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NOTE

Characterizing the Thermal Suitability of Instream Habitat for Salmonids: A Cautionary Example from the Rocky Mountains

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Abstract

Understanding a species' thermal niche is becoming increasingly important for management and conservation within the context of global climate change, yet there have been surprisingly few efforts to compare assessments of a species' thermal niche across methods. To address this uncertainty, we evaluated the differences in model performance and interpretations of a species' thermal niche when using different measures of stream temperature and surrogates for stream temperature. Specifically, we used a logistic regression modeling framework with three different indicators of stream thermal conditions (elevation, air temperature, and stream temperature) referenced to a common set of Brook Trout *Salvelinus fontinalis* distribution data from the Boise River basin, Idaho. We hypothesized that stream temperature predictions that were contemporaneous with fish distribution data would have stronger predictive performance than composite measures of stream temperature or any surrogates for stream temperature. Across the different indicators of thermal conditions, the highest measure of accuracy was found for the model based on stream temperature predictions that were contemporaneous with fish distribution data (percent correctly classified = 71%). We found considerable differences in inferences across models, with up to 43% disagreement in the amount of stream habitat that was predicted to be suitable. The differences in performance between models support the growing efforts in many areas to develop accurate stream temperature models for investigations of species' thermal niches.

Characterization of thermal niches for salmonid species has become increasingly important given the sensitivity of this group of fishes to increasing stream temperatures (Rahel et al. 1996) and the anticipated effects of global climate change (Mohseni et al. 2003; Mantua et al. 2010; Isaak et al. 2012b). Stream temperatures influence food consumption, metabolic costs, growth, and condition for individual salmonids (Elliott 2009; Davidson et al. 2010; Sauter and Connolly 2010; Bal et al. 2011). Stream temperatures can also directly or indirectly influence life history characteristics, recruitment, and population growth rates, as salmonids exhibit indeterminate growth rates and strong, positive length–fecundity relationships (Meyer et al. 2003; Al-Chokhachy and Budy 2008; Jonsson and Jonsson 2009). As a result, the thermal regimes within stream networks often strongly influence the distribution patterns of salmonids, both in allopatry and in sympatry (Dunham et al. 2003; Hasegawa and Maekawa 2008).

Increases in air temperatures over the next 50–100 years are expected to alter or reduce the extent of thermally suitable stream habitat for many species (Parmesan and Yohe 2003; Root et al. 2003; Wenger et al. 2011b). Responses to such changes in thermal regimes are likely to differ considerably across species,

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given our understanding of interspecific differences in thermal tolerances (e.g., Bear et al. 2007). Accurate predictions of where and when species distributions will respond to changing thermal regimes will depend not only upon accurate means of downscaling climate effects on stream temperatures but also upon accurate definitions of thermal niches. Although laboratory studies may accurately describe the thermal niche for a species in the absence of community interactions (i.e., fundamental niche; Connell 1961), there is often substantial disagreement between the thermal niche observed in the laboratory and that observed in natural systems (i.e., realized niche; Huff et al. 2005).

A major hurdle in characterizing thermal niches for aquatic species has been a lack of accurate stream temperature data or predictions that are co-located with fish surveys. Until recently, there have been few extensive data sets of empirical stream temperature measurements. In lieu of these data, biologists have linked stream temperature surrogates (e.g., elevation [McCleary and Hassan 2008] and regional air temperature data) spatially and elevationally calibrated to the specific locations of fish distribution data to characterize species-specific measures of thermal suitability (e.g., Wenger et al. 2011a). As stream temperature databases and modeling abilities continue to improve, however, the ability to interpolate accurate, nearly continuous stream temperature predictions across river networks is becoming more common and provides another means of generating co-located thermal suitability information (Sloat et al. 2005; Doglioni et al. 2008; Isaak et al. 2010; Jones et al., in press).

With the recent development of methods for accurately predicting temperatures throughout stream networks, there have been few efforts to compare these methods with previous surrogates of stream temperature or to evaluate different means of describing thermal niches. Our approach was to compare the predictive performance of three indicators of stream thermal conditions (elevation, air temperature, and stream temperature) when referenced to a common set of fish distribution data. Given the variety of factors that can influence the relationships between stream temperature surrogates (i.e., elevation and air temperature) and local stream temperatures (Caissie 2006), we hypothesized that models based on stream temperature predictions would more accurately reflect fish distributions. Concomitantly, we expected that a model based on stream temperature predictions that were contemporaneous (i.e., during the same year) with fish survey data would exhibit increased predictive performance over a model based on measures of average stream temperature; these expectations were largely based on our understanding of salmonid mobility (Northcote 1997; Hilderbrand and Kershner 2000; Rodríguez 2002) and the ability of salmonids to avoid thermally unsuitable habitat (Kaeding 1996; Young 1999).

