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Accounting for groundwater in stream fish thermal habitat responses to climate change

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Abstract. Forecasting climate change effects on aquatic fauna and their habitat requires an understanding of how water temperature responds to changing air temperature (i.e., thermal sensitivity). Previous efforts to forecast climate effects on brook trout (*Salvelinus fontinalis*) habitat have generally assumed uniform air–water temperature relationships over large areas that cannot account for groundwater inputs and other processes that operate at finer spatial scales. We developed regression models that accounted for groundwater influences on thermal sensitivity from measured air–water temperature relationships within forested watersheds in eastern North America (Shenandoah National Park, Virginia, USA, 78 sites in nine watersheds). We used these reach-scale models to forecast climate change effects on stream temperature and brook trout thermal habitat, and compared our results to previous forecasts based upon large-scale models. Observed stream temperatures were generally less sensitive to air temperature than previously assumed, and we attribute this to the moderating effect of shallow groundwater inputs. Predicted groundwater temperatures from air–water regression models corresponded well to observed groundwater temperatures elsewhere in the study area. Predictions of brook trout future habitat loss derived from our fine-grained models were far less pessimistic than those from prior models developed at coarser spatial resolutions. However, our models also revealed spatial variation in thermal sensitivity within and among catchments resulting in a patchy distribution of thermally suitable habitat. Habitat fragmentation due to thermal barriers therefore may have an increasingly important role for trout population viability in headwater streams. Our results demonstrate that simple adjustments to air–water temperature regression models can provide a powerful and cost-effective approach for predicting future stream temperatures while accounting for effects of groundwater.

Key words: brook trout; climate change; groundwater; headwater streams; Salvelinus fontinalis; *Shenandoah National Park, USA; thermal habitat*

Introduction

Stream temperature is an underlying driver of many biological processes in aquatic systems and consequently a primary factor defining habitat suitability for stream organisms. Regional air temperatures are expected to increase substantially over the next century due to increasing concentrations of greenhouse gasses (Ruosteenoja et al. 2003, Hostetler et al. 2011). Thus, climate change poses a significant threat to the viability of aquatic species, and predicting the ecological consequences of climate warming has become a principal objective of stream ecologists and fisheries managers (e.g., Comte et al. 2013). Warming stream temperatures are of particular concern for salmonids that have high cultural, recreational, and commercial value and low thermal tolerance thresholds (Eaton et al. 1995, Battin et al. 2007, Wehrly et al. 2007, Isaak et al. 2012).

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The historical distribution of native brook trout (*Salvelinus fontinalis*) has been severely reduced due to deforestation, water pollution, and the introduction of nonnative trout, and remaining riverine populations are largely limited to forested headwater streams (i.e., up to third-order streams) throughout much of their native range (Flebbe et al. 1988, Hudy et al. 2008). As a result, the ability of the species to respond to climate change at large spatial scales (e.g., northward migrations) may already be compromised by existing stream network fragmentation and the paucity of cold water mainstem habitats. Brook trout persistence therefore may depend on how headwater stream habitats respond to changing air temperature regimes, and how these changes affect survival and reproduction rates of local populations. Climate change may not only reduce the amount of thermally suitable habitat available for feeding and reproduction, but may also increase stream network fragmentation through the introduction of thermal barriers that restrict dispersal and reduce population viability (Morita and Yokota 2002, Letcher et al. 2007).

The thermal regimes of streams are controlled by energy exchanges across the water surface and the streambed (Webb et al. 2008). Although the direct exchange of heat from warm air to cooler water (i.e., convection) represents a relatively minor influence on stream temperature, air temperature is typically correlated with regional variation in solar radiation that has been implicated as the most influential driver of stream temperature (Caissie 2006, Webb et al. 2008). As a result, air temperature is commonly used as a surrogate for atmospheric energy inputs, especially in large-scale studies of stream temperature dynamics (Johnson 2003). Forecasting climate change effects in freshwater ecosystems requires an understanding of how predicted changes in air temperature will affect stream temperatures (i.e., thermal sensitivity, TS; Kelleher et al. 2012). Previous research predicting climate change effects on fish habitat has assumed strong (e.g., 1:1) and spatially invariant relationships between air and stream temperatures such that stream temperatures were predicted to change as a spatially uniform process matching predicted air temperature changes (e.g., Meisner 1990*a*, Eaton and Scheller 1996, Rahel et al. 1996, Clark et al. 2001, Mohseni et al. 2003, Flebbe et al. 2006, Rieman et al. 2007). This approach has allowed for the development of large-scale models capable of predicting stream temperatures over large regions because only air temperature data are required for stream temperature predictions, and local air temperatures can be obtained from downscaled regional climate data (e.g., Eaton and Scheller 1996) or estimated using surrogates such as elevation and latitude (e.g., Flebbe et al. 2006).

The assumption that stream temperature is highly sensitive to changing air temperature is based on the results of a relatively small number of studies where strong correlations between air and water temperatures were observed over large regions (Stefan and Preud'homme 1993, Pilgrim et al. 1998, Bogan et al. 2003). These empirical observations were derived mainly from data collected from sites in larger streams and rivers where long-term temperature and flow records are prevalent (e.g., U.S. Geological Survey [USGS] gage sites). However, at large spatial scales, stream networks often exhibit patchy thermal conditions due to spatially heterogeneous influences of riparian shading, groundwater upwelling, and valley form and aspect (Constantz 1998, Torgersen et al. 1999, Poole and Berman 2001, Ebersole et al. 2003). These influences appear to be particularly important in headwater areas where flow volumes are low and land–water interactions are strong (Story et al. 2003, Danehy et al. 2005, Tague et al. 2007, Dent et al. 2008). The sensitivity of headwater streams or stream reaches to changing air temperature regimes therefore may vary substantially over relatively small spatial extents, and large-scale models that do not incorporate fine-scale variation in thermal sensitivity may not accurately predict thermal habitat at ecologically relevant spatial scales.

A precise understanding of the drivers of stream temperature requires detailed hydrometerological measurements to inform complex analytical models (Webb et al. 2008). The data demands and costs associated with detailed heat budgets usually preclude their use for characterizing stream temperature and associated drivers at large numbers of sites. As a result, the use of low-cost, automated temperature data recorders has become increasingly popular for the study of stream temperature dynamics because they provide a relatively cost-effective means of assessing thermal conditions at a fine spatial resolution (Dunham et al. 2005, Johnson et al. 2005). Paired air and water temperature data have been found to be useful for characterizing spatial variation in stream temperature patterns (Kelleher et al. 2012, Hilderbrand et al. 2014, Trumbo et al. 2014).

However, the extent to which such correlational data provided by site-specific regression models can be used to predict future stream temperature has not been fully evaluated (Johnson 2003, Arismendi et al. 2014). In particular, the predictive utility of these models may be limited in headwater streams where groundwater contributions are important. Groundwater inputs buffer daily and seasonal extremes, and generally cool stream temperature in summer and warm stream temperature in winter (Caissie 2006, Webb et al. 2008). As a result, air–water temperature regression models are often weaker and more variable in headwater stream sites with large groundwater contributions (Erickson and Stefan 2000, Danehy et al. 2005, Morrill et al. 2005, Kelleher et al. 2012, Hilderbrand et al. 2014). Although site-specific regression coefficients may provide useful information regarding the relative sensitivity of sites to seasonal air temperature changes, they may not provide robust models for predicting current or future water temperatures.

Additionally, such approaches commonly assume that the relative insensitivity of groundwater-dominated streams to seasonal variation in air temperature will persist at longer (e.g., decadal) time scales. This assumption may be reasonable for groundwater originating in karst or relatively young volcanic geologic settings where groundwater is often stored in deep aquifers for extremely long periods of time (e.g., centuries or millennia) prior to discharging into streams (Alley 2001, Hanson and Dettinger 2005, Worthington 2007). However, in older geologic settings, such as the Blue Ridge and Piedmont physiographic provinces of the eastern United States, groundwater is largely stored within shallow residuum deposits with short flow paths to stream discharge points (Lynch 1987). As a result, groundwater residence times are typically short in these regions (e.g., zero to three years; Plummer et al. 2001). Nevertheless, recent evidence suggests that, like deep groundwater, groundwater originating from shallow sources also has a strong moderating effect on seasonal stream temperatures (Story et al. 2003, Johnson 2004, Leach and Moore 2011). In contrast to deep groundwater, however, the temperature of shallow groundwater has been shown to be sensitive to air temperature change over longer time scales using statistical (Kurylyk et al. 2013, Menberg et al. 2014), as well as mechanistic physical models (Taylor and Stefan 2009, Kurylyk et al. 2014) of groundwater temperature, and therefore should be sensitive to climate. New methods are therefore needed to account for uncertainty associated with the effects of changing climate on groundwater temperature over the long term.

In this paper, we describe an approach to account for shallow groundwater influence in statistical models of air–water temperature relationships. We adjusted regression models to assess spatial variation in thermal sensitivity at the stream reach spatial grain, and incorporated spatial variation in thermal sensitivity into simulations designed to forecast climate change effects on brook trout thermal habitat. We compared predictions of future brook trout habitat under climate change derived from these fine-grained regression models to those derived from large-scale modeling approaches. We addressed this research topic in Shenandoah National Park, a critical area for native trout conservation in the Appalachian region (Hudy et al. 2008).

Methods

Study area and site selection

Shenandoah National Park (SNP) is a long narrow protected area located along the spine of the Blue Ridge Mountains of Virginia, USA (Fig. 1). The park ranges in elevation from 168 to 1125 m and encompasses nearly 80 000 ha of mostly forested terrain. The climate is humid temperate, with mean annual air temperatures historically ranging from 7–9°C at higher elevations to 12–14°C at lower elevations (Jastram et al. 2013). The park is underlain by three principle bedrock types: granitic, metabasalts, and siliciclastic rocks (Fig. 1), each of which represent about one-third of the total park area (Gathright 1976, Southworth et al. 2009). Limestone is also present in the park but is rare (<2% of park area). Due to differences in porosity, erodibility, and component mineral profiles, these rock types are primary determinants of soils and vegetation (Young et al. 2009), and water drainage patterns (Mesko et al. 2000, Winter 2001).

Water resources in SNP include over 1000 km of streams draining into the Chesapeake Bay via the Rappahannock, Potomac, and James Rivers. The hydrography of the park is almost entirely headwaters (i.e., less than third order) with 68% of the total stream length represented by first-order streams, 24% by second-order streams, and 8% by third-order streams (Snyder et al. 2013). In addition, perennial springs are prevalent and groundwater is a major driver of streamflow in SNP streams (DeKay 1972, Lynch 1987, Snyder et al. 2013). However, groundwater supplies in the park are largely limited to that contained within shallow (0–9 m thick) layers of residuum and colluvium that overlie bedrock; deeper groundwater, originating from bedrock fractures, represent a minor source of groundwater (Lynch 1987, Plummer et al. 2001, Busenberg and Plummer 2014). Groundwater contributions to surface flow exhibit considerable spatial variation within and among watersheds depending upon complex interactions between bedrock type, depth of regolith, and the steepness of the surrounding terrain (Lynch 1987, Kasahara and Wondzell 2003). Although streams draining most of the park are considered perennial, reaches within them are known to dry periodically during summer base-flow conditions (Lynch 1987).

We used a hierarchical spatial design to select 78 stream reaches within nine focal watersheds for temperature sampling. Focal watersheds were selected to represent park-wide variation in bedrock geology (granitic, basaltic, silicilastic) and solar radiation (kilowatt hours per square meter; Table 1). Site locations within focal watersheds were selected to represent a longitundinal gradient in stream volume and elevation as represented by contributing basin area (site locations were all third order or less). We used USGS 10-m digital elevation models (generalized to a 15-m cell size) in ArcGIS and the ArcHydro extension (Maidment 2002) to generate watersheds above potential sampling points along streams. We summarized bedrock and surficial geology within watersheds using digital maps provided by Morgan et al. (2004). We reclassified the detailed geologic map into broad categories of rock type (silisiclastic, granitic, and metabasalt), and areas with significant alluvial deposits. We computed estimates of summer solar radiation (kW hours/m^2) using the Solar Radiation toolbox in ArcGIS 9.3 (ESRI 2009). These calculations were performed for all raster cells within all major watersheds in the park. We used these landscape attributes as sampling strata because we believed a priori that these broad categories and their correlates would effectively represent park-wide variation in landscape gradients important to air and water temperature.

