

**Conservation of freshwater thermal habitats for Pacific salmon
in a changing climate**

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A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington

2016

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Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

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Abstract

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Climate adaptation strategies for freshwater biota have focused on how water temperature and hydrology will change over time, but understanding spatial patterns in water temperature will also be essential for evaluating vulnerability of biota to future climate and for identifying and protecting diverse thermal habitats. I used high-resolution remotely sensed water temperature data for over 16,000 km of 2nd to 7th-order rivers throughout the Pacific Northwest and California to evaluate spatial patterns of summertime water temperature at multiple spatial scales. I found a diverse and geographically distributed suite of whole-river patterns. About half of rivers warmed asymptotically in a downstream direction, as expected, whereas the rest exhibited complex and unique spatial patterns. Patterns were associated with both broad-scale hydroclimatic variables as well as characteristics unique to each basin. Within-river thermal heterogeneity patterns were highly river-specific, but median size and spacing of cool patches <15 °C were both around 250 m. Patches of this size are large enough for juvenile rearing and for resting during migration, and the distance between patches is well within the movement capabilities of both juvenile and adult salmon. The density, size, and spacing of patches were nonlinearly related to the resolution of water temperature; there was a lot of heterogeneity at very fine scales that may be important to fish that would be missed if data were analyzed at coarser scales. Climate change will cause warmer temperatures overall, but thermal heterogeneity

patterns may remain similar in the future for many rivers. Maintaining this diverse portfolio of habitats will promote resiliency of salmon to natural and anthropogenic disturbance. I also developed an individual-based model to evaluate whether influences of climate change on growth and phenology of juvenile salmon could be mediated by the shape of stream networks. I used three network shapes of increasing spatial complexity: long, typical, and compact. Growth and movement of fish were based on water temperature and conspecific density. Under current-day climate conditions, salmon grew best and were large enough to smolt earliest in the long network. However, salmon grew best and outmigrated earliest in the compact network under future climate scenarios, suggesting that areas of high productivity may shift in the future. Increases in summer maximum temperature had a greater effect on fish responses than did increases in the rate of spring warming or day-to-day variability. Results from my research can be used to inform restoration and conservation strategies that minimize vulnerability of Pacific salmon to climate change and other stressors.

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Acknowledgements

Thanks are due in equal measure to my committee, colleagues, and family. I thank Ashley Steel for continuing to believe in me and for introducing me to the wonderful world of water temperature. I thank Christian Torgersen for truly caring about the details, and for allowing me the opportunity to work on a fabulous project with an amazing dataset. I thank Josh Lawler for providing key critical feedback with a positive attitude and for fostering a stimulating lab environment. I thank Ashley, Christian, and Josh for guiding my small ideas into bigger ones and for introducing me to numerous colleagues that are likely to become lasting relationships. I thank Sándor Tóth for helping me to see that I could understand difficult mathematical concepts if I put in the effort, and for always asking the “so what” questions. I thank Nate Mantua for teaching me about natural climate variability and for welcoming me during my brief stay in Santa Cruz. I thank Jessica Lundquist for agreeing to herd cats and keep us all in line.

I am extremely grateful for the opportunity provided by NOAA Fisheries to pursue this degree. The NOAA Advanced Studies Program provided tuition and time for classes during the first two years. My supervisors Beth Sanderson, John Williams, and Rich Zabel were very supportive in allowing me to pursue research passions that pertained to NOAA’s mission. I thank Joe Ebersole, Scott Leibowitz, Tim Beechie Se-Yeun Lee, Lisa Crozier and others for valuable brainstorming and feedback while developing my research. I am grateful to Russ Faux and Don Essig for allowing me to use the remotely sensed temperature data that they compiled.

Finally, I thank my family for supporting me during this long process. I thank Brian Burke for being not just my best friend and husband, but also my best scientific sounding board. It is very special to be able to talk about science at the dinner table. My children Claire and Derry have hardly known me when I was not a student. I thank them both for their patience and love during the many evenings and weekends I needed to work instead of play. I hope that I have shown them that pursuing higher education is a worthy cause.

Chapter 1. Introduction

1.1. Problem Statement and Need

Temperature controls the rates of many biological processes, and is a key driver of ecological processes controlling population and community structure in aquatic ecosystems (Magnuson et al. 1997, Schlosser et al. 2000, Vinson 2001). For ectotherms such as fish, water temperature regulates rates of physiological, neurological, embryological and behavioral development (Brett 1971, Ficke et al. 2007). Water temperature can alter behavior (e.g., rates of movement), and through its influence on metabolic efficiency and growth, water temperature drives the timing of ontogenetic transitions from one life stage to the next (Ward and Stanford 1979, Beacham and Murray 1990).

Pacific salmonids (*Oncorhynchus* spp.) have evolved in freshwater systems with abundant cold water, and are adapted to the variation in natural thermal regimes over time and across space (Coutant 1999, Poole et al. 2001, McCullough et al. 2009). At broad spatial scales, water temperature partly defines species ranges (Dunham et al. 2001). Spatiotemporal diversity in thermal regimes influences life history diversity (Beechie et al. 2006, Crozier and Zabel 2006, Lisi et al. 2013). At finer spatial scales, thermal heterogeneity can influence connectivity among essential habitats and may provide pockets of refuge during periods of unfavorable temperatures (Torgersen et al. 1999, Ebersole et al. 2003). Temporal patterns in water temperature partly determine timing of transitions among life history stages. For instance, decreasing temperatures trigger upstream migration by adults to the spawning grounds, and temperature is believed to influence the timing of seaward migration.

Human activities such as operation of hydropower dams, development of land adjacent to streams, and water withdrawal for irrigation have altered stream thermal regimes throughout the world (NRC 1996, Bisson et al. 2009, Olden and Naiman 2010). For species already stressed by habitat modification, altered thermal regimes could have substantial consequences. Climate change is predicted to further alter temperature and flow regimes (IPCC 2014). Coupled with natural variability and uncertainty in projections, these conditions may increasingly stress stream organisms (Ficke et al. 2007).

In parts of the Pacific Northwest, summer stream temperatures are expected to reach or exceed thermal tolerances for salmonids by as early as the 2020s (Mantua et al. 2010). Ranges

for bull trout (*Salvelinus confluentus*) are predicted to be restricted (Rieman et al. 2007, Isaak et al. 2010), extinction risk of Chinook salmon (*O. tshawytscha*) populations are predicted to increase (Crozier et al. 2008b), and salmon habitat restoration efforts are expected to have limited effects due to climate change (Battin et al. 2007). Alterations in the magnitude and timing of stream thermal regimes could induce phenological asynchrony, mismatches between evolved life-histories and current environmental conditions that may reduce survival and fitness (Angilletta et al. 2008, Crozier et al. 2008a).

Because of its biological significance and myriad natural and anthropogenic drivers, water temperature is often a “hot” topic of management concern. In a legal context, water temperature in salmon-bearing rivers must remain below levels deemed suitable for protected species (US Clean Water Act; US Endangered Species Act). Although we have a general sense of the thermal requirements of Pacific salmon across the breadth of habitats used during their life cycle, numerous questions persist. For instance, how can complex spatiotemporal patterns be measured and characterized in a way that is meaningful for understanding how they influence fish? What aspects of thermal regimes can we manage in order to conserve thermal diversity? These are difficult questions with no simple answers. For instance, the Oregon Department of Environmental Quality and US Environmental Protection Agency are currently struggling with how to interpret, define, and measure the concept of “sufficiently distributed cold water refuges”.

There has been a great deal of research addressing the thermal requirements of salmonids and how fish respond to temporal patterns in water temperature. However, far fewer studies have attempted to describe historical or future *spatial* patterns in water temperature and evaluate potential consequences for salmon. Therefore, this is the topic on which my dissertation research focused. In Chapter 2, I provide a brief (not exhaustive) review of the literature pertaining to water temperature and its influence on Pacific salmon. Chapters 3 through 5 address the research objectives outlined below. In Chapter 6, I synthesize findings and suggest potentially fruitful future research directions.

1.2. Objectives

My research focused on filling key gaps in our understanding about spatial patterns in water temperature and potential fish response to altered thermal regimes associated with climate change. Specifically, my objectives were to:

- (1) Characterize spatial patterns and potential drivers of summertime water temperature at the scale of whole rivers throughout the Pacific Northwest;
- (2) Compare historical and potential future thermal heterogeneity patterns within rivers (i.e., prevalence, size, and spacing of cold water patches); and
- (3) Consider whether influences of climate change on growth and phenology of juvenile salmon could be mediated by stream network structure.

Each of the following three chapters describes how I evaluated these questions. Together, my analyses should provide information useful for conservation of Pacific salmon and their thermal habitats as the climate continues to change.

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Chapter 2. A brief review of the literature on water temperature as it pertains to Pacific salmon

2.1. Spatiotemporal Patterns in Water Temperature

A stream's thermal regime describes the magnitude, frequency, duration, timing and variability in water temperatures at different spatial and temporal scales (Olden and Naiman 2010, Arismendi et al. 2013). Water temperature at a given location varies across hours, days, months, years, and decades (Webb and Nobilis 1995, Steel and Lange 2007). These temporal patterns in water temperature vary across microhabitats, reaches, streams, watersheds, and river basins (Poole et al. 2001a, Poole et al. 2001b). Both temporal and spatial patterns are predominantly governed by climate forcing at large scales and by local conditions at fine scales (Poole and Berman 2001, Caissie 2006).

Human activities such as thermal pollution, deforestation, flow modification, and climate change have altered thermal regimes (Poole and Berman 2001, Caissie 2006). For instance, large dams alter the magnitude and timing of natural thermal regimes and can dampen variability (Preece and Jones 2002, Steel and Lange 2007, Olden and Naiman 2010). Land conversion and water withdrawal alter stream thermal regimes by increasing the amount of surface area exposed to solar radiation (e.g., from reduced forested buffers or stream widening) or by altering the hydrologic cycle, and therefore the rate of water exchange, both overland and via groundwater recharge (Bisson et al. 2009). Each of these impacts can intensify temporal trends in water temperature causing streams to be warmer during hot periods and cooler during cool periods. And many human activities tend to increase spatial homogeneity of water temperature.

2.1.1. Temporal Variability

Inter-annual and decadal patterns can be complex, as they are driven by climate forcing. Trends over longer time frames are emerging, but our understanding is compromised by the lack of time series of sufficient length (Arismendi et al. 2012, Isaak et al. 2012). Annual patterns are generally similar within geographical regions (Garner et al. 2013, Maheu et al. 2015).

At finer temporal scales, water temperature follows a cyclical pattern, warming during warm-season months and cooling during cool-season months (summer and winter, respectively, in the northern hemisphere). For many regulated rivers, however, water below dams remains relatively warm in winter and relatively cool in summer (Olden and Naiman 2010). Although it

is becoming apparent that the warm season is beginning sooner and lasting longer, it is less clear how the shape of seasonal patterns has changed over time. Much attention has been given to minimum, maximum and mean values or duration exceeding some threshold, but less to the rate of warming and cooling.

Water temperature warms during daylight hours and cools at night (i.e., another cyclical pattern nested within the seasonal pattern). The duration of this wave is related to day length. Systems fed by groundwater tend to be more stable (i.e., have lower amplitude) than those that have few subsurface connections (Tague et al. 2007, Wawrzyniak et al. 2013). Diel variability is typically highest in mid-order reaches (Caissie 2006). In headwaters, water temperature is similar to the more constant temperature of its source (groundwater or snowmelt), and in larger rivers, water temperature is more stable due to the thermal inertia associated with larger volumes. Whereas in mid-order reaches, water temperature may fluctuate daily with change in solar radiation. The hourly, daily, and weekly amplitude in water temperature can be dampened in regulated rivers (i.e., below dams) (Steel and Lange 2007).

2.1.2. Spatial Heterogeneity

Descriptions of comprehensive spatial patterns of water temperature within rivers are scarce in the literature, and spatial patterns throughout river networks are even less well understood. More typically, patterns for one or more point locations within a river are compared to points in other rivers. For instance, Brown and Hannah (2008) found high variability across rivers in France. Makarowski (2009) found no difference in the relationship between water and air temperature among ecoregions, but did find differences among streams within an ecoregion. Snyder et al. (2015) identified spatial variation in thermal sensitivity to climate drivers within and among watersheds.

Within a river, water temperature is believed to generally warm in a downstream direction (Ward 1985, Caissie 2006, Webb et al. 2008). However, within-river thermal heterogeneity can be high. For example, Dent et al. (2008) found spatial variability in longitudinal patterns of headwater streams in Oregon. Variance can also be quite high across a river's floodplain (Arscott et al. 2001, Uehlinger et al. 2003). Tonolla et al. (2010) found variance within the floodplain to be higher than longitudinally along the river.

At riverscape scales (Fausch et al. 2002) and finer, water temperature can be quite patchy. Thermal refuges – patches that are cooler in the warm season or warmer in the cool

season – can be important for stream fishes (Torgersen et al. 1999b, Ebersole et al. 2003b). Drivers of spatial variability in water temperature such as tributaries, groundwater seeps, and localized topographic or vegetative shading are also spatially heterogeneous (Kiffney et al. 2006, Tan and Cherkauer 2013, Ebersole et al. 2015).

2.1.3. Space and Time

Until recently, very little research examined both spatial and temporal patterns in water temperature simultaneously. Often, water temperature is either represented by one location, or is summarized across locations within a river or watershed, in order to evaluate temporal patterns. And evaluation of spatial patterns often means collapsing water temperature over time to the mean annual or summer maximum temperature. It has become less expensive to collect water temperature and exciting new collection and analysis techniques have begun to enable exploration of spatiotemporal patterns. For example, airborne thermal infrared imagery allows examination of water temperature at very high spatial resolution (Torgersen et al. 1999a, Monk et al. 2013). Dugdale et al. (2013) and Wawrzyniak et al. (2016) used airborne remote sensing to survey locations of cold water patches on numerous dates. O'Donnell (2012), Westhoff et al. (2007), and Gryczkowski (2015) used distributed temperature sensors (fiber optic cable) to evaluate longitudinal patterns in water temperature along river reaches throughout the day.

