USING A SPATIALLY EXPLICIT STREAM TEMPERATURE MODEL TO ASSESS POTENTIAL EFFECTS OF CLIMATE WARMING ON BULL TROUT HABITATS

by

Leslie Anne Jones

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Sciences in Land Resources and Environmental Science

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Bozeman, Montana

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March 2012
ACKNOWLEDGEMENTS

Funding was provided by the USGS Global Climate Change Program and the Great Northern Landscape Conservation Cooperative (GNLCC). I sincerely thank Dr. Clint Muhlfeld for the opportunity to work on this project and be a part of his aquatics team in Glacier National Park. I thank my major professor Dr. Lucy Marshall and co-advisor Dr. Brian McGlynn for their amazing guidance and instruction. Lucy is an exceptional mentor and I feel especially grateful for her flexibility in working remotely with me and our many hours of video chatting. I also want to thank Vin, Joe and Brady for endless hours of field reconnaissance and data logging. Most of all I thank my husband for his unwavering support over the years. I could not have done it without his encouragement.
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CHAPTER ONE

INTRODUCTION TO THESIS

Bull Trout in the Flathead River Basin

The Transboundary Flathead Watershed is part of the Crown of the Continent Ecosystem (CCE) and encompasses Glacier National Park, west of the Continental Divide (Figure 1.1). The Flathead Watershed originates in the Rocky Mountains of northwestern Montana (USA) and southeastern British Columbia (Canada) and includes the North Fork, Middle Fork, South Fork, mainstem Flathead rivers, and Flathead Lake. It is referred to as the "headwaters of North America" because the rare Triple Divide Peak in Glacier National Park is the only location in North America that drains water to three oceans: the Pacific, Arctic, and Atlantic (Curtis 2010). The Flathead River Basin has pristine water quality and supports ecologically diverse aquatic life (Hauer and Muhlfeld 2010). Because of its exceptional water quality and inter-connected river and lake system, it has been recognized as a refuge for native fish and aquatic species, including the bull trout (*Salvelinus confluentus*), which is listed as a threatened species under the Endangered Species Act (USFWS 1998).

Although the potential impacts of climate change are now widely recognized (IPCC 2007; Hansen et al. 2005; Durgerov and Meier 2005; Church and White 2006), considerable concern remains about full-scale impacts and how they will be realized at the local scale (Mujumdar and Ghosh 2008). Aquatic ecosystems have been increasingly threatened by global climate change (Poff et al. 2002). Regional warming trends in the
western United States indicate that mountainous ecosystems, such as the CCE, will observe changes in seasonal patterns of precipitation and runoff (Poff et al. 2002; Luce and Holden 2009; Stewart et al. 2005), warmer drier summers (Westerling et al. 2007), reduced summer flows, and increasing water temperatures (Westerling et al. 2007; Pederson et al. 2010). Climatic and hydrological changes can have direct effects on species composition, geographic distribution, ecological interactions, and ecosystem productivity which may interfere with the reproduction and sustainability of many species (Poff et al. 2002; Kaushal et al. 2010). Consequently, understanding how habitats are likely to change and how species may respond to climate warming is critical for developing conservation and management strategies at both local and global scales.

Water temperatures vary spatially and temporally, playing an important role in determining the distribution of many aquatic species (Dunham et al. 2003). This is particularly true for salmonid species (i.e., trout, char, and salmon), which are strongly influenced by changes in temperature, flow, and physical habitat conditions (Williams et al. 2009; Haak et al. 2010). Salmonids are exceptionally vulnerable to a warmer drier climate and can be an important indicator of ecosystem health in the face of climate change (Pederson et al. 2010). Bull trout, in particular, have a limited tolerance to thermal fluctuations in streams and rivers because their body temperature is dependent on the temperature of their surrounding habitat (Rieman et al. 2007). Accordingly, changes in ecosystem processes, combined with species tolerances to thermal regimes, have prompted interest in assessing the thermal sensitivity of aquatic species, possible impacts
to native habitat ranges, and risks to genetic diversity and population persistence (Wenger et al. 2011a; Wenger et al. 2011b).

To study natural systems and understand their functional processes, we need to identify relevant spatial and temporal scales at which they occur. Spatial patterns can be considered an indicator of changes occurring inside of ecosystems and quantifying these ecological patterns requires an iterative approach that, at each iteration, provides some insights about the underlying ecological processes (Fortin and Dale 2005). Spatially explicit landscape models increase our ability to accurately model complex landscapes and quantify changes in ecological patterns over space and time (Dunning et al. 1995). These models can range from empirical to process-based, static to dynamic, simple to complex, and low to high spatial and temporal resolutions (Costanza and Voinov 2004). The simulation of spatially explicit models to assess potential changes in species' habitat distributions has become valuable in the study of population dynamics and the overall assessment of ecosystem functions (Dunning et al. 1995). These models can be used as an important tool to aid in the decision-making process of management strategies in response to both regional and global change processes (Turner et al. 1995).

**Study Objectives and Methods**

As the Flathead River Basin (FRB) undergoes change caused by a warming climate, scientific studies evaluating habitats and species most susceptible to the impacts of climate change will become increasingly important. Here, we seek to identify biologically meaningful physiological thresholds of bull trout in the FRB by modeling
stream temperature and using the model as a tool to predict thermal changes caused by a warming climate. Specifically, we developed a spatially explicit stream temperature model to quantify and explore the potential range of thermal warming effects, using the case study of bull trout populations in the FRB. Our objectives were to: i) compare spatial and non-spatial statistical models used to predict stream temperatures throughout the FRB; ii) apply a spatially explicit model to estimate thermal thresholds for *spawning and rearing* and *foraging migrating and overwintering* bull trout habitats; iii) predict thermal changes under a range of future climate scenarios; and iv) investigate model behavior and inform future research decisions. Development of spatially explicit models, such as the one described here, will create an ideal opportunity to build collaborative relationships through research so that scientists can further understand how climate change will impact freshwater aquatic ecosystems. In particular, model results may be used to perform ecosystem assessments; inform future research needs; and develop conservation plans with broad applications that reach beyond the Flathead system.

**Thesis Organization**

This thesis includes an introduction (Chapter One), a comprehensive explication of the project (Chapter Two), a thesis Summary and Conclusion (Chapter Three) and Appendix. Chapter Two is a manuscript in review in *Canadian Journal of Fisheries and Aquatic Sciences*. This chapter includes a literature review and complete summary of project objectives, methodologies, results and discussion of our findings. Chapter Three is an overview of the projects major findings and a reflection on future model
development efforts. An inclusive assessment of model performance can be found in the Appendix.
Figure 1.1. The Flathead Watershed is part of the Crown of the Continent Ecosystem (CCE) and encompasses Glacier National Park, west of the Continental Divide.
Literature Cited


IPCC. 2007. Climate change 2007: The physical science basis. Contribution of working group i to the fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. Cambridge, United Kingdom and New York, NY, USA.


CHAPTER TWO
USING A SPATIALLY EXPLICIT STREAM TEMPERATURE MODEL
TO ASSESS POTENTIAL EFFECTS OF CLIMATE WARMING
ON BULL TROUT HABITATS

Contributions of Authors and Co-Authors

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Author: Leslie A. Jones
Contributions: Assembled database, analyzed data, and wrote the manuscript.

Co-author: Clint Muhlfeld
Contributions: Obtained funding, assisted with study design, discussed the results and implications and edited the manuscript at all stages.

Co-author: Lucy Marshall
Contributions: Assisted with model development, discussed the results and implications and edited the manuscript at all stages.

Co-author: Brian McGlynn
Contributions: Discussed the results and implications and edited the manuscript.