Temperature data collection and climate forecasting

Water temperature data were collected at all 78 reach locations (Fig. 1) during the summer of 2012 (23 June–7 September). The sample period was selected to incorporate the warmest time of the year when stream temperatures are likely to be most stressful for brook trout (Ensign et al. 1990, Robinson et al. 2010). Temperature was measured every hour with HOBO Pro v2 thermographs (accuracy = 0.2°C, drift = <0.1°C per year; Onset Computer Corporation 2009). Thermographs were installed in nonturbulent flowing water habitats, and were housed within short sections of white polyvinyl chloride (PVC) pipes with holes drilled into the sides to facilitate water exchange and shield them from direct sunlight. Streams dried considerably in late summer, and the complete elimination of streamflow was noted at several sites in mid-August. Thus, we discarded data collected after 10 August at all sites. Maximum summer temperatures in 2012 were found to occur prior to 10 August at all sites with consistent streamflow, and therefore we are confident that the period of record included maximum stream temperatures. From the hourly data we computed daily mean water temperatures (DMWT) for each reach.

We also used HOBO thermographs to measure air temperature at a subset of stream reaches (three reaches per watershed, total of 27 air loggers). Within each focal watershed, we deployed air temperature gages at sites near the top of the watershed (i.e., 100-ha site), the bottom-most site (near the park boundary), and a site intermediate in elevation. At each reach, we attached air temperature gages to the north side of large trees (∼2 m [6 feet] high) in shaded areas near the stream bank. We mounted the air thermographs within PVC pipes to reduce direct light exposure. As with water temperature data, we summarized hourly air temperature data as daily mean air temperature (DMAT).

To estimate air temperature for unsampled reaches, we modeled DMATs across all 27 locations using a multiple regression model that included the grand mean daily air temperature (daily air temperature averaged over all 27 loggers) and site elevation as predictors. Additional predictor variables including measures of solar radiation and canopy cover, as well as all two-way interactions (elevation × grand mean air temperature, elevation × canopy cover, grand mean air temperature × canopy cover, and canopy cover × solar radiation), were incorporated in preliminary models but were found to be uninformative. The air temperature model explained 93.3% of daily variation. We used predicted air temperature values to assess air–water temperature relationships at all 78 sites.

We simulated future summer daily air temperature regimes (i.e., DMATs) for each site under three climate change scenarios: 1.5°C, 3.0°C, and 5.0°C increases in summer mean air temperatures above those observed in 2012. These simulated air temperature increases (SATI) roughly correspond to the range of forecasts for the eastern United States that is expected to occur over the next 50–100 years from alternative general circulation models (GCMs) and scenarios (Ruosteenoja et al. 2003, Hostetler et al. 2011, Rawlins et al. 2012). However, the 12-month period leading up and including our sampling period (September 2011–August 2012) was one of the warmest on record. Over the 74 years of records collected at the SNP weather station located near Luray, Virginia, only two years (i.e., $<3\%$ of records) had warmer average annual air temperatures. Using the 2012 data as a baseline probably overestimates future air temperatures and therefore we view our climate forecasts as representing a worst case scenario. Based on historical records, the 2012 study year was slightly dryer than average (38.8% of records had lower total annual precipitation).

We used the delta method (Fowler et al. 2007) to downscale predictions in mean summer air temperature derived from GCMs to individual sites and daily time steps. For each site, we used the relationship between each DMAT and the overall summer mean observed in 2012 to simulate daily air temperatures under each climate change scenario. Thus, within a site, the *relative* daily temperature pattern observed in 2012 remained the same for simulated future climates, only the overall mean summer temperature changed.

Modeling stream temperature and thermal sensitivity

We used least-squares linear regression methods to predict stream temperatures from air temperature, and to estimate thermal sensitivity. Initially, we used a simple linear regression model that used modeled daily mean air temperature (DMAT) to predict observed daily mean water temperature (DMWT). We also developed models where hourly air and water temperature data were averaged over weekly instead of daily time steps. We found that daily and weekly models were highly correlated (Pearson's $r = 0.96$ and 0.90 for slopes and y-intercepts, respectively), and so inferences regarding among-site differences in air–water temperature relationships would be the same irrespective of the time step used. In contrast to other studies (e.g., Stefan and Preud'homme 1993, Kelleher et al. 2012), we found that regression models based on daily time steps had a better goodness of fit (R^2) for 56 of the 78 sites, suggesting that air–water temperature time lags are less important, and daily time steps may be more appropriate, for smaller streams. We therefore only report results for the daily time step.

We examined plots of DMAT and DMWT through time and found that DMWT did not track daily variation in DMAT at some sites. Rather, these sites exhibited a pattern of gradual warming through the summer (see *Results*). We attribute the observed cumulative heating to the attenuating influence of shallow groundwater and hyporheic exchanges with surface flow on stream temperature. We modeled the observed cumulative heating by adding an additional measure of air temperature to site regression models, the accumulated degree-days above mean summer air temperature (ADD). We used mean summer air temperature as a threshold value for computing ADD because it is directly related to summer ground surface temperature, the actual driver of groundwater temperature during summer (Kurylyk et al. 2013). We used the two-variable regression models to predict DMWT under the current (2012) climate scenario. For each site, the

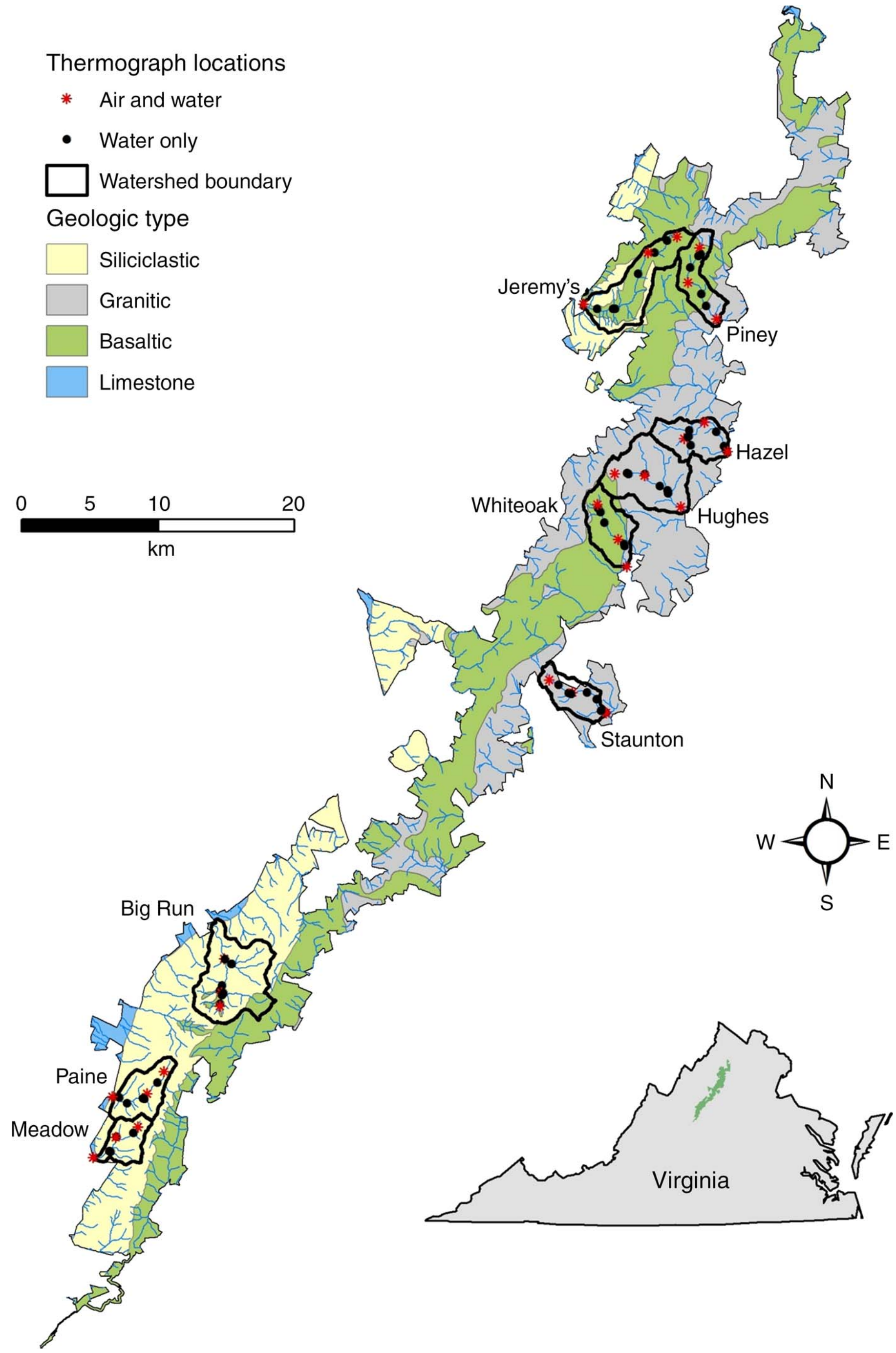

FIG. 1. Shenandoah National Park in northern Virginia, USA. Stream temperatures were measured at 78 sites in nine watersheds within the park that stratified bedrock geology, solar radiance, and elevation and basin area.

multiple linear regression models take the standard form as follows:

$$\mathrm{DMWT}_i = b_0 + (b_1\mathrm{MDAT}_i) + (b_2\mathrm{ADD}_i) \quad (1)$$

where DMWT_i is predicted DMWT at day i in °C, MDAT_i is MDAT at day i in °C, ADD_i is ADD at day i in degree-days, b_0 is the model y-intercept, and b_1 and b_2 are the regression coefficients for the predictor variables MDAT and ADD. We used the partial coefficient of determination for the ADD term (R^2_{ADD}) derived from the model as an estimate of groundwater influence for each site. R^2_{ADD} is a measure of the amount of variation in DMWT explained by ADD, and therefore we argue

TABLE 1. Description of the nine Shenandoah National Park, Virginia, USA, watersheds sampled in this study.

Watershed name	No. sites	Predominant geology type (%)	Basin area (ha)	Solar radiation (kW hours/m^2)
Piney River	7	basaltic (70.1)	1261	621.1
Whiteoak Canyon	8	basaltic (83.6)	1398	632.8
Jeremy's Run	10	basaltic (73.5)	2204	588.7
Staunton River	9	granitic (100)	1073	601.2
Hazel River	9	granitic (100)	1335	599.9
Hughes River	10	granitic (89.1)	2258	605.1
Meadow Run	7	siliciclastic (100)	919	594.8
Paine Run	7	siliciclastic (100)	1269	577.2
Big Run	11	siliciclastic (70.1)	2898	570.8

Note: Values in parentheses are the total cumulative watershed area represented by the predominant geologic type that drains each sample reach.

that it is a reflection of the proportion of streamflow comprised of groundwater. R^2_{ADD} is computed as the product of the standardized regression coefficient and the Pearson correlation coefficient using the equation

$$R^2_{\mathrm{ADD}} = \left[b_2\left(\frac{S_{\mathrm{ADD}}}{S_{\mathrm{DMWT}}}\right)\right] \times \left[\frac{1}{n-1}\sum_{i=1}^{n}\left(\frac{\mathrm{ADD}_i - \overline{\mathrm{ADD}}}{S_{\mathrm{ADD}}}\right)\left(\frac{\mathrm{DMWT}_i - \overline{\mathrm{DMWT}}}{S_{\mathrm{DMWT}}}\right)\right] \quad (2)$$

where b_2 is the regression coefficient for the ADD term from Eq. 1, S_{ADD} is the standard deviation of ADD values, S_{DMWT} is the standard deviation of DMWT values, n is the number of observations (days), ADD_i is ADD at day i (degree-days), DMWT_i is DMWT at day i (in °C), $\overline{\mathrm{ADD}_2}$ is mean ADD, and $\overline{\mathrm{DMWT}}$ is mean DMWT.

