EFFECTS OF STREAM TEMPERATURE AND CLIMATE CHANGE ON FLUVIAL ARCTIC GRAYLING AND NON-NATIVE SALMONIDS IN THE UPPER BIG HOLE RIVER, MONTANA

by

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DEDICATION

This dissertation is dedicated to my loving and supportive family and friends.

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ABSTRACT

The upper Big Hole River basin in southwestern Montana supports one of the last naturally-reproducing populations of fluvial Arctic grayling *Thymallus arcticus* in the coterminous United States. Warm summer water temperatures and negative interactions with non-native fish (brook trout *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta*) have been identified as critical factors constraining this grayling population. Arctic grayling and these non-native fishes are all cold-water species with similar temperature requirements. Understanding when, where, and to what extent water temperatures are suitable for these fishes provides a physical basis for conservation planning. In chapter 2, I used a combination of thermal infrared (TIR) imagery and stationary temperature recorders to estimate water temperatures at a relatively fine spatial (every ~ 100 m of stream length) and temporal (continuous) resolution over a large extent of the Big Hole River (~ 100 km) during the warmest part of the summer in 2008. This modeling revealed considerable spatial and temporal heterogeneity in water temperature and highlighted the value of assessing thermal regimes at relatively fine spatial and temporal scales. In chapter 3, I assessed the potential effects of climate change on thermal suitability of summer water temperatures for these salmonids. Water temperature simulations projected significant warming from the 1980s through the 2060s. Despite this warming, water temperatures in some sections of stream remained below thermal tolerance thresholds through the 2060s. These stream temperature data provide a critical foundation for understanding the dynamic, multiscale habitat needs of these mobile stream fish and can aid in developing conservation strategies for fluvial Arctic grayling.

INTRODUCTION

Humans rely on freshwater ecosystems for multiple purposes, ranging from subsistence to recreation and aesthetics. By exploiting these freshwater resources, or in some cases, removing them (e.g., wetland drainage), humans have drastically altered freshwater ecosystems and, concomitantly, extirpated native species at local, regional, and global scales (Dudgeon et al. 2006). In the western USA, multiple anthropogenic factors, such as overexploitation, habitat degradation, altered discharge regimes, introduced species invasions, and climate change, have imperiled native fish species (e.g., Rieman et al. 2003, Williams et al. 2009). Consequently, fish native to streams and rivers in the western United States are often restricted to small, isolated portions of their historic range, where populations are at increased risk of extirpation (Lee et al. 1997). Fisheries ecologists and natural resource managers face a significant challenge in unraveling and remedying the many interacting factors threatening the persistence of native fish populations.

In response to this challenge, fisheries ecologists have identified a need to understand the interaction between stream habitat conditions and ecological processes that constrain native fish populations. Specifically, it may be useful to perceive lotic systems as complex networks consisting of heterogeneous habitats that are physically and temporally linked by fish movements (Gresswell et al. 2006). Stream fish often migrate between various habitats to find favorable growth conditions, seek refugia from harsh environmental conditions, and reproduce (Schlosser and Angermeier 1995; Figure 1). Understanding the dynamic life history of stream fish requires an evaluation of fish-habitat relationships and biological interactions at multiple spatial and temporal scales (Fausch et al. 2002, Gresswell et al. 2004). Further, the scale of ecological investigations must appropriately characterize the phenomenon of interest (Wiens 2002, Gresswell and Hendricks 2007). Overall, evaluating these ecological processes across multiple scales requires an integration of concepts from disciplines such as landscape ecology, fish biology, and stream ecology.

Evaluating ecological factors constraining the persistence of fluvial Arctic grayling *Thymallus arcticus* in southwestern Montana provides an opportunity to study the conservation of a native stream fish from multiple spatial and temporal scales. Arctic grayling is a circumpolar salmonid species, and historically, there were two disjunct populations that occurred in Michigan and Montana, USA. Grayling became extinct in Michigan circa 1936 (McAllister and Harington 1969 *cited in* Kaya 1992), and although the species still occurs in southwestern Montana, the fluvial (permanently stream dwelling) form has been extirpated from approximately 95-96% of the historic range (Kaya 1992). The last remaining reproductively-viable assemblage of fluvial Arctic grayling is largely limited to the upper 100 km of Big Hole River and its tributaries, and recent monitoring suggests the distribution and relative abundance of this population is declining (Montana Fish, Wildlife and Parks, *unpublished data*). Reduced summer discharge due to irrigation withdrawals, high summer water temperatures, entrainment in irrigation systems, migration barriers, degraded riparian habitat, climate change, and interactions with non-native salmonid species (i.e., brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*) have been identified as factors potentially constraining the distribution and abundance of Arctic grayling in the upper Big Hole River (Lohr et al. 1996, Lamothe et al. 2007).

A diverse group of stakeholders is collaborating to conserve and recover grayling in the upper Big Hole River watershed. In 2008, government agencies and non-government organizations collaborated to fund over a million dollars in stream and riparian habitat restoration projects in the upper Big Hole River watershed. Specifically, these projects are attempting to increase instream discharge, lower summer water temperatures, restore connectivity, and improve riparian habitat conditions throughout the upper basin. In spite of these restoration efforts, summer water temperatures regularly exceed thermal tolerance thresholds for adult Arctic grayling (Lohr et al. 1996, Lamothe et al. 2007).

Although grayling and sympatric fish species have been monitored in the upper Big Hole River basin since the early 1980s, numerous gaps in understanding the basic population ecology of the species still exist. Similarly, physical instream habitat characteristics have been monitored (OEA 1995, TMDL 2008), but inference regarding habitat quality for grayling is limited because of mismatches in the scale of observations and assumptions regarding fish movement (Van Horne 1983, Gresswell and Hendricks 2007, Lamothe and Magee 2004). Further knowledge about the basic population structure of graying and their explicit relationship to habitat conditions in the stream network is essential for effective conservation planning and evaluating ongoing habitat restoration efforts. In particular, documenting thermal habitat complexities and distribution patterns of the fishes currently occupying the upper Big Hole River watershed is integral to interpreting the effects of habitat restoration and climate change..

Within this context, I investigated relationships between thermal habitat conditions and the distribution of Arctic grayling and non-native salmonids in the upper Big Hole River watershed. Specifically, I addressed the following questions within the historic distribution of fluvial Arctic grayling in the Big Hole River watershed upstream of Dickie Bridge:

1- How do physical and biological characteristics of the stream network affect spatial and temporal variation in stream water temperature?

2- How do patterns in stream temperature affect the summer distribution of Arctic grayling and non-native salmonids?

3- How will future changes in climate, instream habitat, and non-native species distributions independently and concomitantly affect the persistence of fluvial Arctic grayling?

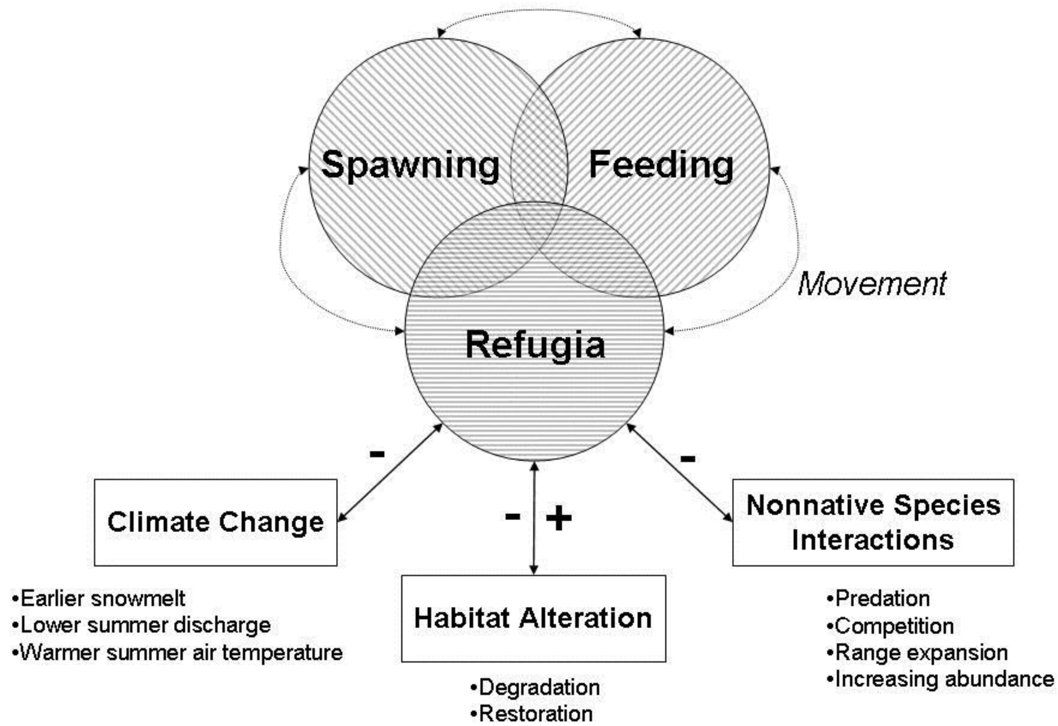

Figure 1. Conceptual diagram of dynamic life history model for fluvial Arctic grayling with factors potentially affecting the availability and use of suitable thermal habitat. Positive and negative signs indicate predicted effects on the availability and use of suitable habitat.

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CHAPTER TWO

QUANTIFYING STREAM THERMAL REGIMES AT MANAGEMENT-PERTINENT SCALES: COMBINING THERMAL INFRARED AND STATIONARY STREAM TEMPERATURE DATA IN A NOVEL MODELING FRAMEWORK

Contributions of Author and Co-Authors

Manuscript in Chapter 2

Author: Shane J. Vatland

Contributions: Conceived the study, collected and analyzed data, wrote the manuscript, and obtained supplemental funding.

Co-author: Robert E. Gresswell

Contributions: Obtained funding, contributed to conceptual framework, assisted with study design, discussed analysis, results, and interpretation, and edited the manuscript at all stages.

Co-author: Geoffrey C. Poole

Contributions: Conceived modeling approach with Vatland and edited manuscript in final stages of preparation.

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RESEARCH ARTICLE

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Key Points:

- A statistical model using diverse data accurately quantified stream temperature
- Evaluating stream temperature at fine scales revealed important heterogeneity
- Temperature data continuous in space and time is critical to guiding monitoring

Supporting Information:

- Readme
- Supporting information

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Quantifying stream thermal regimes at multiple scales: Combining thermal infrared imagery and stationary stream temperature data in a novel modeling framework

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Abstract Accurately quantifying stream thermal regimes can be challenging because stream temperatures are often spatially and temporally heterogeneous. In this study, we present a novel modeling framework that combines stream temperature data sets that are continuous in either space or time. Specifically, we merged the fine spatial resolution of thermal infrared (TIR) imagery with hourly data from 10 stationary temperature loggers in a 100 km portion of the Big Hole River, MT, USA. This combination allowed us to estimate summer thermal conditions at a relatively fine spatial resolution (every ~100 m of stream length) over a large extent of stream (~100 km of stream) during the warmest part of the summer. Rigorous evaluation, including internal validation, external validation with spatially continuous instream temperature measurements collected from a Langrangian frame of reference, and sensitivity analyses, suggests the model was capable of accurately estimating longitudinal patterns in summer stream temperatures for this system (validation RMSEs $< 1°$C). Results revealed considerable spatial and temporal heterogeneity in summer stream temperatures and highlighted the value of assessing thermal regimes at relatively fine spatial and temporal scales. Preserving spatial and temporal variability and structure in abiotic stream data provides a critical foundation for understanding the dynamic, multiscale habitat needs of mobile stream organisms. Similarly, enhanced understanding of spatial and temporal variation in dynamic water quality attributes, including temporal sequence and spatial arrangement, can guide strategic placement of monitoring equipment that will subsequently capture variation in environmental conditions directly pertinent to research and management objectives.

1. Introduction

Stream temperature is a critical attribute of lotic ecosystems. It affects ecological processes, basic biological rates, and stream community composition. The influence of stream temperature is apparent at all levels of biological organization, from individuals to ecosystems, and across trophic levels from primary producers [e.g., *Gudmundsdottir et al.*, 2011], to secondary consumers [e.g., *Hawkins et al.*, 1997], to top instream consumers [e.g., *Lyons*, 1996]. Anthropogenic activities can have significant effects on the thermal regime of streams [*Poole and Berman*, 2001], and there are often unintended consequences to aquatic ecosystems. Thus, understanding stream temperature dynamics can be vital to successful stream research and management.

Accurately quantifying stream thermal regimes can be challenging because stream temperatures are often spatially and temporally heterogeneous. Techniques to collect accurate stream temperature data have improved significantly over the past few decades [*Webb et al.*, 2008]; however, some limitations persist. For example, inexpensive, programmable, digital water temperature recorders have facilitated data collection at multiple locations and user-specified time intervals [*Johnson*, 2003], and quick-responding instream temperature loggers have been used to collect spatially continuous stream temperature profiles over several kilometers of stream [*Vaccaro and Maloy*, 2006]. Satellite, airborne, and ground-based thermal infrared (TIR) imagery have also improved our ability to collect fine spatial resolution surface temperature data over large

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spatial extents [*Torgersen et al*., 2001; *Handcock et al*., 2006; *Cardenas et al*., 2008], but data collection and analysis expenses often limit temporal replication. Using TIR imagery also requires that the stream surface is visible, which restricts use on small streams covered by overhanging riparian vegetation [see *Handcock et al*., 2012 for a detailed discussion on advantages and disadvantages of using TIR imagery in riverine landscapes]. Distributed fiber-optic temperature sensors (DTS) are capable of providing temperature data at fine spatial and temporal resolutions and at spatial extents of up to 30 km [*Selker et al*., 2006], but DTS installation and maintenance are associated with significant logistic constraints [*Deitchman*, 2009]. In sum, there are multiple techniques available for collecting accurate stream temperature data at fine spatiotemporal resolutions, over relatively large spatial extents, and for extended periods, each with its own set of strengths and limitations.

The analysis and modeling of stream temperature data varies considerably in complexity, scale, and theoretical underpinnings. Empirical approaches primarily can be used to accurately quantify spatial or temporal patterns in stream temperature [e.g., *Torgersen et al*., 2001]; whereas mechanistic approaches provide the means to explicitly identify and understand the internal and external forces driving thermal regimes [e.g., *Hebert et al*., 2011]. Mechanistic models can also be used to assess spatial and temporal patterns in stream temperature over relatively large extents of stream [e.g., *Deitchman and Loheide*, 2012], but this requires more extensive and expensive covariate data collection (e.g., channel morphology, discharge, and riparian vegetation) as compared to empirical modeling. Research scale ranges from short-term evaluation of single stream reaches [e.g., *Roth et al*., 2010] to long-term continental trend assessments [e.g., *Kaushal et al*., 2010]. Underlying these diverse approaches to evaluating stream temperature is a common challenge to formulate questions at scales relevant to resource management goals, and subsequently, collect and analyze data at scales pertinent to those goals.

Despite advances in stream temperature data collection, analysis, and modeling, we still often lack stream temperature data at scales appropriate for evaluating critical biological processes and at scales directly applicable to resource management activities [*Fausch et al*., 2002]. For example, resource managers will often monitor stream temperature at a single point and, based on that data, make relevant management decisions for several (10^1) kilometers of stream [e.g., *Montana Fish, Wildlife and Parks et al*., 2006]. However, the spatial and temporal distribution of stream temperature over the area of interest and its relationship to temperature at the monitoring site is usually unknown. In this study, we address these concerns by: (1) using complementary data collection techniques to assess stream temperature data across multiple spatial and temporal scales, (2) employing these data to develop and evaluate a novel statistical stream temperature model, and (3) comparing model results to stream temperature criteria established by local fisheries and water resource managers.

2. Methods

2.1. Study Area

We evaluated stream temperature patterns along approximately 100 km of the Big Hole River in southwestern Montana (Figure 1). The Big Hole River originates in the Beaverhead Mountains and flows north through a wide, flat mountain valley before turning east and entering a relatively narrow segment between the Anaconda Range and the Pioneer Mountains. The study area is located in this valley-bottom stream network, from a point near Jackson, MT, downstream to approximately 10 km northwest of Wise River, MT. Valley fill is predominantly glacial till, outwash, and alluvium, overlying a thick layer of sandstone and siltstone [*Marvin and Voeller*, 2000]. Stream elevation within the study area ranged from 1735 to 1971 m, and channel gradients measured over 1 km intervals ranged from $<$ 0.1 to 0.7 percent. Stream planform was mostly meandering pool-riffle sequences, including a mix of single and anabranching channels. Average-wetted channel widths for the main channel ranged from approximately 10 to 50 m in the autumn (September–November) of 2008.

The study area has a cool, dry, and temperate climate. Daily maximum air temperatures for the coldest (January) and warmest (July) months average -3 and 26°C, respectively (National Climatic Data Center; Wisdom, MT airport; 1933–2010). Mean annual precipitation averages 304 mm, predominately in the form of snow. Peak stream discharge is snow-melt driven, and the lowest flows begin to occur during July and August, when air and water temperatures are also greatest (supporting information Figure S1).

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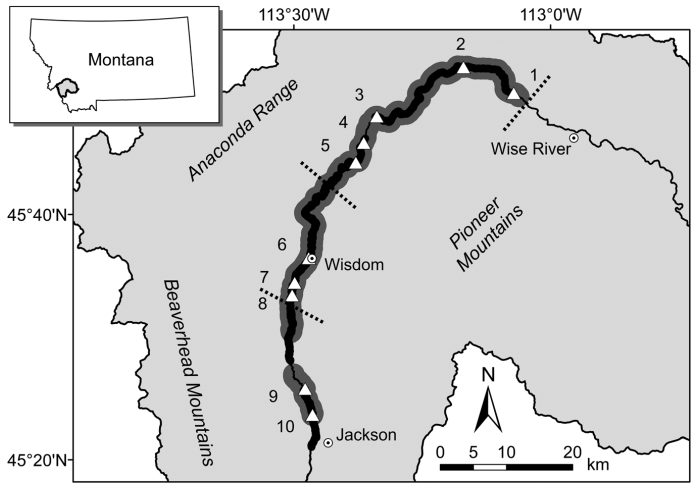

Figure 1. Big Hole River and watershed located in the upper Missouri River basin of southwestern Montana. We collected stream temperature data in the main stem river using three techniques: Langrangian longitudinal profiling (thick black line), thermal infrared (TIR) imagery (wider gray line), and stationary instream temperature-loggers (white triangles, numbered in ascending order from downstream to upstream). Black-dotted lines delineate drought management zone boundaries.

Cattle grazing and grass hay production are the principal land uses in this sparsely populated valley. Stream water is diverted at multiple locations in the watershed for flood irrigation. Riparian vegetation includes a mix of grasses (Poaceae), sedges (*Carex* spp.), and willows (*Salix* spp.). At the downstream end of the study area, the Big Hole River flows through an adjacent coniferous forest.

We selected this study area in relation to a larger research project motivated by a concern for the conservation of fluvial arctic grayling (*Thymallus arcticus*). Fluvial grayling have been extirpated from $>$ 95% of their historic range in the upper Missouri River watershed [*Kaya*, 1992], and the upper portion of the Big Hole River supports one of the last naturally-reproducing populations of fluvial grayling in the coterminous United States. Warm summer stream temperatures have been identified as a critical limiting factor for this cold-water fish species in the Big Hole River [*Lohr et al*., 1996], and reducing summer water temperatures is a primary goal of an extensive stream restoration program.

2.2. Data Collection and Processing

We used three techniques to collect stream temperature data for the main stem Big Hole River in the summer of 2008 (Figure 1). We deployed a network of instream temperature loggers, conducted a thermal infrared (TIR) flight, and collected continuous longitudinal thermal profiles by towing a water temperature probe through the thalweg. These techniques were chosen to provide temperature data with complementary advantages in spatial and temporal scale and cost effectiveness. We focused our efforts on the summer period when stream discharge was relatively low and water temperatures were relatively high (supporting information Figure S1), because this was assumed to be a critical time period for the growth and survival of coldwater fish, including arctic grayling, in the study area.

2.2.1. Stationary Temperature Loggers

We deployed a network of stationary, instream temperature loggers to assess stream temperature at 10 locations in the main stem of the Big Hole River (Figure 1) and in 13 tributaries near their confluences with the main stem. Each of the three models of temperature sensors/loggers (Onset Temp Pro, Temp Pro v2, and Pendant) had a reported accuracy of $\pm 0.2^\circ$C or less. Installation dates ranged from 16 May to 18 July 2008, but most loggers were installed by mid-June. Retrieval dates ranged from 2 October to 16 October 2008. Temperature loggers were secured in well-mixed areas of the stream and calibrated before and after deployment [*Dunham et al*., 2005]. Loggers recorded temperature hourly.

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2.2.2. Airborne Thermal Infrared (TIR)

Thermal infrared and color videography (Watershed Consulting, LLC, Missoula, MT) were used to obtain stream temperature data at a fine spatial resolution ($\sim$ 1 m pixels). An infrared thermal camera (ThermaCAM™ SC640, FLIR Systems, North Ballerica, MA) mounted in a fixed-wing aircraft captured 640 $\times$ 480 pixel imagery from 7.5 to 13 μm of the spectral range. On 30 July 2008 (14:07–16:00 h), the flight was conducted in an upstream direction beginning at the downstream end of the study area. The aircraft flew at a height of 1524 m above ground level for the first 56 km of the study area and at 1219 m for the remaining portion of the study area. Height of the flight was lowered for the upstream segment to allow for sufficient pixel resolution for the narrower stream channels. Weather on the day of the flight was relatively warm (32°C air temperature) and calm with mostly clear skies. Because of pilot error, thermal imagery was not available for approximately 8 km of the river near the upstream end of the study area. Technical problems occurred while collecting videographic images during the initial flight and a subsequent flight was conducted to acquire these images over the same extent of river on 13 August 2008. Videographic images were used to identify pertinent morphological features.

Radiation values from the thermal images were converted to temperature estimates using ThermaCam Researcher software (FLIR™). For calibration, parameters for emissivity, atmospheric temperature, humidity, and flight elevation were adjusted to reflect water temperature measurements recorded by instream stationary temperature loggers during the flight. For this calibration, hourly data from stationary temperature loggers were linearly interpolated to estimate temperature at the exact time the TIR image was taken. After calibration, TIR temperature observations were sampled near the river midline from a circular footprint overlaid on each image, and the mean pixel value from within each footprint was averaged among five or six adjacent images to estimate a mean surface water temperature for approximately 100 m stream length intervals. Interval length varied depending on factors such as air speed, channel pattern, and image angle.

2.2.3. Langrangian Longitudinal Thermal Profiling

We also collected spatially continuous, longitudinal, near-streambed temperature data using methods similar to *Vaccaro and Maloy* [2006], hereafter, referred to as Langrangian longitudinal profiling. The general premise of this technique was to obtain stream temperature data from a Langrangian framework following the downstream movement of a stream water particle as it warmed during the day. To implement this approach, we towed a temperature measuring and recording probe (Levelogger Gold M10; Solinst Canada Ltd., Georgetown, Ontario, Canada; accuracy $\pm$0.05°C; absolute response time $\sim$1°C per minute) in a downstream direction at a velocity similar to, or slightly faster than the stream. The probe was protected within a padded PVC tube, with several holes and an open end to allow for continuous water flow over the temperature sensor. The tube was also weighted to keep the probe near the streambed. Temperature was recorded every second during the survey. Spatial coordinates were simultaneously recorded in a GPS track every 3 s (Garmin GPSMap 76S; WAAS-enabled; approximate position accuracy $\leq$ 5 m).