2.1.4. Biological Consequences of Spatiotemporal Variability

The way that temperature is experienced over time may have direct biological consequences. For instance, in a laboratory experiment (Steel et al. 2012), emergence by Chinook salmon (*Oncorhynchus tshawytscha*) alevins occurred earlier when fish experienced natural variance patterns but was delayed when fish experienced thermal regimes with extreme daily or seasonal variation. Several studies have noted that growth or survival of juveniles changed when stream temperatures were more variable (Hokanson et al. 1977, Boughton et al. 2007, Geist et al. 2010, Xu et al. 2010). Juvenile Atlantic salmon (*Salmo salar*) in the U.K. became nocturnal instead of diurnal when they experienced low temperatures during non-winter periods (Fraser et al. 1995).

Spatial patterns in thermal regimes partly define geographic distributions of fish (Dunham et al. 2001, Lindley et al. 2007, Wenger et al. 2011, Wenger et al. 2013, Warren et al. 2014, Isaak et al. 2015). Diverse thermal habitats promote life history and species diversity (Ruff et al. 2011, Lisi et al. 2013, Griffiths et al. 2014). Thermal heterogeneity at fine scales is

beneficial to fish by providing a range of conditions from which fish can select thermally optimal habitat used for a specific purpose such as feeding or sheltering (e.g., Armstrong et al. 2013).

A key challenge in understanding how thermal regimes influence stream organisms is in determining which metrics, or facets of the thermal regime, are important (Arismendi et al. 2013, Steel et al. 2016, Turschwell et al. 2016). The metrics that are typically monitored may not fully capture the aspects of a thermal regime that are important for stream biota. For instance, in some locations thermal variability during winter months when salmon eggs are incubating may have a bigger effect on population responses than warm temperatures during the growing season.

2.2. Modeling Stream Temperature

As data collection techniques have improved, methods for analyzing empirical data and for using them to make predictions have also evolved. Indeed, numerous models have been developed in the last decade that predict water temperature over space and/or time at high resolutions. Predominantly, models are one of two types: (1) statistical relationships between potential drivers of stream temperature and observed water temperatures, or (2) mechanistic physically-based models that combine first-principles or analytically solve the heat budget equation (Webb et al. 2008). Statistical models may be better for broad spatial application but may not be reliable for conditions beyond which relationships were constructed such as new locations or future times (Caissie 2006). Process-based models are typically applied at finer scales (e.g., for one river reach) and in cases when a better understanding of energy fluxes is important. Because of their reliance on foundational theory about causal links, they may be better for making predictions in unsampled locations or times. Regardless of model type, many challenges remain, particularly with respect to scaling issues (Johnson 2003) and uncertainty (Webb et al. 2008, Wenger et al. 2013).

2.2.1. Drivers of Stream Temperature

For both mechanistic and statistical models, an understanding of expected drivers is key. Water temperature is predominantly governed by climate forcing at broad scales and by local conditions associated with topography, hydrology, and geomorphology at fine scales (Poole and Berman 2001, Caissie 2006) (**Table 2.1**). Water temperature is expected to interact more strongly with atmospheric and climatic conditions in mid-order streams (Caissie 2006). In headwaters, water temperature may be more highly influenced by the temperature of its source.

In larger rivers, water temperature is not as reactive to external conditions due to higher thermal inertia and slower travel time associated with larger volumes (Webb et al. 2008).

Air temperature has often been used as a surrogate for the dominant radiative controls on stream temperature (Walker and Lawson 1977, Caldwell et al. 2015) (**Figure 2.1**). This works well in many circumstances but caution is warranted. The relationship is better characterized as sinusoidal than linear; i.e., stream temperature is not as responsive when air temperatures are extreme (really cold or hot) (Mohseni et al. 1998, Mayer 2012). Moreover, air temperature differs spatially and with terrain (e.g., cold air pooling in complex terrain; Lundquist et al. 2008). There is an increasing lag between air and water temperatures with increasing mean annual discharge (i.e., larger rivers). Such differences are not often accounted for in models of water temperature. Instead, readings from a single weather station are used to represent conditions over a large area, and temporal lags are often ignored.

Stream water at any given location originates from melting snow, surface runoff, underground flow pathways, or upstream (Poole and Berman 2001, Caissie 2006). Precipitation can have strong influences on stream water, both by directly contributing water at a particular temperature, and by contributing to the volume of water in a channel, which increases the buffering capacity (Boyd and Kasper 2003, Story et al. 2003). The timing of water availability is also dictated by climate; if water falls as snow, it is tied up as snowpack, and therefore not available to the stream until it melts (Leibowitz et al. 2012).

Local controls can have substantial influence on water temperature, both in terms of producing patchiness and also by altering mean temperatures over broader spatial scales. For instance, Bogan et al. (2003) found that around 80% of rivers they evaluated were influenced by cold water inputs from groundwater, meltwater and deep reservoir releases, or by warm-water inputs from wastewater, cooling water and lake surface water. Direct inputs from large point sources such as tributaries and side channels can influence stream temperature dramatically (Kiffney et al. 2006, Wawrzyniak et al. 2011, Ebersole et al. 2015). Interaction with subsurface water (e.g., groundwater, hyporheic water) can have a huge effect on stream temperature (Poole and Berman 2001, O'Daniel 2005, Cozzetto et al. 2006, Tague et al. 2007, Arrigoni et al. 2008, Gryczkowski 2015). Glaciers (Fellman et al. 2014), aquifers (Kurylyk et al. 2013, Wigington et al. 2013), riparian vegetation (Imholt et al. 2013, Ryan et al. 2013), and anthropogenic alteration

(Olden and Naiman 2010, Tan and Cherkauer 2013) also play important roles in determining water temperature and in creating thermal heterogeneity.

We know little about how thermal variability over space and time is related to the landscape, and therefore what might be done to conserve natural thermal structure (Chang and Psaris 2013). Landscape features such as the spacing and density of tributary confluences directly influence the presence of localized thermal refuges (Benda et al. 2004, Kiffney et al. 2006, Torgersen et al. 2008). Other, more distributed factors such as network topology, geomorphology, and other local landscape features likely also contribute to thermal heterogeneity (**Table 2.2**) (Torgersen et al. 2012).

2.2.2. Statistical Models

The majority of statistical models make predictions of water temperature from weather data or watershed characteristics (Webb et al. 2008). Predicting stream temperature from air temperature does not always work well, especially when extrapolating beyond the time frame of observations or in regulated rivers (Arismendi et al. 2014). Bal et al. (2014) used more sophisticated time series approaches that incorporated thermal oscillation across time scales in order to translate air temperatures into stream temperatures. Steel and Lange (2007) used wavelet analysis to identify appropriate time scales for considering how water temperature responded to dams. Larnier et al. (2010) used stochastic autoregressive models and Fourier transforms to address seasonal time components of temperatures over 18 years. Spatial variation in water temperature, predictors, and their association has been addressed using random forest models (Hill et al. 2013) and other geostatistical approaches (Gardner et al. 2003, Gardner and Sullivan 2004). An exciting new approach was introduced by McNyset et al. (2015), who used land surface temperature (remotely sensed MODIS satellite data) instead of air temperature as a primary correlate of water temperature. This had the advantage of capturing spatial variation in the predictor, something that is rarely done when using air temperature as a covariate in models. Combining spatial (airborne remotely sensed surveys) and temporal (in-stream loggers) water temperature data, Vatland et al. (2014) developed a model that predicted spatiotemporal patterns of water temperature within a several hundred meter long reach.

An especially exciting new development in recent years is the advent of statistical models capable of properly handling the autocorrelation present in water temperature data. Water temperature at one location is strongly related to water temperature just upstream. However, the

branching structure of stream networks has made it tricky to apply classic one- or two-dimensional autocovariance structures, because incoming tributaries can disrupt expected monotonic patterns. In addition to the typical suite of model covariates (e.g., hydroclimatic or landscape features), spatial stream network models (SSNM) capture the unique branching structure of the river network, flow connectivity, and the effects of streamflow volume and directionality as well as discontinuities that often occur in tributaries just upstream of river confluences (Ver Hoef et al. 2006, Peterson and Hoef 2010, Isaak et al. 2014). Where spatial stream-network models have been applied, accounting for spatial correlation in the data has significantly improved the accuracy of predictions at unsampled locations (Isaak et al. 2010, Ruesch et al. 2012, Peterson et al. 2013). Recently, these models were used to construct spatially continuous predictions of mean summertime water temperature at a 1-km resolution for the entire Pacific Northwest (Isaak et al. 2013).

2.2.3. Process-based Models

A variety of physically-based models have been developed to predict water temperature by solving the heat budget. Many of these models operate at high spatial and temporal resolution for one reach (e.g., 10s to 100s of m). Examples of well used reach-scale models include Heat Source (Boyd 1996, Boyd and Kasper 2003), SNTEMP, the Stream Network Temperature Model (Theurer et al. 1984, Bartholow 2010), and SSTEMP, the Stream Segment Temperature Model (Bartholow 1990). More recently, physically based stream temperature models have been developed and applied to solve real world management problems. For example RAFT, the River Assessment for Forecasting Temperature tool predicts real-time stream temperature for several hundred meters below a hydropower dam to manage timing and magnitude of hypolimnetic releases for coldwater fishes (Danner et al. 2012, Pike et al. 2013). Another process-based model calibrated with water temperature data from distributed temperature sensors (fiber optic cable) has been applied for riparian management in Switzerland (Westhoff et al. 2007, Roth et al. 2010).

As opposed to the difficulty in statistical application to whole stream networks, process-based models are less constrained by autocorrelation and can be applied across watersheds. For instance, HSPF, the Hydrological Simulation Program for FORTRAN (Bicknell et al. 1997) and QUAL2K (Chapra et al. 2005) calculate the temperature of individual reaches and then hydraulically route the heat downstream. Other examples include BasinTemp (Allen et al. 2007)

and WET-Temp, the Watershed Evaluation Tool (Cox and Bolte 2007). The DHSVM-RBM, the product of coupling the Distributed Soil Vegetation Model (Wigmosta et al. 1994) with a Lagrangian temperature model (Yearsley 2012), has been applied to evaluate management concerns (Sun et al. 2015). Related, Wu et al. (2011) and Wu et al. (2012) developed DRTT, the dominant river-tracing-based streamflow and temperature model, by coupling stream thermal dynamics with a source-sink routing model. MacDonald et al. (2014) coupled two process-based models to simulate stream temperature in a groundwater-dominated mountain catchment in Alberta, Canada.

2.3. Thermal Requirements of Salmonids

Salmonids have thermal criteria that are substantially lower than many other freshwater fishes (Brungs and Jones 1977, Eaton et al. 1995). General ranges of temperatures considered to be suitable for each life stage have been well studied for a variety of salmonids (Bjornn and Reiser 1991, McCullough 1999, Elliott and Elliott 2010) (**Table 2.3**). Bull trout (*Salvelinus confluentus*) represent the extreme lower end of the spectrum, and redband trout (*O. mykiss*) represent the upper end. Richter and Kolmes (2005) reviewed and updated the synthesis of our knowledge about requirements for Chinook, coho (*O. kisutch*), chum (*O. keta*), and steelhead (*O. mykiss*) in the Pacific Northwest.

A diverse variety of life history strategies have evolved to best match timing and availability of thermal habitat. For instance, spring Chinook salmon migrate upstream when it is cool and hold in tributaries during warm summer months before spawning in the autumn. Juveniles typically spend an entire year in freshwater before migrating to sea. Whereas fall Chinook migrate upstream during cooler autumn months shortly before spawning. Fall Chinook spawn during autumn and winter months, and juveniles outmigrate the following spring or summer before temperatures get too warm. These patterns suggest that high temperatures may be more limiting to fall-type races than to spring-type races (Coutant 1999). However, the geographic distribution of spring Chinook extends to higher latitudes and elevations than does that of fall Chinook (Taylor 1990).

Direct mortality of fish stressed by temperature is well described in the literature (e.g., Brett et al. 1982). Acute effects are generally more severe at higher temperatures and longer exposures, but differ with fish history including acclimation, environment, and genetic origin (McDermid et al. 2012, Underwood et al. 2012). Upper incipient lethal temperatures (UILT), the

temperature at which 50% of fish survive when exposed for 7 d, are in the vicinity of 27-30 °C. However, fish acclimated at cold temperatures can have upper lethal limits of 3-4 °C lower. Acclimation temperatures above 20 °C produce similar UILTs (McCullough et al. 2001). High temperature is more of a concern than low temperature in most Pacific Northwest rivers; however, in some circumstances (e.g., tailwaters of reservoirs), low temperatures may limit fish growth. The majority of UILT studies were conducted in laboratory settings at constant temperatures. Wehrly et al. (2007) used field-based estimates to suggest that temperature fluctuation during exposure may influence tolerance limits for brook (*S. fontinalis*) and rainbow trout (*O. mykiss*). Recent studies suggest that fish can tolerate warmer temperatures than previously thought in some regions (Clabough et al. 2006, Spina 2007, Geist et al. 2010, Strange 2010); however, delayed effects of exposure to warm temperatures is not well understood.

It is generally recognized that increases in water temperature can limit growth and survival of coldwater fishes, but potential sublethal effects are less clear (McCullough et al. 2009). Many of the effects of temperature on salmonids can have delayed or cumulative effects. Below, I discuss thermal suitability and sublethal effects for each life stage.

