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Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network

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Abstract. Mountain streams provide important habitats for many species, but their faunas are especially vulnerable to climate change because of ectothermic physiologies and movements that are constrained to linear networks that are easily fragmented. Effectively conserving biodiversity in these systems requires accurate downscaling of climatic trends to local habitat conditions, but downscaling is difficult in complex terrains given diverse microclimates and mediation of stream heat budgets by local conditions. We compiled a stream temperature database ($n = 780$) for a 2500-km river network in central Idaho to assess possible trends in summer temperatures and thermal habitat for two native salmonid species from 1993 to 2006. New spatial statistical models that account for network topology were parameterized with these data and explained 93% and 86% of the variation in mean stream temperatures and maximas, respectively. During our study period, basin average mean stream temperatures increased by 0.38°C (0.27°C/decade), and maximas increased by 0.48°C (0.34°C/decade), primarily due to long-term (30–50 year) trends in air temperatures and stream flows. Radiation increases from wildfires accounted for 9% of basin-scale temperature increases, despite burning 14% of the basin. Within wildfire perimeters, however, stream temperature increases were 2–3 times greater than basin averages, and radiation gains accounted for 50% of warming. Thermal habitat for rainbow trout (*Oncorhynchus mykiss*) was minimally affected by temperature increases, except for small shifts towards higher elevations. Bull trout (*Salvelinus confluentus*), in contrast, were estimated to have lost 11–20% (8–16%/decade) of the headwater stream lengths that were cold enough for spawning and early juvenile rearing, with the largest losses occurring in the coldest habitats. Our results suggest that a warming climate has begun to affect thermal conditions in streams and that impacts to biota will be specific to both species and context. Where species are at risk, conservation actions should be guided based on considerations of restoration opportunity and future climatic effects. To refine predictions based on thermal effects, more work is needed to understand mechanisms associated with biological responses, climate effects on other habitat features, and habitat configurations that confer population resilience.

Key words: Boise River basin, Idaho, USA; bull trout; climate change; global warming; Oncorhynchus mykiss; *patch; rainbow trout;* Salvelinus confluentus; *spatial statistical model; stream temperature; thermal habitat; wildfire.*

INTRODUCTION

Environmental trends associated with a warming climate are apparent within the recent instrumental record and are projected to continue and possibly accelerate (IPCC 2007). These trends are causing distributional shifts in many thermally sensitive species as habitats move poleward or towards higher elevations (Parmesan and Yohe 2003, Root et al. 2003). The impacts of climate-induced habitat shifts may be pronounced in stream ecosystems where biota are often ectothermic (Pörtner and Farrell 2008) and movements are constrained to linear networks that are easily fragmented by thermal or structural barriers (Fagan 2002). In streams draining the western United States, this vulnerability may be exacerbated by growing human populations with water supply needs and especially rapid climate change (Diffenbaugh et al. 2008, Saunders et al. 2008). Trends toward warmer air temperatures (Abatzoglou and Redmond 2007, IPCC 2007), increased precipitation variability (Hamlet et al. 2007), decreased snowpack (Hamlet et al. 2005, Mote et al. 2005), and increased wildfire activity (Westerling et al. 2006, Morgan et al. 2008) are already linked to warming streams and rivers (Petersen and Kitchell 2001, Morrison et al. 2002, Bartholow 2005), altered stream

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hydrologies (Stewart et al. 2005, Barnett et al. 2008, Luce and Holden 2009), and increased channel disturbance from flooding and postfire landslides and debris flows (Miller et al. 2003, Istanbulluoglu et al. 2004, Hamlet and Lettenmaier 2007).

Western streams are relatively young (in geologic time), dynamic, and climatically extreme environments with limited species diversity (McPhail and Lindsey 1986, Waples et al. 2008). Salmonid fishes are most common in these environments, have broad societal importance, and are generally thought to be vulnerable to the effects of a warming climate (Keleher and Rahel 1996, Battin et al. 2007, Rieman et al. 2007). A categorical decline is not a forgone conclusion, however, because salmonids have diverse life histories and some flexibility in habitat use that confers resilience to changing environments (Quinn 2005, Crozier et al. 2008), so resolution of potential effects is important.

A growing literature links many aspects of salmonid ecology to a variety of climate-related phenomena (e.g., Mantua et al. 1997, Jager et al. 1999, Fausch et al. 2001, Mote et al. 2003, Brannon et al. 2004), but most studies have focused on thermal considerations, given the requirement of salmonids for cold temperatures (Quinn 2005, Richter and Kolmes 2005). Numerous assessments project the potential effects of increasing temperatures on habitat distributions across broad geographic domains ($>10^5$ km^2; Meisner 1990, Keleher and Rahel 1996, Nakano et al. 1996, Flebbe et al. 2006, Rieman et al. 2007) but, with few exceptions, employ air temperature–elevation relationships as surrogates for stream temperatures (Rahel 2002). This reliance on a surrogate relationship may limit the accuracy of these projections, especially at local scales and in complex terrain where adjacent streams may have very different temperature regimes (Isaak and Hubert 2001). Although broad projections will remain useful for providing strategic assessments that aid in conservation planning, more focused analyses are necessary to document actual rates of change, consider indirect effects (e.g., fire), and validate model projections.

Changes in wildfire extent and severity driven by a warming climate could have important compounding effects on thermal regimes in many western streams (Westerling et al. 2006, Falk et al. 2007). Fires that burn across small streams may cause fish mortalities from excessive temperatures (Hitt 2003), but these effects are often short-term and populations may rebound quickly through immigration from nearby refugia that were not burned (Rieman and Clayton 1997, Dunham et al. 2003*b*). However, fires also alter riparian vegetation and stream shade (Dwire and Kauffman 2003, Pettit and Naiman 2007), resulting in more chronic thermal effects. The importance of these effects depends on the biophysical context and severity of the fire, with some streams showing negligible responses and others heating dramatically (Minshall et al. 1997, Royer and Minshall 1997, Dunham et al. 2007). The persistence of chronic effects varies in length, with recovery occurring over a few years to several decades (Dunham et al. 2007). In certain contexts, temperature increases could become permanent if mesic prefire vegetation types such as trees fail to reestablish under climates that differ from earlier establishment periods (McKenzie et al. 2004, van Mantgem and Stephenson 2007).

Aquatic biota may respond in a variety of ways to shifting thermal conditions. At the scales of individual streams and river networks, thermally suitable habitats may expand or contract, depending on contemporary thermal regimes, the species considered, and geomorphic constraints. Where cold temperatures limit suitability in upstream areas (e.g., Nakano et al. 1996, Isaak and Hubert 2004, Coleman and Fausch 2007), warming could increase the extent of available habitats. Relatively minor temperature increases could substantially increase habitat availability given the dendritic structure of stream networks, as long as constraints associated with stream size, steepness, or anthropogenic barriers did not limit upstream movement (e.g., Rich et al. 2003, Fransen et al. 2006). In many cases, however, these constraints will exist and temperature increases are expected to reduce downstream habitats and may allow nonnative species that are broadly established in downstream areas to invade further upstream (Fausch et al. 2006, Rieman et al. 2006, Rahel and Olden 2008).

Our goal was to explore the influence of recent climate trends and wildfires on stream temperatures and thermal habitat distributions for two salmonid species with contrasting thermal tolerances. We focused on a large river network in a mountainous area of central Idaho where recent trends should be characteristic of changes in many rivers and streams across the region. Our first objective was to develop stream temperature models that accommodated important climate drivers (air temperature and stream flow), fire effects, and geomorphic factors to accurately predict stream temperatures across the network. Our second objective was to use the models to estimate changes in network-scale stream temperature patterns and thermal habitat, while also determining the relative importance of factors responsible for these changes.

METHODS

Study site

The study was conducted in the upper Boise River basin (BRB) in central Idaho, USA (Fig. 1), which is administered primarily by the US Forest Service. The BRB covers 6900 km^2 and is drained by 2500 km of fish-bearing streams ranging in elevation from 900 to 2500 m. The terrain is complex and hillslope and riparian vegetation types vary from trees to grasslands along gradients of elevation, aspect, and precipitation. Lower elevations were historically characterized by low- and mixed-severity fires with return intervals of <35 years;

return intervals for higher elevations may have been an order of magnitude longer (Brown and Smith 2000). Wildfires were relatively rare within the BRB during most of the 20th century, but have become common in the last 20 years. Approximately 14% of the BRB burned from 1993 to 2006 (our study period), but 30% burned from 1992 to 2008 (Fig. 1). Burn severity mapping conducted by the Boise National Forest suggested that areas within wildfire perimeters consisted of relatively similar proportions of high-, medium-, and low-burn severities (Dunham et al. 2007). Forest thinning activities in the northwest portion of the basin were conducted to decrease fire risk to local communities and homes in the wildland–urban interface (J. Thornton, *personal communication*).

Climate is characterized by relatively cold winters with moderate to heavy snow accumulations at higher elevations and hot, dry summers. Stream hydrographs are typical of snowmelt-driven systems in the northern Rockies, with high flows occurring from April through June and low flows during late summer and early fall. Summer thunderstorms may produce locally heavy precipitation and extreme flow events in lower order streams. Average summer air temperatures and stream flows, measured at two USGS flow gages and three NOAA weather stations in or near the basin, have been trending higher and lower, respectively (Fig. 2). These trends are consistent with regional patterns observed over the last 30–50 years (Mote et al. 2005, Stewart et al. 2005, Luce and Holden 2009).