Temperature and spatial data were downloaded following each survey and linked in a database by time. These data were collected from 23 July to 1 August 2008, and the combined spatial extent of the Langrangian longitudinal profiling surveys closely overlapped the extent of the TIR survey (Figure 1). Data were acquired on mostly clear, sunny days (with the exception of some cloudy weather in the late afternoon on 29 July 2008).

2.2.4. Geographic Information System (GIS)

Stream temperature data were spatially referenced and organized in a GIS (ArcGIS 9.3, ESRI, Redland, California). We created a stream line along the center of the main channel of the Big Hole River using visible spectrum aerial photos collected on 13 August 2008. The TIR-derived mean surface water temperatures, stationary temperature logger measurements, and Langrangian longitudinal profiling measurements were linearly referenced to the stream line. For this study, stream location 0 km was at the downstream end of the study area; distance accumulated in the upstream direction.

2.3. Modeling Summer Stream Temperature

2.3.1. General Approach

We developed a statistical modeling framework that estimated spatial and temporal patterns in stream temperature by interpolating between measurements from stationary temperature loggers and TIR imagery. The approach was based on the assumption that daily mean stream temperature increased monotonically from upstream to downstream along the stream course, but range in diel temperature fluctuation was

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variable and required site-specific observations. Integrating two different data types into the modeling framework capitalized on respective temporal and spatial strengths of each. For example, temperature data from stationary loggers formed the foundation for assessing longitudinal patterns in mean stream temperature and the shape and timing of diel fluctuations. The TIR observations provided fine spatial resolution data concerning the magnitude of diel temperature change. Ultimately, we used this approach to estimate stream temperatures at a relatively fine spatial (∼100 m) and temporal resolution (continuous) over a relatively large spatial extent (∼100 km of river) for the warmest period of the summer (July 1 to August 18). We used an independent data set (Langrangian longitudinal thermal profiling) to validate model predictions at a fine spatial resolution. We also used a leave-one-out cross validation (LOOCV) to further evaluate model performance. Last, we compared the fine-scale model estimates to current monitoring data, in the context of management-derived stream temperature thresholds.

2.3.2. Predicting Subdaily Mean Stream Temperature

Theoretical and empirical longitudinal profiles of stream temperature generally reveal a gradual warming trend in daily mean temperatures from upstream to downstream, with the warming rate decreasing as stream size increases [*Theurer et al*., 1984; *Rivers-Moore and Jewitt*, 2004; *Caissie*, 2006]. This general downstream warming trend is not necessarily continuous, because unique geomorphic features of stream networks can reverse expected downstream trends [i.e., *Poole*, 2002; *Fonstad and Marcus*, 2010]. For example, we anticipated a decrease in daily mean temperatures in the downstream 15 km of the study area because of increased groundwater inputs [*Flynn et al*., 2008; *Holmes*, 2000] and a series of cooler tributaries entering the stream [*Vatland et al*., 2009]. Nonetheless, we did hypothesize a downstream warming trend in daily mean stream temperatures for most of the study area.

To predict subdaily mean stream temperature as a function of stream distance, we used a cubic polynomial:

$$T_{mean\,i} = a_i + b_i m + c_i m^2 + d_i m^3 \tag{1}$$

where T (°C) is predicted mean stream temperature at river meter m during time segment i using segment-specific constants (a-d). Time segments consisted of sequential 10 h warming and 14 h cooling periods, 8:00–18:00 and 18:00–8:00 (next day), respectively. Section 2.3.3 (next) details the motivation for using these subdaily time segments. We used the curve-fitting function in NCSS 2007 [*Hintze*, 2009] to fit polynomials to stationary temperature logger data (Figure 1) from 1 July to 18 August 2008. The NCSS software was used for all subsequent model-fitting and statistical analyses.

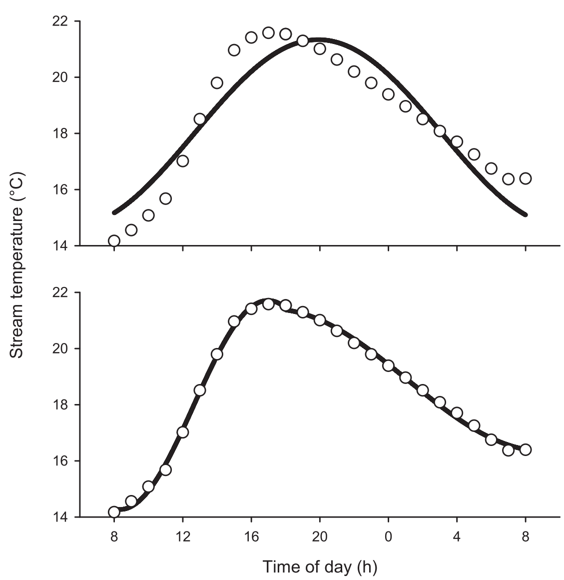

Figure 2. Example of asymmetry in diel stream temperature fluctuation. Black dots are stream temperature observations collected at site 7 near river km 72, beginning at 8:00, 6 August 2008. Black lines are modified sine models (equation (2)) fit to hours 8:00–8:00 (next day) in the top plot, and separately from 8:00–18:00 and 18:00–8:00 (next day) in the bottom plot. RMSE = 0.79, 0.13, and 0.10, respectively. In this example, stream temperature warmed at a faster rate than it cooled, and it cooled to a lesser extent. This illustrates the potential importance of modeling the ascending and descending limbs separately.

2.3.3. Developing A Modified Sine Model

Diel fluctuations in stream temperature are cyclic and can be quantified by oscillating functions such as a sinusoid [e.g., *Arrigoni et al*., 2008]. However, diel fluctuations in stream

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temperature are not necessarily symmetric (vertically or horizontally), and stream temperatures in this system usually warmed faster than cooled during the summer [e.g., *Zimmerman*, 1974; Figure 2]. Accordingly, we split the diel fluctuations of stream temperature into warming and cooling segments to account for these potential asymmetries and improve the model fit of a sinusoid (Figure 2). To quantify temporal variation in summer stream temperature within these sequential warming and cooling time segments, we fit stationary temperature recordings from 1 July to 18 August 2008 to a modified sine function:

$$T_{i,m,t}=A_{i,m}sin\left[2\pi/P_{i,m}\left(t-t_{Tmean\,i,m}\right)\right]+T_{mean\,i,m} \tag{2}$$

where i is time segment; m is distance upstream (m); t is time of temperature measurement (h); A is amplitude (°C); P is period (h); and t_{Tmean} (h) is the phase shift (i.e., time when mean temperature occurs during the time segment). The variable T is predicted stream temperature, and T_{mean} is predicted mean temperature using equation (1). When $t=t_{Tmean}$, $T=T_{mean}$ (to avoid dividing by zero). We constrained P and t_{Tmean} so that estimates of A would be representative of a diel cycle.

We incorporated TIR observations into the sine-based model to estimate stream temperature at a fine spatial resolution between stationary loggers. This required time-specific estimates for P (period) and t_{Tmean} (phase shift), so we averaged P and t_{Tmean} for each subdaily time segment (i) of the time series from 1 July to 18 August 2008. To estimate T_{mean} (vertical offset), we used equation (1). To reduce the influence of outliers, TIR observations were smoothed using a LOESS regression (NCSS 2007, quadratic fit, 4% calculations, one robust iteration). We estimated A at each TIR observation site on the day of the TIR flight using the following equation (Figure 3):

$$A_{TIR\,m}=\left(T_{TIR\,m}-T_{mean\,i,m}\right)/ \\ sin\left[2\pi\;/P_i\left(t_{T_{TIR\,m}}-t_{Tmean\,i}\right)\right] \tag{3}$$

where $i=59$ (warming segment on 30 July 2008), and T_{TIR} (°C) is the TIR temperature observation taken at river meter m at time $t_{T_{TIR}}$ (h). All estimates of A_{TIR} were positive in this study, but other data sets may require a constraint to avoid negative amplitudes.

Estimating stream temperature at TIR observation locations throughout the time series required scaling estimates of amplitude among all time segments. We used A_{TIR} (amplitude estimates during the time segment of the TIR flight) as a baseline. These baseline amplitudes were adjusted for each time segment based on the average proportional change in amplitude at stationary temperature logger sites such that:

$$g_i=\frac{1}{n}\sum_{j=1}^{n}1+\frac{\left(A_{i,j}-A_{TIR,j}\right)}{A_{TIR,j}} \tag{4}$$

where g is the proportional scaling constant for each time segment i, and j represents the number of the stationary temperature logger site ($n=10$ on most days). For example, amplitude estimates at stationary sites were, on average, 23% greater during the warming segment on 31 July 2008 ($i=61$, $g_{61}=1.23$) as compared to the baseline segment on 30 July 2008 ($i=59$, $g_{59}=1.00$).

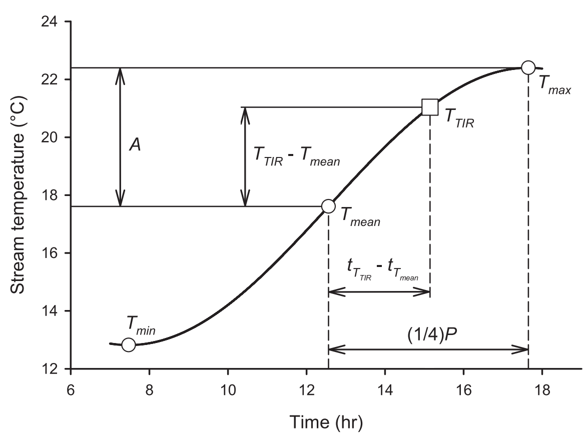

Figure 3. Graphical example using thermal infrared temperature observations (T_{TIR}) to estimate site-specific amplitude (A) in diel temperature fluctuation (equation (3)). Vertical offset (T_{mean}; mean temperature for a given time segment) was estimated as a function of stream distance (m) and time segment (i). Period (P) and phase shift (t_{Tmean}; time of T_{mean}) were averaged across stationary temperature loggers within each time segment. In this specific example, the TIR observation was made at river km 62.57, at approximately 15:09, 30 July 2008.

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We then estimated temperature at TIR observation locations (m) at hourly time steps (t) during all time segments (i), by modifying equation (2) as follows:

$$T_{i,m,t} = g_i A_{TIR\,m} sin[2\pi\ /P_i(t - t_{Tmean\ i})]\ + T_{mean\,i,m} \tag{5}$$

We estimated temperature at 8:00 and 18:00 for each time segment, resulting in concurrent temperature estimates (with the exception of the first and last occurrence in the entire time series). We averaged these coincident temperature estimates.

2.3.4. Evaluating Model Performance

Given the number of parameters in the model and reliance on a relatively small number of stationary temperature loggers in the main stem ($n=10$), we used a LOOCV technique to assess potential overfitting and to identify influential data points. We removed data from one of these stationary temperature loggers, and then calibrated and parameterized the TIR-based sine model using data from the remaining sites and site-specific TIR observations. We then used this LOOCV model to estimate hourly stream temperatures at the removed site for the summer modeling period beginning 10 July 2008. Temperature data were not collected from one to three main stem stationary logger sites on days prior to 10 July 2008, so we did not use the cross validation for these early July time segments. We repeated this procedure for each site. We compared observed and LOOCV-predicted hourly, daily minimum, and daily maximum stream temperatures for each main stem stationary temperature logger location. We evaluated multiple goodness-of-fit metrics (root mean squared error (RMSE), 5th and 95th percentile of error, and mean error) for each of these comparisons.

We also validated TIR-based sine model predictions by comparing them to temperature measurements collected during the Langrangian longitudinal thermal profiling (data independent of the model). Langrangian profiling measurements were matched to the nearest TIR-observation point. All temperature measurements and predictions within 10 m of each other were retained for this external validation. There were several redundant profiling observations for each TIR match, so the profiling observations were averaged within each match. Since the profiling occurred on six different days, including the day of the TIR flight, we performed the external validation separately for each day. Residuals were examined for diel and spatial patterns, and goodness-of-fit was quantified using the same metrics as the internal validation.

2.3.5. Model Sensitivity Analysis

We used a local sensitivity analysis to evaluate the influence of parameter uncertainty on key model results. We used a simple one-factor-at-a-time experimental approach, where we incrementally increased and decreased individual parameters (T_{mean}, t_{Tmean}, P, and T_{TIR}) by up to two standard deviations. By adjusting parameters by standard deviations, we incorporated information on the variability of the parameter and, subsequently, influence on model output [*Hamby*, 1995]. With only one parameter adjusted, we predicted maximum stream temperatures at all the stationary temperature logger sites on 30 July 2008. We then plotted mean error in maximum stream temperature (observed-predicted) and change in parameters (units of standard deviations). Standard deviation of T_{mean} was based on residuals from equation (1), when $i = 59$ (day of TIR flight). Standard deviation for t_{mean} and P were based on variation in parameter estimates among sites for this same time segment. Standard deviation in T_{TIR} was based on deviation in TIR estimates from instream temperature observations at the time of the TIR flight.

2.3.6. Applying the Model to Management Criteria

Local watershed organizations and natural resource managers have collaborated to implement a drought management plan for the Big Hole River. The plan divides the river into three distinct management zones (Lower, Middle, and Upper Big Hole River). The middle and upper zones occur within the study area and range from river km 0–47 and 47–75, respectively. Stream temperature criteria are a major component of the drought management plan, and there is one designated temperature monitoring site within each management zone. When stream temperatures exceed 21°C for more than 8 h per day for three consecutive days at a monitoring site, recreational fishing may be closed in that management zone. We compared the number of hours per day > 21°C at the temperature monitoring sites of the drought management plan to our fine-scale model predictions (approximately every 100 m along the river). This allowed us to evaluate how well single monitoring sites represent summer thermal conditions throughout respective management zones. Details of the drought management plan are described for the year of data collection (2008); minor changes to the plan have occurred in subsequent years.

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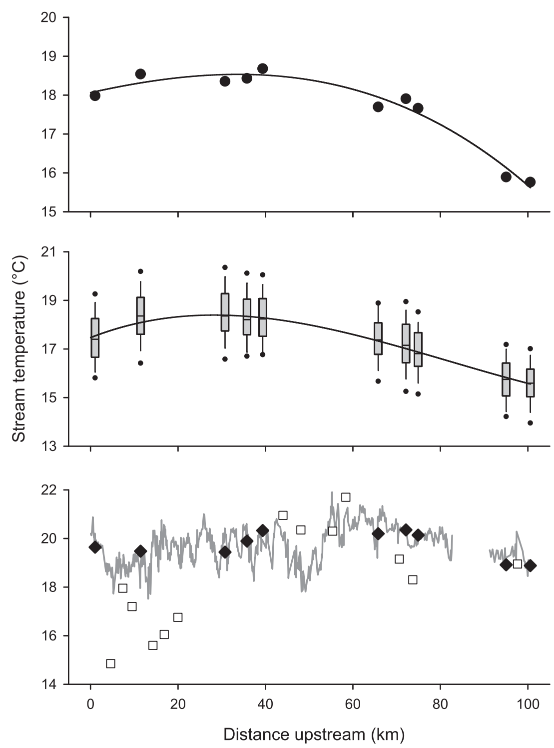

Figure 4. Mean stream temperature as a function of stream distance on 30 July 2008 (day of the TIR data collection; top plot) and from 1 July to 18 August 2008 (summer modeling period; middle plot). A cubic polynomial was fit to all data in the top plot ($r^2 = 0.96$, RMSE = 0.19) and median values in the middle plot ($r^2 = 0.98$, RMSE = 0.12). Box and whisker plots display the median, 10th, 25th, 75th, and 90th percentiles, with 5th and 95th percentiles presented as outliers. (bottom plot) Longitudinal profile of TIR temperature observations in solid gray line and concurrent instream temperature measurement in the main stem (black diamonds) and tributaries (white boxes).

3. Results

3.1. TIR Accuracy and Stationary Loggers

Differences between calibrated TIR observations versus instream main stem temperature measurements were comparable to other TIR studies [~ 0.5°C *Torgersen et al.*, 2001; ~ 1°C *Kay et al.*, 2005]. Minimum error = −0.86; maximum error = 0.64; mean error = 0.00; and RMSE = 0.43 (all error metrics in °C). Tributaries in the downstream portion of the study area were up to 5°C cooler than the main stem during the time of the TIR flight, but stream temperatures of tributaries in the middle and upper portions of the study area tended to be similar to the main stem (Figure 4).

3.2. Predicting Subdaily Mean Stream Temperature Longitudinal Profiles

We observed a consistent longitudinal pattern where subdaily mean stream temperatures gradually increased in a downstream direction except the lower portion of the study area, where it leveled off and decreased slightly. This longitudinal pattern was predictable as a function of river distance during the summer, including the day we collected TIR imagery (Figure 4). Average coefficient of determination (r^2) and RMSE for all subdaily polynomial fits were 0.95 and 0.20°C, respectively (supporting information Table S1).

3.3. Development of the TIR-Based Sine Model

Temperature data from the stationary loggers fit the modified sine function well; average r^2 and RMSE for all fits to equation (2) were 0.99 and 0.19°C, respectively (supporting information Table S2). The few time segments that did not fit the expected sinusoidal pattern occurred on days with sporadic cloud cover, or following rain events (e.g., 8 August 2008). Spatial patterns in period (P), phase shift (t_{Tmean}), and amplitude (A) were consistent throughout the summer modeling period, and parameter estimates during the time segment of the TIR flight were also representative of the summer modeling period. When compared to estimates of P, t_{Tmean} was less variable across space and time (supporting information Table S2). In warming segments, estimates of P tended to be shorter at site 1 and longer at site 2, as compared to the other sites. Amplitude estimates varied spatially and were consistently greater at sites 9 and 10.

Incorporating data from the TIR imagery into the modified sine model allowed us to evaluate full diel cycles in stream temperature at a fine spatial resolution (Figure 5). The model predicted considerable spatial and temporal heterogeneity in stream temperatures during the summer modeling period (1 July to 18 August

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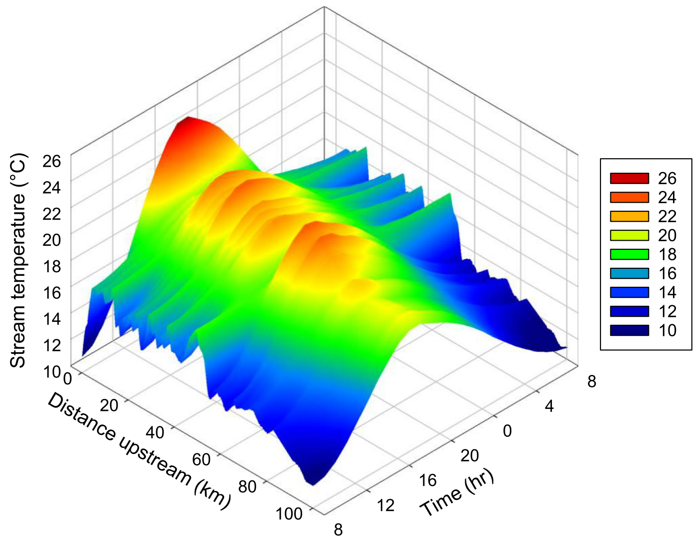

Figure 5. Stream temperature estimates (°C) for the main stem Big Hole River over the entire study area for a 24 h time period beginning at 8:00, 30 July 2008. Estimates are based on a statistical model which incorporates spatial variation from thermal infrared data and temporal variation from stationary temperature loggers. Note changes in spatial heterogeneity across time, with greatest spatial differences occurring at daily maxima and minima.

2008). Indeed, there were areas that were either more or less buffered from diel fluctuations in stream temperature, and predicted range in diel fluctuations on the day of the TIR flight averaged 5.7°C (SD = 2.3°C). Longitudinal patterns in the TIR-based sine model and the TIR temperature observations appeared to be influenced by tributary locations in some cases (Figure 4), contributing to an undulating pattern in daily minima and maxima along the course of the river (Figure 5).

3.4. TIR-Based Sine Model Evaluation

Most errors produced in the LOOCV modeling were <1°C, and the greatest errors were approximately ±3°C (Table 1). Using the LOOCV model, goodness-of-fit metrics were similar for all temperature metrics (hourly, daily minimum, and daily maximum). Mean error was close to zero in all cases, suggesting little overall bias within the range of observed temperatures. However, site-specific evaluation revealed a bias toward overpredicting daily maximum stream temperature at site 1 and, to a lesser extent, underpredicting at sites 2 and 5 (Figure 6). There was a slight bias toward underpredicting the warmest temperatures at all other sites.

External validation results, which compared continuous thermal profiling observation to the TIR-based sine model predictions, were similar to the internal validation (Table 1). Overall, the TIR-based sine model predicted site-specific and time-specific profiling observations well (RMSE $<$ 0.9°C; all days combined). The model fit best in the upstream half of the study area, including the day of the TIR flight (Table 1). The greatest deviations occurred in the downstream end of the study area, especially from river km 10 to 17 (Table 1). This pattern corresponds with spatial trends in error observed at the stationary temperature loggers (Figure 6). Some of the greatest deviations (positive and negative) in the external validation occurred at locations where tributaries and associated groundwater produced lateral (cross-sectional) variation in stream temperature that, in some cases, extended over a kilometer downstream of confluences (e.g., downstream of LaMarche Creek near river km 14).

3.5. Model Sensitivity

Model sensitivity to changes in key parameters varied in magnitude and direction of response (Figure 7). There was a negative linear relationship between mean error and changes in P and T_{TIR}. Although P had the

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Table 1. Goodness-of-Fit Metrics From Internal and External Model Evaluation[a]

Model Evaluation	Time Segment (*i*)	Location (km)	Temperature Metric	RMSE (°C)	5th Percentile Error (°C)	95th Percentile Error (°C)	Mean Error (°C)	*n*
			Internal Validation					
Leave-one-out cross validation	20–97	1.1–100.6	Hourly	0.84	−1.44	1.39	−0.03	10
	20–97	1.1–100.6	Daily maximum	0.88	−1.29	1.52	0.22	10
	20–97	1.1–100.6	Daily minimum	0.80	−1.47	0.83	−0.39	10
			External Validation					
Continuous profiling versus full model	45	96.0–100.6	Explicit	0.13	0.01	0.19	0.11	16
	55	100.6–100.6	Explicit	0.30	n/a	n/a	n/a	1
	57	67.2–82.7	Explicit	0.38	−0.74	0.00	−0.31	85
	59	38.9–65.2	Explicit	0.34	−0.48	0.54	0.07	147
	61	12.2–38.8	Explicit	0.83	−1.44	1.41	−0.03	244
	63	1.1–12.3	Explicit	0.88	−1.47	0.02	−0.66	106
	Combined	1.1–100.6	Explicit	0.68	−1.33	0.80	−0.15	599

[a]Location is distance upstream (km). Time segments (*i*) refer to the sequential 10 h warming and 14 h cooling phases used throughout the manuscript (ranging from 1 July to 18 August 2008). Error terms (°C) are based on differences between observed and predicted temperature metrics. "Explicit" refers to temperature observations and predictions for specific locations and times. *n* is the number of locations used in each validation. See methods for further detail on validation techniques.

greatest standard deviation, model output was relatively insensitive to changes in *P*. The model was most sensitive to changes in T_{TIR}. There was also a negative relationship between t_{Tmean} and mean error, and model predictions were most sensitive to overestimates of t_{Tmean}. This pattern appears to be intuitive, for if t_{Tmean} is erroneously high and close to the time of T_{TIR} (Figure 3), *A* would be overestimated. As a result, daily maximum stream temperature would be overpredicted. There was a positive linear relationship between T_{mean} and mean error, but predictions were relatively insensitive to change in this parameter.