METHODS

*Study area.—*Our study area included the upper portions of the Boise River basin in south-central Idaho; these portions of the basin are primarily under federal ownership (Figure 1). The basin encompasses 6,900 km^2 and is drained by 2,500 km of fish-bearing streams ranging in elevation from 900 to 2,500 m. The terrain is complex, and vegetation types vary from trees to grasslands along gradients of elevation, aspect, and precipitation. Climate within the study area is characterized by relatively cold winters (average temperature = 22.3°C) and hot, dry summers (average temperature = 59.4°C), with an average annual air temperature of 4.7°C at 1,524 m (Western Regional Climate Center; www.wrcc.dri.edu). Much of the average annual precipitation (∼40 cm; Rieman and McIntyre 1995) occurs as snowfall, particularly at higher elevations; average winter snowfall exceeds 200 cm above 1,500 m. Streamflow is characteristic of the northern Rocky Mountains, with high flows in spring (April–June) and low base flows during summer and early fall, varying in magnitude throughout the basin as a function of catchment area.

The ichthyofauna within the Boise River basin is relatively simple, consisting of fewer than 15 species, with headwater streams often supporting fewer than five species. For our analyses, we chose the Brook Trout *Salvelinus fontinalis* because this species has been widely introduced throughout the western United States, a region outside of its natural range, and has exerted considerable negative impacts on a variety of native aquatic fauna (Dunham et al. 2002; Peterson et al. 2004). Furthermore, Brook Trout exhibit a range of thermal suitability that overlaps to a high degree with the thermal suitability ranges of native inland salmonids in the study area and regionally, including the Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*, Rainbow Trout *O. mykiss*, and Bull Trout *S. confluentus* (Bear et al. 2007; McMahon et al. 2007). Few studies have empirically quantified the Brook Trout's thermal niche in situ, and an understanding of its thermal niche is important in the context of conserving native salmonids (e.g., DeHaan et al. 2010); thus, the Brook Trout offers an interesting example species for this effort.

*Distribution data.—*We assembled fish distribution data that were collected across the Boise River basin by state and federal agencies since 1993; these sampling efforts occurred in perennial stream channels and at sites large enough to sustain populations of resident salmonids (e.g., Dunham and Rieman 1999). All data included in the analyses were from surveys conducted via electrofishing methods; however, these efforts involved a variety of different protocols and intensities (i.e., single-pass versus multiple-pass electrofishing). Regardless of method, we constrained the results of each sampling occasion to the presence or absence of Brook Trout at each sampling site. We included only Brook Trout larger than 100 mm to avoid potential identification errors with native Bull Trout at early life stages, but we did not otherwise distinguish size-classes.

To minimize errors associated with unoccupied, suitable habitat, we restricted our analysis to survey data that were collected in subbasins (U.S. Geological Survey [USGS] 8-digit hydrologic unit codes; http://nhd.usgs.gov/) containing Brook

