

ESTIMATING THERMAL REGIMES OF BULL TROUT AND ASSESSING THE POTENTIAL EFFECTS OF CLIMATE WARMING ON CRITICAL HABITATS

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ABSTRACT

Understanding the vulnerability of aquatic species and habitats under climate change is critical for conservation and management of freshwater systems. Climate warming is predicted to increase water temperatures in freshwater ecosystems worldwide, yet few studies have developed spatially explicit modelling tools for understanding the potential impacts. We parameterized a nonspatial model, a spatial flow-routed model, and a spatial hierarchical model to predict August stream temperatures (22-m resolution) throughout the Flathead River Basin, USA and Canada. Model comparisons showed that the spatial models performed significantly better than the nonspatial model, explaining the spatial autocorrelation found between sites. The spatial hierarchical model explained 82% of the variation in summer mean (August) stream temperatures and was used to estimate thermal regimes for threatened bull trout (*Salvelinus confluentus*) habitats, one of the most thermally sensitive coldwater species in western North America. The model estimated summer thermal regimes of spawning and rearing habitats at <13°C and foraging, migrating, and overwintering habitats at <14°C. To illustrate the useful application of such a model, we simulated climate warming scenarios to quantify potential loss of critical habitats under forecasted climatic conditions. As air and water temperatures continue to increase, our model simulations show that lower portions of the Flathead River Basin drainage (foraging, migrating, and overwintering habitat) may become thermally unsuitable and headwater streams (spawning and rearing) may become isolated because of increasing thermal fragmentation during summer. Model results can be used to focus conservation and management efforts on populations of concern, by identifying critical habitats and assessing thermal changes at a local scale. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: stream temperature; spatial statistical model; climate change; bull trout; *Salvelinus confluentus*; thermal habitat; Flathead River Basin

Received 2 August 2012; Revised 26 October 2012; Accepted 4 December 2012

INTRODUCTION

Over the past century, climate warming has increased the planet's mean annual air temperatures by 0.6°C, and temperatures are predicted to rise by as much as 6°C by 2100 (Solomon *et al.*, 2007; Trenberth and Jones, 2007). Water temperatures within aquatic ecosystems are also rising and have been linked to long-term increases in air temperatures (McCullough *et al.*, 2009). These changes are shifting the distribution, abundance, and phenology of many aquatic species (Walther *et al.*, 2002; Parmesan and Yohe, 2003). Therefore, understanding how habitats are likely to change and how species may respond to changes in climatic conditions is critical for developing conservation and management strategies.

Climate warming in the Rocky Mountains of North America is occurring at two to three times the rate of the global average (Hansen *et al.*, 2005; Pederson *et al.*, 2010). Warming trends and regional downscaled climate model simulations indicate that mountainous ecosystems will likely continue to trend towards earlier and more rapid snowmelt in the spring (Luce and Holden, 2009), increased winter precipitation and flooding (Hamlet and Lettenmaier, 2007), warmer, drier summers (Westerling *et al.*, 2007), increased late summer drought (Pederson *et al.*, 2010), and reduced summer flows. These climatic and hydrologic changes contribute to warmer water temperatures in the summer months in many streams and rivers (Kaushal *et al.*, 2010), thereby reducing the amount of thermally suitable habitat for many aquatic species (Isaak *et al.*, 2010; Wenger *et al.*, 2011).

Water temperatures vary spatially and temporally, playing an important role in the distribution of many aquatic species (Dunham *et al.*, 2003). Spatially explicit models

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can be used to capture and quantify these spatial and temporal patterns, which can provide additional information about ecosystem structure and function (Inoue *et al.*, 2009). Both nonspatial and spatial modelling approaches have been used to predict water temperatures in stream networks. For example, simple linear regression models have been used to predict water temperatures using air/water temperature correlations (Mackey and Berrie, 1991; Webb and Nobilis, 1997; Caissie, 2006). These models are generally used for short temporal scales (e.g. 1 year) when water temperature is not autocorrelated within the time series. As temporal scales increase, there can be considerable complexity in air to water temperature relationships, often making simple linear regression ineffective. In these cases, multiple regression models have been used to address model complexity (Jeppesen and Iversen, 1987; Jourdonnais *et al.*, 1992; Caissie, 2006) using a combination of predictor variables in addition to air temperature (Caissie, 2006). More recently, advances in geostatistical modelling of stream systems have greatly improved temperature predictability by using spatial data to explain variation across heterogeneous river networks (Peterson and Ver Hoef, 2010). 'Fine-scale' geostatistical models can incorporate predictors defined at local or small scales (e.g. 30 m) as compared with coarse generalizations often made from broader-scale studies (e.g. watershed scale; Isaak *et al.*, 2010).

Spatial hierarchical modelling is an example of a geostatistical model, which accounts for how stream temperatures are related in groups (e.g. watershed divisions) within a hierarchical framework (McMahon and Diez, 2007). Recently, more sophisticated geostatistical models based on hydrologic relationships have been developed (Peterson and Ver Hoef, 2010). These models use a combination of 'flow-connected' distances, 'flow-unconnected' distances, and Euclidean distances to estimate the spatial relationships (autocorrelation) between stream temperature sites.

Climate trends and projections have prompted interest in assessing the thermal sensitivity of coldwater aquatic species worldwide (Winterbourn *et al.*, 2008; Wenger *et al.*, 2011). This is particularly true for salmonid species (e.g. trout, char, and salmon) that are strongly influenced by changes in temperature, flow, and physical habitat conditions (Haak *et al.*, 2010). Salmonids are especially vulnerable to climate-induced warming in freshwater ecosystems because of the following: (i) they have ectothermic physiologies; (ii) they require streams and lakes with cold, high-quality habitats, which are easily fragmented by thermal or structural barriers; (iii) their distributions and abundances are strongly influenced by temperature and stream flow gradients; and (iv) they have narrow tolerances to thermal fluctuations in cold waters (Dunham *et al.*, 2003; McCullough *et al.*, 2009; Williams *et al.*, 2009; Isaak *et al.*, 2010). Having

one of the lowest upper thermal limits and growth optima of all salmonids in North America, the bull trout (*Salvelinus confluentus*) is an excellent indicator of warming temperatures in stream networks (Selong *et al.*, 2001; Dunham *et al.*, 2003; Rieman *et al.*, 2007). Furthermore, populations of bull trout have declined throughout much of their native range (Rieman *et al.*, 1997), and the species is listed as a threatened species under the Endangered Species Act. Declines are largely attributed to habitat degradation, fragmentation, nonnative invasive species, and climate change (USFWS, 2010).