Co-author: Jeffrey Kershner
Contributions: Obtained funding, discussed the results and edited the manuscript.
Using a Spatially Explicit Stream Temperature Model to Assess Potential Effects of Climate Warming on Bull Trout Habitats

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Key words: stream temperature; spatial statistical model; climate change; bull trout; Salvelinus confluentus; thermal habitat; habitat loss; Flathead River drainage, Montana, USA, British Columbia, Canada.
Abstract

Understanding how species and habitats are likely to respond to climate warming is critical in developing effective conservation and management strategies for freshwater systems. We compiled stream temperature records from 199 sites in the Flathead River Basin (FRB), Montana, USA, and parameterized non-spatial and spatial statistical models to predict temperatures at a 22 meter resolution along the stream network. A spatially explicit hierarchical model was used to predict summer thermal regimes for bull trout spawning and rearing (<13°C) and foraging, migrating and overwintering (<14°C) habitats. Model results indicate that stream temperatures were strongly related to geomorphic (elevation and slope), climatic (air temperature), and lake warming covariates. These covariates explained 82% of the variation in August mean stream temperatures. Climate change simulations were used to quantify potential exceedance of thermal regimes associated with increasing air temperature trends. Analysis of a conservative climate change simulation (ECHAM5 A2 GCM) suggests that approximately 47% of suitable bull trout summer habitat could be thermally exceeded by 2059 and 83% could become thermally unsuitable by 2099. Model predictions suggest that a warming climate will result in warmer water temperatures and a significant loss of thermally suitable summer bull trout habitats. These results illustrate the importance of using fine-scale spatially explicit stream temperature models to explain the local variations of thermal regimes in guiding conservation and management actions.
Introduction

The Earth’s climate is warming at an accelerating pace due to anthropogenic emissions of greenhouse gases (Hansen et al. 2005; IPCC 2007; Christensen et al. 2007). Over the past century, global warming has increased the planet’s mean annual air temperatures by 0.6°C (IPCC 2007) and temperatures are predicted to rise by as much as 6°C by 2100 (Christensen et al. 2007; Trenberth et al. 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 thermally sensitive aquatic species (Parmesan and Yohe 2003; Walther et al. 2002; Root et al. 2003). Understanding how habitats are likely to change and how species may respond to climate warming is, therefore, critical for conservation and management strategies designed to enhance resiliency and adaptation at local and global scales.

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; IPCC 2007; Meehl et al. 2007), resulting in extensive loss of glaciers and snowpack (Hall and Fagre 2003; Pederson et al. 2011; Hamlet et al. 2005; Mote et al. 2005). Warming trends and regional downscaled climate model simulations indicate that mountainous ecosystems will likely continue to trend toward earlier and more rapid snowmelt in the spring (Luce and Holden 2009; Stewart et al. 2005; Rauscher et al. 2008), increased winter precipitation and flooding (Hamlet and Lettenmaier 2007), warmer drier summers (Westerling et al. 2007), increased late summer drought (Westerling et al. 2007; Pederson
et al. 2010), and reduced summer flows. These changes in the hydrological cycle are contributing to warmer water temperatures 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; Williams 2010; Haak et al. 2010; Wenger et al. 2011b; Kaushal et al. 2010).

Water temperatures vary spatially and temporally, playing an important role in determining the distribution of many stream-dwelling species (Dunham et al. 2003). Both non-spatial and spatial modeling 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 (Caissie 2006; Webb and Nobilis 1997; Mackey and Berrie 1991). These models are generally used for short temporal scales (e.g., one yr.) 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; Caissie 2006; Jourdonnais et al. 1992) using a combination of predictor variables in addition to air temperature (Caissie 2006). More recently, advances in geostatistical modeling of stream systems have greatly improved temperature predictability by using fine-scale spatial data to explain variation across heterogeneous river networks. ‘Fine-scale’ models can incorporate predictors defined at local or small scales (e.g., 30 m or the stream reach scale) as compared to coarse generalizations often made from broader scale studies (e.g., watershed scale). These fine-
scale models can be used to capture and quantify high-resolution spatial patterns and make predictions at small scales, which can provide additional information about ecosystem structure and function (Inoue et al. 2009). Spatial hierarchical modeling is an example of a geostatistical model that may be applied at a fine scale, allowing for multiple stream temperature and response relationships to be estimated simultaneously. Hierarchical models describe the relationships between variables at different levels and account for how observations can be related in groups within a hierarchical framework (Singer 1998; Nezlek and Zyzniewski 1998; McMahon and Diez 2007). Recently, more sophisticated geostatistical models based on hydrologic relationships have been developed (Ver Hoef and Peterson 2010; Peterson and Ver Hoef 2010). These models use a combination of "flow-connected" distances, "flow-unconnected" distances and euclidean distances to estimate the covariance components of the spatial relationships between observations.

Climate trends and projections have prompted interest in assessing the thermal sensitivity of coldwater aquatic species in western North America (Wenger et al. 2011a; Wenger et al. 2011b). 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 (Williams et al. 2009; Haak et al. 2010; Isaak et al. 2011; Wegner et al. 2011). Salmonids are especially vulnerable to climate-induced warming in freshwater ecosystems because: (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 characteristically narrow tolerances for thermal fluctuation in cold waters (Williams et al. 2009; Isaak et al. 2010; Keleher and Rahel 1996; McCullough et al. 2009; Dunham et al. 2003). 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 and Isaak 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 primarily due to habitat degradation and fragmentation, invasive species, and climate change.

Fine-scale assessments of species’ sensitivities to climate warming are needed to guide conservation and management actions. The goal of this study was to gain a better understanding of climate change impacts on stream temperatures and critical salmonid habitats. Here, we develop a fine-scale stream temperature model to quantify and explore the potential range of thermal warming effects, using the case study of migratory bull trout populations in the Flathead River Basin (FRB), USA and Canada. Our objectives were to: \( i \) compare spatial and non-spatial model performance to predict stream temperatures throughout the FRB; \( ii \) apply a spatially explicit, fine-scale model to estimate thermal thresholds for migratory bull trout habitats; and \( iii \) predict thermal changes under a range of future climate scenarios.
Materials and Methods

Study Area

The upper FRB originates in the Rocky Mountains of northwestern Montana (USA) and southeastern British Columbia, 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 2.1). The climate is influenced by moist, Pacific maritime air masses, which circulate inland from the Pacific Ocean producing moderate wet weather, while dry, cold continental air masses circulate southerly from Canada bringing cold winters and hot dry summers (Curtis 2010). Average temperatures vary with topography throughout the FRB; however, mean daily winter temperatures can range from -28°C to 0°C (Curtis 2010). Spring and early summer are partly cloudy with rain interspersed with occasionally dry, warm days and average daily summer temperatures range from 21°C to 30°C (Curtis 2010). The intermountain regions of western Montana not only have a large climatological difference in cool and warm season temperatures, but are also prone to large and rapid variations in temperature on extremely short time scales (Pederson et al. 2010). This is particularly true in the late summer season, when temperatures can swing 25°C over the course of a day. The watershed is dominated by snow-melt runoff in the spring, producing high flows from April to June and base flows in August, September and early fall.

Climatological data trends indicate that the FRB is warming. A recent study analyzed over 100 years of daily and monthly temperature data collected in western
Montana to assess long-term changes in seasonal temperature averages and daily extremes (Pederson et al. 2010). The daily temperature time series revealed that extremely cold days (≤-17.8°C) terminated on average 20-d earlier and declined in frequency, whereas extremely hot days (≥32°C) showed a three-fold increase in frequency and a 24-d increase in duration during which they occurred. Western Montana has thus far experienced a +1.33°C (1900 – 2006) rise in annual average temperatures, which is 1.8 times greater than the +0.74°C (1900 – 2005) estimated rise in global temperatures (IPCC 2007). More specifically, average summer air temperatures measured at two NOAA COOP weather stations within the Flathead drainage (at Kalispell and West Glacier) show increasing trends, with summer mean temperatures (1978 - 2007) increasing at the rate of 0.41°C/decade and weekly maximum summer temperatures (1978 - 2007) advancing at 0.76 °C/decade. Mean August discharge rates measured at two USGS flow gages in the Flathead (at Glacier Rim [North Fork] and West Glacier [Middle Fork]) between the years 1950-2008 show significant declines in stream discharge and increasing frequency of low flow events (Leppi et al. 2011; Rood et al. 2005; Rood et al. 2008).

Bull Trout in the Flathead River Basin

The FRB is one of the most intact, biodiverse aquatic ecosystems in North America (Hauer and Muhlfeld 2010), and is a range-wide stronghold for the threatened bull trout (Rieman et al. 1997). Bull trout display migratory life histories (e.g., fluvial and adfluvial) in the upper Flathead River and Lake system (Fraley and Shepard 1989), requiring large, ecologically diverse and connected coldwater habitats to complete their
life cycle (e.g., spawning, rearing, foraging, migrating and overwintering), which is
critical to the long-term persistence of the species (Fraley and Shepard 1989; Rieman and
McIntyre 1995; Muhlfeld and Marotz 2005). Bull trout in the FRB commence spawning
migrations (up to 250 km) from May through July, and spawn in second to fourth-order
streams primarily during September and October. Spawning occurs when water
temperatures fall below 9°C in low-gradient tributary reaches that contain clean gravel,
groundwater influence, and cover (Fraley and Shepard 1989; Muhlfeld et al. 2006; Baxter
and Hauer 2000). Juveniles rear in natal spawning and rearing streams for 1 to 4 years,
and then make complex movements (primarily during high spring flows) to the mainstem
rivers or lakes (e.g., subadult phase) where they grow to maturity (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 which provide the full expression of life history required to maintain genetic
diversity and dispersal among populations (Rieman and Allendorf 2001).