2.3.1. Adult Migration & Holding

Upstream migration by adult anadromous salmon can be blocked at temperatures above 19-23 °C (Richter and Kolmes 2005). Possible mechanisms include increased susceptibility to disease; delay caused by depletion of energy reserves or reduced swimming speed (Hasler et al. 2012); and increased susceptibility to other stressors (Goniaea et al. 2006, Keefer et al. 2008). High temperatures can decrease the success of fish navigating dam passage facilities (Caudill et al. 2013). Pre-spawn mortality may occur at high temperatures (Cramer 2001, Mann 2007, Quinn et al. 2007, Keefer et al. 2009, Hinch et al. 2012). This could be exacerbated in the presence of contaminants (Hooper et al. 2013, Moe et al. 2013). Reproductive success can be decreased for fish holding at high temperatures via suppression of reproductive hormones and reduced gamete viability (Jeffries et al. 2012). Fish have evolved different strategies for coping with warm water during spawning migrations. For instance salmon in the Klamath River basin have multiple life history strategies that minimizing thermal stress based on run timing (Strange 2012). Farrell et al. (2008) and Eliason et al. (2011) found diversity in aerobic scope among life history strategies of sockeye (*O. nerka*) in the Fraser River system. Availability of thermal refuges (e.g., cooler water

for temporary holding) and adequate fat stores for contending with increased metabolic costs can allow fish to migrate through otherwise unsuitably warm waterways.

2.3.2. Spawning

Optimal temperature preferences for spawning balance the needs of adults (better adult condition with moderate to low temperatures) and temperatures at which development of eggs is optimal. Spawning timing is particularly important because it facilitates local adaptation and diversification within river basins. Spawning is generally initiated at temperatures ranging from 7 to 14 °C, but can occur over a much wider range (Poole et al. 2001b). Spawning is usually initiated as temperatures begin to decline. However, during prolonged periods of high temperatures fish may be forced to spawn under suboptimal conditions, resulting in reduced survival and fitness of offspring (Fenkes et al. 2016).

2.3.3. Egg-to-fry

Eggs have the lowest heat tolerance of any life stage (~10°C lower than adults) and rely on being placed in the right location at the right time by adults. Water temperature affects the rate of embryo and alevin development. Higher temperatures generally result in faster development rates and shorter incubation times, but very low temperatures can produce larger alevins, perhaps due to decreased metabolic costs. Elevated incubation temperatures may also increase incidence of mortality. High survival to hatching and emergence tend to occur at temperatures between 4 and 12 °C, with best survival occurring between 6 and 10 °C (Cramer 2001, McCullough et al. 2001). Time to emergence is directly related to temperature, with lower temperatures resulting in slower emergence rates (Cuenco and McCullough 1997). However, temporal variability (i.e., daily, seasonal fluctuations) experienced by embryos can alter both development and emergence rates. For instance, Steel et al. (2012) found that Chinook salmon emerged earlier and were less developed when exposed to naturally varying water temperature but emerged later and more fully developed when exposed to abnormal thermal regimes. Moreover, responses depended on genetic origin. Tolerance to high temperatures differs at various stages of development, and fry may have a higher rate of developmental impairment due to latent effects of early incubation conditions.

2.3.4. Juvenile Rearing

Temperature mainly affects survival of juveniles through its control on growth rate (Cramer 2001). For anadromous salmon, freshwater rearing is a period during which fish must maximize growth in order to survive the early ocean phase of their life histories. Size attained during summer (and winter, depending on species) affects survival and timing of smoltification. Consumption and growth-rate curves are asymmetrical unimodal curves, with optimal temperatures somewhere in the middle and reduced consumption or growth at both higher and lower temperatures (Hanson et al. 1997). Within the optimum range of temperatures encountered by fish, higher temperatures generally allow higher consumption rates, which lead to higher growth rates, provided that food supplies are adequate. Optimum temperatures for feeding and growth range from 12 to 20 °C for many salmonids; but under natural conditions, food availability is much lower and the scope for growth is therefore reduced. Feeding may be inhibited at temperatures above 18 °C, and metabolic costs may inhibit growth at higher temperatures (Chittaro et al. 2014). At temperatures below 6 °C, feeding and activity are low enough to preclude growth (McCullough et al. 2001). Food organisms of salmonids in the freshwater environment (e.g., macroinvertebrates) and the primary production on which they depend are also limited in biomass by temperature. Thus, in very cold headwaters during any season and larger streams during winter, food may be scarce. Even in summer, food may be limiting, and growth rates are often lower than those observed under laboratory conditions (ODEQ 1995). Optimal temperatures also vary among life stages, with younger fish generally preferring warmer water than older fish (Myrick and Cech 2004). Extensive in-stream migration may occur during the freshwater rearing period to maximize preferred temperatures (Sauter et al. 2001).

Biotic interactions can be strongly influenced by temperature (Coutant 1999, Peterson and Kitchell 2001). Fish stressed by increased metabolic rates due to high temperatures may alter their competitive interactions, either increasing or decreasing levels of aggressiveness, and increased temperatures may affect their ability to capture prey. High local fish density can exacerbate conditions for already stressed fish by reducing available food resources. For instance, Harvey and Nakamoto (1996) observed a negative relationship between the growth rate of age-0 coho salmon and the density of steelhead in two California streams. Nonindigenous species (e.g., brook trout or smallmouth bass *Micropterus dolomieu*) can be an added source of

stress as a competitor or predator, especially if they have inherently different temperature requirements that give them an advantage at higher temperatures (Sanderson et al. 2009, Hughes and Herlihy 2012, Lawrence et al. 2014) or as the climate warms (Rahel and Olden 2008, Christensen and Moore 2010). Small fish require more energy than large fish to swim fast, and may not have enough energy at elevated temperatures to out-swim predators (McCullough et al. 2001). Swimming speeds (sustained, prolonged, and burst) may be impaired by high temperatures, and can even be influenced by thermal stress experienced by parents or embryos (Burt et al. 2012).

Temperatures below 12-13 °C are often found to reduce susceptibility to disease, whereas temperatures above 15-16 °C tend to increase risk of disease, and temperatures of 18-20 °C can allow serious outbreaks and high mortality (McCullough et al. 2001, Braden et al. 2010, Bradford et al. 2010, Marcos-Lopez et al. 2010). Hanson and Peterson (2014) reviewed preferences of major salmon pathogens and thermally optimal outbreak conditions. Not only does susceptibility to disease increase with temperature (Ray et al. 2012), but diseases are also often more virulent at higher temperatures (Materna 2001). Stress by pathogens may exacerbate other effects of high temperatures, such as reduced swimming stamina (Kocan et al. 2009). In some cases, the optimum temperature for fish growth may contrast with temperatures necessary to avoid disease, but generally a compromise provides a sustainable, disease-free growth range. The result, considered a physiological optimum, is often the temperature range selected or preferred by fish (McCullough et al. 2001).

2.3.5. Smolt Outmigration

Temperature, either directly or indirectly via its effect on growth, plays a role in the timing of downstream migration and smoltification, which is the transition from the physiological condition adapted to freshwater to the condition capable of saltwater residency. Survival of Chinook and steelhead juveniles migrating downstream was reduced at temperatures > 13 °C (Zabel et al. 2008). Outmigrating juveniles cease seaward migration as temperatures rise above 12-15 °C (Richter and Kolmes 2005). Even at lower temperatures, e.g., 11-13 °C, physiological changes required for smoltification may be hampered, and desmoltification may occur (McCullough et al. 2001). Earlier or later outmigration may lead to stresses in the estuarine and ocean environment. For instance, earlier outmigrants may be too small, and thus susceptible to predation, or may arrive at a time when food resources are scarce. Increased temperatures

during migration may cause local displacements of smolts into the main current, where food is less available and predation risk is increased. Timing of smolt outmigration may be related to the thermal regime during egg incubation; accelerated temperatures during incubation may accelerate growth and result in either earlier outmigration or less successful smoltification (McCullough et al. 2001).

2.3.6. Other Considerations

Materna (2001) discussed interactions between temperature and other stressors affecting salmonids. Effects of such interactions may be synergistic or cumulative (Lee et al. 2012), and depend on acclimation history of fish and duration of exposure. Physical aspects of the aquatic environment affected by temperature include water density and viscosity, depth, discharge, and suspended sediment. For example, low flow conditions allow water to heat quickly; suspended sediment may settle more rapidly at higher temperatures because water is less viscous. Temperature also affects water chemistry. Dissolved oxygen is less soluble at higher temperatures, which can impair fish fitness by reducing availability of dissolved oxygen at the same time as increased metabolism increases oxygen demand. Higher temperatures increase negative effects of pH, water hardness, alkalinity, and ammonia. Toxicity of pollutants (chemical/organic/metal) increases with temperature (Dietrich et al. 2014, Laetz et al. 2014, Sappal et al. 2014).

Ecosystem-wide changes may result from increased temperatures that can negatively affect fish populations. For example, high temperatures may increase algal production, which in turn lowers dissolved oxygen availability. Increased temperatures may also reduce habitat complexity available to fish if they cannot tolerate high temperatures at stream margins. High temperatures can increase stress levels from other factors as well (e.g., angling, migration through reservoirs).

Many studies investigating effects of temperature on salmon have been performed on individual fish in a laboratory setting. Most laboratory studies were conducted on single stressors while holding other factors constant at optimal levels. This does not necessarily translate to viability of populations in natural stream settings, and cannot account for effects of interactions of temperature with other biological or habitat conditions (Poole et al. 2001b). Salmonids in the field may have less time to acclimate than in typical laboratory experiments and may have to pass through multiple areas of thermal stress in conjunction with other stressors. Moreover,

fluctuating temperatures may affect fish response but most studies have evaluated constant temperatures (Cuenco and McCullough 1997).

2.4. Cold Water Refuges

Fish can survive short periods of extreme temperatures, provided there are adequate and well-connected thermal refuges. When water temperature becomes stressful (too warm or too cold), the presence of localized thermal refuges may allow brief respite. Cold water refuges (Torgersen et al. 1999b, Ebersole et al. 2003a) are an important aspect of habitat for salmon during summer and fall. Warm water refuges may be important for overwintering in colder environments like Alaska or at high elevations (Coutant 1999). Cold water refuges may be especially important to fish at the southern limit of their range, those migrating long distances, and those that inhabit marginally suitable habitat (Sauter et al. 2001).

The concept of cold water refuges has featured in the recent national and local news in relation to warm temperatures experienced during the summer of 2015 and to legal action about water quality standards and their bearing on Pacific salmon¹. Existing federal and state regulations necessitate that cold water refuges be a part of the broader definition of what is considered thermally suitable for salmon-bearing streams. For instance, the U.S. Environmental Protection Agency states that inclusion of “cold-water refugia (generally defined as waters that are 2 °C colder than the surrounding water)” are components of natural thermal regimes that should be protected and restored (EPA 2003). The Oregon Department of Environmental Quality more specifically defines cold-water refuges as “those portions of a water body where or times during the diel temperature cycle when the water temperature is at least 2°C colder than the daily maximum temperature of the adjacent well-mixed flow of the water body.” (OAR 340-041-0002 [10]). On 8 August 2013, the US. Environmental Protection Agency (EPA) disapproved the natural conditions criterion contained in Oregon’s water temperature standard². On 4 November 2015, NOAA Fisheries issued a biological opinion stating that the 20 °C criterion would likely jeopardize 8 species of salmon and steelhead protected by the Endangered Species Act and that

¹ http://www.nytimes.com/2015/12/12/us/finding-refuge-for-salmon-cold-water-preferred.html?_r=0;
https://www.washingtonpost.com/national/health-science/as-salmon-vanish-in-the-dry-pacific-northwest-so-does-native-heritage/2015/07/30/2ae9f7a6-2f14-11e5-8f36-18d1d501920d_story.html;
http://www.oregonlive.com/environment/index.ssf/2015/06/more_fish_likely_to_die_as_hig.html

² <http://www.deq.state.or.us/wq/standards/temperature.htm>

the “reasonable and prudent alternative” is to map and protect cold water habitats throughout the Willamette and Columbia rivers available during upstream migration³. The Oregon Department of Environmental Quality and the EPA plan to work together over the next three years to locate, protect and restore zones of cold water habitat for fish in the Columbia and lower Willamette rivers.

Those involved in regulating water temperature standards have found it difficult to interpret how to apply the existing definition of cold water refuge due to the fact that cold water refuges vary over time and space. For the same reason, mapping and protecting cold water refuges is not likely to be straightforward. A definition of what exactly constitutes a refuge will need to be determined, and may differ for different species, across time and among locations (Torgersen et al. 2012). Characterization of cold water refuges, and understanding about how much salmon rely on them in any life stage, requires contextual understanding about geographic location, ecological and environmental conditions, and species. For instance, Torgersen et al. (1999b) found that adult Chinook salmon in the John Day River, Oregon, were spatially associated with thermal refuges in a warmer stream, but less so in a cooler stream.

2.4.1. Refuges Vary in Space and Time

Fish may respond to cold water refuges at a variety of spatial and temporal scales. Salmon have been observed to seek out cool areas along bank margins or areas of localized upwelling (Torgersen et al. 1999b, Ebersole et al. 2003b). A variety of types of fine-scale thermal patches that may be important to fish have been resolved using remote sensing techniques (Monk et al. 2013, Dugdale et al. 2015a, Wawrzyniak et al. 2016). There may also be thermal refuge at depth in larger pools. Use of large patches of cold water such as tributaries and their plumes is well known. For instance, a series of studies using radio-telemetry and archival thermal tags have documented that fish stop and hold in cool tributaries during spawning migrations. Steelhead temporarily held in cooler tributaries for up to several weeks during upstream spawning migrations (Keefer et al. 2009).