To predict DMWT under future climate change, we modified the regression equations to account for *long-term* (e.g., annual or decadal) increases in groundwater temperature that may be expected to accompany climate change (Taylor and Stefan 2009, Kurylyk et al. 2013, Menberg et al. 2014). We use the term long-term groundwater thermal sensitivity ($\mathrm{TS_{GW}}$) to describe the long-term response of groundwater temperature to air temperature change, and define it mathematically as the increase in groundwater temperature per 1°C increase in mean summer air temperature. This is consistent with the terminology used to define stream thermal sensitivity (TS).

For these modifications, we made use of the observation from numerous studies (including this one; see Fig. 2) that, in small forested watersheds, the slope and y-intercept terms of air–water temperature regressions are negatively related such that at groundwater-dominated sites regression slopes are low and y-intercepts approximate mean groundwater temperature; whereas, at runoff-controlled sites, regression slopes are typically high (e.g., >0.7) and y-intercepts approach 0°C (Webb et al. 2003, Caissie 2006, O'Driscoll and DeWalle 2006). For predicting future stream temperatures for reaches where flow is completely comprised of groundwater, the y-intercept term in the regression model therefore should increase by the product of $\mathrm{TS_{GW}}$ and SATI, whereas the y-intercept term should not change at sites where groundwater is unimportant.

In most headwater streams, flow is comprised of water originating from both runoff and groundwater, and therefore, the increase in the y-intercept term under climate change would be a function of the proportion of streamflow as groundwater, current groundwater temperature, and $\mathrm{TS_{GW}}$. To account for this in climate forecasts, we first modeled the relationship between model y-intercepts and R^2_{ADD} values observed under current climate. We found that the following linear model was suitable (i.e., residuals uncorrelated and randomly distributed around zero) and explained 49% of the variation in model y-intercepts:

$$b_0 = 5.75 + (8.87 \times R^2_{\mathrm{ADD}}) + e. \quad (3)$$

We assumed that variation in the y-intercept explained by the R^2_{ADD} term is related to the proportion of streamflow comprised of groundwater. We also assumed that the remaining unexplained variation is indicative of groundwater temperature. That is, we believed much of the unexplained variation (e) in model 3 (Eq. 3) relates to important among-reach variation in groundwater temperature that is a function of latent variables including site elevation, groundwater depth, soil type, and the residence time of hyporheic flow (Johnson 2004, Kurylyk et al. 2013). In this approach, we further assumed that the effects of these latent variables are site-specific and static over time. For predicting new model y-intercepts under climate change, the equation would take the following form:

$$B_{0\mathrm{adj}} = 5.75 + \left[\left(8.87 + (\mathrm{TS_{GW}} \times \mathrm{SATI})\right) \times R^2_{\mathrm{ADD}}\right] + e. \quad (4)$$

$B_{0\mathrm{adj}}$ values estimated from this model were then substituted for b_0 in Eq. 1 for predicting DMWT under climate change yielding the following adjusted regression model:

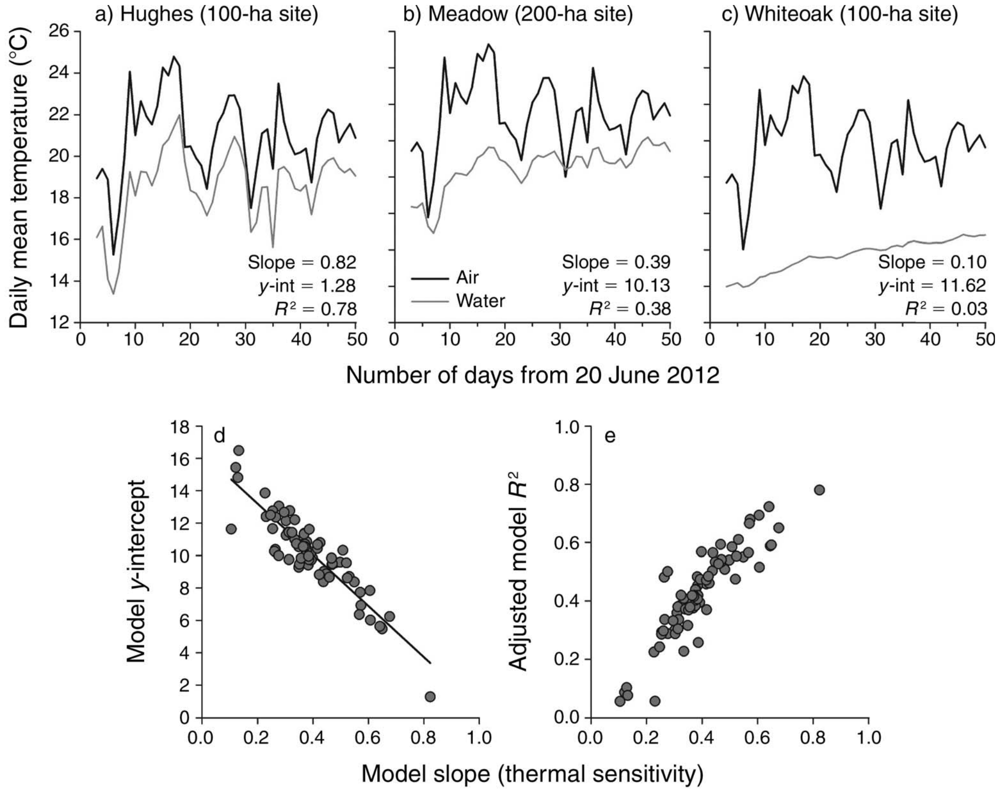

FIG. 2. Relationships between predicted daily mean air temperature (DMAT) and observed daily mean water temperature (DMWT) for reaches in Shenandoah National Park in 2012. Graphs (a), (b), and (c) show three examples that illustrate the range of air and water temperature relationships observed in the park. Regression statistics (slope, *y*-intercept [*y*-int], and adjusted R^2) summarizing the linear relationship between air and water temperature are shown for each example site. Graph (d) shows the relationship between model slope and *y*-intercept for all 78 sites, and graph (e) shows the relationship between model slope and coefficients of determination (adjusted R^2).

$$\mathrm{DMWT}_i = b_{0\mathrm{adj}} + (b_1 \mathrm{MDAT}_i) + (b_2 \mathrm{ADD}_i). \qquad (5)$$

It also follows that, for any SATI–$\mathrm{TS_{GW}}$ scenario, when we solve Eq. 4 for $R^2_{\mathrm{ADD}} = 1$, values of $B_{0\mathrm{adj}}$ represent estimates of summer groundwater temperature (GT). We estimated GT for each site under current and future climates. We compared our model estimates of GT under current climate with empirical GT measurements collected in August and September of 1997 from 40 springs and 20 wells by Plummer et al. (2000). We also compared our GT estimates to model predictions from Collins (1925), in which GTs are approximately equal to the local mean annual air temperature (MAAT) + 1.5°C. The Collins (1925) method has provided reasonable estimates of average GT in forested areas across the native range of brook trout (Meisner 1990*a*). We used monthly air temperature data derived from the Luray weather station in Virginia, USA (latitude 38.6661° N, longitude 78.3727° W, elevation 427 m) to derive regional MAAT, along with the lapse rate equation of 1°C decrease in air temperature per 188-m increase in elevation to estimate MAAT at each site (Meisner 1990*a*). We used air temperature records for the 12-month period leading up to sampling for each data set. Regional MAAT was 12.28°C for the 1997 study year when direct GTs were measured and 13.55°C for the 2012 study year when GTs were modeled.

We used three alternative assumptions regarding $\mathrm{TS_{GW}}$: $\mathrm{TS_{GW}} = 0$ (groundwater temperature is independent of long-term changes in air temperature), $\mathrm{TS_{GW}} = 0.66$ (groundwater temperature will increase 0.66°C per 1°C increase in air temperature), and $\mathrm{TS_{GW}} = 1.0$ (1:1 relationship). The $\mathrm{TS_{GW}} = 0.66$ and $\mathrm{TS_{GW}} = 1.0$ assumptions bracket the ranges reported from recent studies designed to assess thermal responses of shallow groundwater to climate (Taylor and Stefan 2009, Kurylyk et al. 2013) and almost certainly represent more realistic assumptions regarding the long-term sensitivity of groundwater temperature to climate than $\mathrm{TS_{GW}} = 0$. For each reach location, we used adjusted multiple regression models (Eq. 5) to predict DMWT regimes based on different combinations of the three $\mathrm{TS_{GW}}$ assumptions (0.00, 0.66, and 1.00) and the three alternative SATIs (1.5°C, 3.0°C, and 5.0°C).

From our modeling results we computed stream thermal sensitivity for each site. Stream thermal sensitivity (TS) has been defined as the change in mean stream temperature per unit change in mean air temperature (Kelleher et al. 2012) and in linear regression is represented mathematically as the model slope (Mayer 2012, Hilderbrand et al. 2014, Trumbo et al. 2014). However, in our adjusted regression models, the *y*-intercept term changes under TS_{GW} and SATI scenarios, so TS cannot be directly derived from the model parameters, but rather must be estimated empirically. For this, we first simulated a 1°C increase in mean summer air temperature (SATI = 1). We then calculated mean summer water temperature from the distribution of DMWTs from the model outputs from Eq. 5 and computed TS as the difference between the predicted mean summer water temperature at SATI = 1 and observed mean summer water temperature (current climate). We estimated TS from our two-variable models under all three assumptions of TS_{GW}.

We also derived a measure of the thermal resistance of brook trout habitat (TR_{BT}), defined as the increase in mean summer air temperature above current climate required to render a reach unsuitable for brook trout. We used a brook trout thermal threshold of 23.3°C maximum weekly average temperature (MWAT) to define brook trout habitat suitability. The MWAT threshold was derived from a field based assessment of brook trout occurrence patterns across a gradient in temperature and exposure periods in Michigan and Wisconsin, USA (Wehrly et al. 2007). This MWAT threshold corresponded closely with the upper thermal limit of brook trout growth (determined to be 23.4°C) observed in laboratory experiments (Chadwick 2014). MWAT was determined for each site by first calculating the seven-day moving average of DMWT for every seven-day interval throughout the summer, and then selecting the highest value. Sites where MWAT exceed 23.3°C were deemed unsuitable for brook trout occurrence. We used DMWT outputs from our adjusted regression models to estimate MWAT for each TS_{GW}–SATI scenario.

Estimating TR_{BT} is relatively straightforward in this context because just as mean stream temperature is linearly related to mean air temperature, so is MWAT, such that

$$TR_{BT} = \frac{(23.3 - MWAT_{SATI=0})}{(MWAT_{SATI=1} - MWAT_{SATI=0})} \tag{6}$$

where TR_{BT} is change in mean summer temperature, 23.3°C is the brook trout thermal threshold, $MWAT_{SATI=0}$ is maximum weekly average temperature derived from our adjusted regression models under the current climate, and $MWAT_{SATI=1}$ is the MWAT derived from current mean summer air temperature + 1°C. Therefore, the difference between MWAT at SATI = 0 and SATI = 1 is the rate at which MWAT will change per degree change in mean summer air temperature. As with stream TS, we estimated TR_{BT} under all three assumptions of TS_{GW}.

Predicting climate change effects on brook trout habitat

We used three modeling approaches to estimate thermal habitat suitability for brook trout under current and forecasted air temperature regimes. The alternative approaches represent methods currently used to predict potential effects of warming air temperatures on fish habitat in streams, and vary with respect to assumptions regarding air–water temperature relationships (i.e., TS), and the spatial grain at which these relationships vary across the landscape. All three approaches assume that all other factors aside from temperature, including average precipitation and streamflows, would not change in future scenarios.

The first two approaches use our two-variable regression models adjusted for TS_{GW} in combination with a known thermal threshold for brook trout (MWAT = 23.3°C) to infer habitat suitability. The first modeling approach, termed the "reach" method, uses the site-specific parameters from our two-variable regression models to predict daily water temperatures from simulated daily air temperatures. For each climate change scenario, sites where MWAT computed from regression models are predicted to exceed the brook trout thermal tolerance limit are deemed unsuitable. This method evaluates habitat suitability at the stream reach spatial grain and consequently does not assume homogeneity or spatial structure (e.g., upstream to downstream gradients) in TS among sites. There have been few studies designed to assess thermal sensitivity at this fine spatial grain (but see Danehy et al. 2005, O'Driscoll and DeWalle 2006), and to our knowledge, there have been no studies that use fine-grained information to forecast climate change effects on stream fish habitat across the landscape.