Stream Temperature Database

We compiled a database of stream temperature measurements from previous
studies conducted by the U.S. Geological Survey (USGS), U.S. Forest Service, Montana
Fish, Wildlife & Parks, National Parks Service, University of Montana Flathead Lake
Biological Station, as well as current on-going monitoring efforts in the FRB (Figure
2.1). Stream temperatures were measured with digital thermographs (Hobo models; Onset
Computer Corporation, Pocasset, Massachusetts, USA; accuracy = ±0.2°C) that recorded
temperatures 12-24 times daily at bi-hourly or hourly intervals, respectively. 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, behavior, and habitat selection (Selong et al. 2001). Our stream temperature data show that the warmest water temperatures of the year occur during the month of August. Moreover, bull trout migrate to natal spawning streams in the headwater reaches of the FRB during spring and summer months. For these reasons, we focused our stream temperature study on the month of August.

We used August stream temperature records from sites within the FRB for the years of 1998 - 2010. The resultant database consisted of 266,083 data points from 199 unique sites (Figure 2.1). The data were then summarized by three temperature metrics defined as the mean stream temperature for 1-31 August, the maximum stream temperature for this period, and the maximum weekly maximum temperature (MWMT), which is the highest seven-day moving average of maximum daily temperatures. The mean temperature provides an overall indication of thermal suitability and optimal conditions for growth; the maximum provides an indicator of the conditions associated with seasonal extremes; and the MWMT provides an indicator of the duration of seasonal extremes (Isaak et al. 2010).

Stream Networks

We applied two different terrain analysis methods to develop stream networks for the FRB. Both methods are currently used in hydrologic applications (Isaak et al. 2010; Peterson and Ver Hoef 2010) and were employed to compare usability and performance.
The first method utilized two sources of data, including the National Hydrography Dataset from the USGS (NHD 2011) and the National Hydro Network data layers from the Canadian Council on Geomatics (NHN 2011). Due to the transboundary nature of the FRB (USA and Canada), these two source datasets were co-registered across the USA - Canada border to create one continuous stream network. The second stream network used in this study was derived using TauDEM (Terrain Analysis Using Digital Elevation Models) software (Tarboton 2008), which is an ArcGIS tool that extracts hydrologic information from the topographic details represented in a digital elevation model (DEM) and uses that information to delineate stream networks. We used Advanced Spaceborne Thermal Emission and Reflection (ASTER) elevation datasets (National Aeronautics and Space Administration; 22 m cell size) to derive this network using TauDEM software. ASTER datasets were selected as the base DEM for this project because it seamlessly covered both the USA and Canada portions of the FRB. Data co-registered across the border (ASTER and NHD/NHN network) was provided by the Crown Managers Partnership.

**Predictor Variables**

We investigated the influence of geomorphic and climatic covariates (i.e., predictor variables) on stream temperatures and associated variability. Climatic and hydrologic predictors, such as air temperature and stream flow, are known to have a significant 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 simple geomorphic predictor variables (elevation, slope, and aspect), two geographic predictors (latitude and longitude), as well as 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 are used to explain temporal variation in the data. Lastly, we 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) is an important environmental variable that contributes to variability in climatic factors such as air temperatures and snow melt patterns. 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). Therefore, an area-based model was used in ArcGIS to compute solar radiation, calculating surface elevation, orientation (slope and aspect) and shadow effects from the ASTER DEM (22 m grid cells; Dubayah and Rich 1995).

Air temperatures have a similar affect on stream temperatures through heat exchange near the surface of the water (Mote 2006). Mean daily air temperatures for the study period were summarized from three National Climatic Data Center (NCDC) climate stations in the FRB (West Glacier, Hungry Horse and Kalispell Airport; Figure 2.1). Mean daily air temperatures were averaged across all three stations to calculate mean monthly air temperature and MWMT air temperature for the month of August for
each year of our study period. The maximum August temperatures were extracted for
each station individually and were used as possible predictors in the model runs.

As discharge rates decrease, streams become more susceptible to thermal
warming (Hockey et al. 1982; Caissie 2006). Decreased discharge rates, such as those
observed during the month of August, cause streams to have a lower thermal capacity.
Mean daily discharges were obtained from two USGS gauging stations in the basin
(North Fork Flathead- 12355500 and Middle Fork Flathead-12358500; Figure 2.1) and
were averaged to calculate mean August discharges for each year of the study period. The
same summary metrics that were applied to air temperatures were also applied to stream
temperatures (e.g., mean, maximum, and MWMT).

Lakes can have a considerable effect on downstream water temperatures. Lakes
absorb solar radiation resulting in dramatically warmer temperatures at lake outflows
(Garrett 2010; Hieber et al. 2002). We created a categorical predictor variable, lake effect,
which represents lake warming influences on stream temperatures downstream of lakes.
Based on 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 threshold. In order to make temperature predictions throughout the network, stream
segments downstream of lakes within this threshold were considered lake affected and
were digitized as such downstream to the confluence of the next highest stream order.

Slope, aspect and elevation predictors were derived from the ASTER DEM (22
m) using ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands,
California, USA). Predictor values were determined for all segments of the stream
network 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 Metrics

We evaluated mean, maximum and MWMT stream temperature metrics to assess predictor and response relationships within the network. The Akaike Information Criterion (AIC; Akaike 1974) was estimated to select the best set of fixed effects for each temperature metric model. A stepwise technique was then used to remove any insignificant parameters from the model, resulting in the best fit model for each metric. To compare temperature metric predictability, we used a spatial hierarchical model (described below) to explain the spatial dependence of the data, using sub-watershed hydrologic unit code 6 (HUC6; USGS 2011) as the random grouping effect. The temperature metric with the best fit to the observed data was then used to make statistical model comparisons.

Stream Temperature Models

We compared three statistical models used to predict stream temperatures across the FRB stream networks: a fixed effect generalized linear regression model (GLM); a mixed effect generalized linear regression model (GLMM); and a flow-routed stream network model. The generalized linear regression model was defined as (1),

\[ y = X\beta + \epsilon \]

where \( y \) represents a vector of observed data, \( X \) is a vector of explanatory variables, \( \beta \) is a vector of model parameters and \( \epsilon \) is the error term. The GLM 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 GLM 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; Isaak and Hubert 2004). Therefore, we chose a spatial hierarchical model (nested model) or mixed effect generalized linear regression model (GLMM) which uses HUC6 as a random effect to account for potential spatial correlation (i.e., longitudinal connectivity, flow volume, and flow direction) inherent to stream networks (Singer 1998; Deschenes and Rodriguez 2007). This hierarchical mixed model (2),

\[
y_i \sim N(X_i \beta, \sigma^2_y)
\]

has a variance component approach, which allows multiple covariance matrices to be combined to provide a robust and flexible covariance structure. In this case, multiple covariance matrices (\( \sigma^2_y \)) for each HUC6 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 individual temperature locations used for the GLMM runs, where MLE was used to derive the parameter estimates. Additionally, an unconditional means model was used to test the statistical significance of the grouping effect.
The second spatial model used in the model comparisons was a spatially explicit flow-routed network model, which has been gaining popularity in the aquatics community (Isaak et al. 2010; Peterson and Ver Hoef 2010; Gardner and McGlynn 2009). 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. Networks derived from DEMs are routinely used in hydrological applications and were applied in this case using a TauDEM network (Tarboton 2008). Similar to the hierarchical model, the covariance structure for the flow-routed model (3),

\[ y = X\beta + \sigma_{EUC}z_{EUC} + \sigma_{TD}z_{TD} + \sigma_{TU}z_{TU} + \sigma_{NUG}z_{NUG} \]

is also based on a variance component approach (\(\sigma_{EUC}, \sigma_{TD}, \sigma_{TU}, \text{ and } \sigma_{NUG}\)) and uses random effects based on hydrologic distances (\(z_{EUC}, z_{TD}, z_{TU}, \text{ and } z_{NUG}\)). The covariance components are euclidean distance (EUC), "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 any two "flow-unconnected" sites (Peterson and Ver Hoef 2010; Isaak et al. 2010). To implement the model, hydrologic distances and spatial weights matrices were calculated in ArcGIS using the 'Functional Linkage of Water basins and Streams' (FLoWS) toolset and the 'Spatial Modeling in River Networks' toolset (Peterson et al. 2007; Theobald et al. 2006). These matrices were computed from the TauDEM network. Maximum likelihood estimation was used to derive the parameter estimates.
Stream Temperature Predictions and Habitat Simulations