The ichthyofauna within the BRB is relatively simple, consisting of fewer than 15 species, with headwater streams often supporting fewer than five species. We chose bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*) for study, given their conservation significance, wide distributions, well-defined and contrasting thermal preferences, and data available from previous studies (Rieman et al. 1997*a*, Dunham and Rieman 1999, Dunham et al. 2007, Neville et al. 2009). The BRB is near the southern extent of the native range for bull trout (Rieman et al. 1997*b*), but the range of rainbow trout extends much farther south (Currens et al. 2009), and the species has been widely introduced and established throughout the world (Fausch et al. 2001). Rainbow trout prefer temperatures that are several degrees warmer than bull trout (Paul and Post 2001), which have a thermal tolerance that is lower than most other freshwater fishes (Selong et al. 2001, McMahon et al. 2007). Rainbow trout spawn in both headwater and mainstem habitats. They move widely throughout life, but many populations in the BRB appear to consist primarily of resident or nonmigratory individuals (Neville et al. 2009). Rainbow trout populations in the BRB once supported an anadromous life history form, known as steelhead, but this form was extirpated from the basin with construction of downstream dams that blocked fish migrations approximately a century ago. Older bull trout may move extensively throughout larger river basins (Muhlfeld and Marotz 2005, Monnot et al. 2008), but spawning and early juvenile rearing are restricted to the coldest streams and young fish typically live in natal or associated tributary habitats for one to several years (Rieman and McIntyre 1995, Downs et al. 2006). Although bull trout remain widely distributed throughout their range, local extinctions, losses of migratory life history types, and population declines from habitat loss, overharvest, and nonnative species invasions are widely reported (Rieman et al. 1997*b*, Nelson et al. 2002). The species was listed for federal protection under the Endangered Species Act in the late 1990s (USFWS 1998) (see Plate 1).

Stream temperature database

We assembled a database of stream temperature measurements from previous studies (Rieman et al. 2006, Dunham et al. 2007) and routine monitoring efforts conducted by several natural resource agencies in the BRB (Fig. 1 and Appendix A). In 2006 and 2007, we supplemented these data with 152 observations distributed across a representative sample of small (<2350-ha contributing area), medium, and large streams (>10 000-ha contributing area) and the full range of elevations within the BRB. We also examined pre-2006 data to identify types of streams that may have been insufficiently sampled and targeted data collection in these areas to ensure representation of the widest range of conditions affecting stream temperatures.

Stream temperatures were sampled with digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy = ±0.2°C; iButton; Maxim Integrated Products, Sunnyvale, California, USA; accuracy = ±0.5°C) that recorded temperatures a minimum of five times daily (average = 72 times/d). Thermographs were placed in streams before mid-July, georeferenced, and retrieved after mid-September. This sample period encompassed the warmest portion of the year when variation in temperatures among areas is most pronounced and influence on fish growth, behavior, and distribution is potentially greatest (e.g., Scarnecchia and Bergersen 1987, Royer and Minshall 1997). Stream temperatures at other times are often near zero and relatively homothermous. Logistical constraints such as flooding and snow cover also make placement and retrieval of thermographs difficult at those times. After screening to eliminate anomalous temperature records (e.g., those downstream from reservoirs, hot springs, or beaver [*Castor canadensis*] dam complexes), 780 records at 518 unique sites were retained for analysis (Table 1). The mean summer stream temperature, defined as the period from 15 July to 15 September, and the maximum weekly maximum temperature (MWMT), which was the highest seven-day moving average of the maximum daily temperatures, were summarized from each record using

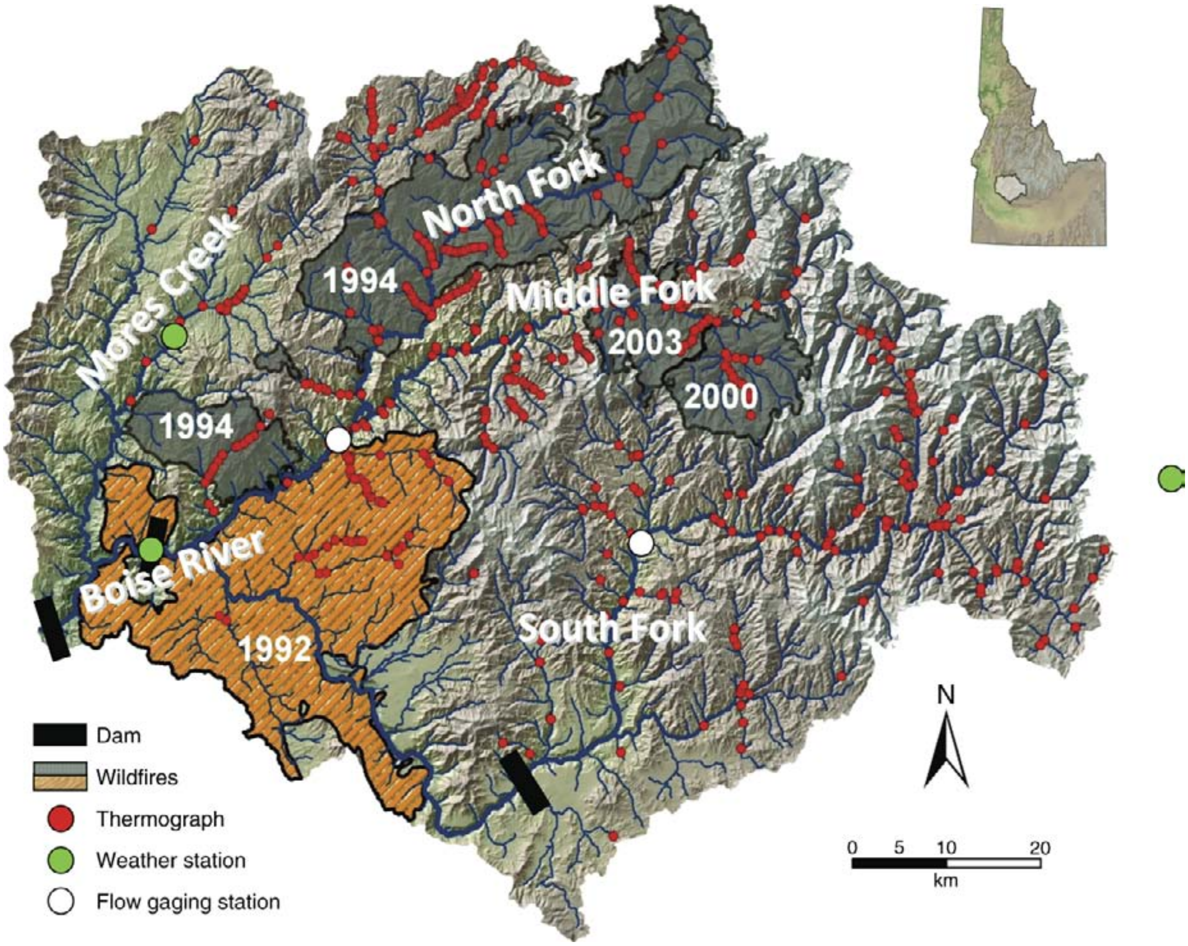

Fig. 1. The Boise River basin in central Idaho, USA. Stream temperatures were measured at 518 unique thermograph sites from 1993 to 2006 to yield 780 temperature records. Air temperatures were recorded at three weather stations, and stream flows were measured at two gages.

a SAS macro (Temperature Data Macro, *available online*).[4] The mean temperature provided a good indicator of overall thermal suitability and conditions for growth, whereas the maximum provided an indicator of transient conditions associated with seasonal extremes.

Predictor variables

We used a statistical approach incorporating predictor variables that represented important components of a stream heat budget. We developed computer scripts that ran in ArcGIS Desktop version 9.2 (Environmental Systems Research Institute, Redlands, California, USA) to quantify many of the predictors from digital map layers in a geographic information system (GIS). Values for all predictors were determined for all portions of the stream network before being matched to stream temperature records at individual locations. The synthetic channel network we used was generated with TauDEM software (Tarboton 2008) using 1 arc second (30-m cell size) USGS National Elevation Dataset (NED) data as input (USGS 2006). The NED data and all predictor grids were co-registered and projected to the UTM, Zone 11, NAD 83 coordinate system.

The temperature at a point on a stream is the result of heat gains and losses that are controlled by upstream conditions (Webb et al. 2008). Conditions immediately upstream generally have greater influence than those farther away, but the extent of the spatial domains over which these conditions are most influential is unclear. Therefore, we quantified predictor variables using distance-weighted averaging for a range of domain sizes. One scheme gave all upstream cells equal weight in estimating the averaged upstream variable. The other three schemes used inverse exponential weights with *e*-folding distances (the distance at which the weight is 1/*e*) of 1 km, 4 km, and 15 km. Along an individual stream this can be estimated as follows:

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[4] ⟨http://www.fs.fed.us/rm/boise/AWAE/projects/stream_temperature.shtml⟩

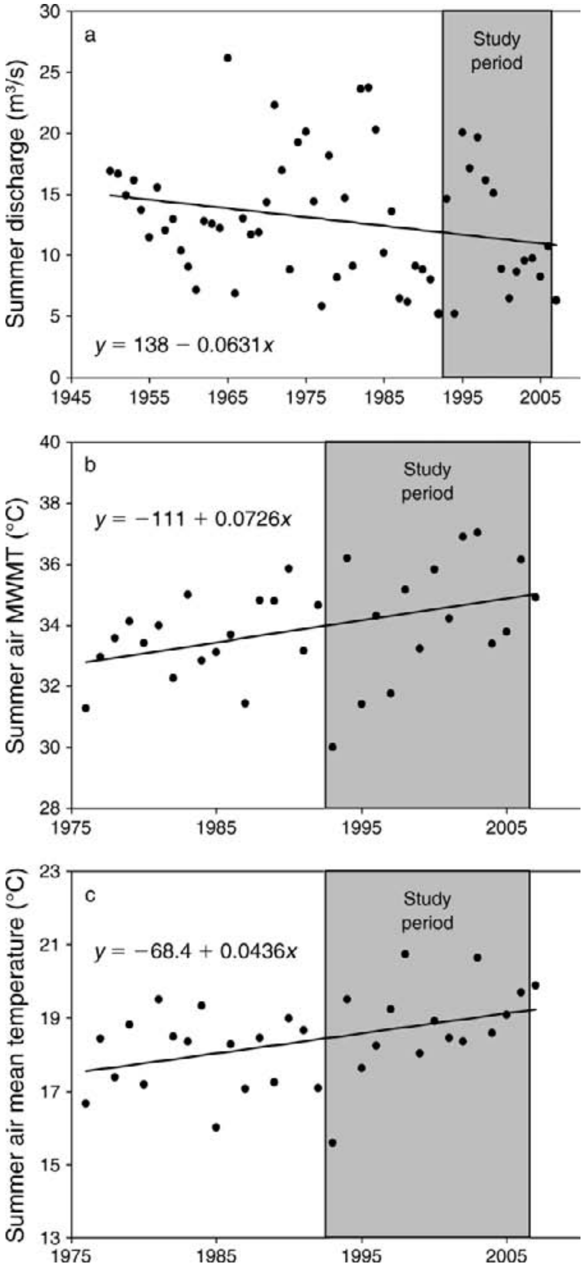

FIG. 2. Trends in (a) summer stream flow and (b, c) air temperatures in the Boise River basin. Shaded areas highlight the period for which stream temperature data were available (1993–2006). MWMT is maximum weekly maximum temperature.

