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**PREDICTING CLIMATE-INDUCED IMPACTS ON SEASONAL STREAM
TEMPERATURES IN THE CROWN OF THE CONTINENT ECOSYSTEM**

By

LESLIE ANNE JONES

M.S. Land Resources and Environmental Science, Montana State University, Bozeman, Montana, 2012

B.S. Statistics, North Carolina State University, Raleigh, North Carolina, 1996

B.S. Environmental Science, North Carolina State University, Raleigh, North Carolina, 1996

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Approved by:

Scott Wittenberg, Dean of The Graduate School
Graduate School

Dr. Erin Landguth, Co-Chair
College of Forestry and Conservation

Dr. Clint Muhlfeld, Co-Chair
College of Forestry and Conservation

Dr. Lucy Marshall
School of Civil and Environmental Engineering
University of New South Wales, Australia

Dr. Ashley Ballantyne
College of Forestry and Conservation

Dr. John Kimball
College of Forestry and Conservation

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Predicting climate-induced impacts on seasonal stream temperatures in the Crown of the Continent

Ecosystem

Chairpersons: Dr. Erin Landguth and Dr. Clint Muhlfeld

Changes in seasonal climate patterns are altering thermal distributions of freshwater ecosystems worldwide. The Crown of the Continent Ecosystem is one of the most biologically diverse ecosystems in North America, spanning northwestern Montana, USA, Alberta and British Columbia, Canada. The fluvial landscape consists of pristine freshwater habitats that provide strongholds for many aquatic species. My dissertation work provides the first broad scale analysis of seasonal climate effects on spatiotemporal patterns of stream temperature in the Crown of the Continent, and a multi-scalar analysis of potential impacts to bull trout (*Salvelinius confluentus*) populations, the most stenothermic cold-water fish in the northern Rocky Mountains.

Seasonal stream temperature models were developed to predict monthly temperatures under current and future climate scenarios. Future climate simulations forecast increasing stream temperatures during spring, summer, and fall, with the largest absolute increases predicted for July, August, and September and the largest increases relative to historic temperatures predicted for April and November. Results portend a temporal shift in seasonal stream temperatures, including an earlier onset and extended duration of warm summer stream temperatures. Stream temperature warming was most pronounced in high-elevation montane and alpine streams, where glacial-fed streams were predicted to experience the largest magnitude (>50%) of change due to the loss of alpine glaciers.

Thermal riverscapes were used to assess spatiotemporal shifts in habitat distributions of bull trout. Models predicted thermal preferences for juvenile bull trout within tributary habitats during the summer months < 12°C, while preferred temperatures for sub-adult and adult bull trout within river habitats were < 15°C. Future stream temperature warming is likely to result in a contraction of thermally optimal habitats, suggesting a shift in the distributional range of bull trout further north in latitudes and higher in elevation. Thermal sensitivities during the summer months are likely to be highest in the southern periphery of their distributional range, while model simulations under extreme climate scenarios predict headwater tributaries within the Oldman, Flathead, and South Fork Flathead basins to provide cold-water refugia into the future. My dissertation work provides a decision support framework for predicting climate-induced stream temperature impacts on freshwater riverscapes and sensitive aquatic species to prioritize climate adaptation strategies in the Crown of the Continent.

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Chapter 1: Introduction

Stream temperature

Stream temperature is a vital component of ecosystem function, influencing the physical, chemical and biological properties of river systems (Caissie 2006, Kelleher et al. 2011). It has both economic and ecological significance and is one of the primary parameters in stream ecology that determines the overall health of aquatic ecosystems (Coutant 1999, Caissie 2006). Stream temperature has tremendous significance for freshwater organisms (Webb et al. 2008); it influences water chemistry and quality, (Ducharme 2008), biotic and abiotic ecosystem productivity (Poff et al. 2002), and the geographic distribution of fish species and other aquatic organisms (Poff et al. 2002, Muhlfeld et al. 2011, Wenger et al. 2011b, Jones et al. 2014).

Stream temperature variation can occur naturally or as a result of anthropogenic effects, such as climate change, deforestation, thermal or industrial pollution, and flow alteration (Johnson and Jones 2000, Lowney 2000, Sinokrot and Gulliver 2000, Schindler 2001). The natural processes contributing to variation are highly dependent on atmospheric (i.e., meteorological) conditions (Caissie et al. 2005). Anthropogenic effects, such as climate change are realized through regional and local scale climate conditions, which can make differentiating between natural and human-induced variations difficult. Nonetheless, anthropogenic effects on stream temperature have been identified as an important component of local and global scale aquatic ecosystem disturbance (Vitousek 1994, Sinokrot et al. 1995, Solomon et al. 2007, Eissa and Zaki 2011, Muhlfeld et al. 2014a), thereby emphasizing the importance of better understanding these interacting processes.

Climate change

Over the past century, climate warming has increased the planet's mean annual air temperatures by 0.74°C and temperatures are predicted to rise by as much as 5°C by 2100 (IPCC 2013). Water temperatures within aquatic ecosystems are also rising and have been linked to long-term increases in air temperatures (McCullough et al. 2009, Isaak et al. 2012). Some studies suggest that mountainous regions

may be more sensitive to global scale climate change and are experiencing warming rates that are greater than the global average (Beniston et al. 1997, Rangwala and Miller 2012). In fact, recent studies have found that 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. 2011). In addition, climate models report an increased sensitivity to warming at high elevations due to enhanced warming effects from lower surface albedo (Pepin and Lundquist 2008, Rangwala and Miller 2012). Other studies have shown that warming trends are most rapid near the 0°C isotherm (i.e., altitude at which the temperature is freezing; Pepin and Lundquist 2008). Therefore, water resources and ecosystems near the 0°C isotherm in the mid-latitude regions are at increased risk from accelerated warming. For all of these reasons, mountainous areas in the mid-latitude regions are good ecological indicators of global warming (Pepin and Lundquist 2008, Pederson et al. 2011).

Projected changes in temperatures and other atmospheric forcings vary considerably depending on Global or Regional Circulation Models (GCMs and RCMs) and/or climate forcings scenario. Nevertheless, thermal energy from elevated air temperatures will transfer to streams directly via sensible heat transfer and long-wave atmospheric radiation and indirectly through altered hydrologic and climatic patterns (Meisner et al. 1988, Schindler 2001). However, the extent of future warming may be mitigated by topographic characteristics, landcover vegetation, and other ecosystem processes, such as groundwater inflows (Arismendi et al. 2013). In fact, processes controlling thermal heterogeneity, operate over different space and time scale (i.e., domain and resolution) with both ‘top-down’ and ‘bottom-up’ interactions and feedbacks (Wiens 2002). Therefore, quantifying thermal sensitivities and identifying dominant process drivers of stream temperature prediction will improve our ability to understand ecosystem changes and inform water resource and ecosystem management.

Both natural and anthropogenic induced variation in climate forcings, such as temperature and precipitation, will be reflected in stream temperatures with consequential impacts to aquatic systems. Seasonal controls on hydroclimatic variability are strongly influenced by natural ocean-atmosphere interactions (Shelton 2009). For the Northern Rocky Mountains, the Pacific Decadal Oscillation (PDO)

and El Niño Southern Oscillation (ENSO) are the dominant drivers of inter-decadal and decadal climate variability (McCabe and Palecki 2006, Zhang and Delworth 2007, Pederson et al. 2011). For example, when the PDO is in phase with warm ENSO years (i.e., sea surface temperatures), winters tend to be warmer and drier than average. Conversely, when PDO is in phase cool ENSO years (i.e., La Niña), winters tend to be cooler and wetter (CIG 2012). Hydroclimatology provides a basis for analyzing how climate conditions influence variations in the hydrologic cycle in space and over time (Shelton 2009). Specifically, patterns of variability in precipitation and air temperature will result in changes to the quantity, quality, and timing of seasonal streamflow and temperature regimes (Cayan et al. 1993, Allen and Ingram 2002, Pederson et al. 2010, Ault et al. 2013).

Since the mid-1980s, studies have shown that in the Northern Rocky Mountains (NRMs), where snowpack is the primary driver of runoff, there has been a substantial decline in peak snowpack conditions, warmer winters and springs (Pederson et al. 2013), and subsequently a reduced and earlier snowmelt runoff (Aguado et al. 1992, Cayan et al. 1993, McCabe and Palecki 2006). Consequently, studies have shown reductions in summer base flows and increasing summer stream temperatures in many streams and rivers (Rood et al. 2008, MacDonald et al. 2011, Isaak et al. 2012). Looking towards the future, climate projections for the Pacific Northwest predict average annual air temperature increases of 1.1°C by the 2020s and 3.0°C by the 2080s and a continuation of altered hydrologic and thermal regimes within freshwater systems (0.1°C to 0.6°C per decade; Mote and Salathé 2010).

Climate prediction involves quantifying risk and probability under conditions of uncertainty (Allen and Ingram 2002). Observed climate records, when and where available, provide constraints for climate predictions and forecasts. Accordingly, forecasted air temperatures are much better constrained by recent climate observations than any other climate variable. Particular details about how precipitation may respond to climate variations and warming are much less clear, as are hydrologic feedbacks (Allen and Ingram 2002). Because precipitation is not well constrained, for lack of available data, climate model bias and prediction errors are amplified, as in comparison with air temperatures (Allen and Ingram 2002).

Aquatic impacts

Water temperature is one of the most important abiotic factors influencing aquatic species survival and performance (Brett 1971). All aquatic organisms have a range of thermal preferences and limits that determine their distribution, abundance, growth, and survival (Sinokrot et al. 1995, Schindler 2001, Selong et al. 2001). Studies have shown that physiological performance is contingent on these thermal preferences and depending on the species, optimal performance centers around a specific temperature value (Brett 1971, Beechie et al. 2013). Spatiotemporal variations in stream temperature, therefore, play an important role in a species' habitat selection, the timing of phenotypic functions, and persistence (Dunham et al. 2003).

Climate trends and projections have stimulated interest in assessing the thermal sensitivity of aquatic species worldwide (Winterbourn et al. 2008, 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 (Haak et al. 2010). In fact, salmonids have evolved due to climate change; where most adaptations are caused by changes in thermal cues for migration and physiological functions (Crozier et al. 2008, Kovach et al. 2012). 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; (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, Haak et al. 2010). For example, having one of the lowest upper thermal limits (20.9°C) and growth optima (13.2°C) of all salmonids in North America, the threatened bull trout (*Salvelinus confluentus*) is an excellent indicator of climate-induced warming in stream networks (Selong et al. 2001, Dunham et al. 2003, Rieman et al. 2007). Understanding how thermal changes will impact potential shifts in habitat distributions and phenotypic functions of climate-sensitive aquatic species, like the bull trout, will be critical for effective ecosystem management in a warmer future.

Microrefugia allows populations of species to persist outside of their main distributions (Dobrowski 2011). Studies indicate that local topography allows for climate patterns to deviate from regional trends creating microclimatic driven refugia (Loarie et al. 2009, Dobrowski 2011). Areas that are isolated from regional patterns maintain suitable habitats similar to historic conditions, as opposed to areas that are tightly coupled to atmospheric forcings (Dobrowski 2011). During periods of elevated stream temperatures, many aquatic species seek thermal refuge (Ebersole et al. 2003, Isaak and Rieman 2013). Cold-water refugia is therefore very important for river ecosystems, potentially mediating the biological impacts of climate warming. This is especially true for cold-water species such as salmonids who seek refuge in small cold-water tributaries (Ebersole et al. 2001). Montane ecosystems, therefore, can provide critical refugia for cold-water species (Paul and Post 2001, Isaak and Rieman 2013).

Stream temperature models

Predictive models are an integral tool of ecosystem analysis allowing physical, chemical, and biological processes to be fully understood (Odum 1994, Waring and Running 2007). Stream temperature models can be classified into three types: (i) deterministic, (ii) regression, and (iii) stochastic. Deterministic models are also referred to as physically based models, using an energy budget approach to predict stream temperatures (Sinokrot and Stefan 1993, Caissie et al. 2007). Regression models use a statistical approach to making predictions from climate data (i.e., air temperature), topography, and catchment characteristics (Neumann et al. 2003, Benyahya et al. 2007), while stochastic models rely on deviations from seasonal trends (Caissie et al. 1998) and the use of equilibrium temperature concepts (Bogan et al. 2004, Caissie et al. 2005). New approaches include the application of geostatistical models and the analysis of spatial and temporal covariance structures for predictions (Gardner et al. 2003, Peterson and Ver Hoef 2010, Jones et al. 2014).

Both non-spatial and spatial statistical modeling approaches have been used to predict stream temperatures in river networks. Historically, stream temperature has been related to air temperature as a surrogate for net heat exchange (Webb et al. 2008). Simple linear regression models have been used to predict stream temperatures using these air-water correlations (Mackey and Berrie 1991, Webb and

Nobilis 1997, Gardner et al. 2003, Caissie 2006) and are generally used for short temporal scales (e.g., one year) when water temperature is not autocorrelated within the time series. As temporal scales increase, there can be considerable complexity in air-water relationships, often making simple linear regression ineffective. In addition, the air-water relationship departs from linearity at low temperatures, high temperatures (Mohseni et al. 1998), and during seasonal snow and ice melt runoff (Webb and Nobilis 1997). Linearity departures also occur in small, headwater streams that have significant contributions from groundwater inflows (Kelleher et al. 2011). 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 modeling of stream networks have greatly improved temperature predictability by using spatially explicit data to explain variation across heterogeneous river networks (Peterson and Ver Hoef 2010). Spatially explicit models can be used to capture and quantify spatial and temporal patterns across the landscape, which can provide additional information about ecosystem structure and function (Inoue et al. 2009). Recent publications have focused on summer models (Isaak et al. 2010, Jones et al. 2014), but none to date include the use of high resolution climate data to capture seasonal atmospheric forcings for every month of the year.

Research objectives

The Crown of the Continent Ecosystem (CCE) is considered one of the most biologically intact temperate ecosystems in the world (Prato and Fagre 2007a). The ecosystem is jurisdictionally fragmented encompassing northwestern Montana, Alberta and British Columbia, Canada (Figure 1; 72,000 km²). Within the United States' portion are five federally protected wilderness areas and Glacier National Park. Within the Canadian portion is Waterton Lake National Park and an adjoining provincial park. Together, Waterton Lake and Glacier National Parks form a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Site and Biosphere Reserve, the world's first International Peace Park (Waterton-Glacier International Peace Park). The CCE forms the headwaters for three of

North America's largest rivers (i.e., the Columbia, Missouri, and Saskatchewan rivers) and is known for ancient geologic formations, as well as glacially carved mountains (Figure 1).

This study focuses on the sensitivity of natural and human induced climate variability on thermal regimes and aquatic species within the Crown of the Continent river and stream ecosystem. More specifically, seasonal stream temperature models were developed to replicate physical processes influencing thermal variation in the CCE. Models were forced and validated with empirical stream temperature data, furthering our understanding of climatic and topographic process drivers. Lastly, the models were used to investigate ecosystem disturbances, such as climate change, and associated impact to bull trout - one of the most stenothermic cold-water salmonids in western North America.

The objective of chapter two was to provide an overview of methods for monitoring stream temperature, characterization of thermal profiles, and modeling approaches to stream temperature prediction. Recent advances in temperature monitoring allow for more comprehensive studies of the underlying processes influencing annual variation of temperatures and how thermal variability may impact aquatic organisms at individual, population, and community based scales. Likewise, the development of spatially explicit predictive models provide a framework for simulating natural and anthropogenic effects on thermal regimes which is integral for sustainable management of freshwater systems.

The primary objective of chapter three was to develop a high-resolution (100 m) monthly stream temperature model for the CCE. Landscape scale empirically based geostatistical models were parameterized with time-series stream temperature data collected throughout the CCE. In addition, a spatial modeling approach was taken, using spatial covariance structures to correct for autocorrelations found in the data (Jones et al. 2014). The temperature models were coupled with high-resolution climate (i.e., air temperature) and land surface (i.e., elevation, slope) data to predict stream temperatures under historic, current conditions, and to forecast future warming patterns across space and time continuums. Additionally, few studies have incorporated important thermal controls such as the presence of lakes and glaciers into regional predictions. This study investigated potential lake and glacier effects on stream

temperatures. This work provides the first broad scale analysis of seasonal climate effects on spatiotemporal patterns of stream temperature in the northern Rocky Mountains.

Life-histories of native salmonids are tightly coupled with local environmental conditions, such as climate and topography, both of which drive the geographic distribution of cold-water refugia (Crozier et al. 2008, Dobrowski 2011). Simulation of climate-induced stream temperature warming, therefore, allows for more comprehensive assessments of species vulnerabilities, by evaluating how thermal habitat distributions may shift in space and time. The objective of chapter four was to investigate seasonal climate impacts to native bull trout habitats and life-history traits. Historic and future climate surfaces (i.e., CMIP5 projections) were used to predict stream temperature regimes throughout the CCE. Thermal preferences and critical thermal thresholds were used to identify the geographic distribution of cold-water refugia and topo-climatic effects driving patterns on the landscape. In addition to spatial shifts in the distribution of thermally suitable habitats, possible temporal shifts in key phenotypic traits were evaluated to further understand climate-induced changes driving species persistence (Fraley and Shepard 1989b, McPhail and Baxter 1996, Swanberg 1997, Baxter and Hauer 2000, Selong et al. 2001, Dunham et al. 2003, Jones et al. 2014).

There is a critical need for landscape scale decision support tools that can provide assessments of climate-induced change within freshwater ecosystems. Managing aquatic ecosystems requires assessing the vulnerability of species and thermal metrics can be used to assess exposure, sensitivity, and adaptability of aquatic species to future climate change (Pacifci et al. 2015). Additionally, climate adaptation planning for aquatic species often involves identifying thermally suitable habitats under future climate scenarios and prioritizing on-the-ground actions towards mitigating climate effects. Modeling frameworks such as the one presented here, can be used to identify populations and habitats at risk; develop monitoring and evaluation programs; 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).



Figure 1. The transboundary Crown of the Continent Ecosystem is jurisdictionally fragmented, encompassing northwestern Montana, Alberta and British Columbia, Canada. The CCE is considered the headwaters of North America and origin for three major continental river drainages, the Columbia, Missouri, and Saskatchewan.

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Chapter 6

Temperature

L. Jones^{1,2}, C.C. Muhlfield^{1,2,3} and F.R. Hauer^{2,3,4}

¹U.S. Geological Survey, Northern Rocky Mountain Science Center, Glacier National Park, West Glacier, MT, USA; ²Systems Ecology, University of Montana, Missoula, MT, USA; ³Flathead Lake Biological Station, University of Montana, Polson, MT, USA;

⁴Center for Integrated Research on the Environment, University of Montana, Missoula, MT, USA

6.1 INTRODUCTION

Stream temperature is a key indicator of ecosystem health because temperature directly and indirectly influences physical, chemical, and biological processes within freshwater systems (Caissie, 2006). Stream temperature can affect abiotic factors such as dissolved gases (e.g., oxygen) and sediment concentrations, toxicity and pH levels, water density and conductivity, and all nutrients cycling within a system. Spatiotemporal heterogeneity in temperature within freshwater systems can influence biotic factors such as photosynthesis rates, physiology (e.g., aerobic respiration, metabolic rates), survival, performance, abundance, distribution, and phenology (e.g., spawning cues, insect emergence) of all aquatic organisms. For these reasons, temperature is one of the most important environmental variables in the biosphere.

Stream temperature is a function of energy fluxes that occur above and below the water surface (Kelleher et al., 2011). Atmospheric energy fluxes (e.g., latent and sensible heat exchanges) occur at the air-water interface. The most significant of these fluxes are (1) solar radiation; (2) net longwave radiation; and (3) evaporative sinks (e.g., energy losses), with direct solar radiation controlling the majority of the energy budget (Webb et al., 2008). Energy exchange that occurs below the water surface (e.g., at the streambed-water interface), can be mainly described through bed conduction, frictional heat transfer, or advective heat exchange through groundwater or *hyporheic flux* (Caissie, 2006; also see Chapter 8). Thermal effects from inflows and outflows of water are often strongly influenced by the thermal characteristics of the source (e.g., tributaries, lakes, glaciers, groundwater, or impoundments) and controlled in part by the volume of water within a stream reach, which correlates directly with the heat energy required to change its thermal mass (Poole and Berman, 2001). Although conductive heat transfer occurs from temperature differences between the atmosphere (e.g., air temperature) and water surface, these exchanges comprise a relatively small portion of the total energy balance (Johnson, 2004).

The magnitude of each process and its relative contribution to the energy budget varies across spatial and temporal domains and scales (e.g., location of the stream, time of year). Alpine streams, for example, are highly influenced by evaporation rates, solar radiation, and discharge contributions (e.g., groundwater, tributaries, snowmelt). Conversely, montane streams and rivers in lower elevations are more closely coupled to atmospheric fluxes at the air-water interface, mainly due to high radiative solar inputs (because of larger channel widths and surface area), limited shading from riparian vegetation, and considerable thermal inertia (Poole and Berman, 2001). Seasonal variation of processes influencing thermal heterogeneity are largely dependent on regional climate patterns (e.g., temperature and precipitation) and hydroclimatic effects (e.g., discharge, snowmelt, precipitation), which are strongly influenced by natural ocean-atmosphere interactions (Shelton, 2009).

Often, temperature from a given stream reach is presented as a single location regime. This leads to the common misconception that stream temperatures are uniform among habitats within a stream reach. On the contrary, stream temperature may be highly variable between habitats only a few meters apart. For example, backwater depositional areas are often much warmer than waters in the stream channel. This would be particularly so in alluvial, gravel-bed rivers, which have high connectivity between channel water and groundwater. Overall, streams express significant changes in temperature from small shaded headwaters to broad, open-canopied river reaches. This is especially true in mountainous regions where a river may originate in alpine environs influenced by glacial and/or snowmelt processes and flow through a much warmer downstream climate before joining larger rivers or discharging into the ocean (Hauer et al., 2000).

2 SECTION | A Physical Processes

Thermal regimes can vary considerably across latitudinal and elevational ranges (e.g., daily, monthly, and annual variations). In temperate regions, water temperature in winter may be at or approach 0°C, whereas summer temperatures may achieve temperatures >30°C (Hauer and Benke, 1987; Lowe and Hauer, 1999). Generally, streams experience *diel temperature flux*, where ranges of more than 5°C are common (Fig. 6.1). Diel temperature flux may also be very high in certain environments; for example, in very small alpine streams that are effected by direct solar radiation, afternoon temperatures in late summer may reach >20°C whereas night temperatures approach 0°C. Even large rivers that have discharges in excess of 500 m³/s may experience diel temperature ranges of 3-5°C. However, because of the high latent heat transfer in larger river systems (which means a large quantity of energy is needed to change even 1°C), stream temperatures tend to vary much more narrowly on a daily basis. Similarly, streams with substantial contributions of groundwater will have a much more narrow range of temperature variability (daily, monthly, and annually). Reaches with extensive groundwater are typically cooler in the summer and warmer in the winter than reaches with little groundwater-surface water interactions (also see Chapter 8).

All aquatic species have a preferred temperature range that limits their geographic distribution, physiological performance, and persistence. *Stenothermic* species, for example, occupy a narrow range of temperatures, whereas *eurythermal* species can thrive in a broad range of temperatures. Critical life history traits of lotic plants and animals (from diatoms and aquatic insects to fish and other *poikilothermic* vertebrates) are regulated by temperature. In fact, many stream organisms use temperature or temperature change as an environmental cue for life history traits, such as spawning migrations (fishes), embryonic development, or larval and egg emergence (aquatic insects and fish fry). Thermal requirements for a given species are typically based on lethal limits (upper thermal tolerance) and temperature optimums for life history traits (e.g., growth, reproduction). Thermal requirements such as these define the “fundamental thermal niche” for a given species and are often used as key metrics in developing thermal protection standards for threatened or endangered species (Bear et al., 2007). Generally, the upper temperature tolerance limits of a given species correlates with the maximum

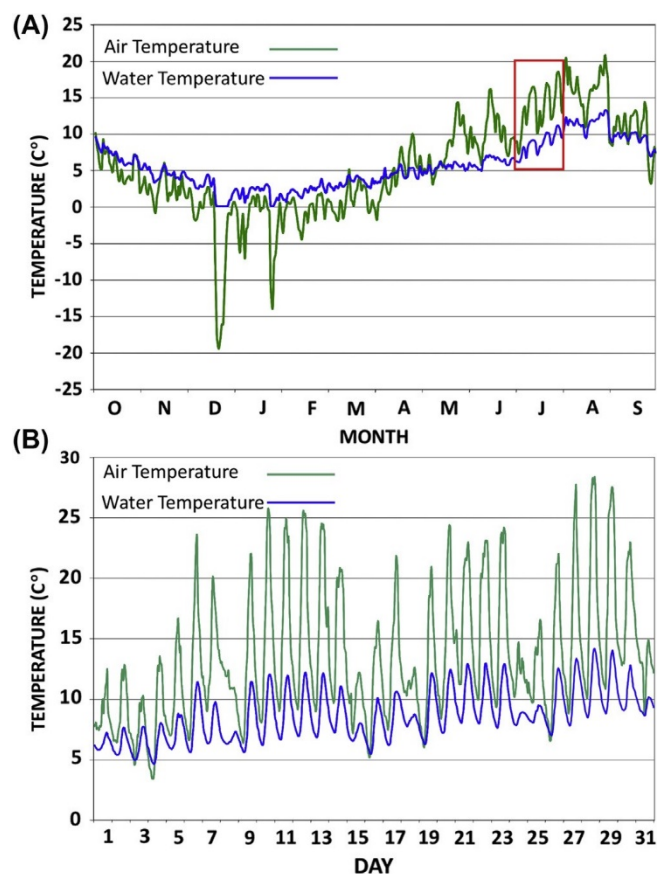


FIGURE 6.1 (A) Daily mean air and water temperatures calculated from hourly means (°C), McDonald Creek, Glacier National Park, Montana (United States), October 1, 1998 to September 30, 1999. (B) Hourly mean air and water temperatures calculated from 5-min interval, instantaneous measures (°C), McDonald Creek, Glacier National Park, Montana (United States), July 1999.

temperatures associated with the lower boundaries of their distribution, while optimum growth temperatures are used as an indicator of the upper range of suitable thermal habitat for their long-term persistence (Dunham et al., 2003). Temperature, therefore, is a fundamental component to the study of bioenergetics where modeling approaches balance energy inputs with outputs to quantify growth response (biomass), predator-prey or trophic interactions, and even carrying capacities of a population (Hansen et al., 1993).