Spatially explicit assessments of species' sensitivities to changing habitat conditions are needed to guide conservation and management actions. The goal of this study was to develop a spatial stream temperature model to quantify and explore the thermal regimes of critical bull trout habitats in the Flathead River Basin (FRB), USA and Canada. Our objectives were as follows: (i) to compare spatial and nonspatial model performance to predict stream temperatures throughout the FRB; (ii) to use a spatially explicit model to estimate thermal regimes for bull trout habitats; and (iii) to predict thermal changes under a range of future climate warming scenarios.

MATERIALS AND METHODS

Study area

The upper FRB originates in the Rocky Mountains of north-western Montana (USA) and south-eastern British Columbia (Canada) and includes the North Fork, Middle Fork, South Fork, mainstem Flathead Rivers, and Flathead Lake. The study area is approximately 14 430 km² and is located in the headwaters of the upper Columbia River Basin (Figure 1). The climate is influenced by moist Pacific maritime air masses, which circulate inland from the Pacific Ocean, producing moderate wet weather, whereas continental air masses circulate southerly from Canada, bringing cold winters and hot dry summers (Curtis, 2010). The watershed is dominated by snowmelt runoff in the spring, producing high flows from April to June that typically recede to base flows in August, September, and early fall.

Bull trout in the Flathead River Basin

The FRB is a range-wide stronghold for the threatened bull trout (Rieman *et al.*, 1997; Hauer and Muhlfeld, 2010). Bull trout display migratory life histories (e.g. fluvial and adfluvial) in the upper Flathead River and Lake system, requiring large, ecologically diverse, and connected coldwater habitats to complete their life cycle [e.g. *spawning and rearing* (SR) and *foraging, migrating, and overwintering* (FMO)], which is critical to the long-term persistence of the species

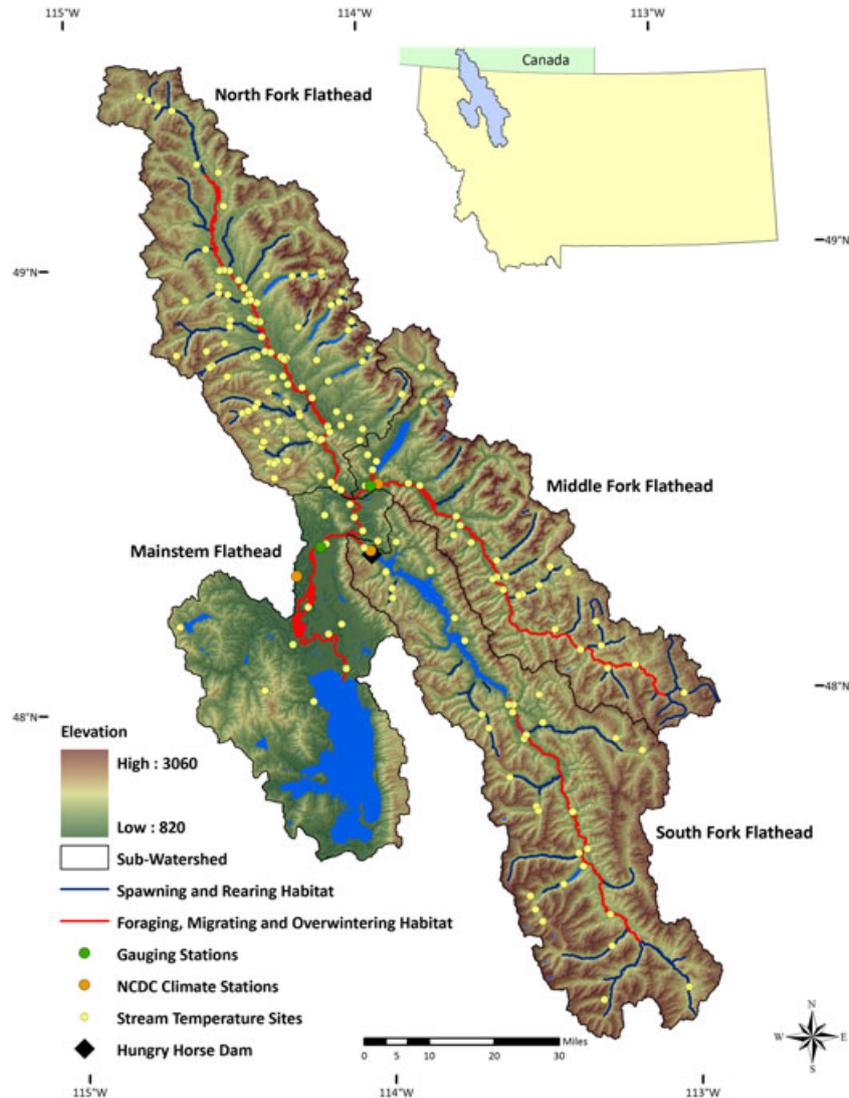


Figure 1. The Flathead River Basin in northwestern Montana (USA) and southeastern British Columbia (Canada). Stream temperatures were measured at 201 thermograph sites. Air temperatures were recorded at three climate stations, and stream discharge rates were measured at two gauge stations. Current bull trout habitat distributions are denoted in red and blue. This figure is available in colour online at wileyonlinelibrary.com/journal/rra.