$$\bar{x}_n = \frac{\sum_{1}^{n} w_i x_i}{n} \tag{1}$$

where $\bar{x}_n$ is the upstream-averaged quantity at the nth cell from the upstream extent of the stream, x_i is the value of the quantity being averaged at each upstream cell, and w_i is the weight at each upstream cell. The x_i were taken from GIS coverages of the quantity of interest (e.g., elevation), and w_i is given by

$$w_i = \exp - (D_{in}/D_c) \tag{2}$$

where D_{in} is the distance between the nth and ith cell along the stream path (using simple eight-direction flow vectors between cells) and D_c is the e-folding distance (i.e., 1 km, 4 km, or 15 km). While Eq. 1 is written as if along one flow line, it can be expanded to encompass any set of contributing cells, including flow lines that include tributaries or every cell within a contributing basin. Final calculations were made using two accumulation routines: (1) network accumulation, in which data were summarized only along cells in stream channels (extracted from the DEM using TauDEM), and (2) catchment accumulation, in which data were summarized using the entire catchment area that drained to a cell on the stream network. For each variable, the averaging method that provided the strongest bivariate correlation with stream temperature was retained for use in temperature model development.

Geomorphic predictors.—Predictors in this category represented relatively static features of the river network, valley bottoms, and upstream watersheds that were hypothesized to affect stream temperatures. Six geomorphic predictors were summarized, including: watershed contributing area (C_A), network drainage density (D_D), elevation (Ele), valley glaciation (G_V), channel slope (SL), and alluviated valley bottom extent (V_B). Table 2 provides additional measurement details and summarizes the rationale for inclusion of the predictor variable and its correlation with stream MWMT across various distances. The strongest correlations generally occurred at shorter distances (1–4 km), suggesting that geomorphic influences on stream heating were relatively localized phenomena. Similar results were observed for mean stream temperature and are not reported.

Solar radiation predictor.—Solar radiation is a primary factor in stream heat budgets (Johnson 2003, Caissie 2006) that can change dramatically when fires burn through riparian areas. To quantify these effects, we used Thematic Mapper (TM) satellite imagery classifications of riparian vegetation linked to field measurements of radiation at the stream surface. Complete imagery sets for the BRB were available for 10 July 2002 (Landsat 7 ETM+) and 14 July 1989 (Landsat 5 TM), which encompassed the majority of wildfire-related vegetation changes during our study period. Classifications were done within a buffer of two grid cells along each bank (120 m total width) of the synthetic stream network. An initial classification signature set was rendered using the ISODATA algorithm (Tou and Gonzalez 1974) and 1-m National Agricultural Imagery Program (NAIP) photography was used to prune high-variance signatures. The remaining set was then input to a maximum-likelihood

TABLE 1. Descriptive statistics for variables in a data set used to build stream temperature models for the Boise River basin, Idaho, USA.

Variable	n	Mean	Median	SD	Minimum	Maximum
C_A (ha)	518	6852	1423	24 148	20	263 131
D_D (km/km^2)	518	1.22	1.21	0.27	0.08	2.14
Ele (m)	518	1799	1791	278	1095	2528
G_V (%)	518	11.0	0.0	25.0	0.0	100.0
SL (%)	518	11.5	10.9	4.4	2.5	29.0
V_B (%)	518	11.7	0.0	19.5	0.0	92.7
Rad (μJ$\cdot$m$^{-2}\cdot$yr^{-1})	518	402	403	74	151	654
Air MWMT (°C)	14	34.2	34.3	2.15	30.0	37.0
Air mean (°C)	14	18.8	18.7	1.29	15.6	20.7
Flow (m^3/s)	14	12.1	10.2	4.8	5.2	20.0
Stream mean (°C)	780	11.9	11.7	2.7	5.4	21.8
Stream MWMT (°C)	780	17.2	16.9	4.2	7.2	30.7

Notes: Variable abbreviations are: C_A, watershed contributing area; D_D, drainage density; Ele, mean basin elevation; G_V, glaciated valley; SL, channel slope; V_B, alluviated valley bottom; Rad, total direct and diffuse incoming radiation; air MWMT, maximum weekly maximum air temperature; air mean, mean air temperature from 15 July to 15 September; flow mean, mean stream flow from 15 July to 15 September; stream mean, mean stream temperature from 15 July to 15 September; stream MWMT, maximum weekly maximum stream temperature.

classifier (Leica Geosystems 2006) to derive final classifications of open, shrub, conifer, or water.

Final classifications were validated by comparison to those made at 158 random points by an independent analyst using the NAIP photography. Overall classification concordance was 80%, with agreement rates of 82% in open areas, 65% in shrub, 90% in conifer, and 82% for water. Additionally, comparisons of vegetation differences between 1989 and 2002 imagery sets confirmed the expected patterns, with vegetation inside fire perimeters trending toward more open riparian conditions (vegetative loss [e.g., tree to open] = 32.6% of cells, gain = 5.13% of cells; Appendices B and C). It was also most common for cells classified as trees to shift to open categories (70.6%). Changes outside fire perimeters also occurred, but tended to offset (gain = 12.5%; loss = 11.3%) and be spatially distributed rather than clustered.

Solar radiation was estimated using hemispherical canopy photography at 181 field sites in 2003. Field sites were visited in June and distributed among a range of riparian vegetation types and stream sizes (C_A = 135–3000 ha). Photographs were acquired using a fish-eye lens and panchromatic film with the camera mounted on a tripod at midstream 1 m above the water surface. The film was analyzed using Hemiview software (Dynamax, Houston, Texas, USA) to estimate total (direct and diffuse) radiation. These values were associated with the vegetation classification cells along the synthetic stream network, and simple power-law relationships were constructed that predicted total radiation from vegetation type and watershed contributing area (Appendix D). Upper radiation limits were imposed at 1000 μJ$\cdot$m$^{-2}\cdot$yr^{-1} to approximate the level at which riparian vegetation would no longer significantly shade large streams. These relationships conformed to general expectations, with radiation levels being higher for open/shrub vegetation classes than for trees and increasing with watershed size (stream width). Radiation values for all remaining cells within the stream network were predicted using these relationships.

Radiation values for years between 1989 and 2002 were calculated by interpolating vegetation classifications and applying the power-law relationships. Interpolations within fire perimeters were made by assuming that losses of vegetation (i.e., tree to shrub, tree to open, or shrub to open) between the two imagery sets occurred in association with the fire. One fire occurred in 2003 after our last TM imagery set. In this instance, radiation values were estimated using fire severity map classifications (high, medium, low, none) as surrogates for vegetation change and assuming that radiation estimates from hemispherical photographs in burned areas were representative of other areas with similar burn severities. Once radiation values were assembled for all years in the study period, this predictor variable was also quantified across several spatial domains, as was the case with geomorphic predictors, to determine the strongest correlation with stream temperature (Table 2).

Climate predictors.—Interannual variation in climatically influenced factors such as air temperature and stream flow have important consequences for stream temperatures. Air temperature affects stream temperature through sensible heat exchange near the surface of the stream and by influencing temperatures of near-surface groundwater, which is an important component of summer flows. Stream flow determines the volume of water available for heating; larger flows have greater thermal capacities and are less responsive to heating (Hockey et al. 1982, Caissie 2006). We used annual summer summaries of each variable to represent interannual differences, or a year effect, common to all observations. Measures of air temperature were derived from time series of average daily temperatures obtained from three NOAA weather stations that are operated in or near the basin (Arrowrock, Idaho City, and Ketchum

TABLE 2. Geomorphic and radiation variables used to predict stream temperatures.

Variable	Rationale	References	Accumulation routine	Correlation with stream temperature			
				1 km	4 km	15 km	Upstream
C_A	Contributing area is a surrogate for stream size. Larger streams have been exposed to insolation over a greater length and are less shaded by adjacent riparian vegetation.	Moore et al. (2005), Brown and Hannah (2008)	watershed	…	…	…	**0.29**
			channel	…	…	…	…
D_D	Drainage density is an indicator of the amount of stream exposed to solar radiation. Higher drainage densities are expected to warm stream temperatures.	Johnson (2003), Caissie (2006), Brown and Hannah (2008)	watershed	…	…	…	…
			channel	**0.30**	0.29	0.26	0.24
Ele	Cooler air temperatures and greater snow accumulations (cooler groundwater inputs) at higher elevations should negatively affect stream temperatures.	Smith and Lavis (1975), Meisner et al. (1988), Sinokrot and Stefan (1993)	watershed	**−0.60**	−0.57	−0.50	−0.43
			channel	−0.59	−0.57	−0.50	−0.44
G_V	Glaciated valleys should cool stream temperatures because these valleys accumulate heavy snowfall and glacial detritus acts as an aquifer that stores and releases cold water during summer.	Brown et al. (2007), Brown and Hannah (2008)	watershed	−0.33	**−0.39**	−0.37	−0.34
			channel	…	…	…	…
SL	Channel slope affects flow velocity and equilibration time to local heating conditions. Steeper slopes and greater velocities should negatively affect stream temperatures because conditions farther upstream at higher elevations have greater influence on local temperatures.	Donato (2002), Sloat et al. (2005), Webb et al. (2008)	watershed	…	…	…	…
			channel	**−0.29**	−0.26	−0.25	−0.23
V_B	Alluviated valley bottoms act as aquifers to enhance hyporheic recharge and cool stream temperatures.	Poole and Berman (2001), Burkholder et al. (2008)	watershed	…	…	…	…
			channel	**0.17**	0.14	0.10	0.10
Rad	Solar radiation is a major factor in stream heat budgets and should increase stream temperature.	Johnson (2003), Caissie (2006)	watershed	…	…	…	…
			channel	0.41	**0.46**	0.46	0.46