3.6. Comparing the Model to Management Criteria

Model predictions of the number of hours per day in excess of 21°C varied across space and time in both drought management zones during the summer period (Figure 8). For example, the mean model prediction among sites in the Upper zone ($n = 174$) from 10 July to 18 August 2008 was 2.0 h $d^{-1} > 21$°C (SD = 1.5), versus 2.2 h $d^{-1} > 21$°C observed at the water temperature monitoring site located at river km 11.4. In the Middle zone, the mean model prediction among sites ($n = 445$) was 2.4 h $d^{-1} > 21$°C (SD = 1.6) for the same time extent, but the mean observed at the monitoring site (river km 65.8) was 3.9 h $d^{-1} > 21$°C. Data for 1 July to 10 July 2008 were not used in this comparison because these data were not available at the monitoring site in the Middle zone. In the summer of 2008, stream temperatures at the monitoring sites did not exceed the drought management plan threshold of three consecutive days with eight or more hours exceeding 21°C. This is not surprising, for 2008 was not a particularly warm or dry summer (supporting information Figure S1). Nonetheless, 33% of model prediction sites exceeded the threshold at least once during the summer.

4. Discussion

In this study, we developed a unique approach to collect and analyze stream temperature data at scales pertinent to biological processes and resource management. We used a novel modeling framework that combined the fine spatial resolution of TIR imagery with hourly stationary temperature logger data. This combination allowed us to estimate summer thermal conditions at a fine spatial resolution (~100 m) over a large extent of stream (~100 km) at any time during the warmest part of the summer. This assessment revealed considerable spatial and temporal heterogeneity in summer stream temperatures (Figure 5) and underscores the potential importance of evaluating thermal regimes at relatively fine spatial and temporal scales. Further, single-point monitoring sites, decisive in drought-management criteria, underestimated the full range of summer thermal conditions in this heterogeneous river (Figure 8).

4.1. Integrating TIR and Stationary Stream Temperature Data

In recent years, TIR imagery has contributed extensively to the understanding of stream thermal regimes, and data of a resolution and extent similar to this study are extremely useful in understanding the dynamic,

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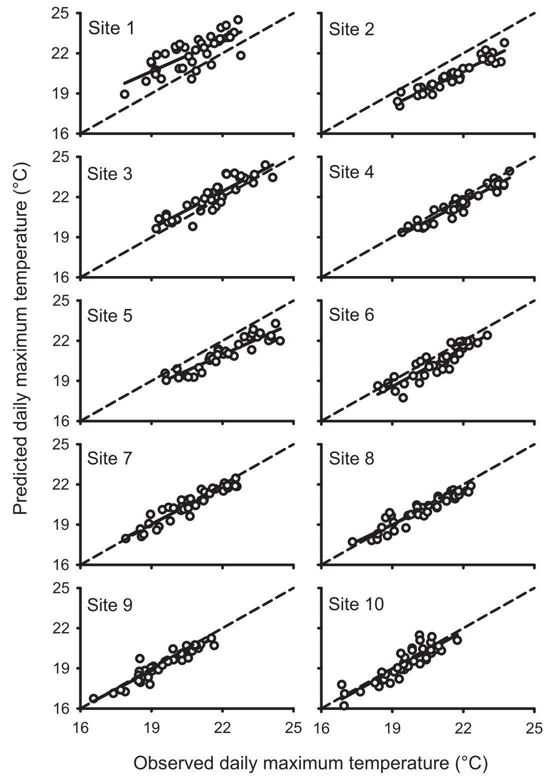

Figure 6. Observed versus LOOCV model-predicted daily maximum stream temperature (°C) at the 10 stationary logger sites from 10 July to 18 August 2008. Dashed lines are 1:1 relationships; solid lines are simple linear regressions.

multiscale habitat needs of mobile stream organisms [e.g., *Torgersen et al*., 1999; *Fausch et al*., 2002; *Wiens*, 2002]. However, collecting fine resolution TIR imagery over extensive study areas introduces implicit time constraints, and longitudinal patterns in TIR temperature observations may be confounded by time and misrepresent spatial patterns. A basic assumption of most TIR studies is that sequential images provide a synoptic view of surface temperature because: (1) data were collected when rate of change in temperature was relatively low (i.e., near the daily maximum or minima); or (2) the study area was small, and data were collected over a brief time period [e.g., *Loheide and Gorelick*, 2006]. In this study, we collected TIR imagery in a flight that lasted ~2 h and covered ~100 km of river, and this rate of TIR image collection is comparable to other aerial TIR surveys of sinuous rivers [*Torgersen et al*., 2001]. Stream temperatures can increase at ~1°C per hour during summer afternoons in the study area. Thus, a potential ~2°C difference in TIR temperature observations between upstream and downstream ends of the study area was attributable solely to the time data were collected (Figure 4; bottom plot). We overcame this limitation by incorporating TIR imagery and stationary temperature logger data into a modified sine model, and this allowed us to effectively compare synoptic temperature estimates throughout a relatively large study area.

4.2. Model Evaluation

Rigorous evaluation, including internal validation, external validation, and sensitivity analyses, suggests model estimates of longitudinal patterns in summer stream temperatures are accurate for this system. Validation errors (RMSEs < 1°C) were comparable to other studies evaluating thermal regimes using statistical modeling approaches [e.g., *Benyahya et al*., 2007]. The model was most sensitive to the accuracy of the

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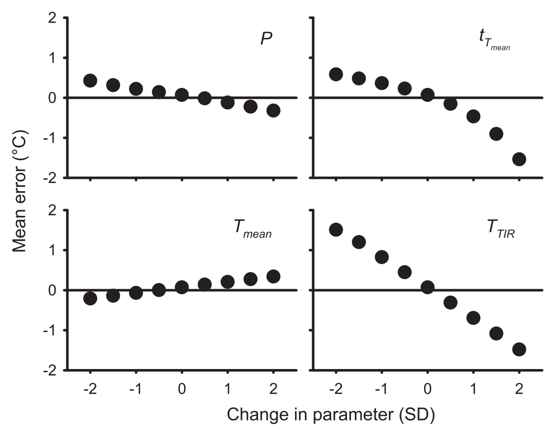

Figure 7. Local sensitivity analysis for four parameters (P, t_{Tmean}, T_{mean}, and T_{TIR}) used in the TIR-based sine model. Mean error was based on the difference between observed and predicted daily maximum stream temperature on 30 July 2008 at stationary temperature loggers. Standard deviations (SD) for P, t_{Tmean}, T_{mean}, and T_{TIR} were 2.06 h, 0.34 h, 0.20°C, and 0.45°C, respectively.

calibrated TIR observations, as opposed to derived parameters within the model, but accuracy of TIR observations in this study was comparable to prior research [~ 0.5°C *Torgersen et al.*, 2001; ~ 1°C *Kay et al.*, 2005]. It was also encouraging that model predictions were relatively insensitive to parameters with the greatest uncertainty, such as P (period of the sine function).

External validation was used to estimate the accuracy of longitudinal patterns in stream temperature, but vertical and lateral variation in stream temperature also occurs in streams. We did not directly assess vertical differences in stream temperature because we assumed the river was well mixed. *Torgersen et al.* [2001] found minimal vertical stratification in a range of stream types, but this phenomenon can vary considerably within and among stream networks [*Webb et al.*, 2008]. For example, *Krause et al.* [2012] observed streambed temperatures up to 1.5°C cooler near groundwater upwellings as compared to the ambient temperature, but there was no measurable evidence that the upwellings influenced surface water temperatures. Thus, it is possible that some of the error in external validation was related to differences in measurements taken near the streambed (longitudinal thermal profiling) and surface water estimates (TIR-based sine model).

Lateral variation in stream temperature and mismatched sampling contributed to error in our external validation. For example, we sampled TIR data from the midline of the stream channel and measured longitudinal thermal profiles along the thalweg. Consequently, longitudinal profiling sometimes measured nearshore water, but TIR data were sampled from midchannel water. This becomes an issue when cooler or warmer point-source inputs contribute to incomplete lateral mixing. Other studies have highlighted significant differences in spatial and temporal stream temperature patterns between adjacent main stem and side channel areas [*Arrigoni et al.*, 2008; *Carrivick et al.*, 2012]. Similarly, *Cardenas et al.*, [2011] used TIR data to illustrate lateral variation between a main stem river and geothermally heated tributaries in Yellowstone National Park, and lateral variation in stream temperature persisted several channel widths downstream of confluences.

Uncertainty in model predictions was greatest in the downstream portion (~20 km) of the study area. For example, the model overpredicted daily maximum temperature at site 1 and underpredicted daily maximum temperature at site 2 (Figure 6). Much of this error can be attributed to differences in measurements associated with the two techniques (T_{TIR} and stationary temperature loggers). Further, measurement error was amplified in estimates of daily maxima in this area because TIR measurements at these two sites were made closer in time to t_{Tmean} than at upstream sites. Estimates of P for sites 1 and 2 also differed considerably from the mean value used in the model. The combination of these three factors resulted in the biased predictions; this outcome underscores a potential weakness in the model, where a combination of parameter uncertainty can result in bias.

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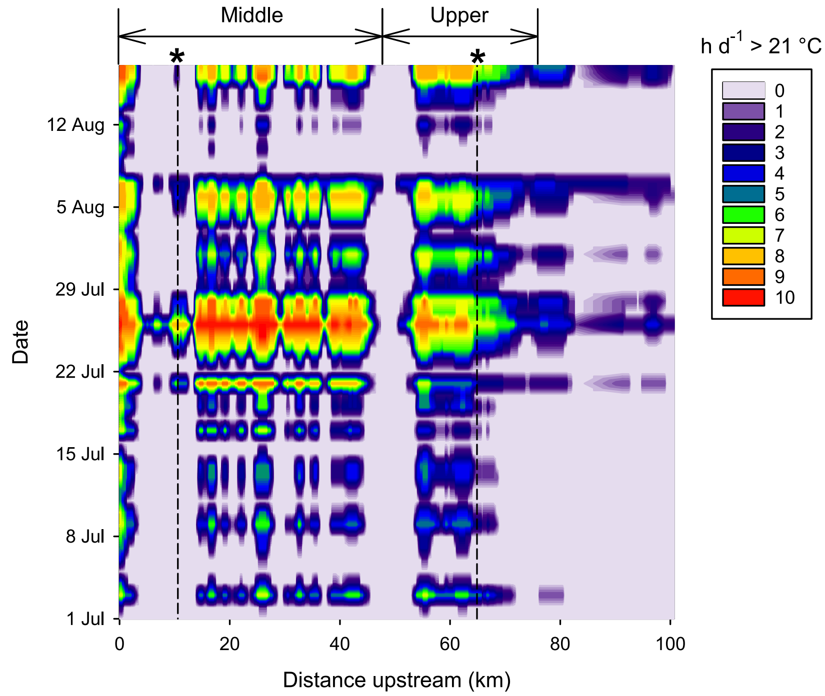

Figure 8. Predicted number of hours per day > 21°C in the main stem Big Hole River (~ every 100 m of stream length) from 1 July to 18 August 2008. Drought management plan zones are indicated above the plot. Asterisks and vertical-dashed lines mark the location of temperature monitoring sites used within respective management zones in 2008.

The statistical modeling approach used to estimate stream temperature patterns in this paper relied on two fundamental assumptions: (1) longitudinal patterns in daily mean stream temperatures can be predicted accurately during summer baseflow conditions, and (2) diel fluctuations in stream temperature can be accurately quantified with a modified sine function. Based on model evaluations, longitudinal patterns in daily mean stream temperature were predictable and consistent during this study, and the multiphase sine function accurately fit fluctuating stream temperatures. It was particularly important that both of these assumptions were valid because error in the initial modeling phases could propagate to subsequent steps. Additionally, hydrologic conditions were assumed to be relatively stable during the modeled time period, and validity of this approach for modeling systems with dynamic flow regimes is unknown. Overall, the usefulness in applying this modeling framework in other systems (or in other seasons or years in this system) largely depends on the robustness of these underlying assumptions.

In this study, we parameterized the model based on our understanding of the upper Big Hole River, and we summarized data to answer specific management questions. However, there is flexibility in this modeling framework. For example, sine-model parameters could be estimated for individual stream segments based on geomorphic characteristics of the stream and the valley in which it flows. Temperature estimates could also be summarized to meet alternative study objectives and to evaluate different biotic thresholds, such as daily minima. Other studies have incorporated lateral variation in stream temperature into longitudinal analyses [e.g., *Cristea and Burges*, 2009] and quantified indices of spatial heterogeneity [e.g., *Carrivick et al.*, 2012] using thermal data similar to this study.

The continuous stream temperature data produced using the statistical modeling framework of this study are accurate when model assumptions are met, but this approach has limitations and uncertainties. The model was developed to quantify spatial and temporal patterns in stream temperature by capitalizing on

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the strengths of otherwise disparate stream temperature data types. The framework was not designed to identify factors producing the stream temperature patterns, although empirical approaches can be useful in identifying important correlations [e.g., *Dugdale et al*., 2013]. Alternatively, a mechanistic model could be used to predict fine-scale changes in stream thermal regimes over time and to investigate factors driving the resulting patterns [e.g., *Deitchman and Loheide*, 2012].

Overall, TIR still appears to be an exceptional tool for identifying fine-scale spatial variation in stream temperature in main stem, side channels, and floodplains [*Torgersen et al*., 2001], but collecting airborne TIR imagery is relatively expensive. Other techniques can be used to collect fine-resolution spatial data of stream temperature. For example, Langrangian longitudinal thermal profiling (used as an independent data set for external validation in this study) is a relatively inexpensive alternative to TIR [*Vaccaro and Maloy*, 2006]. Langrangian profiling could also be integrated with the temperature modeling framework presented in this study, and sampling near the diel extremes (daily maximum or daily minimum) should provide the most reliable temperature predictions. Distributed fiber optic temperature sensors (DTS) is also an emerging technology with the potential to evaluate stream temperature at fine spatial and temporal resolutions and at spatial extents of up to 30 km [*Selker et al*., 2006], and these data, where logistically feasible and affordable, could provide a powerful alternative to the approaches presented in this study.

4.3. From Theory to Application

Poole [2002] portrayed river reaches as unique segments nested within an interconnected spatial and temporal hierarchy, and this framework revealed largely discontinuous patterns in stream characteristics while acknowledging the persistence of some coarse-scale longitudinal patterns. Embracing this hierarchical perspective, we coupled fundamentally different data types in our stream temperature modeling to estimate summer stream temperatures at a fine spatial resolution over a large spatial extent. This approach resulted in a physical template with which we could match scales of data collection and analysis with management criteria [i.e., *Fausch et al*., 2002; *Wiens and Bachelet*, 2010]. Further, this provided sufficient stream temperature data to compare a comprehensive thermal regime to conventional temperature monitoring and management thresholds [i.e., *Poole et al*., 2004].

Our comparison of stream temperature monitoring and modeling revealed potential concerns with the ability of single-site monitoring plans to capture important attributes of summer thermal regimes. For example, temperature monitoring in the Upper management zone of the study area represented average thermal condition for that section of river, but monitoring in the Middle zone did not. Furthermore, neither monitoring site captured the relatively large range in thermal conditions observed within respective management zones (Figure 8). High-resolution spatial data, such as the TIR imagery and modeling employed in this study, can be used to develop monitoring plans that strategically place monitoring sites to capture a range of thermal conditions pertinent to management objectives [e.g., *Faux et al*., 2001].

Thermal criteria are included in most water quality assessments because of the critical role of water temperature in stream ecosystems, and these criteria can be evaluated using TIR imagery. For example, assessments of TMDL (Total Maximum Daily Load, section 3.3(d) Clean Water Act) have used TIR imagery, in combination with stationary sensors and mechanistic stream temperature modeling, to evaluate thermal criteria in streams [e.g., *Cristea and Burges*, 2009]. In this study, we provide a unique framework for incorporating spatial advantages of TIR imagery with temporal advantages of stationary sensors, and thus, inference from the TIR imagery increased. Accordingly, we support the use of multiple data collection and modeling techniques to evaluate stream thermal regimes [e.g., *Doyle and Ensign*, 2009]. In addition, explicitly evaluating data in the context of current management critieria can be revealing, and it provides tangible paths for communicating and applying research results.

5. Conclusions

The modeling framework presented in this paper combines different stream temperature data sets continuous in either space or time to create a new data set continuous in both space and time, and this comprehensive data set can aid in quantifying important complexities of stream thermal regimes across multiple scales. Preserving spatial and temporal variability and structure in abiotic stream data provides a critical foundation for understanding the dynamic, multiscale habitat needs of mobile stream organisms [e.g., *Fausch et al*., 2002; *Wiens*, 2002, *Carbonneau et al*., 2012]. Similarly, enhanced understanding of spatial and temporal variation in dynamic water quality attributes, including temporal sequence and spatial arrangement, can help ensure that water quality standards target conditions conducive to the beneficial uses of streams [*Poole et al*., 2004]. As our ability to measure and estimate abiotic components of stream ecosystems advances, it will be critical that we explicitly address the data needs of resource management and conservation biology and engender a reciprocal integration between research and management. Spatially and temporally continuous data sets of dynamic stream attributes, such as that created in this study, provide an opportunity for researchers and managers to explicitly consider the spatial and temporal context within which ecological processes are driving water resources. Further, these data can guide strategic placement of monitoring equipment that will subsequently capture variation in environmental conditions directly pertinent to management objectives.

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CHAPTER THREE

EFFECTS OF CLIMATE CHANGE ON THE THERMAL HABITATS OF ARCTIC GRAYLING AND NON-NATIVE STREAM SALMONIDS

Contributions of Author and Co-Authors

Manuscript in Chapter 3

Author: Shane J. Vatland

Contributions: Conceived the study, collected and analyzed data, wrote the manuscript, and obtained supplemental funding.

Co-author: Robert E. Gresswell

Contributions: Obtained funding, contributed to conceptual framework, assisted with study design, discussed analyses, results, and interpretation, and edited the manuscript at all stages.

Co-author: Steve Hostetler

Contributions: Discussed modeling approaches, data analysis, and edited manuscript.

Co-author: Alexander V. Zale

Contributions: Edited manuscript and discussed methods, results, and interpretation.

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Title page

Effects of climate change on the thermal habitats of Arctic grayling and non-native stream salmonids

Running head: Climate effects on thermal habitat

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Keywords: Climate change, air temperature, water temperature, dynamically downscaled regional climate model, thermal tolerance, Arctic grayling, brown trout, brook trout, rainbow trout

Original Research: Primary Research Article

Abstract

Climate change is projected to increase summer stream water temperatures and alter the distribution of suitable habitat for cold-water fish in the Rocky Mountain region of western North America. Understanding when, where, and to what extent climate will change thermal conditions provides a physical basis for strategic climate adaptation planning. We used a statistical modeling approach to evaluate the effects of climate on summer water temperatures in the valley-bottom stream network of the upper Big Hole River watershed in southwestern Montana. Thermal suitability was assessed for fluvial Arctic grayling and non-native salmonids using chronic and acute thermal tolerance thresholds (21 °C and 25 °C, respectively), based on previously published research. Air temperature and water temperature were highly correlated, suggesting that meteorological control of thermal habitat was much stronger than groundwater control. Simulations projected significant stream warming because of climate change from the 1980s through the 2060s. Water temperatures in half of the stream network exceeded the chronic threshold 15% or more of the summer in the 1980s, and exceedance increased to 50% or more of the summer in the 2060s. None of the stream network had water temperatures that exceeded the acute threshold in the 1980s, but temperatures in 35% of the stream network were projected to exceed the acute threshold at some point during the summer in the 2060s. Despite projected warming of the stream network, water temperatures in some sections of stream remained below both thermal tolerance thresholds through the 2060s and could provide refugia critical to the persistence of grayling and non-native salmonids. Relationships between riparian vegetation and summer water temperature suggest that

restoring riparian vegetation, at least in tributaries, could be a viable adaptation tool. This modeling approach can be used to develop strategic climate adaptation plans, especially when considered within broader ecological and socioeconomic contexts.

Introduction

Climate is a dynamic factor affecting the structure and function of freshwater ecosystems (Grimm et al., 2013). In lotic systems, climate affects discharge and water temperature, which in combination with substrate, can control the distribution and abundance of organisms (Allan & Castillo, 2007). Stream water temperature is particularly vital to the ecology of poikilotherms, such as fish, because it mediates bioenergetic processes (Beamish et al., 1975; Tytler & Calow, 1985). Climate in the Rocky Mountain region of the USA warmed over the last half of the 20th century (Pederson et al., 2010; Isaak et al., 2010; McGuire et al., 2012), and air temperature is expected to increase throughout the 21st century (Hostetler et al., 2011; Rangwala et al., 2012). Consequently, future stream water temperatures are also projected to increase in this region (Al-Chokhachy et al., 2013; Jones et al., 2014; Isaak et al., 2015).

Evaluating effects of climate change on the habitat of animal populations requires consideration of spatial and temporal scale, spatial arrangement, temporal sequence, and connectivity (Wiens & Bachelet, 2010; McCluney et al., 2014). Further, the influence of global climate change on environmental conditions that animals experience will depend on both regional variation in climate and local landscape characteristics (Poff, 1997; Griffiths et al., 2014). Climate change evaluations often focus on shifts in the central tendency of environmental parameters, such as temperature, but shifts in the range of conditions and frequency of extremes can also have important effects on biota (e.g., Fig. 1; Jenstch et al., 2007; Pederson et al., 2010; Vasseur et al., 2014).

Water temperature limits the distribution of native salmonids in the Rocky Mountain region (e.g., Keleher & Rahel, 1996; Dunham et al., 2003a and 2003b). Furthermore, the viability of many populations is threatened by land and water use, habitat fragmentation, and non-native species. A projected shift to warmer water temperatures further threatens these imperiled populations (Williams et al., 2009; Wenger et al., 2011; Isaak et al., 2012). Thus, identifying and prioritizing areas likely to have thermally suitable habitat in the future has become critical to long-term conservation planning (i.e., Isaak et al., 2015).

For example, fluvial Arctic grayling *Thymallus arcticus* in the Big Hole River in southwestern Montana represent the southernmost extent of the distribution of the species. This watershed supports one of the last naturally-reproducing populations of fluvial Arctic grayling in the conterminous United States, but habitat degradation, loss of hydrologic connectivity, entrainment in irrigation ditches, and non-native salmonid introductions limit the population (Kaya, 1992a, 1992b). Indeed, non-native salmonids (brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*) that occur in the watershed have thermal niches that are similar to grayling (Eaton et al., 1995).

Chronic irrigation withdrawals, removal of natural riparian vegetation, and intensive grazing in riparian areas are directly associated with stream segments that are relatively wide, shallow, and warm (Montana Fish, Wildlife and Parks et al., 2006). Warm summer water temperatures affect thermal habitat suitability for both grayling and non-native salmonids and potentially influence negative interactions (i.e., competition and predation) among species. Addressing these concerns requires an understanding of the spatial and temporal distribution of suitable thermal habitat. In this study, we evaluated the influence of climate and land use on current patterns (1980s through 2000s) of summer water temperature suitable for grayling and non-native salmonids. Subsequently, we estimated changes in summer water temperature from the 1980s through the 2060s, given potential climate change scenarios. Finally, we assessed effects of spatial and temporal patterns in water temperature on grayling conservation strategies.