The second approach we termed the "watershed" method. This method is the same as the reach method, except that instead of using air–water temperature relationships derived from each site, only the relationships derived from the lower most site in each watershed (i.e., the pour-point) is used in modeling. Air–water temperature relationships determined from each pour-point site are applied at all sites within the watershed (i.e., nine regression models instead of 78 in our case). This approach recognizes among-watershed variation, but, in contrast to the reach modeling approach, assumes thermal air–water temperature relationships will be uniform among reaches within watersheds. Similar watershed-scale approaches have been used to assess TS and controls on stream temperature for salmonid habitat (Isaak and Hubert 2001, Trumbo et al. 2014).

The third approach we termed the "boundary" method. In contrast to the first two approaches, the boundary method does not use air–water temperature data or relationships directly in habitat assessments. Instead, this approach relies on empirical relationships between air temperature, latitude, and elevation in combination with current trout distribution data to infer regional estimates of current and future trout habitat suitability. This approach was used by Flebbe et al. (2006) to estimate climate change effects on trout habitat in the southern Appalachians. Their method links a boundary model of current trout distribution (defined by minimum elevation) across a gradient in latitude, with a lapse rate model that defines the change in air temperature with elevation to estimate change in trout habitat with increasing air temperature. For areas north of 35 degrees latitude (including all of SNP and most of the range of eastern brook trout), their model was

$$\begin{aligned}\mathrm{ELE} = -\exp[-163 + (9.23 \times L) - (0.126 \times L^2)] \\ +(188 \times \Delta T) \qquad (7)\end{aligned}$$

where ELE is minimum elevation in meters, L is latitude in decimal degrees, and ΔT is the change in mean air temperature (i.e., $\Delta T = \mathrm{SATI}$ with values of 1.5°C, 3.0°C, and 5.0°C). The boundary model thus predicts minimum elevation of suitable trout habitat under current ($\Delta T = 0$) and forecasted air temperature regimes. A site is deemed unsuitable if the site elevation is lower than the modeled minimum elevation for a given climate scenario. Implicit in the model is the assumption that atmospheric factors such as air temperature are the primary drivers of stream temperature, and that thermal sensitivity of streams is invariant. Specifically, the Flebbe et al. (2006) model assumes that a 1°C change in air temperature corresponds to a 1°C change in water temperature at all sites. Similar boundary methods have been widely used to predict changes in salmonid habitats over large areas associated with climate change (Meisner 1990*a*, Keleher and Rahel 1996, Rahel et al. 1996, Rieman et al. 2007).

Results

Modeling stream temperature and thermal sensitivity

Linear relationships between modeled DMAT and DMWT were highly variable among the 78 sites in SNP. Air–water relationships ranged from highly sensitive sites where water temperature tracked daily variation in air temperature (Fig. 2a) to more resistant sites where water temperature increased through the summer, but did not track daily variation in air temperature (Fig. 2c). Water temperatures at most sites showed patterns intermediate to the two extremes (Fig. 2b). Linear regression slopes (i.e., TS) ranged from 0.10 to 0.82 (mean = 0.39). Linear model *y*-intercepts ranged from 1.2 to 16 (mean = 10.2) and were negatively related to model slopes (Fig. 2d). Model fits of individual regression models were also highly variable, with adjusted R^2 values ranging from 0.03 to 0.72 (median = 0.41), and were positively correlated with model slope (Fig. 2e).

Including the ADD as a predictor variable into regression models improved model fit substantially (Fig. 3a, b, c). Model fit improved for all 78 sites with adjusted R^2 values for the two-variable models ranging from 0.43 to 0.99 (median = 0.87; Fig. 3d). Average improvement in adjusted R^2 over the single-variable (DMAT) model was 43.5% and ranged from 2.8% to 95.5% (Fig. 3e). Although model strength improved for all sites, it was most pronounced for sites less sensitive to DMAT (Fig. 3e).

The relative importance of the two predictor variables (DMAT and ADD) varied substantially among sites (Fig. 4a). Although both variables explained a significant fraction of the total variation in daily water temperature at most sites, ADD explained more variation than DMAT at 67.9% ($n = 53$) of the sites (Fig. 4a). Inferred effects of groundwater on stream temperature varied widely within and among watersheds (Fig. 4b). Groundwater influence was relatively consistent in some watersheds like Meadow Run, Piney River, and Hughes River, whereas it varied substantially in others such as Big Run, Paine Run, and Jeremy's (Fig. 4b). However, on average, variation in the relative influence of groundwater was greater within individual watersheds (mean SD within watersheds = 0.54) than among them (SD among watershed means = 0.08).

On average, estimates of GT for the 78 stream reaches in 2012 derived from our two-variable regression models showed an approximately 1:1 relationship with mean annual air temperature of the preceding year (MAAT), though there was considerable variation in estimates for individual reaches around the trend line (Fig. 5a). For instance, MAAT explained only 34% of the variance in GT among reaches and the root mean squared error estimate (RMSE) was 1.33°C. Similar patterns were observed for direct measurements of GT collected from 60 wells and springs in the park in 1997 (Fig. 5a). Observed GT also showed an approximately 1:1 relationship with MAAT, and similar levels of among-reach variance were observed ($R^2 = 0.50$, RMSE = 1.30°C). The relationships of both modeled and observed GT with MAAT were similar to predictions of mean GT from the simple regional model that assumes GT is approximately MAAT plus 1.5°C (Fig. 5a).

Estimates of future groundwater temperatures for the 78 reaches depended upon assumptions regarding the sensitivity of groundwater temperature to *long-term* changes in air temperature ($\mathrm{TS_{GW}}$). Modeled mean GT for 2012 was 14.62°C and was not predicted to change with climate change under the assumption that $\mathrm{TS_{GW}} = 0$ (Fig. 5b). However, under more realistic assumptions of $\mathrm{TS_{GW}}$ (i.e., 0.66–1.00), mean GT increases substantially under climate change, and differences in estimates of mean GT among $\mathrm{TS_{GW}}$ assumptions become increasingly significant with larger simulated increases in climate (SATI). For instance, with a 1.5°C SATI, mean GT increases to 15.61°C with $\mathrm{TS_{GW}} = 0.66$ and 16.12°C with $\mathrm{TS_{GW}} = 1.00$, but differences were not statistically different ($P > 0.05$). However, with a 5.0°C SATI, mean GT increases to 17.92°C for $\mathrm{TS_{GW}} = 0.66$, and 19.62°C for $\mathrm{TS_{GW}} = 1.00$, and differences were significantly different among $\mathrm{TS_{GW}}$ assumptions (Fig. 5b).

Increases in GT and assumptions regarding $\mathrm{TS_{GW}}$ would have obvious implications on stream TS. Under

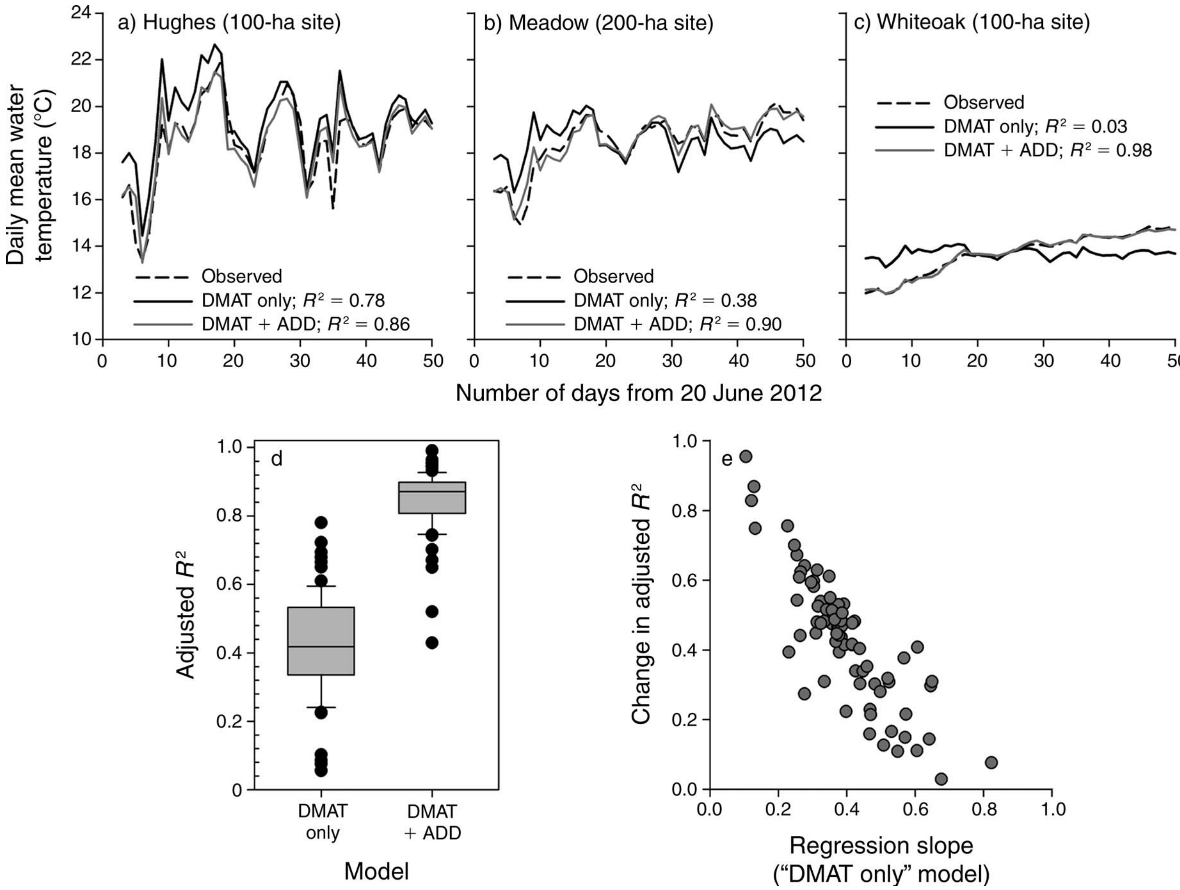

FIG. 3. Comparisons of predictions of daily mean water temperatures (DMWT) for stream reaches in Shenandoah National Park between regression models that used only daily mean air temperature (DMAT) as a predictor, and two-variable models that used both DMAT and accumulated degree-days above mean summer air temperature (ADD) as predictors. Graphs (a), (b), and (c) show observed and modeled MDWT for three example sites. Adjusted R^2 values are shown for both single- and two-variable models. Graph (d) compares the distribution of adjusted R^2 values for all 78 sites for both models. Graph (e) shows the relationship between the single-variable model slope and improvement in adjusted R^2 observed from incorporating the additional ADD model term into the model.

the assumption that $TS_{GW} = 0$, predicted stream TS declines sharply with increasing groundwater influence, with predictions ranging from 0.69 for reaches with no groundwater influence (i.e., $R^2_{ADD} = 0$) to 0.08 for reaches completely comprised of groundwater (i.e., $R^2_{ADD} = 1$; Fig. 6a). In contrast, mean TS predictions are largely invariant to groundwater influence at $TS_{GW} = 0.66$ with predictions ranging from 0.69 at $R^2_{ADD} = 0$ to 0.74 at $R^2_{ADD} = 1$ (Fig. 6b); and increase substantially at $TS_{GW} = 1.00$ with predictions from 0.69 at $R^2_{ADD} = 0$ to 1.08 at $R^2_{ADD} = 1$ (Fig. 6c). In contrast, the relationship between groundwater influence and TR_{BT} was consistently negative, irrespective of assumptions regarding TS_{GW}, though the magnitudes of expected changes vary considerably. For instance, estimates of TR_{BT} for reaches at $R^2_{ADD} = 0$ range between 1.25°C and 1.5°C for all three assumptions regarding TS_{GW}. However, at $R^2_{ADD} = 1$, estimates of TR_{BT} are 43.2°C for $TS_{GW} = 0$ (Fig. 6d), 10.7°C for $TS_{GW} = 0.66$ (Fig. 6e), and 7.4°C for $TS_{GW} = 1$ (Fig. 6f).