Notes: Reported correlations were with maximum weekly maximum temperature (MWMT); values in boldface indicate upstream distance associated with predictor used in stream temperature models. C_A was calculated by accumulating the number of upslope grid cells that contributed to a cell on the synthetic stream network; D_D was computed by dividing the contributing area for a grid cell into the upstream channel length; Ele was the average for grid cells within a contributing area or cells on the stream network; G_V was estimated as a percentage of C_A after identifying glaciated valleys on a digital elevation model (DEM); SL was calculated as change in elevation per length between stream confluences; V_B was estimated as a percentage of C_A using an ArcGIS script that delineated flat, unconfined areas adjacent to the stream network. Accumulation routine was measured along the upstream channel network or watershed contributing area. Ellipses (. . .) indicate that the calculations were not made.

stations; Fig. 1). These data were strongly correlated ($r = 0.74–0.91$), so the individual time series were averaged and the same summary metrics that were applied to stream temperatures were applied here (i.e., summer mean and MWMT). Flow data were obtained from two USGS stream gages in the basin (Twin Springs and Featherville gages; Fig. 1). These two sets of data were also strongly correlated ($r = 0.97$) and were averaged to calculate annual mean flow from 15 July to 15 September.

Stream temperature models

Climatic influences on stream temperatures are often assessed using mechanistic models (Caissie 2006), but data requirements limit their utility in remote areas and in smaller streams where microclimates associated with riparian vegetation strongly affect local heat budgets. Statistical models, though correlative, require less parameterization of physical constants, provide estimates of parameter precision, and can be applied across a range of spatial scales when linked to a GIS. Therefore, we used multiple regressions to model the relationship between our stream temperature observations and predictor variables. Because our temperature observations came from multiple sources and were collected using a variety of sampling designs, the data could not be considered random. Fitting these data with a model that did not account for spatial structure could produce biased parameter estimates and autocorrelated error structures (Legendre 1993). To circumvent these problems, we applied recently developed spatial statistical models that account for the unique forms of spatial dependence (e.g., longitudinal connectivity, flow volume, and flow direction) inherent to stream networks

(Peterson and Ver Hoef 2010, Ver Hoef and Peterson 2010). Previous applications of these models suggest they provide valid covariance structures for streams and yield significantly improved predictive power when spatial autocorrelation is present in stream data (Peterson et al. 2006, 2007).

Because patterns in stream temperature are spatially complex, we used a stream network model with a mixed-model error structure developed by Ver Hoef and Peterson (2010). The mixed model is essentially a variance component approach, which allows multiple covariance matrices to be combined to provide a robust and flexible covariance structure. Here, covariances based on Euclidean distance are combined with "tail-up" and "tail-down" covariances. Tail-up covariances are based on hydrologic distance, but restrict spatial correlation to "flow-connected" sites (water must flow downstream from one site to another). In addition, spatial weights are incorporated to account for the disproportionate effects that tributaries of differing size may have on downstream areas. Tail-down covariances allow spatial correlation between any two "flow-unconnected" sites, meaning that they reside on the same network (share a common outlet downstream). The mixed models were fit using three covariance component models; the exponential tail-up, the exponential Euclidean, and the linear-with-sill tail-down components. The exponential tail-up autocovariance between flow-connected locations on the stream network is

$$C_{\mathrm{TU}}(s_i, s_j \mid \boldsymbol{\theta}) = \begin{cases} 0 & \text{if } s_i \text{ and } s_j \text{ are flow-unconnected} \\ \prod_{k \in B_{s_i s_j}} \sqrt{w_k}\, C_1(h \mid \boldsymbol{\theta}) & \text{if } s_i \text{ and } s_j \text{ are flow-connected} \end{cases} \tag{3}$$

where

$$C_1(h \mid \boldsymbol{\theta}) = \sigma^2_{\mathrm{TU}} \exp\left(\frac{-h}{\alpha}\right).$$

Here,

$$\prod_{k \in B_{s_i, s_j}} \sqrt{w_k}$$

represents the spatial weights, h is the total hydrologic distance between locations s_i and s_j, and $\boldsymbol{\theta}$ is the parameter vector containing $\sigma^2_{\mathrm{TU}} > 0$ (the tail-up partial sill or variance component in the mixed model) and $\alpha > 0$ (the spatial range parameter). Also note that $C_1(h \mid \boldsymbol{\theta})$ is an unweighted exponential autocovariance function. When used in the tail-up model, it is not guaranteed to produce a valid covariance matrix until it has been weighted appropriately using the spatial weights matrix (Ver Hoef et al. 2006). However, if h in $C_1(h \mid \boldsymbol{\theta})$ were to be replaced with Euclidean distance, there would be no need for weighting and the product would be a valid exponential Euclidean distance matrix (Cressie 1993). The linear-with-sill tail-down autocovariance function represents both flow-connected and flow-unconnected locations and is constructed as follows:

$$C_{\mathrm{TD}}(s_i, s_j \mid \boldsymbol{\theta}) = \begin{cases} \sigma^2_{\mathrm{TD}}\left(1 - \dfrac{\max(a,b)}{\alpha}\right) I\left(\dfrac{\max(a,b)}{\alpha} \le 1\right) \\ \qquad \text{if } s_i \text{ and } s_j \text{ are flow-unconnected} \\ \sigma^2_{\mathrm{TD}}\left(1 - \dfrac{h}{\alpha}\right) I\left(\dfrac{h}{\alpha} \le 1\right) \\ \qquad \text{if } s_i \text{ and } s_j \text{ are flow-connected} \end{cases} \tag{4}$$

where a and b represent the hydrologic distance from sites s_i and s_j to the nearest common downstream confluence between the two locations, $\boldsymbol{\theta}$ is the parameter vector containing $\sigma^2_{\mathrm{TD}} > 0$ (the tail-down partial sill or variance component in the mixed model) and $\alpha > 0$ (the spatial range parameter), and $I(\cdot)$ is the indicator function.

The data to run the spatial models included the temperature observations, predictor variables, x, y coordinates for each location, a matrix containing the hydrologic distance between all sites (both predicted and observed), and a spatial weights matrix. The hydrologic distances and spatial weights were calculated in ArcGIS using customized scripts and the functional linkage of water basins and streams (FLoWS) toolset (Theobald et al. 2006, Peterson et al. 2007). These matrices were computed from the TauDEM vector stream network to ensure alignment with each of the predictor variable grids used in the study. The spatial weights were based on watershed contributing area, which was used as a surrogate for stream size and discharge.

Our stream temperature data set contained sites that were sampled in multiple years, but the spatial statistical models we employed were not true space–time models. To accommodate the temporal dimension of our data, we adjusted the location of repeat observations slightly upstream or downstream (<100 m) from the original site location to create small nonzero distances. These observations retained the same set of geomorphic predictors associated with the original site, but were assigned different sets of air temperature, stream flow, and radiation values based on their respective year. This adjustment effectively translated temporal variation to the climatic and radiation variables that were of primary interest and treated the climate variables as class variables affecting all sites similarly within a given year.

To determine which fixed effects would constitute the best stream temperature models, a set of a priori candidate models was developed. This set included a simple "elevation-only" model, a global model with all predictors, the global model with significant interactions, and several reduced forms that combined different subsets of predictors (e.g., geomorphic predictors, climate predictors, etc.). To provide a reference point for the spatial model results, we also parameterized these candidate models using traditional, nonspatial regression methods. All parameters were derived using maximum-likelihood estimation. Standard diagnostic tests were performed, including checks for residual normality and calculation of variance inflation factors (VIFs) to assess potential problems with multicollinearity (Helsel and Hirsch 1992).

For model comparisons, we calculated spatial Akaike information criterion (AIC) values (Hoeting et al. 2006), which are similar to standard AIC, but penalize models for the number of parameters used to estimate the autocovariance structure. Although information theoretic procedures such as AIC have rapidly become the norm in many model selection contexts (Burnham and Anderson 2002), models used for bioclimatic predictions are often criticized for insufficient spatial and temporal validation (Dormann 2007). To minimize these concerns, we split our data into a training set used for preliminary model fits ($n = 728$) and a validation set composed of temperature observations that were spatially isolated from other sites ($n = 52$). In earlier spatial analyses of stream temperature data, distances of 5–15 km were reported between spatially independent sites (Gardner et al. 2003, Peterson et al. 2006), so we exceeded this distance when selecting observations for the spatial validation data.

Models were fit using the training data, and the universal kriging algorithm (Cressie 1993) was used to predict temperatures at validation sites in the spatial models. Predictive accuracy was assessed by calculating the squared Pearson correlation coefficient (r^2) between predicted and observed values. Leave-one-out cross-validation predictions were also generated using the training data for each model and used to calculate the root mean square prediction error (RMSPE). After the models with the best set of fixed effects were identified, the models were refit to the pooled set of observations from the training and validation sets.

Stream temperature predictions

Final models were used to make stream temperature predictions at both the basin scale and within burned areas by adjusting input values for air temperature, flow, and radiation to match the "average" set of conditions at the beginning and end of the study period. The radiation values used were from 1993 and 2006. Average stream flow values for these years were derived from a regression of flow on year for the 56-year period from 1950 to 2006 (Fig. 2). Air temperature values were derived similarly, but using a shorter, 30-year period from 1976 to 2006 to accommodate warming rates that are accelerating through time (IPCC 2007). Climate data were obtained from the same air temperature and flow stations described above (see *Methods: Climate predictors*) and regressions were based on averages across stations. The rates of change described by the regressions were comparable to recent global circulation model (GCM) projections for the Pacific Northwest (Mote et al. 2008).