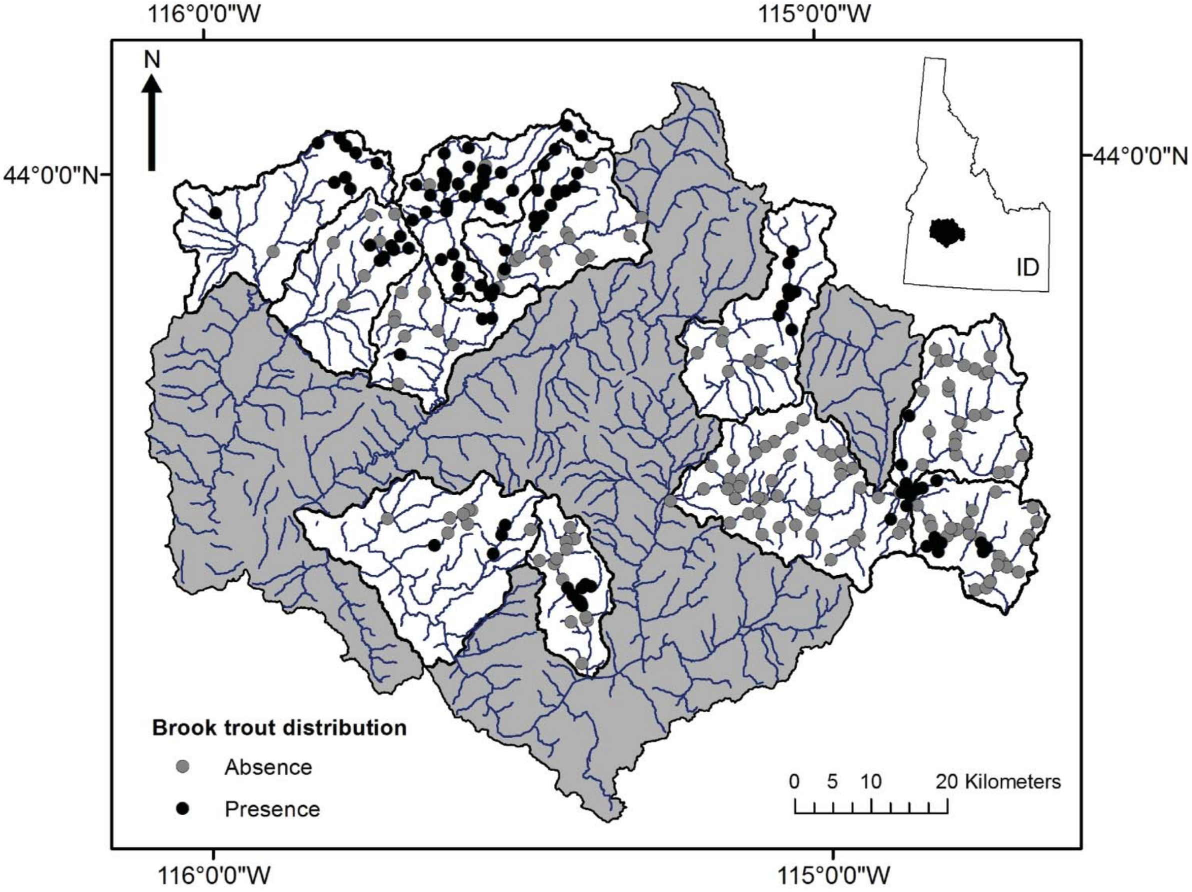

FIGURE 1. The Boise River basin in central Idaho, showing subbasins from which sample data were included in the analyses (i.e., subbasins that were occupied by Brook Trout; white areas) and the sample locations where Brook Trout were present (black circles) or absent (gray circles). [Figure available online in color.]

Trout. Because the number of sites where Brook Trout were absent ($n = 236$) greatly exceeded the number of sites where Brook Trout were present ($n = 102$), we partitioned the original data set by year and randomly selected from the candidate absence data within each year to match the total number of sites that contained Brook Trout. Thus, we attempted to maintain a balance of sample sizes across years and roughly equal numbers of presence and absence data.

Analyses.—We used four separate approaches to characterize the thermal conditions at each survey site. The first measure of thermal conditions included only elevation, which was used as a surrogate for stream temperature. We quantified the elevation at fish survey sites by using digital elevation models available from the 30-m-resolution National Hydrography Dataset. For the second approach, we used mean air temperature (AirT) data that were corrected for differences in elevation at each of the fish survey sites (Wenger et al. 2011a); again, AirT was used as a surrogate for stream temperature. Briefly, this approach used statistical relationships to compute local air temperatures for the centroid of each 0.0625° grid cell from weather station data; these values were then adjusted by using an elevation lapse rate of −6.0°C per kilometer (Rieman et al. 2007) to compute mean summer air temperatures at fish survey sites. For the third and fourth approaches, we used outputs from a stream temperature model developed for the Boise River basin from a large temperature database (described by Isaak et al. 2010). The temperature model, which was based on the spatial statistical network models developed by Ver Hoef and Peterson (2010), included predictors for elevation, solar radiation, and interannual differences in air temperature and discharge at monitoring stations in the basin. Stream temperature data from 780 locations were used to calibrate the model, which accounted for 93% of the variation in mean summer temperatures. The model was used to predict mean summer temperatures based on universal kriging at a resolution of 1 km throughout the stream network (Isaak et al. 2010). Predicted stream temperatures were then cross-referenced with the locations of the fish survey data for the third and fourth approaches to depict the site-specific thermal regimes. For the third approach to characterizing thermal conditions, year-specific stream temperature (YSST) predictions were matched to the locations of fish surveys conducted in the same year (i.e., predictions were contemporaneous with fish survey data). We computed the YSST predictions at each survey site by inputting the values of air temperature and discharge observed during a specific year at the climate stations in the basin. Finally, for the fourth approach, we matched a "composite" or average set of historical stream temperature predictions (composite stream temperature [CST]) to the locations of fish survey data. The CST predictions were based on the 2006 values of running averages in air temperature and discharge determined from simple linear regressions of each variable versus time, as described by Isaak et al. (2010).