As an exercise to show model applicability, we simulated a baseline current conditions model and three future climate change scenarios. After choosing the statistical model with the best fit to mean August stream temperatures, parameter estimates were used to predict stream temperatures for 22 m grid cells along the NHD/NHN stream network. A mean August air temperature for the study period (1998-2010) was used as the air temperature parameter in the baseline predictions to characterize average thermal conditions during our study period. The baseline simulation represents current thermal habitat conditions within the network, which was then used to estimate current thermal regimes in foraging, migrating and overwintering (FMO) and spawning and rearing (SR) bull trout habitats. Foraging, migrating, and overwintering habitat are defined (USFWS 1998) as relatively large streams and mainstem rivers, including lakes or reservoirs, estuaries, and nearshore environments, where subadult and adult migratory bull trout forage, migrate, mature or overwinter. This habitat is typically downstream from spawning and rearing habitat and contains all the physical elements to meet criteria for overwintering, spawning migration, and subadult and adult rearing needs. Spawning and rearing habitat are defined as stream reaches and associated watershed areas that provide all habitat components necessary for spawning and juvenile rearing for a local bull trout population. Basin-wide redd counts were conducted by natural resource agencies to delineate current locations of SR habitats in the FRB (USWFS 1998; C. Muhlfeld, unpublished data; Deleray et al. 1999). Current delineations of FMO and SR habitat distributions were then digitized onto the FRB stream network using ArcGIS (Figure
2.1), where stream temperature predictions were used to create a baseline scenario of thermal ranges preferred for each habitat type. The thermal habitat regimes predicted from the baseline simulation were then used to quantify habitat impacts due to temperature changes resulting from three future climate projections.

Three future climate scenarios were used in the habitat simulations and were based on predicted air temperatures for the next 100 years in the Pacific Northwest (PNW) Region. For this model application, we used expected air temperature changes output from three GCMs, ECHAM5 (ECHAM5 2011), IPSL CM4 (IPSL 2011) and the GISS ER (NASA 2011) to represent a range of potential climate responses due to General Circulation Model (GCM) uncertainties. The ECHAM5 (Max-Planck-Institute fur Meteorologie) and IPSL CM4 (Institut Pierre Simon Laplace) 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 (IPCC 2007). The GISS ER (Goddard Institute for Space Studies) 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 (IPCC 2007). All GCM simulations were prepared for the Fourth Intergovernmental Panel on Climate Change (IPCC) Assessment by the Center for Science in the Earth System (CSES) at the University of Washington. Results from the IPCC Assessment Report 4 (AR4) simulations suggest that the ECHAM5 SRES A2 GCM is a "middle of the road" climate scenario, the IPSL CM4 A2 GCM is the "highest warming scenario" and the GISS ER B1 GCM is the "lowest
warming scenario”. All models were downscaled to daily 1/8-degree data for the Pacific Northwest (PNW) region (CSES 2010).

We used all three climate scenarios to predict distributional changes in thermally suitable bull trout habitats based on predicted changes in average August air temperatures from 2000 to year 2059 and year 2099. Specifically, the ECHAM5 21st century climate simulations predict that summer air temperatures will rise 3.28°C from 2000 to 2059 and 5.46°C from 2000 to 2099 in the PNW. The IPSL CM4 simulations predict that summer air temperatures will rise 3.6°C between the years 2000 and 2059 and 6.06°C between the years 2000 and 2099. Lastly, the GISS ER simulations predict that summer air temperatures will rise 1.22°C between the year 2000 and 2059 and 2.0°C between the year 2000 and 2099. We applied these predicted changes to our baseline air temperature (18.11°C) to predict stream temperatures throughout the FRB under varying climate change scenarios. Stream temperature predictions from the climate change scenarios were then used to assess potential summer habitat loss caused by increasing air temperatures. Potential habitat loss was defined as bull trout habitat (SR and FMO) where stream temperature predictions exceed the thermal regimes and thresholds estimated under the baseline scenario.

Results

Stream Temperature Model

The best model fits were obtained for each temperature metric model, with the mean temperature model resulting in the highest $r^2$ value ($r^2>0.82$) of all three metrics
Furthermore, all predictors in the mean model (i.e., fixed effects: elevation, lake effect, August mean air temperature and slope) were statistically significant ($p<0.0003$; Table 2.2). The mean metric also characterizes optimal conditions for growth and thermal suitability of bull trout, therefore, the mean temperature metric was used in subsequent analyses to compare non-spatial and spatial model performances.

Using the mean temperature metric, we found that the spatial models performed significantly better than the non-spatial equivalent (Table 2.2), as indicated by the higher $r^2$ values. Scatter plots of the predicted and observed values are shown for all three models supporting the improved accuracy of the spatial models relative to the non-spatial model (Figure 2.2). Although the GLMM model shows a slight potential bias towards underestimating temperatures in the warmest streams and overestimating temperatures in the coldest streams, the model predicts equivalently to that of the flow-routed model (Figure 2.2). To substantiate the grouping effect used in the spatial hierarchical model, we ran an unconditional means model (intercept only) using HUC6 as the random effect and found a statistically significant group effect ($p<0.0001$). The results showed that 66% of the total variation in stream temperatures existed between groups (HUC6) and 34% existed within these watershed delineations, justifying the requisite for the random grouping effect to account for the spatial dependence. By adding this random effect we explain 50% of the between HUC6 variance and 33% of the within HUC6 variance. In addition, we contrasted the spatial autocorrelation of model residuals for the non-spatial and spatial models and observed that the spatial models significantly reduced the spatial
autocorrelation by explaining portions of the spatial variance. Parameter estimates for the non-spatial and spatial mean temperature models are summarized in Table 2.2.

We observed a significant warming effect of stream temperatures for all sites downstream of lakes in our study ($p<0.0001$). As a result, we used the smallest lake as a lower lake threshold (area > 0.32 km$^2$) and digitized network segments downstream of these lakes as being lake-influenced. The lake effect influencing these downstream segments culminates in a +3.09°C increase in stream temperatures as compared to stream segments that are not lake–influenced (Table 2.2).

Habitat Simulations

Our baseline (current conditions) model estimates that 97.93% of August FMO habitat exists at water temperatures less than 14°C and 83% of the predicted temperatures ranged from 11°C to 14°C (Figure 2.3a). Thermal estimates of current FMO habitat decreased significantly below 10°C (3.59%) and ceased to exist above 16°C. Baseline stream temperature predictions suggest that 95.82% of August spawning and rearing habitat exists below 13°C and 78.37% of the estimated temperatures are between 9°C and 12°C (Figure 2.3b). Thermal predictions of current SR habitat decreased significantly below 8°C (2.85%) and above 12°C (2.79%). As a result of the baseline predictions, climate simulations used 14°C as a critical thermal threshold for FMO conditions and 13°C as a critical thermal threshold for SR conditions during the month of August. Stream temperature conditions corresponding to existing FMO and SR habitat increased significantly under the ECHAM5 2059 and 2099 climate simulations, exceeding the thermal thresholds predicted under the baseline model (Figure 2.3).
We evaluated the potential loss of habitat (temperatures above thermal thresholds) for a range of climate change scenarios (Figure 2.4). Stream temperature simulations predicted a 24.19 - 61.30% loss of FMO bull trout habitat for air temperature increases associated with the 2059 simulations (Table 2.3). In addition, a 37.65 - 91.21% loss of current FMO habitat was estimated for air temperature increases associated with the 2099 simulations. Similarly, the stream temperature model predicted a 3.78 - 42.75% loss of current SR habitat for the 2059 simulations and a 13.05 - 81.73% loss of current SR habitat for the 2099 simulations.

Discussion

Stream Temperature Models

Similar to most ecological data, stream networks are hierarchically structured where each level of the stream habitat hierarchy corresponds to a specific spatial scale, from drainages to valley segments to stream reaches to channel bedform units (pool-riffle) (Frissell et al. 1986; Fausch et al. 2002). For this reason, multiple types of spatial autocorrelation may be present and may vary depending on the spatial scale of the data (Inoue et al. 2009). Because of the wide range of spatial variation associated with environmental characteristics, broad-scale studies at the watershed scale or larger often do not capture the detail and heterogeneity that exists at the stream reach scale. Accordingly, ecologists are moving towards using fine-scale, spatially explicit modeling approaches to understand habitat relationships for management of aquatic ecosystems (Dunham et al. 2003; Gollock et al. 2009; Baxter et al. 1999). Fine-scale studies of
habitat relationships, as described in our study, help to understand the localized variation in biological processes and can prove to be an important tool for predicting potential future warming effects on habitats and biota in complex riverscapes.