Materials and methods

Study area, focal species, and thermal tolerance thresholds

We investigated the effects of climate on summer water temperatures in the valley-bottom stream network of the upper Big Hole River and the lower reaches of its tributaries in southwestern Montana (Fig. S1) derived from the National Hydrography Dataset (2011 high resolution; http://viewer.nationalmap.gov). Misnamed or mislocated channels were edited or removed in a GIS (ArcMap 10.1, ESRI, Redlands, California, USA). Analysis was limited to named streams with perennial discharge in the valley bottom because fluvial Arctic grayling are restricted to relatively low gradient (< 1%) stream segments (Hubert et al., 1985; Kaya, 1992a). The extent of the study area was equivalent to the historic distribution of fluvial Arctic grayling within the upper watershed. Mountain whitefish *Prosopium williamsoni*, a native salmonid, also occupied the study area, but stream fish biomass and abundance were predominately made up of non-native brook trout, rainbow trout, and brown trout (Cayer & McCullough, 2012).

The study area was a wide, flat mountain valley. Climate in the valley was cool, dry, and temperate. Cattle grazing and grass hay production were the most common land uses; stream water was diverted at multiple locations for irrigation. Riparian vegetation included a mix of grasses, sedges (*Carex spp.*), willows (*Salix spp.*), and limited coniferous forest dominated by lodgepole pine *Pinus contorta* along the valley margins. Peak stream discharge was snow-melt driven, and the lowest discharges typically occurred mid-to-late summer, when air and water temperatures were highest (Fig. S2).

We used the weekly mean of the daily maximum (WMDM) water temperature to evaluate the effects of summer thermal conditions on the distribution of Arctic grayling and non-native salmonids. The WMDM water temperature metric has been used in (or related to) thermal tolerance assessments for the focal species (Arctic grayling, brook trout, brown trout, and rainbow trout), and thus it provided a basis for establishing biologically-relevant standards with which to evaluate past, present, and future patterns in summer water temperatures. We defined chronic (21 °C) and acute (25 °C) WMDM water temperature thresholds to assess summer thermal conditions.

The chronic threshold (21 °C) characterized stream conditions that were detrimental (but sub-lethal) to Arctic grayling and non-native salmonids. When the WMDM met or exceeded the threshold, we assumed that metabolic rates (Cho et al., 1982), competition (Reeves et al., 1987; McMahon et al., 2007), and predation risk would increase and growth would decrease or stop (e.g., Reeves et al., 1987; Bear et al., 2007; Al-Chokhachy et al., 2013). Reproductive success would also be negatively affected. For example, the probability of juvenile brown trout and rainbow trout presence declined in a Georgia stream network where the annual maximum WMDM exceeded 21.5 °C (Jones et al., 2006). Abundances could decrease and patchiness and isolation of individuals could increase (e.g., Torgersen et al., 1999; Ebersole, 2003; Isaak et al., 2010). In the Boise River basin, rainbow trout densities decreased significantly between mid-July and mid-September when maximum WMDM water temperatures exceeded 20 °C (Isaak et al., 2010). Moreover, under the Arctic grayling management plan for the study area, 21 °C was a general stress threshold for the species (Montana Fish, Wildlife & Parks et al., 2006). Therefore, using 21 °C for the chronic threshold in this study provided context for evaluating climate change effects on fisheries management. However, consideration of the temporal aspects of the criterion is critical in such comparisons (i.e., Wehrly et al., 2007).

When the acute threshold (25 °C WMDM) was met or exceeded, we expected death or permanent emigration of individuals, extirpation of populations, or both. In Michigan and Wisconsin, for example, brook and brown trout were limited to areas where maximum WMDM were less than 25.4 °C (Wehrly et al., 2007). Furthermore, the 7-d upper incipient lethal temperature (UILT; the constant temperature at which 50% of a test population survives for 7 days in the laboratory) of brown trout is 24.7 °C (Elliott, 1981); the analogous value for brook trout is 24.5 °C (Selong et al., 2001). This similarity between UILTs and field-based occupancy thresholds is especially meaningful because the *in situ* fish were only exposed to that maximum water temperature part of each day, but exposure to the threshold temperature was constant in the UILT lab experiments. Additional environmental stressors or an accumulation of stressors may affect this convergence (Todd et al., 2008), but UILTs are similar to WMDM occupancy thresholds for stream salmonids (McCullough, 2010) and therefore represent distribution thresholds for cold-water species. Furthermore, Lohr et al. (1996) reported a 7-d UILT for juvenile Arctic grayling of 25.0 °C. The mean 7-d UILT for rainbow trout from multiple laboratory studies was 25.7 °C (McCullough, 1999). Although thermal tolerances of salmonids differ, the four cold-water species of interest in this study have documented UILTs within 1 °C of the acute threshold that we used.

Water temperature modeling overview

We used a statistical modeling approach to evaluate the effects of climate on summer water temperature. The approach comprised four steps: 1) we quantified relationships between air temperature and water temperature at sites throughout the study area during the months of June, July, and August (JJA) from 2005–2010; 2) we used these site-specific air-water temperature relationships to predict JJA water temperatures at these same locations using observed air temperatures from 1980–2009 and climate model-projected air temperatures from 2020–2069; 3) we quantified spatial relationships between landscape variables and summer water temperatures during a relatively warm summer (2007); and 4) we combined steps 2 and 3 in a two-step model to predict decadal trends in summer water temperatures throughout the stream network from 1980–2069. A combination of NCSS (Hintze, 2009) and R statistical software was used for the following analyses.

Stream water and air temperature measurements

We used digital data recorders to measure water temperature from 2007–2010, and additional data (2005–2010) were gathered from several government agencies. We placed recorders instream to fill spatial gaps in the data collected prior to 2007, and to provide a systematic assessment of water temperatures in the study area. These measures resulted in a large data set of water temperatures collected throughout the study area over numerous durations ranging from 2005–2010. Erroneous or misleading measurements were removed (e.g., times when the sensor was out-of-water). We excluded records with recording intervals longer than one hour because these were less probable to capture daily maximum temperatures (Dunham et al., 2005).

Daily maximum air temperature measurements were available from three weather stations located within or adjacent (< 5 km) to the study area (Fig. S1). These data were part of the Cooperative Observers Program (COOP) and available from the National Climatic Data Center (http://www.ncdc.noaa.gov). To prevent the inclusion of biased air temperature data associated with changes in equipment, protocol, or site conditions (i.e., Peterson et al., 1998), we examined relationships among measurements at the three sites during June, July, and August from 1980 through 2010. Based on that preliminary assessment, daily maximum air temperatures at the three sites were highly correlated (Pearson pair-wise correlations among the three sites = 0.87, 0.88, and 0.92), and daily maximum air temperatures at the three sites were similar in magnitude (mean difference among sites = 1.1 °C). The mean of daily maximum air temperatures at the sites was used to estimate valley-bottom air temperature for water temperature modeling.

Site-specific climate forcing on water temperature

We initially considered two climate-related variables (air temperature and stream discharge) as potential temporal predictors of summer water temperature. In a preliminary assessment, we evaluated correlations between air temperature, stream discharge, and water temperature at a site centrally-located in the study area (near Wisdom, Montana, USA) because it yielded the longest time series of observations for all three variables. Air temperature was positively correlated with water temperature and explained 86% of variation during JJA from 1998–2010 (Fig. S3; Table S1). Stream discharge was negatively correlated with water temperature and explained 45% of variation for the same time series. Using air temperature and discharge as predictors in multiple linear regression models yielded little additional explanatory power (Table S1; *cf.* van Vliet et al., 2011).

We ultimately used air temperature as the sole temporal predictor of past, present, and future climate forcing on summer water temperature, based in part on the preliminary analyses. Moreover, air temperature is a useful surrogate for solar radiation, the primary component driving diurnal heating of stream waters (Webb et al., 2008), and air temperature is a reliable statistical predictor of water temperature in several streams (e.g., Webb & Nobilis, 1997; Erickson & Stefan, 2000; Morrill et al., 2005; *cf.* Arismendi et al., 2014). We used a weekly mean daily maximum (WMDM) temperature metric in the following analyses because 1) weekly correlations between air and stream water temperature are usually stronger than daily or hourly correlations (Pilgrim et al., 1998; Morrill et al., 2005); 2) weekly metrics avoid problems of serial correlation often present in daily water temperature data (Stefan & Preudhomme, 1993; Erickson & Stefan, 2000), and 3) the biological pertinence of a weekly metric (e.g., Wehrly et al., 2007; McCullough, 1999; Parkinson et al., 2015).

We quantified relationships between valley-bottom air temperature and water temperature using simple linear regressions at stream sites with water temperature data from at least 12 weeks during JJA of each year for at least 3 years from 2005–2010. This ensured at least 36 weeks of data were included in each regression. Twenty-four sites, 11 in the Big Hole River and 13 in its tributaries, met these criteria (Fig. S1). We conducted regressions and evaluated standard diagnostics using data collected at each site. We compared the resultant regression coefficients among sites and to regression results in other studies to gain insight into the relative influence of groundwater and meteorological control of summer water temperatures (O'Driscoll & DeWalle, 2006; Krider et al., 2013).

We considered using a nonlinear model instead of a linear model because evaporative cooling tends to decrease the influence of solar radiation on water temperature at water temperatures above 25 °C (Mohensi et al., 1998; Bogan et al., 2003; Webb et al., 2008), and extrapolation beyond the observed range of data could be misleading. However, this potential bias was not a major concern in this study because we evaluated the time water temperature exceeded two thresholds, 21 °C and 25 °C.

Potentially over-predicting water temperatures already above 25 °C would have no influence on threshold exceedance, and the range of observed water temperature data used to parameterize the linear regressions approached 25 °C at several sites in this study. Further, the relationship between air and water temperature appeared linear over the range of observed data, so we opted for the parsimonious linear model (Al-Chokhachy et al., 2013).

Future air temperature scenarios

We evaluated the timing and magnitude of changes in summer air temperature using a dynamically downscaled regional climate model (RegCM3; Hostetler et al., 2011). Boundary conditions for the regional model were set using three different global climate models (GFDL CM 2.0 [GFDL], PSU/OSU GENMOM [GMOM], and MPI ECHAM5 [EH5]). Emissions scenarios for each global climate model included the 20th century and A2 time series of atmospheric conditions prepared for the IPCC AR4 (Intergovernmental Panel on Climate Change, 2007). The A2 scenario depicted increasing rates of global greenhouse gas emissions in the future, and trends in global CO_2 emissions produced by fossil fuel consumption from 2000–2010 generally tracked or exceeded the A2 scenario (Boden et al., 2013). The A2 scenario was similar to the RCP8.5 developed for the AR5 (Intergovernmental Panel on Climate Change, 2013).

We graphically evaluated temperature patterns in the 30 RegCM3 15 × 15 km grid cells within the study area, but we limited our quantitative analysis to the three grid cells that encompassed the weather stations described above. The RegCM3 simulations were evaluated separately for each of the different global climate models (GCMs). Daily maximum air temperature estimates for JJA from 1980-2009 and 2020-2069 were adjusted using a lapse rate of -6.5 °C km^{-1} to account for elevation differences between the average elevation of the RegCM3 grid cells and the elevation of the weather stations. The mean lapse rate-adjusted air temperature for all three grid cells was used to represent a valley-bottom air temperature. These daily valley-bottom air temperature estimates were then averaged by week and ranked from coolest to warmest week within each month-decade combination. For example, the coolest WMDM air temperature projected for July during the 2040s was 16.7 °C (rank = 1), and the warmest was 28.9 °C (rank = 50; based on EH5 boundary conditions). We ranked the data in this manner to facilitate comparisons of same-ranked weeks among decades.

We used observed summer air temperatures (1980-2010) as a baseline climate condition and used RegCM3 to estimate changes in air temperature from this baseline; this technique is commonly referred to as the delta change method or delta method (Hay et al., 2000). Using the delta method limited the influence of a cold-bias in RegCM3 predictions for this region (Hostetler et al., 2011), and we assumed RegCM3 depicted relative changes in air temperature over time better than it accurately portrayed recent conditions (Hay et al., 2000). Specifically, future changes in air temperature (ΔT) were calculated by subtracting air temperature estimates for each week in the 1980s from the same-ranked future air temperature estimates as follows:

$$\Delta T_{ijk} = T_{ijk} - T_{ij1980s}$$

where i is the ith ranked week, within month j, during decade k. Weeks were ranked from coolest to warmest within each month-decade combination. These calculations were estimated separately for each of the different GCMs. Projected temperature differences over time (ΔT) were then added to observed data (T_{obs}) from the same-ranked week i and month j during the 1980s to estimate future air temperatures (T_{est}) in all future decades k using the following equation:

$$T_{est,ijk} = T_{obs,ij1980s} + \Delta T_{ijk}\,.$$

By ranking and retaining each week of air temperature data, we preserved variation in the distribution of air temperature data that could have been masked if decadal or monthly means were used to calculate air temperature change. We preserved potential seasonality in the data (e.g., shifts in the timing of warm summer conditions) by ranking values within months.

Summer air temperature estimates were grouped by decade for each of the models (GFDL 2040-2069; GMOM 2020-2069; and EH5 2020-2069) and compared to observed summer air temperature from 1980–2009. We evaluated differences among model results driven by the different GCM boundary conditions to gain information on the range of thermal conditions predicted by the different models. We also calculated a mean model (MM) that consisted of an average of projected temperatures among the weekly data using each of the different GCM boundary conditions; however, the MM was only calculated from 2040-2069, when data for all three GCMs was available.

Modeling site-specific water temperature change over time

We estimated decadal distributions of summer water temperature for 22 stream sites using site-specific air-water linear regressions and either observed or modeled air temperatures as predictors in each regression, depending on decade. We used observed air temperature data from 1980–2009 and MM-based projections of air temperature for 2040–2069. Projected distributions in water temperature were graphed to detect patterns in the exceedance of the chronic and acute thermal tolerance thresholds. To compare patterns among relatively cool, moderate, and warm sites, we grouped sites into thirds based on average summer water temperature in the 1980s, and we subsequently evaluated patterns for each site, groups of sites, and all sites combined.

We also assessed the influence of current (2000s) water temperatures and sensitivity to climate change on future water temperature projections. Specifically, we evaluated pair-wise scatter plots and correlations between mean summer water temperatures in the 2000s (an index of current thermal conditions), the slope of air-water temperature regressions (an index of sensitivity to climate change), and exceedance of chronic and acute thresholds in the 2060s (biologically relevant indices of future thermal conditions).

Modeling spatial patterns of summer water temperature

We used a statistical modeling approach to identify key landscape variables correlated with spatial patterns in summer water temperature. We initially developed an *a priori* set of candidate regression models that included one or two predictor variables hypothesized to affect the summer heat budget of the stream network. We limited the number of predictors in each candidate model because of the relatively small number of water temperature data collection sites (n = 34). We excluded models with predictors that were highly correlated with one another (r > 0.5) to avoid multicollinearity. Main stem and tributary sites were assessed separately because stream sizes of the two groups differed, and we assumed that the thermal dynamics of the two groups would vary accordingly (Poole & Berman, 2001). Prior to modeling, we also hypothesized the type of correlation (positive or negative) between predictor variables and summer water temperature: channel slope (negative; Donato, 2002; Sloat et al., 2005, Webb et al., 2008), contributing area (positive; Moore et al., 2005; Brown & Hannah, 2008), elevation (negative; Smith & Lavis, 1975; Meisner et al., 1988; Sinokrot & Stefan, 1993), riparian vegetation (negative; Tabacchi et al., 1998; Poole & Berman 2001), and potential solar radiation (positive; Johnson, 2003; Caissie, 2006; Isaak et al., 2010).

We used a variety of sources to construct data for the predictor variables. Elevation attributes were derived from the National Elevation Dataset (10 m, NED, US Geological Survey). Vegetation data were extracted from the National Land Cover Database 2006 (30 m resolution, NLCD 2006, US Geological Survey). The NLCD raster data were transformed into binary data. One land cover category included vegetation that can reduce or buffer summer water temperature (shrub vegetation, wetlands, and forest; Tabacchi et al., 1998; Poole & Berman, 2001); the other category included all other land cover types. We then quantified the percent of area in the first category (riparian vegetation) that occurred within 90 m buffers of each side of the stream. Potential solar radiation was estimated using the ArcGIS Spatial Analyst extension and accounted for topographic shading but not vegetative shading.

The maximum WMDM water temperature between 1 July and 15 August 2007 was used as the response variable to evaluate candidate models. We chose this set of data because 2007 included the most water temperature data collection sites of all the years in our dataset, and it was the warmest year during data collection and probably more representative of future climate conditions than other years of observed water temperature data. The WMDM metric was used to maintain consistency with the air-water temperature regressions.

Water temperature is affected by a combination of factors upstream of a given point in a stream network (Webb et al., 2008). However, the distance upstream and degree to which factors influence water temperature are uncertain. Few prior studies using a statistical modeling approach have explicitly addressed uncertainty in the spatial extent of influence by predictors (but see Isaak et al., 2010). We evaluated correlations between water temperature and channel slope, riparian vegetation, and potential solar radiation over 1, 5, 10, and 15 km linear stream distances upstream of temperature observation sites. The upstream distance for each variable that had the highest bivariate correlation with water temperature was included in the candidate models. We did not evaluate varying spatial extents for elevation or contributing area because upstream elevation information was already captured by the channel slope variable, and contributing area included, by definition, all upstream drainages.

Standard diagnostics were evaluated for each candidate regression model, including an assessment of multicollinearity for the two-predictor models. We also used Moran's I simulations for small sample sizes to test for spatial autocorrelation of residuals. Models were validated internally using LOOCV (leave-one-out cross validation). Model fit was evaluated using a combination of corrected Akaike information criterion (*AICc*), coefficient of determination (r^2), and root mean squared error (*RMSE*). Goodness-of-fit was evaluated separately for the full data set and the LOOCV models. Ultimately, the main-stem and tributary candidate models with the lowest LOOCV *RMSE* were chosen as the predictive models for the combination space-time modeling (see next section). One extreme outlier was removed from the riparian vegetation data set for the tributary sites. This site had relatively cool water temperatures and was located directly downstream of a large beaver dam complex, but riparian vegetation upstream of this site was misclassified as grassland (not wetland or shrubs). We excluded models with potential solar radiation as a predictor because topographic shading had minimal influence on radiation along the stream network.

Combining models to predict water temperature across space and time

The air-water temperature regressions (temporal model) were combined with the landscape-water temperature regressions (spatial model) to quantify water temperature throughout the study area in recent decades (1980s and 2000s) and under projected future climate scenarios (2040s and 2060s). This approach was similar to methods used by Hrachowitz et al. (2010). Initially, we created prediction points every 500 m along the stream network. Landscape variables were estimated at prediction points and at sites used in the air-water temperature regressions. Next, we regressed landscape variables (variable selection process described in the previous section) against water temperature estimates from the site-specific air-water temperature regressions. The resulting coefficients were used to predict water temperature at each prediction point in the stream network for each weekly time step. This was repeated for each summer week from the 1980s through the 2060s. Model results for the 2040s and 2060s were based on the MM GCM. Landscape variables were the same for each model and based on conditions in the 2000s. Water temperature estimates were evaluated for exceedance of the chronic and acute thresholds. For each decade, threshold exceedance was mapped and cumulative distributions were plotted.

We used a Monte Carlo approach to estimate uncertainty resulting from the combination of two regression models. Ten thousand simulations of the model were constructed for each weekly set of data. For each simulation, water temperature values were randomly drawn from the normally-distributed uncertainty associated with each air-stream water regression estimate. This set of randomly drawn temperature estimates was regressed against landscape covariates to produce coefficients for the spatial model. As before, main-stem and tributary sites were modeled separately, and the coefficients of each spatial model were used to estimate water temperatures at all predictions sites. The resulting distributions of 10,000 temperature estimates at each location for each week of data were used to approximate uncertainty. Specifically, we averaged the standard deviations of these distributions for main-stem sites and, separately, for tributary sites.

These two average standard deviations were then used to approximate 90% confidence limits for water temperature estimates in the main stem and tributaries.

Results

Air-water temperature relationships

Air temperature was positively correlated with water temperature, and simple linear regressions explained a majority of the variation in water temperature at 23 of the 24 sites (Table 1). The relationship between air and water temperature at sites 12 and 22 appeared linear at some times and unrelated or nonlinear at other times, especially during the month of August (see Fig. S4). Correspondingly, these two sites had smaller slopes, greater intercepts, and more influence from groundwater than all other sites (Fig. 2). These two sites were excluded from summary statistics and future water temperature predictions. The slope of regressions at the 22 other sites ranged from 0.53–0.79 (mean = 0.65; SD = 0.08) and intercepts ranged from -4.0–7.4 (mean = 3.1; SD = 2.7). Air and water temperature observations used to fit the regressions ranged from 11.6–31.0 °C and 7.4–26.7 °C, respectively. Overall, site-specific regressions were accurate predictors of water temperature (*RMSE* mean = 1.3 °C; SD = 0.3 °C).

Air temperature changes

Timing and magnitude of projected changes in WMDM air temperature varied among models, but temperatures increased from the 1980s through the 2060s (Fig. 3). Observed July air temperatures in the 2000s were about two degrees warmer than in the two prior decades, and these temperatures were similar to future July projections based on the EH5 and GMOM models. GFDL-based projections were the warmest of the three GCMs and increased about 4 to 6 °C from the 1980s through the 2060s, with the greatest increases occurring in July. The greatest increases in temperature for the EH5-based model occurred in June, illustrating a potential shift in seasonality to an earlier occurrence of warm summer temperatures. The EH5-based model depicted slightly cooler temperatures in August during the 2020s and 2040s but warming to a similar level as the other models by the 2060s. In each summer month, MM-based air temperature projections increased about 3 °C from the 1980s through the 2060s.

Projected changes in summer water temperatures at observation sites

Stream water temperature estimates increased from the 1980s through the 2060s at all 22 sites, and chronic (21 °C) and acute (25 °C) thermal tolerance thresholds were exceeded more often as the time series progressed (Fig. 4; see Table S2 for results from all models and decades). At the group of relatively cool sites, water temperatures did not exceed the acute threshold in any summer weeks in the 2060s projections, but exceedance of the chronic threshold still increased over time at these sites. When all sites were combined, the proportion of JJA weeks that water temperatures exceeded the chronic threshold increased from 0.20 to 0.44 from the 1980s through the 2060s, and the number of sites where water temperature exceeded the chronic threshold at least once during these same decades increased from 17 to 22 (out of 22). All sites combined, the proportion of JJA weeks that water temperatures exceeded the acute threshold increased from < 0.01 to 0.05 from the 1980s through the 2060s, and the number of sites where water temperatures exceeded the acute threshold at least once during these same decades increased from 1 to14 (out of 22).

Sites that were relatively warm (or cool) in the 2000s were projected to be relatively warm (or cool) in the 2060s, independent of sensitivity to climate change. For example, water temperatures in the 2000s were strongly correlated with chronic threshold exceedances in the 2060s (r = 0.97), but slopes of air-water temperature regressions were moderately correlated with chronic exceedances in the 2060s (r = 0.54). Similarly, thermal conditions in the 2000s were moderately correlated with acute threshold exceedances in the 2060 (r = 0.66), but slopes of air-water temperature regressions were not correlated with acute exceedances in the 2060s (r = 0.02). The relationship between thermal conditions in the 2000s and the slopes of air-water regressions was also weak (r = -0.13).