Simple logistic regressions performed via the glm procedure in R (R Development Core Team 2004) were used to describe the probability of Brook Trout occurrence relative to the four different measures of thermal conditions. For each logistic regression model, we included the site-specific measure of thermal conditions (elevation, AirT, YSST, or CST) as the independent variable and the presence or absence of Brook Trout at each site as the dependent variable. Given our understanding of niche suitability for most salmonids (Selong et al. 2001; Bear et al. 2007; Wenger et al. 2011b), we used a quadratic relationship (e.g., elevation + elevation^2) to represent the Brook Trout response to thermal conditions. A quadratic relationship takes the form of the classical bell-shaped response of species occurrence to a resource gradient (Austin 2002). We assumed a prediction cutoff of 0.5 in our logistic model to denote the probability of presence (>0.5) or absence (<0.5) given our balanced data set, and we assessed the significance of parameters by using an α value of 0.05.

We assessed model accuracy through resubstitution and the following measures: percent correctly classified (PCC), specificity, sensitivity, and Cohen's kappa (hereafter, "kappa"; Manel et al. 2001). Briefly, specificity and sensitivity provide measures of how well a model predicts absences and presences, respectively, while kappa describes the proportion of the presence and absence data that is correctly predicted. Kappa values range from −1 to 1, with the former indicating complete disagreement and the latter indicating complete agreement.

We mapped the reaches within the stream network that were predicted to be thermally suitable for Brook Trout from each of the models (probability cutoff = 0.5), and we summarized the total number of suitable stream kilometers. For the two models based on stream temperature predictions (YSST and CST), we also graphically compared the inferences from the logistic regression models with laboratory-based temperature–growth predictions for Brook Trout as reported by McMahon et al. (2007).

RESULTS

Our analyses included 215 survey sites from 11 subbasins within the Boise River basin; Brook Trout were present at 102 of these sites. Correlations between the four measures of thermal conditions (elevation, AirT predictions, YSST predictions, and CST predictions) at the survey sites varied considerably. The correlation coefficient (*r*) was highest between the YSST predictions and CST predictions ($r = 0.95$) and was lowest between the YSST predictions and AirT predictions ($r = 0.54$; Table 1). The coefficients for the different measures of stream temperature in each of the four logistic regression models were significant (Table 2). We found that the YSST model had the highest overall performance accuracy, with a PCC of 71% and a kappa of 0.41 (Table 3). Both the CST model and the elevation-based model resulted in similar measures of PCC (67%), but the kappa value for the CST model (0.41) was considerably higher than that observed for the elevation-based model (0.34). Overall, we found the poorest fit for the model based on AirT predictions, as evidenced by PCC (65%) and kappa (0.31) statistics.

The two methods of defining thermal niches relative to stream temperature (YSST and CST) resulted in different ranges of Brook Trout thermal suitability (Figure 2). These differences were observed both in the model parameter estimates and in the predicted range of Brook Trout presence. The CST approach suggested a slightly cooler range of thermal suitability

TABLE 1. Matrix illustrating the correlation coefficients (*r*; below the diagonal) and pairwise adjusted *P*-values (above the diagonal) between the four different measures of thermal conditions at the Boise River basin, Idaho, survey sites used in the logistic regression analyses (AirT = air temperature predictions; YSST = year-specific stream temperature predictions [i.e., contemporaneous with fish survey data]; CST = composite stream temperature predictions).

Measure of thermal conditions	Elevation	AirT[a]	YSST	CST
Elevation	—	<0.001	<0.001	<0.001
AirT	−0.87	—	<0.001	<0.001
YSST	−0.67	0.54	—	<0.001
CST	−0.68	0.57	0.95	—

[a] Air temperatures were modeled as average summer air temperatures at each point (1985–2004; see Wenger et al. 2011a for details).

TABLE 2. Logistic regression model intercepts, coefficients for the quadratic parameters (with SE in parentheses), and statistical significance (*P*-values) for each of the four approaches describing the relationship between the probability of Brook Trout occurrence and thermal conditions in the Boise River basin (AirT = air temperature predictions; CST = composite stream temperature predictions; YSST = year-specific stream temperature predictions).

