hydrology (i.e., MDAT + ADD in groundwater-dominated streams, MDAT + precipitation in runoff-dominated streams) allows fisheries and aquatic resource professionals and policy makers to use hydrology as a criterion for selecting stream temperature models. Although a groundwater/precipitation modeling approach diverges from previous models (e.g., spatial network models in western USA streams; Peterson & Ver Hoef, 2010), Michigan stream thermal dynamics are different from those in the western USA: relatively little elevation change, greater groundwater influence, more precipitation as rain, and less snowmelt over a shorter annual period. Therefore, stream temperature modeling in the present study required an approach focused on groundwater inputs and precipitation as rain. Previous authors have acknowledged the importance of accounting for precipitation dynamics in stream climate change modeling (Snyder et al., 2015), but few accurate, cost-effective, management-relevant models that include precipitation have been generated prior to this research. The stream temperature modeling approach developed herein is readily transferable to streams outside Michigan where the primary drivers of stream temperature are air temperature, precipitation as rain, and groundwater rather than elevation change or snowmelt.

Signs (i.e., \pm) of the ADD and precipitation coefficients in stream temperature models were consistently negative in 2016 and 2017 in all streams (Table 1), indicating thermal buffering effects of both groundwater and precipitation in summer. Precipitation coefficients generally declined from 2016 to 2017, reflecting cool, wet weather in the latter year (EAWSN, 2018) and demonstrating an overall cooling effect of summer precipitation on runoff-dominated stream temperatures driven by increased stream discharge and water volume. Such a cooling effect may offset, to some extent, stream temperature warming resulting from increased air temperatures in a changing climate (Merriam et al., 2017). In addition, modeling stream temperatures under divergent weather conditions (i.e., warm/dry, cool/wet) enabled

us to generate a diversity of models that encompassed the range of temperature and precipitation conditions that Michigan streams currently experience and are projected to experience in the future. This, in turn, provides fisheries and aquatic resource professionals with a flexible thermal modeling approach for forecasting stream temperatures along a gradient of future air temperature and precipitation regimes (Primack, 2000; Parry et al., 2007; Stoner et al., 2013).

Results of this study have important implications and applications for brook charr management within and beyond Michigan. Managing coldwater streams and their thermally sensitive fish populations for thermal resilience (i.e., ability to absorb temperature changes and retain ecosystem structure and function; Holling, 1973) will be increasingly important as climate change continues to degrade coldwater habitats throughout the world (Almodóvar et al., 2012; Isaak et al., 2012; Santiago et al., 2015). Amid limitations in fisheries management resources (e.g., money, time, personnel), fisheries and aquatic resource professionals will benefit from accurate, cost-effective, management-relevant stream temperature models such as those described herein. In turn, lower resource expenditure on temperature data collection and model development will allow greater resource allocation toward thermal habitat management activities.

For instance, resource managers can form public–private partnerships to protect stream groundwater resources (e.g., springs, seeps), limit groundwater withdrawal from aquifers, and identify groundwater-limited streams where thermal habitat management is most needed. They can also work with policymakers to provide incentives (e.g., financial assistance, open space tax deduction, fast-track permitting; Knight 2009) for land developers and property owners to protect coldwater habitats and thermal buffering mechanisms on their lands (e.g., grassland watersheds, sandy soils that promote groundwater recharge; Waco & Taylor, 2010). In addition, fisheries and aquatic resource professionals should focus on preserving and rehabilitating riparian trees and plants that provide favorable thermal conditions for brook charr growth and survival via stream shading, water infiltration, and percolation (Siitari et al., 2011). Fisheries and aquatic resource professionals can also promote thermally resilient brook charr populations by installing fish ladders at roadside crossings/culverts and removing

dams where appropriate to enable fish movement between coldwater habitats (Hayes et al. 2006). Overall, results from this study indicate that resource managers should prioritize brook charr management in runoff-dominated streams capable of thermal habitat rehabilitation—particularly those predicted to experience increased precipitation and an associated cooling effect—and in groundwater-dominated streams where management activities produce tangible returns on investment in terms of brook charr survival and growth. It would be inefficient, for example, to expend management resources in runoff-dominated streams that exceed brook charr temperature tolerances or, alternatively, groundwater-dominated streams that can sustain their thermal habitat conditions without human intervention (e.g., cold streams such as the East Branch Fox River).

Collectively, the strategies described above can be used to develop resilience-based management programs for coldwater streams and their ecologically, socioeconomically important brook charr fisheries (Carlson et al., 2016). Resilience-based management involves collaboration among scientists, biologists, policy makers, and public stakeholders to cultivate fisheries ecosystems that are robust to local and global change (e.g., climate change, land use alteration) and, likewise, management systems that can withstand environmental and socioeconomic stressors (Paukert et al., 2016). For example, managers can increase fisheries ecosystem resilience by protecting diverse brook charr age/size classes, genetic stocks, and prey resources that tolerate wide-ranging temperatures expected in a changing climate (Hansen et al., 2015); instituting angling regulations (e.g., reduced creel limits, protected slot limits) that preserve brook charr populations during thermally stressful times; and monitoring precipitation levels and associated thermal effects in runoff-dominated streams. Similarly, resource managers can enhance management system resilience by developing outreach programs that inform policymakers and public stakeholders about thermal habitat management, prepare them for realistic stream fish community outcomes amid climate change (e.g., salmonid decline, centrarchid expansion; Pease & Paukert, 2014), and garner their support for resilience-based management.

In conclusion, we developed a methodology for, and demonstrated the advantages of, modeling effects of air temperature, precipitation, and groundwater input on stream thermal regimes in an accurate, cost-effective,

management-relevant manner. The modeling approach described herein allows fisheries and aquatic resource professionals to forecast and respond to effects of climate change on populations of brook charr and other fish species in management-relevant ways. Methods used in this study are widely applicable throughout the range of brook charr (and other species), beyond the headwater reaches emphasized herein, and over different temporal scales (e.g., annual, autumnal) because they only require readily available (or easily collectable) air/stream temperature and precipitation data. Moreover, our stream temperature modeling approach is flexible because it is applicable in streams with diverse air temperature, precipitation, and groundwater regimes, and it can incorporate potential climate-induced changes in these factors within individual streams. As a result, methods used herein expand the scope of groundwater-focused models (Snyder et al., 2015) and help fill knowledge gaps regarding the effects of precipitation dynamics (e.g., thermal sensitivity, magnitude, timing) on stream temperature. Overall, precipitation- and groundwater-corrected stream temperature models are useful for reliable thermal forecasting and associated brook charr management efforts ranging from groundwater conservation to riparian/watershed habitat rehabilitation and public engagement. In turn, these activities will promote sustainable, resilience-based management of coldwater streams and their ecologically and socioeconomically important brook charr fisheries in a changing climate.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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