Stream temperature warming within aquatic ecosystems has been linked to long-term increases in air temperatures, altered hydrologic regimes, and land-use/land-cover changes (Kaushal et al., 2010). Natural- and anthropogenic-caused thermal variation within freshwater *riverscapes* can lead to long-term ecological and environmental impacts such as loss of community biodiversity, genetic hybridization, and species extinction. Long-term monitoring and use of empirical data for predictive modeling is, therefore, fundamental to understanding the patterns, processes, and ecology of freshwater systems and to improving our ability to forecast both future changes in temperature and ecological effects within streams and rivers.

6.2 GENERAL DESIGN

6.2.1 Data Collection

Digital temperature data loggers (e.g., thermographs) are the most common instruments used for monitoring stream temperatures. Important features to consider when choosing a thermograph include accuracy, precision, memory capacity, durability, battery life, resolution, and programmability. Frequently used thermographs include the Hobo Water Temp Pro v2 and Tidbit v2 Temp sensor (Onset Computer Corporation), both of which have a 5-6 year battery life, 0.02°C resolution, and $\pm 0.2^\circ\text{C}$ accuracy. After a data logger is chosen and prior to installation, it should be placed in a durable housing unit (e.g., PVC pipe or radiation shield) that protects the thermograph from damage, while also shielding the unit from direct solar radiation (Johnson and Wilby, 2013; EPA, 2014). If the housing unit absorbs any solar radiation or if the thermograph is installed without a shield, heat conduction to the sensor will bias temperature readings. Prior to deployment, any such device should be checked for accuracy and precision against a thermometer certified by the National Institute of Standards and Technology (NIST, formerly the National Bureau of Standards). A simple method for performing accuracy checks on the sensor prior to deployment is the “ice bucket” method by which loggers are placed in an ice bath for several hours and temperature recordings are checked against readings from the NIST certified thermometer (EPA, 2014). Both digital and nondigital NIST certified thermometers can also be used for instant readings at sample site locations.

Recent advancements in installation methods of thermographs have made it possible to establish annual monitoring sites that collect continuous data recordings for a given sampling interval over the entire hydrologic cycle. In the past decades (1980 – present), monitoring was predominantly conducted during low-flow seasons, resulting in seasonal snapshots of temperature regimes. Underwater epoxy methods are now being used to attach sensors (e.g., TidbiT, Onset Computer Corporation, Pocasset, Massachusetts, United States) to the downstream side of large rocks and cement bridge supports (Isaak and Horan, 2011). Other installation methods include cabling the sensor to rebar, stable in-stream structures, or bank vegetation (EPA, 2014). Stream substrate is an important factor to consider when choosing an installation method. For example, the epoxy method is likely better suited for larger main stem rivers, where boulders are present, grain size is cobble or larger, and bed load transport is minimal. In areas with fine substrate (e.g., gravel or sand) and higher bed load transport, loggers are prone to being buried in the sediment; therefore site selection and installation methods are important considerations.

Stream temperature monitoring has dramatically increased in the past decade due to availability of relatively inexpensive loggers that are easy to install and capable of collecting large amounts of data. With continuous data recordings, it is possible to characterize the timing, magnitude, and duration of thermal events (e.g., seasonal means and variance, date of spring onset, annual degree days), which have direct implications on aquatic species distributions. Additionally, long-term (e.g., multiple decades) monitoring will increase our understanding of temperature trends and variability, especially within the context of climate change. The rapid accumulation of temperature data, monitoring sites, and online data sources (Isaak et al., 2011) will ultimately improve our ability to understand thermal variation; however, there can be challenges associated with availability and use of such data (e.g., reliability, accuracy, missing data). Clear objectives and research questions should be defined to ensure the appropriate use of the data collected or downloaded, including spatial and temporal domains, resolutions, and relevant sampling designs. Quality assurance and quality control (QA/QC) procedures should also be performed after the data are offloaded or downloaded to verify the quality of the data and check for potential errors or missing time-series data. Data errors can occur when the logger is dewatered during low flow events or potentially buried in sediment. A list of additional error sources and screening procedures can be found in Sowder and Steel (2012).

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Sampling intervals (i.e., time) and site selection (i.e., space) are important elements to consider when designing a study. The sampling intervals at which data are collected can greatly bias temperature metrics (Dunham et al., 2005). For example, longer sampling intervals (i.e., lower temporal resolution) may not adequately describe thermal variations within a system, thereby underestimating thermal maximums and overestimating thermal minimums. Because minimum and maximum temperatures occur only briefly within the day, longer sampling intervals are likely to miss the true values of those metrics. Thus if the daily range of temperatures is large, a high frequency sampling interval should be used. Higher sampling frequencies, however, require more memory capacity and may increase site visits to offload data. When choosing a sample site location, data loggers should be placed in areas of well-mixed moving water, both horizontally and vertically. The thermograph should also be placed in sufficient water depth to keep the sensor submerged year round, avoiding reaches with high gradients ($>7\%$; sensor retention rates are inversely related to slope). Additionally, sample sites located in high traffic areas, backwater pools, or tributary confluences should not be selected. The distribution of sample sites across a chosen study area will be determined by the research question of interest, scale of analysis, chosen data sources, and modeling methods.

Thermal infrared remote sensing provides an alternative method to in situ measurements as a means of characterizing thermal distributions of river systems. Radiant temperature measurements (e.g., thermal emission data) taken by thermal infrared sensors provide a spatially continuous map of temperatures across a watershed (Fig. 6.2). Thermal imagery is useful for (1) identifying groundwater inflows, the analysis of floodplain hydrology, and (2) identifying thermal processes across riverscapes. While thermal imaging allows broad area analysis, it has the disadvantage of being restricted to measuring emission radiation and thus can only measure surface temperatures. Satellite-based, airborne (i.e., aircraft or drone), or ground-based imaging have specific pros and cons depending on the spatiotemporal resolution or data collection methods, which are discussed in detail in Handcock et al. (2012). Thermal sensors can also be deployed at a single location and used over an extended time to characterize temperature variation along a specific channel segment.

Statistical summaries or “metrics” of stream temperature describe important characteristics of thermal regimes and are useful for investigating thermal sensitivities influencing aquatic species. In biological applications, thermal metrics can be used to characterize fundamental life history traits such as growth, survival, and reproductive success (Hasnain et al., 2013). Thermal maximums influence species survival rates and species abundance and can be an excellent indicator of “thermal resistance” in river systems, thereby resulting in loss or fragmentation of thermally suitable habitat. Maximum temperatures are also commonly used in regulatory compliance, water quality standards, and thermal protection standards for aquatic species. Additionally, temperature extremes such as minimums and maximums affect competitive interactions among species and are important for identifying overlapping habitats of native and invasive species (Isaak et al., 2016). Average (e.g., mean) temperature summaries can be useful (1) for aggregating space and time scales and (2) when

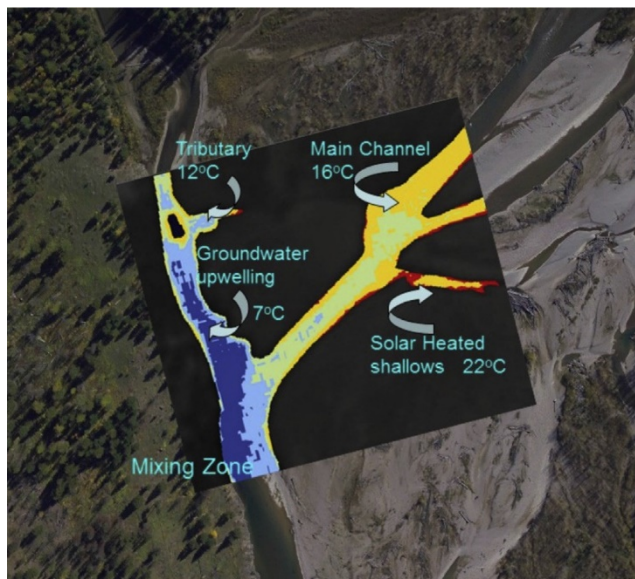


FIGURE 6.2 Thermal infrared (near IR) image classified by temperature and superimposed on an aerial image of the Nyack floodplain, Middle Fork Flathead River in Montana. The image illustrates the spatial variation in temperature distributed across a riverscape and the utility of IR imagery in landscape scale study.

conducting change analysis associated with historic and future temperature simulations (Fig. 6.2). Mean metrics also provide a good representation of average ambient energy and insight into system behavior.

6.2.2 Stream Temperature Modeling

Stream temperature models can be used to evaluate underlying physical processes or predict thermal distributions across space and through time (Webb et al., 2008). Ultimately, the accuracy and potential success of modeling stream temperature is dependent on the proper description of energy exchange processes within the appropriate context of scale. Temperature models generally fall into two categories: (1) physically based or deterministic models and (2) empirically based statistical models. Physically based models employ the use of energy fluxes and solving heat budget equations, while statistical models rely on correlative relationships between atmospheric conditions and catchment characteristics.

Physically based models can simulate stream temperatures in one or more dimensions. One-dimensional models are typically applied to streams and rivers that are well mixed, while higher-dimensional models may be necessary in more heterogeneous environments. The objective of physically based models is to quantify total energy fluxes occurring at both the air-water and streambed-water interfaces. Generally, physically based models require a significant quantity of data inputs (e.g., meteorological data, stream geometry, land-cover classifications, riparian shading, soil moisture indices, hydrology etc.). These models vary in their methods used to estimate stream temperature, with some requiring hydrology as an input and others dynamically modeling hydrology and stream flow (Ficklin et al., 2012). One advantage of physically based models is the ability to incorporate water fluxes. Therefore these models should be chosen in areas of high inflow, outflow, or groundwater exchanges. Another advantage of physically based models is the broad application for quantifying thermal responses to nonstationary changes which may occur within a given system, such as land use (e.g., mining or logging), land cover (e.g., wildfire or deforestation), altered hydrologic regimes, thermal pollution, and water diversions or impoundments.

The most common forms of statistical stream temperature models are regression models (e.g., linear or multiple), stochastic models, and logistic models, all of which require significantly less input data than physically based models and rely mostly on air-water temperature correlations (Benyahya et al., 2007). Regression models use a statistical approach to making predictions from climate data, topography, and catchment characteristics. Both nonspatial and spatial statistical modeling approaches have been used to predict stream temperatures in river networks using air temperature as a proxy for net radiation exchanges. These models are predominantly driven by air-water temperature correlations across space and time continuums (Webb et al., 2008). It is critical, however, to recognize the difference between correlation and causation, as well as the associated limitations of using air temperature as a proxy for energy balance processes (Johnson, 2003; Letcher et al., 2016). Nonetheless, statistical models are commonly used to simulate future climate impacts on stream temperature by correlating air temperature and water temperature and predicting a system response based on future air temperature values (Jones et al., 2014).

Simple linear regression models have been used to predict stream temperatures using air-water temperature correlations and are generally used for short time periods when water temperature is not autocorrelated within the time series. Correlations between air and water temperature increase from daily to weekly to monthly time scales, but this trend does not continue for annual means (see Fig. 6.1; and Mohseni and Stefan, 1999). Important to note is that the air-water temperature relationship fails to remain linear at the extreme bounds of the air temperature range, near or below 0°C, when air temperatures dip below the freezing limit, and at high temperature ranges (e.g., 20°C), when evaporative cooling slows the warming effect (Letcher et al., 2016). Nonlinearity also occurs in streams that have significant contributions from groundwater inflows (Fig. 6.1) during seasonal snow and ice melt runoff, increased precipitation rates, and temporal lags caused by thermal inertia (Caissie, 2006; Webb et al., 2008; Letcher et al., 2016). Because many statistical models rely on air-water correlations, they fail to quantify interactions or feedback processes between the atmosphere and land surface, such as emissivity rates, solar radiation, surface albedo, and latent energy exchanges from soil moisture or vegetation. Land surface temperature (i.e., land skin temperature) is a remote sensing product that accounts for land-cover shading from net radiation effects, soil and ground emissivity rates, and surface albedo. Recent studies have used land skin temperature in lieu of air temperature to predict stream temperature where empirical data is not available, where it is not feasible to deploy sensors or to explain spatially variable relationships between land surface and water temperature (e.g., surface geology, vegetation, physiography; McNyset et al., 2015).

Multiple regression models have been used to address thermal complexities using a combination of predictor variables in addition to air temperature. The choice of these variables is dependent on the scale and spatial domain of the study, but typically involves catchment level characteristics, such as elevation, geology, slope, aspect, stream order, and/or stream reach level characteristics, such as land cover. Advances in geostatistical modeling of stream networks have greatly

improved temperature predictability by using spatially explicit models to account for spatial autocorrelations found in temperature observations. Autocorrelation occurs when data points in space or time are not independent, and it is a very common issue in estimation. *Geostatistical models* are attractive because of their ability to capture and quantify spatial and temporal patterns across large landscapes by incorporating spatially continuous predictor variables at reach scale resolutions (Fig. 6.3). Spatial hierarchical modeling is an example of a geostatistical modeling approach that accounts for spatial covariance structures by incorporating random effects into a generalized multiple regression model (Jones et al., 2014). Hierarchical models with random effects across space and time can also accommodate missing data in sample site time series (Letcher et al., 2016). More sophisticated geostatistical models, referred to as “flow-routed models,” address spatial autocorrelation through hydrologic relationships (Peterson and Ver Hoef, 2010). These models use a combination of “flow-connected,” “flow-unconnected,” and Euclidean distances to estimate the covariance components of the spatial relationships between observations. This modeling approach, however, requires a dense network of sample sites, longitudinally placed within a catchment, to adequately explain the flow-connected covariances.

In fluvial landscape ecology, scale and domain are perhaps the most critical of elements of any study, where challenges are produced by temporal variation (e.g., nonstationarity; daily to seasonal patterns) and variations in space (e.g., basin,

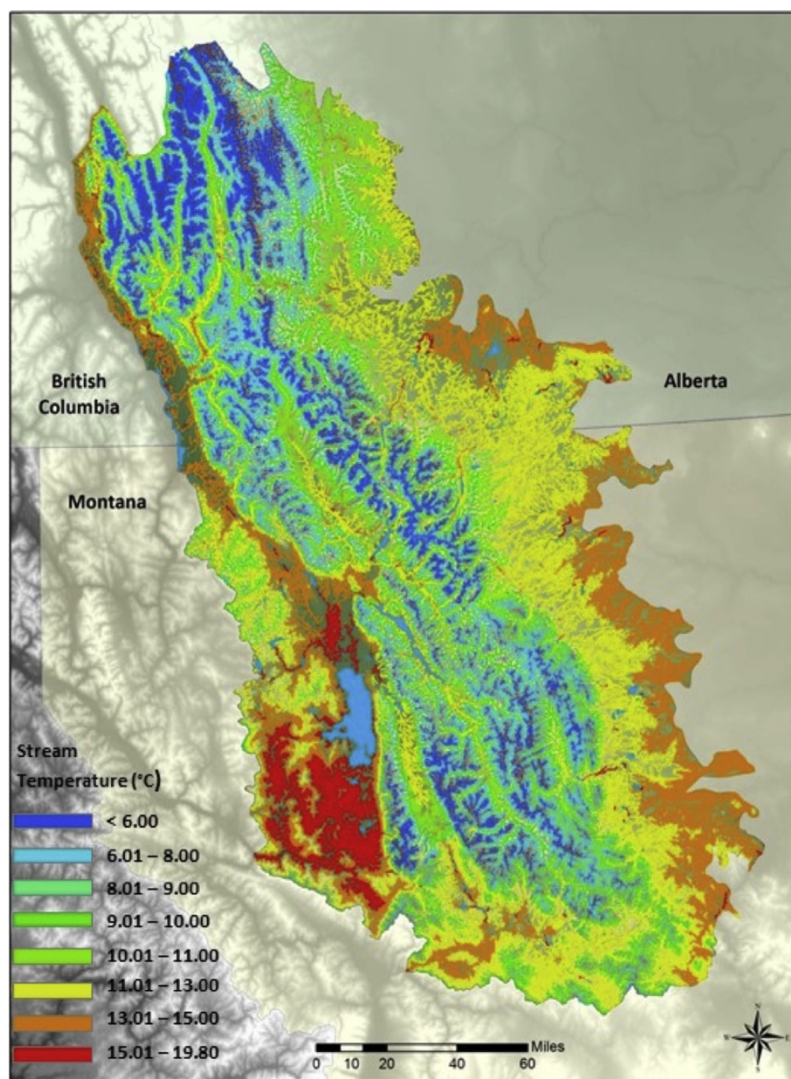


FIGURE 6.3 Mean August stream temperatures for the historic period (1986-2005), Crown of the Continent Ecosystem, Montana (United States), and Alberta and British Columbia, Canada. Empirical data was used to inform a spatial hierarchical statistical model using air temperature, elevation, slope, lake effect, glacier effect, and a spatial random effect to explain autocorrelation. Parameter estimates were used to interpolate predictions at a 100 m resolution.

watershed, stream reach or microhabitat patterns and hierarchy). Applications of fluvial landscape ecology integrate concepts of pattern, process, hierarchy, scale, directionality, and connectivity to explain relationships between system structure and function (Poole, 2002). Choice of sampling techniques and modeling approaches, therefore, will ultimately hinge on the abiotic or biotic research question of interest. Additionally, careful consideration of scales relevant to your research question, spatial and temporal domains of your study, spatial and temporal resolutions of your data inputs and outputs, and how these relationships may be extrapolated across space and time continuums will be most important when choosing appropriate methods for any stream temperature study.

6.3 SPECIFIC METHODS

6.3.1 Basic Method 1: Illustrating the Spatial Variation of Temperature

1. Choose sections of a study stream that have readily apparent differences in landscape, channel form, and/or ground-water interactions (see Chapters 1, 2, 5, and 8). Select specific locations that also capture a range of variation in solar radiation from being relatively open to being heavily shaded by riparian vegetation or by geophysical features. Stream study sections should consist of at least one riffle-pool-run sequence, if possible. Within each stream section, select and mark at least five cross-stream transects. The distance between transects will depend upon the length of each section, but transects should be at least several meters apart and intersect different and representative habitat types.
2. Measure temperature at a series (9-15) of equidistant points across each transect, including points at both edges of the stream. Measure water temperature at the surface and as close to the stream substratum as possible.
3. Begin measurements at the downstream transect and work across each transect before moving to the next upstream transect. Measure and record as quickly as possible to reduce the confounding effects of temporal variation.
4. For each transect, graph temperature versus transect position (m) for each data point at the surface and near the substratum. Conduct an analysis of variance (ANOVA) to determine whether there is greater variation between points within transects or between transects.
5. Stratify each data collection point across each transect into habitats (e.g., riffle, pool, thalweg, bank margin). Combine temperature data from each habitat type. Calculate mean, standard error, and coefficient of variation for each habitat type; compare habitats.

6.3.2 Advanced Method 1: Spatially Explicit Geostatistical Stream Temperature Modeling-Developing a Spatial Hierarchical Model to Predict August Stream Temperatures at the Watershed Scale

1. Select a watershed (i.e., hydrologic unit code (HUC) 4; [USGS, 2013](#)) that has smaller subwatershed divisions (i.e., HUC 6). Choose monitoring sites that cover a range of topographic gradients (e.g., headwaters to main stem) and sub-watershed divisions ([Fig. 6.4](#)). Use an appropriate sampling method to collect continuous temperature readings at bihourly intervals for the month of August. Using a handheld GPS unit, georeference each site location.

Alternate approach: Find an online stream temperature database (NorWeST; [Isaak et al., 2011](#)) and download temperature records and locations (i.e., latitude and longitude coordinates) for a selected watershed. Choose a watershed with adequate sample sites and continuous data recordings for the month of August (Note: temporal domain of this analysis can be >1 year).
2. QA/QC data and summarize temperature records to mean August temperatures for each site and year in your study. Append all site records into one data matrix that includes a site ID code, mean August temperature (°C), year, and latitude/longitude coordinates of the sample site ([Table 6.1](#)).
3. Download georeferenced data layers to be used in a geographic information system (GIS) software: (1) stream network (i.e., National Hydrography dataset); (2) digital elevation model (DEM); and (3) subwatershed boundary (i.e., HUC 6) for your selected watershed ([USGS, 2013](#)).
4. Project (i.e., map) the layers in GIS and calculate a slope raster surface from the DEM.
5. Project the data table from step 2 in GIS using the latitude and longitude coordinates and attribute each data record with an elevation, slope, and subwatershed identification code using the GIS layers acquired.

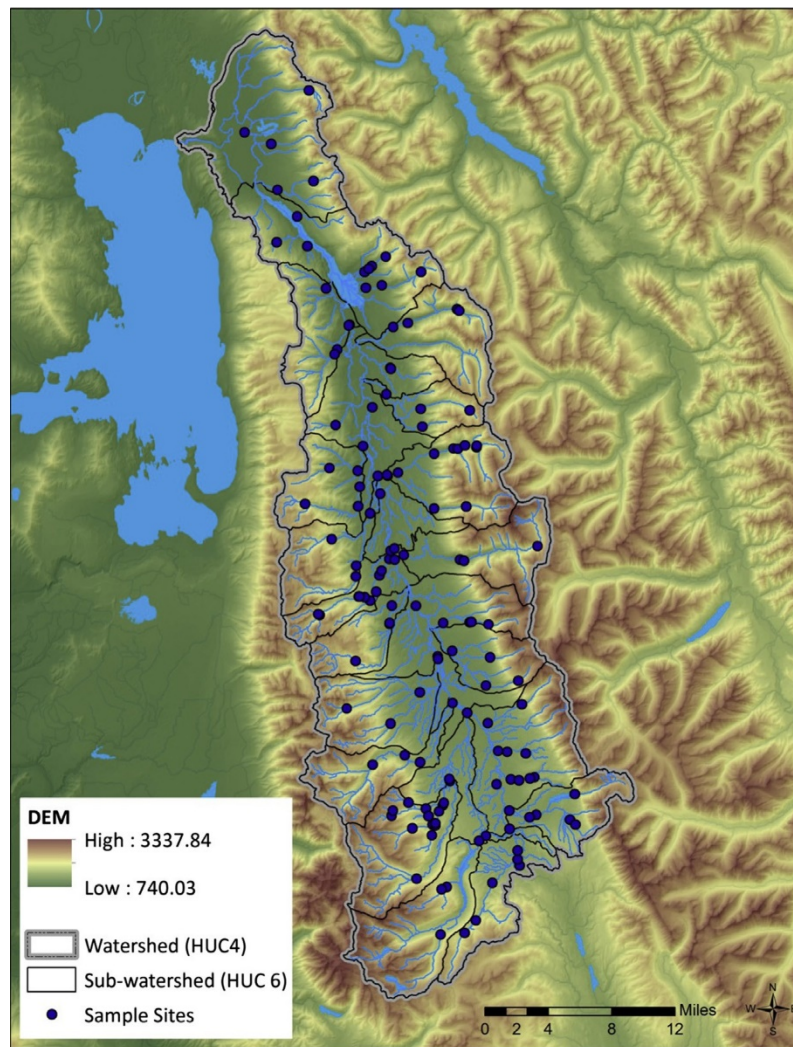


FIGURE 6.4 Hydrologic unit code (HUC) 4 watershed and HUC 6 subwatershed divisions used for spatial hierarchical statistical model. Sample sites were chosen to cover topographic gradients and subwatershed divisions.