(Rieman and McIntyre, 1995; Rieman and Allendorf, 2001). Bull trout in the FRB commence spawning migrations (up to 250 km) from May through July and spawn in second-order to fourth-order streams primarily during September and October. Juveniles rear in natal spawning and rearing streams for 1 to 4 years and then make complex movements to the mainstem rivers or lakes where they grow to maturity (Fraley and Shepard, 1989; Muhlfeld *et al.*, 2003; Muhlfeld and Marotz, 2005). Therefore, loss of habitat connectivity, due to thermal, hydrological, or physical barriers, can be especially detrimental to migratory populations. Consequently, conservation efforts have focused on maintaining natural connections of coldwater

habitats, as well as protecting and restoring critical or unique habitats, which provide the full expression of life history required to maintain genetic diversity and dispersal among populations (Rieman and Allendorf, 2001; Muhlfeld and Marotz, 2005).

Stream temperature database

A database of stream temperatures was compiled from previous studies conducted by the US Geological Survey (USGS), US Forest Service, Montana Fish, Wildlife, & Parks, National Park Service, and the University of Montana's Flathead Lake Biological Station, as well as current ongoing monitoring

efforts in the FRB. August stream temperatures were recorded at 201 sites within the FRB during the years of 1998–2010 (Figure 1). Stream temperatures were measured with digital thermographs (Hobo models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy = $\pm 0.2^\circ\text{C}$) that recorded temperatures at bi-hourly or hourly intervals, resulting in a database of 266 083 raw data points from 201 unique sites. These bi-hourly and hourly recordings were then summarized to mean August temperatures for each site and year of the study period ($n=371$). Thermograph locations were georeferenced at the time of installation.

Physiological stresses due to warm water temperatures and base flows can have a significant impact on fish growth, behaviour, and habitat selection (Selong *et al.*, 2001). The summer month of August is an important time for bull trout feeding and spawning migrations and can also sustain some of the warmest water temperatures of the year. For these reasons, we focused our stream temperature study on the summer month of August. Previously, we found that the mean temperature metric explained the variation in our data better than the *maximum* or *maximum weekly maximum temperature* metrics (Jones, 2012). Furthermore, the mean metric provides an overall indication of thermal suitability and optimal conditions for growth of bull trout (Isaak *et al.*, 2010).

Stream networks

We applied two different terrain analysis methods in developing stream networks for the FRB. Because of the transboundary nature of the FRB, two datasets were co-registered across the USA–Canada border. This network utilized the National Hydrography Dataset from the USGS (NHD, 2011) and the National Hydro Network (NHN, 2011) from the Canadian Council on Geomatics. The second stream network used in this study was derived using TauDEM (Terrain Analysis Using Digital Elevation Models) version 5 software (Tarboton, 2008), which delineates stream networks from topographic details represented in a digital elevation model (DEM). We used Advanced Spaceborne Thermal Emission and Reflection (ASTER) elevation datasets (NASA; 22-m resolution) to derive this network and used it as the base DEM for this project because it seamlessly covered both the USA and Canada portions of the FRB.

Predictor variables

A particular challenge of transboundary river basins, such as the FRB, is the development of consistent and harmonized geographic information system (GIS) databases. Here, we investigated the influence of simple geomorphic, geographic, and climatic covariates on stream temperatures and associated variability. Climatic and hydrologic predictors, such as air

temperature and stream flow, are known to have an effect on stream temperatures and annual variability (Isaak *et al.*, 2010). Furthermore, in heterogeneous stream and river networks, such as the FRB, thermally suitable habitats may not only vary with climatic changes but may depend largely on physical and geomorphic constraints (Rieman *et al.*, 2007). Therefore, we considered three geomorphic predictor variables (elevation, slope, and aspect), two geographic predictors (latitude and longitude), and three climatic predictors (solar radiation, air temperature, and discharge). Elevation, slope, aspect, latitude, longitude, and solar radiation represent spatial attributes in the landscape, whereas air temperature and discharge were used to explain temporal variation in the data. We also included a categorical predictor variable to account for the presence of lakes, which are known to influence downstream thermal regimes (Mellina *et al.*, 2002).

Solar radiation (insolation) contributes to stream temperatures and variability in climatic factors such as air temperatures and snowmelt patterns (Webb *et al.*, 2008). Spatial variability of insolation is strongly affected by topographical features including elevation, orientation (slope and aspect), and shadows cast by topographic features (Kumar *et al.*, 1997). We used an area-based model in ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California, USA) to compute solar radiation, calculating surface elevation, orientation, and shadow effects from the ASTER DEM.

Air temperatures have a similar effect on stream temperatures through heat exchange near the surface of the water (Mote, 2006). Mean daily air temperatures were summarized from three National Climatic Data Center climate stations in the FRB (West Glacier, Hungry Horse, and Kalispell Airport; Figure 1) and were averaged together, resulting in a mean August air temperature for each year of our study period.

As discharge rates decrease, streams become more susceptible to thermal warming. Consequently, lower discharges in August typically result in lower thermal capacity (Caissie, 2006). Mean daily discharges were obtained from two USGS gauging stations in the basin (North Fork Flathead-12355500 and Middle Fork Flathead-12358500; Figure 1) and were averaged to calculate mean August discharges for each year of the study period. These averaged air and discharge values represent regional patterns of flow and air temperatures within the FRB.

Lakes have a considerable effect on downstream water temperatures, absorbing solar radiation and resulting in dramatically warmer temperatures at lake outflows as compared with inflow streams (Hieber *et al.*, 2002). We created a categorical predictor variable, *lake effect*, which represents lake warming influences on stream temperatures downstream of lakes. From empirical data used in the

model, we created a lake size threshold for the warming effect, where the smallest lake within our study was used to designate the lower lake size threshold. To make temperature predictions throughout the network, we considered stream segments downstream of lakes as lake affected and digitized them as such to the confluence of the next highest stream order.

Slope, aspect, and elevation predictors were derived from the ASTER DEM using ArcGIS. Predictor values were calculated at a 22-m resolution, before being attributed to stream temperature records at individual locations. All predictors and grids were projected to the UTM, Zone 11, NAD 83 coordinate system.