Eighty-two percent 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 and flow-routed model equally explained the temperature variation throughout the network. Flow-routed models can have extremely good predictive power, but typically require large quantities of flow connected temperature records, depending on the size of the study area. Sample size and data availability can be a challenge in most ecological studies making models like these a difficult alternative. DEM derived networks can also have a large degree of error propagation caused by DEM resolution and terrain complexity. Errors such as these are noticeable once evaluated against ground-truthed data or networks such as the NHD, which can complicate management efforts and field reconnaissance (Hengl et al. 2010). In addition, the time and cost required to build DEM derived networks and flow-routed models is very demanding. Our results illustrate how spatial hierarchical models can be used with existing stream networks to accurately predict stream temperatures and emphasizes the time/cost tradeoffs for different modeling approaches.

**Bull Trout Thermal Preferences**

Salmonids are directly affected by water temperature changes associated with climate change because of their ectothermic physiologies and movements constrained to stream networks. Typically, physiological functions, such as growth, food consumption,
and activity, 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 (Saffel and Scarnecchia 1995; Fraley and Shepard 1989; Goetz 1997; Rieman et al. 1997; Rieman and Chandler 1999; Haas 2001). Our results support the optimal thermal ranges for feeding and growth, where peak thermal preferences (83%) during the month of August for FMO were predicted at temperatures >11°C and <14°C.

**Bull Trout Habitat Loss**

Our results support other studies that suggest that a warming climate will likely fragment stream and river habitats during the summer months, possibly putting many extant populations at high risk of further declines and possible extirpation (Poff et al. 2002; Wenger et al. 2011b; Rahel 1997; Rieman and Isaak 2007; Williams et al. 2009). Rieman et al. (2007) modeled the relationships between the lower elevation limits of bull trout and mean annual temperature to explore the implications of climate warming across the species’ potential range in the interior Columbia River Basin of the USA. 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 over the predicted range of bull trout. However, the authors suggest that more detailed models (fine-scale) are needed to prioritize conservation management at local scales. Isaak et al. (2010) employed fine-scale, 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 southern margin of the species’ range. The models estimated that from 1993 to 2006 bull trout lost 11 - 20% of headwater spawning and rearing streams.

We found that approximately 47% of suitable bull trout summer habitat could be thermally exceeded by 2059 and 83% could become thermally unsuitable by 2099 (Figure 2.5). Our models estimate that approximately 43% (348 km) of optimal FMO habitat (>11°C and <14°C) could become thermally unsuitable if air temperatures increase 3.28°C and 72% (575 km) may become thermally unsuitable if air temperatures were to increase 5.46°C. Correspondingly, our model predicts that 52% (499 km) of optimal SR habitat (>9°C and <12°C) could be lost if air temperatures were to increase 3.28°C and that 72% (686 km) could be lost if air temperature increase 5.46°C. It is important to note that the uncertainty of these model simulations and potential future impacts is not fully addressed within, emphasizing the intent of this study to illustrate quantitative methods in simulating and predicting potential impacts to aquatic species distributions.
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 summer months. Use of FMO habitat as migratory corridors is essential to maintaining genetic and life history diversity for bull trout, while cold headwater spawning and rearing streams are vital for survival and reproduction, providing thermal refugia from nonnative trout invasions (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 due to increasing thermal fragmentation during the summer months. How the FRB bull trout populations will respond and adapt to the warming of migratory corridors, feeding areas and overwintering habitats is uncertain.

Potential climate warming in stream environments may shift habitat distributions of bull trout both spatially and temporally. Although our study focuses on simulating potential loss of existing habitat associated with increasing air temperatures, future studies will explore possible spatial shifts in habitat distributions caused by altered climatic and hydrologic relationships. For example, bull trout habitat distributions could shift spatially due to decreases in food availability, increased competition with species, thermal refugia, prey availability and could shift temporally in timing of life history transitions (Rieman and Isaak 2010). Projected temperature changes may also shift habitat distributions to higher latitudes and elevations, exacerbating native and nonnative species interactions (Jonsson and Jonsson 2009). In addition, increasing frequency of rain on snow events during the winter months could have considerable effects on scouring of
tributary gravels (Tonina et al. 2008). Scouring events caused by higher flows during the winter months may have severe impacts on embryonic survival of bull trout, further exacerbating the effects of climate change on bull trout populations.

Model Development to Assess Ecosystem Impacts

Increasing air temperatures and changes in the hydrological cycle have been correlated with increasing stream temperatures, which have direct effects on aquatic ecosystems and ecological organization at a variety of spatial scales (Petersen and Kitchell 2001; Isaak et al. 2010; Morrison et al. 2002; Bartholow 2005; Kaushal et al. 2010). As warming air and water temperatures are accompanied by hydrologic changes such as magnitude, frequency, duration, timing, and rate of change in discharge patterns (Jager et al. 1999; Henderson et al. 2000), populations may become more susceptible to local extinctions (Haak et al. 2010). Watersheds may experience a decrease in aquifer recharge, making less water available for groundwater inputs to streams, which may intensify the warming effects on aquatic ecosystems. At present, efforts are being made to incorporate a distributed hydrologic model to assess the impacts of hydrology on stream temperatures within our network. In addition, future models will integrate a geomorphic model and/or geologic variable to understand how spawning and rearing habitats that are characterized by bounded alluvial reaches with hyporheic exchange may or may not be affected by warming temperatures (Baxter and Hauer 2000). Existing efforts also include deployment of an air temperature sensor network that will be used to quantify air temperature variation at a finer scale throughout the FRB. Currently, this stream temperature model is being used in collaboration projects to assess how climate
warming will influence the spread of introgressive 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. 2011), further illustrating the importance of models like these in evaluating and predicting aquatic ecosystem impacts.

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, and how individual species or ecosystem processes will integrate and respond to these changes. The models developed here and integration of other stream network models will improve the ability to characterize ecosystem processes by reducing much of the imprecision associated with larger-scale models.

As climate change continues, managers will need to understand how predicted changes may affect the conservation efforts of many species, how current threats will evolve with a changing climate, and what new stresses might emerge as a result. Developing conservation strategies that incorporate scientific studies, such as this, will be important for managing populations and ecological systems and processes (Haak et al. 2010). Spatially explicit forecasts of habitat conditions, species distributions, genetic
diversity, and probabilities of persistence are possible using fine-scale spatial models (Nelitz et al. 2009; Wenger et al. 2010; Landguth et al. 2011). We believe that models such as these will be important to explaining local variations of habitat relationships and predicting vulnerability of critical habitat niches and resources at risk, which will help direct conservation planning and management efforts at scales relevant to local population persistence. For 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 a changing climate and invasive species and to ensure the evolutionary legacy of this species.

Acknowledgments

We would like to thank Montana Fish Wildlife & Parks, U.S. Forest Service, National Park Service, Crown Managers Partnership, and The University of Montana Flathead Lake Biological Station for data collaboration. We thank the USGS Global Climate Change Program and the Great Northern Landscape Conservation Cooperative (GNLCC) for funding this research. 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.
Figure 2.1. The Flathead River Basin in Northwest Montana, USA and southeast British Columbia, Canada. Stream temperatures were measured at 199 unique 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.
Figure 2.2. Scatter plots of predicted vs. observed stream temperatures from the non-spatial (a) and spatial models (b, c). The black line is a 1:1 regression line, illustrating probable bias associated with each model.
Figure 2.3. Stream temperature predictions for current *foraging, migrating and overwintering* habitat (a) and *spawning and rearing* habitat conditions (b). Yellow bars represent current habitat conditions predicted by the model, orange bars represent predicted habitat conditions for 2059 and red bars represent predicted habitat conditions for 2099.

Figure 2.4. Percent of thermally suitable habitat predicted under various climate simulations. Climate simulations are defined by increasing air temperatures.
Figure 2.5. Current bull trout habitat distribution throughout the Flathead River Basin (a) and potential loss of habitat (exceedance of thermal thresholds) associated with 2059 (b) and 2099 (c) climate simulations.
Table 2.1. Statistically significant parameters and associated $r^2$ values for fitted temperature metric models.