Thermal refuges can be variable over time (Dugdale et al. 2013, Ebersole et al. 2015, Wawrzyniak et al. 2016), and salmonids are known to move into and out of different locations in order to take advantage of optimal water temperature at different times (Belchik and Turo 2003,

³ <http://yosemite.epa.gov/opa/admpress.nsf/0/7AC162A9568E994885257EF20077CC15>

Ebersole et al. 2006, Reid 2007, Sutton et al. 2007, Macdonald et al. 2010, Hague et al. 2011, Martins et al. 2011, Brewitt and Danner 2014). For instance, body temperatures of adult fall Chinook salmon migrating up the Columbia River were lower than ambient river temperatures (Keefer and Caudill 2015). Moreover, because fish are mobile, they may be able to capitalize on optimal thermal conditions by swimming small distances throughout the day (Torgersen et al. 2012, Armstrong and Schindler 2013).

2.4.2. Refuge Use During Spawning Migration

The relevance of cold water refuges to salmon depends on what species and life stages are present during potentially stressful summertime conditions. Both adults and smolts migrate over a wide variety of months throughout the Pacific Northwest; timing depends on species, life history, geographical position, and environmental conditions (Quinn 2005). Pacific salmon spawn in the fall, but they often begin upstream migration many months earlier. For instance, the Chinook salmon migrating up the Columbia River pass the lowest dam (Bonneville, rkm 234) in peak numbers during April (spring run) and August-September (fall run)⁴. The majority of sockeye, steelhead, and coho pass in June, July-August, and September-October, respectively. Timing can differ significantly in other Pacific Northwest rivers, and from year to year. Chum and pink salmon (*O. gorbuscha*) also exhibit protracted spawning periods beginning in June and lasting through October, depending on the river. Species that run early need sufficient thermal habitat in tributaries in which to hold in until they are ready to spawn, whereas species that run later must contend with warmer conditions during migration and may rely on cold water habitats as “stepping stone” refuges along the way. Successful migration to the spawning grounds may be directly related to the availability of cold water refuges along the way (Mathes et al. 2010).

Cold water refuge use by adult salmon during spawning migrations is well documented. Summer steelhead migrating up the Columbia River used cold tributaries to a greater extent than did fall Chinook salmon, although refuge use by Chinook dramatically increased at temperatures over 20 °C (Keefer and Caudill 2015). Many Chinook salmon slowed migration and used cold tributaries, but some fish continued migrating through presumably stressful conditions (Gonia et al. 2006). Spring Chinook salmon migrating up the Willamette River rarely exhibited thermoregulation, even at presumably stressful temperatures (Keefer et al. 2015). There is less

⁴ source: www.fpc.org/adultsalmon_home.html

information about whether and under what conditions adults use non-tributary habitats as thermal refuges. Tributary plumes provide stable sources of cool water whereas smaller refuges are only intermittently present and therefore may not be used for thermoregulation (Dugdale et al. 2013, Dugdale et al. 2015b).

Movement among cold water refuges by adults depends on their swimming ability. Adults can swim at speeds of around 0.5-2 km per h (Hanson et al. 2008), at rates of 5-65 km per day (Salinger and Anderson 2006) for distances up to 2000 km (Keefer et al. 2006) during spawning migrations. Using radiotelemetry to track fish during upstream migration of steelhead, Keefer et al. (2004) found that migration rates dropped from around 20-60 km per day during cooler periods (spring, fall) to zero during late summer, when fish instead sought refuge in cooler tributaries. They found that Chinook salmon migrated more rapidly as temperature and date increased, and in low flow years.

2.4.3. Refuge Use During Summer Rearing

Coho, steelhead, and certain races of Chinook salmon spend summers rearing in streams before migrating to sea the following year (as do many non-migratory trout species) whereas juvenile pink and chum salmon generally aren't present in streams during warm summer months. Following emergence, pink and chum salmon head directly toward seawater as smolts in their first spring. Typically, summer rearing occurs in parts of stream networks that have cold enough water such as headwater tributaries or mid-order reaches, rather than in large mainstem reaches (Burnett et al. 2007, Ebersole et al. 2009, Flitcroft et al. 2012). However, many complex life history strategies have evolved to hedge bets given varying environmental conditions; in many species, a portion of the progeny begin emigrating only a few weeks after emerging from redds. These fish move progressively downstream, rearing in mainstem rivers and their associated floodplain habitats, and then in estuaries, before finally heading to sea (Greene and Beechie 2004, Schroeder et al. 2015).

Smaller fish have lower metabolic costs than adults (e.g., the optimal temperature for growth for age-0 Chinook salmon is over 20 °C; Plumb and Moffitt 2015), so it is less likely that juveniles are stressed enough by summer temperatures in order to seek refuge in cooler habitats. In fact, fish may seek out warmer temperatures where growth opportunities are higher (Satterthwaite et al. 2012, Boughton et al. 2015). However, in rivers that have been disturbed by wildfire or have otherwise had drastic alterations to shade or hydrology, summer temperatures

could become stressful (Isaak et al. 2010). Small fish or juveniles could potentially squeeze into small patches of cool water, but at a potential cost to growth, survival, and fitness.

Salmon tend to remain within a home range during non-migratory periods, moving less than 200 m and often less than 50 m as juveniles (Rodriguez 2002, Kanno et al. 2014). Petty et al. (2012) found that juvenile brook and brown trout (*Salmo trutta*) moved farther in mainstem habitat than in tributary habitat in search of sources of cold water. Some studies suggest that fish become less mobile at high temperatures whereas others suggest that fish become more mobile. Juveniles have been observed swimming long distances to access cold water refuges (Dugdale et al. 2015b).

2.4.4. Refuge Use During Smolt Outmigration

Smolts migrate downstream over a wide span of time, and wild fish move downstream over a more protracted period than do hatchery-reared fish (Melnychuk et al. 2010). The majority of yearling Chinook salmon, sockeye (*O. nerka*), steelhead, and coho pass Bonneville Dam by the end of June⁵ and similar outmigration patterns have been observed in the Willamette River, Oregon (Schroeder et al. 2015), Nechako River, British Columbia (Sykes et al. 2009), and elsewhere (Quinn 2005). However, some fish smolt during fall of their first (e.g., subyearling Chinook) or subsequent (yearling Chinook, coho steelhead) years. Less is known about whether smolts use cold habitats during their seaward migration. Archival temperature tags have not been used on juveniles due to their small size. Studies using passive integrated transponder (PIT) tags and coded wire tags have been helpful for understanding when the majority of fish migrate, and movement rates between fixed points. But quantification of refuge use has been scarce.

Movement among cold water refuges by smolts depends on their swimming ability. Smolts swim from less than one to nearly 100 km per day (Aarestrup et al. 2002). Across 49 watersheds in British Columbia Canada, downstream migration by steelhead was slower on average than other salmon, and hatchery fish were slower than wild fish (Melnychuk et al. 2010). Downstream travel time for salmon in the Columbia River tagged between 1998 and 2013 was about 2 to 6 weeks over ~ 235 km⁶; this equates to migration rates of about 6 to 17 km per day

⁵ source: www.fpc.org/smolt_home.html

⁶ source: www.fpc.org/survival/smp_multiyear_survival_query.html

on average. Most movement occurs as fish passively ride the current, periodically hanging out in slower water (Moser et al. 1991, Fångstam 1993).

2.5. Climate Change

2.5.1. Anticipated Changes in the Pacific Northwest

Air temperature has increased and will continue to increase globally (IPCC 2014) and throughout the Pacific Northwest (Mote et al. 2008). Extreme events are also expected to increase in frequency. Regional models suggest that the Pacific Northwest will see warmer drier summers and wetter winters, and in many mid-elevation areas, winter precipitation that previously fell as snow will fall as rain (Dalton et al. 2013, Hamlet et al. 2013, Mote et al. 2013). Correspondingly, snowpack levels will decrease (Klos et al. 2014). Transitional areas may see increased “rain-on-snow” events that cause increased peak flow. Climate change will also influence ocean conditions; see Crozier (2014) for a summary of published expectations.

Water temperature will be influenced by climate change because it is controlled to some extent by atmospheric forcing. Indeed, river temperatures have warmed globally (Webb and Nobilis 1995) as well as in the USA (Kaushal et al. 2010). Kurylyk et al. (2013) found increases in both surface and groundwater temperature in New Brunswick, Canada. Summer flows are projected to decrease across most of the Pacific Northwest due to decreased snowpack storage, reduced summer precipitation, and higher evaporation caused by warmer summer temperatures (Jefferson 2011, Leibowitz et al. 2012, Tohver et al. 2014). Effects are expected to be greatest in rain-dominated and transitional (i.e., rain-on-snow hydrology) basins, mainly because the most arid regions are already very dry. Lower flows will enhance stream warming during summer because of lower water volumes (i.e., reduced thermal inertia). Wu et al. (2012) predicted an increase of 0.55 and 1.68 °C in mean annual stream temperatures for 12 Pacific Northwest rivers by the 2020s and 2080s, respectively.

However, responses of water temperature to climate change will differ with time and location (van Vliet et al. 2011, Durre et al. 2013, Luce et al. 2014). For instance, warming has occurred for Pacific Northwest rivers in some seasons but not others (Isaak et al. 2012, Mayer 2012), and in some streams but not others (Arismendi et al. 2012). Sensitivity of stream temperature to climate change will depend on the level of interaction with subsurface flow pathways (i.e., hyporheic and ground water) (Waibel et al. 2013, Luce et al. 2014), glacier coverage (Fellman et al. 2014), stream size (Kelleher et al. 2012), base flow (Deitchman and

Loheide 2012, Carlson et al. 2015), or a combination of factors. For example, Null et al. (2014) found differences in susceptibility of California rivers to climate-induced warming depending on mean annual flow, runoff and timing of low flows. Chang and Psaris (2013) found differences among river sensitivity depending on distance to the Pacific coast, base flow index, and contributing watershed area. They also found that spatial scale influenced which factors were most influential.

2.5.2. Predicted Impacts to Salmon

Crozier (2014) reviewed the literature between 2010 and 2014 and concluded: “Anthropogenic climate change will likely cause moderate to severe declines in most west coast salmon, especially when interacting factors are incorporated into the analysis (e.g., existing threats to populations, water diversion, accelerated mobilization of contaminants, hypoxia, and invasive species). Salmon will adapt their behavior and possibly physiology, but these responses are unlikely to prevent long-term declines.” Climate change may cause shifts in species distributions, reduced growth and survival, altered phenology, and decreased life history diversity (Jonsson and Jonsson 2009, Crozier and McClure 2015). Increased vulnerability is due in part to altered thermal regimes, and in part to altered hydrologic regimes.

Analyses of the factors correlated with past salmon extinctions in California (Zeug et al. 2011) and Japan (Fukushima et al. 2011) point to changes in flow regimes and rising air temperatures. Vulnerability analyses for extant populations of Pacific salmon have predicted that large portions of species ranges within freshwater environments will become unsuitable in the future (Mantua et al. 2010, Wenger et al. 2011, Ruesch et al. 2012, Isaak and Rieman 2013, Wade et al. 2013). Coupled with other stressors such as acidification (McDonnell et al. 2015) or fire (Falke et al. 2015), habitats could become even more limited. This is true also for the marine environment, where Abdul-Aziz et al. (2011) modeled a contraction of 30-50% of the summer thermal range suitable for chum, pink, coho, sockeye and steelhead and a contraction of ~85% for Chinook salmon by the 2080s.

Risk is expected to increase for salmon across their existing range because thermal and hydrologic conditions will negatively influence growth and survival. For instance, Xu et al. (2010) found a direct link between increased summer temperature and decreased survival in brook trout in Massachusetts. For spring Chinook salmon in Idaho, Crozier and Zabel (2006) identified relationships between survival and water temperature (negative) and flow (positive),

and Crozier et al. (2010) found decreases in growth with increasing water temperature and fish density. Walters et al. (2013) predicted substantial reductions in survival for Chinook salmon in the Lemhi River, Idaho, where climate change effects were exacerbated by high rates of water withdrawal. Growth and survival may be influenced indirectly via effects of climate on competitors (Wenger et al. 2011) or predators (Lawrence et al. 2014).

Changing climate conditions are also likely to affect phenology (timing of life history events or ontogenetic shifts) in salmon. Crozier and Hutchings (2014) reviewed changes in the timing of migration and reproduction, age at maturity, age at juvenile migration, growth, survival and fecundity for a variety of fish. They found that altered timing was primarily associated with changes in temperature. There is already evidence for shifting phenology. For instance, Otero et al. (2014) found that Atlantic salmon smolt timing in 67 rivers has shifted by about 2.5 days earlier per decade. Kovach et al. (2013) examined 5 salmon species representing 14 life histories in Alaska and found that migration events have occurred earlier (1.7 d per decade for the last 3-5 decades) and the duration of migration events has decreased by 1.5 d per decade. In contrast to earlier shifts observed for pink, chum, and coho, they found that sockeye were migrating later. The spawn date for fall Chinook salmon in the Columbia River has shifted to a week later as water has warmed by 2°C since 1950 (Hayes et al. 2014), and steelhead spawning runs have been earlier in the Columbia (Robards and Quinn 2002). Achord et al. (2007) found a significant relationship between earlier smolt migration timing and higher water temperature for spring Chinook salmon in the Snake River, as did Sykes et al. (2009) for Chinook salmon migrating out of the Nechako River, British Columbia.