Forecasting climate change effects on brook trout habitat

In 2012, observed water temperatures indicated substantial among-site variation in MWAT. Observed MWAT ranged from 14.7°C to 23.7°C and only two of the 78 sites exceeded the 23.3°C MWAT threshold for brook trout habitat suitability (Fig. 7). The distribution of MWAT predictions derived from our two-variable *reach* regression models under the current climate closely matched the distribution of observed MWAT (Fig. 7). Reach-specific differences between observed and modeled MWAT ranged from 0.005°C to 0.825°C (mean difference = 0.160°C), and predictions regarding habitat suitability were only slightly different with all 78 regression models predicting suitable habitat (Fig. 7).

Predicted stream temperature and habitat suitability changes were sensitive to TS_{GW} assumptions, especially at larger simulated increases in mean summer air temperature (Fig. 7). Under the 1.5°C SATI scenario, variation in the ranges of predicted stream temperatures

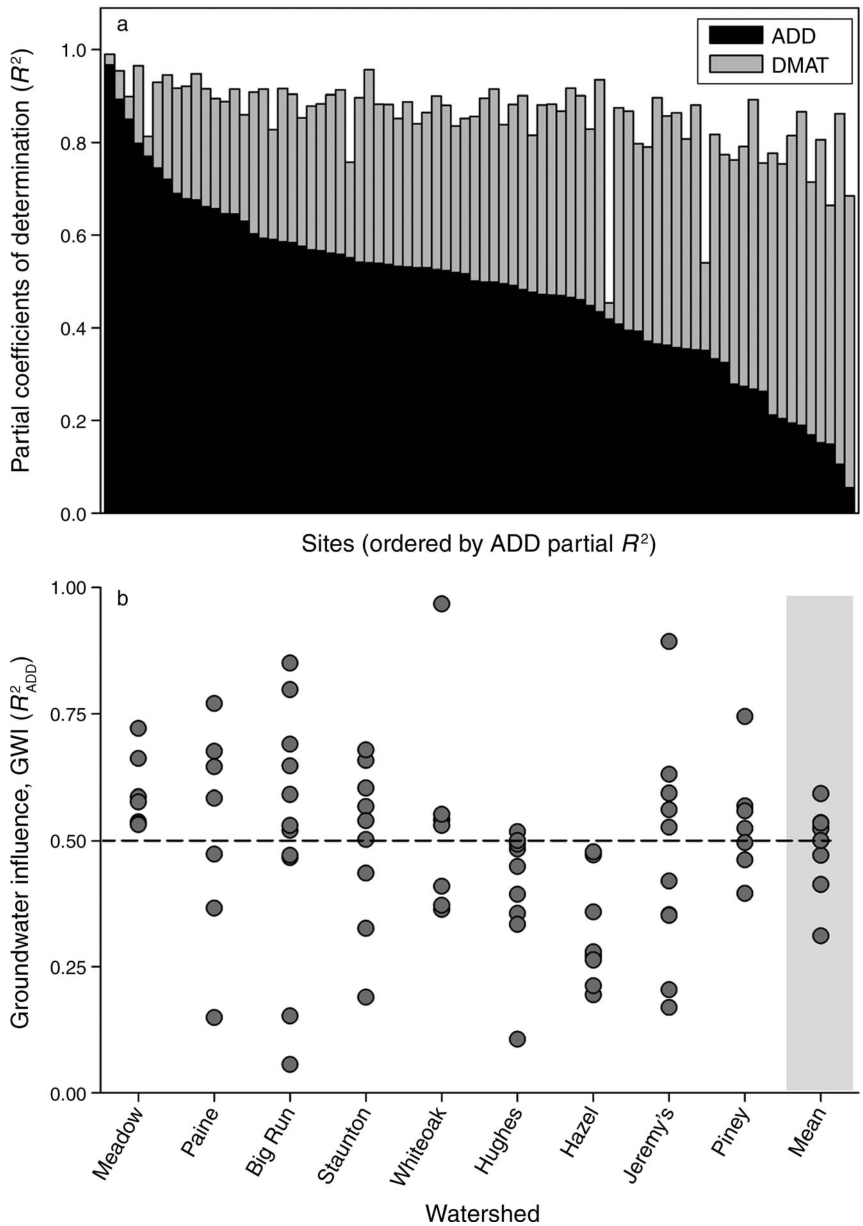

FIG. 4. Graph (a) shows the relative importance (partial R^2 values) of the two model terms, daily mean air temperature (DMAT) and accumulated degree-days above mean summer temperature (ADD), in predicting daily mean water temperature (DMWT) for all 78 stream sites in Shenandoah National Park. Graph (b) shows the relative importance of groundwater within each of the nine watersheds evaluated in the park.

and estimates of park-wide habitat suitability were relatively consistent among models with varying TS_{GW} assumptions. Median MWAT ranged from 20.37°C to 21.28°C, and habitat suitability ranged from 94.87% to 92.31% (Fig. 7). However, differences in stream temperature predictions among TS_{GW} assumptions became increasingly important at greater future air temperature scenarios. At 5.0°C SATI, median MWAT ranged from 21.75°C to 24.60°C, and habitat suitability ranged from 75.35% to 15.38% (Fig. 7).

Park-wide predictions of water temperature (MWAT) and habitat suitability were also highly dependent on spatial grain as defined by the three alternative modeling approaches. As expected, all three approaches predicted 100% of sites in the park were thermally suitable in 2012 (Fig. 8), which compares favorably with observed data (97.4% suitable, 76/78 sites). However, predicted future habitat suitability for brook trout deviated sharply among the three modeling approaches. Declines predicted from the reach models were less extreme than for

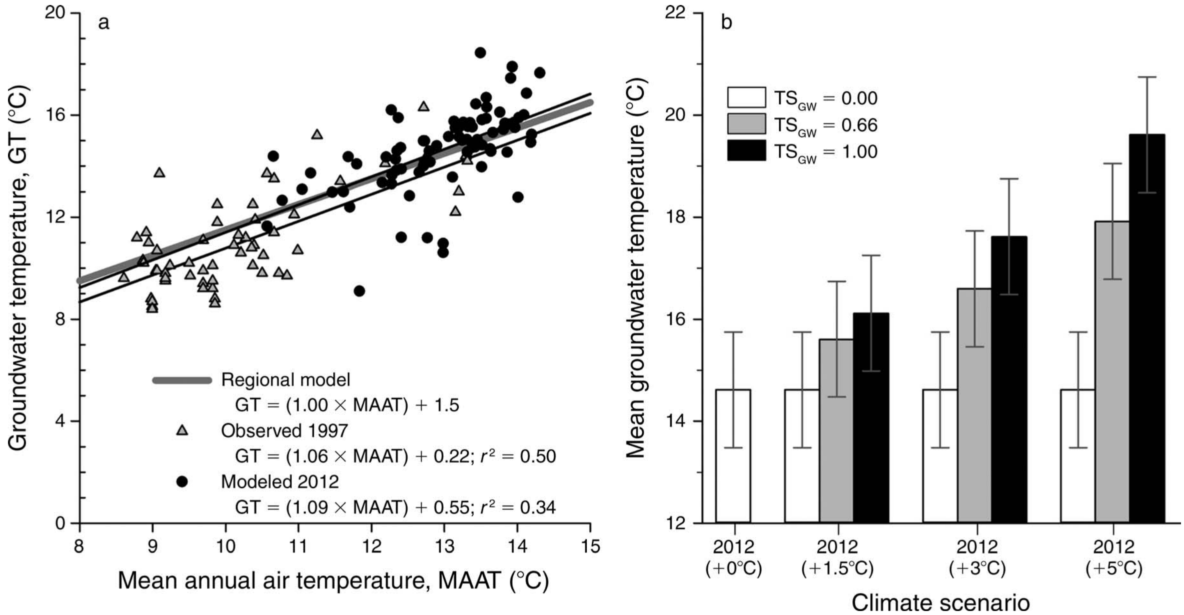

FIG. 5. Groundwater temperatures (GT) measured and modeled in Shenandoah National Park. Graph (a) compares the relationships between mean annual air temperature of the 12-month period leading up to temperature measurements (MAAT) and (1) GT estimated from two-variable regression models for 78 stream reaches in 2012; (2) direct GT measurements collected from 44 springs and 16 wells in the park in 1997 by Plummer et al. (2000); and (3) predictions from a simple regional model (Meisner 1990*a*). Graph (b) shows the influence of assumptions regarding long-term sensitivity of groundwater temperature (TS_{GW}) on predictions of mean GT (±95% confidence limits) derived from our two-variable regression models under the three climate change scenarios: 1.5°C, 3.0°C, and 5.0°C increases in summer mean air temperatures above those observed in 2012.

watershed or boundary modeling approaches. For instance, under the 1.5°C SATI with $TS_{GW} = 1.0$ scenario (i.e., maximum groundwater sensitivity to air temperature), the reach models predicted 92.3% of stream habitat in the study area would remain thermally suitable for brook trout compared to 74.3% for the watershed approach and only 39.7% for the boundary approach (Fig. 8). For the 5.0°C SATI scenario, the reach models predicted over 15.4% of available stream habitat would remain thermally suitable, whereas both the watershed and boundary approaches predicted that no thermally suitable habitat would remain in the study area (Fig. 8).

We also detected important differences in the spatial patterns of habitat loss among the three modeling approaches. For this assessment, we controlled for differences in the total amount of habitat loss by using the respective modeling approaches to empirically derive the SATI required to cause equivalent and moderate declines in suitable habitat. We found that 20 of the 78 reaches (25.6%) would become thermally unsuitable with a 2.67°C increase for the reach approach, a 1.50°C increase for the watershed approach, and a 0.70°C increase for the boundary approach (Fig. 9). The results indicate substantial differences in spatial patterns of habitat decline within and among watersheds for the three modeling approaches. Both the watershed and boundary modeling approaches predicted that reaches within watersheds would become progressively unsuitable in an upstream direction as air temperatures increase over time (Fig. 9). In contrast, the reach modeling approach predicted a more patchy spatial distribution of habitat suitability within watersheds. For instance, high-elevation reaches in Paine, Big Run, Hughes and Jeremy's watersheds were predicted to become unsuitable prior to reaches lower in elevation (Fig. 9). The three modeling approaches also predicted different habitat decline patterns among watersheds. The boundary model predicted more uniform patterns of decline among watersheds because elevation ranges were similar for most watersheds (Fig. 9). In contrast, the watershed models predicted highly heterogeneous patterns of decline, wherein whole watersheds are predicted to be comprised of either largely suitable or unsuitable habitats (Fig. 9). The reach models predicted habitat losses among watersheds that were intermediate to those of the watershed and boundary approaches.