6. Download gridded air temperature surfaces (Daymet; [Thornton et al., 2012](#)) or nearest climate station data ([NOAA, 2016](#)) and summarize mean August air temperatures for each year for which you have acquired data. Attribute each site-specific temperature record with air temperature values ($^{\circ}\text{C}$) for the corresponding years. Export the attribute table to use as an input data matrix-to-temperature model ([Table 6.1](#)).
7. Using statistical software, run a generalized linear hierarchical model using fixed effects: air temperature, DEM, slope, and random effect: subwatershed (i.e., HUC 6). The model should return parameter estimates for fixed effects and a random effect for each subwatershed in your study. Calculate root mean square error (RMSE) and r^2 to evaluate model performance.
8. Select a year or temporal period for which you want to interpolate temperatures in your watershed. Summarize mean air temperature surfaces or records for that chosen period (see [Fig. 6.5](#)).
9. Using GIS, partition the stream network into 1 km reaches (or desired resolution) and attribute network with average elevation, slope, subwatershed identification, longitude/latitude centroids for each stream segment, and air temperature values for the chosen time period. The resulting attribute table is a matrix of covariates, with each row representing a given stream segment (y_i).

TABLE 6.1 Example Data Matrix of Fixed and Random Effects for Spatial Hierarchical Model

Site ID	Year	Month	StreamT_mean	AirT_mean	Longitude	Latitude	Digital Elevation Model	Slope	HUC 4	HUC 6
SR_001	2012	8	14.46076075	17.93548387	-113.7479711	47.46802634	1222.02	1.72556	17010211	170102110104
SR_001	2013	8	15.3068703	18.74193548	-113.7479711	47.46802634	1222.02	1.72556	17010211	170102110104
SR_002	2012	8	13.14247648	17.12096774	-113.7823626	47.44376308	1419.78	5.54878	17010211	170102110104
SR_003	2012	8	11.73960081	16.45967742	-113.8055231	47.44974051	1749.39	15.9515	17010211	170102110104
SR_003	2013	8	12.73767602	17.04032258	-113.8055231	47.44974051	1749.39	15.9515	17010211	170102110104
SR_006	2012	8	10.47466532	15.22580645	-113.8264927	47.44297079	1847.91	21.1355	17010211	170102110104
SR_007	2012	8	13.84928629	17.59677419	-113.7591653	47.44635787	1302.75	2.6348	17010211	170102110104
SR_008	2012	8	13.94698858	17.2983871	-113.7793076	47.43689004	1381.18	4.81162	17010211	170102110104
SR_008	2013	8	15.07811425	17.97580645	-113.7793076	47.43689004	1381.18	4.81162	17010211	170102110104
SR_009	2012	8	12.92858333	17.59677419	-113.7647599	47.44047267	1338.27	6.25897	17010211	170102110104
SR_010	2013	8	14.38856586	17.97580645	-113.7713126	47.42987555	1413.57	5.59554	17010211	170102110104
SR_011	2012	8	10.49327151	16.65322581	-113.7753591	47.41906881	1504.95	7.92619	17010211	170102110104
SR_011	2013	8	11.11436559	17.30645161	-113.7753591	47.41906881	1504.95	7.92619	17010211	170102110104
SR_012	2012	8	10.95194556	15.86290323	-113.8013859	47.42605745	1589.22	5.89411	17010211	170102110104
SR_012	2013	8	12.8447836	16.40322581	-113.8013859	47.42605745	1589.22	5.89411	17010211	170102110104
SR_021	2012	8	9.778231855	18.41935484	-113.8150007	47.74922187	1003.65	2.0148	17010211	170102110303

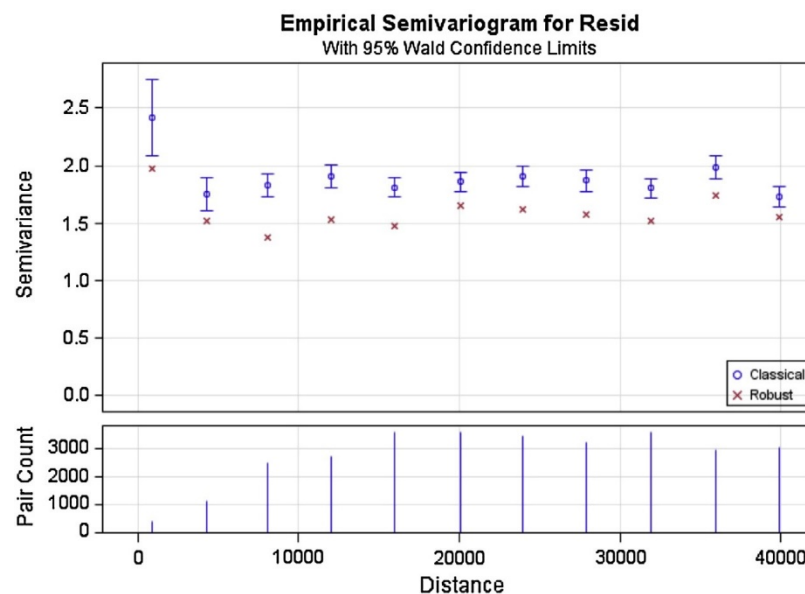


FIGURE 6.5 Example semivariogram of spatial hierarchical model residuals based on Euclidean distances between pairs of sample locations.

10. Using a statistical software package or GIS, predict mean stream temperatures for any given time period using the covariate matrix from step 9. Parameter estimates from step 7 should be used in the following equation to perform your predictions:

$$\hat{y}_i = \hat{\beta}_0 + \hat{\beta}_1 * airT_i + \hat{\beta}_2 * dem_i + \hat{\beta}_3 * slope_i + \hat{\sigma}_z^2,$$

where $\hat{\beta}_0$ is the parameter estimate for the intercept, remaining $\hat{\beta}$'s represent parameter estimates for corresponding covariates, and $\hat{\sigma}_z^2$ is variance estimate for the associated subwatershed in which the stream segment (y_i) is located.

11. Use latitude and longitude coordinates to project model predictions as point locations in GIS. Spatially join point attributes to the stream network layer (1 km resolution) and use colored symbology to visualize temperature gradients (see Fig. 6.4).

6.4 QUESTIONS

1. Identify the spatial variation in temperature in the study stream. What appears to be the sources of variation? Are the sources of variation random or predictable? What is the role of habitat type?
2. Many investigations characterize stream temperature at a particular site in a stream based on measurements taken at a single point. Based on your data, how accurately would a measurement at a single point reflect these conditions for the stream section(s) you chose?
3. What is the spatial and temporal domain of your study? What is the spatial and temporal resolution of your data inputs, model, and predictions?
4. Are all parameters in your model statistically significant ($p < .05$)? Based on RMSE and r^2 , how would you evaluate model performance? What parameters in the model are explaining the largest variance in the data?
5. Plot predicted temperatures versus observed temperatures for all sample sites and investigate sites with high residual error. Is there a pattern in sites with high error rates (e.g., site location, elevation, cold vs. warm sites)? What other covariates might you include in your model to explain this error?
6. Using residual errors from model output, plot a *semivariogram* for all sites in your model (Supplemental Figure 2). Did you adequately explain the spatial autocorrelation found in your data?
7. How might you simulate future climate scenarios and compare current thermal regimes to future thermal regimes? Where do you expect future warming will be greatest?
8. Think about possible model applications. To which abiotic or biotic research questions would this model be appropriately applied? Why?

6.5 MATERIALS AND SUPPLIES

Basic Materials and Supplies

Field notebook
 Measuring tapes
 Transect markers (rebar, plastic flagging, etc.)
 Electronic thermistor ($\pm 0.1^{\circ}\text{C}$)

Field Equipment for Monitoring

Thermographs ($\pm 0.2^{\circ}\text{C}$)
 Handheld GPS unit
 Radiation shields
 Cable or epoxy for installation

Advanced Temperature Modeling

Thermograph software (i.e., HOBOWare)
 Statistical software
 GIS software

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12 SECTION | A Physical Processes

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In review at *Climatic Change*

**Chapter 3: Projected warming portends seasonal shifts of stream temperatures
in the Northern Rocky Mountains, USA and Canada**

Leslie A. Jones^{1,2}, Clint C. Muhlfeld^{1,3}, and Lucy A. Marshall⁴

¹ U.S. Geological Survey, Northern Rocky Mountain Science Center, West Glacier, MT, USA

² Department of Biological Science, University of Montana, Missoula, MT, USA

³ Flathead Lake Biological Station, University of Montana, Polson, MT, USA

⁴ School of Civil and Environmental Engineering, University of New South Wales, Sydney, NSW, AU

Leslie Jones: lesliejones123@gmail.com; 406-223-2827; fax (406) 888-7923

Clint Muhlfeld: cmuhlfeld@usgs.gov; 406-600-9686; fax (406) 888-7923

Lucy Marshall: lucy.marshall@unsw.edu.au; (+61 2) 9385-7944; fax (+61 2) 9385-6139

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Abstract

Climate warming is expected to increase stream temperatures in mountainous regions of western North America, yet the degree to which future climate change may influence seasonal patterns of stream temperature has not been evaluated. In this study, a geostatistical model framework was integrated with empirical stream temperature data (~4 million bi-hourly recordings) and high resolution climate and land-surface data to predict monthly stream temperatures and associated change under future climate scenarios in the Crown of the Continent Ecosystem of the Rocky Mountains, USA and Canada (106,700 km stream network). Moderate and extreme climate simulations forecast increasing stream temperatures during spring, summer, and fall, with the largest increases predicted during summer (July, August, and September). Additionally, thermal regimes characteristic of current August temperatures, the warmest month of the year, are likely to be exceeded during July and September, suggesting an earlier onset and extended duration of warm summer stream temperatures. Models predict the largest magnitude of temperature warming relative to current conditions will be observed during the shoulder months of winter (April and November). Summer stream temperature warming will be most pronounced in high-elevation montane and alpine streams, where glacial-fed streams are predicted to experience the largest magnitude (> 50%) of change due to the loss of alpine glaciers. We provide the first broad scale analysis of seasonal climate effects on spatiotemporal patterns of stream temperature in the northern Rocky Mountains and spatially explicit forecasts for better understanding climate change impacts on freshwater habitats and guiding conservation and climate adaption strategies.

Keywords: geostatistical models, stream temperature, aquatic ecosystems, thermal variation, seasonal, climate change

1 Introduction

Stream temperature is a fundamental driver of abiotic and biotic processes within freshwater ecosystems (Kelleher et al. 2011). Climatic changes associated with atmospheric warming are causing increases in temperatures within many streams and rivers worldwide, altering physical, chemical, and biological processes in aquatic ecosystems (Shelton 2009). Increasing water temperatures caused by climate warming can impact abiotic characteristics of freshwater systems by decreasing oxygen levels, increasing toxicity and pH levels, and modifying biogeochemical processes (Poff et al. 2002).

Additionally, thermal variations due to climate warming can impact biotic components of aquatic ecosystems, such as aquatic metabolism (i.e., photosynthesis rates), and the physiology, survival, abundance, distribution, and phenology of aquatic organisms (Schindler 2001). An important component of understanding climate impacts on freshwater systems, therefore, will be predicting climate-induced change across multiple time and space domains, so that ecosystem response can be better understood.

Over the past century, the northern Rocky Mountains have warmed two to three times the rate of the global average, causing seasonal shifts in temperature and precipitation patterns (Pederson et al. 2010). Winter and spring warming and declining snowpack have resulted in an earlier onset of spring snowmelt (~2-3 weeks) and declining baseflows during the summer and fall months (Rood et al. 2008). Climate records indicate an earlier onset and later extension of the summer season, with extremely hot days (>32°C) occurring 24 days earlier and lasting 14 days longer than early 20th century (Pederson et al. 2010). Stream temperatures are also rising and have been linked to long-term increases in air temperatures and associated changes in the hydrological cycle (Isaak et al. 2012). Consequently, trend analyses of stream temperature records in the Pacific Northwest show increases in the magnitude and duration of warm summer temperatures, with estimated increases up to 0.22°C/decade (1980-2009; Isaak et al. 2012) and warmer temperatures beginning a full month earlier and persisting 2-3 weeks later (1950-2006; Crozier et al. 2008). Climate model simulations forecast that these mountainous systems will likely continue to trend towards an earlier onset of spring runoff (Rood et al. 2008), warmer drier summers (Westerling et al. 2007), reduced summer flows, increased late summer drought (Pederson et al. 2010),

and warmer summer stream temperatures (Jones et al. 2014; Isaak et al. 2015). Despite future forecasts of climatic warming and increased variation, changes in seasonal thermal distributions of stream systems and linkages with future climate change have not been assessed across broad geographic regions of the Rocky Mountains.

Stream temperature models can be used to evaluate underlying physical processes affecting thermal dynamics in freshwater ecosystems and predict thermal distributions across space and time continuums (Webb et al. 2008). Physically based models are useful for quantifying total energy fluxes occurring at both the air-water and streambed-water interfaces, but require significant amount of data inputs (e.g., meteorological data, stream geometry, land cover classifications, riparian shading, soil moisture indices, hydrology). Therefore, physically based models are generally applied across small spatial domains, at coarse resolutions, or at individual site locations (Wu et al. 2012, MacDonald et al. 2014). Geostatistical stream temperature models are frequently used to simulate thermal changes in freshwater ecosystems and are effective for describing landscape scale patterns of climate induced temperature change and potential impacts on ectothermic organisms. Common applications of such landscape scale models include stream temperature estimation during the warmest month of the year (e.g., August), when aquatic species are assumed to be most thermally sensitive (Isaak et al. 2010, Jones et al. 2014). Generally, these models are employed in a ‘climate envelope’ type approach, where summer temperatures are used to define climatic conditions (i.e., thermal niches) under which species are likely to occur, and future distributions are forecasted by extending these relationships to future climate scenarios. Such temporally constrained models, however, are limited to spatial pattern analysis and do not allow for a holistic approach to understanding potential climate impacts on aquatic species and critical habitats. Creating frameworks that link seasonal climate patterns with stream temperature variations to forecast spatiotemporal changes in thermal distributions at the landscape scale are needed to strengthen our understanding of potential impacts to aquatic species (i.e., spatial distributions and phenology) and provide an integral resource for guiding conservation and climate adaptation strategies.

Here, we compiled a comprehensive database of stream temperature records and high-resolution climate data to predict current and future stream temperatures across one of the most ecologically diverse ecosystems in the Rocky Mountains of North America – the Crown of the Continent Ecosystem (CCE), USA and Canada. This transboundary ecosystem is considered a regional and range-wide stronghold for many native aquatic species (Hauer and Muhlfeld 2010), and spans several management jurisdictions in Montana, USA, and Alberta and British Columbia, Canada. As tools for collaborative landscape conservation and climate adaptation planning are critically needed, we provide the first broad scale analysis of spatiotemporal patterns of stream temperature change in the northern Rocky Mountains. Specifically, we used spatially explicit geostatistical stream temperature models to predict mean monthly stream temperatures across the CCE under current and future climate conditions. Simulated model results were then used to assess the magnitude and variation of predicted change across time (i.e., months) and space. The model framework described within provides a relatively simple approach for analyzing spatiotemporal patterns of climate induced change in thermal riverscapes and is potentially transferrable across domains.

2 Data and methodology

2.1 Study area and stream temperature data

The CCE (72,000 km²) is considered the hydrologic apex of North America and source for three major continental river drainages, the Columbia, Missouri, and Saskatchewan, that flow to the Pacific, Atlantic, and Arctic Oceans, respectively. The CCE is bounded by the Rocky Mountain Trench on the west and the prairie foothills on the east, while the interior consists of a complex topographic landscape shaped from belt series mountain ranges, with elevational gradients ranging from 740 m to 3338 m. As a result, the region consists of headwaters streams that originate in high alpine environments, subalpine streams that flow through forested watersheds, and low-elevation or valley bottom streams, which are generally characterized by alluvial floodplains. The ecosystem is composed of watersheds in various stages of deglaciation - large valleys where glaciers retreated 15,000 years ago and high-elevation valleys where glaciers are still retreating today (Pederson et al. 2007). Climate is driven by a unique convergence

of climate zones along the narrowest point along the Rocky Mountain cordillera. Pacific Northwest Maritime weather patterns control the climate west of the Continental Divide and continental air masses (e.g., northern boreal Arctic, and eastern Great Plains) moving from the north and south drive climate patterns east of the divide (Hauer et al. 2007).

We assembled an extensive stream temperature database consisting of ~4 million bi-hourly measurements from natural resource agencies throughout the CCE. Monitoring sites ranged from mainstem rivers to forested headwater and alpine streams, including glacial and lake systems. Stream temperatures were recorded at 743 sites ($N_{\text{summer}} = 720$; $N_{\text{fall}} = 297$; $N_{\text{spring}} = 407$) during the years of 1990-2013 (Fig.1) with digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy $\pm 0.2^{\circ}\text{C}$) at bi-hourly or hourly intervals. Temperature measurements were then summarized to mean monthly temperatures for each site and year of the study period.

2.2 Model drivers and hydrography

First order processes influencing thermal heterogeneity of freshwater ecosystems begin at the largest spatial scale and include regional and seasonal climate patterns (i.e., temperature and precipitation; Kelleher et al. 2011). Because air temperature has strong direct (i.e., sensible heat transfer and long-wave atmospheric radiation) and indirect effects (i.e., hydrologic patterns, climate warming) on stream temperatures, it is commonly used in statistical stream temperature prediction as a surrogate to net radiation exchange (Webb et al. 2008). Therefore, we used Daymet air temperature surfaces (1km resolution; Thornton et al. 2012) that were temporally joined to each site specific temperature record as the principle climate driver influencing stream temperature. This statistical approach relies on the correlative and linear nature of the air-water temperature relationship to predict climate induced stream temperature change (Benyahya et al. 2007). Because this relationship fails to remain linear at the lower bounds of the air temperature range, near or below 0°C (e.g., when air temperatures are below the freezing limit; Letcher et al. 2016), the winter season was excluded from subsequent analyses.

Local topography can cause climate patterns to deviate from regional trends influencing temperature gradients and creating microclimates (Loarie et al. 2009). Therefore, topographic predictor variables (elevation, slope, and aspect) were used to represent second order effects (i.e., watershed scale) accounting for geomorphic features influencing stream temperature. Third order effects included the presence of lakes and glaciers at the stream reach scale. Because model simulations predict that most glaciers in the CCE will disappear by 2030 (Hall and Fagre 2003), our model simulations included a null glacier effect for all future climate scenarios. A *month effect* was also included in each seasonal model to account for temporal variation found at the monthly time scale.

Due to the transboundary nature of the CCE, a stream network was developed by merging USGS National Hydrographic Datasets (NHD) with NHD Harmonized datasets for the U.S.-Canada transboundary watersheds, and National Hydrographic Networks datasets for the remaining watersheds in Alberta and British Columbia. All covariates were attributed to stream temperature records at the individual locations for model parameterization and then to the stream network (106,700 km; 100 m resolution) for model interpolations.

2.3 Geostatistical models and climate change analysis

Because temperature variation is driven by seasonal processes and patterns, seasonal temperature models were used to predict monthly stream temperatures across the CCE. Seasons were partitioned based on historic temperature data and monthly correlations as follows: summer (July, August, and September: $n = 2301$); fall (October and November: $n = 1150$); and spring (April, May, and June: $n = 1716$). A spatial hierarchical model framework (e.g., mixed effect generalized linear regression model) was used to parameterize seasonal temperature models (SAS version 9.4; Jones et al. 2014). Watershed divisions (Hydrologic Unit Code 4) were treated as a random effect to account for spatial autocorrelation among sample sites. The Akaike Information Criterion (AIC) was used to subset the best set of fixed-effects across all models, while a combination of forward and backward stepwise elimination methods was used to remove insignificant parameters, resulting in the most parsimonious model with fewest predictor variables. We used cross-validation to compare the predictive accuracy of each model, where

data was split into a training set and a validation set composed of an equal percentage (10%) of sites randomly sampled from each watershed (Hydrologic Unit Code 4). Root mean square error of model predictions (RMSE) and Pearson correlation coefficients (r) between predicted and observed values were used to assess predictive accuracy of each model iteration. Prior to model interpolations, each model was refit to the pooled set of observations from the training and validation sets.

Coupled models from the Canadian Centre for Climate Modeling and Analysis and the Intercomparison Project 5 (CMIP5) were used as the basis for the future climate projection analysis, where the Canadian Regional Climate Model 4 (CanRCM4) is nested within the second generation Canadian Earth System Model 2 (CanESM2). Two Representative Concentration Pathway (RCP) scenarios, RCP 4.5 and RCP 8.5, from the Fifth-Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC 2013) were chosen to describe future climate warming. The RCP scenarios are based on the peak or stabilization value of the radiative forcing by 2100. These scenarios span a range of greenhouse gas emission scenarios between moderate (RCP 4.5) and extreme scenarios (RCP 8.5). The RCP 4.5 scenario accounts for stabilization at 4.5 Watts/meter² (Wm²) around 2100, while the RCP 8.5 scenario implies a radiative forcing of 8.5 Wm² by 2100 and further rising beyond this point.

Simulating future stream temperatures based on climatic changes relies on predictive models that predict baseline conditions from which future changes can be assessed (Elliott and Elliott 2010). For the *baseline* model simulations, mean monthly air temperature surfaces (Daymet) were summarized for the period (1986-2005) and used in the seasonal models to predict average monthly temperatures. Global temperature anomalies, whether above or below historic averages are directly reflected in thermal distributions of freshwater ecosystems (Isaak et al. 2012). To evaluate model capability of capturing year to year variability within the *baseline* period, stream temperature predictions were created for a colder than average year (1993) and a warmer than average year (2003). Climate records indicate 1993 was the last year that daily average lows outnumbered daily record highs, while 2003 was one of the top 10 warmest years on record (Pederson et al. 2010, NOAA 2015). To predict future conditions, gridded air

temperature changes from the RCP 4.5 and 8.5 scenarios (1-km resolution) were summarized for the near-future 2026-45 (2035) and mid-future periods 2066-85 (2075). These surfaces were then added to the *baseline* surfaces and used in a delta-change approach to assess future air temperature warming effects on stream temperatures.

To estimate the magnitude of stream temperature change predicted from the climate simulations, we calculated mean absolute and relative change (i.e., percent change) from the *baseline* to future periods and examined potential shifts in the onset and duration of seasonal temperatures based on current temperature regimes. Additionally, thermal maps of absolute change were generated to describe spatial and temporal variation across the stream network. Variability (i.e., dispersion) of model predictions was evaluated by calculating the coefficient of variation (CV), while Kolmogorov-Smirnov nonparametric tests were used to examine statistical significance of change in thermal distributions (i.e., empirical distribution functions) between the *baseline* and future scenarios.

3 Results

3.1 Stream temperature models

Seasonal models were parameterized with *air temperature, elevation, slope, lake, glacier, and month* covariates. All predictors were statistically significant ($p < 0.05$) and parameter signs in agreement with their expected influence across seasons (Table 1). We chose seasonal models that performed best with the validation data (*spring*: $r = 0.90$ and $RMSE = 1.31^{\circ}C$; *summer*: $r = 0.90$ and $RMSE = 1.38^{\circ}C$; *fall*: $r = 0.86$ and $RMSE = 1.06^{\circ}C$) and retained good predictive ability with the training data (*spring*: $r = 0.91$ and $RMSE = 1.17^{\circ}C$; *summer*: $r = 0.90$ and $RMSE = 1.23^{\circ}C$; *fall*: $r = 0.90$ and $RMSE = 0.91^{\circ}C$; Table 1). A significant warming effect of stream temperature was observed for all sites downstream of lakes ($p < 0.0001$); this effect was estimated at $+3.05^{\circ}C$ during the summer season, $+1.53^{\circ}C$ during the fall season, and $+0.83^{\circ}C$ during the spring season. Conversely, a significant cooling effect was observed for sites downstream of glaciers ($p < 0.0001$). This effect was estimated as a $-2.15^{\circ}C$ cooling effect during the summer season, $-0.79^{\circ}C$ during the fall season, and $-1.61^{\circ}C$ during the spring season. The model clearly captured year to year variability in thermal conditions for two years representing global

anomalies in historic air temperatures (Fig. 2); average stream temperature for 1993 was 8.7°C and average temperature in 2003 was 11.9°C.

3.2 Predicted stream temperature change

Projections under moderate and extreme climate change scenarios forecast that the largest increases in stream temperatures will occur during the summer months (July, August, and September). While predicted temperature increases for the RCP 4.5 and 8.5 scenarios were similar in magnitude for 2035, predicted increases under the RCP 8.5 scenario were about 40 – 100% greater than the RCP 4.5 scenario for 2075 (Table 2). Thermal distributions show that for all future climate simulations mean July stream temperatures are predicted to exceed *baseline* August conditions (Fig. 3). Similarly, September stream temperatures are predicted to approximate *baseline* August temperatures for all future climate scenarios except RCP 8.5 (2075) where temperatures are anticipated to far exceed average August temperatures (Fig. 3). Relative change statistics show notable increases for the shoulder months of winter (i.e., April and November), while relative changes are considerably lower for May and October (Table 2). Although calculations of CV reveal high variability in model predictions for spring, particularly April, variability for the summer and fall months is comparably low (Table 2). Kolmogorov-Smirnov tests for significant change between the *baseline* and future scenarios were statistically significant ($p < 0.0001$), indicating significant differences in the empirical distributions of temperatures.