Model	Parameter	Parameter estimate (SE)	*P*
Elevation	Intercept	−19.5 (7.2)	0.007
	Elevation	0.024 (0.008)	0.004
	Elevation^2	−0.0000074 (0.0000024)	0.002
AirT	Intercept	−199.1 (49.7)	<0.001
	AirT	21.1 (5.3)	<0.001
	AirT^2	−0.56 (0.14)	<0.001
CST	Intercept	−8.8 (3.3)	0.008
	CST	1.56 (0.57)	0.006
	CST^2	−0.068 (0.024)	0.005
YSST	Intercept	−12.3 (4.0)	0.002
	YSST	2.00 (0.65)	0.002
	YSST^2	−0.079 (0.026)	0.002

TABLE 3. Measures of resubstitution model accuracy for each logistic regression model, including percent correctly classified (PCC), specificity, sensitivity, and Cohen's kappa from four different approaches for modeling Brook Trout thermal suitability in the Boise River basin (AirT = air temperature predictions; CST = composite stream temperature predictions; YSST = year-specific stream temperature predictions).

Model	PCC (%)	Specificity (%)	Sensitivity (%)	Kappa
Elevation	67	69	65	0.34
AirT	65	52	79	0.31
CST	67	69	65	0.41
YSST	71	75	67	0.41

(9.7–13.3°C) than the YSST approach, which differed by more than 1°C (10.8–14.5°C).

Across the four measures of thermal conditions, the differences in model predictions were apparent both spatially and in the total extent of the stream network. Spatial differences were evident when comparing the portions of the stream network that were deemed suitable (Figure 3). The median elevations of habitat predicted as suitable were consistent among the models based on elevation, AirT predictions, and CST predictions (range of median elevations = 1,615–1,629 m), but these elevations were noticeably higher than the median suitable habitat elevation based on the YSST model (median = 1,531 m; Figure 4). The four models also differed considerably in the range of elevations (i.e., minimum–maximum elevations) and total kilometers of stream that were predicted as suitable within these subbasins. With the elevation-based model, we found a relatively narrow range of elevations (range = 1,396–1,821 m; Figure 4) and the lowest amount of habitat predicted as suitable (534 km; Figure 3). The range of habitats predicted as suitable was relatively consistent between the AirT-based model (range = 1,629–2,141 m) and the CST model (range = 1,623–2,109 m); however, we did find a considerably higher amount of the stream network predicted as suitable from the CST model (767 km) than from the model based on AirT (718 km). Predictions of thermally suitable habitat from the YSST model included the greatest range in elevations (range = 1,081–2,101 m), with markedly lower elevations of streams but an intermediate amount of habitat predicted as suitable (692 km). Overall, we found that 419 km of stream were consistently predicted as suitable habitat across all four models (i.e., representing the overlap in predictions).

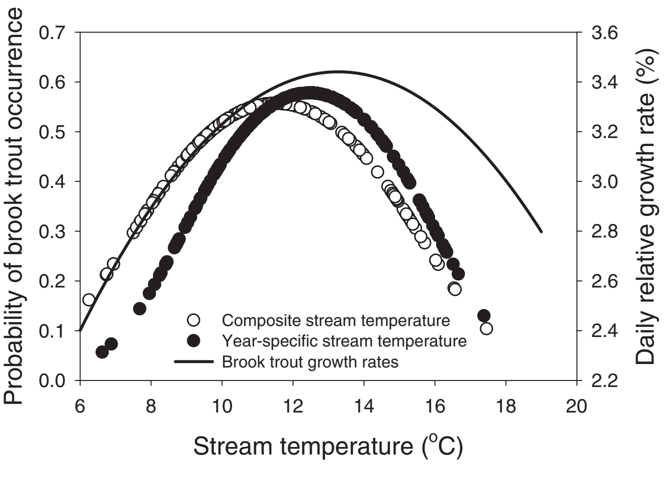

FIGURE 2. Model predictions of the probability of Brook Trout presence as a function of composite stream temperature predictions (black circles), which are reflective of the years including and immediately preceding 2006; or year-specific stream temperature predictions (white circles), which were matched with the year of Brook Trout sampling. The predicted daily relative growth rate of Brook Trout (black line) as a function of temperature is from McMahon et al. (2007).