DISCUSSION

Modeling stream thermal sensitivity

Our analysis of air–water temperature relationships revealed important discontinuities in TS and DMWT regimes. Simple linear regression models indicated that thermal patterns in SNP ranged from highly sensitive reaches where summer stream temperatures closely tracked daily variation in air temperature to relatively insensitive reaches where stream temperatures were largely independent of short-term variation in air

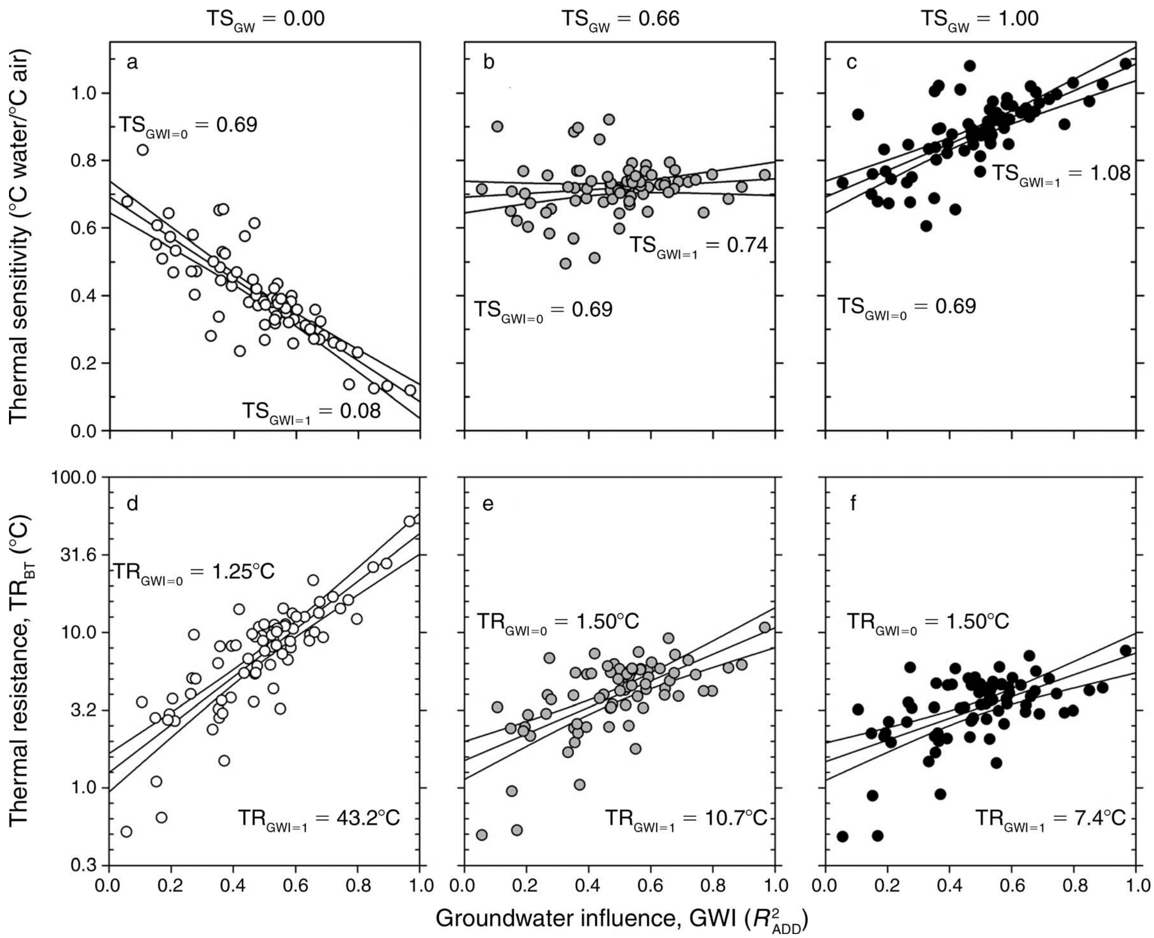

FIG. 6. Relationships between modeled stream thermal sensitivity (TS, top panels) and brook trout site thermal resistance (TR_{BT}, bottom panels) and groundwater influence (GWI) under three alternative assumptions of long-term groundwater sensitivity (TS_{GW}). Predictions for GWI = 0 (streamflow completely comprised of surface runoff) and GWI = 1 (streamflow completely comprised of groundwater) are shown for each graph.

temperature (Fig. 2). This is in contrast to larger streams and rivers where TS is consistently high (linear regression slopes >0.7; Stefan and Preud'homme 1993, Pilgrim et al. 1998, Erickson and Stefan 2000, Bogan et al. 2003) and stream temperature varies in a directional fashion along gradients in elevation and latitude (Arscott et al. 2001, Morrill et al. 2005, Caissie 2006, Kelleher et al. 2012, Hilderbrand et al. 2014). Our findings suggest that, unlike larger streams, where climatic variables such as solar radiation are the principle drivers of stream temperature (Webb et al. 2008), thermal patterns in forested headwater streams are strongly influenced by hydrologic controls that vary at smaller spatial scales (Constantz 1998, Story et al. 2003, Tague et al. 2007). Predicting stream temperature in headwater streams and forecasting climate change responses will therefore require an understanding of TS at fine spatial grains, and the use of statistical models that rely on air temperature alone and assume uniform air–water temperature relationships over larger areas may not be appropriate. Our results also demonstrate that process-based analytical modeling approaches that require detailed hydrometerological data may be impractical for assessing thermal patterns at ecologically relevant spatial scales.

Regression-based statistical models that incorporate the direct measurement of both local air and water temperatures may provide an alternative approach for assessing stream temperature dynamics that is conducive to ecological assessments. This approach has become increasingly popular due to the relatively low cost of automated temperature loggers (Dunham et al. 2005, Johnson et al. 2005) and has been used to characterize TS patterns at fine spatial grains across broad landscapes (Kelleher et al. 2012, Mayer 2012, Hilderbrand et al. 2014, Trumbo et al. 2014). However, recent research has shown that these simple air–water regression models derived from short-term (i.e., sub-annual) data sets may provide limited value in terms of predicting future stream temperatures in headwater areas for two reasons. First, these simple models do not directly account for non-climatic influences, such as groundwater inputs on

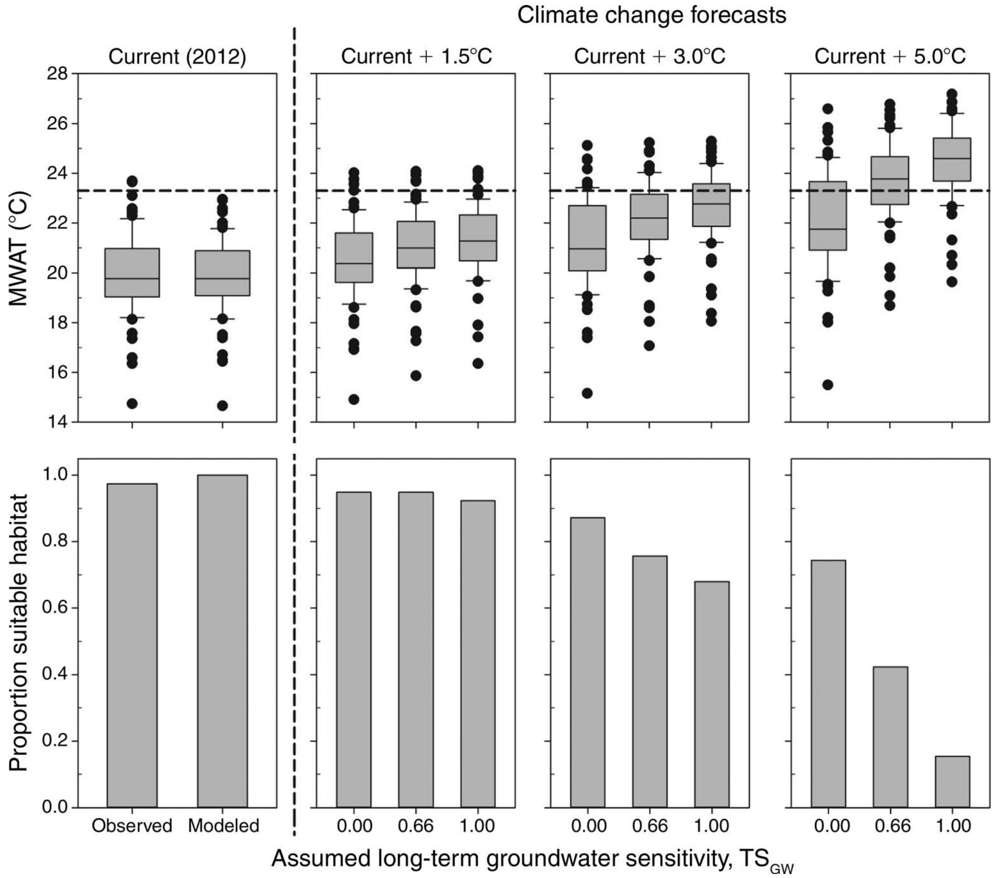

FIG. 7. Park-wide predictions of maximum weekly average temperatures (MWAT) and the proportion of thermally suitable habitat under current (2012) and three future climate change scenarios. Predictions were derived from the reach-specific air–water temperature regression models ($N = 78$) using three alternative assumptions regarding long-term sensitivity of groundwater temperature to changing air temperature (TS_{GW}). Top panels (box plots) show the distribution of MWAT for the 78 stream reaches, and bottom panels show the proportion of thermally suitable habitat in the park (i.e., MWAT < 23.3°C). For box plots, black lines within boxes depict medians, the upper and lower limits of the box define the 25th and 75th percentiles, and whiskers define the 10th and 90th percentiles.

stream temperature (Arismendi et al. 2014, Gu et al. 2014). As a result, these models tend to underfit the data, especially at sites with large groundwater contributions. This underfitting is exemplified by the strong positive correlation we observed between estimates of model fit (adjusted R^2) and model slopes (i.e., TS) of simple air–water temperature regression models (Fig. 2e), and the observation that residuals generated from air–water temperature regressions showed a biased distribution for sites where model slopes and partial R^2 values were low (not shown, but can be inferred by Fig. 3c). Secondly, these simple models do not account for increases in GT that are likely to accompany increasing climate over long time periods. Therefore, directly using parameters derived from these short-term models essentially assume that groundwater is not sensitive to changing air temperature. This is not a reasonable assumption, as GT has been shown to be highly sensitive to changing air temperatures over annual and longer time scales (Kurylyk et al. 2013, Menberg et al. 2014). This may be particularly important in landscapes where groundwater is stored in relatively shallow aquifers such as SNP (Lynch 1987, Plummer et al. 2001, Busenberg and Plummer 2014).

We show that intuitive adjustments to simple air–water temperature models may allow for the estimation of groundwater influence on stream temperatures, and that these adjusted models can be used to incorporate more realistic assumptions regarding the long-term effects of increasing climate on GT (i.e., TS_{GW}) and consequent effects on stream TS. Specifically, we were able to model the moderating effect of groundwater on summer DMWT, and improve the model fit of short-term regression models by incorporating the ADD term into site regression models. This additional measure of air temperature tracked the cumulative heating of stream temperature through the summer that is associated with groundwater intrusion. Inclusion of the ADD term improved estimates of model fit at all 78 stream reaches studied, but improvements were most pro-

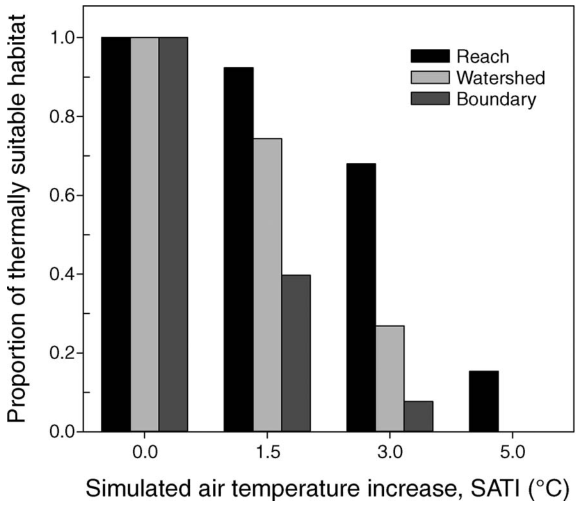

FIG. 8. Park-wide predictions of the proportion of thermally suitable brook trout habitat predicted by the three different modeling approaches (reach, watershed, and boundary) under current and three simulated future climate scenarios. The long-term sensitivity of groundwater temperature to air temperature (i.e., TS_{GW}) is assumed to be 1.0 for all three modeling approaches.

nounced at sites that were less sensitive to air temperature (Fig. 3e). Previous efforts to incorporate stream hydrology variables into stream temperature regression models have largely relied on direct measures of streamflow gains and losses derived from remote gaging stations. For instance, in an assessment of TS of 99 small streams in Maryland (USA), Hilderbrand et al. (2014) found that incorporating mean daily discharge derived from the nearest gaging station significantly improved the predictive capacity of air–water temperature regressions, and improvements were greatest at sites with low TS, as we observed in SNP. However, these improvements were relatively modest (mean R^2 increased from 0.61 to 0.73). Using similar approaches for 104 sites in the Pacific Northwest, Mayer (2012) also found significant, but modest improvements (mean R^2 increased from 0.61 to 0.68) in summer air–water temperature regressions after including gage-derived estimates of flow. In contrast, addition of the ADD term into our regression models more than doubled the median adjusted R^2 values (0.41 to 0.87; Fig. 3d).