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<th>Model Type</th>
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<th>p-value</th>
<th>$r^2$</th>
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<td>0.47</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.0075 (0.00057)</td>
<td>-13.07</td>
<td>&lt; 0.0001</td>
<td></td>
</tr>
<tr>
<td>Lake Effect</td>
<td>2.23 (0.32)</td>
<td>7.03</td>
<td>&lt; 0.0001</td>
<td></td>
</tr>
<tr>
<td>Air Temperature</td>
<td>0.63 (0.13)</td>
<td>5.00</td>
<td>&lt; 0.0001</td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>-0.11 (0.025)</td>
<td>-4.28</td>
<td>&lt; 0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.2. Parameter estimates and summary statistics for non-spatial and spatial models estimated.
<table>
<thead>
<tr>
<th>Model Description</th>
<th>Change in Air Temperature</th>
<th>Percent of Habitat within Thermal Preference (%)</th>
<th>Deviation from Baseline Conditions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2059</td>
<td>2099</td>
<td>Baseline</td>
</tr>
<tr>
<td>Spawning and Rearing Current Conditions (&lt;= 13°C)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GISS ER B1 GCM</td>
<td>+1.22</td>
<td>+2.04</td>
<td>95.82</td>
</tr>
<tr>
<td>ECHAM A2 GCM</td>
<td>+3.28</td>
<td>+5.46</td>
<td></td>
</tr>
<tr>
<td>IPSL CM4 A2 GCM</td>
<td>+3.64</td>
<td>+6.06</td>
<td></td>
</tr>
<tr>
<td>Foraging, Migrating and Overwintering Current Conditions (&lt;= 14°C)</td>
<td></td>
<td></td>
<td>97.92</td>
</tr>
<tr>
<td>GISS ER B1 GCM</td>
<td>+1.22</td>
<td>+2.04</td>
<td></td>
</tr>
<tr>
<td>ECHAM A2 GCM</td>
<td>+3.28</td>
<td>+5.46</td>
<td></td>
</tr>
<tr>
<td>IPSL CM4 A2 GCM</td>
<td>+3.64</td>
<td>+6.06</td>
<td></td>
</tr>
</tbody>
</table>

Note: GISS ER B1 GCM represents the lowest warming scenario. ECHAM5 A2 GCM represents the middle of the road warming scenario. IPSL CM4 A2 GCM represents the highest warming scenario.

Table 2.3. Percent of thermally suitable bull trout habitat and potential habitat loss predicted for each GCM climate simulation. Climate simulations are defined by corresponding air temperature increases.
Literature Cited


IPCC. 2007. Climate change 2007: The physical science basis. Contribution of working group i to the fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. Cambridge, United Kingdom and New York, NY, USA.


Rieman, B. E. and Isaak, D. J. 2010. Climate change, aquatic ecosystems and fishes in the Rocky Mountain west: Implications and alternatives for management. USDA Forest Service, Rocky Mountain Research Station, GTR-RMRS-250, Fort Collins, CO.


CHAPTER THREE

SUMMARY AND CONCLUSION

Bull Trout in the Flathead Watershed

Changes in ecosystem processes caused by global warming may already be impacting aquatic systems in the Rocky Mountain region. The Crown of the Continent Ecosystem, for example, has lost 66% of its glacial and perennial snow and ice cover since 1900 (Fountain et al. 2007), significantly impacting base flows and stream temperatures during the hot, dry summers (Pederson et al. 2010). For cold-water dependent species, such as those found in the Flathead Watershed, regulation of thermal extremes is critical in controlling the distribution and abundance of invertebrates (Hauer et al. 1997) and fish (Dunham et al. 2003). Accordingly, scientific studies will be essential in better understanding the potential impacts of climate change and how they may affect thermal regimes of aquatic systems.

Bull trout in the Flathead Watershed are a migratory metapopulation, growing to maturity in the larger rivers and lakes and migrating upriver into natal headwater tributaries to spawn (Fraley and Shepard 1989). They require cold, connected and complex habitats for growth, survival, and population persistence. Bull trout have the lowest mean tolerance for high water temperatures of any North American salmonid (Selong et al. 2001); therefore, thermal fluctuations in stream and river temperatures may have severe impacts on habitat distributions and species perseverance. In our efforts to
better understand climate change impacts on stream temperatures and critical bull trout habitats, we developed a spatially explicit stream temperature model to quantify the potential range of thermal warming effects. Specifically, we compared spatial and non-spatial model performance, estimated biologically meaningful physiological thresholds, and predicted probable thermal changes under various climate scenarios.

**Model Results**

Our results support the conclusion that the spatial statistical models performed significantly better than the non-spatial equivalent when simulating the spatio-temporal variability of stream temperature in large stream networks. More specifically, our spatial hierarchical stream temperature model with fixed effects elevation, lake effect, mean air temperature, and slope, combined with a sub-watershed grouping as the mixed effect explained 82% of the variation in stream temperatures throughout the Flathead River Basin (FRB). Empirical semivariograms (Appendix A) show that the spatial hierarchical model significantly reduced the spatial autocorrelation between sites within our study as compared to non-spatial and flow-routed models. This suggests improved model predictions when spatial structure is included in model simulations.

One benefit of fine-scale stream temperature models, such as the one developed in this study, is the ability to characterize local variation across river networks. As part of our model assessments in Appendix A, we found that the model predicted better for 2nd, 3rd and 4th order streams, while correlation coefficients between predicted and observed were considerably lower for 5th and 6th order streams. We found that lake affected sites
were on average 3°C warmer than sites which are not lake affected. However, lake
affected sites higher than 1,300 meters in elevation and part of a chain of upper elevation
lakes were somewhat overestimated by the model. We also found local variations in
geology to be highly influential in terms of stream temperature. One site in the
headwaters of Logan Creek is significantly influenced by bedrock and we found that the
site was considerably underestimated. This site was on average 6°C warmer than another
site 435 meters away. From these assessments (Appendix A) we learn which aspects of
the system are most in need of further study, where more empirical data are needed and
we will in turn use this information as input to future model development and data
collection efforts.

Habitat Simulations

We evaluated model predictions at the current extent of bull trout *spawning and
rearing* (SR) and *foraging, migrating and overwintering* (FMO) habitats in the FRB and
found that optimal thermal regimes for SR habitat were <13°C, while optimal regimes for
FMO were <14°C. These predicted values were used to determine critical thermal
thresholds for bull trout in the FRB and conduct habitat simulations using projected
climate warming scenarios. The ECHAM5 2050 climate simulation predicted 59.8% of
SR habitat to be thermally suitable with lower and upper 90% prediction bounds of 96.3
and 8.7%. The same model predicted 40.2% of FMO habitat to be thermally suitable with
lower and upper 90% prediction bounds of 97.9 and 3.3%. Similarly, the ECHAM5 2090
model predicted 19.8% of SR and 11.5% of FMO habitat within the corresponding
thermal ranges with lower and upper limits (84.7 - 1.4%) and (63.0 - 0.2%), respectively. Bull trout in the Flathead Watershed have very narrow thermal preferences. More specifically, 83% of FMO habitat falls within a 3°C thermal range, while 78% of SR habitat falls within a 2°C range. In calculating the upper and lower limits of the 90% prediction bounds a ±2.08°C change in stream temperatures were applied to the model predictions of the climate simulations. This small thermal fluctuation results in a potential loss/gain of 78% of SR habitat, further supporting the sensitivity of bull trout thermal ranges. Therefore, it should be noted that the wide range in the upper and lower limits of the prediction bounds are directly influenced by bull trout's narrow range in thermal preferences.

Model simulations show that lower portions of the FRB drainage (FMO habitat) may become thermally unsuitable and upstream habitats (SR) could become isolated due to increasing thermal fragmentation during the summer months. Bull trout habitat distributions could shift spatially due to decreases in food availability, increased competition with species, thermal refugia, prey availability and could shift temporally in timing of life history transitions (Rieman and Isaak 2010). Projected temperature changes may also shift habitat distributions to higher latitudes and elevations, potentially exacerbating native and nonnative species interactions (Jonsson and Jonsson 2009).

**Future Model Development**

As aforementioned and discussed in the Appendix, there is a wide range of uncertainty associated with model simulations in our study. Future work will be aimed at
further model refinement and expansion to address this predictive uncertainty and improve model predictions. Specifically, future work will incorporate a distributed hydrologic model to assess the impacts of hydrology and better understand how changes in magnitude, frequency, duration, and timing will effect stream temperatures. We will also integrate a geomorphic model and/or geologic component to learn how spawning and rearing habitats may be impacted by hyporheic exchange and how changes in geology may effect stream temperatures. In addition, current efforts are underway to incorporate an air temperature sensor network that can be used to quantify air temperature variation at a finer scale throughout the FRB. We will also further investigate how lakes affect stream temperatures and how the potential loss of glacier and permanent ice fields impact aquatic systems in the Crown of the Continent Ecosystem.

As global warming continues, scientific studies with a multitude of perspectives are needed to anticipate impacts to regional and local resources. Due to the uncertainty of climate change and inconclusiveness about how large-scale changes in the atmosphere will be conceived locally, model simulations and future model development efforts can be used as a tool to quantify and explore potential changes to ecosystem process, habitat distributions and to assess species vulnerabilities. With this study and the development of future stream network models we will improve our understanding of aquatic systems and guide conservation efforts into the future.
Literature Cited


Rieman, B. E. and Isaak, D. J. 2010. Climate change, aquatic ecosystems and fishes in the Rocky Mountain west: Implications and alternatives for management. USDA Forest Service, Rocky Mountain Research Station, GTR-RMRS-250, Fort Collins, CO.