Spring model simulations show that spatial warming patterns for April and May vary longitudinally, increasing from east to west, whereas warming patterns for June are strongest in the southern and central portions of the ecosystem (Fig. 4-5). Warming patterns for the summer months are most prominent in the central portion of the ecosystem, which consists of montane watersheds and higher elevation streams (Fig. 6-7). Fall patterns are highly variable minus a clear pattern in the mid-future November simulations which shows increased warming in the western extents with maximum warming occurring in the lower elevation streams around Flathead Lake in Montana (Fig. 8-9).

4 Discussion and summary

4.1 Climate effects on seasonal stream temperature distributions

For mountain ecosystems, such as the northern Rocky Mountains, atmospheric warming has resulted in temporal shifts in seasonal windows, including a later onset of fall and winter and earlier onset of spring and summer (Pederson et al. 2010). These patterns have led to a narrowing of the winter season and extended duration of the summer season. Our results suggest similar patterns are expected for stream temperature regimes throughout the northern Rocky Mountains. *Baseline* model simulations show the warmest average stream temperature conditions are observed during August. Our future model simulations predict the most significant increases will occur during the summer months, where thermal conditions characteristic of current August regimes are predicted to be exceeded during July and September. These results imply that stream temperatures consistent with current August temperatures are likely to begin a month earlier (July) and persist a month later (September), resulting in an earlier onset and extended duration of warm summer stream temperatures. Seasonal models also predict that forecasted temperature increases during the shoulder seasons of spring and fall (April and November) may be larger in magnitude relative to current conditions, with the most dramatic temperature changes occurring in the seasonal transitions into and out of winter (i.e., shortening of the winter season). These results indicate that future climate warming is likely to result in seasonal shifts in stream temperatures in the northern Rocky Mountains, including an earlier onset of temperatures characteristic of spring and summer and later onset of temperatures characteristic of fall and winter.

Stream temperature predictions during the summer months show increased warming throughout the central mountainous regions of the CCE. In addition, glacial-fed streams may observe warming rates 50% larger in magnitude with the complete loss of glacial masses. These findings corroborate other studies suggesting that mid-latitude, high-elevation mountainous systems are particularly sensitive to recent and projected climate change (Diaz et al. 2003), due to enhanced warming effects from lower surface albedo and decreased exchanges of latent energy fluxes (Rangwala and Miller 2012). Other studies have also shown that minimum air temperatures are rising faster than maximum air temperatures

in these mountainous regions, a trend notably observed during the summer months (Pederson et al. 2010, IPCC 2013). Furthermore, temperature changes in streams located along the 0°C isotherm are likely to be heightened due to significant changes in snowpack patterns, which in turn influence surface albedo feedbacks, soil moisture content, evaporation rates, and vegetation composition (Pepin and Lundquist 2008). As anthropogenic warming increases, causing a decrease in winter snowpack and an earlier onset of spring snowmelt, late summer drought conditions in montane stream systems may be exacerbated, which are likely to increase the magnitude of future stream temperature warming (Cook et al. 2015).

4.2 Model uncertainty and future research needs

Evaluation of model predictions show decreased uncertainty in the summer and fall models, while variability in spring predictions were relatively high. In snowmelt driven systems, such as the CCE, annual stream flow regimes are driven by accumulation of winter snow-pack, spring precipitation rates, and the seasonal timing of snowmelt (Pederson et al. 2011). Thermal variations during the spring season, therefore, are strongly influenced by hydrologic processes (i.e., snowmelt, rain vs. snow, flow accumulation). The relatively high variation of predicted change (CV) for April simulations indicates some level of uncertainty in model predictions. Summer and fall stream temperatures are highly correlated with ambient air temperatures and are less influenced by hydrology due to observed baseflow conditions. Because air temperature is the main climatic driver in model simulations, CV found in the summer and fall models is relatively low. April uncertainty is likely reflected in model parameterization, indicating a need for a more process based approach (i.e., hydrology) for analyzing climate impacts. Climate models predict that warmer winter temperatures are likely to result in a significant decrease in winter snowpack and a higher frequency of rain on snow events (Klos et al. 2014). While statistical models are useful for inferring landscape scale patterns, evaluating complex ecosystem process feedbacks and interactions and incorporating this information into landscape-scale analysis remains a challenge.

Complex interactions and feedbacks between regional scale (e.g. climate patterns), watershed scale (e.g., topography) and channel or stream reach processes (e.g. riparian shading, geomorphology, evapotranspiration, groundwater) influence spatiotemporal patterns of thermal heterogeneity (Allan

2004). Landscape scale analyses provide insights into the broad patterns of ecosystem response and are useful to describe the relative nature of change across broad geographic areas. However, these approaches generally do not capture thermal variations occurring at the lowest hierarchical levels of stream networks, such as specific habitat units or stream reach scales (i.e., groundwater, riparian shading, channel depth; Snyder et al. 2015). Recent studies have questioned the non-stationarity of processes across spatial and temporal domains and scales and have begun to emphasize the importance of geomorphology, hydrology, and ecosystem processes influencing stream temperature variation and the potential of these controls to mediate the sensitivity of thermal warming to climatic changes (Arismendi et al. 2014, Khamis et al. 2015, Lisi et al. 2015). In the application of statistical stream temperature models the non-stationarity of heat flux process extends to the assumed air-water temperature relationship. By developing seasonal models, we demonstrate the temporal variability of the air-water temperature relationship. This dynamic approach allows for the air-water temperature relationship and contributing response from predictor variables to vary across seasons. It is less certain, however, in what manner these relationships may change as models are extrapolated outside the spatial and temporal domains of the data and into the future (Arismendi et al. 2014).

4.3 Model application

The CCE was recently selected as one of the seven new *Resilient Landscapes* to highlight landscape scale management approaches toward building climate resilience through cooperative, inter-agency institutions and partnerships in the United States and Canada (USDA 2014). This study was developed as part of a decision support framework for setting conservation goals and implementing climate adaptation strategies for conservation of aquatic species and habitats in the CCE. Specifically, we provide a spatial and temporal framework for identifying future cold-water refugia and predicting future shifts in distributions of thermally suitable habitats and critical life history traits of aquatic organisms in the CCE. Ectothermic organisms are particularly sensitive to stream temperature warming because thermal distributions within rivers and streams influence physiology, survival, performance, abundance, distribution, and phenology (Schindler 2001). Rising stream temperatures will likely cause the

distributions of many species to shift or contract as they differentially track their thermal niches (Isaak and Rieman 2013), and depending on thermal tolerances of a given species may result in increased thermal stress, particularly during the summer months. Thermal changes during spring and fall are likely to drive species response to temperature optimums and thermal cues related to critical life history traits (i.e., reproduction and migration cues). For aquatic species, adaptations to climate induced stream temperature variations will require phenotypic (short-term) or genetic (long-term) responses based on physiological and behavioral sensitivities to change (Muñoz et al. 2015b). Such capacities for adaptation are key determinants of how populations and species can persist into the future. This study provides a useful research and conservation management tool for assessing aquatic species' impacts and vulnerabilities to both short-term and long-term temperature change (Crozier et al. 2008).

Climate in the next century will likely be characterized by shifts in global weather patterns and climate regimes, with increases in mean temperatures, changes in patterns of precipitation, and increasing incidence of extreme climatic events (IPCC 2013). Impacts of climate change on plant and animal species, and ecosystems can already be observed (Parmesan and Yohe 2003). However, considerable uncertainty remains concerning the extent of change on a regional basis (Harris et al. 2006). For freshwater ecosystems, biotic exchange (i.e., non-native invasions) may be most at risk to climatic change (Sala et al. 2000). In the CCE, ecological connectivity is one of the primary factors driving biotic resilience and both terrestrial and aquatic habitat fragmentation threatens biological diversity. Predicting biological response to climate change, therefore, plays an important role to informing scientists and decision makers of potential risks and providing a means to support the development of proactive strategies to reduce climate impacts on species and biodiversity. Our models provide spatially explicit climate change projections of seasonal stream temperature warming and a crucial decision support tool for guiding conservation and climate adaptation strategies in one of the most biodiverse aquatic ecosystems in North America.

Authors Attribution

L.A.J., C.C.M., and L.A.M. designed the study. L.A.J. and C.C.M. collected and assembled the data. L.A.J. performed analysis, modeling and cartography; L.A.J. and C.C.M. wrote the paper. All authors discussed the results and commented on the manuscript.

Table 1 Parameter estimates and summary statistics for seasonal stream temperature models

Model Coefficients	<i>b</i> (SE)	<i>p</i> -value	<i>Pooled data</i>		<i>Training data</i>		<i>Validation data</i>	
			<i>r</i>	<i>RMSE</i>	<i>r</i>	<i>RMSE</i>	<i>r</i>	<i>RMSE</i>
Spring hierarchical model			<i>n = 1716</i>		<i>n = 1539</i>		<i>n = 177</i>	
Intercept	8.05 (0.65)		0.91	1.16	0.91	1.17	0.90	1.31
Elevation	-0.004 (0.0002)	<0.0001						
Slope	0.021 (0.0006)	0.0002						
Air temperature	0.37 (0.02)	<0.0001						
Lake effect	0.83 (0.09)	<0.0001						
Glacier effect	-0.61 (0.17)	0.0005						
Month - <i>April</i>	-1.03 (0.22)	<0.0001						
<i>May</i>	-0.89 (0.11)							
<i>June</i>	0.0 (0.0)							
Summer hierarchical model			<i>n = 2301</i>		<i>n = 1954</i>		<i>n = 347</i>	
Intercept	7.32 (0.52)		0.90	1.2	0.90	1.23	0.90	1.38
Elevation	-0.003 (0.0001)	<0.0001						
Slope	-0.038 (0.006)	<0.0001						
Air temperature	0.613 (0.02)	<0.0001						
Lake effect	3.05 (0.09)	<0.0001						
Glacier effect	-2.15 (0.18)	<0.0001						
Month - <i>July</i>	-1.06 (0.11)	<0.0001						
<i>August</i>	-0.29 (0.10)							
<i>September</i>	0.0 (0.0)							
Fall hierarchical model			<i>n = 1150</i>		<i>n = 1054</i>		<i>n = 96</i>	
Intercept	5.56 (0.30)		0.89	0.93	0.90	0.91	0.86	1.06
Elevation	-0.002 (0.0002)	<0.0001						
Slope	0.012 (0.005)	0.02						
Air temperature	0.29 (0.02)	<0.0001						
Lake effect	1.53 (0.08)	<0.0001						
Glacier effect	-0.79 (0.14)	<0.0001						
Month - <i>October</i>	1.27 (0.10)	<0.0001						
<i>November</i>	0.0 (0.0)							

Table 2 Monthly change statistics representing magnitude, variation, and significance under RCP 4.5 and 8.5 scenarios

Month	Baseline	Absolute Δ ($^{\circ}\text{C}$)				CV				Relative Δ (%)			
		RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5	
		2035	2075	2035	2075	2035	2075	2035	2075	2035	2075	2035	2075
April	3.86	0.53*	0.89*	0.42*	1.27*	23.74	20.62	42.45	12.60	16.95	28.15	13.56	40.27
May	5.02	0.43*	0.85*	0.3*	1.17*	13.98	12.86	26.30	8.62	11.25	22.30	7.91	30.54
June	6.78	0.69*	1.2*	0.73*	1.7*	12.06	5.28	11.22	4.88	12.83	22.44	13.39	31.63
July	9.84	1.38*	2.52*	1.66*	3.84*	11.03	7.16	9.14	4.48	16.93	30.95	20.21	46.69
August	10.42	1.5*	2.63*	1.9*	4.35*	11.98	7.95	9.28	6.40	17.04	29.82	21.55	49.20
September	7.99	1.84*	2.18*	1.24*	4.41*	9.86	7.23	12.73	3.31	28.93	34.20	19.53	69.88
October	4.64	0.34*	0.72*	0.52*	1.23*	16.54	8.12	12.19	4.88	8.61	17.85	13.00	30.47
November	2.35	0.53*	0.68*	0.41*	1.19*	11.23	13.53	9.72	5.58	24.96	32.06	19.52	57.23

* statistically significant kolmogorov-smirnov test ($p < 0.0001$)



Fig. 1 Stream temperature monitoring sites ($N = 743$ sites) in the Crown of the Continent Ecosystem, USA and Canada. Temperature was measured using digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy $\pm 0.2^{\circ}\text{C}$) that recorded temperatures at bi-hourly or hourly intervals

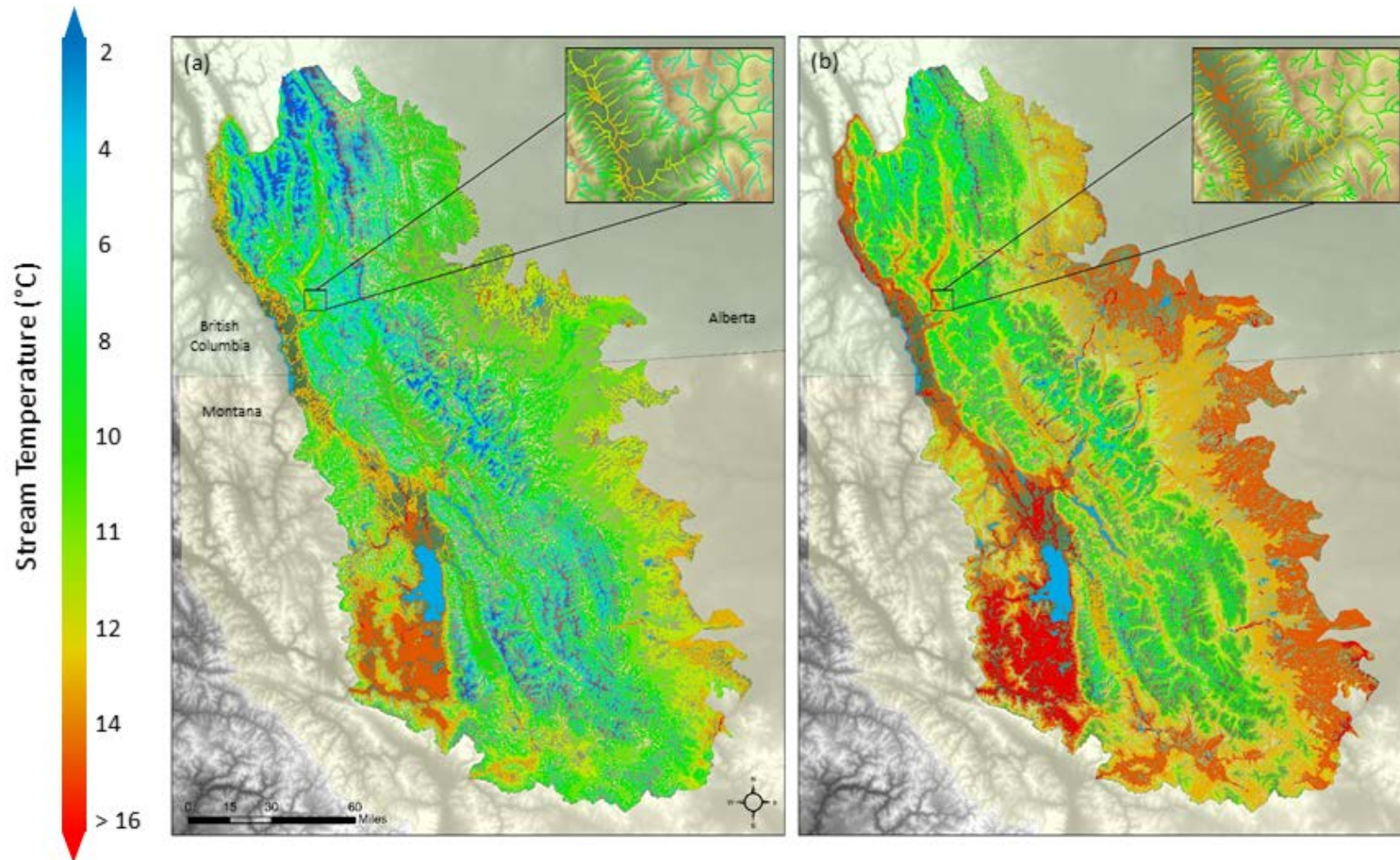


Fig. 2 Average August stream temperatures ($^{\circ}\text{C}$) are shown for 1993 (a), a colder than average year and 2003 (b), one of the top ten warmest years on record

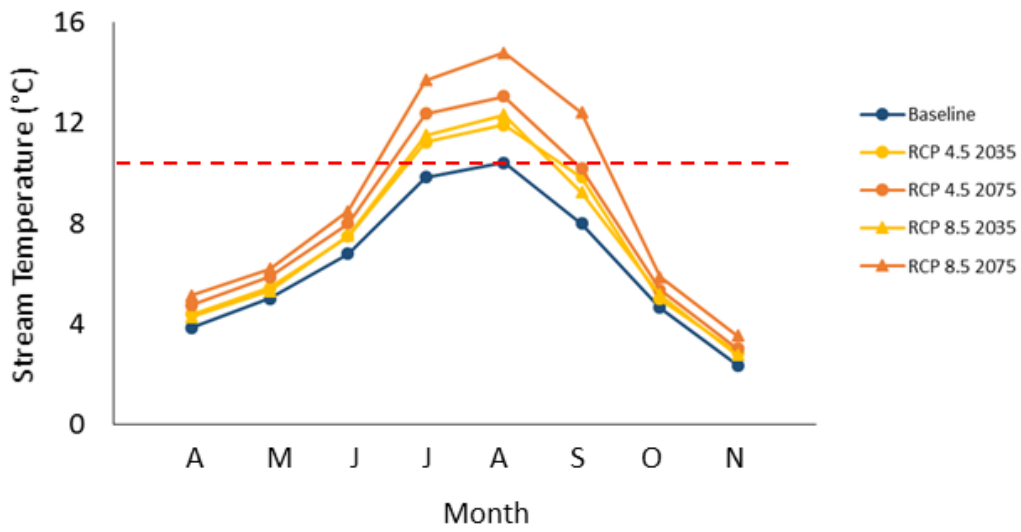


Fig. 3 Mean monthly stream temperatures under *baseline* (1986-2005) and future climate scenarios. Warmest temperature regimes under *baseline* simulations (August) are emphasized with red dotted line. See Table 1 for details including mean stream temperatures, predicted change, and coefficient of variation

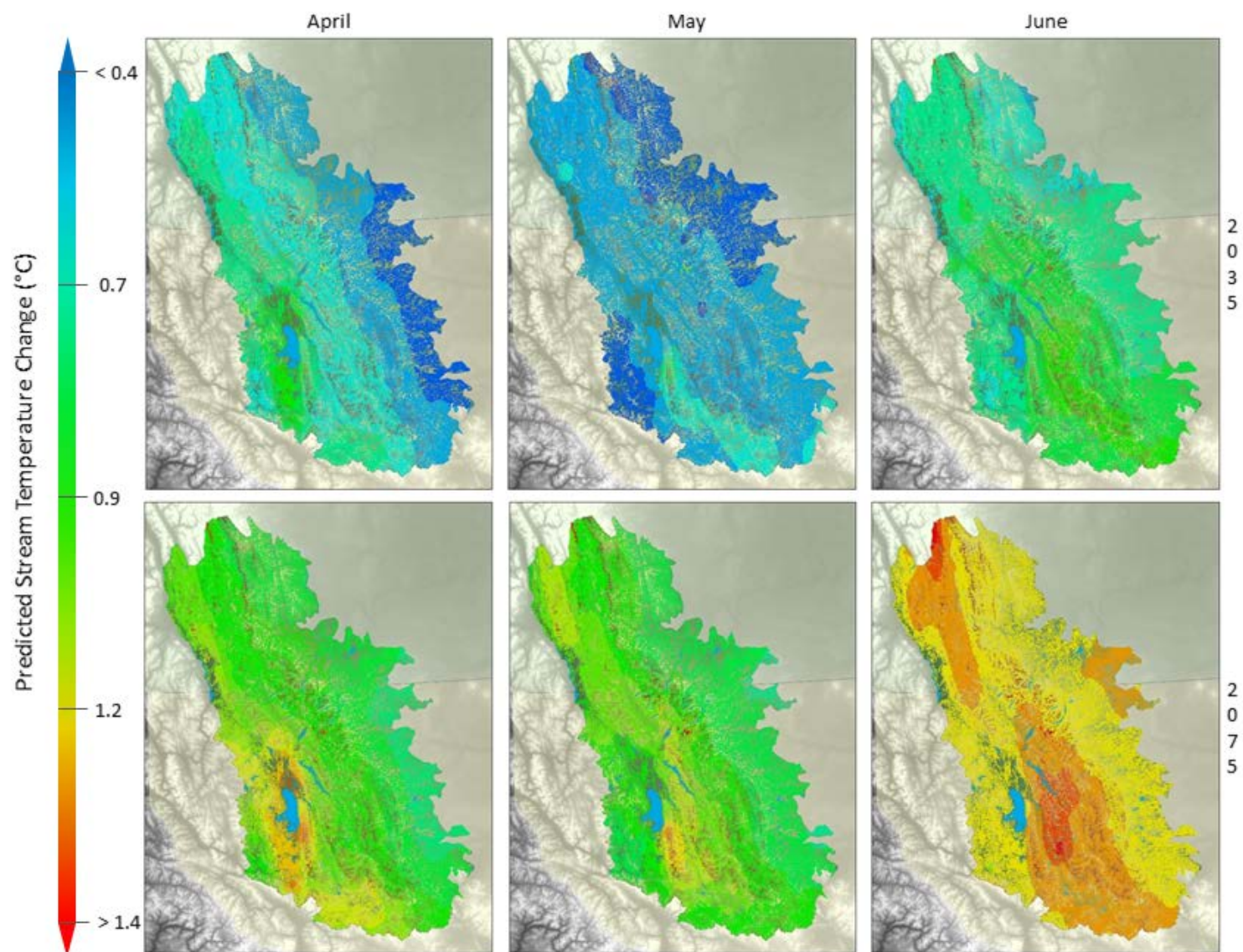


Fig. 4 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the *baseline* and RCP 4.5 scenarios for spring season (April, May, and June)

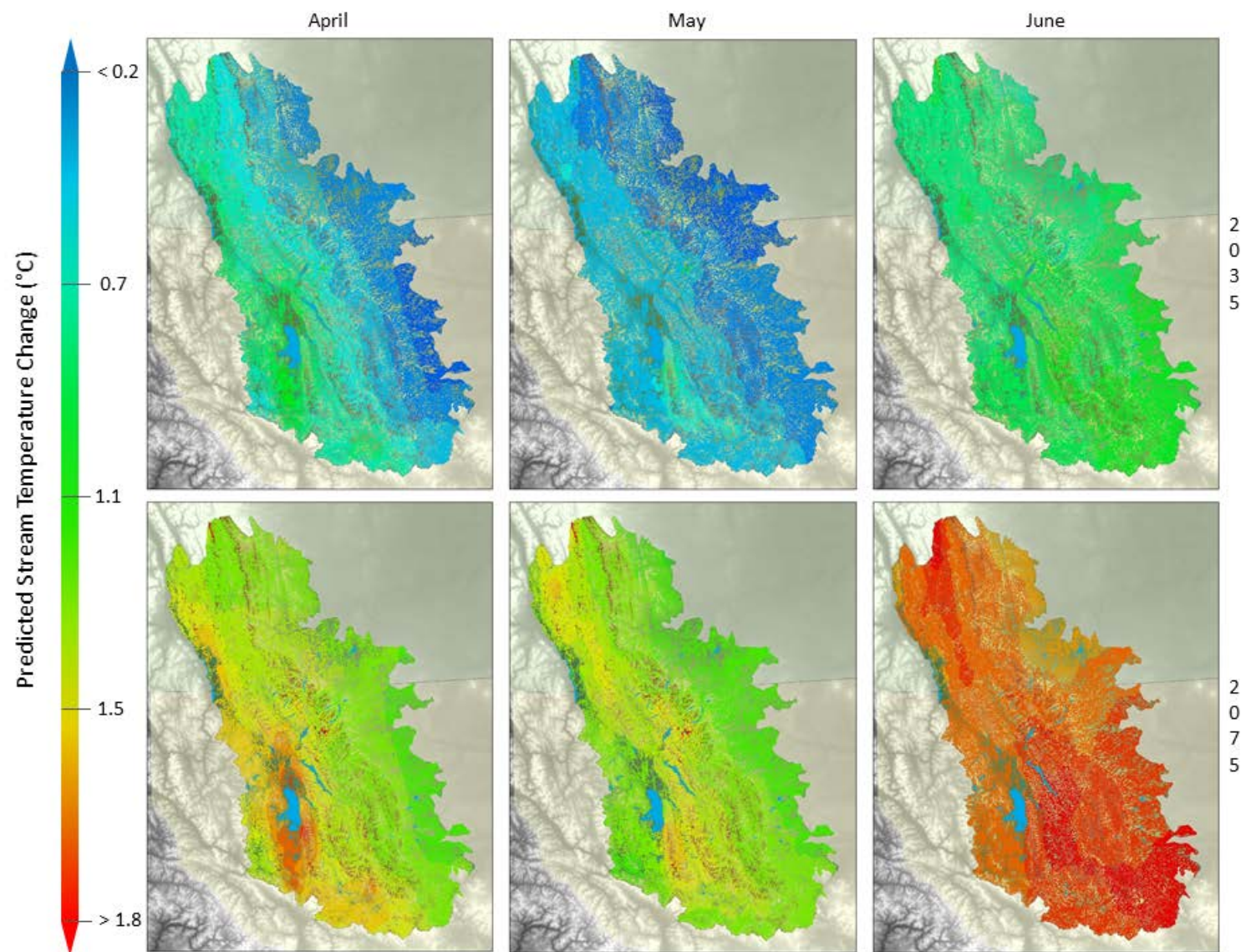


Fig. 5 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the *baseline* and RCP 8.5 scenarios for spring season (April, May, and June)