Others have used geostatistical modeling approaches developed specifically for stream networks (Peterson and Ver Hoef 2010) to account for spatial autocorrelation of

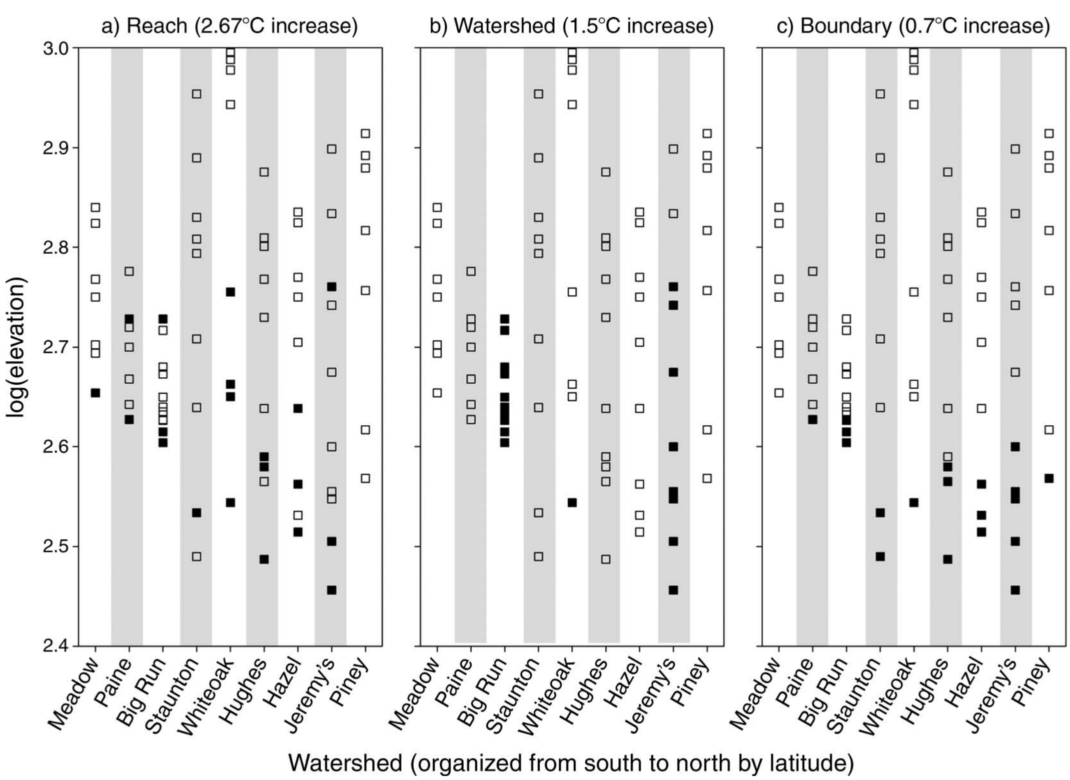

FIG. 9. Comparisons of the predictions of the spatial patterns of thermal habitat loss among three modeling approaches: (a) reach regression, (b) watershed regression, and (c) boundary model. Graphs show predictions of habitat suitability (open squares show suitable habitat; solid squares show unsuitable habitat) for all stream reaches with each of the nine watersheds as a function of position in the watershed (i.e., elevation [measured in meters]). We controlled for differences in the total amount of habitat loss by using the respective modeling approaches to empirically derive the increase in mean summer temperature required to cause equivalent and moderate declines in suitable habitat (i.e., 25.6% or 20 of 78 reaches as unsuitable).

thermal patterns associated with flow connectivity. These methods have been successfully applied to western drainages and have been found to improve stream temperature models by accounting for gradients in stream size, elevation, and tributary effects on stream temperature that change in a directional fashion along stream corridors (Isaak et al. 2010, Jones et al. 2013). However, we found that adding elevation or basin area measures as additional predictor variables to simple air–water temperature models did not significantly improve predictions of current or future stream temperatures in SNP (not shown). We hypothesize that processes controlling TS vary over larger spatial scales in western vs. eastern streams in North America. For instance, snowmelt represents a considerable source of surface flow during significant periods of the summer, potentially overwhelming groundwater effects that may vary over smaller spatial scales. Moreover, the effect of snowmelt on stream temperature correlates with topographical features such as elevation and stream size that, like air temperature, vary in an upstream to downstream direction (Isaak et al. 2010, Hunsaker et al. 2012). Thus, the mechanistic processes controlling stream temperatures and TS may be different and operate over different spatial scales in eastern and western North America. Many GCMs predict a decrease in spring snowpack, a transition from snow to rain, and reduced summer streamflows across the western United States by 2040 (Ashfaq et al. 2013), and these predictions are supported by recent observations (Mote et al. 2005, Hunsaker et al. 2012). If these trends continue, groundwater may become an increasingly important driver of future summer stream temperatures in western stream networks, and spatial patterns of thermal heterogeneity may begin to resemble those in eastern stream networks as shown here. We conclude from these patterns that the ADD term provides a robust and reach-specific measure of groundwater importance that does not rely on assumptions that groundwater influence correlates with regional gradients. Our approach is conceptually comparable to field methods that use heat flux measurements as a tool to quantify surface–groundwater interactions and define complex flow paths in headwater streams (Anderson 2005, Constantz 2008, Leach and Moore 2011, Westhoff et al. 2011).

Our development of a predictor variable that tracks groundwater influence (i.e., ADD) allowed for the estimation of two related parameters, the proportion of streamflow comprised of groundwater (inferred by the R^2_{ADD}) and actual groundwater temperature (GT, computed as the y-intercept when $R^2_{\mathrm{ADD}} = 1$) at each stream reach. Our results suggest that stream temperature regimes described by summer DMWT patterns can be largely explained by net atmospheric energy fluxes, as inferred by R^2_{DMAT}, and advective heat exchanges associated with shallow groundwater inputs and hyporheic flow, as inferred by R^2_{ADD}. With only a few exceptions, >80% of the variation in DMWT was explained by these two predictor variables (Fig. 4a). Although net solar radiation is frequently implicated as the most important driver of stream temperatures (Caissie 2006, Webb et al. 2008), our observation that R^2_{ADD} was greater than R^2_{DMAT} at most sites (Fig. 4a) suggests the pervasive influence of shallow groundwater on headwater stream temperatures. This finding is consistent with the results of intensive thermal and hydrologic investigations conducted within selected headwater stream reaches in other areas that have shown that advective heat exchanges can have profound effects on thermal sensitivity and stream temperatures in small streams (Story et al. 2003, Johnson 2004, Constantz 2008, Leach and Moore 2011). We also showed that groundwater influence is more variable within watersheds than among them (Fig. 4b), and this has significant implications for the appropriate spatial scale required for thermal condition assessments in headwater stream networks.

Estimates of 2012 GT derived from our models were consistent with direct GT measurements collected from wells and spring sources in the park in 1997 (Plummer et al. 2000), providing independent validation for our two-variable reach models. Both modeled and measured mean GT showed an approximately 1:1 relationship with local MAAT and similar ranges of variation among GT values for individual sites (Fig. 5a). These MAAT–GT relationships also approximate predictions from a simple regional model of GT that has been applied to the range of eastern brook trout (Meisner 1990*a*). In particular, the relationship from our modeled data corresponded almost exactly with the regional model (Fig. 5a). Relative to MAAT, observed GT measurements were ~0.66°C cooler on average than modeled values. This difference may be due to the fact that GT measurements were taken from wells and spring sources that reflect subsurface GT, whereas modeled values represent GT at the stream surface. Much of the variation in GT not explained by MAAT (50% for observed measurements; 66% for modeled estimates) is likely due to site-specific variation in the depth of groundwater sources, the distance from groundwater sources, soil types, and other latent variables known to influence GT (Kurylyk et al. 2013, Menberg et al. 2014). We argue that these factors primarily represent physical characteristics of individual stream reaches that are not likely to change over ecologically relevant time scales, and so our adjusted regression models should provide reasonable estimates of future GT. However, we acknowledge that these models ignore the effects of changing precipitation patterns on groundwater influence that may occur under future climates, and which would likely have strong effects on stream thermal regimes (see *Conclusions and limitations* section below).

The strong (1:1) relationships observed between MAAT and GT suggests that GT may be highly sensitive to MAAT over even short time lags. In our case, we used the 12-month period prior to temperature measurements to define MAAT, which suggests that GT in SNP may be driven by relatively recent air temperature patterns. Recent research on GT responses to air temperature change suggests that, for shallow aquifers, the lag time between air temperature warming and associated increases in GT is usually less than five years and often less than one year (Menberg et al. 2014). Moreover, others have shown that GT at depths of as much as 30 m may show significant annual variability due to interannual changes in air temperature (e.g., Lesperance et al. 2010). In addition, investigators using both detailed analytical heat budget models (Kurylyk et al. 2014, Menberg et al. 2014) and statistical analyses of GT samples (Kurylyk et al. 2013, Menberg et al. 2014) have shown that the sensitivity of shallow GT to changing air temperatures (i.e., TS_{GW}) typically ranges between 0.66 and 1.0 depending on depth, soils, and other factors (Kurylyk et al. 2013, Menberg et al. 2014). These patterns suggest that, although groundwater dominated streams exhibit highly damped responses to daily and seasonal variation in stream temperature, they are highly sensitive to changes in air temperature that occur over time periods commensurate with climate change (e.g., years or decades).

Predictions of future GT derived from our adjusted regression models were highly dependent on assumptions of TS_{GW} (Fig. 5b). It necessarily follows then that estimates of stream TS also depend upon TS_{GW}. For instance, assuming $TS_{GW} = 0$, stream TS declines sharply with groundwater influence suggesting that groundwater-dominated sites are less sensitive to air temperature change. This is consistent with inferences of stream TS typically drawn from the slope coefficients of air–water temperature regression models derived from annual or sub-annual data (Kelleher et al. 2012, Mayer 2012, Hilderbrand et al. 2014, Trumbo et al. 2014). Such evaluations of stream TS based on this short-term perspective have led some to suggest that groundwater-dominated streams or reaches are more resistant to climate change, and that they may offer refugia for fishes and other biota in the face of an increasing climate (Ficklin et al. 2014, Kløve et al. 2014). However, we show that under more realistic assumptions of TS_{GW}, stream TS is shown to be equally ($TS_{GW} = 0.66$), or even more, sensitive ($TS_{GW} = 1.00$) to air temperature increases than runoff-dominated reaches (Fig. 6, top panels). These results highlight the importance of incorporating a longer temporal perspective in assessments of stream TS.

However, estimates of stream TS may not be sufficient by themselves to predict ecological responses to climate change. This is because aquatic species are typically adapted to specific thermal regimes and their distribution is often defined by thermal thresholds (Eaton et al. 1995, Beitinger et al. 2000, Wehrly et al. 2007). Thus, the rate at which stream temperatures are expected to increase per unit increase in air temperature (i.e., stream TS) represents only one important aspect of site vulnerability. Current stream temperatures are also important because the difference between current stream temperature and any biologically meaningful thermal tolerance threshold defines the extent a stream needs to warm before becoming thermally unsuitable.

Our measure of thermal resistance (TR_{BT}) is an estimate of the increase in air temperature required to render a site unsuitable to brook trout, and incorporates measures of both stream TS and current stream temperature, as well as the thermal threshold for brook trout thermal habitat suitability. This measure is simple to compute and although it is specific to brook trout habitat suitability, the approach could be used to estimate site thermal resistance for any biological endpoint that can be defined by a threshold temperature. However, because our estimate of TR_{BT} was derived from a linear model, it should only be interpreted as a *relative* measure of site thermal resistance only. This is because stream temperatures typically deviate from linearity as air temperatures exceed about 25°C (Mohseni and Stefan 1999, Bogan et al. 2006), which, in our case, would be anything above about a 3°C increase above current climate (mean 2012 summer air temperature = 22.07°C). Thus, these values almost certainly represent pessimistic estimates of TR_{BT}; nonlinear models would yield higher estimates of TR_{BT}.