DISCUSSION

Recent changes in the climate of North America illustrate the importance of identifying the extent of thermally suitable habitat for native and nonnative species (Isaak et al. 2012a). Using nonnative Brook Trout as an example, we illustrated how the use of different approaches for characterizing stream thermal conditions can influence assessments of in situ measures of a species' niche. The improvements in performance for models based on stream temperature predictions (YSST and CST) versus surrogates (elevation and AirT) support the growing efforts in many areas to develop accurate stream temperature models (e.g., Flint and Flint 2008; Isaak et al. 2010). The importance of field-based and analytical efforts to characterize thermal conditions of streams is highlighted in our results, as we found that stream temperature predictions alone resulted in over 70% correct classification of Brook Trout presence or absence.

Our results indicate that models based on stream temperature predictions provide more accurate species–climate relationships than assessments based on surrogates for stream temperature, such as air temperature and elevation. Among the two measures of stream temperature, we found the highest accuracy for the YSST model, in which stream temperature predictions were contemporaneous with fish sampling data. The wider range of elevations and warmer stream temperatures predicted as suitable from the YSST model are likely due to year-to-year fluctuations in stream temperature at any given site (Kaushal et al. 2010; Isaak et al. 2012b). These results suggest the importance of considering interannual differences in climate conditions when developing niche models, particularly in situations where populations are not constrained by barriers and individuals are allowed to move in response to ambient conditions (e.g., Kaeding 1996).

The poor performance of the stream temperature surrogates used in our analyses is likely a result of the myriad of factors (in addition to elevation) that control stream temperature (e.g., aspect, stream size, and groundwater) and the fact that correlations between air temperatures and stream temperatures can vary considerably across streams (Caissie 2006). The inadequacy of using surrogates in complex, mountainous regions