Stream temperature models

This study examined three model types used to predict stream temperatures at sites within our study area: a nonspatial model and two spatial models. The nonspatial model selected was a fixed-effect generalized linear regression model. The two spatial models chosen were a mixed-effect generalized linear regression model, also known as a spatial hierarchical model and a spatial flow-routed model. The nonspatial model (fixed-effect generalized linear regression model) was defined as

$$y = X\beta + \varepsilon \quad (1)$$

where y represents a vector of observed stream temperatures, X is a matrix of predictor variables, β is a matrix of model parameters, and ε is the error term. The nonspatial model uses maximum likelihood estimation (MLE) to derive parameter estimates, and the residual errors are assumed to be normally distributed, $\varepsilon \sim N(0, \sigma^2)$. The NHD/NHN stream network was used to assign predictor variables to individual temperature locations used for the nonspatial model runs. This model is a fixed-effect model and does not incorporate any spatial index for explaining spatial dependency within the data.

Many studies have shown that fitting spatially dependent data with a model that does not account for spatial structure can produce biased parameter estimates and autocorrelated error structures (Legendre, 1993; Peterson *et al.*, 2007). Therefore, we chose a spatial hierarchical model or a mixed-effect generalized linear regression model, which uses USGS Hydrologic Unit Code 6 sub-watershed divisions as a random effect to account for potential spatial correlation (i.e. longitudinal connectivity, flow volume, and flow direction) inherent to stream networks (Deschenes and Rodriguez, 2007; USGS, 2012). This spatial hierarchical model,

$$y_i \sim N(X_i\beta, \sigma^2_y) \quad (2)$$

has a variance component approach, which allows multiple covariance matrices to be combined simultaneously. In this case, covariance matrices (σ^2_y) for each USGS Hydrologic Unit Code 6 watershed ($X_i\beta$) were combined to improve the model's predictive power. The NHD/NHN stream network was used to assign predictor variables to the study sites, and MLE was used to derive the parameter estimates.

The second spatial model used in the model comparisons was a spatial flow-routed model, which has recently emerged as a new methodology of evaluating hydrologic parameters (Isaak *et al.*, 2010; Peterson and Ver Hoef, 2010). Flow-routed models can use existing stream networks, such as the NHD, or a DEM-derived network to describe spatial dependencies in the model predictions. Similar to that of the spatial hierarchical model, the covariance structure for the spatial flow-routed model,

$$y = X\beta + \sigma_{EUC}z_{EUC} + \sigma_{TD}z_{TD} + \sigma_{TU}z_{TU} + \sigma_{NUG}z_{NUG} \quad (3)$$

is also based on a variance component approach (σ_{EUC} , σ_{TD} , σ_{TU} , and σ_{NUG}) and uses random effects based on hydrologic distances (z_{EUC} , z_{TD} , z_{TU} , and z_{NUG}). The covariance components are Euclidean distance (EUC) and 'tail-up' (TU) and 'tail-down' (TD) hydrologic distances, as well as a nugget effect (NUG). Tail-up covariances are based on hydrologic distances between flow-connected sites, and tail-down covariances allow spatial correlation between flow-unconnected sites (Isaak *et al.*, 2010; Peterson and Ver Hoef, 2010). To implement the model, we calculated hydrologic distances and spatial weight matrices in ArcGIS using the 'Functional Linkage of Water Basins and Streams' toolset and the 'Spatial Modelling in River Networks' toolset (Theobald *et al.*, 2006; Peterson *et al.*, 2007). These matrices and predictor variables were computed from the Terrain Analysis Using Digital Elevation Models network, and MLE was used to derive the parameter estimates.

Model selections were based on a combined Akaike information criterion and stepwise approach. The Akaike information criterion was estimated to select the best set of fixed effects for each model. A stepwise technique was also used to remove any insignificant parameters, resulting in the most parsimonious model with the fewest parameters. Because the model is used to predict thermal conditions throughout the network, we used cross-validation to compare the predictive power of each model. We split our data into a training set used for preliminary model fits ($n=345$) and a validation set composed of temperature observations that were spatially isolated from the other sites ($n=26$). In earlier spatial analyses of stream temperature data, distances of 5–15 km were reported between spatially independent sites (Isaak *et al.*, 2010), so we exceeded this distance when randomly selecting observations for the

spatial validation. We also chose no more than one site per sub-watershed division.

Predictive accuracy was assessed by calculating the squared Pearson correlation coefficient (r^2) between predicted and observed values. Leave-one-out cross-validation was also performed for each model to calculate the root mean square prediction error. After the best model was identified via cross-validation and r^2 , the model was refit to the pooled set of observations from the training and validation sets. The non-spatial and spatial hierarchical models were fit in SAS version 9.2 (PROC MIXED, Cary, North Carolina, USA), whereas the spatial flow-routed model was estimated in R version 2.11.

Stream temperature predictions and habitat simulations

As an exercise to show model application, we simulated a baseline current condition model and three future climate warming scenarios to assess bull trout habitat vulnerability to climate change. The parameter estimates for the spatial hierarchical model (pooled data) were used to predict stream temperatures for 22-m grid cells along the stream network. The mean August air temperature for the study period (1998–2010) was used as the air temperature parameter for the baseline model, which represents current thermal habitat conditions within the network. These predictions were then used to estimate the thermal regimes of currently designated FMO and SR bull trout habitats. Current designation of critical bull trout habitat was defined by the Montana Fish, Wildlife, & Parks and is included as part of the US Fish and Wildlife Service (2010) federal register that designates critical habitat for threatened bull trout in the conterminous USA. Current delineations of FMO and SR habitat distributions were digitized onto the FRB stream network (Figure 1), with the mainstems of the forks providing FMO habitat and the tributary reaches providing SR habitat. Stream temperature predictions were then used to identify thermal ranges preferred for each habitat type and to quantify potential impacts to current habitat distributions caused by warming air and stream temperatures.