Spatial predictors of summer water temperatures

Relationships between summer water temperatures and landscape variables differed between the main stem and tributaries (Table 2). Water temperatures in the main stem were highly correlated with elevations, contributing areas, and channel slopes, and poorly correlated with proportions of riparian vegetation. Water temperatures in the tributaries were correlated the strongest with channel slopes and proportions of riparian vegetation, moderately correlated with elevations, and weakly correlated with contributing areas. In the main stem, correlation between water temperatures and channel slopes was highest at the 15-km spatial extent, but correlations differed minimally among the 5-, 10-, and 15-km scales. In contrast, correlation between water temperatures and channel slopes was highest at the 1-km scale in tributaries, and correlations decreased at longer spatial extents. The nature of most relationships (positive or negative correlations) between landscape variables and water temperatures matched our hypotheses, with a few exceptions. Correlations between water temperatures in the main stem and proportions of riparian vegetation were weak, and either negative or positive depending on spatial extent; tributary sites at lower elevations were generally cooler than sites at higher elevations. These cooler tributaries in the lower portion of the study area had more natural riparian vegetation than tributaries in the mid and upper parts of the study area.

Main-stem regression models were more accurate and precise than tributary models (Table 3). Channel slope and riparian vegetation were key predictors in the top main-stem and tributary models, respectively. Goodness-of-fit metrics for each one-predictor model were similar for the full data set and LOOCV, but the two-predictor models appeared to be over-fitted because of larger differences between results from the full data set and LOOCV, as compared to one-predictor models. Results of Moran's I simulations yielded no evidence of spatial structure in the residuals from the top main-stem (15-km channel slope) or tributary (5-km riparian vegetation) models.

Projected changes in summer water temperatures throughout the study area

Water temperatures increased with time such that exceedance of chronic and acute thresholds increased from the 1980s through the 2060s in the entire stream network and at the air-water regression sites (Fig. 5). For example, water temperatures in half of the stream network exceeded the chronic threshold 15% or more of the time in the 1980s, but this exceedance increased to 50% or more of the time in the 2060s (Fig. 6). In the 1980s, water temperatures in 20% of the stream network never exceeded the chronic threshold, but temperatures in the entire stream network were projected to exceed the chronic threshold at least 6% of the time in the 2060s (Fig. 6). Temperatures in the warmest stream reaches exceeded the chronic threshold 50% of the time in the 1980s and nearly 70% of the time in the 2060s (Fig. 6). In the 1980s, water temperatures did not exceed the acute threshold anywhere in the stream network, but temperatures in 35% of the network exceeded the acute threshold at some point in the summer in the 2060s (Fig. 7). The warmest stream reaches were projected to exceed the acute threshold > 20% of the time in the 2060s (Fig. 7).

Spatial patterns in water temperature predictions remained relatively consistent across time (Fig. 5). Projected main-stem water temperatures were coolest upstream, warmest in the middle of the study area, and slightly cooler in the furthest downstream reaches than in the middle. Water temperatures in the tributaries were generally cooler in the downstream section of the study area and near the valley margins, and warmer mid-valley. Overall, spatial variation in projected water temperatures was higher within and among tributaries than within the main stem. Monte Carlo realizations of water temperature at each site-week combination resulted in uncertainty estimates of ± 1.09 °C in the tributaries and ± 0.88 °C in the main stem (90% confidence limits).

Discussion

Water temperature simulations projected significant warming as a result of climate change in the stream network of the upper Big Hole River watershed, and summer water temperatures appeared to be relatively sensitive to climate change in comparison to systems with stronger groundwater control (e.g., O'Driscoll & DeWalle, 2006; Krider et al., 2013; Snyder et al., 2015). Consequently, suitability of the thermal habitat of Arctic grayling and non-native salmonids appears to be closely related to climate during the summer in most of the study area. However, implications of this climate-driven warming on these cold-water species will vary depending on a suite of abiotic and biotic factors (e.g., Wenger et al., 2011), including the rate, variation, and magnitude of warming (Jentsch et al., 2007; Vasseur et al., 2014).

Evaluating spatial patterns in recent and future thermal conditions, in combination with sensitivity to climate change, can aid conservation planning (e.g., Trumbo et al., 2014). Temperate stream systems with relatively warm summer water temperatures, such as this study area, may be more sensitive to climate change than cooler stream networks (Luce et al., 2014), and thermal conditions in the 2000s were correlated with future thermal conditions in this study. However, sensitivity to climate change (air-water temperature regression slopes) was not strongly correlated with future thermal conditions. Additionally, warming rates may be amplified with elevation (Mountain Research Initiative Working Group, 2015), and the stream network in this study ranged from 1730 to 2130 m in elevation, which is relatively high. Nonetheless, water temperatures in some of the stream network were predicted to remain below thermal tolerance thresholds through the 2060s. These cooler stream sections could be critical to the persistence of grayling and non-native salmonids and, consequently, provide examples of potential conservation priority areas (i.e., Isaak et al., 2015).

Contiguous sections of the study area projected to exceed chronic and acute thresholds could act as thermal barriers to fish migration, especially in the main stem of the Big Hole River (Fig. 5). These thermal barriers could negatively affect populations with migratory life history components, including fluvial Arctic grayling (Shepard & Oswald, 1989; Northcote, 1995; Vatland et al., 2009). Warm river reaches limit other salmonid migrations (Meisner, 1990; Bumgarner et al., 1997 as cited by McCullough, 1999), and fragmentation and lack of connectivity are already major concerns for most cold-water fish populations in this region (Rieman et al., 2003; Gibson et al., 2009; Haak et al., 2010). Fittingly, connectivity is fundamental to climate adaptation planning for freshwater species conservation (Nel et al., 2009), and considering the effects of projected thermal barriers on connectivity may benefit such planning.

Water temperature simulations were useful for evaluating the exceedance of thermal tolerance thresholds throughout the stream network and among decades, but these simulations probably underestimated biologically important spatial and temporal variation in water temperature (i.e., Vatland et al., 2015). Two water temperature monitoring sites that showed evidence of groundwater control were excluded from simulations (Fig. 2), but areas with groundwater influence (such as the excluded sites) may provide cold-water refugia for juvenile rearing and adult survival, especially during the latter part of the summer (i.e., Fig. S3). In addition, the biological importance of thermal refugia may be disproportionately greater than their quantity in the stream network because juvenile and adult salmonids are capable of seeking out these preferable habitats (e.g., Berman & Quinn, 1991; Armstrong et al., 2013; Dugdale et al., 2015). Availability of thermal refugia has also been correlated with population-level benefits for salmonids (Torgersen et al., 1999; Ebersole et al., 2003), but the interannual persistence of refugia, especially at fine spatial scales, is uncertain (but see Dugdale et al., 2013). As stream networks warm, thermal refugia may become increasingly important to the dynamics of cold-water fish populations, and therefore, models that capture variation in water temperature at scales relevant to fishes in stream environments will become increasingly critical for developing management strategies.

Persistence of cold-water fish populations in warming streams may necessitate adaptation, either genotypic, phenotypic, or both (i.e., Williams et al., 2008). Phenotypic change in response to environmental change can occur quickly in fish populations (Hendry et al., 2008), but whether animal populations persisting near upper thermal tolerance thresholds will have the capacity to adapt to rapid environmental change is uncertain (Somero, 2010; Sinervo et al., 2010; Hoffman & Sgrò, 2011). The rate of expected climate change in the 21st century will exceed (by orders of magnitude) previously observed niche evolution rates for vertebrates (Quintero & Wiens, 2013), but the potential evolution rates of individual fish species are unknown. Nonetheless, the persistence of grayling and non-native salmonids in the upper Big Hole River watershed will probably depend on some form of adaption if the rate of warming forecasted in this study is realized.

Warming summer water temperatures may have already influenced the distribution and abundance of cold-water fish in the Big Hole River. For example, warming that occurred from the 1980s through the 2000s corresponded with increased patchiness, contracted distribution, and reduced abundance of Arctic grayling (Montana Fish, Wildlife & Parks et al., 2006; Vatland et al., 2009). Concurrently, the distribution of bull trout *Salvelinus confluentus* (another cold-water species) contracted from low elevation stream sites in an adjacent watershed as water temperatures increased (Eby et al., 2014). In contrast, warming could also provide ecological opportunities, such as improved thermal conditions for fish growth and survival in relatively cold stream reaches (e.g., Al-Chokhachy et al., 2013). Indeed, warming could benefit cold-water fish able to access cooler high-elevation stream reaches, upstream of the current study area. However, summer warming is unlikely to benefit the cold-water fish that remain in the relatively warm, valley-bottom stream network examined in this study.

Inference from water temperature modeling was constrained because projections were based on a static landscape. Landscape parameters (stream gradient and riparian vegetation) were held constant from the 1980s through the 2060s, and water use for irrigation was not explicitly simulated. However, changes to the landscape, water use, precipitation, or a combination could alter the spatial distribution of water temperature and indirectly affect the stability of air-water temperature relationships (i.e., Arismendi et al., 2014). Reach-scale stream gradient typically adjusts to landscape change over longer time frames than those modeled in this study (Knighton, 1998), and assuming stream gradient would not change may be reasonable for the main-stem Big Hole River simulations. However, riparian vegetation, the spatial predictor used for the tributaries, could change significantly over decades, and restoring riparian vegetation in the tributaries may be a viable climate-adaptation strategy. In addition, water temperature and discharge were negatively correlated, so reducing irrigation withdrawals could potentially moderate summer water temperatures. Further, reduced irrigation in combination with the restoration of riparian vegetation could be an especially effective adaptation tool. We also hypothesized that beaver dams, flood irrigation, natural wetlands, or a combination of these factors can contribute to shallow ground water contributions to instream flows in late July and throughout August, and as a result, cool maximum water temperatures in the late summer (Fig. S4). In summary, land use, water use, and climate change can have complex interactions, and quantifying and interpreting the relative importance of these major components of stream heat budgets will be critical to effective climate adaptation planning (Webb et al., 2008; Daraio & Bale, 2014).

We focused on the warmest period of the year because we identified summer water temperature as a key stressor to Arctic grayling and non-native salmonids, but the influence of environmental factors on the distribution and abundance of these fish may fluctuate with seasonal changes. For example, cold water temperatures and ice conditions can limit the distribution and abundance of salmonid populations in the winter (Cunjak & Power, 1986; Huusko et al., 2007). Climate change could alter the timing and magnitude of snow-melt driven runoff and increase the probability of winter floods in temperate regions (Stewart et al., 2004, 2005; Hamlet & Lettenmaier, 2007). Changes in discharge regime could affect spawning success, early life-stage survival (e.g., Fausch et al., 2001;

Lytle & Poff, 2004; Wenger et al., 2011), and the survival of older life-stages of salmonids (Berger and Gresswell, 2009). Shifts in the timing and length of seasons (e.g., Fig. 3) could also alter growth patterns in stream fish. For example, annual growth could shift from a peak during the summer (unimodal) to a bimodal growth pattern with a peak in growth in both the spring and autumn (Berger & Gresswell 2009; Al-Chokhachy et al. 2013). As climate change assessments progress beyond a singular focus on summer water temperature, incorporating other seasonal dynamics will aid in predicting changes in the distribution and abundance of cold-water fishes (e.g., Wenger et al., 2011; Power et al., 2013).

We used the same tolerance thresholds to evaluate thermal suitability for grayling and non-native salmonids, but the effects of an altered thermal regime may differ among species. Water temperature can mediate interactions among salmonids (e.g., DeStaso & Rahel, 1994; Taniguchi et al., 1998; McMahon et al., 2007), and harsh thermal conditions could exacerbate negative interactions (i.e., competition and predation) between grayling and non-native salmonids. Negative interaction with non-native trout is considered a major factor in the extirpation of fluvial grayling from more than 95% of their historic range in the upper Missouri River watershed (Vincent, 1962; Kaya, 1992b), and Arctic grayling are capable of persisting in marginal habitat in the absence of non-native trout species (Barndt, 1996). No evidence for negative competitive interactions between Arctic grayling and brook trout existed in two streams within this study area at water temperatures ranging from 3-22 °C (Byorth & Magee, 1998). The fundamental and realized thermal niche for rainbow and brown trout may also include slightly warmer temperatures than for grayling (McCullough, 1999; Selong et al., 2001; Wehrly et al., 2007; Todd et al., 2008). Furthermore, grayling are generally limited to low-gradient stream systems, and non-native salmonids may have a greater capacity to access cooler waters in higher gradient, higher elevation streams (Hubert et al., 1985; Kaya, 1992a). Overall, it appears non-native salmonids have a competitive advantage over grayling under the water temperature changes projected in the upper Big Hole River watershed, but the extent and magnitude of warming will probably have negative effects on all these cold-water species.

The dynamic nature of lotic ecosystems complicates forecasting the effects of climate change on stream fish, but developing reliable water temperature predictions is a useful initial step (e.g., Isaak et al., 2010, 2015; Ruesch et al., 2012; Al-Chokhachy et al., 2013). Temperature predictions can be incorporated into simple or complex decision-support tools (e.g., spatial prioritization of limited conservation resources; Peterson et al., 2013), and these data have utility beyond species-specific conservation concerns, including community and landscape conservation planning (i.e., Shaffer, 2015). However, modelers should proceed cautiously, and acknowledge and clearly communicate the uncertainties and limitations of such analyses. Ultimately, modeling efforts, such as those conducted here, can greatly aid in developing strategic climate adaptation plans, especially when considered within broader ecological and socioeconomic contexts, and empirical evaluations of climate adaptation efforts can facilitate adaptive management.

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Tables

Table 1. Site-specific linear regressions using weekly mean daily maximum (WMDM) air temperature (°C) as the predictor and WMDM stream water temperature (°C) as the response. Sites 1-11 were in the mainstem Big Hole River and 12-24 in tributaries.

Site ID	n	r^2	Intercept	SE	Slope	SE	*RMSE*
1	39	0.88	2.5	1.1	0.74	0.05	1.2
2	39	0.90	2.9	1.0	0.75	0.04	1.1
3	65	0.92	1.9	0.7	0.74	0.03	1.0
4	64	0.87	6.1	0.6	0.53	0.03	0.9
5	39	0.92	3.8	0.7	0.57	0.03	0.8
6	52	0.73	4.7	1.3	0.60	0.05	1.7
7	51	0.87	5.8	0.7	0.55	0.03	1.0
8	65	0.75	3.3	1.2	0.70	0.05	1.8
9	51	0.85	-0.6	0.9	0.65	0.04	1.2
10	39	0.85	3.5	1.2	0.70	0.05	1.3
11	64	0.89	5.4	0.7	0.61	0.03	0.9
12*	39	0.04	14.4	3.3	0.16	0.13	3.5
13	65	0.90	0.5	0.8	0.73	0.03	1.1
14	65	0.86	1.3	0.8	0.64	0.03	1.2
15	39	0.87	5.9	0.9	0.57	0.04	1.1
16	39	0.78	-4.0	1.7	0.79	0.07	1.9
17	77	0.80	5.8	0.7	0.54	0.03	1.2
18	52	0.89	2.5	0.8	0.71	0.03	1.1
19	64	0.77	2.6	1.1	0.65	0.05	1.6
20	39	0.75	0.0	1.7	0.70	0.07	1.7
21	77	0.76	6.3	0.9	0.57	0.04	1.5
22	51	0.53	9.7	1.4	0.42	0.06	1.8
23	38	0.74	7.4	1.3	0.53	0.05	1.4
24	51	0.80	1.1	1.3	0.73	0.05	1.5
Overall mean*	53	0.83	3.1	1.0	0.65	0.04	1.3

Notes: Standard error (SE) follows the corresponding coefficient. Root mean squared error abbreviated as *RMSE*.
*Regression for Site 12 was the only one that $p > 0.05$. Sites 12 and 22 were excluded from the overall mean.

Table 2. Correlation of spatial variables with summer water temperatures at varying spatial extents.

	Correlation with water temperature									
	Mainstem					Tributaries				
Variable	At site	1 km	5 km	10 km	15 km	At site	1 km	5 km	10 km	15 km
Elevation	**-0.86**	–	–	–	–	**0.44**	–	–	–	–
Contributing area (log)	**0.89**	–	–	–	–	**0.17**	–	–	–	–
Channel slope	–	-0.60	-0.92	-0.91	**-0.92**	–	**-0.72**	-0.67	-0.62	-0.49
Riparian vegetation (square root)	–	**0.19**	0.03	-0.11	-0.17	–	-0.44	**-0.68**	-0.68	-0.54

Notes: Pearson pairwise correlation values for Big Hole River sites and tributary sites. Bold values are the spatial extent used for each variable in subsequent modeling. Two variables were transformed to improve normality of regression residuals.

Table 3. Summary statistics of candidate regression models for predicting spatial variation in summer water temperatures in the mainstem Big Hole River and tributaries.

			Full data set			LOOCV	
Linear regression model	*n*	*K*	ΔAICc	r^2	*RMSE*	r^2	*RMSE*
Mainstem							
Channel slope (15 km)	**16**	**2**	**0.0**	**0.85**	**0.73**	**0.80**	**0.83**
Channel slope (15 km) + Contributing area (log)	16	3	1.7	0.86	0.72	0.78	0.90
Channel slope (15 km) + Elevation	16	3	2.1	0.86	0.73	0.77	0.93
Channel slope (15 km) + Riparian vegetation (1 km)	16	3	2.9	0.85	0.75	0.75	0.96
Contributing area (log)	16	2	5.0	0.79	0.85	0.75	0.94
Contributing area (log) + Riparian vegetation (1 km)	16	3	6.9	0.81	0.85	0.69	1.07
Elevation	16	2	9.0	0.73	0.96	0.66	1.09
Riparian vegetation (1 km) + Elevation	16	3	11.6	0.74	0.98	0.60	1.22
Riparian vegetation (1 km)	16	2	29.5	0.04	1.83	-0.20	2.04
Tributaries							
Riparian vegetation (5 km)	**17**	**2**	**0.0**	**0.62**	**1.25**	**0.51**	**1.43**
Riparian vegetation (5 km) + Elevation	17	3	1.4	0.65	1.24	0.45	1.56
Riparian vegetation (5 km) + Contributing area (log)	17	3	2.5	0.63	1.28	0.46	1.56
Riparian vegetation (5 km) + Channel slope (1 km)	17	3	3.0	0.62	1.30	0.45	1.57
Elevation + Channel slope (1 km)	18	2	7.1	0.58	1.56	0.37	1.84
Contributing area (log) + Channel slope (1 km)	18	2	8.4	0.54	1.62	0.34	1.89
Channel slope (1 km)	18	2	9.6	0.51	1.62	0.40	1.80
Riparian vegetation (5 km)	18	2	11.6	0.46	1.71	0.34	1.88
Elevation	18	2	18.7	0.19	2.09	0.00	2.32
Contributing area (log)	18	2	22.1	0.03	2.29	-0.25	2.60

Notes: Regression models selected to predict spatial patterns indicated in bold. Distance upstream of prediction points that spatial variables were quantified indicated in parentheses following the variable name.

Figures

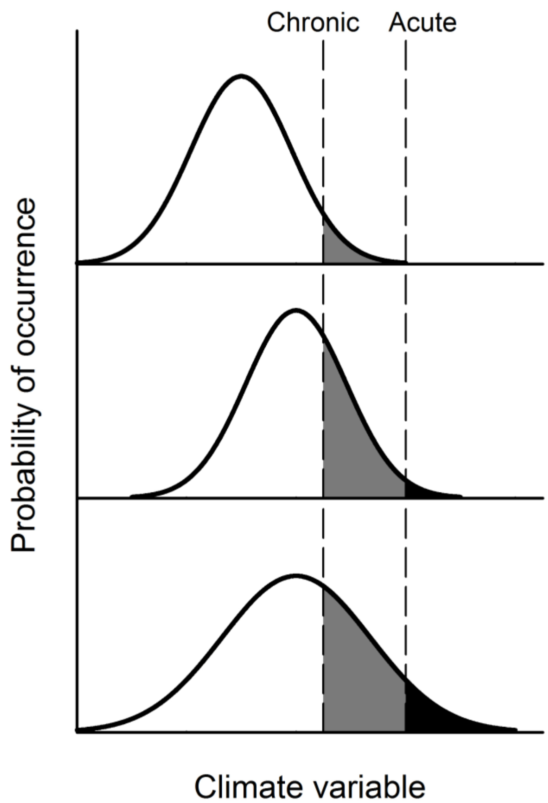

Fig. 1 Hypothetical changes in the probability distribution of a climate variable from present climate (top) to a shift in the central tendency (middle) or a shift in the central tendency and an increase in variation (bottom). Vertical dashed lines represent hypothetical tolerance thresholds for biota. Exceeding chronic thresholds could result in reduced fitness of individuals, temporary emigration of individuals, reduced abundance of populations, or increased patchiness and isolation of populations. Exceeding acute thresholds could result in death or permanent emigration of individuals, extirpation of populations, or both. Adapted from Jentsch et al. (2007).

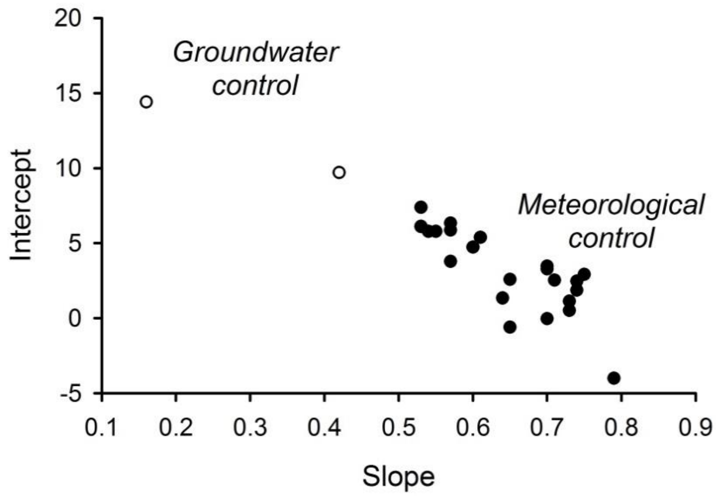

Fig. 2 Slope and intercept estimates from simple linear regressions between air and water temperatures in the study area. Water temperature controls are indicated along a hypothetical gradient between groundwater and meteorology (for comparisons see O'Driscoll and DeWalle 2006; Krider et al. 2013; Snyder et al. 2015). Black circles (n = 22) represent sites used to predict water temperatures based on changes in air temperatures; white circles (n = 2) represent sites not used for air-temperature-based predictions (see Fig. S4 for details).