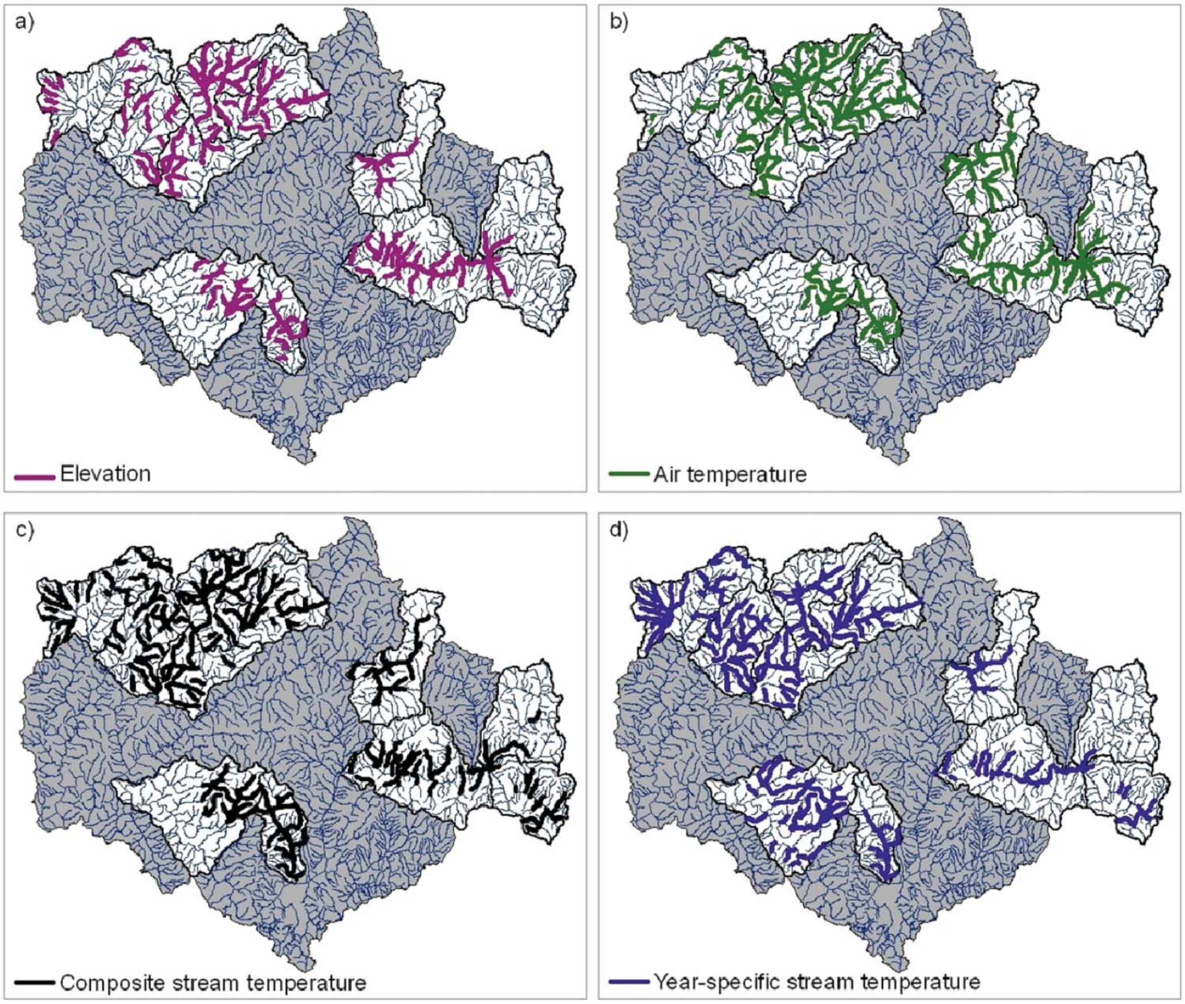

FIGURE 3. Predictions of Brook Trout thermal suitability from models based on **(a)** elevation, **(b)** air temperature, **(c)** composite stream temperature predictions, and **(d)** year-specific stream temperature predictions matched with sample year (shown here for 2006 temperatures) in subbasins with existing Brook Trout populations in the Boise River basin. [Figure available online in color.]

of the Rocky Mountains is further illustrated by the differences in model performance and inferences of suitable habitat (Figures 3, 4). Air temperatures can be influenced by a variety of local controls (Holden et al. 2011) that can lead to variable lapse rate corrections for elevation across watersheds (Minder et al. 2010), thus rendering the extrapolations to large basins difficult. Because air temperature and elevation data are readily accessible, the use of these surrogates for stream temperature will likely continue in areas where there is a paucity of existing stream temperature data. We acknowledge that under situations in which stream temperature data are not available, air temperature and elevation data may be particularly useful in directing field efforts for collecting empirical stream temperature and fish distribution data.

Although much attention has been given to the different sampling approaches for minimizing bias in niche modeling (e.g., Araújo and Guisan 2006), our results highlight the value of incorporating year-specific measures of attributes, such as climate variables (e.g., temperature and precipitation), that can exhibit substantial interannual variability. Year-to-year differences in abiotic factors such as stream temperature are likely to vary considerably within and across streams, largely as a result of interannual climate effects, stream discharge, and the extent of groundwater contribution to streams (Caissie 2006; Isaak et al. 2012b). Concomitantly, biologists often must rely on using species distribution data collected over multiple years or even decades to investigate factors that are associated with spatial patterns across landscapes (e.g., Wenger et al. 2011b). This was the case with our data, which spanned 15 years and a period in which the monthly average air temperature for July in the Boise River basin varied from 9.8°C to 19.7°C (U.S. Department of Agriculture, Natural Resources Conservation Service, Snowpack Telemetry system; www.wcc.nrcs.usda.gov/nwcc/site?sitenum=496&state=id). As such, it is not surprising

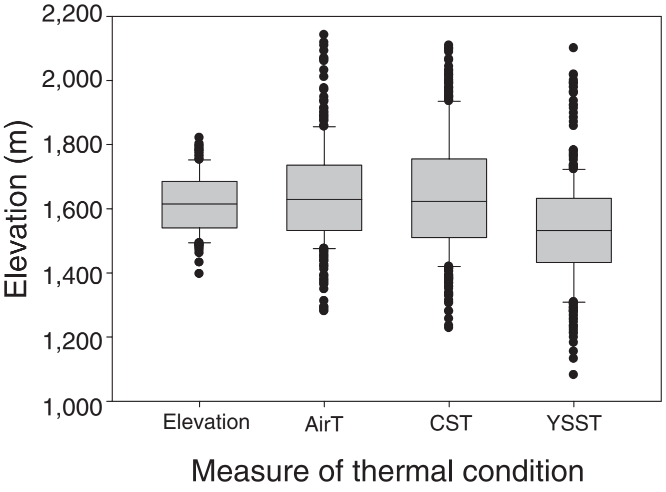

FIGURE 4. Range of elevations for portions of the stream network that were predicted as suitable for Brook Trout from logistic regression models based on elevation data, air temperature (AirT) data, composite stream temperature (CST) data, and year-specific stream temperature (YSST) data from the Boise River basin; box plots illustrate the median value (horizontal line within the box), the 25th and 75th percentiles (ends of the box), the 5th and 95th percentiles (ends of whiskers), and all outliers (black circles).

that our YSST model, which matched contemporaneous temperature predictions with Brook Trout occurrence data, exhibited the highest measures of accuracy.