Migration timing is both genetically and plastically determined (Waples et al. 2009, Reed et al. 2011). Ultimately, the ability of a species to cope with climate change will depend on genetic diversity, phenotypic plasticity, and dispersal ability (Beever et al. 2015, Nicotra et al. 2015). The capacity for Pacific salmon to adapt may already be in their genetic code (Miller et al. 2012). However, selection pressures at different life stages may be in opposite directions and selection pressures may interact with plastic responses. Crozier et al. (2008) proposed the direction of likely shift (earlier or later) for each Pacific salmon life stage (e.g., upstream migration, spawning, egg emergence, downstream migration, and ocean entry) in response to climate change, and whether shifts are plastic or adaptive. Altered timing could lead to mismatches in when fish arrive in a habitat and when resources in that habitat are optimal. For

instance, Gharrett et al. (2013) suggested a tradeoff between earlier migrating adults, which had lower freshwater survival but higher marine survival. Changes are likely to differ by species. For example, Beer and Anderson (2013) predicted that Chinook would spawn later but that steelhead would not. Migration timing can be influenced additionally by non-climatic factors such as dams (Angilletta et al. 2008). Peer and Miller (2014) found interactions in the effect of climate and fishing pressure on altered phenology for striped bass (*Morone saxatilis*). Similarly, size-selective predation (e.g., by killer whales; Ford and Ellis 2006) could also interact with climate to alter phenology. Finally, it is worth noting that a focus on individual life stages may occlude population-level responses to climate change (Healey and Bradford 2011, Pankhurst and Munday 2011).

A species' vulnerability to climate change can be described as the product of its sensitivity to stressful environmental conditions and its likely future exposure to those conditions (Füssel and Klein 2006), as well as its adaptive capacity (Beever et al. 2015, Nicotra et al. 2015). For Pacific salmon, vulnerability to altered thermal regimes caused by climate change is best considered hierarchically. At the broadest level, this entails identifying the places and times that salmon are likely to be most limited by altered thermal regimes (and to other changes such as altered hydrology). This step should help to clarify which regions may become unsuitable in the future versus which regions may still be suitable under certain conditions (Isaak and Rieman 2013, Isaak et al. 2015). Then, for those areas, analyses are needed that can help elucidate whether variation in water temperature over space or time might allow salmon to persist, keeping in mind that they may be capable of adapting to physical challenges (Crozier et al. 2008) if the pace of change is not too rapid (Loarie et al. 2009, Schloss et al. 2012).

2.5.3. Climate-ready Conservation Planning

Although our awareness about potential impacts of climate change is growing, climate change has been a relatively low priority in the design and implementation of conservation plans (Ellenwood et al. 2012). Lawler et al. (2010) recommended the following strategies for making populations more resilient to climate change: 1) develop adaptive management plans with prescribed alternative strategies; 2) implement actions to remove other threats to populations, such as removing non-indigenous species and maintaining habitat connectedness and availability; and 3) conduct extensive monitoring of climate conditions and a population's response to climate. Adelman et al. (2012) provide guidance on planning for multiple aspects of

climate change in Washington State. With respect to conservation of salmon and other wildlife, they recommend adaptation strategies that include conservation of habitat and protection of connectivity among critical habitats to allow species to move in response to climate change. Keppel et al. (2015) developed a general framework for quantifying the capacity of potential climate refugia and for prioritizing them.

Concern over climate change has resulted in its explicit inclusion in recent recovery planning for salmon in the Columbia River basin (see Biological Opinions, the 2009 Adaptive Management Implementation Plan, and Climate Change Excerpts, available here: http://www.westcoast.fisheries.noaa.gov/fish_passage/fcrps_opinion/federal_columbia_river_power_system.html). In California, Katz et al. (2013) incorporated climate change into status assessments for all salmonids, and Zeug et al. (2012) used a life cycle model to evaluate the certainty of obtaining results from various management/conservation options for Sacramento River Chinook, given the likely effects of climate change.

Habitat restoration has been a prominent approach for recovery of endangered species (Haines et al. 2006, Prather et al. 2008). Approximately \$1 billion was spent annually on river restoration in the United States between 1990 and 2003 (Bernhardt et al. 2005), and Roni et al. (2008) estimated that hundreds of millions of dollars are spent annually on habitat restoration for Pacific salmon. Given observed and expected changes to stream thermal regimes, effective conservation of thermally suitable habitat for coldwater species like salmonids will require managers to consider whether existing or planned restoration actions will be effective under future climate scenarios. For instance, Cristea and Burges (2010) found that warming will likely offset gains provided by improved riparian vegetation (and the shade it provides). Whereas, Sun et al. (2015) suggested that restoration of riparian vegetation could have a bigger effect than warming in a small urban watershed. Battin et al. (2007) suggested that habitat restoration at lower elevations in the Snohomish River basin would be most effective because these are areas least likely to be altered by climate change.

Beechie et al. (2010) and Beechie et al. (2012) promoted strategies that would recover or preserve natural processes that create thermally diverse habitats. Torgersen et al. (2012) suggested that restoration of cold water refuges needs to consider the myriad factors controlling or influencing them – physical factors, biological interactions, and human effects including climate change. In some locations, active intervention may be required. Kurylyk et al. (2015)

provided some tips for maintaining and constructing thermal refuges. Hatcher and Jones (2013) illustrated that managed releases from dams can have dramatic effects on stream thermal regimes. Based on this principle, Danner et al. (2012) and Pike et al. (2013) developed a model to provide real-time information about how much water needs to be released in order to meet the thermal requirements of salmon downstream during critical periods. Maintaining discharge in streams during low flow periods can reduce water temperature locally (Kurylyk et al. 2013). This can be accomplished by decreasing water withdrawals during critical periods, and by improving hydrological connections vertically to subsurface flow pathways and laterally to floodplains.

Another common stop-gap measure used in salmon recovery has been propagation of hatchery-reared fish. Hanson and Peterson (2014) cautioned that there may be a shortage of sufficiently cool water available to hatcheries in the future. There are also concerns about hatchery influence on wild fish fitness, including that selection pressures in hatcheries may be in opposite directions as those from climate change (Buhle et al. 2009, Ford et al. 2015).

Provision of thermal habitats necessary for salmon into the future will entail: (1) identifying and monitoring existing cold water patches; (2) protecting, restoring, or creating cold water patches deemed important for fish; and (3) protecting or restoring watershed processes that promote thermal diversity. Monitoring environmental conditions responsive to climate change, such as water temperature and flow, species demographics, and other indicators of species responses through time will continue to be important (Levin and Schwing 2011). It is only with long-term data that trends begin to emerge, and with sufficient monitoring, we can begin to understand the consequences of past actions. If we could identify characteristics of watersheds in which fish are less susceptible to anthropogenic and climate effects, we would be better able to assess long-term viability risk, and to identify priority areas for conservation or restoration.

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Table 2.1. Potential covariates of stream temperature.

Driver	Example	Common covariates
Climate	Radiation (e.g., solar, atmospheric, longwave)	Air temperature, Aspect, Riparian cover, Upstream insolation
	Precipitation	Rainfall, Snowfall
Watershed characteristics	Topography	Elevation, Glacial extent, Network position
	Geology (aquifer)	Impervious vs. Alluvial
	Geomorphology	Gradient, Channel type, Sinuosity, Depth
	Hydrology	Discharge, Base flow, Drainage area
	Vegetation	Riparian (cover, community)
Anthropogenic alterations	Development	Land use, Water withdrawal (irrigation)
	Hydropower	Dams
	Climate change	Air temperature, Precipitation

Table 2.2. Potential drivers of cold water refuges.

Driver	Example	Potential covariates	Effect scale
Surface water input	Tributaries, side channels	Network topology, Drainage density, Characteristics (e.g., size, elevation) of channel relative to mainstem	Localized
	Dams, outflows	Discharge or temperature at point	
Subsurface pathways	Alluvial floodplains	Valley width to bankfull width ratio	Distributed
	Bounded valleys	Channel confinement	Localized
Groundwater input	Head differential	Channel gradient	Localized
	Permeable aquifer	Alluvial geology types	Distributed
Shading	Vegetation	Riparian (cover, community)	Both
	Topography	Aspect, Sinuosity; Depth; Channel incision; Stream wall steepness	Both
	Substrate	Channel gradient; Geology type	Distributed

Table 2.3. Generalized summary of thermal conditions required by anadromous salmonids, representative not of rigid criteria but of temperatures beyond which deleterious effects are more likely to occur; adapted from Poole et al. (2001b).

Consideration	Temperature Requirements
Temperature of common summer habitat use	10-17 °C
Lethal temperatures (one week exposure)	Adults: >21-22 °C Juveniles: >23-24 °C
Adult migration	Blocked: >21-22 °C
Swimming speed	Reduced: >20 °C Optimal: 15-19 °C
Gamete viability during holding	Reduced: >13-16 °C
Disease rates	Severe: >18-20 °C Elevated: 14-17 °C Minimized <12-13 °C
Spawning	Initiated: 7-14 °C
Egg incubation	Optimal: 6-10 °C
Optimal growth	Unlimited food: 13-19 °C Limited food: 10-16 °C
Smoltification	Suppressed: >11-15 °C

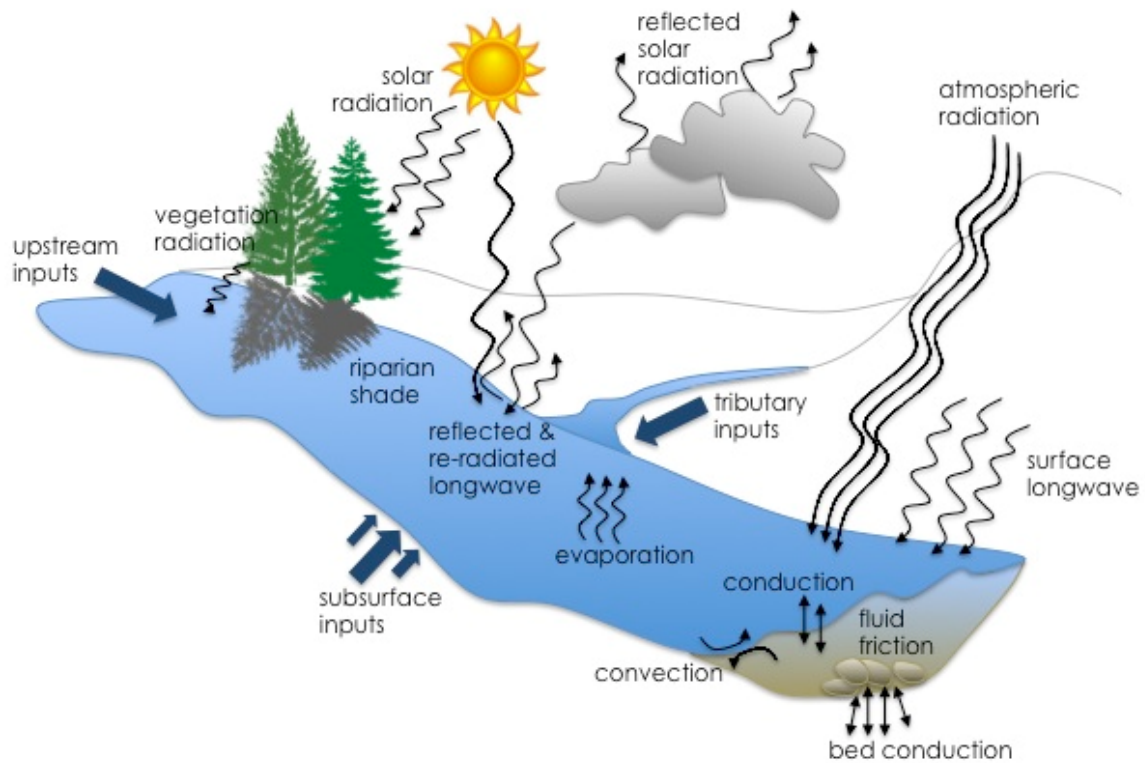


Figure 2.1. Energy balance inputs and outputs as controls on stream temperature. Adapted from Figure 2 in Tague et al. (2007).

Chapter 3. Rethinking the longitudinal stream temperature paradigm

Published as:

Fullerton, A.H., C.E. Torgersen, J.J. Lawler, R.N. Faux, E.A. Steel, T.J. Beechie, J.L. Ebersole, and S.G. Leibowitz. 2015. Rethinking the longitudinal stream temperature paradigm: region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. *Hydrological Processes* **29**: 4719-4737. DOI: 10.1002/hyp.10506.

3.1. Abstract

Prevailing theory suggests that stream temperature warms asymptotically in a downstream direction, beginning at the temperature of the source in the headwaters and leveling off downstream as it converges to match meteorological conditions. However, there have been few empirical examples of longitudinal patterns of temperature in large rivers due to a paucity of data. We constructed longitudinal thermal profiles (temperature versus distance) for 53 rivers in the Pacific Northwest (USA) using an extensive dataset of remotely sensed summertime river temperatures and classified each profile into one of five patterns of downstream warming: *asymptotic* (increasing then flattening), *linear* (increasing steadily), *uniform* (not changing), *parabolic* (increasing then decreasing), or *complex* (not fitting other classes). We evaluated (1) how frequently profiles warmed asymptotically downstream as expected, and (2) whether relationships between river temperature and common hydroclimatic variables differed by profile class. We found considerable diversity in profile shape, with 47% of rivers warming asymptotically, and 53% having alternative profile shapes. Water temperature did not warm substantially over the course of the river for coastal *parabolic* and *uniform* profiles, and for some *linear* and *complex* profiles. Profile classes showed no clear geographical trends. The degree of correlation between river temperature and hydroclimatic variables differed among profile classes, but there was overlap among classes. Water temperature in rivers with *asymptotic* or *parabolic* profiles was positively correlated with August air temperature, tributary temperature and velocity, and negatively correlated with elevation, August precipitation, gradient, and distance upstream. Conversely, associations were less apparent in rivers with *linear*, *uniform*, or *complex* profiles. Factors contributing to the unique shape of *parabolic* profiles differed for coastal and inland rivers, where downstream cooling was influenced locally by climate or cool water inputs, respectively. Potential drivers of shape for *complex* profiles were specific to each river. These thermal patterns indicate diverse thermal habitats that may promote resilience of

aquatic biota to climate change. Without this spatial context, climate change models may incorrectly estimate loss of thermally suitable habitat.