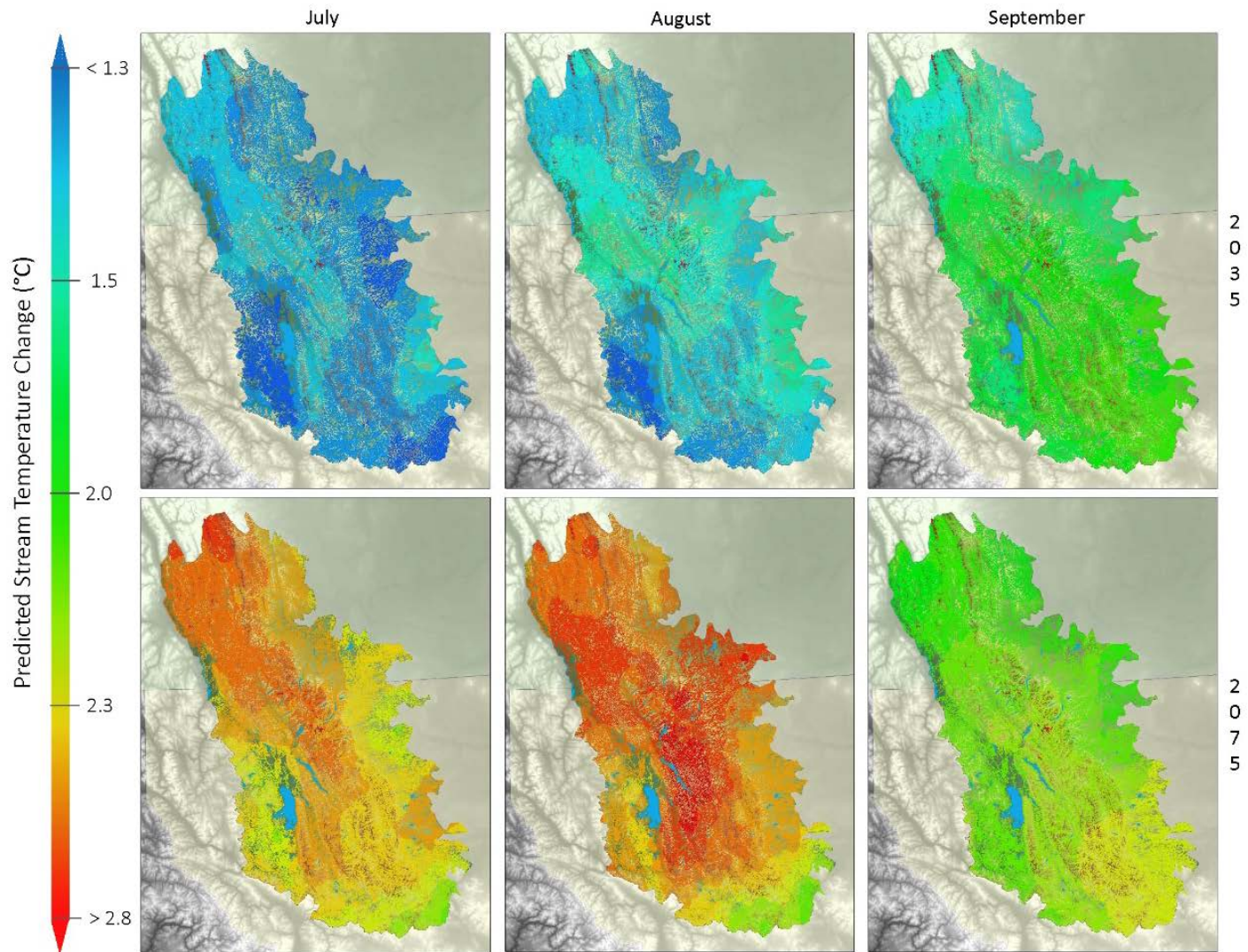


Fig. 6 Predicted absolute stream temperature warming (°C) between the *baseline* and RCP 4.5 scenarios for summer season (July, August, and September)

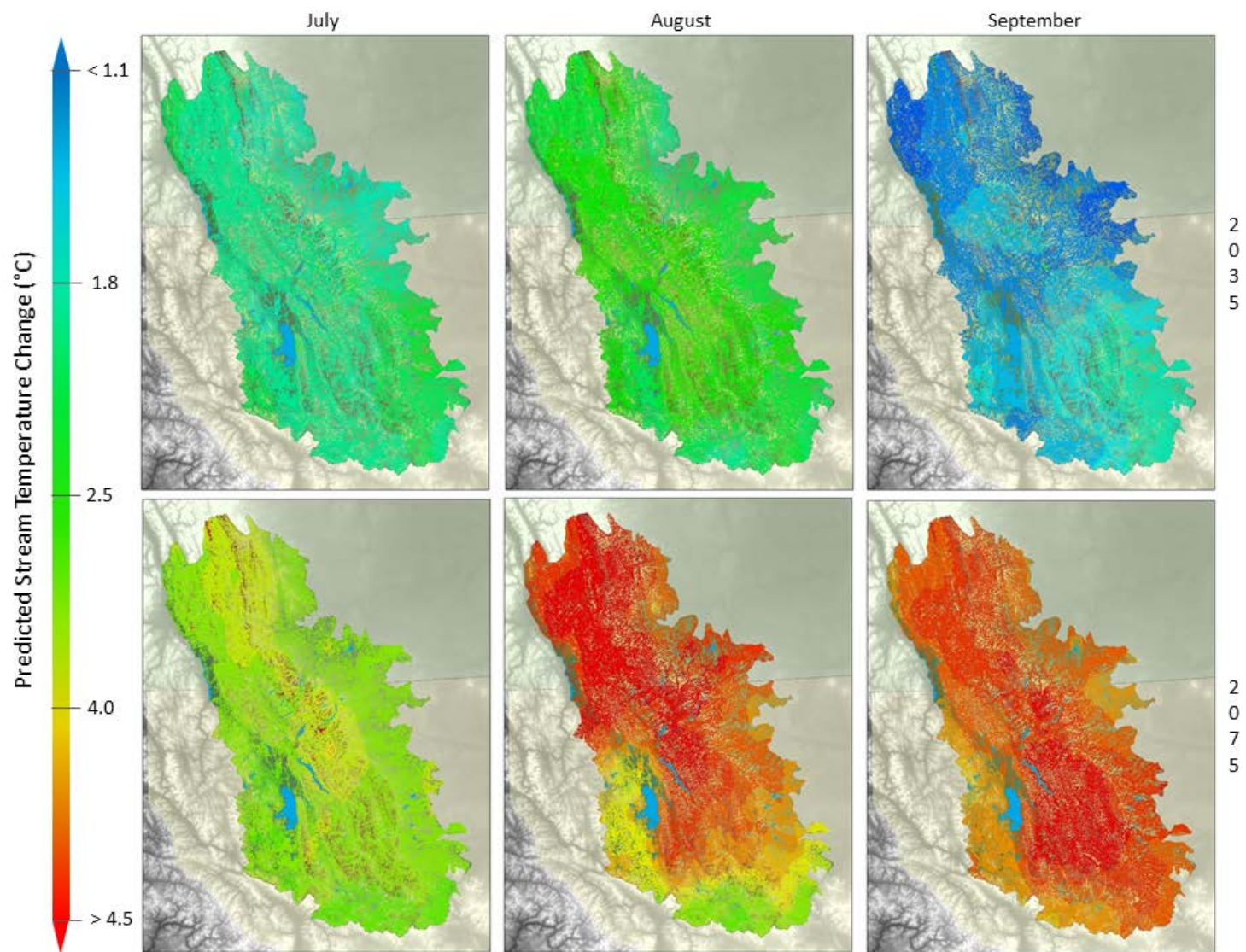


Fig. 7 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the *baseline* and RCP 8.5 scenarios for summer season (July, August, and September)

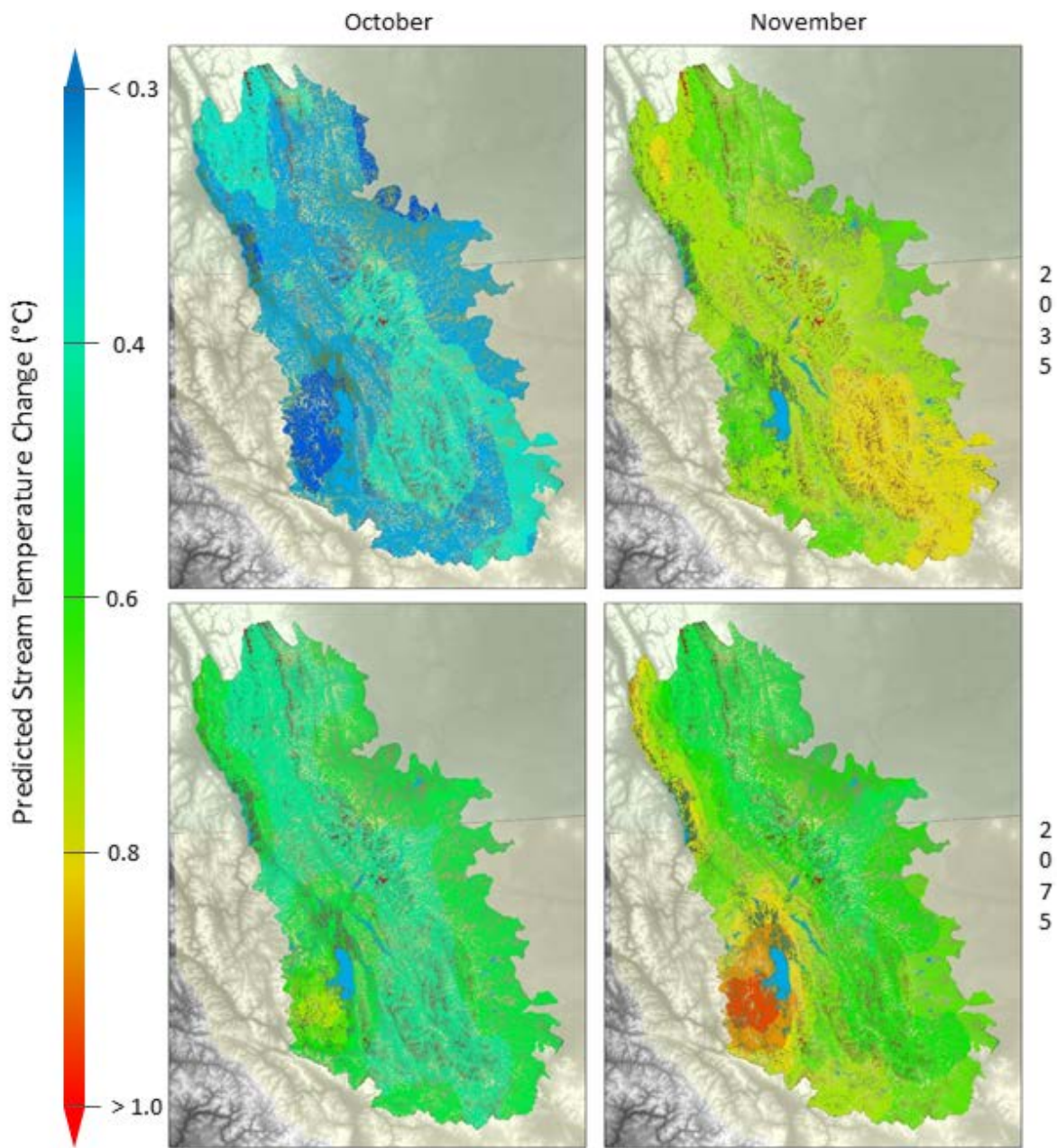


Fig. 8 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the *baseline* and RCP 4.5 scenarios for fall season (October and November)

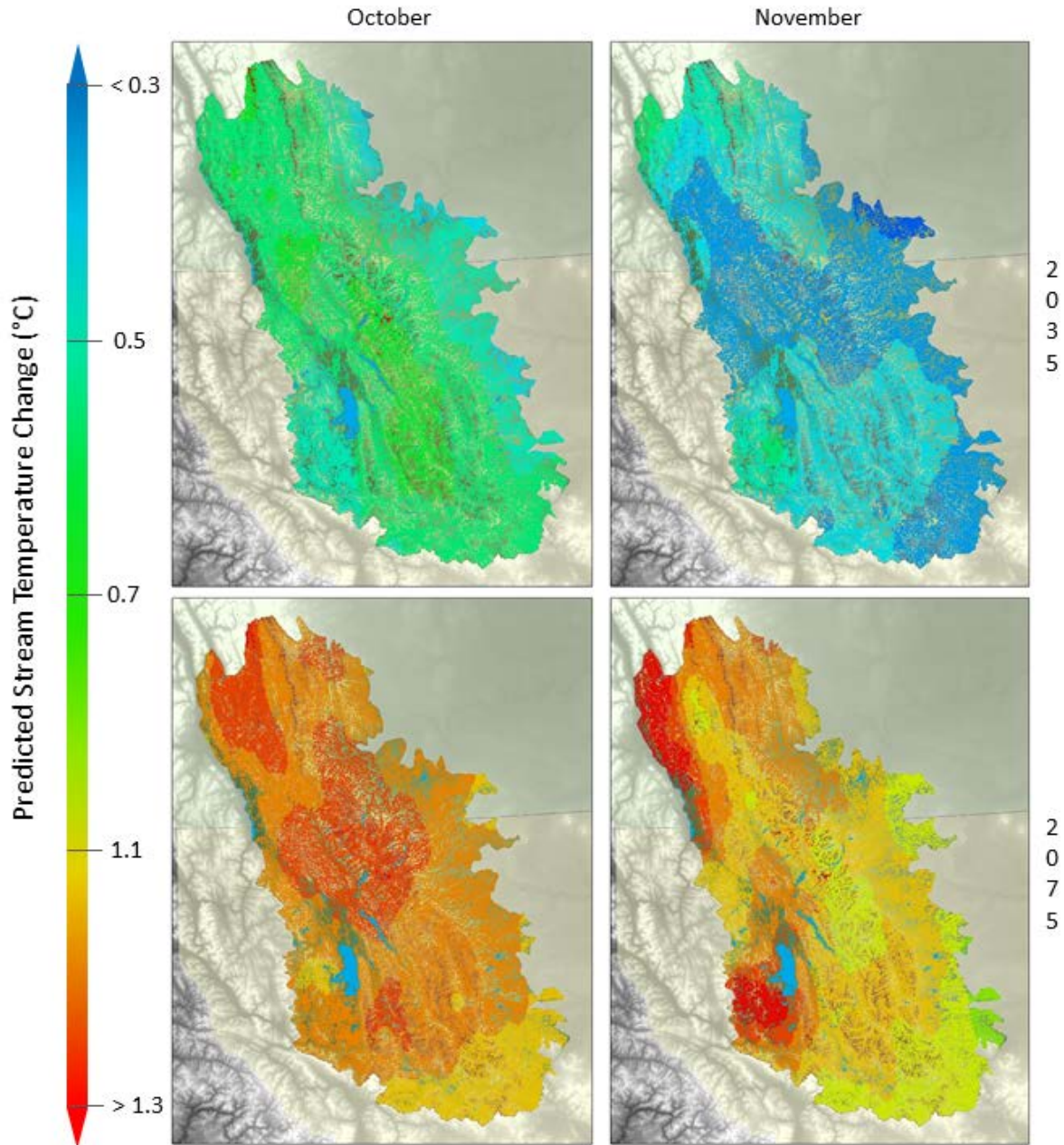


Fig. 9 Predicted absolute stream temperature warming ($^{\circ}\text{C}$) between the *baseline* and RCP 8.5 scenarios for fall season (October and November)

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Chapter 4:

Spatiotemporal impacts of climate-induced stream temperature warming on bull trout: a multi-scalar analysis in the Crown of the Continent Ecosystem, USA and Canada

Leslie A. Jones^{1,2}, Clint C. Muhlfeld^{1,3}

¹ U.S. Geological Survey, Northern Rocky Mountain Science Center, West Glacier, MT, USA

² Department of Biological Science, University of Montana, Missoula, MT, USA

³ Flathead Lake Biological Station, University of Montana, Polson, MT, USA

Leslie Jones: lesliejones123@gmail.com; 406-223-2827; fax (406) 888-7923

Clint Muhlfeld: cmuhlfeld@usgs.gov; 406-600-9686; fax (406) 888-7923

Abstract

Context Climate change is dramatically altering thermal regimes of freshwater ecosystems worldwide, yet future shifts in seasonal thermal regimes and potential impacts on cold-water species and their habitats are poorly understood. There is an imperative need for decision support tools that provide multi-scalar assessments of climate-induced spatiotemporal changes for climate adaptation planning and mitigation.

Objective We forecast climate-induced stream temperature patterns throughout the Crown of the Continent Ecosystem, USA and Canada (104,700 km stream network), and evaluate impacts to critical bull trout (*Salvelinius confluentus*) habitats, one of the most stenothermic cold-water salmonids in western North America.

Methods A geostatistical model framework was used to predict monthly stream temperatures and associated change under current and future climate scenarios. Thermal riverscapes were then used to assess the magnitude of predicted warming across bull trout habitats, spatiotemporal shifts in thermal habitat distributions, and thermal sensitivities at the landscape (regional), basin (meta-population), and watershed (local population) scales.

Results Climate simulations predict that stream temperature warming will be greatest during the summer months (July, August, and September), causing a contraction of thermally optimal habitats (adult < 15°C and juvenile < 12°C) north in latitudes and higher in elevations. Meta-populations occupying the southern range are likely to be most sensitive to warming, while local populations in headwater streams and northern latitudes may be least sensitive to future climate change.

Conclusion Our spatiotemporal stream temperature modeling framework provide a means for prioritizing climate adaptation strategies for conservation of freshwater species across biological and conservation hierarchies.

Keywords: aquatic species, climate change, freshwater ecosystems, geostatistical models, phenology, salmonids, seasonal stream temperature, thermal distributions, thermal heterogeneity

Introduction

The Earth's climate has warmed 0.74°C over the past century, and global mean temperatures are projected to rise an additional 4.3 (\pm 0.7°C) by 2100 (IPCC 2013). The effects of global warming will be realized across all regions of the world, yet the nature of these impacts and associated vulnerabilities will vary geographically, resulting in regional and local effects (IPCC 2013). There is now ample empirical evidence of ecological impacts of climatic change across organizational and biological hierarchies (Walthers et al. 2002), with warming trends generally shifting species distributions towards the poles and higher altitudes (Parmesan 2006). Freshwater ectothermic organisms are particularly sensitive to climatic change because they have relatively narrow thermal range for growth and survival and optimums for key life history traits (Pörtner and Farrell 2008). Uncertainty remains, however, concerning the seasonal impacts of climate warming in freshwater environments and impacts on cold-water species at regional scales (Harris et al. 2006). Regional assessments of climate-induced warming of freshwater ecosystems, therefore, are critical for understanding how ectothermic organisms may respond to spatiotemporal shifts in stream temperature regimes, and to identify climate mitigation strategies for conservation and management programs.

The northern Rocky Mountain region of western North America is warming two to three times the rate of the global average, causing seasonal shifts in temperature and precipitation patterns (Hansen et al. 2005, Pederson et al. 2010). Climatic trends over the past several decades show substantial declines in annual snowpack, an earlier onset and reduction of spring snowmelt, and reductions in summer base flows, which are changing hydrologic and thermal regimes (MacDonald et al. 2011, Pederson et al. 2013). Stream temperatures are rising and are directly linked to long-term increases in air temperatures and associated changes in the hydrological cycle (Isaak et al. 2012). Although few long-term stream temperature records exist, reconstructions of seasonal warming trends estimate stream temperatures in the northwestern U.S. have increased up to 0.3°C/decade (1980-2009; Isaak et al. 2012). Future climate projections for the Pacific Northwest predict average annual air temperature increases of 1.1°C by the

2020s and 3.0°C by the 2080s (0.1°C to 0.6°C per decade) and a continuation of altered hydrologic and thermal regimes within freshwater systems (Mote and Salathé 2010). Despite future forecasts of climatic warming, linkages between seasonal climate patterns and thermal warming within freshwater systems of the northern Rocky Mountain region have not been assessed.

Thermal distributions within rivers and streams influence physiology, performance (e.g., optimal growth), abundance, distribution, phenology (e.g., life history traits), and survival of aquatic organisms (Schindler 2001). Salmonid fishes (i.e., trout and char) are cold-water specialists whose life histories are directly linked to environmental conditions driven by climate and stream temperature variations. The most stenothermic salmonid species in the northern Rocky Mountains is the bull trout (*Salvelinus confluentus*), which is listed as a threatened species under the U.S. Endangered Species Act, a threatened species in Alberta, Canada, and a species of special concern in British Columbia, Canada (USFWS 2010, COSEWIC 2012). Bull trout are especially vulnerable to climatic warming because they have one of the lowest upper thermal limits and growth optima of all salmonids and very narrow tolerances to thermal fluctuations (Dunham et al. 2003, Rieman et al. 2007). To assess vulnerabilities to climatic change, thermal metrics are used estimate the magnitude of climate-induced variation within habitats (i.e., exposure), the ability of a species to tolerate climatic variations (i.e., sensitivity), and the capacity of a species to conform to those changes (i.e., adaptability; Pacifici et al. 2015). Quantifying thermal metrics of exposure and associated sensitivity of ectothermic species, such as bull trout, across multiple spatial and temporal scales enables prioritization of conservation needs across organizational and biological hierarchies (Pettit et al. 2012, Whited et al. 2013).

Climate adaptation planning for cold-water species, such as bull trout, often involves identifying thermally suitable habitats (i.e., cold-water refugia) under future climate scenarios and prioritizing on-the-ground actions to mitigate climate effects. Geostatistical stream temperature models are commonly used to simulate thermal changes in freshwater ecosystems (Isaak et al. 2010, Jones et al. 2014) and are an effective tool for assessing landscape scale patterns of temperature change and impacts on ectothermic organisms. Biological model applications typically include ‘climate envelope’ approaches during the

warmest month of the year (e.g., August), when aquatic species are assumed to be most thermally sensitive, including bull trout (Isaak et al. 2010, Jones et al. 2014). In this approach, modeled stream temperatures are used to define thermal niches under which a species is likely to occur and forecasts are made by extending these relationships under future climate scenarios. Seasonal climate impacts on thermal habitat distributions of bull trout, however, have not been made and future predictions remain unknown.

Applications of fluvial landscape ecology integrate concepts of pattern, process, hierarchy, scale, and connectivity to explain relationships between system structure and function (Fausch et al. 2002, Poole 2002). In statistically based stream temperature prediction, hierarchical patterns are assumed to represent underlying physical and ecological processes influencing variation. As spatial and temporal scales (i.e., domain) of the model change, the relative importance of these processes change (Figure 1; Webb et al. 2008). The intent of landscape scale ecosystem analysis is to represent the dominant processes that explain broad patterns of variability (Waring and Running 2007). In the context of landscape scale stream temperature modeling, regional climate patterns represent the most dominant processes. It is unreasonable to assume that models at this scale can simultaneously describe stream reach level processes and characterizations (i.e., groundwater, micro-habitat). For these reasons, landscape scale models are most appropriate for population-based biological assessments, whereas stream reach scale models are more appropriate for individual organisms (i.e., habitat selection and movements). Choosing appropriate scales for biological applications of stream temperature models, therefore, is extremely important to delivering scientific tools for effective management.

In this study, we develop seasonal stream temperature models to examine spatial and temporal climate warming patterns on critical bull trout habitats in the Crown of the Continent Ecosystem (CCE), USA and Canada. Bull trout populations in the CCE are structured in a hierarchical manner, representing reproductive communities of individuals that share evolutionary histories and futures (Whitesel et al. 2004). More specifically, meta-populations are defined as a group of local, discrete and connected populations that collectively represent the regional population in the CCE (Hanski 1998, Rieman and

Dunham 2000). Our objective was to predict monthly stream temperatures under current and future climate scenarios and assess temporal shifts in thermally optimal bull trout habitats at three spatial scales: (1) landscape (regional population), basin (meta-population), and watershed scale (local populations). Our collective results provide a decision support framework for prioritizing climate adaptation strategies in the CCE.