Because stream TS depends on TS_{GW}, estimates of TR_{BT} also vary with respect to $TS_{GW.}$ We show however that, in contrast to stream TS, TR_{BT} increases with the relative contribution of groundwater (i.e., R^2_{ADD}) irrespective of TS_{GW} assumptions (Fig. 6, bottom panels). These analyses indicate that higher thermal resistance of groundwater-dominated sites has more to do with cooler current stream temperatures than lower stream TS. Even when we assume reaches dominated by groundwater will warm more quickly than runoff-dominated reaches (i.e., higher TS; e.g., when $TS_{GW} = 1.00$), groundwater-dominated streams would still require larger increases in air temperature before becoming thermally unsuitable (Fig. 6). These findings support the conclusion of Mayer (2012) that accurate assessments of spatial variation in current stream temperature regimes are just as important as thermal sensitivity for assessing potential climate change impacts. Trumbo et al. (2014) also considered measures of current stream temperatures in addition to stream TS to characterize thermal vulnerability. The authors used TS derived from short-term air–water regression models and a measure of current exposure to temperatures above a critical thermal threshold (comparable to our MWAT threshold) to rank site vulnerability to climate change. However, their estimate of stream TS did not account for $TS_{GW,}$ and their measure of current exposure did not fully account for near-threshold conditions. That is, sites that were exposed to summer stream temperatures that were currently very near, but not above, the thermal threshold were ranked the same as sites where summer stream temperatures were not anywhere near the thermal threshold. In contrast, our TR_{BT} measure incorporates both TS_{GW} and current stream temperatures into a single continuous value that describes the relative resistance of sites to climate change.

Implications for brook trout habitat prediction

Our predictions for future brook trout thermal habitat in SNP were sensitive to assumptions regarding TS_{GW} (Fig. 7). However, within the realistic range of TS_{GW} of 0.66 to 1.0, differences in future habitat predictions were relatively minor except for the most pessimistic climate scenario (i.e., 5.0°C SATI) where model predictions of remaining thermally suitable habitat varied between 28.2% ($TS_{GW} = 1.0$) and 51.3% ($TS_{GW} = 0.66$). We found no differences for the 1.5°C-increase scenario and only minor differences (<4%) for the 3.0°C-increase scenario when comparing TS_{GW} between 0.66 and 1.0 (Fig. 7). In contrast, we found that estimates of suitable habitat based upon the assumption of $TS_{GW} = 0$ were far too optimistic. For instance, even under the 5.0°C increase in mean summer air temperature scenario, nearly 76% of available habitat in the park is predicted to remain thermally suitable. Moreover, differences in habitat predictions under climate change associated with varying assumptions regarding TS_{GW} were relatively minor compared with differences associated with measurement grain. Even when using the most pessimistic assumptions regarding TS_{GW} (i.e., $TS_{GW} = 1.0$), climate change predictions derived from our fine-grained reach models suggest that forested headwater streams are substantially less vulnerable to climate warming than previously estimated from large-scale boundary models that assume high and spatially uniform thermal sensitivities across the region (Fig. 8). For example, Eaton and Scheller (1996) used downscaled climate change predictions (mean summer increase = 4.4°C) and a uniform air–water temperature relationship of 0.9 to project a 54.8% decline in brook trout habitat nationwide. Clark et al. (2001) used a uniform air–water temperature relationship of 0.7 to estimate an 80% decline in trout habitat in the Appalachians associated with a 1.5–2.5°C increase in air temperature. Likewise, Flebbe et al.'s (2006) boundary model assumed a uniform air–water temperature relationship of 1.0 and predicted that trout habitat in the southern Appalachians would decline 21.6% with a 1.5°C increase in annual air temperature, and 97.3% with a 5.0°C increase. That model also predicted the complete elimination of trout habitat in Virginia under a 5.0°C in mean annual temperature scenario, which is consistent with our boundary model predictions in SNP where we noted complete elimination of suitable habitat at a 5.0°C increase in summer temperature (Fig. 8; Flebbe et al. 2006). In contrast, our models that incorporated reach-specific information on thermal sensitivity predicted brook trout habitat in SNP to decline only 5% with a 1.5°C increase in summer mean temperature, and 71% with an increase of 5.0°C (Fig. 8). These findings are particularly significant when we consider that the baseline mean summer air temperatures (i.e., 2012 study year) were relatively high: The historical mean summer air temperature at the SNP weather station in Luray, Virginia was 12.1°C compared with 13.5°C for the 2012 study year. Moreover, only 3% ($n = 2$) of the observations over the 77-year period of record exceeded the mean summer air temperature observed in 2012. Thus, our simulated future climate regimes and our modeled future water temperatures probably represent a scenario of maximum potential change in brook trout thermal habitat.

The watershed-scale models also overestimated habitat loss, though not to the extent of the boundary models (Fig. 8). In this case, the overestimate is more related to a spatial bias in the sampling design (i.e., using models from the downstream extent or pour point sites of the watershed to represent the entire watershed) than measurement grain per se. In SNP, sites located near the bottom of their watersheds were frequently "losing" reaches where streamflow is lost to the underlying hyporheic zone (Lynch 1987). Thus, streamflow in these areas tends to be comprised largely of surface runoff and are therefore warmer. We found no examples of previous studies that used watershed-scale air–water temperature regression models to predict future stream temperatures or habitat loss from climate change. However, researchers have used sampling designs that rely on a single paired air–water temperature model, often developed from pour point sites near streamflow gaging stations, to estimate stream TS and rank watersheds in terms of vulnerability to climate change (e.g., Kelleher et al. 2012, Trumbo et al. 2014). The assumption here is that watershed models would effectively represent elevation and other factors that affect local variation in air temperature, and that other important drivers of TS such as groundwater influence is organized at the watershed scale. However, our analyses indicate that there is as much variation in groundwater influence within these small watersheds as among them in SNP (Fig. 4b).

We also predicted large differences in the spatial pattern of thermal habitat loss due to climate change among the three modeling approaches. The boundary and watershed modeling approaches predicted thermally suitable habitat would decline in a downstream to upstream direction in response to increasing air temperatures (Fig. 9). This finding is largely tautological, as both of these larger grain modeling approaches assume uniform thermal sensitivities within watersheds. Therefore, air temperature is the only driver of stream temperature that varies within watersheds in these models, and air temperature is largely a function of elevation for both modeling approaches. In contrast, results inferred from our reach models indicate that future habitat decline patterns will actually exhibit a more patchy spatial distribution within watersheds (Fig. 9). This suggests that, despite the important and directional influence of air temperature on stream temperatures, the fine-scale and nondirectional thermal heterogeneity associated with groundwater has a strong influence on both current and future stream temperatures and habitat suitability. Kanno et al. (2013) reached a similar conclusion in a study of thermal heterogeneity in two brook trout streams in Connecticut, USA.

Our findings have important implications for brook trout conservation and management. On the one hand, fine-scale reach models show that brook trout habitat losses expected from climate change are likely to be less severe than previously estimated from large-scale models. However, spatial patterns of habitat loss predicted by our reach models suggest that a warming climate will increase stream network fragmentation and isolation of brook trout populations. At the watershed scale, brook trout habitat is already highly fragmented throughout much of the historical range due to deforestation, water pollution, and the paucity of connected cold-water mainstems (Flebbe et al. 1988, Hudy et al. 2008, Stranko et al. 2008). Our results suggest that additional fragmentation within headwater streams may become increasingly important over time. Brook trout are expected to move within and between connected streams to access thermal refugia (Meisner 1990*b*, Petty et al. 2012) and recolonize areas after natural disturbances (Roghair and Dolloff 2005). Future thermal fragmentation therefore may compound effects of existing natural and anthropogenic barriers to fish movement, potentially decreasing population viability (Morita and Yokota 2002, Letcher et al. 2007).

Conclusions and limitations

Our findings have important implications for predicting stream thermal regimes and thermal habitat suitability patterns under climate change. In particular, we show that, with relatively simple adjustments, paired air–water temperature relationships can be used to discriminate the relative effects of groundwater and air temperature on stream thermal regimes of forested headwater streams. Moreover, these improved regression models allow for the incorporation of more realistic assumptions regarding GT and TS_{GW} into climate change forecasts. Thus, we conclude that such regression-based models based on paired air–water temperature measurements may provide the most realistic approach for assessing and forecasting stream thermal regimes at ecologically relevant spatial scales.

The regression models we used are based upon several key assumptions and have important limitations. First, these models assume that precipitation patterns are temporally static. That is, inferences derived from short-term air–water temperature correlations are not merely site specific, but *site–year* specific. Recent studies have shown that coefficients and statistics derived from air–water temperature regression models vary significantly among years, at least in headwater areas (Kanno et al. 2013, Trumbo et al. 2014), and regression models developed from one time period may not accurately predict future stream temperatures (Arismendi et al. 2014). Such temporal variation should not be surprising in light of the importance that hydrologic variables exert on stream temperature and the larger interannual variation in precipitation patterns for the region. The magnitude and timing of precipitation would be expected to affect the relative contribution of surface runoff and groundwater to streamflow (Kurylyk et al. 2014), which, as we showed, is a primary driver of TS in SNP streams. Total precipitation during the 2012 study year was only slightly lower than the long-term average measured within the park (97 cm compared with 101 cm). Therefore, assuming that total annual precipitation represents a legitimate measure of precipitation patterns related to stream hydrology, and that total precipitation does not change in the future, then stream temperature and TS predictions derived from our adjusted models probably reflect realistic changes in average thermal conditions that can be expected with climate change. In some respects, this assumption may be reasonable, as most GCMs predict no significant changes in mean annual precipitation amount or the frequency of extreme precipitation events (floods or droughts) for the northeastern United States over the next few decades (Kunkel et al. 2013). However, longer term predictions indicate that mean annual precipitation will likely change significantly, though, in contrast to temperature predictions, there is little agreement among the GCMs in even the likely direction of change (i.e., wetter or drier; Ruosteenoja et al. 2003, Kunkel et al. 2013). Despite considerable uncertainty regarding future precipitation patterns, methods are needed that incorporate meaningful precipitation measures into temperature regression models so that the sensitivity of stream temperature to precipitation patterns can be evaluated. This will require assessments of air–water temperature relationships over long periods of time that include a range of precipitation regimes. Currently, long-term stream temperature data are sparse, especially for headwater areas. Thus, improving our understanding of future climate effects on stream ecosystems would benefit greatly from a national stream temperature monitoring network comparable to streamflow monitoring network operated by the U.S. Geological Survey.

Second, we used a linear modeling approach, whereas air–water temperature relationships typically exhibit nonlinear patterns when examined over a wide range in potential air temperatures. Specifically, stream temperatures tend to asymptote at very low (i.e., $\leq 5°C$) and high (i.e., $>25°C$) air temperatures (Mohseni and Stefan 1999, Bogan et al. 2006). Nevertheless, for many objectives related to climate change forecasting (including our objective of estimating trout habitat change), we believe linear models are appropriate because the primary concern is predicted changes in summer stream temperatures up to a relatively low critical summer threshold (in our case, 23.3°C MWAT), above which habitat becomes thermally unsuitable. This assumption is probably true for assessing climate change effects on most salmonids and other cold-water species. However, other objectives will require a broader perspective on stream temperature change. For instance, Mohseni et al. (2003) showed that the distribution of a large number of warm-water fish species are limited by constraints imposed by lower winter temperature thresholds. Therefore, comparable methods to directly account for groundwater influence in nonlinear modeling approaches will be required.

Additional research is needed to characterize groundwater sensitivity to changing climate across different ecosystem types and at various spatial scales. In this study, we assumed a wide range of TS_{GW} to define the boundaries of stream temperature and thermal habitat predictions. However, this range was based on a very small number of studies (Taylor and Stefan 2009, Kurylyk et al. 2013, Menberg et al. 2014). We argue that further increases in our fundamental understanding of thermal drivers such as groundwater inputs and how they vary in space and time will require field studies that link the results of detailed heat budget analyses from selected sites with air–water correlations measured across the broader landscape.

Finally, our predictions regarding future brook trout habitat are also predicated on important assumptions regarding biological responses to increasing air temperatures. Perhaps most importantly is the assumption that the thermal niche or thermal threshold defined under current climate does not change under future climates. Specifically, we assumed that MWAT of 23.3°C is, and will continue to be, an accurate measure of thermal habitat suitability for brook trout. However, the effects of chronic thermal stresses on thermal tolerance in fishes are poorly understood, particularly in complex, fluctuating thermal regimes (Bevelhimer and Bennett 2000). On the one hand, the accumulated stress of increasing stream temperature through time could reduce average individual fitness thereby effectively reducing the thermal threshold for habitat suitability. On the other hand, chronic thermal stresses could increase tolerance through either acclimation (Kelsch and Neill 1990) or adaptation (Hansen et al. 2012, Crozier and Hutchings 2013). Despite the limitations, we believe the work described here increases our understanding of thermal processes at ecologically relevant spatial scales, and provides a physical template on which ecological and evolutionary questions can be tested in future research.

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Supplemental Material

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.th6g8