3.2. Introduction

Temperature drives vital rates in aquatic biota and is a key determinant of ecological processes that control population and community structure in aquatic ecosystems (Allan and Castillo 2007, Webb et al. 2008). Substantial effort has focused on understanding temporal patterns in water temperature across hours, days, months, and years (Webb and Nobilis 1995, Steel and Lange 2007, Arismendi et al. 2013), and recent research has underscored the biological significance of altered timing in riverine thermal regimes (Crozier et al. 2008, Isaak et al. 2012, Steel et al. 2012). Spatial patterns in water temperature are also paramount to aquatic biota. For example, water temperature partly defines species distributions within and across river basins (Arscott et al. 2001, Buisson et al. 2008). At finer spatial scales (e.g., reaches of 1-10 km), water temperature can influence connectivity between reaches used during different life stages such as foraging and breeding (Tonolla et al. 2010, Armstrong et al. 2013).

There has been little evaluation of longitudinal spatial patterns in water temperature in large rivers. Therefore our understanding of thermal profiles and potential drivers remains incomplete. Prevailing theory dictates that stream temperature warms asymptotically in a downstream direction, beginning at the temperature of the source (e.g., groundwater or snowmelt) in the headwaters and leveling off downstream as it converges to an equilibrium determined by meteorological conditions (Vannote et al. 1980, Theurer et al. 1985, Ward 1985, Bogan et al. 2003). In downstream reaches, higher water volume increases thermal inertia, reducing the likelihood of rapid change in water temperature. It is now widely recognized that temperature can exhibit a high degree of variability between headwaters and the mouth (Poole et al. 2001a, Poole 2002, Brown and Hannah 2008). However, the literature reveals that asymptotic warming is still generally the operating conceptual paradigm for longitudinal stream temperature patterns (Caissie 2006, but see Dent et al. 2008). Increasingly, large datasets are available that include water temperature compiled from point locations in many tributaries throughout and across watersheds (e.g., Isaak et al. 2013). These data should improve our understanding about spatial patterns of water temperature, especially in wadeable streams where most empirical data are collected. Nevertheless, the degree of thermal complexity within and across large rivers remains unknown. Moreover, there have been few empirical studies examining the factors that

drive these patterns (Deitchman and Loheide 2012, Monk et al. 2013, Dugdale et al. 2015). Conceivably, climate is the dominant driver of temperature in some rivers, whereas landscape features such as terrain, geomorphology, and vegetation are more important in others. Evaluation of these concepts will directly influence our understanding of anthropogenic impacts such as climate change on spatial patterns in river temperature.

In this paper, we use spatially continuous water temperature data from remote sensing to explore longitudinal patterns in synoptic summertime water temperature for 53 rivers throughout the Pacific Northwest (USA). Our objectives were to (1) classify river temperature profiles based on their shape and determine what proportion of profiles conform to the theoretical expectation of asymptotic downstream warming, and (2) evaluate whether relationships between river temperature and hydroclimatic variables differ by profile class. This work provides a spatial context for understanding long-term stream temperature predictions, which are instrumental to conservation planning.

3.3. Methods

3.3.1. Study Area

We considered a sample of watersheds across Washington, Oregon, Idaho, and northern California (USA). Precipitation in the region occurs predominantly from October to March and falls as snow or rain, depending mainly on elevation and proximity to the Pacific Ocean. Snowmelt contributes significantly to stream flow from April to September in snowmelt-dominated and transitional watersheds (Hamlet 2010). Human population density in the study watersheds ranges from low (e.g., roadless areas in Idaho) to high (e.g., near major cities). Human influences on processes controlling hydrology and temperature include large hydropower facilities, water diversion for irrigation, forest management, and altered riparian vegetation associated with agriculture and urban development.

3.3.2. Water Temperature Data

River temperature surveys were conducted using airborne thermal infrared (TIR) remote sensing (Torgersen et al. 2001, Madej et al. 2006, Handcock et al. 2012, Monk et al. 2013). Thermal images measuring radiant temperature of surface water were acquired while flying directly over the river. The majority of surveys were conducted by Watershed Sciences Inc., Corvallis, OR (USA), using the approach described in Torgersen et al. (2001) and Monk et al.

(2013). Different TIR sensors were used depending on the technology available at the time of the survey, but the sensor systems had comparable performance characteristics. All were similar in terms of wavelength range (8-12 μ m), radiometric calibration, and sensitivity. Earlier surveys (before 2001) used scanned arrays whereas later surveys (2001 and after) used focal plane array sensors. Surveys in the Salmon and Clearwater rivers in Idaho were conducted by IRZ Consulting, Hermiston, OR (USA), using similar methods and a focal plane array sensor (ID DEQ 2000, 2001). All surveys occurred during the afternoon in July or August between 1994 and 2007, when water temperatures were expected to be near the daily and annual maximum and likely to be most limiting to aquatic biota (see **Table 3.1** for specific dates). Instream thermal sensors were used to ground-truth remotely sensed temperatures; mean (\pm standard deviation) accuracy was 0.44 ± 0.37 °C (**Table 3.1**). Thermal image data were georeferenced and water temperatures were subsampled from images at approximately 150- to 200-m intervals along the thalweg of each river. We created longitudinal profiles for each river using plots of water temperature versus distance from the downstream end of the survey.

To maximize the extent of river available for characterizing the longitudinal thermal profile from headwaters to mouth, we combined adjacent surveys to construct profiles. For 14 profiles, we combined adjacent surveys conducted on the same day (see **Table S 3.1**). Separate surveys in upstream and downstream sections were flown continuously (i.e., without stopping) on the same day for 8 profiles. For the remaining 6 profiles, surveys were separated by ≤ 1 h (5 surveys) and 2.5 h (1 survey). Differences in water temperature at the junction between upstream and downstream sections were only visible for 2 of 14 profiles and both of these discrepancies were attributable to tributary confluence effects. For another 14 profiles, we combined adjacent surveys that were flown at similar times but on separate days (see **Table S 3.2**). Weather conditions were alike on days during which combined surveys occurred. Seven of these profiles exhibited differences in water temperature at the junctions between surveys; these differences were due to tributary confluences in 5 cases. Two profiles had unexplained discrepancies at junctions between surveys but these differences did not influence our interpretation of the shapes of the profiles.

Flight duration and direction may influence the interpretation of the shape of longitudinal thermal profiles because daily maximums are typically reached earlier in upstream reaches (downstream reaches warm more slowly due to thermal inertia of larger volumes). For example,

Torgersen et al. (2001) found that temperatures increased at a maximum rate of about 1°C h^{-1} in upper reaches and at slower rates in lower reaches. Therefore, the potential for misclassification increases with survey duration. In our study, combined flight time averaged 1.6 h for profiles constructed from surveys conducted on the same day and 3.0 h for surveys conducted on separate days. The combined flight time for profiles constructed from multi-day surveys tended to be longer overall, but surveys were conducted during the same window of time each day; individual surveys on a given day averaged 1.45 h. Changes in water temperature over the course of each survey measured with instream sensors were typically 0.5°C but were as high as 2°C in one survey. Although most surveys proceeded in an upstream direction, 14 profiles were flown at least partly in a downstream direction; 9 of these profiles were combined surveys (**Table 3.1**). If flight direction biased our interpretation of longitudinal profile shapes (see **Table S 3.3**), it was in the same direction for most surveys. Bias is likely to be greatest for profiles surveyed in a downstream direction and in small rivers. Our profiles that were surveyed in a downstream direction occurred in rivers with a mean stream order of 4.8 ± 0.9 ; the longitudinal thermal profiles for two rivers with stream orders <4 had strong shapes unlikely to have been influenced by flight direction.

To be included in our analysis, a profile dataset had to meet the following criteria: (1) total surveyed length of the river was at least 50 km; (2) surveyed length was no less than 50% of total river length, measured from the mouth (the ocean or confluence with a larger river) to the top of the uppermost second-order reach in a 1:100,000-scale digitized stream network (NHDPlusV2; McKay et al. 2012); (3) the profile spanned at least two Strahler stream orders; and (4) the midpoint of the profile was located within the middle one-third of the river. These criteria ensured that we had sufficient longitudinal data to describe temperature profiles and to make comparisons among rivers. Using these criteria, we retained 58 profiles in 53 rivers from an initial population of nearly 500 surveys (see **Figure S 3.1**).

Surveys were conducted twice over approximately the same extent in 4 rivers: the Applegate (1998, 1999), Middle Fork John Day (1998, 2003), Sprague (1999, 2007) and Walla Walla (2000, 2003). Surveys covered overlapping but different reaches in the Scott River (2003, 2006). Longitudinal profiles from repeat surveys demonstrate consistent spatial patterns among years (**Figure 3.1**).

Contemporaneous discharge data was available for 44 profiles and enabled us to identify profiles that may have been influenced by unusual flow conditions (**Table 3.1**) or by dams (**Table 3.2**). For each of these profiles, we used data from all USGS gages located within the same spatial extent covered by TIR surveys to compute the average discharge for the month and year in which the TIR survey occurred. We then compared this value to the monthly average (for the same month) from gage data over the period of record for that location. We also evaluated the influence of our selection criteria on our conclusions by examining whether the relative proportion of rivers in each profile class differed when we relaxed the criteria (see **Table S 3.4** for descriptions of additional profiles that were considered).

3.3.3. Statistical Analysis

Preliminary inspection of thermal profiles suggested five classes of longitudinal pattern (described below, plots and equations in **Figure 3.2**). We hypothesized geographic locations where each pattern was likely to occur and the factors that may drive its configuration. We then evaluated the proportion of empirical profiles that fit these classes, examined their geographic distribution, and compared relationships between river temperature and hydroclimatic and network variables for rivers in each profile class. The five profile classes and their hypothesized characteristics are listed below:

Asymptotic: nonlinear warming from headwaters to the mouth in a saturating pattern. Originates at high elevations and moves downstream into arid flatlands where water is exposed to solar radiation with few opportunities for cooling by riparian shading or groundwater. We hypothesized that this type is likely to occur in areas of the Columbia Plateau (Theurer et al. 1985, Ward 1985, Caissie 2006, Allen 2008).

Linear: constant warming from headwaters to the mouth. Originates at high elevations and progresses downstream over steep slopes with few discontinuities in the heat budget (e.g., having numerous small but few large groundwater or tributary inputs, and gradual changes in riparian vegetation). We hypothesized that this type would be likely to occur on the slopes of mountain ranges such as the western Cascade Range in Oregon (USA) (Torgersen et al. 1999a, Tague et al. 2007, Tague et al. 2008).

Parabolic: rapid warming from headwaters to a maximum, and then cooling again downstream. Originates at high elevations, transitions through wide alluvial valleys with increased exposure to solar radiation, then flows through a zone of cooling downstream. Cooling

may be caused by local climate (e.g., coastal fog), influx of groundwater, impermeable geology and steep topography, or a combination of the above factors. Examples found along the Pacific coast (Madej et al. 2006).

Uniform: temperature remains constant with distance. Streams flow through relatively homogenous terrain (i.e., with similar geology and little change in elevation) with shading or groundwater inputs that prevent warming. We hypothesized that this type was likely to occur in flat portions of the Interior Columbia basin (Allan and Castillo 2007).

Complex: profiles with multiple discontinuities (increasing and/or decreasing). Discontinuities may be caused by stream topology (i.e., position and layout of tributaries in the stream network), geomorphology, interaction with groundwater, or other local controls (natural or anthropogenic, such as the presence of dams). We hypothesized that this type would be likely to occur in topographically complex areas (ODEQ et al. 2001, Kiffney et al. 2006).

3.3.3.1. Model Selection

We classified each empirical profile as *asymptotic*, *linear*, *parabolic*, or *uniform*. If none of these models was appropriate, the profile was considered *complex*.

We used generalized least squares regression (Pinheiro and Bates 2000) to fit each of four model forms to each river temperature profile (see **Figure 3.2** for equations). Water temperatures within a river were always highly spatially autocorrelated ($\Phi \sim 0.8$ to 0.99), with temperature at one location being dependent on temperature just upstream. Inspection of autocorrelation and partial autocorrelation functions suggested that a first-order autoregressive error process was appropriate, so we included this error structure when fitting models. Analyses were conducted in R (R Development Core Team 2015) using the *gls* and *gnls* functions with a *corAR1* error structure (Pinheiro et al. 2014). We used the following constraints when fitting each model: (1) a *linear* model had a negative slope, cooler in headwaters than near the mouth ($m < 0$); (2) a *parabolic* model was convex with a maximum not located at the river mouth ($a < 0$, $b > 0$); (3) an *asymptotic* model increased rapidly near the headwaters and then gradually toward the mouth ($a < 0$, $m > 0$); (4) a *uniform* model was an intercept-only model with a slope of 0. If the conditions for a thermal profile were violated, that model was discarded from that profile's candidate set. The best model among the remaining candidate models was the one having the greatest Akaike weight (Burnham and Anderson 2002). To be conservative, we chose *parabolic* only when its

ΔAIC was >10 units better than any other model, which placed a greater burden of proof on finding this unusual pattern.