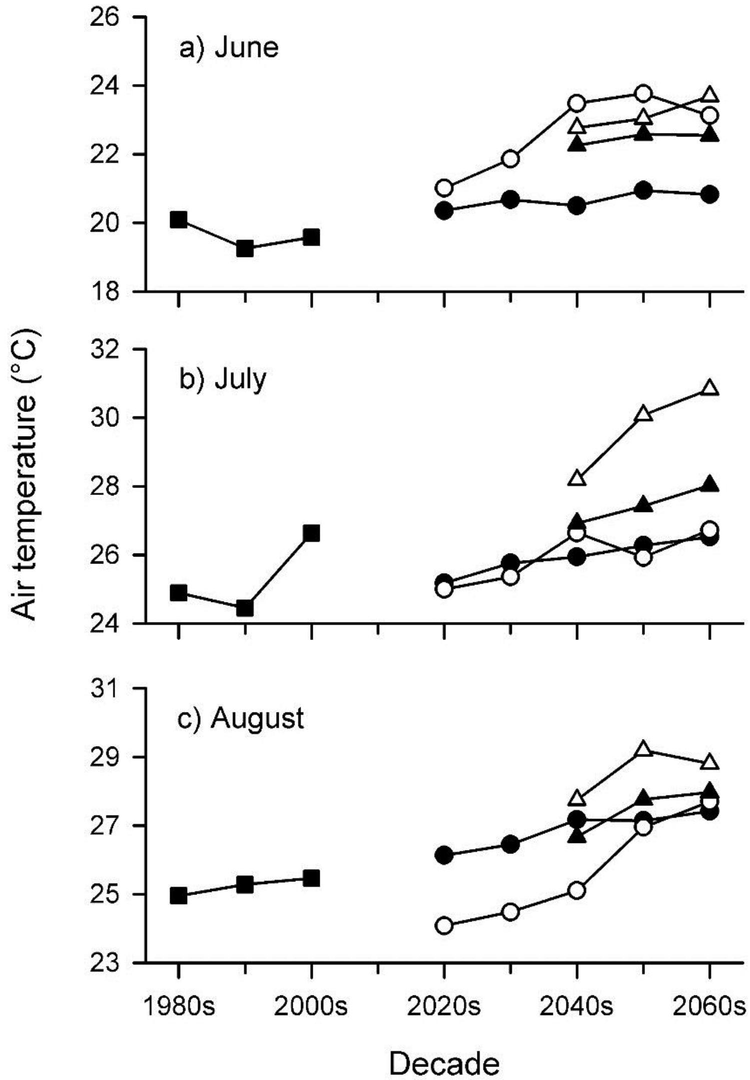

Fig. 3 Decadal averages by month of weekly mean daily maximum (WMDM) air temperatures. Black squares are observed air temperatures in the study area from 1980 to 2009. Future air temperatures are based on regional climate model simulations with boundary conditions set by three different global climate models: EH5 (white circles, 2020-2069); GMOM (black circles, 2020-2069); GFDL (white triangles, 2040-2069); and a mean of the three climate models (MM; black triangles; 2040-2069). See text for model details and bias correction. Note y-axis scale difference among panels.

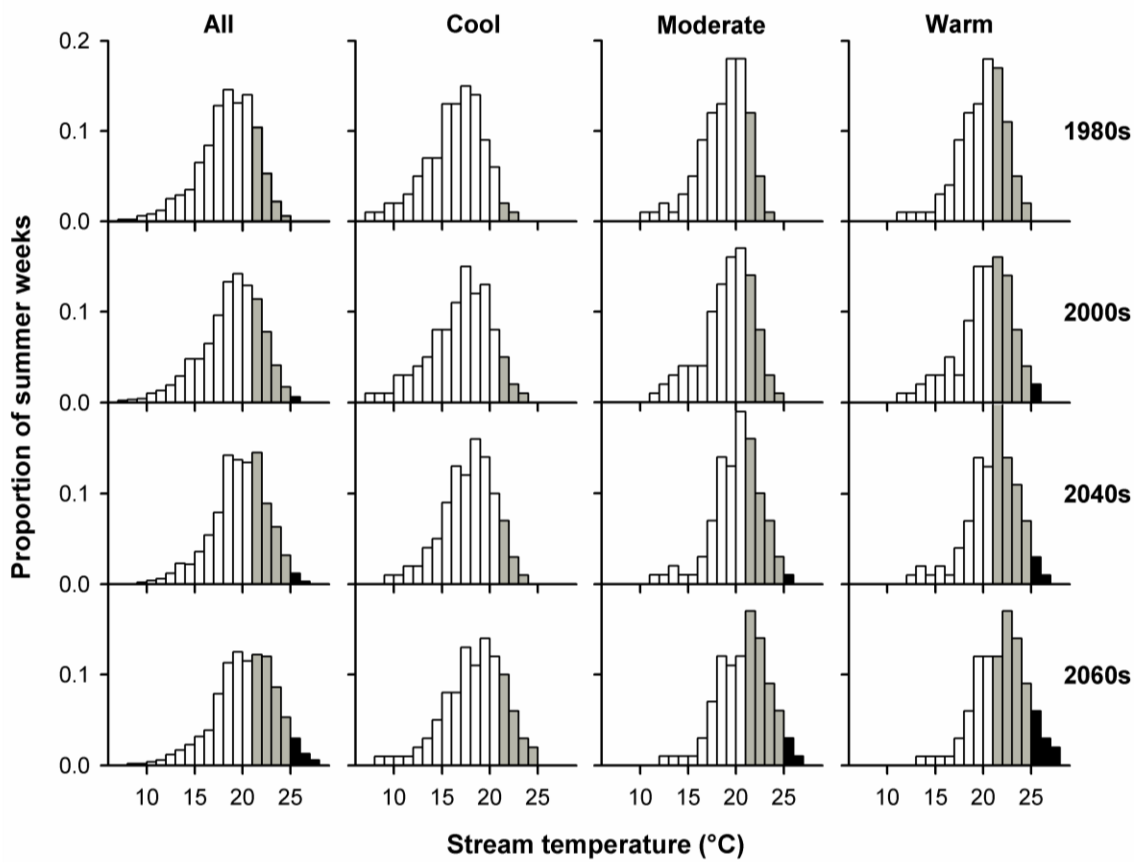

Fig. 4 Decadal frequency distribution of weekly mean daily maximum (WMDM) water temperature estimates for June, July, and August. Estimates based on site-specific air temperature-water temperature linear regressions. Air temperature inputs are from observed data for both the 1980s and 2000s and from future air temperature predictions (MM) for both the 2040s and 2060s. Water temperatures for all sites (n = 22) were combined in the left column, and subsequent columns contain the coolest (n = 7), moderate (n = 8), and warmest sites (n = 7). Weeks that exceed the chronic (21 °C) and acute (25 °C) thermal tolerance thresholds are colored in gray and black, respectively.

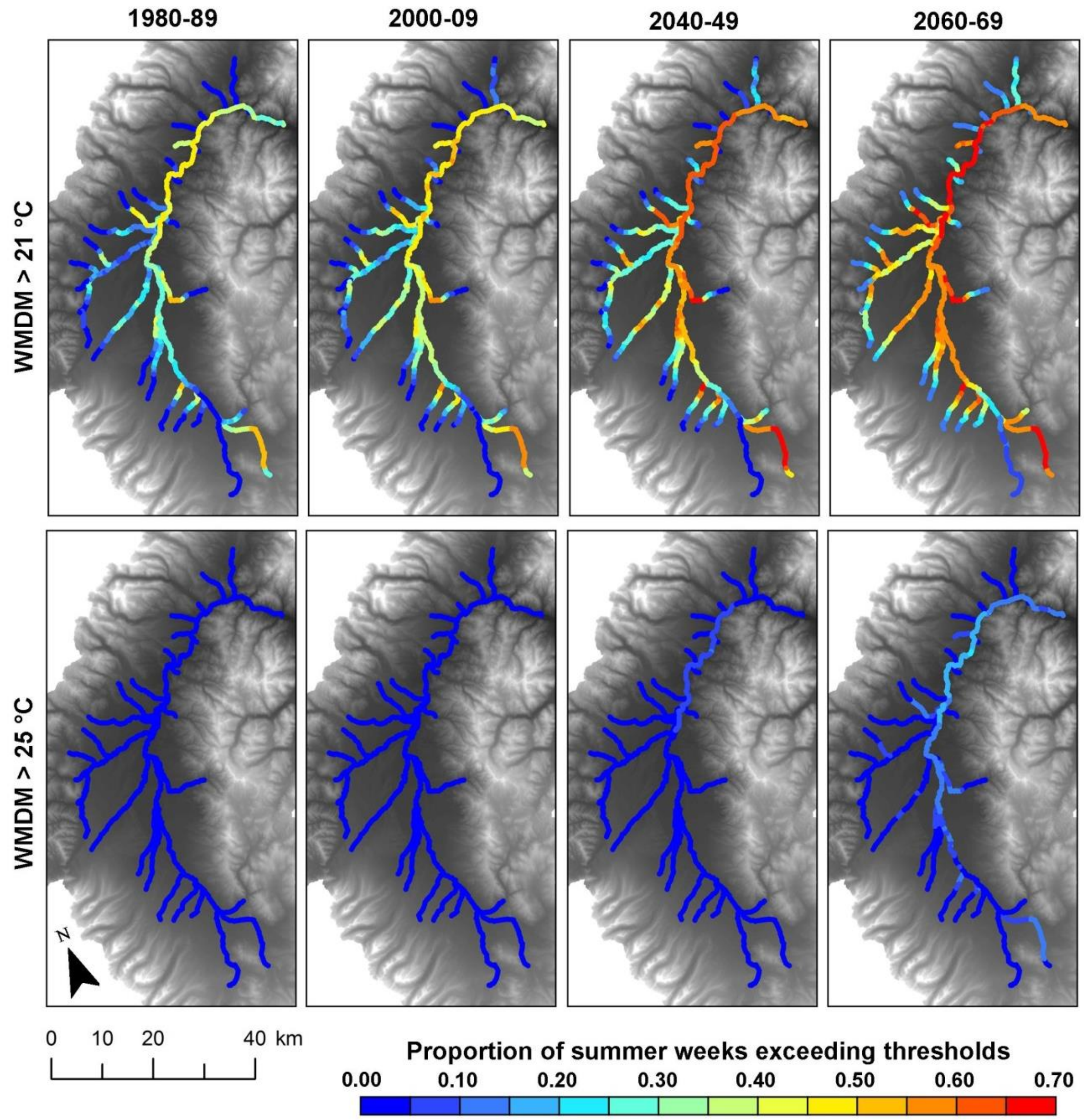

Fig. 5 Proportions of summer weeks (June, July, and August) predicted to exceed chronic and acute water temperature thresholds during the 1980s, 2000s, 2040s, and 2060s. Prediction points located every 500 m throughout the study area.

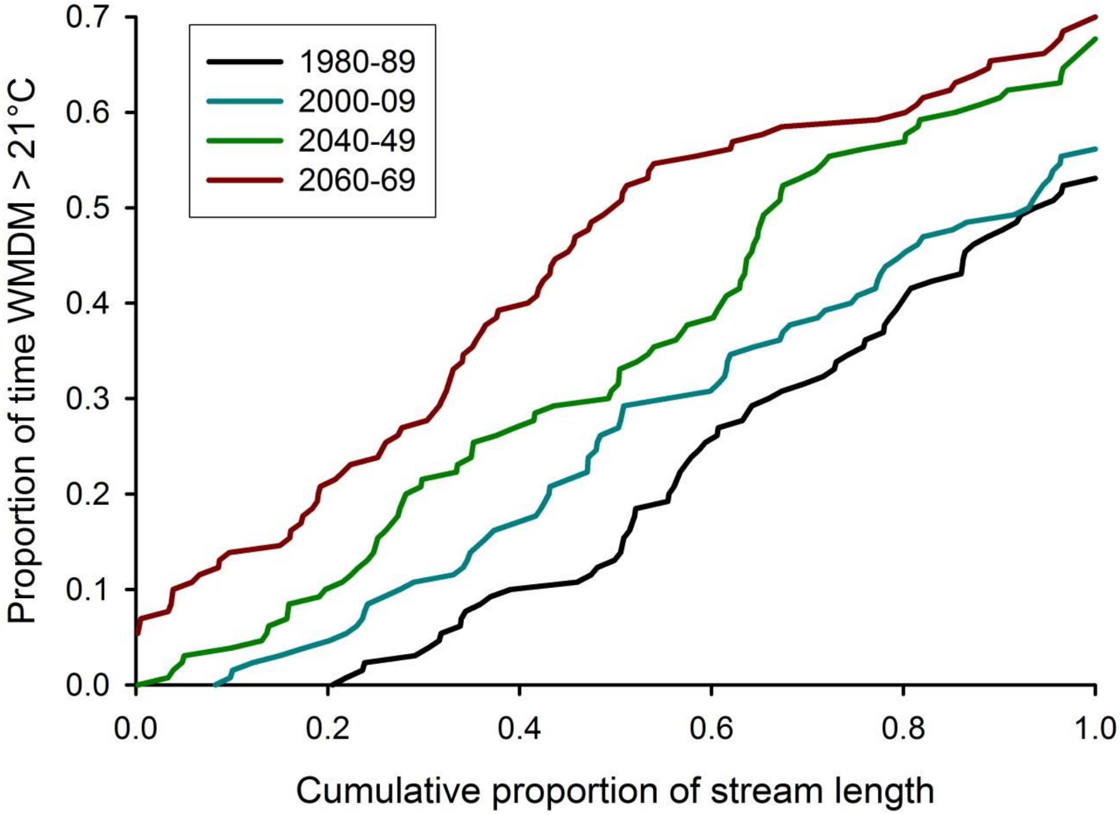

Fig. 6 Cumulative proportion of stream network based on proportion of time that summer water temperatures exceeded the chronic threshold of 21 °C. Cumulative curves presented by decade. 2040s and 2060s based on bias-corrected MM air temperature predictions, but the 1980s and 2000s were based on observed air temperatures.

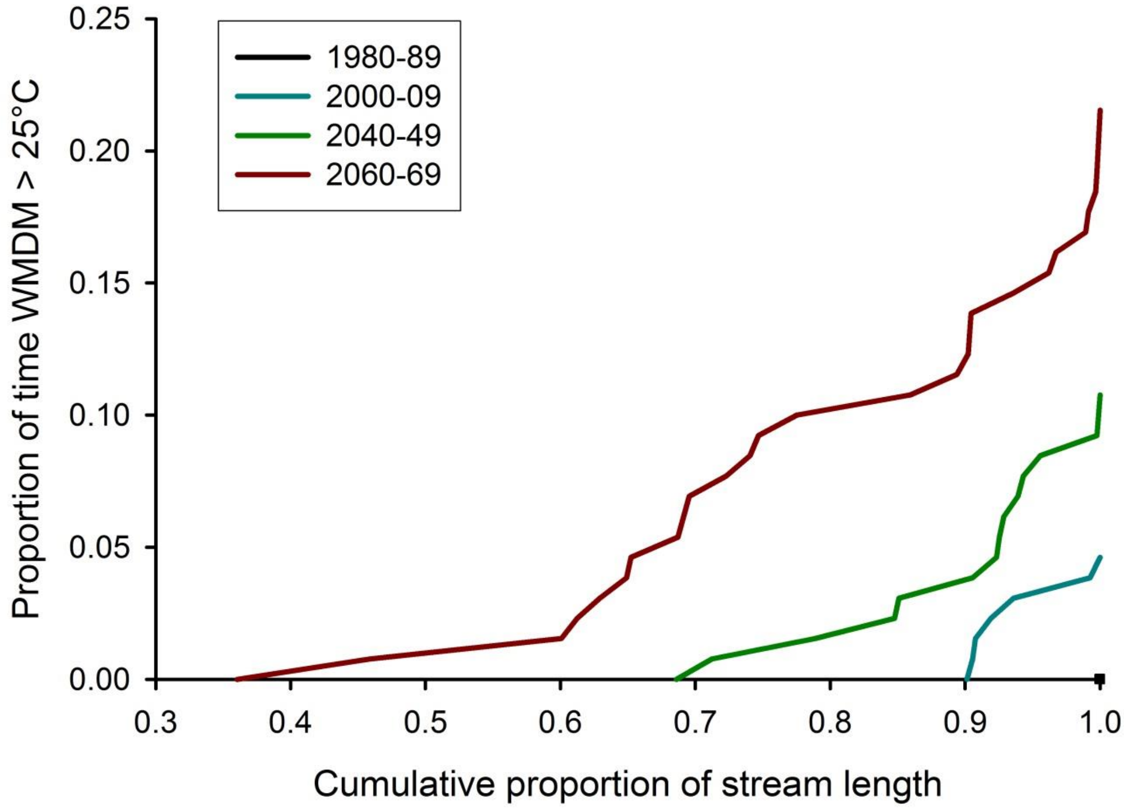

Fig. 7 Cumulative proportion of stream network based on proportion of time that summer water temperatures exceeded the acute threshold of 25 °C. Cumulative curves presented by decade. 2040s and 2060s based on bias-corrected MM air temperature predictions, but the 1980s and 2000s were based on observed air temperatures. Note that none of the stream network exceeded the acute threshold in the 1980s, so itis only a dot at 1.0 on the x-axis.

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CONCLUSIONS

In this dissertation, I evaluated stream temperature patterns in the upper Big Hole River basin with a focus on information pertinent to the conservation of fluvial Arctic grayling *Thymallus arcticus*. The study area supports one of the last naturally-reproducing populations of fluvial Arctic grayling in the conterminous United States. Warm summer stream temperatures are a critical factor constraining grayling, but summer stream temperatures may also limit non-native trout (brook trout *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta*). Accordingly, I investigated the suitability of thermal habitat for grayling and non-native salmonids by estimating summer stream temperatures across multiple spatial and temporal scales and under regional climate change scenarios. These data were critical to understanding spatial and temporal variation in stream temperature and the effects of temperature on the distribution of these salmonids in the upper Big Hole River basin.

In Chapter 2, I used a combination of thermal infrared (TIR) imagery and stationary temperature recorders to estimate stream water temperatures at a relatively fine spatial resolution over a large extent of the Big Hole River during the warmest part of the summer in 2008. The modeling framework combined water temperature data continuous in either space or time, to create a new data set continuous in both space and time. Results revealed complexities of stream thermal regimes across multiple scales. Preserving spatial and temporal variability and structure in water temperature data provided a foundation for understanding the dynamic habitat requirements of grayling and non-native trout (e.g., Fausch et al. 2002; Wiens 2002, Carbonneau et al. 2012). In addition, these fine-scale data can guide strategic placement of monitoring equipment that will capture variation in environmental conditions directly pertinent to grayling conservation and fisheries management.

In Chapter 3, I assessed potential effects of climate change and land use on summer water temperatures and thermal suitability for fluvial Arctic grayling and non-native salmonids. We used chronic and acute thermal tolerance thresholds (21 °C and 25 °C, respectively), based on previously published research. Air temperature and water temperature were highly correlated in most of the study area, suggesting that meteorological control of thermal habitat was much stronger than groundwater control. Stream water temperature simulations projected significant warming from the 1980s through the 2060s. Despite projected warming, water temperatures in some stream sections remained below thermal tolerance thresholds throughout the study period. Relationships between riparian vegetation and summer water temperature suggested that increasing natural riparian vegetation could moderate water temperatures and be a viable climate adaptation strategy as conditions warm in the coming decades.

Overall, the stream temperature data collected and modeled in this dissertation provide a critical foundation for understanding the distribution of suitable thermal conditions for fluvial Arctic grayling and non-native salmonids. Developing reliable stream temperature predictions is a critical step in evaluating the potential effects of climate and land use change on the distribution of these cold-water species (e.g., Isaak et al., 2010, 2015; Ruesch et al., 2012; Al-Chokhachy et al., 2013). Temperature predictions can be incorporated into simple or complex decision-support tools (e.g., spatial prioritization of limited conservation resources), and these data have utility beyond species-specific conservation concerns (e.g., community and landscape conservation planning). Such modeling can also aid in developing strategic climate adaptation plans, especially when considered within broader ecological and socioeconomic contexts.

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APPENDICES

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2

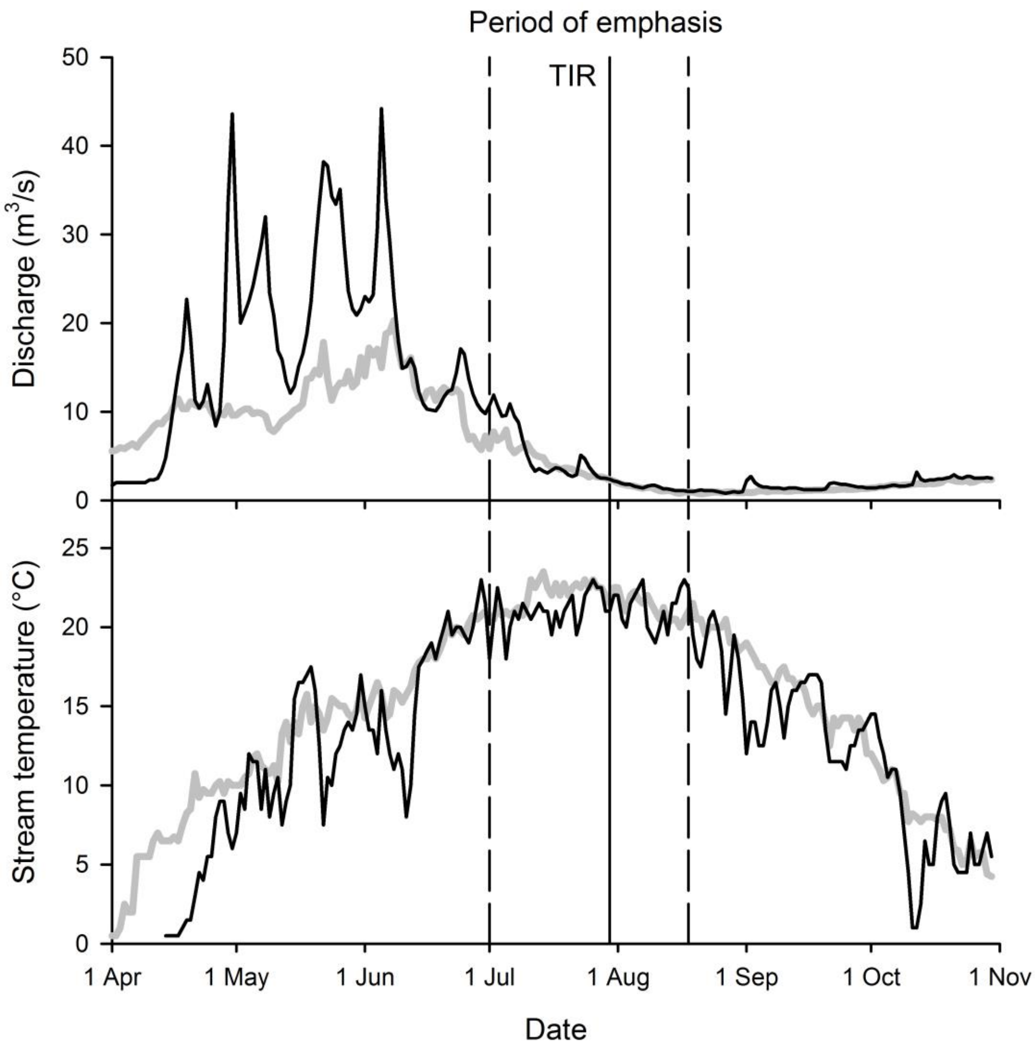

Figure S1. Big Hole River discharge and stream temperature data collected near the center of the study area (USGS gage #06024450, near Wisdom, MT). Median period-of-record values for daily mean discharge (1988-2011) and daily maximum stream temperature (1997-2011) are depicted as thick gray lines, and 2008 data are presented as solid black lines. The solid black vertical line indicates the day thermal infrared (TIR) imagery was collected (30 July 2008). Dashed vertical lines bracket the 7-week period emphasized in this study (1 July - 18 August 2008), when stream discharge was relatively low and stream temperatures were relatively high.