To represent the wide range of potential climate responses due to general circulation model (GCM) and emissions scenario uncertainties, we selected three future climate warming scenarios used in the habitat simulations. These scenarios were based on results from the Intergovernmental Panel on Climate Change Fourth Assessment Report climate simulations conducted by the Center for Science in the Earth System's (CSES, 2010) group at the University of Washington. Potential air temperature increases were predicted over the next 100 years for the Pacific Northwest region. We used expected air temperature change output from three GCMs to represent a range of potential climate responses: ECHAM5 (Roeckner, 2003), Institut Pierre Simon Laplace (IPSL) CM4 (Marti, 2006), and the Goddard Institute for

Space Studies (GISS) ER (Schmidt, 2006). The ECHAM5 (Max-Planck-Institute fur Meteorologie) and IPSL CM4 models were simulated for the Special Report on Emissions Scenario (SRES) A2. The 'A2 scenario' is defined as a very heterogeneous world with continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other scenarios (Solomon *et al.*, 2007). The GISS ER model was simulated for the SRES B1, which is defined as a convergent world with a global population that peaks in mid-century and declines thereafter (Solomon *et al.*, 2007). Results from the Intergovernmental Panel on Climate Change Fourth Assessment Report simulations suggest that the ECHAM5 SRES A2 GCM is a 'conservative' climate scenario, the IPSL CM4 A2 GCM is the 'highest warming scenario', and the GISS ER B1 GCM is the 'lowest warming scenario', best representing a range of plausible warming scenarios (CSES, 2010).

We used all three climate scenarios to predict distributional changes in thermally suitable bull trout habitats from predicted increases in average August air temperatures from 2000 to 2059 and 2099. Specifically, the ECHAM5 21st-century climate simulations predict that summer air temperatures will rise by 3.3°C from 2000 to 2059 and by 5.5°C from 2000 to 2099. The IPSL CM4 simulations predict that summer air temperatures will rise by 3.6°C between 2000 and 2059 and by 6.1°C between 2000 and 2099. Lastly, the GISS ER simulations predict that summer air temperatures will rise by 1.2°C between 2000 and 2059 and by 2.0°C between 2000 and 2099. We applied these predicted air temperature increases to our baseline model parameter (18.1°C) to predict stream temperatures for the currently designated bull trout habitats in the FRB. These predictions were then used to assess potential loss of thermally suitable habitat caused by increasing air and stream temperatures. Potential habitat loss was defined as exceedance of the thermal regimes and thresholds estimated under the baseline model.

RESULTS

Stream temperature model

We found that the spatial models performed significantly better than the nonspatial model. Because we wanted a model that best predicted stream temperatures across the FRB, we chose the spatial model that performed best with the validation data ($r^2=0.48$) and retained good predictive ability with the training data ($r^2=0.82$; Table 1). This model included predictors for elevation, lake effect, air temperature, and slope output from the spatial hierarchical model. Scatter plots of the predicted and observed values are shown for all three models, supporting the improved

Table I. Parameter estimates and summary statistics for nonspatial and spatial models estimated

Model type	b (SE)	t	p -value	Pooled data ($n = 371$)		Training data ($n = 345$)		Validation data ($n = 26$)	
				r^2	RMSPE	r^2	RMSPE	r^2	RMSPE
Spatial hierarchical model									
Intercept	7.45 (1.85)	4.02	<0.0001	0.82	1.27	0.82	1.28	0.48	1.90
Elevation	-0.0053 (0.00068)	-8.33	<0.0001						
Lake effect	3.09 (0.37)	8.38	<0.0001						
Air temperature	0.58 (0.094)	6.19	<0.0001						
Slope	-0.084 (0.023)	-3.62	0.0003						
Spatial flow-routed model									
Intercept	11.46 (1.53)	7.49	<0.0001	0.82	1.27	0.69	2.34	0.48	1.90
Elevation	-0.0056 (0.00089)	-6.26	<0.0001						
Lake effect	3.42 (0.48)	7.12	<0.0001						
Air temperature	0.40 (0.05)	7.70	<0.0001						
Slope	-0.10 (0.031)	-3.31	0.00102						
Nonspatial model									
Intercept	135.15 (30.31)	4.46	<0.0001	0.49	2.11	0.49	2.13	0.56	1.88
Elevation	-0.0067 (0.0006)	-11.22	<0.0001						
Lake effect	2.54 (0.32)	7.97	<0.0001						
Air temperature	0.54 (0.12)	4.34	<0.0001						
Slope	-0.11 (0.024)	-4.27	<0.0001						
Longitude	-0.00003 (7.39E-6)	-3.67	0.0003						
Latitude	-0.00002 (4.75E-6)	-4.14	<0.0001						

RMSPE, root mean square prediction error.

accuracy of the spatial models relative to the nonspatial model (Figure 2). In addition, we contrasted the spatial autocorrelation of model residuals for the nonspatial and spatial models and observed that the spatial models significantly reduced the spatial autocorrelation by explaining portions of the spatial variance (Jones, 2012).

A significant warming effect of stream temperatures was observed for all sites downstream of lakes in our study ($p < 0.0001$). As a result, the smallest lake was used as a lower lake size threshold (area $> 0.32 \text{ km}^2$), and digitized network segments downstream of these lakes was considered as being lake influenced. The spatial hierarchical model estimated this warming effect at $+3.09^\circ\text{C}$ for sites downstream of lakes (Table 1).

Habitat simulations

Our baseline model estimated 97.9% of August FMO habitat at water temperatures less than 14°C . More interestingly, 95% of FMO habitat was predicted at $>10^\circ\text{C}$ and $<14^\circ\text{C}$ (Figure 3a). Similarly, for SR habitat, the baseline model estimated 95.8% of August SR habitat at water temperatures less than 13°C and 94% of the habitat at $>8^\circ\text{C}$ and $<13^\circ\text{C}$ (Figure 3b). These predictions were used to establish optimal habitat conditions and thermal thresholds used in the climate simulations. For FMO habitat, we used 14°C (97.9% of predictions) as the upper thermal threshold of

preferred habitat conditions during the month of August. For SR, that thermal threshold was 13°C (95.8%). Results from the conservative climate simulations (ECHAM5 2059 and 2099) show the thermal conditions of current SR and FMO habitat increasing significantly as air temperatures warm (Figure 3).

We evaluated the potential loss of critical bull trout habitats (exceedance of the thermal thresholds established in the baseline model) for a range of climate warming scenarios (Figure 4). Stream temperature simulations predicted a potential 24.2–61.3% loss of FMO bull trout habitat for air temperature increases associated with the 2059 simulations. In addition, a 37.7–91.2% loss of current FMO habitat was estimated for air temperature increases associated with the 2099 simulations (Table 2). Similarly, the stream temperature model predicted a 3.8–42.7% loss of current SR habitat for the 2059 simulations and a 13.1–81.7% loss of current SR habitat for the 2099 simulations (Table 2).