To determine the relative importance of the three dynamic predictors in any stream temperature changes that occurred during the study period, we also predicted temperatures by holding input values for two predictors at their 1993 values and changing the value of the third predictor between its 1993 and 2006 values. The process was repeated for each of the predictors and the stream temperature change associated with each predictor was divided by the total basin scale stream temperature change (or total burned area stream temperature change) that occurred between 1993 and 2006, as described in the previous paragraph.

After setting the input values for the various comparisons, temperature predictions were made using the universal kriging algorithm at 2487 points spaced at 1-km intervals throughout that portion of the stream network where contributing areas exceeded 400 ha. Smaller contributing areas rarely support streams wider than 2 m in this region, which appears to be a minimum for providing the necessary perennial flow and habitat volume to support a resident fish population (Dunham and Rieman 1999, Rich et al. 2003).

Effects on thermal habitat

Basin-scale maps of predicted stream temperatures were converted to thermally suitable habitats for each species by applying different temperature criteria. These criteria were derived from field samples of fish densities at 249 sites on 20 central Idaho streams conducted in 2007 (Appendix E). We considered suitable thermal habitats to be those in which each species occurred regularly and high-quality habitats to be those temperatures with the highest densities of individuals. For bull trout, we further refined these criteria by focusing on the distribution of juveniles (<150 mm) that are indicative of spawning and rearing habitats (Rieman and McIntyre 1995, Dunham and Rieman 1999). This targeted our analysis on a critical subset of habitats required for bull trout population persistence and should have provided a more precise climatic assessment for this species. Portions of the stream network with MWMT < 17.5°C (means < 12°C) were considered to be suitable habitat for bull trout, whereas high-quality habitats were defined where MWMTs were <15°C (means < 10°C). Similar precision in defining thermal habitats for rainbow trout was not possible because juveniles are more widely distributed. So instead we relied on the occurrence of fish of all ages and areas with MWMT > 15°C and < 20°C (mean > 11°C and <14°C) were considered high-quality habitats and areas with MWMTs > 12.5°C (means > 9°C) were considered suitable habitats. We did not define an upper temperature limit for rainbow trout habitat suitability because it appears to be warmer than the temperatures regularly observed in the Boise (McCullough et al. 2001, Dunham et al. 2007). With this exception, our temperature

TABLE 3. Summary statistics for candidate multiple regression models used to predict stream maximum weekly maximum temperature (MWMT).

Model description	Fixed effects	Model type	p	ΔAIC	Training data (n = 728)		Validation data (n = 52)	
					r^2	RMSPE	r^2	RMSPE
1) Global + interactions	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A, C_A × Rad, Air_MWMT × Rad, Air × Flow, Ele × G_V	spatial	20	0	0.880	1.41	0.476	2.85
2) Global	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A	spatial	16	35	0.878	1.42	0.545	2.66
3) Simple hybrid	**Ele, Rad, Air_MWMT, Flow**	**spatial**	12	**51**	**0.874**	**1.45**	**0.612**	**2.51**
4) Dynamic predictors	Rad, Air_MWMT, Flow	spatial	11	77	0.870	1.47	0.468	2.84
5) Geomorphic predictors	Ele, G_V, V_B, SL, C_A	spatial	13	204	0.849	1.58	0.511	2.71
6) Elevation	Ele	spatial	9	222	0.845	1.60	0.560	2.57
7) Global + interactions	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A, C_A × Rad, Air_MWMT × Rad, Air × Flow, Ele × G_V	nonspatial	13	768	0.586	2.62	0.369	3.12
8) Global	Ele, G_V, V_B, Rad, Air_MWMT, Flow, SL, C_A	nonspatial	9	808	0.562	2.70	0.428	2.98
9) Simple hybrid	**Ele, Rad, Air_MWMT, Flow**	nonspatial	5	**838**	**0.542**	**2.76**	**0.495**	**2.78**
10) Geomorphic predictors	Ele, G_V, V_B, SL, C_A	nonspatial	6	955	0.463	2.99	0.318	3.31
11) Elevation	Ele	nonspatial	2	1023	0.408	3.13	0.288	3.37
12) Dynamic predictors	Rad, Air_MWMT, Flow	nonspatial	4	1137	0.308	3.39	0.130	3.63

Notes: Models are ordered based on Akaike information criterion (AIC) values; p is the number of parameters. Final models are in boldface. RMSPE is root mean square prediction error. See Table 2 for explanations of variable abbreviations.

criteria were generally consistent with others reported in the literature for these species (Bjornn and Reiser 1991, Ebersole et al. 2001, McCullough et al. 2001, Dunham et al. 2003*a*, Isaak et al. 2009).

Areas meeting these criteria were summarized based on the absolute amount of habitat, as well as the number and size of discrete habitat areas or "patches" (i.e., a continuous network of thermally suitable habitat). The size of individual habitat patches appears to be particularly relevant to persistence in many salmonid species (Isaak et al. 2007, Dunham et al. 2008). Larger patches tend to support larger populations that are less susceptible to extirpations through small population effects and probably contain a greater diversity of habitats to provide resilience against environmental stochasticity (White and Pickett 1985, Sedell et al. 1990). Previous studies with bull trout in the BRB support this notion, suggesting patches > 3000 ha (~10 stream km) have a 50% probability of occupancy, whereas patches > 10 000 ha (~40 stream km) have a 90% probability of occupancy (Rieman and McIntyre 1995, Dunham and Rieman 1999).

Results

The stream temperature database encompassed substantial interannual variation in climatic and solar radiation conditions across a diversity of local geomorphologies and streams (Table 1; Fig. 2). Observed mean stream temperatures ranged from 5.4° to 21.8°C (mean = 11.9°C) and MWMTs ranged from 7.2° to 30.7°C (mean = 17.2°C). Correlations among predictor variables were not particularly strong, with the exception of the two air temperature measures. Stream temperature was most strongly correlated with elevation, but also had moderate correlations with radiation and several other factors (Appendix F).

Stream temperature models

Summary statistics for candidate models predicting stream MWMT are provided in Table 3. Spatial models, despite having larger numbers of parameters, significantly outperformed their nonspatial counterparts, as indicated by lower RMSPE and AIC values, and greater predictive ability with training data (spatial $r^2 \sim 0.87$ vs. nonspatial $r^2 \sim 0.55$). Spatial models also performed better than the nonspatial models at the validation sites, although the differences were smaller. The highest AIC ranking was for a spatial model that included all predictor variables and four interactions. When applied to validation data, however, this model had poorer predictive ability than several others. Because we wanted a model that best predicted stream temperatures across the BRB, we chose a simpler model (eight fewer parameters) that performed best with the validation data ($r^2 = 0.61$) and retained good predictive ability with training data ($r^2 = 0.87$). This model included predictors for elevation, radiation, air MWMT, and stream flow. Results for mean stream temperature models were similar and are not shown.

Parameter estimates and summary statistics for the spatial and nonspatial versions of the final temperature models based on the reconstituted database are summarized in Table 4. The RMSPE for the spatial MWMT model was 1.54°C, a significant improvement over 2.75°C for the nonspatial model. Approximately two-thirds of the variance explained in the spatial MWMT

TABLE 4. Parameter estimates and summary statistics for nonspatial and spatial parameterizations of final stream temperature models (all $P < 0.001$).

Predictor	b (SE)	t	r^2	RMSPE	Variance component: Fixed effect (%)	Variance component: Spatial error (%)
MWMT						
Spatial						
Intercept	14.3 (2.45)	5.86	0.857	1.54	62.8	37.2
Elevation	−0.00573 (0.000789)	−7.27				
Radiation	0.0156 (0.00201)	7.78				
MWMT air	0.234 (0.0353)	6.61				
Mean flow	−0.125 (0.0209)	−5.98				
Nonspatial						
Intercept	18.8 (2.61)	7.19	0.543	2.75	100	. . .
Elevation	−0.00795 (0.000385)	−20.7				
Radiation	0.0189 (0.00138)	13.8				
MWMT air	0.212 (0.0625)	3.38				
Mean flow	−0.255 (0.0355)	−7.19				
Mean						
Spatial						
Intercept	8.20 (1.23)	6.64	0.925	0.736	72.3	27.7
Elevation	−0.00447 (0.000438)	−10.2				
Radiation	0.00850 (0.00108)	7.90				
Mean air	0.479 (0.0225)	21.3				
Mean flow	−0.111 (0.00878)	−12.7				
Nonspatial						
Intercept	13.3 (1.23)	10.8	0.679	1.53	100	. . .
Elevation	−0.00637 (0.000216)	−29.5				
Radiation	0.0104 (0.000765)	13.6				
Mean air	0.392 (0.0549)	7.14				
Mean flow	−0.173 (0.0176)	−9.85				

Notes: RMSPE is root mean square prediction error. MWMT is maximum weekly maximum temperature.

model could be attributed to fixed effects and one-third to spatial structure in model residuals. All parameter estimates were significantly different from zero ($P < 0.001$) and their signs were in agreement with the expected influence. Contrasts between the spatial and nonspatial versions of the mean temperature model were similar to those associated with the MWMT models, but the mean stream temperature models predicted this metric more accurately and a larger proportion of explained variation was attributable to the fixed effects. Scatter plots of predictions from the final models vs. observed temperatures confirmed the improved accuracy of the spatial models relative to the nonspatial models (Fig. 3), but a slight bias towards over- (under-) predictions in the coldest (warmest) streams remained. Additional details regarding the final spatial models are given in Appendices G and H, including the relative contributions of each covariance type in the mixed-model structure and empirical semi-variograms that describe spatial trends in model residuals.