Recently, there have been considerable efforts to develop predictive stream temperature and climate models (Sloat et al. 2005; Isaak et al. 2010; Jones et al., in press), yet our knowledge of how fishes respond to ambient temperatures—particularly in the context of interactions with conspecifics and food resources—has not progressed at a similar pace in natural systems. The need for more studies that integrate the different biotic and abiotic factors influencing fish distributions was demonstrated by Xu et al. (2010), who found that the effect of stream temperature on Brook Trout growth rates was largely context dependent as a function of the time of year, streamflow, and fish density. Although we do not deny the importance of laboratory studies for providing valuable insight into the upper and lower thermal limits in controlled settings, further research is needed to evaluate how the apparent physiological constraints translate to species responses in stream networks. For example, recent efforts by Howell et al. (2010) using archival tags in eastern Oregon found that Bull Trout used habitat with 7-d average daily maximum temperatures up to 25°C—among the highest temperatures observed for fluvial Bull Trout. The temperatures observed by Howell et al. (2010), however, are considerably higher than the thermal cutoff observed for the cessation of feeding (22°C) and lower than the critical thermal maximum (28.9°C) reported for Bull Trout in laboratory studies (Selong et al. 2001). Inferences of Brook Trout thermal niches from our field-based distribution models (Figure 3) were considerably narrower than niches observed in laboratory settings (McMahon et al. 2007). The two measures of stream temperature (YSST and CST) captured certain characteristics of the laboratory-based results, yet both measures suggested considerably lower thermal constraints. Clearly, these differences illustrate the need for more research to better understand how factors such as community interactions, forage availability, local habitat characteristics, genotypic variability through local adaptations, or a combination thereof can lead to such disparities.

We acknowledge that some uncertainty still remains as to which of our models most accurately represents the thermal niche of Brook Trout in the Boise River basin. This uncertainty is largely driven by the fact that our models were parameterized with "found" data, which were collected to answer a variety of conservation and management-based decisions in the Boise River basin; none of those survey efforts was specifically focused on answering the question of how climate influences the distribution of Brook Trout. This predicament is not unique to our data set, as biologists often gather as much available information as possible to help parameterize their models and build upon existing infrastructure. However, without accurate assessments of fish distributions, particularly at the upstream and downstream extents (e.g., Thurow et al. 2001), our understanding of how climate (e.g., stream temperature) may influence fish distributions within natural systems may be imprecise. This imprecision is especially troubling because these distributional extents are critical for identifying invasion fronts (Muhlfeld et al. 2009) and potential management opportunities (e.g., determining areas in which to focus removal efforts or the placement of barriers).

Development of strategies for conserving and managing fishes under future climate change scenarios has become a priority at both the national and regional levels (USFWS 2010). With limited resources available, there is a need to identify how thermally sensitive species are associated with ambient thermal conditions (among other factors) to help prioritize areas for future management actions (Rahel et al. 2008). Increasingly, biologists are integrating species–climate relationships to help guide explicit discussions of triage and climate adaptation through decision-support modeling frameworks (Peterson et al. 2013). The efficacy of such efforts, however, hinges upon developing accurate assessments of the extent of thermal suitability. As documented here, the way in which temperature thresholds are described influences the interpretations of suitable habitat and likely affects the accuracy of our assessment of the impacts of future climate changes (Wenger et al. 2011b).

As stream temperature and fish distribution databases and modeling abilities continue to improve, there will be increasing opportunities to extract additional, more accurate information for defining thermal niches and relationships with other environmental variables over large spatial scales (McIntire and Fajardo 2009). In many cases, the collection of additional stream temperature data will improve the capacity of temperature models to account for unique features that are important for salmonids, such as groundwater (Fausch et al. 2002), and will be useful in further evaluations of how fish are associated with finer temporal patterns of climate conditions (e.g., diel fluctuations in temperature). Continuing to improve the representation of ambient thermal and hydrologic conditions will likely improve our understanding of species–climate relationships beyond that demonstrated here. Continued comparison and validation of inferences across these different approaches will be important to identify the most effective methods for characterizing the ecology of fishes and the potential management and conservation opportunities across relevant spatial and temporal scales.

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