DISCUSSION

Stream temperature model

Spatially explicit studies of habitat relationships, as described in our study, help us to understand the localized variation in suitable habitat and can prove to be an important tool for

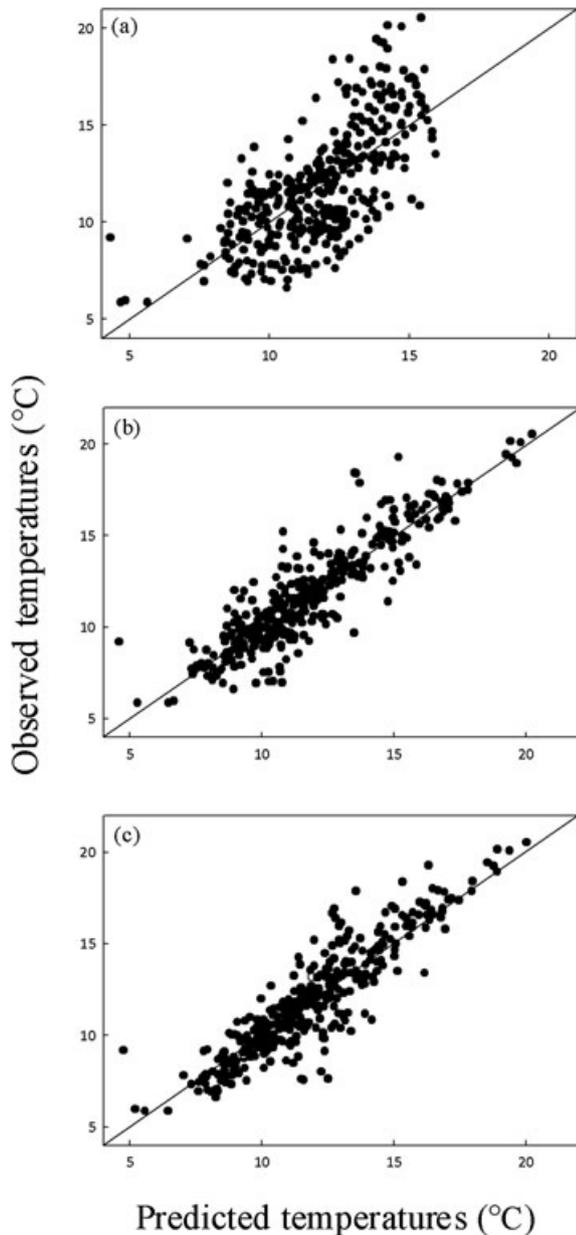


Figure 2. Scatter plots of predicted versus observed August stream temperatures from the nonspatial (a), spatial flow-routed (b), and spatial hierarchical models (c). The black line is a 1:1 regression line, illustrating probable bias associated with each model.

predicting climatic impacts to habitats and biota in complex riverscapes. Currently, this stream temperature model is being used in collaboration efforts to forecast the effects of climate warming on the spread of hybridization between native and nonnative trout (Muhlfeld *et al.*, 2009), to predict the distribution of aquatic invasive species (Schweiger *et al.*, 2011), and to assess the genetic and demographic vulnerability of native fisheries (Landguth *et al.*, 2012),

further illustrating the importance of models like these in understanding how changes or trends in habitats and populations have occurred, as well as assessing species vulnerability and habitats at risk.

Eighty-two per cent of the variation in stream temperatures within the FRB was explained by the spatial hierarchical model parameterized in this case study. We found that the spatial hierarchical model explained the variation throughout the network as well as that of the spatial flow-routed model. Flow-routed models can have extremely good predictive power but can also require large quantities of flow-connected temperature records, depending on the size of the study area. For this large-scale study, we found that more flow-connected temperature records are needed to improve the predictive power above that of the spatial hierarchical model. This is especially reflected in the cross-validation results where the loss of flow-connected records in the training data resulted in a significant decrease in model performance (Table 1). We also found that the DEM-derived networks can have a large degree of error propagation caused by resolution and terrain complexity. Errors such as these are noticeable once evaluated against ground-truthed data or networks such as the NHD. Our results illustrate how a more simplistic approach, using a spatial hierarchical model with readily available data, can be used with existing stream networks to reduce spatial autocorrelation and accurately predict stream temperatures.

Bull trout thermal preferences

Physiological functions of bull trout, such as growth rate and food consumption, increase with increasing temperature to some critical threshold, after which the rates rapidly decline (Selong *et al.*, 2001). The most sensitive physiological function is growth rate, which is critical to all physiological responses. In a laboratory study, Selong *et al.* (2001) reported that 95% of the peak feeding and growth temperatures for bull trout occurred in the range of 10.9–15.4°C and decreased significantly above and below this range. More specifically, peak consumption was predicted at 13.3°C, and estimates decreased significantly below 10.3°C and above 16.3°C. In addition, studies in the natural environment show that bull trout occurrence is typically rare where maximum temperatures exceed 15°C (Fralely and Shepard, 1989; Rieman *et al.*, 1997; Rieman and Chandler, 1999). Our results support the optimal thermal ranges for feeding and growth, where peak thermal preferences during the month of August for FMO were predicted at >10°C and <14°C, decreased significantly below 10°C (3.6%), and ceased to exist above 16°C. These results further support the very narrow thermal preferences of this threatened species.