Stream temperature and habitat predictions

The difference between basin-scale stream temperatures predicted at the beginning and end of the study period suggest that mean summer stream temperatures increased by 0.38°C (0.27°C/decade) and MWMTs increased by 0.48°C (0.34°C/decade); Figs. 4 and 5). These temperature increases correlated most strongly with trends in air temperature and secondarily with stream flow. Radiation increases, primarily associated with the wildfires that burned 14% of the basin, accounted for ~9% of basin-scale warming. Within wildfire perimeters, however, temperature increases were 2–3 times greater than the basin averages and radiation gains played a much larger role, accounting for 50% of total stream warming. Maps of the 1993–2006 mean stream temperature changes indicated that all portions of the BRB network warmed, with the smallest increases occurring in the southern half of the basin and the largest increases within wildfire perimeters (Fig. 5). Larger-than-average temperature increases were also observed in the northwest portion of the basin outside fire perimeters, probably in response to forest thinning activities.

Stream temperature increases had different effects on thermal habitat for bull trout and rainbow trout. Rainbow trout habitats encompassed much of the stream network in 1993 and the total amount of estimated habitat was not substantially affected by warming trends (Table 5, Fig. 6). The most notable changes were small habitat gains at higher elevations (sometimes accelerated within wildfire perimeters) as unsuitably cold areas became thermally suitable. Bull trout natal habitats, in contrast, initially encompassed approximately half the BRB stream network and experienced systematic declines because these areas

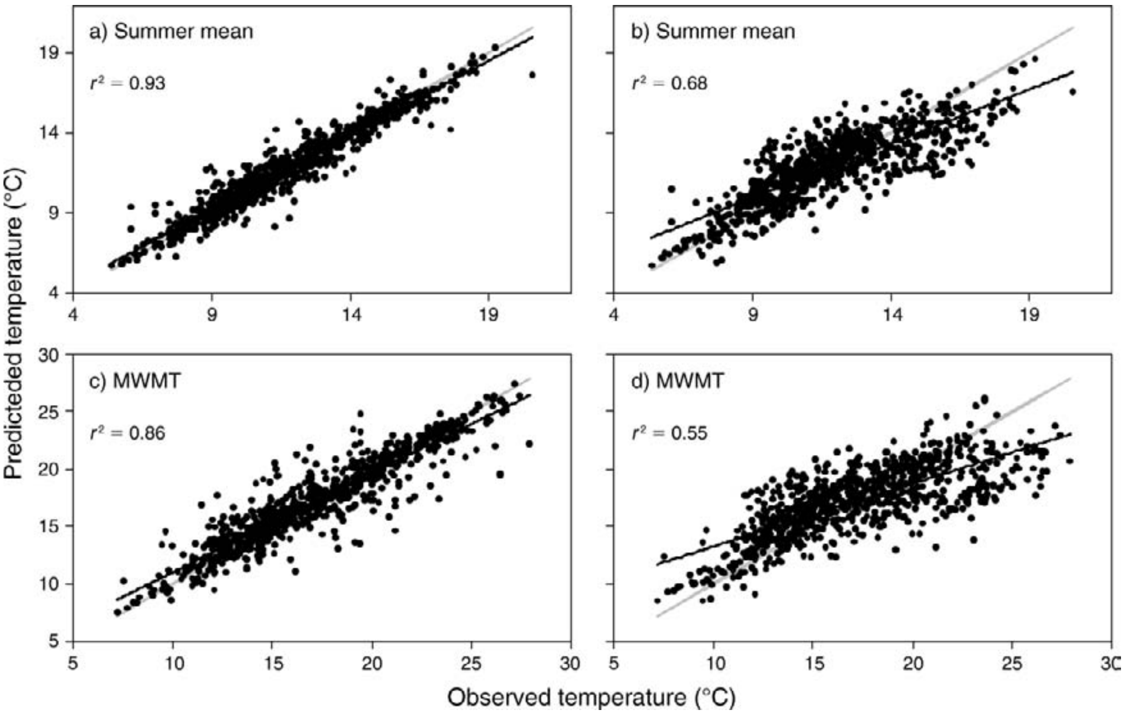

FIG. 3. Scatter plots of stream temperatures predicted from the (a, c) final spatial and (b, d) nonspatial models vs. observed values. The gray line indicates a 1:1 relationship; the black line is the simple linear regression between predicted and observed. MWMT is maximum weekly maximum temperature.

already occurred at the upper terminus of the network and losses in low-elevation sites were not offset by gains farther upstream (Table 5, Fig. 6). The total length of thermally suitable stream based on mean temperature criteria decreased by 11–20% (8–16%/decade), and the size of remaining natal patches was reduced by 10–18%. The greatest reductions occurred within wildfire perimeters and for the coldest, high-quality habitats because these areas comprised a smaller area at the outset of the study and changes relative to this baseline were amplified.

DISCUSSION

Our results suggest that environmental trends associated with a warming climate have begun to alter temperatures and thermal habitat distributions in streams across the BRB. Given the geographic breadth of recent wildfires (Westerling et al. 2006, Morgan et al. 2008), air temperature increases (Mote et al. 2005, Abatzoglou and Redmond 2007), and summer stream flow decreases (Stewart et al. 2005, Luce and Holden 2009) across much of the western United States, we believe similar thermal alterations are likely in many river networks. Whether these alterations have significant biological implications ultimately depends on local conditions. For a relatively mobile species such as rainbow trout, which has widely distributed and well-connected habitats in the BRB, the effects may be relatively benign. With some exceptions associated with structural barriers, rainbow trout populations should be able to track upstream shifts in habitat. Moreover, the wildfires associated with climate change may increase stream productivity, the availability of important forage

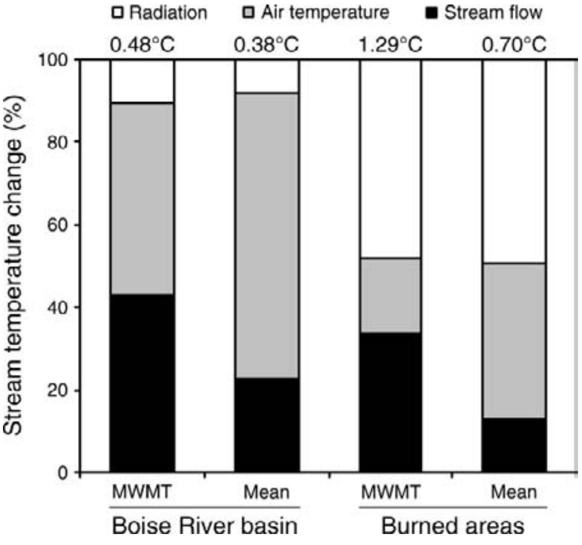

FIG. 4. Percentage of stream temperature change from 1993 to 2006 within burned areas and across the Boise River basin that was attributable to radiation gains associated with fires and long-term trends in air temperature and stream flow. Values above bars are total stream temperature increases. MWMT is maximum weekly maximum temperature.

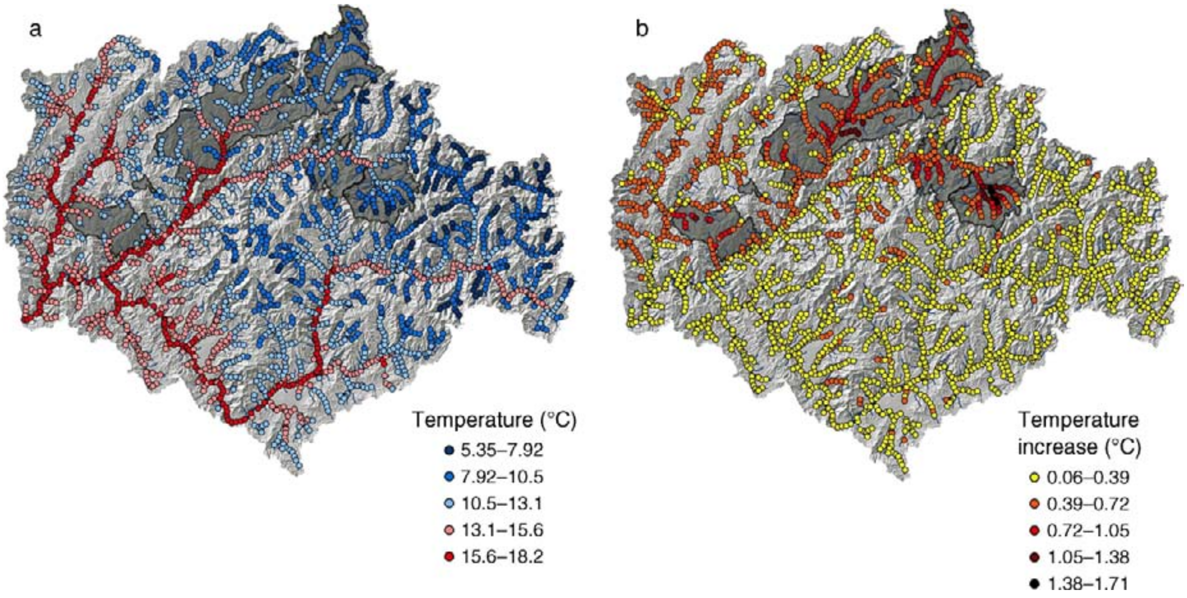

FIG. 5. Thermal maps for the Boise River basin of (a) predicted mean stream temperatures in 2006 and (b) mean temperature changes from 1993 to 2006. Dark gray shaded areas show wildfire perimeters from 1993 to 2006.

TABLE 5. Changes in basin-scale bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*) thermal habitats due to stream temperature trends from 1993 to 2006.

Habitat quality	Year	Habitat patches	Suitable stream length (km)	Patch size (km)		No. patches	
				Mean	Maximum	>10 km	>40 km
Bull trout, mean							
High	1993	158	697	4.41	58.0	13	2
	2006	153	555	3.63	58.0	8	2
	Change	−3%	−20%	−18%	0%	−38%	0%
Suitable	1993	184	1393	7.57	107.4	28	7
	2006	183	1246	6.81	107.4	25	6
	Change	−1%	−11%	−10%	0%	−11%	−14%
Bull trout, MWMT							
High	1993	162	557	3.44	58.0	10	1
	2006	150	433	2.89	55.0	7	1
	Change	−7%	−22%	−16%	−5%	−30%	0%
Suitable	1993	212	1234	5.82	107	22	7
	2006	211	1086	5.15	90.8	17	5
	Change	0%	−12%	−12%	−15%	−23%	−29%
Rainbow trout, mean							
High	1993	185	938	5.07	50.1	23	2
	2006	194	993	5.12	49.5	27	4
	Change	5%	6%	1%	−1%	17%	100%
Suitable	1993	1	2353	2353	2353	1	1
	2006	1	2443	2443	2443	1	1
	Change	0%	4%	4%	4%	0%	0%
Rainbow trout, MWMT							
High	1993	214	1361	6.36	83.5	33	5
	2006	236	1337	5.67	77.2	30	5
	Change	10%	−2%	−11%	−8%	−9%	0%
Suitable	1993	1	2592	2592	2592	1	1
	2006	1	2634	2634	2634	1	1
	Change	0%	2%	2%	2%	0%	0%

Note: MWMT is maximum weekly maximum temperature.