Table S1. Parameter estimates and goodness-of-fit measures from Equation 1 cubic polynomial fits, including all time segments *i* from 1 July - 18 August 2008. Odd time segments are 10-h warming phases and even segments are 14-h cooling phases. Error terms (°C) are based on differences between observed and predicted mean temperature at stationary temperature loggers (*n* = number of loggers) during segment *i*.

i	*n*	*a*	*b* (10^{-5})	*c* (10^{-9})	*d* (10^{-15})	r^2	RMSE	Minimum error	Maximum error
1	8	15.99	5.32	-0.63	-1.26	0.99	0.13	-0.21	0.25
2	8	15.58	6.64	-1.38	5.14	0.98	0.15	-0.27	0.22
3	8	15.75	3.69	-0.20	-2.46	0.98	0.09	-0.13	0.13
4	8	16.63	10.24	-1.73	6.75	0.98	0.10	-0.17	0.13
5	8	17.65	4.11	-0.31	-2.28	0.97	0.14	-0.22	0.23
6	8	18.47	10.21	-2.08	9.72	0.98	0.14	-0.22	0.19
7	8	18.25	7.50	-1.40	5.14	0.99	0.11	-0.12	0.20
8	7	17.46	8.50	-1.77	7.77	1.00	0.06	-0.10	0.09
9	7	16.32	4.74	-0.54	-0.75	0.96	0.17	-0.32	0.24
10	7	16.20	6.27	-1.42	6.70	0.96	0.14	-0.16	0.25
11	7	16.41	3.80	-0.39	-0.93	0.97	0.11	-0.16	0.18
12	7	16.81	8.92	-1.78	7.86	0.99	0.07	-0.12	0.11
13	7	16.96	4.59	-0.63	0.10	0.98	0.14	-0.22	0.22
14	7	17.11	10.11	-2.26	11.37	0.99	0.08	-0.14	0.16
15	8	17.44	3.16	-0.50	-0.25	0.98	0.13	-0.23	0.20
16	8	17.56	8.56	-2.02	10.26	0.99	0.08	-0.13	0.11
17	8	17.60	5.38	-0.90	1.77	0.99	0.11	-0.20	0.17
18	8	18.02	9.63	-2.23	11.58	1.00	0.06	-0.10	0.11
19	8	17.96	4.96	-0.85	1.94	0.99	0.08	-0.17	0.13
20	8	16.99	7.50	-1.77	8.95	0.99	0.06	-0.10	0.08
21	10	16.29	2.85	0.02	-5.13	0.92	0.28	-0.31	0.47
22	10	15.85	8.27	-2.01	10.39	0.93	0.23	-0.42	0.48
23	10	15.98	6.92	-1.10	1.96	0.95	0.24	-0.27	0.44
24	10	16.69	13.29	-3.26	18.14	0.97	0.19	-0.26	0.39
25	10	16.77	8.30	-1.32	3.04	0.95	0.24	-0.25	0.45
26	10	17.07	11.86	-2.80	14.87	0.96	0.20	-0.24	0.42
27	10	17.18	7.63	-1.39	4.46	0.94	0.24	-0.27	0.47
28	10	17.27	10.18	-2.30	11.83	0.97	0.15	-0.16	0.30
29	10	16.71	6.09	-0.72	-0.38	0.91	0.27	-0.32	0.60
30	10	16.34	11.25	-1.91	7.22	0.98	0.12	-0.18	0.26
31	10	15.93	11.85	-2.34	9.90	0.95	0.25	-0.34	0.44
32	10	15.64	12.74	-2.91	14.59	0.98	0.19	-0.21	0.43
33	10	17.04	9.81	-2.08	8.91	0.98	0.18	-0.22	0.31
34	10	18.12	12.53	-3.38	18.82	0.99	0.13	-0.16	0.25

35	10	17.76	2.60	-0.54	0.21	0.97	0.19	-0.23	0.43
36	10	16.60	3.33	-0.80	2.87	0.94	0.20	-0.20	0.40
37	10	16.92	5.05	-0.78	0.78	0.96	0.20	-0.25	0.35
38	10	17.36	9.66	-2.22	10.79	0.99	0.09	-0.09	0.19
39	10	16.50	6.73	-1.03	1.67	0.93	0.27	-0.35	0.46
40	10	17.86	8.82	-2.04	9.76	0.96	0.22	-0.20	0.46
41	10	18.59	9.52	-1.96	8.05	0.96	0.22	-0.34	0.36
42	10	19.38	9.53	-2.77	15.20	0.99	0.11	-0.16	0.20
43	10	17.65	7.16	-1.85	9.12	0.94	0.28	-0.35	0.61
44	10	17.15	3.39	-1.16	5.70	0.96	0.20	-0.25	0.48
45	10	17.84	3.25	-0.78	2.15	0.92	0.28	-0.37	0.52
46	10	18.49	6.26	-1.62	7.51	0.99	0.12	-0.13	0.22
47	10	19.02	5.33	-1.23	4.00	0.97	0.23	-0.34	0.38
48	10	18.61	8.39	-2.15	10.87	0.99	0.11	-0.15	0.27
49	10	18.64	7.32	-1.58	5.72	0.95	0.28	-0.48	0.45
50	10	19.20	9.97	-2.52	13.06	0.99	0.13	-0.17	0.29
51	10	19.48	7.77	-1.68	6.42	0.96	0.25	-0.50	0.39
52	10	19.60	9.08	-2.22	10.76	0.99	0.14	-0.18	0.28
53	10	19.29	5.98	-1.10	2.41	0.97	0.22	-0.35	0.36
54	10	19.02	6.60	-1.73	8.58	0.96	0.22	-0.26	0.48
55	10	18.94	7.26	-1.44	4.73	0.95	0.27	-0.49	0.43
56	10	18.66	9.15	-2.02	9.11	0.99	0.12	-0.18	0.30
57	10	18.23	7.49	-1.40	4.12	0.97	0.21	-0.31	0.28
58	10	17.61	3.48	-0.84	2.61	0.95	0.23	-0.28	0.56
59	10	18.06	2.52	-0.25	-2.37	0.96	0.19	-0.25	0.23
60	10	17.19	6.82	-1.57	6.74	0.96	0.21	-0.35	0.46
61	10	17.51	2.52	-0.14	-3.29	0.94	0.23	-0.38	0.34
62	10	17.69	7.24	-1.33	4.72	0.95	0.20	-0.21	0.47
63	10	18.02	3.80	-0.25	-3.18	0.93	0.26	-0.49	0.39
64	10	18.48	5.88	-1.10	3.14	0.96	0.19	-0.27	0.40
65	10	18.61	3.68	-0.61	-0.47	0.98	0.17	-0.27	0.29
66	10	17.39	6.42	-1.63	6.84	0.97	0.23	-0.32	0.36
67	10	17.34	4.60	-0.99	2.81	0.98	0.16	-0.33	0.17
68	10	16.97	11.41	-2.84	14.72	0.97	0.24	-0.33	0.42
69	10	17.59	6.96	-1.37	4.14	0.94	0.29	-0.60	0.38
70	10	17.78	10.74	-2.41	10.72	0.97	0.23	-0.35	0.47
71	10	17.84	9.05	-1.77	6.53	0.94	0.30	-0.72	0.46
72	10	18.59	8.11	-1.93	9.12	0.96	0.21	-0.25	0.43
73	10	18.27	8.21	-1.67	6.26	0.93	0.32	-0.70	0.44
74	10	19.13	7.88	-1.70	7.99	0.99	0.09	-0.12	0.15
75	10	19.49	5.58	-0.77	0.17	0.92	0.28	-0.69	0.42
76	10	18.84	2.43	-0.55	0.19	0.95	0.25	-0.37	0.41
77	10	17.86	3.29	-0.79	2.13	0.97	0.19	-0.23	0.35
78	10	17.19	9.48	-2.18	10.73	0.98	0.15	-0.15	0.34
79	10	17.01	6.89	-1.58	6.46	0.97	0.21	-0.32	0.39
80	10	16.51	8.33	-2.23	11.88	0.96	0.21	-0.27	0.43
81	10	17.36	4.48	-1.44	7.66	0.94	0.25	-0.61	0.32
82	10	16.44	5.87	-1.69	8.82	0.95	0.23	-0.29	0.47

83	10	16.08	4.39	-0.78	1.75	0.83	0.36	-0.88	0.47
84	10	15.66	8.52	-1.73	7.47	0.95	0.20	-0.23	0.37
85	10	16.03	9.12	-1.67	6.38	0.85	0.38	-0.94	0.45
86	10	16.48	8.31	-1.76	8.11	0.91	0.25	-0.33	0.46
87	10	15.13	10.01	-1.68	5.56	0.92	0.28	-0.60	0.41
88	10	15.81	8.47	-1.69	6.67	0.96	0.21	-0.24	0.42
89	10	16.46	9.95	-2.00	8.68	0.88	0.35	-0.82	0.50
90	10	17.07	4.75	-0.94	2.85	0.88	0.31	-0.53	0.60
91	10	17.03	6.27	-1.16	3.71	0.89	0.32	-0.77	0.52
92	10	17.55	2.69	-0.65	2.00	0.87	0.28	-0.45	0.62
93	10	17.18	9.39	-1.79	6.94	0.82	0.46	-1.02	0.61
94	10	18.36	6.52	-1.35	4.75	0.93	0.30	-0.46	0.68
95	10	17.74	9.42	-1.72	6.24	0.89	0.37	-0.81	0.55
96	10	18.46	2.82	-0.40	-1.09	0.90	0.31	-0.63	0.66
97	10	17.86	8.50	-1.52	4.86	0.91	0.34	-0.71	0.55

Table S2. Parameter estimates and goodness-of-fit measures from Equation 2 modified sine-function fits, including all time segments *i* from 1 July - 18 August 2008. Odd time segments are 10-h warming phases and even segments are 14-h cooling phases. Error terms (°C) are based on differences between observed and predicted hourly temperatures at stationary temperature loggers (*n* = number of loggers) during segment *i*. Standard deviation among logger sites is displayed in parenthesis.

i	*n*	*A* (°C)	*P* (h)	t_{Tmean} (h)	r^2	RMSE (°C)
1	8	1.1 (0.2)	22.0 (2.8)	13.2 (0.6)	0.95 (0.03)	0.18 (0.04)
2	8	2.2 (0.2)	30.5 (2.1)	9.9 (1.2)	0.99 (0.00)	0.14 (0.03)
3	8	3.4 (0.8)	21.7 (1.9)	13.1 (0.1)	0.99 (0.00)	0.19 (0.06)
4	8	2.5 (0.9)	30.8 (1.7)	9.8 (1.0)	0.98 (0.02)	0.18 (0.07)
5	8	3.4 (0.8)	20.9 (1.9)	13.1 (0.2)	0.99 (0.00)	0.19 (0.09)
6	8	2.7 (0.8)	31.7 (0.4)	9.1 (0.2)	0.99 (0.01)	0.16 (0.10)
7	8	1.9 (0.6)	16.0 (0.0)	12.4 (0.3)	0.94 (0.06)	0.31 (0.10)
8	8	2.1 (0.5)	30.2 (2.9)	9.8 (0.9)	0.98 (0.02)	0.17 (0.05)
9	7	1.4 (0.6)	20.5 (3.5)	12.9 (0.6)	0.96 (0.03)	0.19 (0.04)
10	7	2.1 (0.5)	29.3 (2.1)	10.6 (1.3)	0.98 (0.02)	0.19 (0.09)
11	7	3.1 (0.6)	21.8 (1.8)	13.0 (0.2)	1.00 (0.00)	0.11 (0.03)
12	7	2.8 (0.7)	31.3 (1.9)	9.5 (1.0)	0.99 (0.01)	0.17 (0.07)
13	7	3.1 (0.7)	20.1 (0.9)	13.1 (0.2)	1.00 (0.00)	0.14 (0.09)
14	8	3.0 (0.5)	31.9 (0.1)	9.1 (0.1)	0.99 (0.01)	0.22 (0.07)
15	8	3.2 (0.7)	20.8 (0.9)	13.1 (0.2)	1.00 (0.00)	0.13 (0.08)
16	8	3.1 (0.5)	32.0 (0.1)	9.1 (0.1)	0.99 (0.01)	0.20 (0.07)
17	8	3.5 (0.7)	21.0 (0.4)	13.1 (0.2)	1.00 (0.00)	0.14 (0.08)
18	8	3.2 (0.7)	31.6 (0.6)	9.2 (0.3)	0.99 (0.00)	0.15 (0.04)
19	8	3.0 (0.7)	20.7 (1.4)	12.9 (0.2)	1.00 (0.00)	0.12 (0.06)
20	10	3.7 (0.6)	31.4 (1.5)	9.1 (0.1)	0.98 (0.02)	0.23 (0.14)
21	10	3.3 (0.5)	20.8 (1.7)	13.0 (0.4)	0.99 (0.01)	0.14 (0.12)
22	10	3.5 (0.3)	31.6 (0.7)	9.1 (0.2)	0.99 (0.01)	0.26 (0.16)
23	10	4.1 (0.4)	21.5 (1.3)	13.0 (0.3)	1.00 (0.00)	0.15 (0.11)
24	10	3.5 (0.4)	31.2 (1.2)	9.5 (0.6)	0.99 (0.00)	0.18 (0.07)
25	10	3.9 (0.4)	21.1 (0.9)	13.0 (0.3)	1.00 (0.00)	0.14 (0.09)
26	10	3.5 (0.4)	31.7 (0.4)	9.1 (0.3)	0.99 (0.01)	0.20 (0.09)
27	10	3.7 (0.5)	20.6 (1.2)	13.0 (0.4)	1.00 (0.00)	0.16 (0.08)
28	10	3.4 (0.5)	31.4 (0.9)	9.2 (0.4)	0.99 (0.00)	0.15 (0.06)
29	10	3.1 (0.3)	22.6 (1.4)	13.0 (0.5)	0.99 (0.01)	0.17 (0.06)
30	10	2.9 (0.4)	31.7 (0.4)	9.1 (0.2)	0.99 (0.01)	0.15 (0.06)
31	10	2.1 (0.3)	17.3 (2.4)	12.9 (0.5)	0.95 (0.03)	0.36 (0.12)
32	10	2.5 (0.3)	31.6 (0.5)	9.2 (0.3)	0.99 (0.01)	0.14 (0.08)
33	10	3.7 (0.4)	19.9 (1.9)	12.9 (0.3)	1.00 (0.01)	0.14 (0.10)

34	10	3.1 (0.4)	31.8 (0.3)	9.2 (0.2)	0.99 (0.01)	0.19 (0.08)
35	10	2.5 (0.5)	17.4 (1.9)	12.6 (0.4)	0.97 (0.03)	0.29 (0.14)
36	10	3.0 (0.3)	31.8 (0.3)	9.2 (0.3)	0.99 (0.00)	0.19 (0.07)
37	10	4.0 (0.3)	21.2 (1.5)	13.0 (0.3)	1.00 (0.00)	0.13 (0.09)
38	10	3.6 (0.4)	30.8 (1.1)	9.6 (0.4)	1.00 (0.00)	0.14 (0.05)
39	10	3.5 (0.2)	18.1 (2.5)	13.3 (0.4)	0.98 (0.02)	0.31 (0.16)
40	10	3.0 (0.3)	31.4 (0.5)	9.3 (0.4)	1.00 (0.00)	0.13 (0.07)
41	10	3.6 (0.3)	18.1 (1.5)	12.8 (0.4)	0.99 (0.00)	0.21 (0.07)
42	10	2.8 (0.2)	31.7 (0.3)	9.1 (0.1)	0.99 (0.01)	0.20 (0.06)
43	10	1.7 (0.2)	16.5 (1.7)	12.8 (0.6)	0.86 (0.08)	0.49 (0.12)
44	10	2.4 (0.2)	30.8 (1.5)	9.7 (0.9)	0.99 (0.01)	0.17 (0.06)
45	10	3.6 (0.2)	19.9 (1.5)	13.0 (0.4)	1.00 (0.00)	0.11 (0.08)
46	10	2.9 (0.4)	31.7 (0.2)	9.2 (0.2)	1.00 (0.00)	0.13 (0.03)
47	10	3.5 (0.3)	20.6 (1.3)	13.0 (0.4)	1.00 (0.00)	0.10 (0.08)
48	10	3.6 (0.3)	31.8 (0.2)	9.1 (0.1)	0.99 (0.01)	0.21 (0.08)
49	10	3.9 (0.3)	20.4 (0.9)	13.0 (0.4)	1.00 (0.00)	0.10 (0.09)
50	10	3.5 (0.3)	31.7 (0.3)	9.1 (0.2)	1.00 (0.00)	0.15 (0.05)
51	10	3.9 (0.4)	20.0 (0.9)	13.0 (0.4)	1.00 (0.00)	0.11 (0.07)
52	10	3.6 (0.4)	31.8 (0.3)	9.1 (0.2)	0.99 (0.01)	0.20 (0.08)
53	10	3.3 (0.5)	19.4 (2.2)	12.9 (0.4)	1.00 (0.00)	0.13 (0.06)
54	10	3.4 (0.4)	31.6 (0.5)	9.2 (0.3)	0.99 (0.01)	0.18 (0.09)
55	10	3.7 (0.3)	20.3 (1.6)	12.9 (0.4)	1.00 (0.00)	0.12 (0.05)
56	10	3.6 (0.2)	31.8 (0.2)	9.1 (0.2)	0.99 (0.01)	0.24 (0.09)
57	10	2.8 (0.3)	16.6 (0.9)	12.5 (0.4)	0.96 (0.04)	0.39 (0.18)
58	10	2.8 (0.4)	31.5 (0.6)	9.1 (0.4)	0.99 (0.01)	0.21 (0.09)
59	10	3.3 (0.3)	20.4 (2.1)	12.9 (0.3)	1.00 (0.00)	0.15 (0.07)
60	10	3.6 (0.3)	31.6 (0.5)	9.1 (0.3)	0.99 (0.01)	0.26 (0.11)
61	10	4.1 (0.4)	20.2 (1.1)	13.0 (0.3)	1.00 (0.00)	0.13 (0.07)
62	10	3.5 (0.4)	31.7 (0.4)	9.2 (0.3)	1.00 (0.00)	0.14 (0.03)
63	10	3.8 (0.4)	19.5 (1.1)	12.9 (0.4)	1.00 (0.00)	0.13 (0.05)
64	10	3.3 (0.4)	31.7 (0.5)	9.2 (0.3)	1.00 (0.00)	0.15 (0.08)
65	10	2.7 (0.3)	16.2 (0.4)	12.5 (0.3)	0.97 (0.02)	0.34 (0.15)
66	10	3.2 (0.2)	31.6 (0.5)	9.2 (0.3)	0.99 (0.00)	0.17 (0.05)
67	10	3.2 (0.3)	19.3 (3.1)	12.8 (0.4)	0.98 (0.02)	0.27 (0.14)
68	10	3.2 (0.2)	31.3 (1.0)	9.4 (0.9)	0.99 (0.00)	0.18 (0.05)
69	10	4.0 (0.4)	19.5 (1.6)	13.0 (0.4)	1.00 (0.01)	0.15 (0.11)
70	10	3.6 (0.3)	31.6 (0.4)	9.2 (0.3)	0.99 (0.00)	0.20 (0.06)
71	10	4.1 (0.4)	19.3 (1.4)	13.0 (0.4)	1.00 (0.00)	0.13 (0.07)
72	10	3.7 (0.2)	31.4 (0.6)	9.3 (0.6)	0.99 (0.01)	0.18 (0.09)
73	10	3.9 (0.4)	19.8 (1.9)	13.0 (0.5)	1.00 (0.00)	0.16 (0.07)
74	10	2.8 (0.3)	31.3 (1.4)	9.4 (0.8)	0.99 (0.01)	0.22 (0.09)
75	10	2.9 (0.4)	16.6 (1.7)	12.4 (0.6)	0.94 (0.03)	0.50 (0.16)
76	10	2.4 (0.2)	31.2 (0.9)	9.2 (0.3)	0.98 (0.02)	0.23 (0.09)
77	10	1.6 (0.4)	24.0 (0.0)	13.3 (0.6)	0.85 (0.03)	0.45 (0.13)
78	10	2.4 (0.3)	30.1 (2.6)	10.1 (1.6)	0.99 (0.01)	0.17 (0.06)
79	10	2.2 (0.2)	17.3 (2.1)	13.1 (0.6)	0.98 (0.01)	0.23 (0.08)
80	10	2.7 (0.2)	31.3 (1.0)	9.4 (0.7)	0.99 (0.00)	0.14 (0.05)
81	10	3.1 (0.5)	17.1 (1.6)	12.7 (0.6)	0.99 (0.01)	0.24 (0.05)

82	10	3.2 (0.3)	31.6 (0.4)	9.2 (0.4)	0.99 (0.01)	0.21 (0.10)
83	10	3.7 (0.5)	19.0 (1.4)	13.0 (0.5)	1.00 (0.01)	0.09 (0.08)
84	10	3.4 (0.4)	31.6 (0.4)	9.2 (0.4)	0.99 (0.01)	0.20 (0.09)
85	10	4.2 (0.4)	19.1 (1.2)	13.0 (0.5)	1.00 (0.00)	0.09 (0.08)
86	10	3.5 (0.3)	31.4 (0.5)	9.2 (0.4)	0.99 (0.01)	0.21 (0.08)
87	10	3.0 (0.4)	21.2 (2.6)	13.2 (0.5)	0.99 (0.01)	0.21 (0.05)
88	10	3.0 (0.3)	30.7 (1.0)	9.7 (1.0)	0.99 (0.01)	0.18 (0.07)
89	10	4.2 (0.4)	19.1 (0.9)	13.0 (0.5)	1.00 (0.00)	0.09 (0.05)
90	10	3.7 (0.2)	31.3 (0.7)	9.3 (0.5)	0.99 (0.01)	0.26 (0.15)
91	10	4.1 (0.4)	19.3 (0.8)	13.0 (0.4)	1.00 (0.00)	0.08 (0.04)
92	10	3.8 (0.3)	31.5 (0.7)	9.2 (0.4)	0.99 (0.01)	0.28 (0.12)
93	10	4.6 (0.6)	20.0 (1.3)	13.1 (0.5)	1.00 (0.01)	0.15 (0.10)
94	10	3.9 (0.4)	30.9 (1.4)	9.5 (1.1)	0.99 (0.01)	0.25 (0.14)
95	10	4.3 (0.5)	19.0 (1.3)	13.0 (0.5)	1.00 (0.00)	0.10 (0.05)
96	10	4.0 (0.5)	31.3 (1.0)	9.3 (0.7)	0.99 (0.01)	0.25 (0.14)
97	10	4.2 (0.4)	18.5 (1.1)	13.0 (0.5)	1.00 (0.00)	0.10 (0.04)

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER 3

Table S1 Linear models for predicting stream temperatures in the Big Hole River near Wisdom, Montana, USA. Corresponding data displayed in Fig. S3.

Predictor	Number of independent variables	*P*	r^2	*RMSE*
Air temperature	1	< 0.01	0.862	1.063
Stream discharge (sqrt)[a]	1	< 0.01	0.446	2.132
Air temperature + stream discharge (sqrt)[a]	2	< 0.01	0.869	1.041
Air temperature * stream discharge (sqrt)[a]	3	< 0.01	0.874	1.024

[a] Stream discharge transformed with a square root function.

Table S2. Decadal means of weekly mean daily maximum stream temperature estimates for June, July, and August.