Methods

Study Area

The CCE is one of the most intact aquatic ecosystems in North America, and is recognized as a regional and range-wide stronghold for many aquatic species, including bull trout (Prato and Fagre 2007b). The CCE is jurisdictionally fragmented encompassing northwestern Montana, USA, and southwestern Alberta and southeastern British Columbia, Canada (Figure 2; 72,000 km²), and includes five federally protected wilderness areas and the world's first International Peace Park, Waterton-Glacier International Peace Park. The CCE includes the headwaters of three major continental river drainages, the Columbia, Missouri, and Saskatchewan River drainages. Belt series mountains shape the complex interior topography, where elevational gradients range from 740 m to 3338 m. Consequently, the fluvial landscape consists of headwaters streams that originate in high alpine environments, subalpine streams that flow through forested watersheds, and low-elevation mainstem rivers, characterized by alluvial floodplains. Watersheds within the CCE are in various stages of deglaciation consisting of large valleys where glaciers retreated 15,000 years ago and high-elevation valleys where glaciers still remain (Pederson et al. 2007). Climate is driven by three unique climate zones, which converge on the narrowest point along the Rocky Mountain cordillera; Pacific Northwest Maritime weather patterns control climate west of the Continental Divide and continental air masses (e.g., northern boreal Arctic, and eastern Great Plains) moving from the north and south drive climate patterns east of the divide (Hauer et al. 2007).

Geostatistical models

Stream temperature models were forced with empirical stream temperature data collected by natural resource agencies across the study area. Stream temperatures were recorded at 743 sites

(summer=720; fall=297; spring=407) during the years of 1990-2013 with digital thermographs (Hobo and Tidbit models; Onset Computer Corporation, Pocasset, Massachusetts, USA; accuracy $\pm 0.2^{\circ}\text{C}$). These recordings were then summarized to mean monthly temperatures for each site and year of the study period. Because temperature variation is driven by seasonal processes and patterns, seasonal temperature models (summer, spring, and fall) were used to predict monthly stream temperatures. Seasons were partitioned based on historic temperature data and monthly correlations as follows: summer (July, August, and September: $n = 2301$); fall (October and November: $n = 1150$); and spring (April, May, and June: $n = 1716$).

Spatial hierarchical models (e.g., mixed effect generalized linear regression model) were used to parameterize seasonal temperature models (SAS version 9.4; Jones et al. 2014), in which watershed divisions (Hydrologic Unit Code 4) were used as a random effect to account for spatial autocorrelation found between sample sites (USGS 2013). Cross-validation was used to compare the predictive accuracy of each model, by splitting data into a training set and a validation set composed of an equal percentage (10%) of sites randomly sampled from each watershed (Hydrologic Unit Code 4). Root mean square error of model predictions (RMSE) and Pearson correlation coefficients (r) between predicted and observed values were used to assess predictive accuracy of each model iteration. In addition, residual plots and empirical semivariograms for residuals were used to test assumptions of normality and independence. Prior to model interpolations, each model was refit to the pooled set of observations from the training and validation sets.

Model drivers and hydrography

Regional climate patterns influence thermal regimes of freshwater ecosystems (i.e., temperature and precipitation; Kelleher et al. 2011). Air temperature has direct (i.e., sensible heat transfer and long-wave atmospheric radiation) and indirect effects (i.e., hydrologic patterns) on stream temperatures (citations). Because water temperature and air temperature are primarily heated through solar radiation, air temperature is commonly used as a proxy in stream temperature models for explaining net radiation exchange at the air-water interface (Webb et al. 2008). Therefore, we used Daymet air temperature raster

layers (1 km resolution; Thornton et al. 2012) that were temporally joined to each site specific stream temperature record and used as the primary driver in the seasonal models. The winter season was excluded from this analyses because statistically based stream temperature prediction relies on the correlative and linear nature of the air-water temperature relationship (Benyahya et al. 2007) and this relationship fails to remain linear at the lower bounds of the air temperature range (e.g., when air temperatures are below the freezing limit), near or below 0°C (Letcher et al. 2016).

Landscape structure as delineated by geologic history and topographic characteristics (i.e., elevation, slope, and aspect), can cause climate patterns to deviate from regional trends influencing temperature gradients and creating microclimates (Figure 1; Loarie et al. 2009). Topographic landforms define catchment structure and hydrologic divisions at a hierarchy of spatial scales (i.e., basin, watershed, stream reach). Elevation and slope (30 m resolution) were used as topographic predictors in the seasonal models to account for geomorphic features. In addition to regional and watershed scale covariates, categorical effects were used to account for the presence of lakes and glaciers at the stream reach scale. Model simulations predict that most glaciers in the CCE will fully recede over the next two decades (Hall and Fagre 2003); therefore, our models included a null glacier effect for all future climate scenarios. A *month effect* was also included in each seasonal model to account for temporal variation found at the monthly time scale.

Because the CCE is a transboundary ecosystem, a stream network was created by merging USGS National Hydrographic Datasets (NHD) for the U.S. portion, including the NHD Harmonized datasets for the U.S. - Canada transboundary watersheds, and National Hydrographic Networks datasets for other watersheds in Alberta and British Columbia. All covariates were attributed to stream temperature records at the individual locations for model parameterization and then to the stream network (100 m resolution) for model interpolations.

Climate change simulations

A coupled General Circulation Model (GCM) and Regional Climate Model (RCM) from the Canadian Centre for Climate Modeling and Analysis were used as the basis for the climate change

analysis. In this coupled model framework, the Canadian Regional Climate Model 4 (CanRCM4) is nested within the second generation Canadian Earth System Model 2 (CanESM2) and used in a delta-change approach to future air temperature warming. Two Representative Concentration Pathway (RCP) scenarios, RCP 4.5 and RCP 8.5, from the Fifth-Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) were chosen to describe future climate change. The RCP scenarios span a range of greenhouse gas emission scenarios between moderate (RCP 4.5) and extreme scenarios (RCP 8.5). The scenarios are based on the peak or stabilization value of the radiative forcing by 2100, where RCP 4.5 scenario accounts for stabilization at 4.5 Watts/m² (Wm⁻²) around 2100, while the RCP 8.5 scenario implies a radiative forcing of 8.5 Wm⁻² by 2100 and further rising beyond this point.

Use of predictive models in simulating climate change scenarios requires baseline forecasts of current or historic conditions from which future changes can be assessed (Elliott and Elliott 2010). Here, mean monthly air temperature surfaces (Daymet) for the *baseline* period (1986-2005) were used to predict average monthly temperatures under current conditions. Gridded air temperature changes from the RCP 4.5 and 8.5 scenarios (1km resolution) were summarized for the near-future 2026-45 (2035) and mid-future periods 2066-85 (2075). To forecast future stream temperatures, delta-change surfaces were added to the *baseline* layers and used to assess future air temperature warming effects on stream temperatures.

Bull trout in the Crown of the Continent

Bull trout require large, ecologically diverse, and connected cold-water habitats to complete their life cycle in the CCE (Rieman and Allendorf 2001, Muhlfeld and Marotz 2005). Bull trout grow to maturity in rivers and lakes (foraging, migrating, and overwintering areas; FMO) and then begin spawning migrations from May through July, traveling up to 250 km upriver to natal tributaries to spawn (Fraley and Shepard 1989a, Swanberg 1997). Spawning occurs from late August through early October, when water temperatures decline to below 9°C in low-gradient reaches with extensive hyporeic and groundwater-surface water exchange (Baxter and Hauer 2000; Muhlfeld et al. 2006; Bean et al. 2015). Juveniles rear in natal spawning and rearing streams (SR) 1-3 years and then emigrate (primarily during high spring flows) to the rivers or lakes (i.e., subadult phase; Muhlfeld and Marotz 2005). For this study,

we used current designations of bull trout *spawning and rearing* (SR) and *foraging, migrating, and overwintering* (FMO) habitats (Figure 2) in the CCE as defined by management agencies, including Montana Fish, Wildlife, & Parks, U.S. Fish and Wildlife Service, National Park Service, Parks Canada, Alberta Environment and Parks, and B.C. Ministry of Environment (USFWS 2010, COSEWIC 2012).

Thermal habitat distributions and multi-scalar analysis

Simulated stream temperature model predictions were attributed to bull trout SR and FMO habitats to characterize thermal regimes and habitat distributions under current and future scenarios. To estimate the magnitude of predicted stream temperature warming, we calculated mean monthly statistics of absolute and relative change (i.e., percent change) from the *baseline* to future periods for SR and FMO habitats across the CCE. Stream temperature predictions under the *baseline* scenario were used to identify optimal thermal ranges used by bull trout in SR and FMO habitats during the summer months. Thermal optimums and thresholds were then used to investigate exceedance patterns across multiple spatial scales (see below) relevant to bull trout ecology (Figure 2). At each spatial scale, stream lengths (km) of thermally suitable habitats were aggregated and used to derive percentages of total habitat under current and future climate simulations. Calculations were based on total SR or FMO habitats at each spatial scale, providing a multi-scalar approach to estimating future changes in thermally suitable habitats.

Thermal sensitivities were evaluated at three hierarchical scales: (1) landscape (regional population), (2) river basin (meta-population), and (3) watershed scale (local populations). Landscape scale analyses provide a regional assessment of bull trout across the CCE, which consists of several collective groups of meta-populations, defined as interacting breeding populations (USFWS 2010). Major river basins are generally consistent with meta-populations in the CCE and were delineated by hydrologic and biologic connectivity (i.e., major dams, reservoirs, migratory life-history). River basins include the Blackfoot, Flathead, South Fork Flathead (SF Flathead), Kootenay, Oldman, St. Mary, Elk, and Swan (Figure 2). Collective groups of local populations interact to form meta-populations (Whitesel et al. 2004). The third hierarchical scale used in this analysis were watershed divisions, which represent major

SR tributaries. Watershed divisions are consistent with local populations of bull trout within major river basins (i.e., meta-populations).

Results

Stream temperature model

Seasonal models were parameterized with hierarchical covariates: air temperature, elevation, slope, lake, glacier, and month effects (Table 1). Predictors were statistically significant ($p < 0.05$) and parameter signs in agreement with their expected influence across seasons. Random effect for watershed (HUC 4) was statistically significant (*spring*: $p = 0.02$; *summer*: $p = 0.01$; *fall*: $p = 0.03$) and plots of residuals showed that spatial autocorrelation was adequately explained and assumptions of normality were successfully met. Seasonal models performed well with the validation data (*spring*: $r = 0.90$ and RMSE = 1.31°C ; *summer*: $r = 0.90$ and RMSE = 1.38°C ; *fall*: $r = 0.86$ and RMSE = 1.06°C ; Table 1) and maintained good predictive ability with the training data (*spring*: $r = 0.91$ and RMSE = 1.17°C ; *summer*: $r = 0.90$ and RMSE = 1.23°C ; *fall*: $r = 0.90$ and RMSE = 0.91°C ; Table 1). A significant warming effect of stream temperature was observed for all sites downstream of lakes in our study ($p < 0.0001$). Seasonal models estimated this effect at $+3.05^{\circ}\text{C}$ during the summer, $+1.53^{\circ}\text{C}$ during the fall, and $+0.83^{\circ}\text{C}$ during the spring (Table 1). Similarly, a significant cooling effect was observed for sites downstream of glaciers ($p < 0.0001$). Glacial cooling effects were estimated as a -2.15°C cooling effect during the summer, -0.79°C during the fall, and -0.61°C during the spring (Table 1). Thermal riverscapes under *baseline* and RCP 4.5 scenarios for the month of August show consistent warming patterns, with the highest temperatures predicted in the southern latitudes, eastern prairies, lake affected reaches, and lower elevation mainstem rivers (Figure 3). Mean August temperature under *baseline* model simulations was 10.3°C (SD = 3.3°C), while mean temperature under 2035 and 2075 were 11.8°C (3.3°C) and 12.9°C (3.3°C), respectively.

Model application

Seasonal models predict stream temperature warming for bull trout SR and FMO habitats during the spring, summer, and fall seasons, with the greatest increases to occur during the summer months. Specifically, thermal regimes characteristic of current August temperatures may be exceeded during July and September under both near-future and mid-future scenarios (Figure 4). These results imply that stream temperatures consistent with current August temperatures are likely to begin a month earlier (July) and persist a month later (September), resulting in an earlier onset and extended duration of warm summer temperatures. Predicted temperature increases for SR and FMO habitats under the RCP 4.5 and 8.5 scenarios were similar in magnitude for 2035, while predicted increases under the RCP 8.5 scenario were about 40 – 100% greater than the RCP 4.5 scenario for 2075 (Figure 4; Table 2). Relative change statistics show notable increases in stream temperatures in SR and FMO habitats for late fall (November), late summer (September) and spring (April; Table 2).

Habitat simulations

Average monthly stream temperatures for current SR habitats ranged from 1.96°C in November to 10.34°C in August, while average conditions for FMO habitats were slightly higher and varied from 2.61°C in November to 12.56°C in August (Table 2; Figure 4). *Baseline* model simulations estimated approximately 90% of August FMO habitats at water temperatures less than 15°C. Similarly, for SR habitat, the baseline models estimated 90% of August SR habitat at water temperatures less than 12°C. These predictions were used to identify optimal thermal habitat conditions and thermal thresholds for the climate model simulations; 15°C was used as an upper thermal threshold of preferred summer habitat conditions for FMO habitats and 12°C for SR habitats.

Landscape scale analysis

Landscape scale analyses of thermal exceedance percentages during August show an upstream contraction of thermally suitable habitats. Results suggest that the regional distribution of bull trout in the CCE will be pushed further north in latitudes and higher in elevation (Figure 5). *Baseline* model

simulations show exceedance of thermally optimal temperature regimes are highest in the southern latitudes and western longitudes of the CCE (Figure 5). Models predict that as thermal warming increases, exceedance patterns for FMO habitats will shift upstream within the major river basins (Figure 5). Similarly, thermal exceedance patterns for SR habitats are predicted to shift into lower reaches of tributaries under near-future scenarios (2035) and further upstream under mid-future scenarios (2075; Figure 5). Although climate simulations predict the distribution of thermally suitable habitats under the near-future scenarios are similar for both RCP scenarios, mid-future simulations under the extreme scenario (RCP 8.5) predict that most bull trout habitats will be at risk to thermal warming during the warm summer months (Table 3 - 4).

Basin scale analysis

Basin scale analyses of thermal exceedance percentages show that the Clark Fork and Flathead River basins currently have the highest magnitude of FMO habitats thermally exceeded during August (85% and 30%, respectively; Figure 6). Near-future (2035) model simulations for RCP 4.5 and 8.5 scenarios predict the greatest decreases in thermally suitable FMO habitats will occur in the Kootenay and Flathead basins during July and August, with amplified reductions forecasted for the Blackfoot, St. Mary, and Elk basins under the mid-future (2075) scenarios (Figure 6 - 7; Table 3). Models predict thermal sensitivities of FMO habitats during August may be highest for the Kootenay, Flathead, and Blackfoot (Figure 6). For SR habitats, the Clark, Blackfoot, and Kootenay River basins currently have the highest percentage of tributary habitats thermally exceeded during August (Figure 8). Moderate climate simulations (RCP 4.5) predict the highest magnitude of change in thermally suitable SR habitats may occur within the Elk, Swan, South Fork Flathead, Flathead, and St. Mary basins (Figure 8 - 9; Table 4). Estimated reductions in thermally suitable SR and FMO habitats was lowest for the Oldman River basin under all future scenarios (Figures 6 - 9; Tables 3 - 4).

Watershed scale analysis

Watershed scale (i.e., within basin) summaries of thermal exceedance percentages show that under current conditions, lower elevation tributaries and/or lake effected tributaries are most thermally

sensitive during August (Figure 10). These patterns are most prevalent for the Blackfoot, Kootenay, and Flathead River basins. Moderate climate simulations predict significant increases in thermal sensitivities for low elevation watersheds and watersheds with limited availability of stream habitat (Figure 10). Under the mid-future scenario thermal sensitivity patterns are correlated with tributaries lower in the Flathead, SF Flathead, and Swan River basins. As climate continues to warm and stream temperatures increase, watersheds consisting of higher elevation habitats are likely to be least sensitive to thermal warming during the summer months. Tributaries within the Flathead, South Fork Flathead, and Oldman River basins have similar characteristics and are likely to be least sensitive to thermal warming. Even under extreme climate scenarios these tributaries may be identified as future areas of cold-water refugia (Figure 10). Our models also predict that current cold-water limited habitats (i.e., headwater and glacier fed tributaries) could provide thermally optimal habitats as they warm in the future.

Discussion

Linking seasonal and regional climate patterns with landscape structure help to improve our understanding of spatiotemporal climate-induced impacts on stream temperature and aquatic species distributions. Results from this study can be used as critical components to vulnerability assessments, by quantifying magnitude of predicted change (i.e., exposure) and thermal sensitivities of aquatic species, such as bull trout. This study further illustrates the importance of quantifying change across multiple spatial and temporal scales using spatially explicit predictive models to understand potential changes in habitats and populations.

Bull trout thermal preferences and sensitivities

Models predict thermal preferences for juvenile bull trout within tributary habitats (SR) during the summer months $< 12^{\circ}\text{C}$, while preferred temperatures for sub-adult and adult bull trout within mainstem habitats (FMO) were $< 15^{\circ}\text{C}$. These results are consistent with studies that have shown juvenile bull trout occurrence is typically rare where mean summer temperatures exceed 12°C (Rieman and Chandler 1999, Dunham et al. 2003, Isaak et al. 2015). Although adult bull trout have been shown to occupy habitats as much as $5\text{-}10^{\circ}\text{C}$ warmer than juvenile bull trout (Howell et al. 2010), mean summer

water temperatures exceeding 15°C limit bull trout distributions considerably (Fraley and Shepard 1989a, Rieman and Chandler 1999).

Based on thermal optimums for bull trout during the summer months, thermal sensitivities under future climate scenarios are likely to be highest for FMO and SR habitats during August with similar sensitivities expected for July. Landscape scale assessments show the most thermally sensitive habitats are distributed within low-elevation habitats in mainstem and tributary reaches. As model results are downscaled, we learn that river basins consisting of higher elevation habitats may be least sensitive to warming and are likely to be most resilient to climatic change. As results are downscaled to the watershed scale, these findings are further supported, where model results identify headwater tributaries within the Flathead, South Fork Flathead, and Oldman River basins to be least resilient to climate change, likely providing cold-water refugia into the future.

Habitat fragmentation

Models predict thermal sensitivities of FMO habitats during summer months may be highest for the Kootenay, Flathead, and Blackfoot River basins. Thermal warming during the summer months may cause a contraction and/or fragmentation of thermally suitable riverine habitats, potentially altering adult and sub-adult summer foraging and migration patterns. There is a clear understanding that habitat connectivity strongly influences the persistence of salmonid populations (Rieman and Dunham 2000). Bull trout utilize patchy distributions of suitable habitats within streams, seeking out areas of groundwater upwelling and microhabitats (e.g., deep pools), which are significantly colder than average temperatures (Rieman and McIntyre 1995, Al-Chokhachy and Budy 2007). Our models do not account for stream reach characteristics such as these that may buffer climate warming effects and predicted habitat fragmentation patterns. It is feasible, therefore, that individuals will utilize these microhabitats allowing movement through migration corridors or thermally fragmented habitats to more optimal temperature conditions. This is likely the case in the southern periphery of their distributional range and river basins such as the Blackfoot where thermal sensitivities and temperatures are already high.

Both habitat loss and fragmentation have considerable effects on population dynamics and are extremely important in evaluating conservation priorities. From an ecological perspective, major causes of population and species extinction are habitat fragmentation and degradation. Habitat fragmentation can lead to smaller isolated populations, increasing extinction risk through demographic and environmental stochasticity (Schindler et al. 2010, Kovach et al. 2016). Demographic stochasticity increases inbreeding probabilities and genetic drift, thereby decreasing genetic variation and adaptation capacities (Wang et al. 2002, Harmon and Braude 2010). Stream reach scale analyses are needed to differentiate between habitat loss and fragmentation, potential isolation of meta-populations, loss of migratory life histories, and consequential effects to bull trout populations in the CCE.

Species response to thermal warming and seasonal shifts

The adaptive capacity of salmonids, including bull trout, is dependent on the ability of populations track environmental changes, such as stream temperature (Muñoz et al. 2015a). Species response include adapted shifts in behavior and physiology, which directly influence life-history attributes such as time of spawning, rate of embryonic development, egg hatching, growth, sexual maturation, and life span (Crozier et al. 2008). Model simulations predict a decrease in thermally optimal FMO habitats beginning as early as July under near (2035) and mid-future (2075) scenarios. These results suggest that sub-adult and adult bull trout in Flathead, Blackfoot, Kootenay, and St. Mary river basins may be forced to adapt to an earlier warming of mainstem habitats by commencing migrations (i.e., upstream movements) toward natal spawning tributaries earlier in the year. Additionally, as mainstem and tributary habitats warm toward thermal optimums earlier and persist later, growth seasons may increase in duration. Laboratory studies have shown optimal feeding and growth temperatures between 10.9 - 15.4°C, with peak consumption at ~13°C (Selong et al. 2001). Local bull trout populations in thermally sensitive river basins, such as the Blackfoot may find that metabolic costs of growth will increase due to high stream temperatures, restricting annual growth rates (Jonsson and Jonsson 2009). Conversely, higher elevation streams may warm towards optimal temperatures for growth earlier in the year, creating a longer within-year growth period (Beer and Anderson 2011, Al-Chokhachy et al. 2013). Seasonal models

predict that temperature increases during November and April may be larger in magnitude relative to current conditions, with the most dramatic temperature changes occurring in the seasonal transitions into and out of winter, which could imply a shortening of the winter season. Considering spring fry emergence in fall-spawning salmonids is dependent on degree-days required for winter egg incubation, warming stream temperatures and narrowing of the winter season would suggest shorter durations of embryonic development (Carlson and Seamons 2008, Mantua et al. 2015).

An extension of warm summer temperatures and delayed onset of stream temperature cooling during fall season could indicate temporal shifts in spawning related cues. Due to natal homing, it is reasonable to assume that populations exhibit adaptations regarding spawning time, dependent on thermal cues from stream temperatures (Jonsson and Jonsson 2009). Studies have shown significant differences in spawning times between fall spawning salmonid populations, where spawning cues commence earliest in the coldest uppermost tributaries of river systems (i.e., northern latitudes and headwater streams) and become progressively later in downstream tributaries which remain warmer longer in the year (Summers 1996, Webb and McLay 1996). Watershed scale results emphasize similar patterns in thermal sensitivities, where watersheds consisting of higher elevation habitats are likely to be least sensitive to change. Differences in the timing of spawning cues have also been found in relation to embryonic development, where spawning cues begin later in populations where embryonic development occurs in warmer streams, and earlier in colder streams, which require longer incubation periods (Unwin et al. 2000, Quinn et al. 2001, Warren et al. 2012). As variability in seasonal temperatures increase, and temperatures remain warmer longer in the year, spawning times will likely continue to track these trends, while simultaneously shifting life history stages.

For aquatic species, adaptations to climate driven thermal variations requires phenotypic (short term) or genetic (long-term) responses based on physiological and behavioral sensitivities to change (Wang et al. 2002, Muñoz et al. 2015b). Migratory salmonids display plasticity to temperatures, shifting the timing of life history traits to reduce probability of exposure to change (Kovach et al. 2012, Wade et al. 2013). However, because salmonids display phenotypic plasticity (Jonsson and Jonsson 2009, Crozier

et al. 2011) and can proliferate effects across generations, differentiating between plastic and genetic responses and predicting how populations may respond to climate change can be challenging (Mantua et al. 2015, Muñoz et al. 2015b). Currently, scientific data on adaptive plastic responses are extremely limited for species of conservation concern, such as bull trout, and until adaptive markers are identified and quantified, most vulnerability assessments will continue to be built from conceptual models, including theoretical metrics identifying adaptive capacity (Wade et al. 2016).

Climate adaptation planning for bull trout in the Crown of the Continent

Conservation efforts within the transboundary CCE rely on decision support tools, which can be used to inform policy across many jurisdictional boundaries. Results of this study provide a multi-scalar and temporal assessment of future climate impacts to freshwater habitats linking current monitoring efforts (i.e., empirical data), climatic projections, geomorphology, and species habitat distributions which can be used directly in risk planning and vulnerability assessments. Climate adaptation planning for cold-water salmonids in the CCE consists of three stages: 1) identifying conservation goals related to climate suitability (e.g., temperature and stream flow), non-native species threats (e.g., competition, predation, hybridization), and habitat connectivity (e.g., migrations, isolation of meta-populations); 2) considering climate adaptation strategies that support each goal; 3) and targeting on-the-ground actions to accomplish a given strategy (Cross et al. 2013). This simulation modeling tool supports the first stage of this process and can be used to identify thermally suitable habitats (i.e., cold-water refugia), potential shifts in species phenology, habitats at risk of non-native invasions and disease outbreaks (Muhlfeld et al. 2014b), and loss of habitat connectivity (i.e., increased fragmentation). Full assessments of species vulnerabilities, however, should consider regulatory, social, economic and locally driven factors (i.e., hydrology, food web, land-use) relevant to climatic exposure, sensitivity and adaptive capacities (Cross et al. 2013, Kovach et al. 2016).