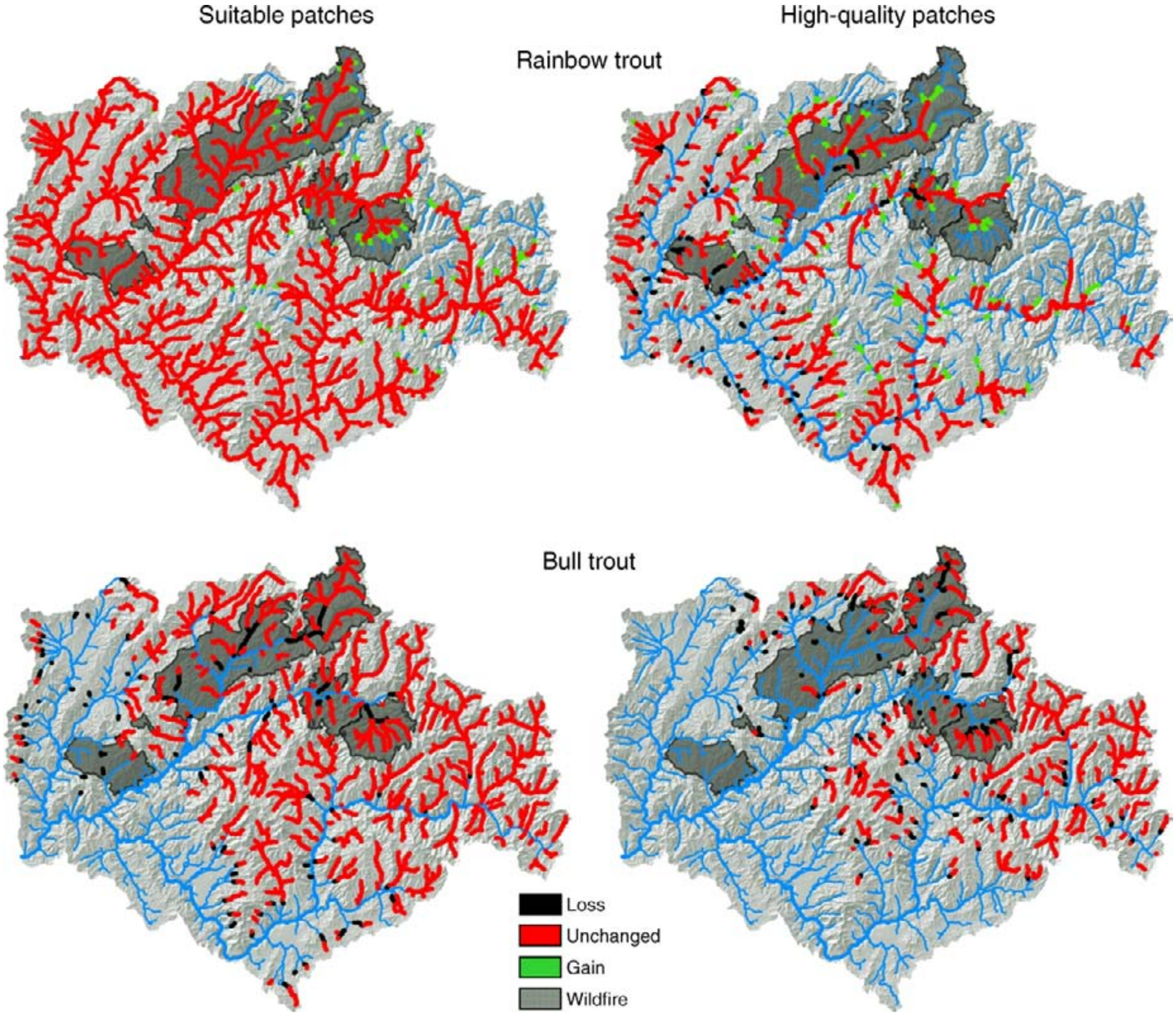

FIG. 6. Shifts in distribution of thermally suitable stream habitat for rainbow trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*) natal areas in the Boise River basin from 1993 to 2006 based on observed fires and long-term trends in stream flow and air temperature. Dark gray shaded areas show wildfire perimeters from 1993 to 2006.

items, and increase fish growth rates and densities (Rieman et al. 1997*a*, Dunham et al. 2007, Koetsier et al. 2007). Upstream habitats that become thermally suitable for rainbow trout may also be in better physical condition than lower elevation streams that tend to be more accessible and compromised by human activities (e.g., Rieman et al. 2000). Although differences in physical characteristics between gained and lost habitats could have important implications for the expression of different life histories (e.g., Brannon et al. 2004), at this point it does not appear that the effects of climate change will dramatically alter the status of rainbow trout in this basin.

Bull trout appear to be more vulnerable. Our results suggest that climate change may be rendering 8–16% of thermally suitable natal stream lengths unsuitably warm each decade. If recent trends continue in the future (when most climate models project accelerated warming), bull trout may lose half of their habitat in the BRB by mid-century. These losses would be exacerbated by fragmentation of large habitat patches and decreases in connectivity among remaining habitats (Rieman et al. 2007). Because the occurrence of bull trout populations is strongly associated with the size and isolation of habitat patches (Rieman and McIntyre 1995, Dunham and Rieman 1999), ongoing reductions would almost certainly be problematic for persistence of many populations. Moreover, predicted loss rates for the coldest, high-quality habitats were greater than loss rates of suitable habitats. Especially cold streams may be disproportionately important for bull trout persistence within a landscape because they provide thermal environments that are less susceptible to nonnative trout invasions (Rieman et al. 2006, McMahon et al. 2007) and support higher densities of individuals that could provide emigrants and demographic support to weaker populations.

Most stream temperature increases and habitat shifts within the BRB were related to trends in air temperature and stream flow, but wildfires also had important effects. Our estimates of temperature increases associated with fire were smaller (typically <1°C) than the several degree increases that are often reported (e.g., Minshall et al. 1997, Dunham et al. 2007, Leach and Moore 2008), but our study averaged across multiple burn severities and stream types within burn perimeters. Moreover, conclusions from previous studies are difficult to generalize, given their opportunistic nature and tendency to focus on severely burned streams. Despite a smaller estimated effect, however, the wildfires within the BRB effectively doubled or tripled stream warming rates relative to basin averages and caused some of the most dramatic shifts in thermal habitat. If the frequency and extent of wildfires continues to increase (McKenzie et al. 2004, Westerling et al. 2006), greater overlap with shrinking bull trout habitats could foreshadow a difficult future for the conservation of this species in some portions of its range (Rieman et al. 2007).

Within this evolving context, key questions emerge regarding where future fires and other disturbances are likely to occur, their extent, grain of fire behavior and severity, and the processes of postfire population and habitat recovery. In some instances, we have partial answers to these questions or the tools necessary to begin to address them. For example, fire behavior models exist that could be used to simulate wildfire behavior across complex landscapes, but these have yet to be applied in ways that might inform assessments of thermal conditions in streams (Whitlock et al. 2003). We also know that thermal recovery from fires happens, but the process is complex and dependent on prefire vegetation types, burn severity and extent, stream size, and postfire channel disturbances such as debris flow torrents that can retard recovery of riparian areas (Dunham et al. 2003*b*, Pettit and Naiman 2007). In some streams, thermal effects are minimal and recovery is rapid, but in others, changes may persist for decades after a fire (Minshall et al. 1997, Dunham et al. 2007). Moreover, changing climatic conditions could alter disturbance and recovery trajectories, either by increasing the extent or severity of fires and postfire disturbances or prolonging, possibly even preventing, regrowth of prefire vegetation types (Whitlock et al. 2003, van Mantgem and Stephenson 2007). More details regarding these uncertainties and the changing role of wildfire are needed to refine current understanding and incorporate potential effects into future risk assessments for bull trout or other aquatic species (Bisson et al. 2003, Dunham et al. 2003*a*).

Whether bull trout are yet responding to habitat shifts, as has been documented for numerous other plant and animal taxa, is unknown (Parmesan and Yohe 2003, Hari et al. 2006, Heino et al. 2009). Although climate-related reductions of natal habitats may have been ongoing for several decades, systematic and spatially representative population monitoring has not been conducted over a similar time frame. Where long-term distributional data do exist for bull trout or other salmonid species, monitoring has typically focused on areas with high fish abundance in the best habitats, which may also be some of the slowest to change (Rieman and McIntyre 1997, Isaak and Thurow 2006). Recognizing this, we have begun to conduct our own distributional assessments, wherein bull trout are resampled along longitudinal profiles that span the lower elevation limit of juvenile fish (Rieman et al. 2006; D. Isaak, *unpublished data*). Preliminary results from 12 streams in central Idaho (seven were in the BRB) suggest that the lower elevation limit of juvenile bull trout did not change consistently across streams between 1997 and 2007, except in three streams affected by fires. Interannual variation may have been too great or the monitoring period too short to detect any population shifts. Because bull trout are a relatively long-lived species (generation time of 5–7 years) with diverse life histories, population responses could be protracted (Morris et al. 2008). Resolving the mechanisms by which climate affects recruitment processes and restricts distributions in streams will ultimately be necessary to accurately predict population responses, but appropriate monitoring strategies are also needed to provide early indications of population shifts and determine rates of change (e.g., Isaak et al. 2009). Monitoring that focuses on the thermally sensitive downstream limits of distributions (e.g., Rieman et al. 2006) could be particularly effective at resolving biological responses in headwater species such as bull trout.