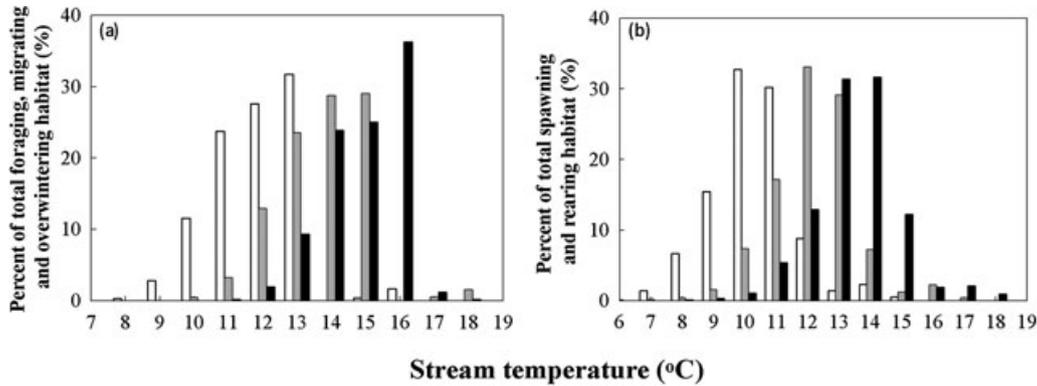


Figure 3. Stream temperature predictions for current bull trout foraging, migrating, and overwintering habitat (a) and spawning and rearing habitat conditions (b). White bars represent predictions from the baseline model, grey bars represent predictions from the ECHAM5 2059 climate simulation, and black bars represent habitat conditions for the 2099 simulation.

Bull trout habitat loss

Simulation of climatic conditions is possible with the model described herein and could be used to identify where future changes may occur and where they are likely to exceed important thermal thresholds. Results of this study substantiate other literature that suggest that a warming climate will likely fragment stream and river habitats, putting many extant populations at high risk of further declines and possible extirpation (Rieman *et al.*, 2007; Williams *et al.*, 2009; Wenger *et al.*, 2011). Rieman *et al.* (2007) modelled the relationships between the lower elevation limits of bull trout and mean annual temperature to explore the implications of climate warming in the interior Columbia River Basin. The predicted changes suggest that warming temperatures could result in the loss of 18–92% of thermally suitable natal habitat area and 27–99% of large (>10 000 ha) habitat patches. However, the authors suggest that more detailed models

(fine-scale) are needed to prioritize conservation management at local scales. Isaak *et al.* (2010) employed spatially explicit, spatial statistical models to retrospectively estimate the effects of climate change and wildfire on stream temperatures and critical bull trout habitats in the Boise River Basin in central Idaho. The models estimated that from 1993 to 2006 bull trout lost 11–20% of headwater spawning and rearing streams. We found that a conservative climate warming scenario (ECHAM5), as defined by the CSES, estimated a potential 58% loss of FMO habitat and a 36% loss of SR habitat if air temperatures were to rise by 3.28°C. Correspondingly, our model predicted a potential 86% loss of currently designated FMO habitat and a 76% loss of SR habitats if air temperature increases by 5.5°C.

How bull trout may respond to climate changes

Our results suggest that future climate warming may result in a substantial decrease in thermally suitable bull trout habitat during the month of August. Use of FMO habitat as migratory corridors is essential to maintaining genetic and life history diversity for bull trout, whereas cold headwater spawning and rearing streams are vital for survival and reproduction (Rieman *et al.*, 2006). Model simulations show that lower portions of the FRB drainage (FMO habitat) may become thermally unsuitable and upstream habitats (SR) could become isolated because of increasing thermal fragmentation during the summer months (Figure 5). How the FRB bull trout populations will respond to these changes is uncertain; however, climate warming may shift the habitat distributions both spatially and temporally. Spatial shifts may be caused by decreases in food availability, increased competition with species, thermal refugia, and prey availability. Temporal shifts may occur in timing of life history transitions, such as spawning and feeding migrations (Rieman and Isaak, 2010). Model results presented here

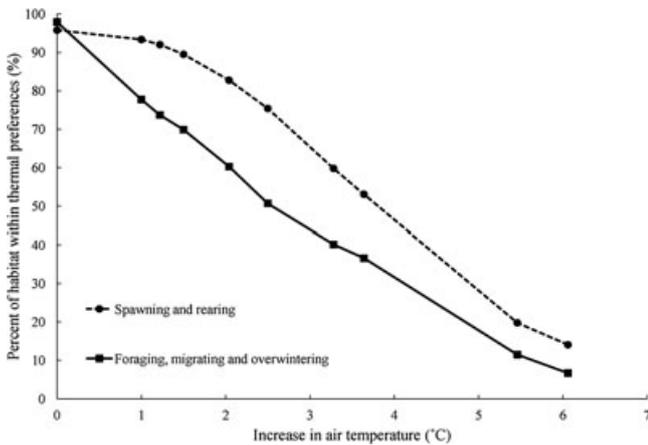


Figure 4. Per cent of thermally suitable habitat predicted under various climate simulations. Climate simulations are defined by increasing air temperature.

Table II. Per cent of thermally suitable bull trout habitat and potential habitat loss predicted for each general circulation model climate scenario

Model description	Change in air temperature (°C)		Baseline	Per cent of habitat within thermal regime (%)		Deviation from baseline model (%)	
	2059	2099		2059	2099	2059	2099
Spawning and rearing (<13°C)							
GISS ER B1 GCM	+1.2	+2.0	95.8	92.0	82.8	-3.8	-13.0
ECHAM A2 GCM	+3.3	+5.5		59.8	19.8	-36.0	-76.0
IPSL CM4 A2 GCM	+3.6	+6.1		53.1	14.1	-42.7	-81.7
Foraging, migrating, and overwintering (<14°C)							
GISS ER B1 GCM	+1.2	+2.0	97.9	73.7	60.3	-24.2	-37.7
ECHAM A2 GCM	+3.3	+5.5		40.2	11.5	-57.8	-86.4
IPSL CM4 A2 GCM	+3.6	+6.1		36.6	6.7	-61.3	-91.2

GISS, Goddard Institute for Space Studies; IPSL, Institut Pierre Simon Laplace. Climate simulations are defined by corresponding air temperature increases.

could be used by managers in the FRB to inform decisions, such as use of a selective withdrawal and thermal control device on the Hungry Horse Dam, to prevent water temperatures from exceeding the temperature ranges preferred by bull trout for FMO in the lower reaches above Flathead

Lake (Figure 1). Accordingly, use of a fine-scale spatially explicit model to focus efforts on populations of concern, weigh vulnerability, and identify critical habitats will be an important tool in prioritizing conservation and management actions.