Mitigation strategies for stream temperature warming in the Crown of the Continent

Results from this study can be used to inform climate adaptation strategies and target streams and watershed for mitigation actions by identifying currently occupied streams and cold-water limited habitats

that may provide thermal refugia in the future. Within the CCE thermal adaptation strategies for native cold-water fish include efforts to ameliorate increasing temperatures, protect and restore cold-water habitats, and re-connect local populations caused by thermal fragmentation. Strategies to ameliorate stream temperature warming include restorative actions that promote physical and biological processes thereby increasing resiliency of habitats and populations to climate variability (Waples et al. 2009, Beechie et al. 2013). Local restoration efforts should focus on restoring lateral, longitudinal and vertical connectivity, such as reconnecting stream channels with active floodplains to facilitate groundwater contributions and re-establishing riparian vegetation buffers (Pierce et al. 2014). Mitigation strategies to restore habitat connectivity among local populations (i.e., maintaining genetic diversity), however, may be most important to the overall persistence of bull trout in the CCE. Climate-induced actions are those that ameliorate stream temperature warming, as mentioned above, and facilitate thermal connectivity. Loss of habitat connectivity, however, can also result from instream barriers or lack thereof (i.e., waterfalls, dams or culverts). In some cases removal of barriers or installation of appropriate culverts will facilitate movement between local populations, increasing genetic diversity and resilience to climate-induced change and stressors (i.e., non-native invasions; Schmetterling 2003). Strategies for protecting bull trout populations include addressing any additional threats to current or future thermally suitable habitats. This may include natural or human-induced threats such as mining, logging, recreational activities, roads, wildfires, non-native invasions, or hydrology (i.e., connectivity, flooding).

Climate change is expected to significantly alter invasive species distributions worldwide (Rahel and Olden 2008). Non-native aquatic species generally occupy broader latitudinal ranges and have higher tolerances for temperature variability and extremes (Bates et al. 2013). Stream temperature warming is likely to facilitate expansion of non-native distributions, invasions into native species habitats, and increase risk of hybridization (Rahel and Olden 2008). Because bull trout are one of the most thermally sensitive species in western North America, populations exposed to higher temperatures may be at risk to non-native invasions, such as brook trout, brown trout, and lake trout (Kovach et al. 2015). Recent studies have shown a negative correlation between the genetic diversity within bull trout populations, higher

stream temperatures (Kovach et al. 2016), and higher summer air temperatures (Wenger et al. 2011a). Therefore, implementing removal strategies to suppress non-native species, proactively preventing expansion of invasive species in streams (i.e., barriers), or translocating native species to isolated habitats likely to provide thermal refugia in the future will be an important climate mitigation strategy for bull trout in the CCE (Schmetterling 2003, Al-Chokhachy et al. 2014, Williams et al. 2015, Galloway et al. 2016) .

Connecting science with conservation - scale matters

Thermal heterogeneity within streams and rivers is driven by interactions and feedbacks between hierarchical processes. Coarser scale processes can influence the effects of finer scale processes, while finer scale local processes can alter ecosystem function and mitigate effects of larger scale processes (Figure 1; Poole 2002). It is important to recognize the potential for “bottom-up” effects from the lowest hierarchical levels and the potential of these controls to reduce the sensitivity of thermal warming to climatic changes (i.e., air temperature; Poole 2002, Khamis et al. 2015, Lisi et al. 2015). This concept of scale dependency transfers over to climate change projections and our ability to predict impacts on freshwater systems. Climate change is driven by global and continental scale processes that are realized at regional and local scales. When applying climate projections at landscape scales, the coarse resolution and uncertainties of global and regional climate models may be less important than the broad scale patterns revealed about future conditions. However, at finer scales, local processes often alter broad scale effects further increasing climate change and model parameter uncertainties. Landscape scale climate change modeling, therefore, is about providing probabilities and likelihoods about what to expect in the future, establishing priorities, and using this information to influence conservation and management of habitats and species. In this study, we match our climate modeling framework to appropriate biological, and management scales – providing a comprehensive regional (i.e., landscape scale) and meta- population (i.e., basin scale), and local population (i.e., watershed scale) assessments of climate impacts to bull trout in the CCE.

Conclusion

Climate-induced warming within freshwater ecosystems has significant implications to aquatic species distributions and overall biological diversity (Sala et al. 2000, Bellard et al. 2012, Isaak et al. 2016). For conservation and management, assessing climatic, ecological, and biological impacts across multiple spatial and temporal scales will provide a more holistic approach for better understanding threats to species persistence and identifying appropriate mitigation strategies across political and conservation jurisdictions. In the CCE, understanding how climate change may impact threatened species such as the bull trout, is a priority for conservation management because of their cultural, economic, and ecological value (USFWS 2010). For this large, ecologically diverse landscape protecting high-quality habitats and maintaining complex, connected cold-water habitats that support life history diversity will increase population resilience and ultimate persistence of this keystone species (Rieman and Allendorf 2001, Beechie et al. 2013).

Acknowledgments

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Table 1. Parameter estimates and summary statistics for seasonal stream temperature models.

Model Coefficients	<i>b</i> (SE)	<i>p</i> -value	<i>Pooled data</i>		<i>Training data</i>		<i>Validation data</i>	
			<i>r</i>	<i>RMSE</i>	<i>r</i>	<i>RMSE</i>	<i>r</i>	<i>RMSE</i>
Spring hierarchical model			<i>n = 1716</i>		<i>n = 1539</i>		<i>n = 177</i>	
Intercept	8.05 (0.65)		0.91	1.16	0.91	1.17	0.90	1.31
Elevation	-0.004 (0.0002)	<0.0001						
Slope	0.021 (0.0006)	0.0002						
Air temperature	0.37 (0.02)	<0.0001						
Lake effect	0.83 (0.09)	<0.0001						
Glacier effect	-0.61 (0.17)	0.0005						
Month - <i>April</i>	-1.03 (0.22)	<0.0001						
<i>May</i>	-0.89 (0.11)							
<i>June</i>	0.0 (0.0)							
Summer hierarchical model			<i>n = 2301</i>		<i>n = 1954</i>		<i>n = 347</i>	
Intercept	7.32 (0.52)		0.90	1.2	0.90	1.23	0.90	1.38
Elevation	-0.003 (0.0001)	<0.0001						
Slope	-0.038 (0.006)	<0.0001						
Air temperature	0.613 (0.02)	<0.0001						
Lake effect	3.05 (0.09)	<0.0001						
Glacier effect	-2.15 (0.18)	<0.0001						
Month - <i>July</i>	-1.06 (0.11)	<0.0001						
<i>August</i>	-0.29 (0.10)							
<i>September</i>	0.0 (0.0)							
Fall hierarchical model			<i>n = 1150</i>		<i>n = 1054</i>		<i>n = 96</i>	
Intercept	5.56 (0.30)		0.89	0.93	0.90	0.91	0.86	1.06
Elevation	-0.002 (0.0002)	<0.0001						
Slope	0.012 (0.005)	0.02						
Air temperature	0.29 (0.02)	<0.0001						
Lake effect	1.53 (0.08)	<0.0001						
Glacier effect	-0.79 (0.14)	<0.0001						
Month - <i>October</i>	1.27 (0.10)	<0.0001						
<i>November</i>	0.0 (0.0)							

Table 2. Average monthly temperature conditions for bull trout *spawning and rearing* (SR) and *foraging, migrating, and overwintering* (FMO) habitats for the current *baseline* period (1986-2005) and absolute and relative increases predicted under the RCP 4.5 and 8.5 scenarios.

Month	Baseline	Absolute Increase (°C)				Relative Increase (%)			
		RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5	
		2035	2075	2035	2075	2035	2075	2035	2075
Spawning and rearing (SR) Bull Trout habitats									
April	3.21	0.57	0.95	0.51	1.32	17.76	29.60	15.89	41.12
May	4.35	0.46	0.93	0.34	1.25	10.57	21.38	7.82	28.74
June	6.47	0.73	1.23	0.74	1.73	11.28	19.01	11.44	26.74
July	9.72	1.40	2.57	1.66	3.86	14.40	26.44	17.08	39.71
August	10.34	1.52	2.68	1.95	4.40	14.70	25.92	18.86	42.55
September	7.77	1.89	2.20	1.25	4.45	24.32	28.31	16.09	57.27
October	4.58	0.36	0.73	0.55	1.25	7.86	15.94	12.01	27.29
November	1.96	0.50	0.68	0.41	1.19	25.51	34.69	20.92	60.71
Foraging, migrating, and overwintering (FMO) Bull Trout habitats									
April	4.3	0.59	0.96	0.50	1.33	13.72	22.33	11.63	30.93
May	5.95	0.43	0.87	0.31	1.19	7.23	14.62	5.21	20.00
June	8.26	0.66	1.19	0.69	1.67	7.99	14.41	8.35	20.22
July	11.99	1.36	2.54	1.63	3.83	11.34	21.18	13.59	31.94
August	12.56	1.47	2.65	1.88	4.37	11.70	21.10	14.97	34.79
September	9.96	1.78	2.13	1.19	4.39	17.87	21.39	11.95	44.08
October	5.55	0.34	0.72	0.52	1.24	6.13	12.97	9.37	22.34
November	2.61	0.53	0.68	0.42	1.23	20.31	26.05	16.09	47.13

Table 3. Exceedance statistics of thermal preferences for FMO habitats during August. Relative occurrence in streams (km) and percent of total habitat within major river basins in the CCE.

Scenario (< 15°C)	Flathead		Elk		Oldman		St. Mary		SF Flathead		Swan		Clark Fork		Kootenay		Blackfoot	
	%	km	%	km	%	km	%	km	%	km	%	km	%	km	%	km	%	km
July																		
Baseline	91	653	100	314	100	455	100	441	97	115	100	150	18	37	99	372	100	233
RCP 4.5 2035	54	387	96	302	100	455	91	400	93	110	83	124	9	18	17	63	87	202
RCP 4.5 2075	51	370	77	244	100	455	85	378	92	109	81	122	2	3	4	15	62	145
RCP 8.5 2035	53	382	95	298	100	455	90	399	93	110	83	124	5	11	11	40	80	187
RCP 8.5 2075	27	196	58	183	80	368	43	188	84	99	50	75	0	0	3	13	3	8
August																		
Baseline	70	499	99	313	100	455	98	435	95	112	88	132	15	31	84	315	98	229
RCP 4.5 2035	52	374	91	286	100	455	90	399	93	110	83	124	3	7	7	27	74	172
RCP 4.5 2075	39	282	68	216	98	448	61	272	92	109	79	118	0	0	3	13	30	72
RCP 8.5 2035	52	370	80	251	100	455	87	386	92	109	80	121	1	2	5	18	64	150
RCP 8.5 2075	13	95	35	111	47	214	9	41	36	43	12	18	0	0	1	3	1	2
September																		
Baseline	96	684	100	314	100	455	100	441	100	117	100	150	89	184	99	372	100	233
RCP 4.5 2035	92	662	100	314	100	455	100	441	100	117	100	150	20	42	99	372	99	232
RCP 4.5 2075	91	653	100	314	100	455	100	441	98	116	100	150	18	37	99	372	99	232
RCP 8.5 2035	93	667	100	314	100	455	100	441	100	117	100	150	33	68	99	372	99	232
RCP 8.5 2075	52	374	84	265	100	455	87	386	92	109	81	122	2	4	7	25	65	153

Table 4. Exceedance statistics of thermal preferences for SR habitats during August. Relative occurrence in streams (km) and percent of total habitat within major river basins in the CCE.

Scenario (< 12°C)	Flathead		Elk		Oldman		St. Mary		SF Flathead		Swan		Clark Fork		Kootenay		Blackfoot	
	%	km	%	km	%	km	%	km	%	km	%	km	%	km	%	km	%	km
July																		
Baseline	94	1061	88	242	99	380	89	172	99	524	98	270	49	22	62	244	54	411
RCP 4.5 2035	82	924	59	164	99	380	81	156	86	450	75	207	20	9	52	205	26	198
RCP 4.5 2075	56	632	28	76	85	325	45	88	57	299	40	111	16	7	34	134	11	83
RCP 8.5 2035	78	879	52	144	99	380	72	140	80	418	64	176	18	8	50	196	21	159
RCP 8.5 2075	29	324	12	32	52	199	13	24	21	111	22	61	13	6	10	38	4	27
August																		
Baseline	91	1028	80	220	99	380	87	168	98	515	97	266	34	15	59	232	41	307
RCP 4.5 2035	65	731	39	108	97	374	56	109	66	348	50	137	17	8	43	171	16	120
RCP 4.5 2075	38	431	18	50	68	262	20	39	34	181	27	75	13	6	19	76	6	43
RCP 8.5 2035	56	627	31	85	89	342	45	87	55	289	38	104	16	7	38	149	10	75
RCP 8.5 2075	11	119	6	2	23	88	9	11	9	46	13	36	8	3	3	13	1	9
September																		
Baseline	99	1121	99	276	100	384	98	189	100	525	100	275	70	32	97	385	96	728
RCP 4.5 2035	95	1064	91	252	99	380	89	173	99	524	98	270	49	22	67	264	58	435
RCP 4.5 2075	94	1060	87	241	99	380	88	171	99	524	98	270	46	21	63	247	49	367
RCP 8.5 2035	96	1080	98	270	99	380	91	176	99	524	99	272	61	27	73	288	86	654
RCP 8.5 2075	59	665	31	85	84	321	40	78	57	297	41	112	16	7	38	151	12	90

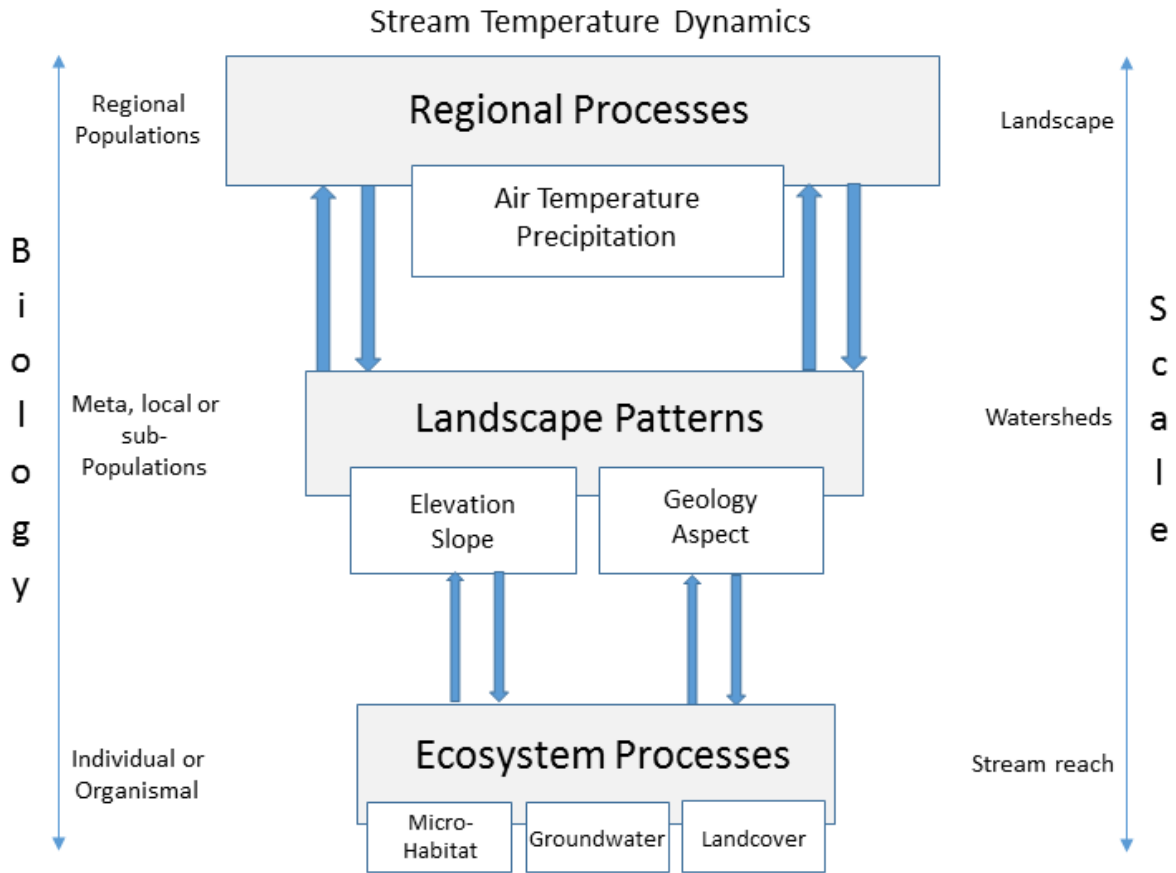


Figure 1. Hierarchical processes influencing stream temperature dynamics and appropriate scales for spatial and biological application of models.



Figure 2. The Crown of the Continent Ecosystem, Montana (USA), British Columbia and Alberta (Canada), and major river basins. Map and table denotes current bull trout *spawning and rearing* and *foraging, migrating, and overwintering* habitat distributions and seasonal use of habitats associated with critical life history traits.

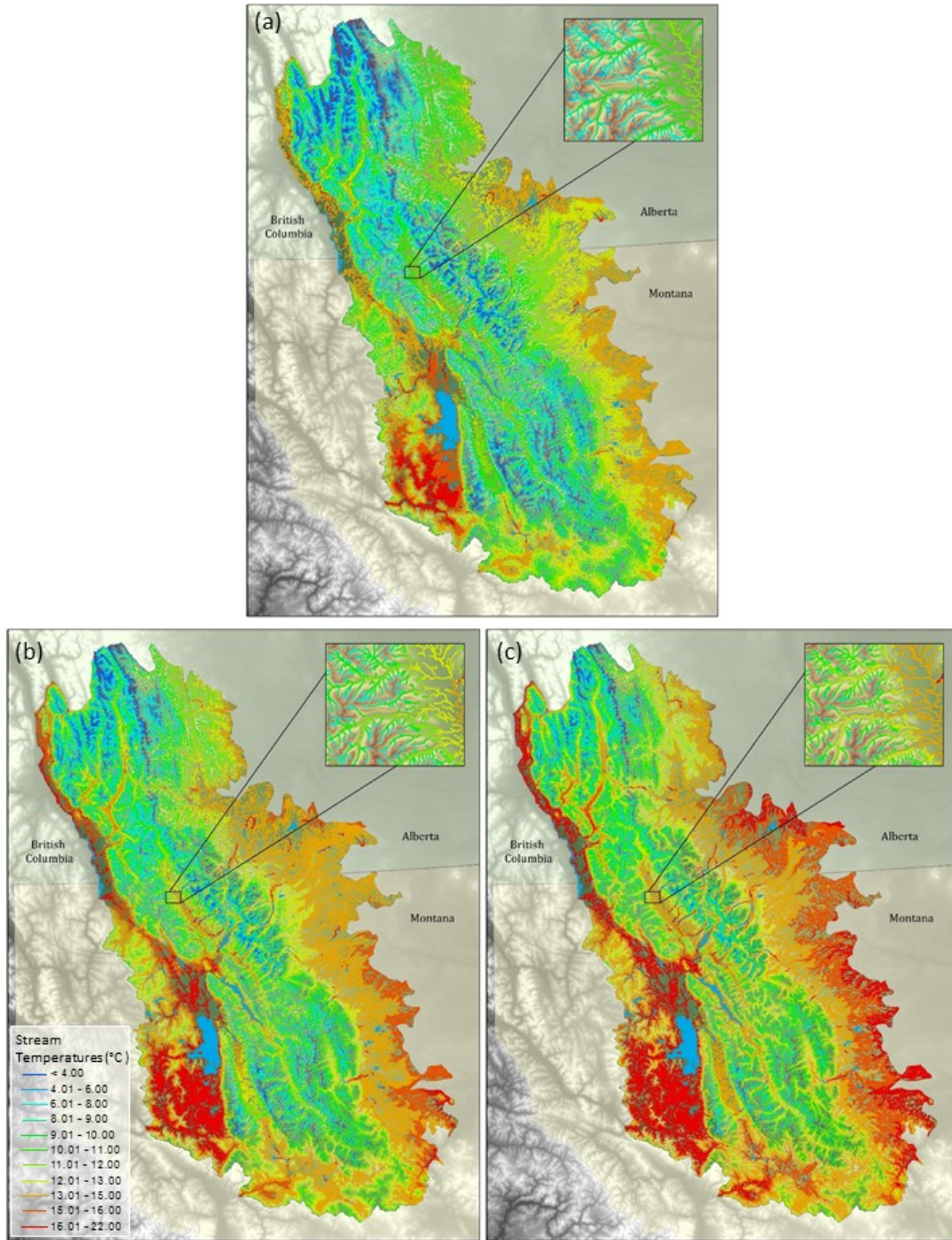


Figure 3. Mean August stream temperatures for the *baseline* period (1986-2005) (a) and RCP 4.5 2035 (b) and 2075 (c) scenarios. Summer model parameters were used to interpolate temperatures across the Crown of the Continent Ecosystem (100 m resolution).

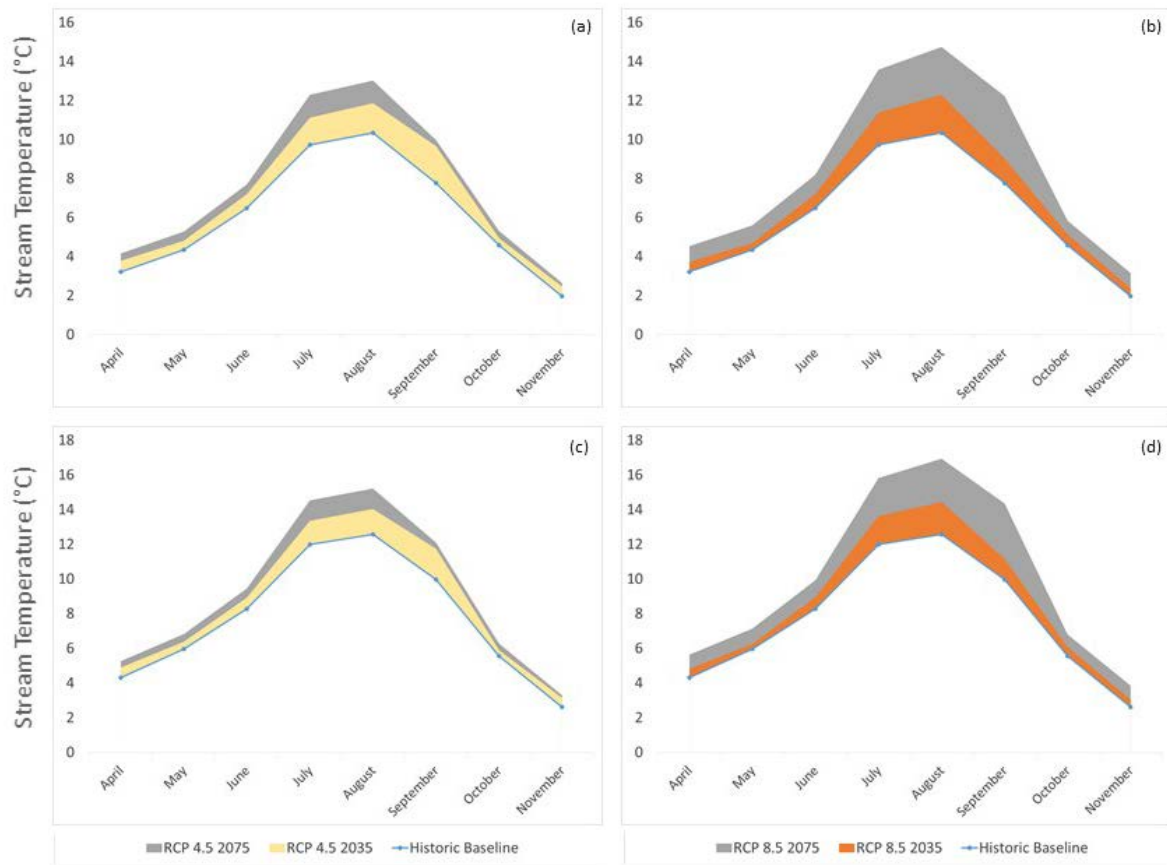


Figure 4. Simulated stream temperature model results characterizing thermal regimes for SR habitats under RCP 4.5 (a) and 8.5 (b) scenarios and FMO habitats under RCP 4.5 (c) and 8.5 (d) scenarios. Mean monthly predictions were averaged over habitat types and used to construct thermal habitat distributions characterizing current and future conditions.