Spatial statistical stream temperature models

Climate change effects on stream temperatures have been assessed in large rivers using mechanistic models (e.g., Gooseff et al. 2005, Flint and Flint 2008) and based on simple statistical relationships between air temperatures and stream temperatures (e.g., Eaton and Scheller 1996, Mohseni et al. 2003). Both approaches provide limited spatial inference, however, because of difficulties associated with extrapolating beyond areas where measurements are obtained. The ability to make valid spatial inference is greatly improved by Ver Hoef and Peterson's new spatial models for streams (Ver Hoef et al. 2006, Ver Hoef and Peterson 2010). These models overcome many of the problems that have limited statistical analyses of stream systems by accommodating spatially complex covariance structures associated with network topology, flow volume, and flow direction (Peterson et al. 2006, Peterson and Ver Hoef 2010, Ver Hoef and Peterson 2010). Incorporating a realistic covariance structure minimizes potential bias in parameter estimates that could arise from spatial autocorrelation (Legendre 1993) and makes the models well-suited for application to "found" databases such as our

PLATE 1. Adult bull trout staging near a spawning area in central Idaho's Salmon River basin (USA). Photo credit: Russ Thurow.

temperature data that are often characterized by clustering and nonrandomness (e.g., Kadmon et al. 2004, High et al. 2009). Moreover, at least from a spatial modeling perspective, spatial autocorrelation is clearly a positive characteristic because it improves the predictive ability of the models (Ver Hoef 2002), as local deviations from the mean response can be modeled using the spatial autocorrelation between nearby sites (Cressie 1993).

Current applications of the stream spatial models have been limited primarily to understanding water chemistry attributes (e.g., Peterson and Urquhart 2006, Peterson et al. 2006, Gardner and McGlynn 2009), but comparable benefits may be expected for biological attributes of stream networks and numerous applications can be envisioned that draw on large georeferenced databases now routinely compiled by natural resource agencies. The integration of spatial models for stream networks with improving ability to characterize important landscape and stream habitat features through GIS promises to significantly advance understanding of lotic ecosystems by reducing much of the imprecision associated with larger-scale inquiries (Fausch et al. 1988, McIntire and Fajardo 2009) and should be particularly useful for understanding relationships at landscape to regional scales.

Air temperature–stream temperature relationships

Air temperature serves a useful role in understanding temporal variability in stream temperature (Mohseni et al. 1998, Caissie 2006) and is commonly used as a surrogate in assessing potential climate change impacts (e.g., Keleher and Rahel 1996, Rieman et al. 2007). Although our analysis suggested air temperatures played a dominant role in stream temperature increases across the BRB, air temperature parameters were considerably less than 1 (MWMT = 0.23; mean = 0.48) and were at the low end of the range reported by Morrill et al. (2005) in a recent review of the subject. Morrill et al. (2005) also note that the smallest air temperature parameters were associated with high-elevation streams, which implies some generality among these systems that may make them less sensitive to future air temperature increases. Multiple factors could contribute to decreased sensitivity, but at the global scale considered by Morrill et al. (2005), strong distinctions would certainly be expected between lowland streams characterized by rainfall hydrology and high-elevation streams dominated by snowmelt runoff and seasonal influxes of cold groundwater. And even within high-elevation streams, variation in sensitivity to air temperatures is apparent seasonally due to variation in snowmelt inputs (Webb and Nobilis 1997, Mohseni et al. 1998) and might also be expected along an elevational gradient from greater snow accumulation and persistence at higher elevations (Luce and Tarboton 2004).

Within the BRB, we speculate that a similar elevational mechanism, perhaps enhanced by greater proportional influences of glacial valleys at high elevations, could have accounted for the small bias in our final temperatures models wherein over- (under-) predictions were made for the coldest (warmest) streams. Because the spatial models we applied lacked a true temporal component, they could not account for spatially varying sensitivities to air temperature, but instead assumed a spatially uniform effect across the basin. The accuracy of our final stream temperature models attests to the general adequacy of this approach, but an important area of future research would explore the factors responsible for spatial variation in warming rates within and among streams.

Management implications

Our models suggest climate change will have important implications for species such as bull trout, although biologically significant changes may take a decade or more to occur. This time lag may provide a window of opportunity for management actions to conserve or recover some resilience in vulnerable populations. One alternative is to mitigate past habitat disruptions to minimize cumulative stresses and increase resilience against future climate effects. Fortunately, the thermal gains associated with many stream modifications and natural disturbances may be similar to, or larger than, those expected from future climate warming. Riparian vegetation, for example, strongly affects near-stream microclimates (Moore et al. 2005), and minimizing near-stream disturbances associated with grazing, road-building, and timber harvest, or facilitating rapid vegetative recovery after these disturbances, could help buffer many streams from additional warming. Suppression of fires in riparian areas may preclude the most dramatic stream temperature increases and might be warranted where critical habitats or small populations of sensitive fishes occur, but such effects must be weighed against longer-term benefits to stream and forest diversity (Reeves et al. 1995, Rieman et al. 2000). Restoring stream flows or precluding future water abstractions through water right acquisitions are yet other options for buffering streams against warming where flow diversion is an issue.

In addition to thermal mitigation, efforts to increase biological resilience will also be important. Structural barriers associated with road crossings, water diversions, or dams often impede fish movements but can be modified to facilitate fish passage (Fausch et al. 2006). Improved passage promotes connectivity among habitats and may allow populations the flexibility to track habitat distributions that shift with warming or to use refugia when large disturbances occur. If costs of passage improvements are prohibitive, human-assisted migrations may be an option in extreme cases (McLachlan et al. 2007). Within certain contexts, populations of brook trout (or other nonnative salmonids) that constrain downstream distributions of bull trout (or other native species) may be controlled to expand access to local habitats (Moore et al. 1986, Peterson et al. 2008). Promoting diversity, both in terms of life histories (Rieman and Clayton 1997, Isaak et al. 2003) and heterogeneity of stream and forest habitats, could also minimize risks from large, synchronous disturbances. Although rarely viewed as a viable option, letting populations go in areas where climate impacts will overwhelm restoration potential may also become necessary so that limited resources can be expended more effectively elsewhere. Exercising this option, however, is likely to encounter significant socio-political impediments and will require explicit recognition of management priorities and trade-offs (Bottrill et al. 2008).

Conclusion

Mountain streams in the western United States figure prominently in regional conservation efforts for many species (Thurow et al. 1997, Lee et al. 1998, Kareiva et al. 2000) because they provide relatively pristine habitats in comparison to lower elevation streams where anthropogenic impacts are pervasive. In an era of global warming, however, mountain environments can no longer be viewed as refugia from these impacts. Our work and that of many others (Mote et al. 2005, Westerling et al. 2006, Abatzoglou and Redmond 2007, Hamlet and Lettenmaier 2007, Hamlet et al. 2007, Barnett et al. 2008, Morgan et al. 2008) suggest that rapid climate change within the western United States is effecting profound changes in many environmental drivers that either directly or indirectly affect stream ecosystems. Alteration of stream thermal regimes is likely to be one of the most important environmental changes that aquatic organisms experience, given the strong control that temperature has on distribution, abundance, growth, and population persistence. Some species in certain contexts will benefit from temperature increases, whereas others will experience habitat declines that could significantly reduce the probability of population persistence within individual landscapes or across distributional ranges (Battin et al. 2007, Rieman et al. 2007). But even where negative impacts are anticipated, many populations may persist, especially with assistance from informed, proactive management.

A key challenge will be predicting relative vulnerabilities of populations and habitats so that prioritization can proceed accordingly. Because conservation needs will often exceed available resources, potential management interventions should be viewed in larger contexts to identify those areas where investments are most likely to yield meaningful biological returns (Roni et al. 2002). Broadscale assessments of climatic threats could be used to provide strategic overviews (e.g., Battin et al. 2007, Rieman et al. 2007) and differentiate portions of a species range into future strongholds, lost causes, and areas where management could play a decisive role. In this latter category, more detailed analyses are warranted and could be used to guide conservation planning and project-level implementation at scales relevant to local population persistence. Our approach to statistically downscaling climate change effects on thermal regimes in river networks is a useful step in this regard that helps reduce many key uncertainties. Although thermal effects will be a first-order determinant for many aquatic species, these considerations need to be supplemented and refined by a better understanding of the mechanisms associated with biological responses, climate effects on other habitat features, and habitat configurations that confer population resilience. As these uncertainties are resolved, those working with stream ecosystems will be increasingly well equipped to conserve biodiversity in a warming world.

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APPENDIX A

Temporal sequence of stream temperature records from the Boise River basin (BRB) used to parameterize temperature models (*Ecological Archives* A020-046-A1).

APPENDIX B

Changes in riparian vegetation determined from Thematic Mapper satellite imagery relative to wildfire perimeters within the BRB between 1989 and 2002 (*Ecological Archives* A020-046-A2).

APPENDIX C

An example of riparian vegetation classifications derived from Thematic Mapper satellite imagery before a wildfire in 1989 and after fire in 2002 (*Ecological Archives* A020-046-A3).

APPENDIX D

Relationships between radiation, watershed area, and vegetation class used to predict radiation values for the stream network in the BRB (*Ecological Archives* A020-046-A4).

APPENDIX E

Stream temperature thresholds used to delineate habitat quality for bull trout and rainbow trout (*Ecological Archives* A020-046-A5).

APPENDIX F

Correlations among variables at 780 sites used in stream temperature models for the BRB (*Ecological Archives* A020-046-A6).

APPENDIX G

Semi-variograms of the residuals from the final maximum weekly maximum temperature (MWMT) and summer mean spatial stream temperature models (*Ecological Archives* A020-046-A7).

APPENDIX H

Percentage of the residual error structures in the final spatial stream temperature models attributable to tail-up, tail-down, Euclidean, and nugget portions of the covariance structure (*Ecological Archives* A020-046-A8).