We evaluated whether the best model fit the data using four metrics: (1) root mean squared error (RMSE; Eq. 3.1), (2) the Nash-Sutcliffe model efficiency coefficient (NSC; Nash and Sutcliffe 1970; Eq. 3.2), (3) p-values from a Glejser test for heteroscedasticity (Glejser 1969), and (4) the difference between RMSE for the best model and RMSE for a smoothed model (20-knot general additive model; GAM). The fourth metric represented spatial structure not captured by the trend in the best model. The first two metrics were computed respectively as:

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^N (F_i - O_i)^2} \quad [\text{Eq. 3.1}]$$

$$NSC = 1 - \frac{\sum_{i=1}^N (F_i - O_i)^2}{\sum_{i=1}^N (O_i - \bar{O})^2} \quad [\text{Eq. 3.2}]$$

where O_i is observed temperature at point i of the survey, F_i is fitted temperature from the best model, and N is the number of observations along the length of the profile.

We used a point system to decide whether to classify a profile as *complex*. We assigned points ranging from 1 (a good fit) to 4 (a poor fit) to each of the 4 metrics. Scores corresponded to quartiles for each metric computed across the set of profiles. We summed the 4 scores to get a total score ranging between 4 and 16. Profiles having scores of 10 or lower (i.e., having adequate fits) retained their classification as *asymptotic*, *linear*, *parabolic*, or *uniform*, while those having scores of 14 or more (i.e., failing most diagnostics) were classified as *complex*. Profiles with scores between 11 and 13 and profiles with scores <11 but having $\Delta AIC < 2$ better than the second best model retained their original classification, but we highlighted them as profiles for which classification was less certain. We inspected four types of diagnostic plots to evaluate the scores: (1) observed versus expected values, (2) residuals from the best model, (3) residuals from the smoothed model, and (4) fitted values from a 5-knot GAM compared to those from the best model.

Additionally, we compared profile shapes selected quantitatively (as described above) with qualitative visual assignments. Four of the authors (not including the lead author) each

assigned a shape, a level of confidence in their assessment, and potential alternative shapes to each profile; this was a blind process, i.e., authors did not know the names of the rivers they were assessing. We used the majority class from the qualitative assessments for each profile to evaluate robustness of the quantitative classification.

3.3.3.2. Associations with Hydroclimatic and Network Variables

We evaluated whether relationships between river temperature and hydroclimatic variables (described below) differed among profile classes. For each thermal profile, we evaluated correlations between water temperature and hydroclimatic variables discretized at 1-km intervals along the length of the profile after accounting for spatial autocorrelation. First, we binned mean values of both river temperature and hydroclimatic variables (described below) at 1-km intervals to ensure that water temperature and hydroclimatic variables were spatially matched at the same resolution along the length of each river (Welty 2015, Welty et al. 2015). Then, for each profile, we computed the partial correlation coefficient between water temperature and each hydroclimatic variable. Partial correlation coefficients were computed as the correlation between (1) the residuals of a linear model between river temperature and distance upstream and (2) the residuals of a linear model between a given hydroclimatic variable and distance upstream. The goal of this approach was to examine relationships between river temperature and hydroclimatic variables after we had accounted for their mutual correlation with space (Legendre 1993). We also computed the correlation coefficient between river temperature and distance upstream.

We considered variables that are frequently used in predictive models of water temperature and in response to climate change impacts: mean August air temperature ($^{\circ}\text{C}$), mean August precipitation (mm), elevation (m), discharge (m^3s^{-1}), velocity (ms^{-1}), stream gradient (%), and water temperature in tributaries ($^{\circ}\text{C}$). Data for the first 6 explanatory variables came from attributes of 1:100,000-scale stream reaches in NHDPlusV2 (McKay et al. 2012), which is a geospatial framework of surface-water data products based partly on the U.S. National Hydrography Dataset (see **Table S 3.5**). The NHDPlusV2 is a geographic information system (GIS) dataset comprising estimates of elevation, gradient, air temperature, precipitation, discharge and stream velocity for all reaches within rivers of the United States. Elevation, gradient and velocity were derived from a 10-m digital elevation model. Air temperature and precipitation estimates were derived from the PRISM model (www.prismclimate.org). Discharge

and velocity were calculated using the enhanced runoff method (EROM), and values were adjusted to gages at the bottom of each reach (McKay et al. 2012). Tributary temperatures were sampled at the confluence of the tributary with the main river from TIR imagery.

We used partial correlation coefficients as inputs to a principal components analysis (PCA) to visualize groups of profile classes in relation to hydroclimatic variables. Using partial correlation coefficients in the PCA, as opposed to aggregate metrics summarized across all reaches in a profile, allowed us to examine the spatial relationship between hydroclimatic variables and river temperature over the profile length. We expected that profiles of the same class would be clustered in the PCA if river temperature was spatially correlated with the same suite of hydroclimatic variables as other profiles in that class.

We also evaluated relationships between profile classes and 3 network variables: (1) significant confluence density, where significant confluences were defined as tributary confluences contributing more than 10% of mainstem flow, (2) stream density, or length of streams per catchment area, and (3) basin shape, defined as the drainage area divided by the square of the mainstem length. We anticipated that *complex* thermal profiles would be associated with streams having larger values of significant confluence density, stream density and basin shape (Benda et al. 2004).

3.4. Results

3.4.1. Profile Classification

We classified 27 longitudinal thermal profiles as *asymptotic*, 9 as *linear*, 8 as *parabolic*, 4 as *uniform*, and 10 as *complex* (**Figure 3.3**; also see **Figure S 3.2**). For 25 thermal profiles, classification was not definitive (**Table 3.3**). In 2 of these cases, the *asymptotic* model did not converge. For these rivers (John Day and NF John Day), the fit of the next best model (*linear*) was relatively poor (goodness of fit scores of 16 and 12, respectively), so we used the qualitative assignment of *asymptotic* assessed visually by the coauthors. In three other cases (Grande Ronde River, Whychus Creek and Williamson River), the best models selected were *linear*, *linear* and *uniform*, respectively. However, we assigned these profiles as *complex* because quantitative fits were relatively poor (goodness of fit scores of 13, 12, and 11 points, respectively, and Δ AIC of <1 between best and second best models). Moreover, qualitative assessments by the coauthors were unanimous in classifying these profiles as *complex*. We list the best and second choices in **Table 3.1**. For profiles classified as *complex*, we list the best quantitative assignment as the

second choice. Distributions of profiles among classes based on the second choice were similar to ‘best’ choices; the most notable difference was that there were more *linear* and *complex* profiles and fewer profiles in the other classes (see **Table S 3.6**). The shapes of the profiles were consistent from year to year for rivers that had been surveyed multiple times: Applegate, Middle Fork John Day, Sprague, and Walla Walla rivers (**Figure 3.1**; **Table 3.1**).

Qualitative assessments were consistent with the quantitative approach for 41 profiles (71%). Disagreement between the qualitative and quantitative approaches occurred among all five classes. Using the majority class visually assessed by 4 coauthors, profiles assigned as *asymptotic* by the quantitative method were described as *linear* (5 cases), *uniform* (2 cases), or *complex* (2 cases) by the visual assessments; *linear* profiles were described as *uniform* (1 case) or *complex* (2 cases) by the visual assessments; 1 *uniform* profile was described as *complex*; and 1 *complex* profile was described as *asymptotic* by the visual assessments. For profiles classified as *parabolic* by the quantitative approach, 4 were classified as *asymptotic* by visual assessments: Eightmile Creek, Fifteenmile Creek, and Walla Walla River in both 2000 and 2003. These 3 rivers are inland tributaries to the Columbia River, whereas the other 4, upon which both qualitative and quantitative classification agreed were truly *parabolic* shapes, flowed directly to the Pacific Ocean. We treated these cases separately in subsequent analyses and address these points in the discussion.

Contrary to our expectations, the spatial distribution of profile classes did not suggest any clear geographical patterns (**Figure 3.4**). One exception is that the 4 profiles classified as *parabolic* by both quantitative and qualitative methods were located on the Pacific coast.

3.4.1.1. Influence of Discharge, Dams, and Flight Direction

Profile shape may have been influenced by flow conditions during the survey year (**Table 3.1**). In 10 cases, rivers were surveyed during years in which discharge was substantially higher than average (i.e., above the 75th percentile over the period of record for that location); 8 surveys occurred during low-discharge years (i.e., below the 25th percentile). However, the distribution of profile shapes was similar for high and low flow years, with 6 and 5 *asymptotic*, 4 and 3 *linear*, 1 and 0 *parabolic*, 0 and 1 *uniform*, and 1 and 0 *complex*, respectively. Conditions differed between years for repeat surveys in the Middle Fork John Day and Sprague rivers; discharge was high in only the first year for the former and low in only the second year for the latter. Discharge

was high in both years for the Applegate River, and normal in both years for the Walla Walla River. Profile classification was consistent between years for all repeat surveys.

Our ability to distinguish profile shape may also have been influenced by dams (**Table 3.2**). It is possible that dams located in the upper reaches of surveys (5 cases) may have influenced upstream thermal conditions (*sensu* Ward and Stanford 1983). However, it is unlikely that the *asymptotic* shape of the Rogue River would change in the absence of the dam because there was a strong downstream warming trend for >150 km. The Applegate River, Cow Creek, and Russian River also likely would remain *asymptotic* in the absence of a dam upstream; however, downstream warming trends were less pronounced in these rivers so it is possible that their profiles would be *linear* if the effect of the dams was to cool the upper reaches of the profile (i.e., downstream from dams). The Shasta River, classified as *linear*, could possibly be *asymptotic* if the effect of the dam was to moderate temperatures in upper reaches. Two of the profiles classified as complex showed potential dam influences in the middle of the profile. The large decrease in water temperature in a downstream direction in the Tualatin River was due to inputs of cold water from Scoggins Creek, which originated as bottom releases from Scoggins Dam. The Tualatin River profile may otherwise have been *asymptotic* or *linear*. The Crooked River was also strongly influenced by Arthur R. Bowman Dam near Prineville, OR (USA), which lowered water temperatures substantially in the middle section of the longitudinal thermal profile. This river would have been classified as *complex* regardless of the dam, due to inputs of large volumes of cooler water via lava tubes and other subsurface pathways.

It is also possible that flight direction influenced classification. For rivers surveyed in an upstream direction, it is possible that true *asymptotic* profiles may have been classified as *linear* or *uniform* if headwaters warmed rapidly (see **Table S 3.3**). Conversely, for rivers surveyed in a downstream direction, true *linear* or *uniform* profiles may have been misclassified as *asymptotic* if headwaters were surveyed before they reached their maximum temperature.

3.4.1.2. Inclusion Filter Criteria

The inclusion criteria that we applied to ensure that the profiles were representative of whole-river patterns were generally similar across profile classes (**Table 3.3**); these inclusion criteria were river length, proportion of river surveyed, survey midpoints, the number of stream orders spanned and the mean stream order. Profiles classified as *uniform* and *linear* tended to be slightly shorter, covered a smaller proportion of the river and fewer stream orders, and had

midpoints downstream compared to other classes. Profiles classified as *parabolic* and *complex* were the longest, had the highest proportion of river surveyed and had the greatest range in stream order. *Asymptotic* profiles had intermediate values for most metrics. Coastal *parabolic* rivers had lower mean stream order than other types. Had we used relaxed criteria, we would have included an additional 10 profiles, with 3 included by removing the stream order criterion and 7 by relaxing the longitudinal position criterion (to allow midpoints centered between 25 and 75% of river length). With these additional profiles, the percent of profiles in each shape class remained within ~2% of original numbers (see **Table S 3.6**).

3.4.2. Associations with Hydroclimatic and Network Variables

3.4.2.1. Hydroclimatic Variables

Correlations between river temperature and hydroclimatic variables differed among profile classes (**Table 3.4**). In particular, we noticed high variability across classes in the correlation between water temperature and August air temperature after accounting for correlation with distance upstream (see **Table S 3.7**). For rivers classified as *asymptotic* and for inland *parabolic* rivers, water temperature was positively correlated with August air temperature, tributary temperature and velocity, and negatively correlated with elevation, August precipitation, gradient, and distance upstream (**Table 3.4**). Partial correlation coefficients for coastal *parabolic* profiles were smaller but in the same direction as coefficients for inland *parabolic* profiles for elevation, mean August Air temperature, mean August precipitation, gradient, and tributary temperature. Coastal profiles had a more negative coefficient for discharge, whereas inland profiles had a more negative coefficient for distance upstream. In contrast, for rivers classified as *linear*, *uniform*, or *complex*, partial correlation coefficients were small for most hydroclimatic variables. Water temperature for rivers with *linear* profiles was negatively correlated with distance upstream; this coefficient was larger than coefficients for hydroclimatic variables. Water temperature was more strongly correlated with tributary temperature for rivers with inland *parabolic*, *complex*, and *uniform* profiles than for other profile shapes. Water temperature was negatively correlated with distance upstream for *asymptotic*, *linear*, and inland *parabolic* profiles but poorly correlated for coastal *parabolic* rivers and rivers classified as *uniform* or *complex*.

Differences among profile classes in relationships between river temperature and hydroclimatic variables were visually apparent when we plotted the profiles on the same scale.

For instance, after accounting for the shared correlation with distance upstream, water temperature was more positively correlated with August air temperature for *asymptotic* and *parabolic* profiles than for *linear*, *uniform*, or *complex* profiles (**Figure 3.5**). **Figure 3.5** also illustrates that many profiles (e.g., coastal *parabolic*, *linear*, *uniform*, *complex*, and even some *asymptotic* profiles were relatively flat over their course. These patterns persisted when we included profiles that met a relaxed set of criteria.