APPENDIX A

MODEL ASSESSMENT
Overview

The models developed as part of this research provide insights for understanding the stream temperature data collected within the Flathead River Basin. In addition to the model assessments made in Chapter 2, we used supplemental methods to further understand the performance of the spatial hierarchical model. Model assessment can highlight which aspects of the system are most in need of further study, and where more empirical data are most needed (Oreskes et al. 1994). The information gathered in this Appendix will be used as input to future model development and data collection efforts.

Model Uncertainty

Despite their usefulness, model projections have many sources of uncertainty including, the accuracy of model inputs, uncertainty of parameter values, and model bias. Residual variance calculated from the hierarchical model predictions was used to compute 90% prediction bounds for the ECHAM5 2050 and 2090 climate change simulations (Table A.1). The ECHAM5 2050 model predicts 59.8% of spawning and rearing (SR) habitat to be thermally suitable with lower and upper limits of 96.3 and 8.7%. The same model predicts 40.2% of foraging, migrating and overwintering (FMO) habitat to be thermally suitable with lower and upper bounds of 97.9 and 3.3% (Figure A.1). Similarly, the ECHAM5 2090 model predicts 19.8% of SR and 11.5% of FMO habitat within the corresponding thermal ranges with lower and upper limits (84.7 - 1.4%) and (63.0 - 0.2%), respectively (Figure A.2). In these simulations, model uncertainty varies with respect to the estimated preferred thermal ranges of SR and FMO.
habitat, which were predicted with the baseline model and directly affect habitat suitability and habitat loss predictions under the climate simulations. Bull trout in the Flathead Watershed have very narrow thermal preferences. More specifically, 83% of FMO habitat falls within a 3°C thermal range, while 78% of SR habitat falls within a 2°C range. In calculating the upper and lower limits of the 90% prediction bounds a ±2.08°C change in stream temperatures were applied to the model predictions of the climate simulations. This small thermal fluctuation results in a potential loss/gain of 78% of SR habitat, further supporting the sensitivity of bull trout thermal ranges. Therefore, it should be noted that the wide range in the upper and lower bounds of the predictions are directly influenced by bull trout's narrow range in thermal preferences.

Furthermore, according to Huth (2004), estimates based on downscaling of GCM outputs have different levels of uncertainty related to inter-model variability, inter-scenario uncertainty, parameter uncertainty and uncertainty regarding downscaling methodologies. These uncertainties are particularly acute in complex topographies where changes in climate may be amplified or attenuated by large variability in elevation and topography (IPCC 2001). Model projections will become more accurate as our understanding of key processes improve and supporting databases and collaboration efforts expand. As we look to the future, we will be able to refine model simulations for the latest climate scenarios and use these models as a tool for forecasting habitat conditions, species distributions, and probabilities of persistence.
Spatial and Temporal Assessments

Predicted versus observed stream temperature values were plotted to assess spatial and temporal performance of the hierarchical model. We aggregated the data based on sub-watershed Hydrologic Unit Code 4 divisions (HUC4) to evaluate how the model performed spatially (HUC 2011). This plot represents predictions attributed to each fork of the Flathead River (North Fork, South Fork, Middle Fork and Flathead Lake; Figure 2.1) within our study area (Figure A.3). Figures A.3 and A.4 show that selected sites within the North Fork and Middle Fork drainages of the Flathead River have the highest residual error, as compared to Flathead Lake and South Fork watersheds. In addition, sites with higher stream temperatures within the North Fork were underestimated by the model (Figure A.3). In stream systems draining glaciated terrain, such as the Flathead River, studies have indicated that valley geomorphology and the presence of bounded alluvial valley segments are influenced by reach-scale downwelling and upwelling (Stanford and Ward 1993; Baxter and Hauer 2000; Anderson 2002). Localized variation caused by hyporheic exchange may dominate some sites within our study. We hypothesize that characteristics such as these may contribute to high predictive error seen in some of the model results.

To examine the temporal performance of the model, the data were aggregated by year (Figure A.5). The warmest steam temperature in our dataset was observed during the year 2003, which also recorded the warmest mean August air temperature for our study period (20.16°C). A cluster of year 2002 predictions can be seen in the lower range of this plot, also representing the coolest mean August air temperature for our study period.
(16.12°C). A plot of model residuals aggregated by year supports that no temporal patterns were observed in the model fit (Figure A.6).

**Lake Effect Assessment**

To assess the model *lake effect* predictor we stratified the data based on this critical covariate (Figure A.7). In general, lake affected sites are repeatedly warmer than sites that are not lake affected. In this plot, we observe a cluster of lake affected sites that sustain cooler stream temperatures than the other lake affected sites. These sites are also somewhat overestimated by the model because they experience less of a warming effect than the other lake affected sites. After further examination, we found that the sites within this cluster are downstream of lakes over 1300 meters in elevation; sites that are found within a chain of upper elevation lakes. This cluster of points represents multiple years of observations from two sites that are above Bowman Lake and below Pocket Lake; as well as two sites that are above Quartz Lake and below Cerulean Lake. These sites are higher in elevation than most sites within our study area and are downstream of high alpine lakes. We investigated the influence of the *lake effect* predictor on upper elevation sites by testing for a *lake effect* on sites above 1300 meters in elevation. We found that the *lake effect* was still statistically significant, regardless of elevation ($p<0.0001$). We also tested for a *lake*elevation interaction, which was not significant ($p = 0.4208$). After examining lake affected sites that were underestimated by the model we found that many of these sites were in close proximity to lake outlets as compared to other lake affected sites. These observations support the idea that sites further downstream from lake outlets
observe a cooling effect caused by mixing of lower stream order tributaries (Mellina et al. 2002). Inquiries such as these will aid future efforts in better understanding lake effects, evaluating how lake size may play a role in the warming of stream temperatures and how temperatures decay with distance from lake outlets.

**Magnitude of Stream Order, Air Temperature and Discharge Rates**

Pearson correlation coefficients were used to examine whether the magnitude of stream order or ranges in air temperature and flow rates (low or high) contributed to model performance. We aggregated the data by stream order to evaluate possible bias associated with model predictions. Correlation coefficients were higher for 2nd, 3rd and 4th order streams (Table A.2), while 5th and 6th order stream coefficients were significantly lower. We did not find any patterns when assessing whether warmer summer years (air temperature) predicted better than cooler years (Table A.3). Similarly, no patterns were found when evaluating the magnitude of flow years (Table A.4).

**Semivariograms of Non-Spatial and Spatial Models**

Semivariograms are used to assess the nature and structure of spatial autocorrelation in observations at sample locations for the non-spatial generalized linear model (GLM), the spatial flow-routed model and the spatial hierarchical model. We used classical and robust estimates of semi-variance based on euclidean distances between sites to evaluate the variation in residual error with respect to distance between pairs of sampled locations. A robust semi-variance estimator is used to weaken the effect that
outliers may have on the semi-variance of that particular grouping (Cressie and Hawkins 1980). Empirical semivariograms for the non-spatial generalized linear model (GLM) residuals (Figures A.8) and spatial flow-routed model residuals (Figure A.9) indicate potential spatial correlation up to a lag of 4,000 meters. The stochastic nature of the semi-variance between groupings shows that the model has not resolved the total autocorrelation that exists between the pairs. The covariance estimated for the spatial flow-routed model is based on flow-routed distances rather than euclidean distances. Figure A.9 illustrates that spatial autocorrelation based on euclidean distance still exists for the flow-routed model. The empirical semivariogram for the spatial hierarchical model residuals shows stable (equivalent) semi-variance between groups (Figure A.10). This shows that the spatial hierarchical model significantly reduced the spatial autocorrelation between sites within our study as compared to the other two models. Moran's I also supports a significant decrease in spatial autocorrelation between the non-spatial GLM and spatial hierarchical model, where $I = 0.910$ and 0.558 for each model respectively (Moran 1950). The higher semi-variance in the first group is potentially caused by outliers due to the low number of observations in the grouping and significantly lower robust estimator.