	Estimates of stream temperature (°C) based on:								
	Observed air temperature			GFDL			MM		
Site	1980s	1990s	2000s	2040s	2050s	2060s	2040s	2050s	2060s
1	19.8 (2.9)	19.6 (3.2)	20.3 (3.2)	22.0 (3.1)	23.0 (3.3)	23.2 (3.6)	21.3 (2.9)	21.8 (3.0)	22.0 (3.3)
2	20.5 (2.9)	20.3 (3.2)	21.0 (3.3)	22.8 (3.2)	23.7 (3.4)	24.0 (3.6)	22.0 (3.0)	22.5 (3.0)	22.7 (3.3)
3	19.2 (2.9)	19.0 (3.2)	19.7 (3.2)	21.4 (3.1)	22.3 (3.3)	22.6 (3.6)	20.7 (2.9)	21.1 (3.0)	21.4 (3.3)
4	18.5 (2.1)	18.4 (2.3)	18.9 (2.3)	20.1 (2.2)	20.8 (2.4)	20.9 (2.6)	19.6 (2.1)	19.9 (2.1)	20.1 (2.4)
5	17.2 (2.2)	17.0 (2.5)	17.6 (2.5)	18.9 (2.4)	19.6 (2.6)	19.8 (2.8)	18.3 (2.3)	18.7 (2.3)	18.8 (2.5)
6	18.9 (2.4)	18.7 (2.6)	19.3 (2.6)	20.7 (2.5)	21.4 (2.7)	21.7 (2.9)	20.1 (2.4)	20.5 (2.4)	20.6 (2.7)
7	18.6 (2.1)	18.4 (2.3)	18.9 (2.4)	20.2 (2.3)	20.9 (2.5)	21.1 (2.6)	19.7 (2.2)	20.0 (2.2)	20.2 (2.4)
8	19.7 (2.7)	19.5 (3.0)	20.1 (3.1)	21.7 (2.9)	22.6 (3.2)	22.9 (3.4)	21.1 (2.8)	21.5 (2.8)	21.7 (3.1)
9	14.7 (2.6)	14.5 (2.8)	15.1 (2.8)	16.6 (2.7)	17.4 (2.9)	17.7 (3.2)	16.0 (2.6)	16.4 (2.6)	16.6 (2.9)
10	19.8 (2.7)	19.6 (3.0)	20.3 (3.1)	21.9 (2.9)	22.8 (3.2)	23.0 (3.4)	21.2 (2.8)	21.7 (2.8)	21.9 (3.1)
11	19.6 (2.4)	19.4 (2.6)	20.0 (2.7)	21.4 (2.6)	22.2 (2.7)	22.4 (2.9)	20.8 (2.4)	21.2 (2.5)	21.4 (2.7)
13	17.6 (2.9)	17.4 (3.1)	18.1 (3.2)	19.8 (3.1)	20.7 (3.3)	21.0 (3.5)	19.1 (2.9)	19.6 (2.9)	19.8 (3.3)
14	16.3 (2.5)	16.1 (2.7)	16.8 (2.8)	18.2 (2.7)	19.0 (2.9)	19.3 (3.1)	17.6 (2.5)	18.0 (2.6)	18.2 (2.8)
15	19.3 (2.2)	19.1 (2.5)	19.7 (2.5)	21.0 (2.4)	21.7 (2.6)	21.9 (2.8)	20.4 (2.3)	20.8 (2.3)	20.9 (2.5)
16	14.5 (3.1)	14.2 (3.4)	15.0 (3.4)	16.8 (3.3)	17.8 (3.6)	18.1 (3.8)	16.0 (3.1)	16.5 (3.2)	16.8 (3.5)
17	18.4 (2.1)	18.3 (2.3)	18.8 (2.4)	20.0 (2.3)	20.7 (2.4)	20.9 (2.6)	19.5 (2.1)	19.8 (2.2)	20.0 (2.4)
18	19.1 (2.8)	18.9 (3.0)	19.6 (3.1)	21.2 (3)	22.1 (3.2)	22.4 (3.4)	20.5 (2.8)	21.0 (2.9)	21.2 (3.1)
19	17.9 (2.6)	17.7 (2.8)	18.4 (2.9)	19.9 (2.8)	20.7 (3.0)	20.9 (3.2)	19.2 (2.6)	19.6 (2.6)	19.8 (2.9)
20	16.3 (2.7)	16.1 (3.0)	16.8 (3.0)	18.4 (2.9)	19.3 (3.1)	19.5 (3.4)	17.7 (2.8)	18.1 (2.8)	18.3 (3.1)
21	19.7 (2.2)	19.5 (2.4)	20.1 (2.5)	21.4 (2.4)	22.1 (2.6)	22.3 (2.8)	20.8 (2.3)	21.2 (2.3)	21.4 (2.5)
23	19.9 (2.1)	19.7 (2.3)	20.2 (2.3)	21.4 (2.2)	22.1 (2.4)	22.3 (2.6)	20.9 (2.1)	21.2 (2.1)	21.4 (2.4)
24	18.2 (2.9)	18.0 (3.1)	18.7 (3.2)	20.4 (3.1)	21.3 (3.3)	21.6 (3.5)	19.7 (2.9)	20.1 (2.9)	20.3 (3.2)
All sites combined	18.4 (3.0)	18.1 (3.2)	18.8 (3.3)	20.3 (3.2)	21.1 (3.4)	21.3 (3.5)	19.6 (3.1)	20.1 (3.1)	20.2 (3.3)
Mean among sites	18.4 (2.5)	18.1 (2.8)	18.8 (2.8)	20.3 (2.7)	21.1 (2.9)	21.3 (3.1)	19.6 (2.6)	20.1 (2.6)	20.2 (2.9)

Note: standard deviations follow means. See Methods for model descriptions.

Table S2 (continued). Decadal means of weekly mean daily maximum stream temperature estimates for June, July, and August.

	Estimates of stream temperature (°C) based on:									
	GMOM					EH5				
Site	2020s	2030s	2040s	2050s	2060s	2020s	2030s	2040s	2050s	2060s
1	20.3 (3.2)	20.6 (3.1)	20.7 (3.2)	20.9 (3.3)	21.0 (3.4)	19.9 (3.2)	20.3 (3.1)	21.2 (2.7)	21.4 (2.8)	21.7 (3.1)
2	20.9 (3.2)	21.3 (3.1)	21.4 (3.2)	21.6 (3.3)	21.7 (3.4)	20.6 (3.3)	21.0 (3.1)	21.9 (2.8)	22.1 (2.8)	22.4 (3.1)
3	19.6 (3.2)	19.9 (3.1)	20.1 (3.2)	20.3 (3.3)	20.4 (3.3)	19.3 (3.2)	19.6 (3.1)	20.5 (2.7)	20.8 (2.8)	21.0 (3.1)
4	18.8 (2.3)	19.0 (2.2)	19.2 (2.3)	19.3 (2.3)	19.4 (2.4)	18.6 (2.3)	18.8 (2.2)	19.5 (1.9)	19.7 (2.0)	19.8 (2.2)
5	17.5 (2.4)	17.7 (2.4)	17.9 (2.5)	18.0 (2.5)	18.1 (2.6)	17.2 (2.5)	17.5 (2.4)	18.2 (2.1)	18.4 (2.2)	18.6 (2.4)
6	19.2 (2.6)	19.5 (2.5)	19.6 (2.6)	19.8 (2.7)	19.9 (2.7)	18.9 (2.6)	19.2 (2.5)	20.0 (2.2)	20.2 (2.3)	20.4 (2.5)
7	18.9 (2.3)	19.1 (2.3)	19.2 (2.4)	19.4 (2.4)	19.5 (2.5)	18.6 (2.4)	18.9 (2.3)	19.5 (2.0)	19.8 (2.1)	19.9 (2.3)
8	20.1 (3.0)	20.4 (2.9)	20.5 (3.0)	20.7 (3.1)	20.8 (3.2)	19.7 (3.0)	20.1 (2.9)	20.9 (2.6)	21.2 (2.6)	21.4 (2.9)
9	15.0 (2.8)	15.3 (2.7)	15.5 (2.8)	15.6 (2.9)	15.7 (2.9)	14.7 (2.8)	15.1 (2.7)	15.8 (2.4)	16.1 (2.5)	16.3 (2.7)
10	20.2 (3.0)	20.5 (2.9)	20.7 (3.0)	20.9 (3.1)	21.0 (3.2)	19.9 (3.0)	20.3 (2.9)	21.1 (2.6)	21.3 (2.6)	21.6 (2.9)
11	20.0 (2.6)	20.2 (2.5)	20.4 (2.6)	20.5 (2.7)	20.6 (2.7)	19.7 (2.6)	20.0 (2.5)	20.7 (2.2)	20.9 (2.3)	21.1 (2.5)
13	18.1 (3.1)	18.4 (3.0)	18.5 (3.2)	18.7 (3.2)	18.8 (3.3)	17.7 (3.2)	18.1 (3.1)	18.9 (2.7)	19.2 (2.8)	19.5 (3.0)
14	16.7 (2.7)	17.0 (2.7)	17.1 (2.8)	17.3 (2.8)	17.4 (2.9)	16.4 (2.8)	16.7 (2.7)	17.5 (2.3)	17.7 (2.4)	17.9 (2.7)
15	19.6 (2.4)	19.8 (2.4)	20.0 (2.5)	20.1 (2.5)	20.2 (2.6)	19.3 (2.5)	19.6 (2.4)	20.3 (2.1)	20.5 (2.2)	20.7 (2.4)
16	14.9 (3.4)	15.3 (3.3)	15.4 (3.4)	15.6 (3.5)	15.8 (3.6)	14.5 (3.4)	14.9 (3.3)	15.9 (2.9)	16.2 (3.0)	16.4 (3.3)
17	18.7 (2.3)	19.0 (2.2)	19.1 (2.3)	19.2 (2.4)	19.3 (2.4)	18.5 (2.3)	18.7 (2.3)	19.4 (2.0)	19.6 (2.0)	19.8 (2.2)
18	19.5 (3.0)	19.8 (2.9)	20.0 (3.1)	20.2 (3.1)	20.3 (3.2)	19.2 (3.1)	19.5 (3.0)	20.4 (2.6)	20.6 (2.7)	20.9 (2.9)
19	18.3 (2.8)	18.6 (2.7)	18.7 (2.8)	18.9 (2.9)	19.0 (3.0)	18.0 (2.8)	18.3 (2.7)	19.1 (2.4)	19.3 (2.5)	19.6 (2.7)
20	16.7 (3.0)	17.0 (2.9)	17.2 (3.0)	17.3 (3.1)	17.4 (3.2)	16.4 (3.0)	16.7 (2.9)	17.6 (2.6)	17.8 (2.6)	18.1 (2.9)
21	20.0 (2.4)	20.3 (2.4)	20.4 (2.5)	20.5 (2.5)	20.6 (2.6)	19.7 (2.5)	20.0 (2.4)	20.7 (2.1)	20.9 (2.1)	21.1 (2.4)
23	20.2 (2.3)	20.4 (2.2)	20.5 (2.3)	20.6 (2.3)	20.7 (2.4)	19.9 (2.3)	20.2 (2.2)	20.8 (2.0)	21.0 (2.0)	21.2 (2.2)
24	18.6 (3.1)	18.9 (3.0)	19.1 (3.1)	19.3 (3.2)	19.4 (3.3)	18.3 (3.2)	18.7 (3.0)	19.5 (2.7)	19.8 (2.7)	20.0 (3.0)
All sites combined	18.7 (3.2)	19.0 (3.2)	19.1 (3.2)	19.3 (3.3)	19.4 (3.4)	18.4 (3.3)	18.7 (3.2)	19.5 (2.9)	19.8 (2.9)	20.0 (3.2)
Mean among sites	18.7 (2.8)	19.0 (2.7)	19.1 (2.8)	19.3 (2.9)	19.4 (2.9)	18.4 (2.8)	18.7 (2.7)	19.5 (2.4)	19.8 (2.4)	20.0 (2.7)

Note: standard deviations follow means. See Methods for model descriptions

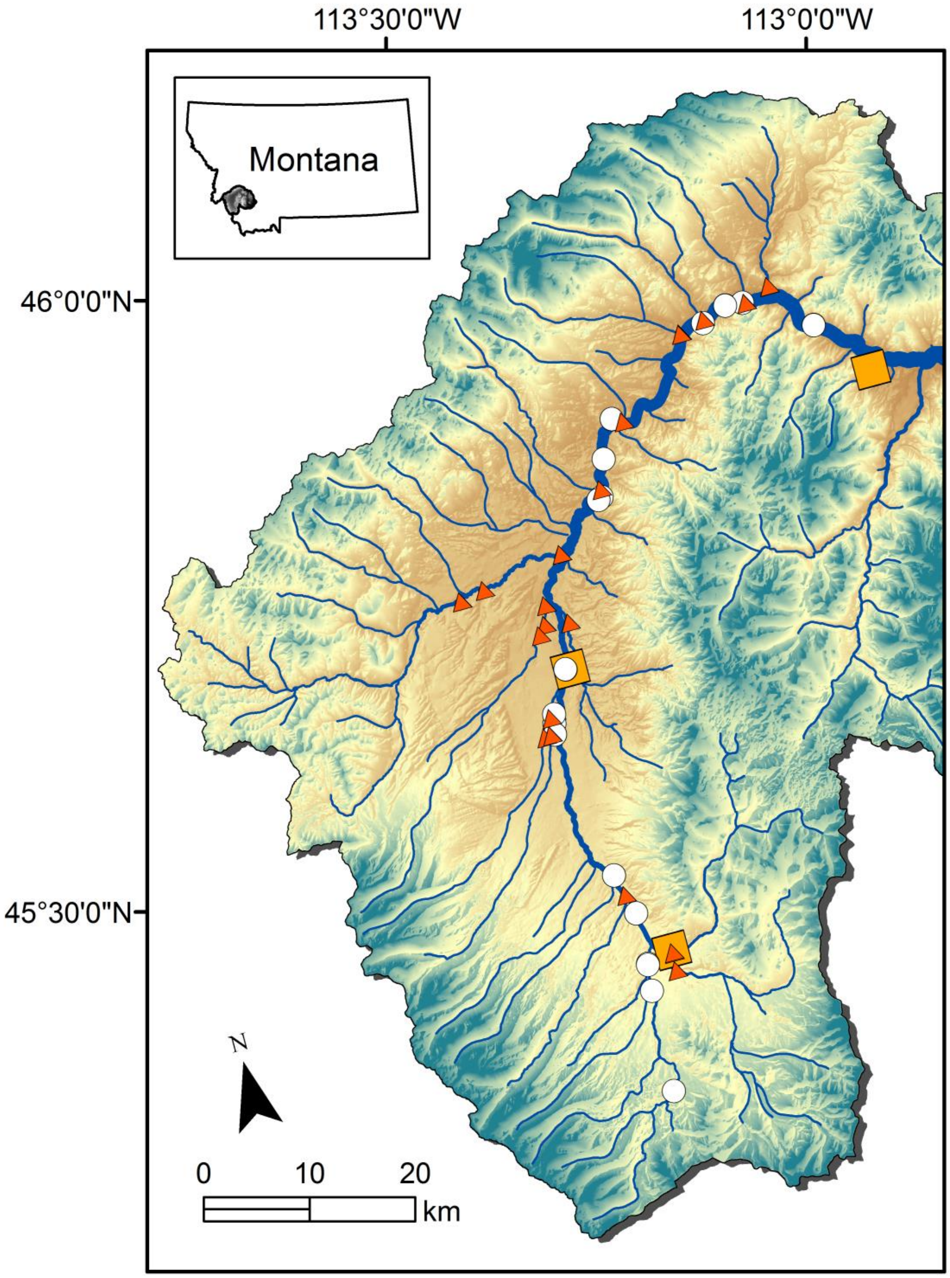

Fig. S1 Upper Big Hole River watershed and stream network (stream line width correlated with drainage area). Multiple data collection sites included on the map: red triangles = tributary temperature loggers; white circles = Big Hole River temperature loggers; orange squares = air temperature observation sites. Background color = elevation gradient increasing from brown to green.

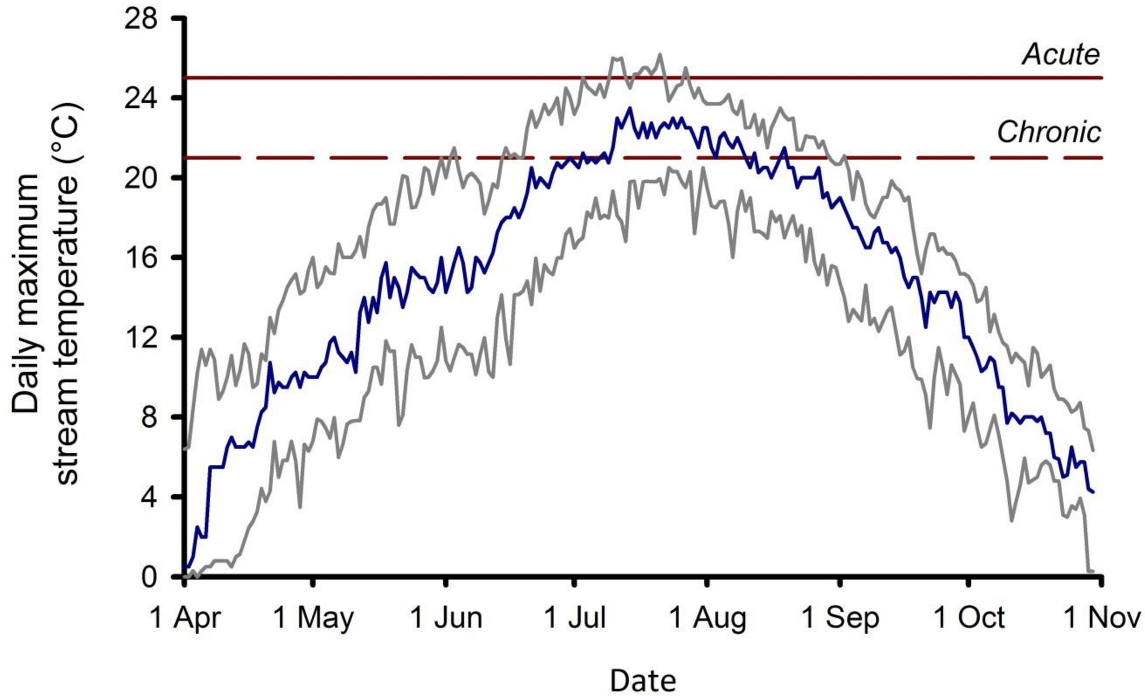

Fig. S2 Daily maximum stream temperatures measured in the Big Hole River near the center of the study area (USGS gage #06024450 near Wisdom, MT). Median period-of-record values (1997-2011) are depicted by the blue line and 5^{th} and 95^{th} percentile values by the gray lines. Chronic (21 °C) and acute (25 °C) thermal tolerance thresholds are indicated by the dark red horizontal lines.

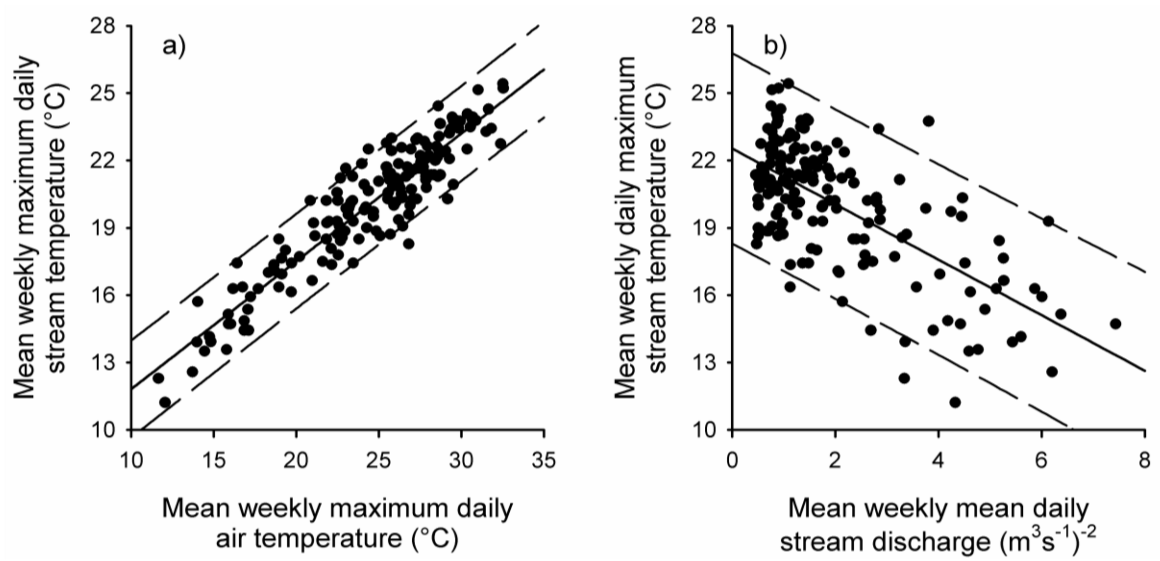

Fig. S3 Big Hole River summer stream temperatures as a function of a) air temperatures and b) stream discharges. Data collected near Wisdom, Montana, USA, from 1998–2010. Only data from June, July, and August were included. All values are weekly averages of the daily maximum for temperature or daily mean for discharge. Solid black lines are linear regression predictions and dashed lines are the 95% prediction interval bands. Stream discharge was transformed with a square root function to improve normality of residuals.

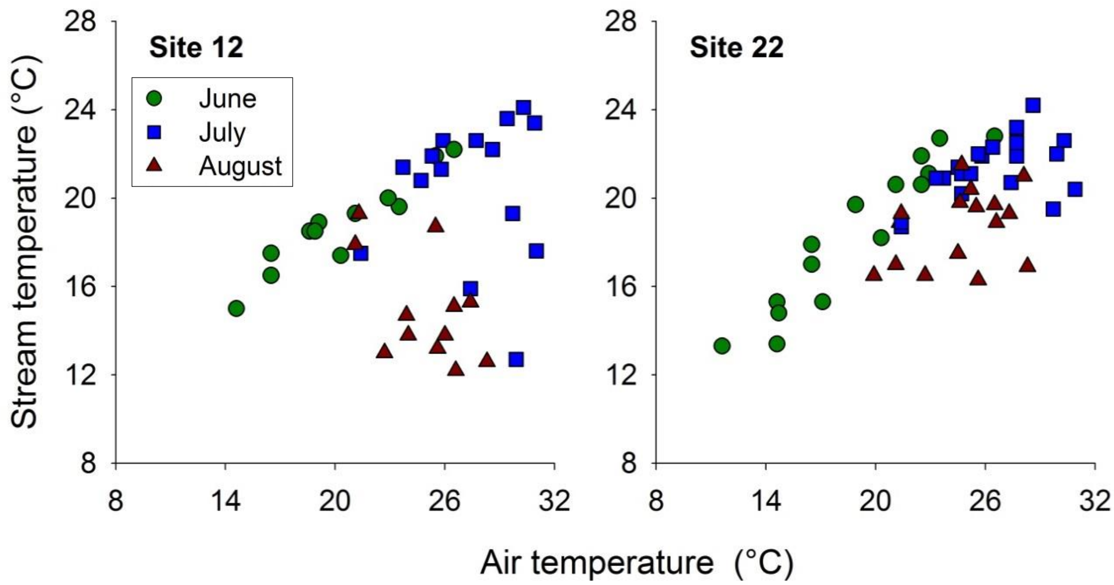

Fig. S4 Weekly mean daily maximum (WMDM) air and stream temperature relationships at site 12 (near the mouth of Big Lake Creek) and site 22 (near the mouth of Swamp Creek and Lower North Fork Road) during June, July, and August. Includes all available data from 2005–2010. We hypothesized that beaver dams, flood irrigation, natural wetlands, or a combination of these factors occurring upstream of sites resulted in proportionally greater shallow ground water contributions to instream flows in late July and throughout August in some years. As a result, maximum stream temperatures in the late summer were cooler, and the relationship with air temperature was weak (in comparison to all other monitoring sites).