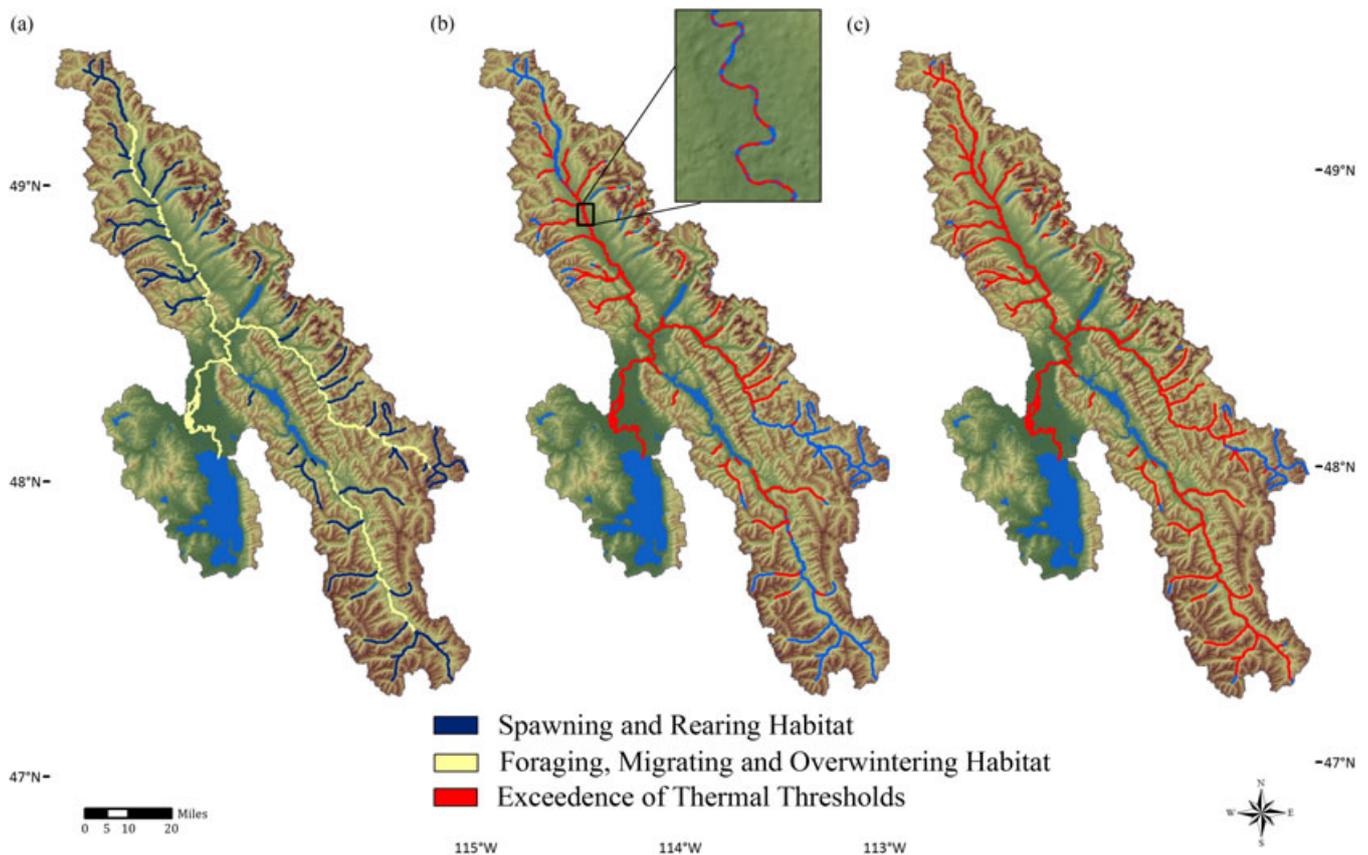


Figure 5. Critical bull trout habitat distributions throughout the Flathead River Basin (a) and potential loss and fragmentation of thermally suitable habitat associated with ECHAM5 2059 (b) and 2099 (c) climate warming simulations. This figure is available in colour online at wileyonlinelibrary.com/journal/rra.

CONCLUSIONS

Comprehensive assessments of regional and local climate trends and trajectories will be integral for assessing potential impacts of climate warming in aquatic ecosystems (Pederson *et al.*, 2010). The single largest source of uncertainty is simply how much and how fast the Earth's climate will warm. Additional inconclusiveness exists about how large-scale changes in the atmosphere will be realized at regional and local scales. Understanding the interactions between climate shifts and existing stressors is important to identifying which species and ecosystems are likely to be affected by projected changes and why they are likely to be vulnerable. Vulnerability assessments using models such as the one here can be used to identify populations and habitats at risk, develop monitoring and evaluation programmes, inform future research and conservation needs, and develop conservation delivery options (e.g. adaptation strategies) in response to or in anticipation of climatic changes and other important cumulative stressors (e.g. habitat loss and invasive species).

Climate adaptation planning requires assessing the vulnerability of aquatic species, habitats, and ecosystems to future climate change scenarios. Accordingly, management options are identified and implemented to reduce sensitivity and exposure to existing and future stressors, thereby increasing resiliency and adaptive capacity across large spatial scales. In some cases, climate change may result in the expansion of suitable habitats, but for many coldwater-dependent species, these changes are likely to restrict and further reduce suitable habitats to headwaters streams, resulting in highly fragmented habitat networks (Isaak *et al.*, 2010; Rieman *et al.*, 2007). For migratory salmonids, such as bull trout in the FRB, conserving the connectivity, size, and extent of existing high-quality habitats will be an important conservation strategy, as well as helping to guide restoration opportunities to mitigate the effects of climate change.

ACKNOWLEDGEMENTS

We thank the National Climate Change and Wildlife Science Center of the US Geological Survey and the Great Northern Landscape Conservation Cooperative (GNLCC) for funding this research, as well as Jack Stanford and Brian Marotz for reviews of the previous drafts. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. This research was conducted in accordance with the Animal Welfare Act and its subsequent amendments.

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