Local Variation

The benefit of fine-scale models such as the one developed in this paper is the ability to characterize local variation in river networks. Figure A.11 illustrates local variation in the model predictions where fragmentation in the river system is caused by
variability in the warming of stream temperatures. Models such as these will be especially important for conservation efforts in identifying vulnerable habitat niches or areas of special concern. First order streams can be largely influenced by variation in geology, geomorphology, slope, aspect and many other predictors governed by geography. A site on McGee Creek (114° 2' 21.31"W and 48° 35' 54.66" N) is an example of a first order stream in our study of which the model was not able to capture local variations. Three consecutive years of predictions show a high residual error (Table A.5) as compared to the mean residual error of the model (1.039e-14) and associated standard deviation (1.27). Correspondingly, two upper elevation sites in the headwaters of Logan Creek demonstrate local variations not captured by the model. Upper and Lower Logan Creek sites are located at 2,120 and 2,056 meters in elevation, respectively, and are 435 meters apart. Our data show a significant difference in stream temperatures despite the proximity between sites (Figure A.12). The lower Logan Creek site is significantly influenced by bedrock, which may be impacting the groundwater system causing a significant warming effect within this small headwaters stream. As a result, lower Logan Creek was significantly underestimated by our model. Local variations such as these observed within our study support the need for characterizations of geologic formations and possible influences on stream temperature variation. Model assessments such as these described in the Appendix will prove to be invaluable when building future modeling efforts.
Figure A.1. Thermally suitable habitat predicted from ECHAM5 2050 climate simulations (b), as well as lower (a) and upper (c) 90% prediction bounds.
Figure A.2. Thermally suitable habitat predicted from ECHAM5 2090 climate simulations (b), as well as lower (a), and upper (c) 90% prediction bounds.
Figure A.3. Spatial hierarchical model predicted versus observed values aggregated by sub-watershed Hydrologic Unit Code 4 (HUC4).

Figure A.4. Sub-watershed Hydrologic Unit Code 4 (HUC 4) residuals calculated from the spatial hierarchical model results.
Figure A.5. Spatial hierarchical model predicted versus observed values aggregated by year.
Figure A.6. Residuals output from the spatial hierarchical model aggregated by year.

Figure A.7. Spatial hierarchical model predicted versus observed values aggregated by lake effect.
Figure A.8. Empirical semivariogram of the non-spatial generalized linear model (GLM) residuals based on euclidean distances between pairs of sampled locations.
Figure A.9. Empirical semivariogram of the spatial flow-routed model residuals based on euclidean distances between pairs of sampled locations.
Figure A.10. Empirical semivariogram of the spatial hierarchical model residuals based on euclidean distances between pairs of sampled locations.
Figure A.11. Local variation and fragmentation of river network caused by warming stream temperatures predicted from the climate model simulations.
Figure A.12. Upper and lower Logan Creek sites illustrate variability in stream temperatures caused by local variation in geologic features and the groundwater system.
Table A.1. Model uncertainty (90% prediction bounds) for ECHAM5 2050 and 2090 climate change simulations.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Percent of Thermally Suitable Habitat (%)</th>
<th>2059</th>
<th>2099</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spawning and Rearing (&lt; 13°C)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ECHAM5 GCM</td>
<td>59.8</td>
<td>19.8</td>
<td></td>
</tr>
<tr>
<td>90% Upper Bounds</td>
<td>96.3</td>
<td>84.7</td>
<td></td>
</tr>
<tr>
<td>90% Lower Bounds</td>
<td>8.7</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td><strong>Foraging, Migrating and Overwintering (&lt; 14°C)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ECHAM5 GCM</td>
<td>40.2</td>
<td>11.5</td>
<td></td>
</tr>
<tr>
<td>90% Upper Bounds</td>
<td>97.9</td>
<td>63.0</td>
<td></td>
</tr>
<tr>
<td>90% Lower Bounds</td>
<td>3.3</td>
<td>0.2</td>
<td></td>
</tr>
</tbody>
</table>

Table A.2. Pearson correlation coefficients of predicted versus observed stream temperature values from the spatial hierarchical model aggregated by stream order.

<table>
<thead>
<tr>
<th>Stream Order</th>
<th>Number of Observations</th>
<th>Correlation Coefficient</th>
<th>Mean Observed Temperature (°C)</th>
<th>Mean Predicted Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>57</td>
<td>0.78</td>
<td>10.5</td>
<td>11.0</td>
</tr>
<tr>
<td>2</td>
<td>121</td>
<td>0.85</td>
<td>10.5</td>
<td>10.7</td>
</tr>
<tr>
<td>3</td>
<td>128</td>
<td>0.90</td>
<td>12.2</td>
<td>12.0</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
<td>0.97</td>
<td>13.5</td>
<td>13.2</td>
</tr>
<tr>
<td>5</td>
<td>28</td>
<td>0.46</td>
<td>14.1</td>
<td>13.4</td>
</tr>
<tr>
<td>6</td>
<td>17</td>
<td>0.54</td>
<td>16.8</td>
<td>16.4</td>
</tr>
</tbody>
</table>
Table A.3. Pearson correlation coefficients of predicted versus observed stream temperature values from the spatial hierarchical model aggregated by annual summaries of mean August air temperatures.

<table>
<thead>
<tr>
<th>Number of Observations</th>
<th>Year</th>
<th>Correlation Coefficient</th>
<th>August Mean Air Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>1998</td>
<td>0.89</td>
<td>18.7</td>
</tr>
<tr>
<td>2</td>
<td>1999</td>
<td>NA</td>
<td>18.9</td>
</tr>
<tr>
<td>28</td>
<td>2000</td>
<td>0.92</td>
<td>18.0</td>
</tr>
<tr>
<td>13</td>
<td>2001</td>
<td>0.91</td>
<td>19.1</td>
</tr>
<tr>
<td>14</td>
<td>2002</td>
<td>0.97</td>
<td>16.1</td>
</tr>
<tr>
<td>24</td>
<td>2003</td>
<td>0.95</td>
<td>20.2</td>
</tr>
<tr>
<td>21</td>
<td>2004</td>
<td>0.93</td>
<td>18.3</td>
</tr>
<tr>
<td>35</td>
<td>2005</td>
<td>0.92</td>
<td>17.2</td>
</tr>
<tr>
<td>39</td>
<td>2006</td>
<td>0.95</td>
<td>17.6</td>
</tr>
<tr>
<td>38</td>
<td>2007</td>
<td>0.94</td>
<td>18.2</td>
</tr>
<tr>
<td>55</td>
<td>2008</td>
<td>0.83</td>
<td>18.4</td>
</tr>
<tr>
<td>51</td>
<td>2009</td>
<td>0.84</td>
<td>18.0</td>
</tr>
<tr>
<td>43</td>
<td>2010</td>
<td>0.85</td>
<td>16.7</td>
</tr>
</tbody>
</table>
Table A.4. Pearson correlation coefficients of predicted versus observed stream temperature values from the spatial hierarchical model aggregated by annual summaries of mean August flow rates.

<table>
<thead>
<tr>
<th>Number of Observations</th>
<th>Year</th>
<th>Correlation Coefficient</th>
<th>August Mean Discharge (cfs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>1998</td>
<td>0.89</td>
<td>1159.7</td>
</tr>
<tr>
<td>2</td>
<td>1999</td>
<td>N/A</td>
<td>1963.6</td>
</tr>
<tr>
<td>28</td>
<td>2000</td>
<td>0.92</td>
<td>1040.8</td>
</tr>
<tr>
<td>13</td>
<td>2001</td>
<td>0.91</td>
<td>746.1</td>
</tr>
<tr>
<td>14</td>
<td>2002</td>
<td>0.97</td>
<td>1360.9</td>
</tr>
<tr>
<td>24</td>
<td>2003</td>
<td>0.95</td>
<td>790.7</td>
</tr>
<tr>
<td>21</td>
<td>2004</td>
<td>0.93</td>
<td>1648.9</td>
</tr>
<tr>
<td>35</td>
<td>2005</td>
<td>0.92</td>
<td>877.2</td>
</tr>
<tr>
<td>39</td>
<td>2006</td>
<td>0.95</td>
<td>802.1</td>
</tr>
<tr>
<td>38</td>
<td>2007</td>
<td>0.94</td>
<td>739.9</td>
</tr>
<tr>
<td>55</td>
<td>2008</td>
<td>0.83</td>
<td>1399.7</td>
</tr>
<tr>
<td>51</td>
<td>2009</td>
<td>0.84</td>
<td>1339.9</td>
</tr>
<tr>
<td>43</td>
<td>2010</td>
<td>0.85</td>
<td>1217.4</td>
</tr>
</tbody>
</table>

Table A.5. Residual error associated with yearly predictions of first order stream temperatures from McGee Creek site.

<table>
<thead>
<tr>
<th>Year</th>
<th>Predicted Stream Temperature (°C)</th>
<th>Observed Stream Temperature (°C)</th>
<th>Residual Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>12.5</td>
<td>7.6</td>
<td>4.9</td>
</tr>
<tr>
<td>2009</td>
<td>12.2</td>
<td>8.0</td>
<td>4.2</td>
</tr>
<tr>
<td>2010</td>
<td>11.5</td>
<td>7.6</td>
<td>3.9</td>
</tr>
</tbody>
</table>
Literature Cited


LITERATURE CITED


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