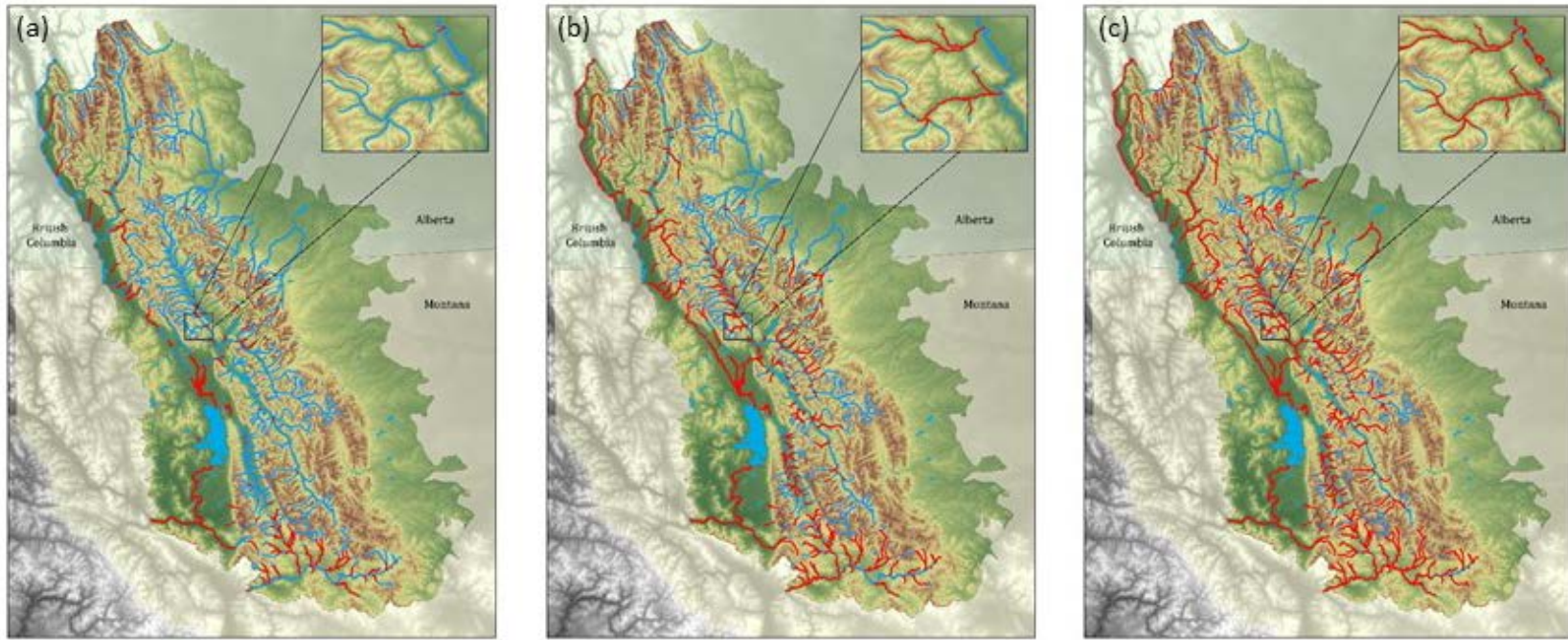


Figure 5. Mean August temperatures under the *baseline* (a), RCP 4.5 2035 (b) and 2075 (c) scenarios. Red lines represent predicted stream temperatures $>12^{\circ}\text{C}$ for SR and $>15^{\circ}\text{C}$ for FMO habitats.

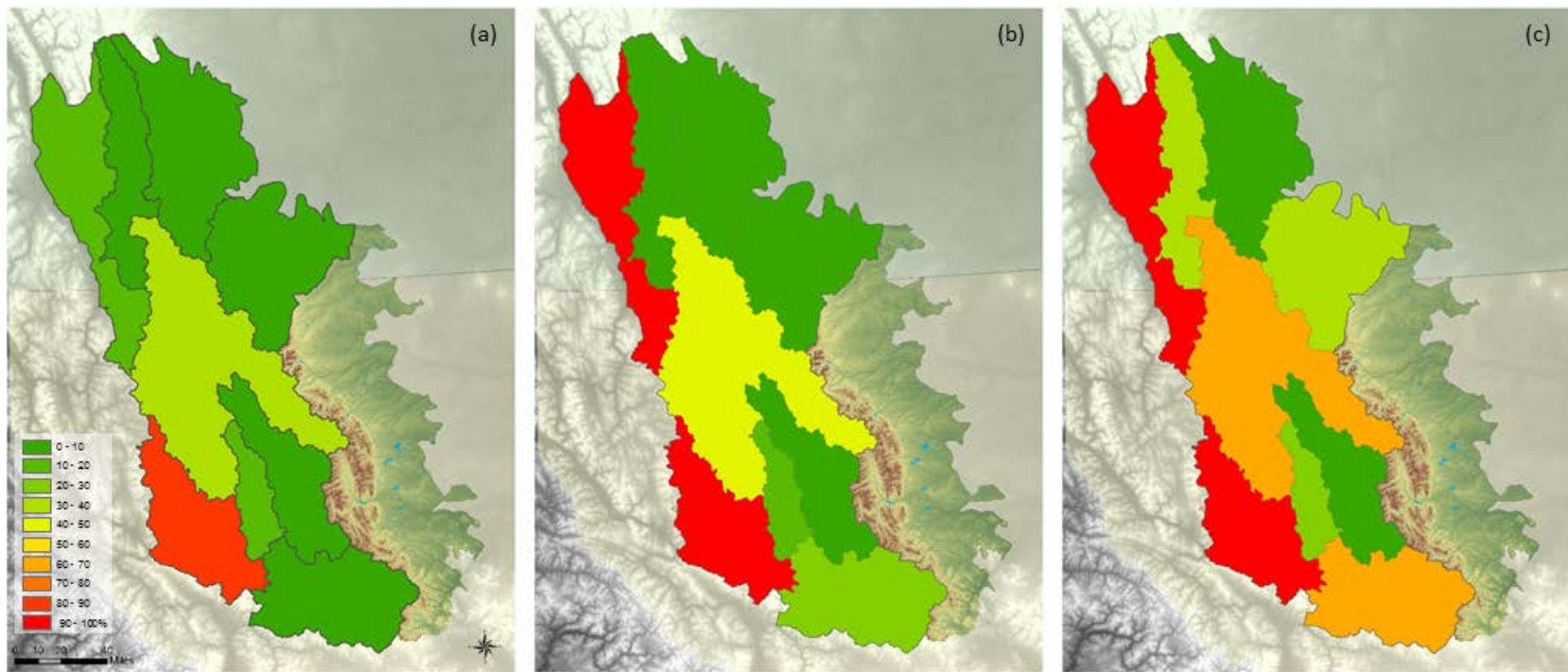


Figure 6. Thermal sensitivity of bull trout FMO habitats for *baseline* (a) and RCP 4.5 2035 (b) and 2075 (c) scenarios by river basin.

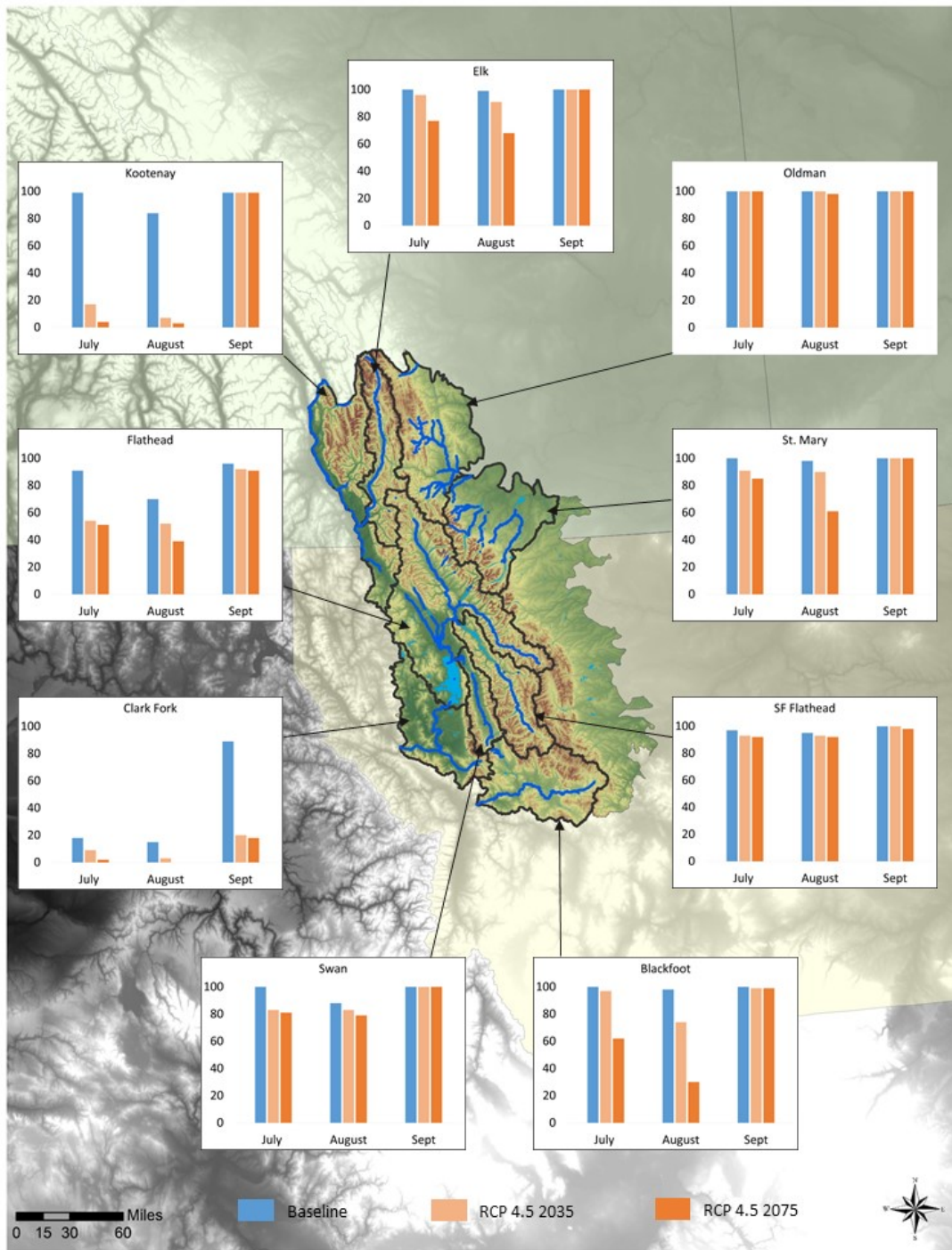


Figure 7. Percent thermally suitable bull trout FMO habitats under *baseline* and future climate scenarios, by river basin.

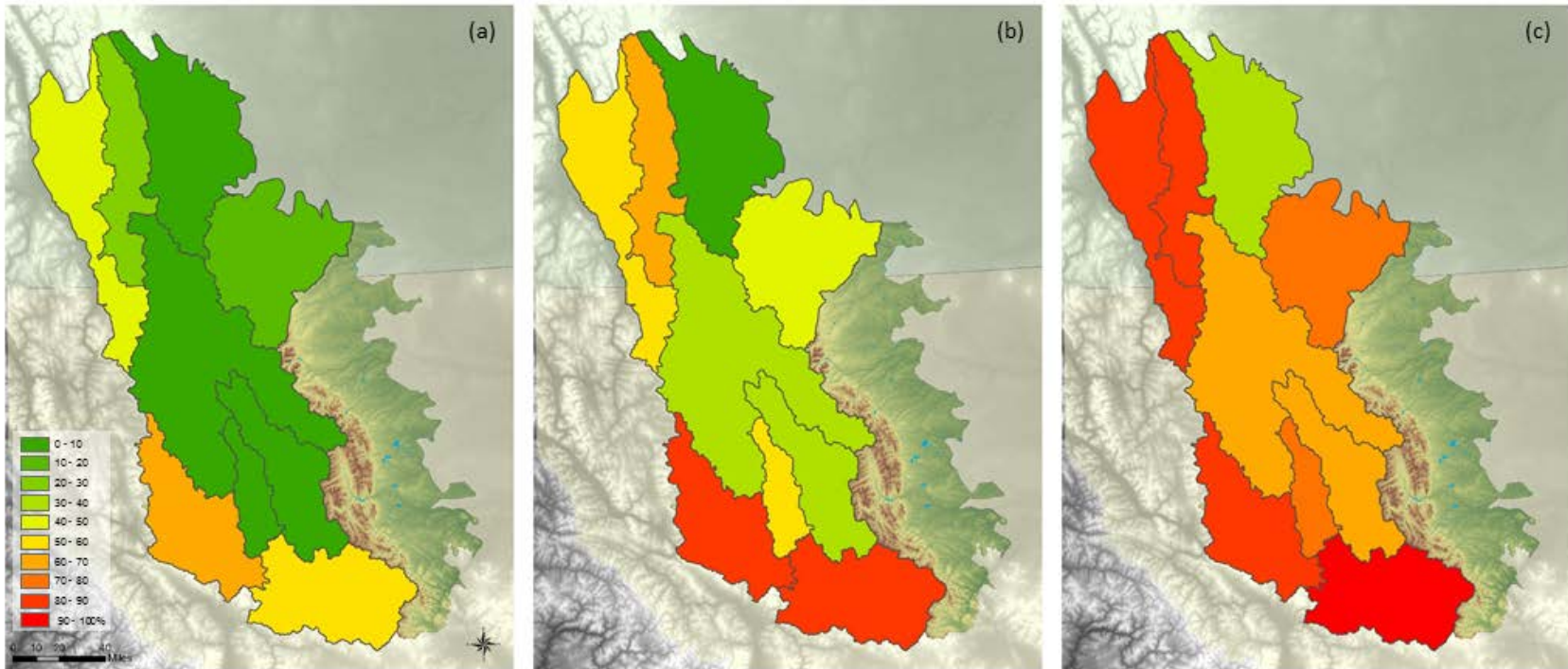


Figure 8. Thermal sensitivity of bull trout SR habitats for *baseline* (a) and RCP 4.5 2035 (b) and 2075 (c) scenarios by river basin.

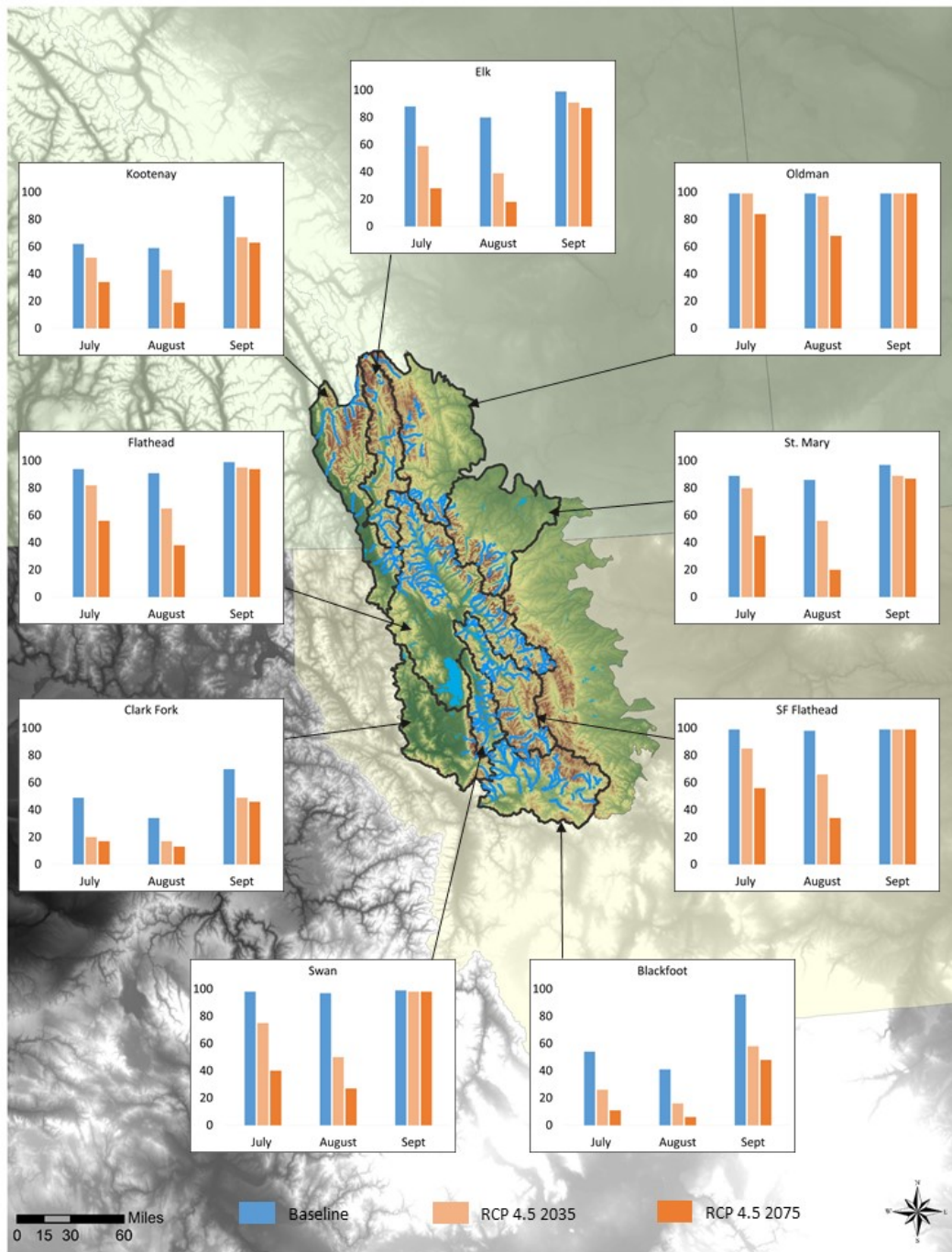


Figure 9. Percent thermally suitable bull trout SR habitats under *baseline* and future climate scenarios, by river basin.

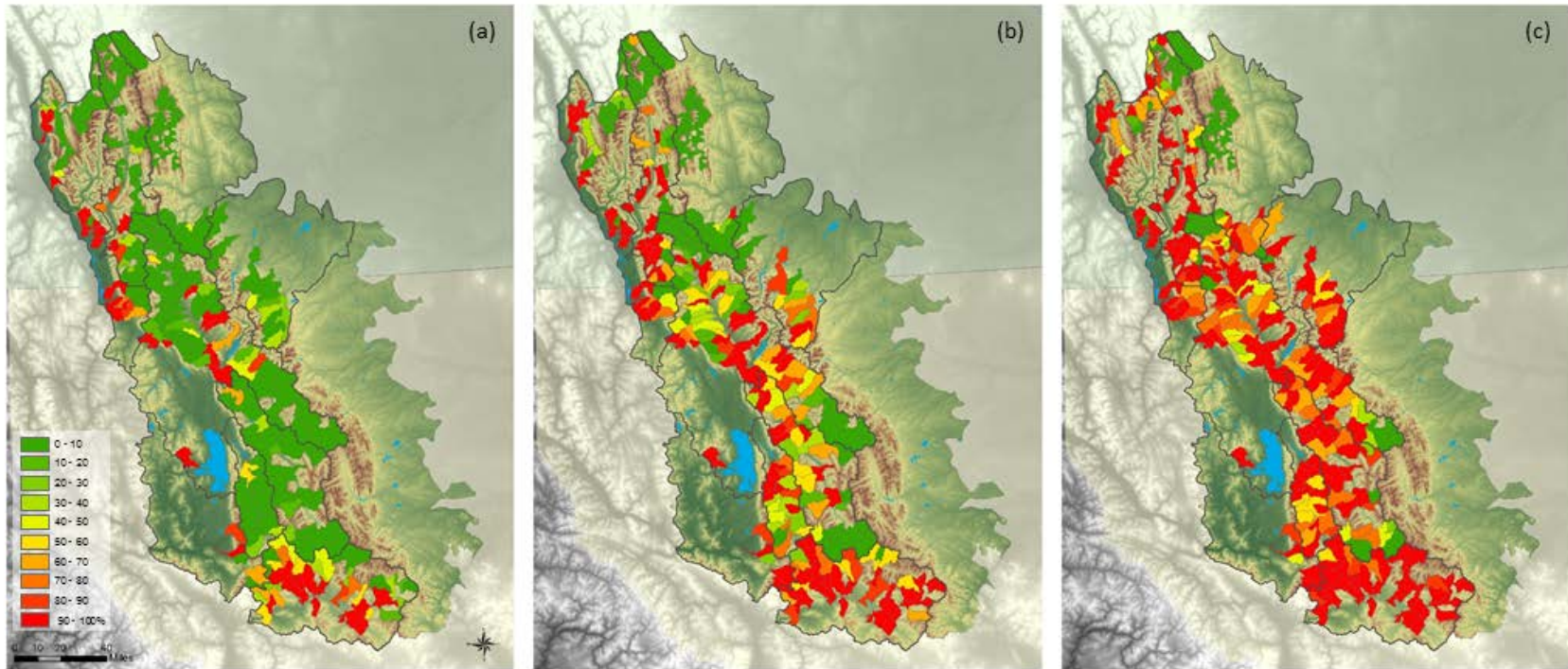


Figure 10. Thermal sensitivity of bull trout SR habitats for *baseline* (a) and RCP 4.5 2035 (b) and 2075 (c) scenarios by watershed.

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Chapter 5: Conclusion and Broader Impacts

Conclusion

My dissertation work furthers landscape-scale aquatic conservation in the Crown of the Continent Ecosystem (CCE) by linking ecosystem and biological monitoring efforts with climate and land-surface data to better understand thermal responses of aquatic habitats and a cold-water specialist. My objectives were to develop systematic methods for monitoring and predicting stream temperatures in the CCE, synthesize a database of historic and current temperature recordings, and use this data to explore linkages between climate and thermal heterogeneity across time and space. This work assessed how future climate variations may impact seasonal stream temperatures, quantified thermal warming patterns across space and time continuums, and related these findings to critical bull trout habitats and populations in the CCE.

Atmospheric warming in the CCE has resulted in temporal shifts in seasonal climate windows, including a later onset of fall and winter and earlier onset of spring and summer. Results from Chapter 3 suggest similar patterns are expected for stream temperature regimes throughout the CCE. Seasonal stream temperature models predict the largest stream temperature increases will occur during the summer months, resulting in an earlier onset, extended duration, and heightened severity of warm stream temperatures. Stream temperature predictions during the summer months show increased warming throughout the central mountainous regions of the CCE. In addition, warming rates for glacial-fed streams were 50% larger in magnitude with complete loss of glacial masses over the next two decades. These findings corroborate other studies suggesting that mid-latitude, high-elevation mountainous systems are particularly sensitive to recent and projected climate change. Additionally, predicted temperature increases during spring and fall were larger in magnitude relative to current temperature regimes, with the most dramatic temperature changes occurring in seasonal transitions into and out of winter (April and November). My findings indicate that future climate warming is likely to result in seasonal shifts in stream temperatures in the CCE, including an earlier onset of temperatures characteristic of spring and summer and later onset of temperatures characteristic of fall and winter.

In Chapter 4, application of thermal riverscapes to critical bull trout habitats revealed similar linkages between seasonal climate patterns and temperature regimes. Models forecasted that stream temperatures consistent with current August temperatures in bull trout *spawning and rearing* (SR) and *foraging, migrating, and overwintering* (FMO) habitats are likely to begin a month earlier (July) and persist a month later (September). Average monthly stream temperatures for current SR habitats are predicted to range between 1.96°C in November to 10.34°C in August, while average temperatures for FMO habitats were slightly higher and varied from 2.61°C in November to 12.56°C in August. Thermal preferences for bull trout during the summer months were used to conduct a multi-scalar analyses of thermal sensitivities. Landscape scale assessments of thermally optimal habitats under future climate scenarios show a contraction and/or fragmentation of thermally suitable habitats, suggesting a northward movement (i.e., latitudinal) and higher altitudinal shift in the distributional range of bull trout in the CCE. Basin scale assessments predict that thermal sensitivities will be highest for populations in the southern periphery of their distributional range (i.e., Blackfoot), where tributary habitats within the Oldman, Flathead, and South Fork Flathead basins were predicted to be least sensitive to thermal warming, potentially providing cold-water refugia in the future.

Broader Impacts

There is an urgent need for landscape-scale decision support tools that provide quantitative assessments of climate-induced change within freshwater ecosystems. In the transboundary CCE, such tools are used to inform policy across many jurisdictional boundaries. Development of my stream temperature modeling framework is timely, as stream temperature regimes shift throughout western North America under ongoing and future climatic variability. My dissertation work will be used to strengthen our understanding of potential climate change effects on freshwater habitats, aquatic species (e.g., distribution and phenology), and guide conservation and climate adaptation strategies across a hierarchy of biological and management scales.

This work provides landscape-scale analyses of ecosystem response between air temperature trends, stream temperature, and topography. Landscape scale models are valuable in providing estimates

of future conditions, yet they do not address in-stream thermal complexities or local scale ecosystem processes that may mediate the sensitivity of stream temperature to atmospheric warming. Thermal heterogeneity within streams and rivers is driven by complex interactions and feedbacks between processes occurring over a range of hierarchical scales. As we look towards the future, in snowmelt driven systems, such as the CCE, it will be imperative to address hydrologic impacts on thermal variations across time and space. Annual flow regimes in these mountainous systems are driven by accumulation of winter snowpack, spring precipitation rates, and the seasonal timing of snowmelt. I believe that future approaches to stream temperature prediction should challenge how physical processes driving stream temperature can be spatially represented. More specifically, by integrating the technical abilities of both process based and statistically based stream temperature models into one centralized framework. Landscape scale models are particularly useful for directing future research needs and downscaling efforts. I emphasize the need for better understanding ecosystem processes, interactions, and feedbacks that influence thermal heterogeneity at the stream reach scale and coupling finer scale analysis of these processes with larger scale models for a more comprehensive methodology to simulating ecosystem response.

Ultimately, understanding spatiotemporal variation in ecosystem processes and biodiversity will improve our ability to perceive how ecosystems function. Geographical shifts in different components of ecological and biological diversity under changing environments will impact ecosystem services in the short- and longer-term futures. Knowledge and understanding of such changes, therefore, will help us to develop more informed models and to respond through developing and implementing adaptation and mitigation measures.