The different profile classes fell into relatively distinct but overlapping domains in multivariate space (**Figure 3.6**). The first and second principal components of the PCA accounted for about 36 and 19% of the variance, respectively; only the first two axes were significant ($p < 0.001$). Profiles in the *uniform* and *linear* classes were most different from the *asymptotic* class along the first axis (PC1); this pattern was evident primarily in the strength of correlations between river temperature and climate variables. Profiles in the *linear* and *asymptotic* classes were most different from the *uniform* and *parabolic* profiles along the second axis (PC2), which indicates gradients in hydrologic variables and distance upstream. The position of rivers in the *parabolic* class depended on regional location. Inland *parabolic* profiles (4 surveys in 3 rivers) overlapped with *asymptotic* profiles, whereas coastal *parabolic* profiles (4 rivers) were intermediate between *asymptotic* and *uniform* classes. Profiles in the *complex* class overlapped with other classes in ordination space, which is consistent with the observed high variance in correlations between water temperature and most variables for *complex* profiles.

3.4.2.2. Network Variables

We did not detect any strong associations between profile classes and network variables (i.e., there was high within-class variability; **Table 3.5**), but profiles that did not exhibit warming in a downstream direction (e.g., coastal *parabolic* and *uniform*) tended to have a higher density of significant confluences. Contrary to expectations, *complex* profiles had the lowest stream density and also had moderate values for the density of significant confluences and basin shape. Coastal *parabolic* profiles were the least compact in shape (i.e., more likely to be rectangular than heart or pear shaped; sensu Benda et al. (2004)), which is consistent with their generally lower stream order.

3.5. Discussion

3.5.1. Rethinking the Downstream Warming Paradigm

River scientists have recognized that the conceptual model of asymptotic stream warming from headwaters to mouth may not apply in all rivers (Moore et al. 2005, Brown and Hannah 2008, Dent et al. 2008). However, the high-resolution spatial data needed to evaluate longitudinal profile patterns in and across large rivers has been lacking until now. Using an extensive, detailed dataset of spatially continuous summertime river temperatures, we found that water temperature did not always warm asymptotically in a downstream direction, as expected. Rather, we found evidence of at least four other profile shapes. Although *complex* and *linear* shapes were expected based on the literature, the *uniform* and *parabolic* shapes were unexpected. Our intent was not to promote our particular profile classification scheme *per se*; rather, we wanted to illustrate that there are rivers that exhibit alternative and sometimes unexpected longitudinal profile shapes. Matching profile classifications from repeat surveys of four rivers suggest that patterns were consistent among years, but additional data are needed to fully assess temporal stability of patterns.

Asymptotic downstream warming represents the foundation of a longitudinal stream temperature typology for many rivers. It is possible that some of the rivers that we classified as *linear* or *uniform* may represent adjacent parts of a larger asymptotic warming pattern if (1) these profile classes were shorter as a proportion of total river length than other classes, (2) *linear* profiles occurred closer to headwaters than other classes, and (3) *uniform* profiles occurred closer to river mouths than other classes. In our analyses, both *linear* and *uniform* rivers were shorter on average and were shorter as a proportion of total river length than other classes (**Table 3.3**). Thus, it is possible that we misclassified some *asymptotic* rivers as (1) *uniform* because the surveys did not include colder headwater stream reaches, or (2) *linear* because the surveys did not extend far enough downstream to detect the asymptote. Rivers classified as *uniform* did tend to occur close to river mouths; however, rivers that were classified as *linear* also occurred near river mouths.

We expected that many rivers would exhibit downstream sections with little or no increases in temperature in a downstream direction based on the asymptotic conceptual model for downstream warming. However, rivers that we classified as *uniform* (e.g., Deschutes [Puget Sound] and Pudding rivers) were surveyed from the headwaters to the mouth. Furthermore,

many of the rivers that we classified as *asymptotic* could have been classified as *linear* or *uniform* because their downstream inflection points were not very pronounced and their rates of warming were minimal (see **Figure S 3.2**). In fact, many of the visual assessments did assign these rivers to *linear* or *uniform* classes (e.g., the Hoh River).

Parabolic or *complex* profile types may indicate an underlying asymptotic downstream warming pattern that is influenced by local factors that disrupt the expected downstream warming trend. We did not find any examples for either shape that could have been caused by surveying an incomplete portion of the river; *parabolic* and *complex* profiles covered 92% and 97% of total river length, respectively, and both shapes were centered within rivers (**Table 3.3**). These patterns were more common than we expected based on the literature. Moreover, we found other examples of rivers that fit alternative patterns of downstream warming when we examined longitudinal profiles of recently published modeled mean August (1993-2011) water temperature from the NorWeST project (Isaak et al. 2013).

Our analysis focused on trends in river temperature at very broad spatial scales (>50 km), but more research is needed to examine longitudinal complexity in stream temperature at finer spatial scales using alternative metrics. For example, Dugdale et al. (2013) quantified thermal complexity in an Atlantic salmon (*Salmo salar*) river using the standard deviation of derivatives of the long profile calculated within a 1-km moving window, and Dent et al. (2008) quantified the length of reaches in coastal Oregon headwater streams that were decreasing, constant, or increasing in temperature. Spatially continuous river-temperature data, such as the TIR dataset used in this study, are becoming more available, as are spatially continuous modeled stream temperature maps that cover broad spatial extents (Isaak et al. 2013, Peterson et al. 2013, Isaak et al. 2014). These datasets are powerful tools that will make it possible to better quantify complex thermal patterns in rivers.

3.5.2. Potential Drivers of Longitudinal Spatial Patterns

Spatial relationships between river temperature and hydroclimatic variables suggest that longitudinal thermal profile shapes are influenced by local and regional conditions. Rivers that originated at higher elevations with higher precipitation and flowed through arid regions tended to be cool in the headwaters and warm rapidly or steadily as the river progressed downstream. In these rivers, the headwaters may be cool due to a combination of snowmelt, relatively greater riparian shading than downstream, and steeper gradient (i.e., less time to equilibrate with air

temperatures). These patterns were associated with *asymptotic*, *linear*, and inland *parabolic* profile types, which also had lower densities of significant confluences than other profile shapes (**Table 3.5**).

Water temperature in rivers that did not warm substantially in a downstream direction (i.e., *uniform*, *complex*, coastal *parabolic*, and some *linear* profiles) was less correlated with many of the hydroclimatic variables that we tested. For rivers exhibiting the *parabolic* pattern, there were at least two potential mechanisms controlling cooling near the mouth: local climate conditions and cold water inputs. In coastal rivers, reduced water temperature occurred in downstream reaches and may be influenced by fog cover (Madej et al. 2006) (**Figure 3.6**). The cooling mechanism for these rivers may be reduced solar radiation reaching the river under heavy fog and an increased contribution of atmospheric moisture to the river (i.e., condensed and trapped in riparian areas; Harr 1982). In contrast, inland rivers had air temperatures that were generally warmer near the river mouth, suggesting that cooling was more likely driven by inputs of cool water from tributaries, surficial aquifers (Arrigoni et al. 2008, van Vliet et al. 2013, Ebersole et al. 2015), or other influences, such as shading from riparian vegetation or evaporative cooling from strong winds (**Figure 3.6**). The relatively constant temperatures in *uniform* and coastal *parabolic* rivers may be moderated by surficial or subsurface inputs of cooler water throughout, as evidenced by higher densities of streams and significant confluences. Rivers with *uniform* or coastal *parabolic* shapes also did not have large changes in elevation over the course of the river.

In rivers with *complex* profile shapes, and in many rivers with other shapes, abrupt changes in temperature were apparent at finer spatial scales that obscured broader patterns. Anomalies within thermal profiles may arise from local conditions that differ across the landscape (Ward and Stanford 1983, Stanford and Ward 2001, Poole 2002). Discontinuities in thermal profiles can be caused by tributaries (Rice et al. 2001, Kiffney et al. 2006, Ebersole et al. 2015) or surface-groundwater exchange (Constantz 1998, Keery et al. 2007), which can contribute a substantial volume of water of a different temperature to the river. Discontinuities also may be due to localized shade produced by riparian vegetation (Beschta 1997, Brosofske et al. 1997) or to topographic characteristics such as aspect or valley confinement (Constantz 1998, Poole 2002). Tributaries and surface-groundwater exchange can decrease water temperatures directly via inputs of cooler water, whereas shade and topography prevent warming over a given

distance by decreasing the duration that water is exposed to solar radiation. Moreover, factors contributing to discontinuities in the longitudinal thermal profile are likely to be different in different parts of the river. Poole and Berman (2001) suggested that riparian shading may be a more important determinant of locally cool conditions in headwaters, whereas surface (and subsurface) inputs may dominate in downstream reaches. Discontinuities also can be caused by human impacts. For example, dams can change downstream thermal conditions depending on how water is released from reservoirs (i.e., surface or bottom releases), as we saw for the Tualatin and Crooked rivers. The Crooked River also was influenced by high-volume subsurface inputs of cool water near the mouth via lava tubes and other subsurface pathways.

Associations between water temperature and hydroclimatic and network variables generally supported our hypotheses about potential drivers of longitudinal river temperature patterns. However, many of our hypotheses were incorrect about where the different types of profiles were likely to occur geographically. With the exception of coastal *parabolic* rivers being located along the Pacific coast, rivers with similar longitudinal profile shapes were not associated with specific physiographic regions and landscape features in the Pacific Northwest.

3.5.3. Implications for Ecology and Conservation

Our results have implications for biological conservation and management of riverine thermal regimes (Hamlet 2010, Kaushal et al. 2010, IPCC et al. 2014), aquatic biota, and ecosystem processes (Ficke et al. 2007, Mantua et al. 2010), which respond to climate change and other anthropogenic impacts. First, our findings illustrate the variety of spatial patterns of summertime thermal habitat present within and among rivers. Cold-water organisms in rivers may be able to use thermal diversity in rivers to survive in a warming climate. Concepts from metapopulation biology (Hanski 1998) and portfolio theory (Schindler et al. 2010) suggest that diverse habitats may promote resilience to disturbance, such as warmer water temperature. Although we did not investigate thermal patterns at finer spatial scales in this paper, the variability in spatial patterns in river temperature that we observed suggest the presence of potential cold-water refuges at multiple spatial scales. Such refuges are used by aquatic organisms in their movement among breeding, foraging and rearing habitats (Schlosser 1995, Torgersen et al. 1999b, Dugdale et al. 2013, Ebersole et al. 2015).

An understanding of locations where local controls such as geomorphology, tributary influence, groundwater exchange points, and riparian vegetation may outweigh climate effects

could provide a sense of a river's "natural" thermal regime (Hill et al. 2013), its sensitivity to change (Luce et al. 2014, Snyder et al. 2015), and its potential for restoration (Ebersole et al. 1997). Such information will be essential for prioritizing conservation actions that provide long-term benefits. Spatially continuous data on stream temperature from remote sensing and modeling provide a context for understanding longitudinal thermal profiles and establishing total maximum daily load (TMDL) thermal requirements to enhance water quality in rivers.

Models predicting the response of water temperature to climate change will need to consider spatial patterns of water temperature and the drivers of riverine thermal regimes. Existing models that assess climate-change effects on river temperatures at broad scales (i.e., large in extent and coarse in resolution) have generally predicted that future river temperatures will exhibit a pattern of asymptotic warming from headwaters to mouth (e.g., Allen 2008) and that water temperature will respond similarly across space to changes in air temperature and stream flow (van Vliet et al. 2011, Mayer 2012, Wu et al. 2012). Our study found that existing river temperature profiles are complex and variable with respect to basic climate variables, suggesting that climate change may affect river temperature differently among rivers.

3.5.4. Conclusions

Until recently, data to characterize spatial patterns in river temperature over broad spatial extents were unavailable. In our analysis of remotely sensed water temperature data, we did not expect to find that many rivers throughout the Pacific Northwest (USA) did not warm asymptotically in a downstream direction. Instead, more than half of the rivers we evaluated exhibited one of several unusual longitudinal profile patterns, and many rivers were too complex to classify with a simple model. Moreover, relationships between water temperature and basic hydroclimatic variables differed among profile classes. Our approach and results may serve as a starting point for classifying longitudinal thermal profiles and assessing potential human impacts on stream temperature patterns at scales of tens of kilometers. Without this spatial context, climate impacts to thermal habitat may be difficult to predict because longitudinal patterns are influenced by myriad local and regional controls that may respond differently to changes in climate.

3.6. Acknowledgements

Individual river temperature surveys and image processing were conducted by R. Faux, Watershed Sciences Inc., except for rivers in the Salmon and Clearwater basins in Idaho, the data

for which were provided by D. Essig of the Idaho Department of Environmental Quality. We are grateful to the many local, state, federal, tribal and nongovernmental organizations that funded the collection of these data for water quality monitoring and assessment. AHF was supported by the Northwest Fisheries Science Center and the NOAA Advanced Studies Program. We thank P.M. Kiffney, N.J. Mantua, S.G. Smith and three anonymous reviewers for helpful discussions and reviews of earlier versions of the manuscript, and B.J. Burke for statistical advice. The information in this document has been subjected to peer and administrative review and is approved for publication by NOAA, USGS, EPA, and USFS. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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Table 3.1. Attributes of remotely sensed profiles of summertime river temperature used in analyses.

Basin/River (Map Reference)	First day of survey	Total length surveyed (km)	Flight duration (h)	Proportion of river surveyed	Strahler stream orders (n)	Distance- weighted mean Strahler order ⁵	Survey midpoint (km from mouth / total km)	TIR Accuracy (mean \pm sd, °C) ⁶	Discharge in survey year (percentile) ⁷	Profile class (second choice)
<i>Bear</i>										
Cub (1)	29 Jul 06	56	1.11	0.94	2	3.6	0.47	0.1 \pm 0.08	0.50	A (C)
<i>Deschutes</i>										
Crooked ¹ (2)	6 Aug 2005 ²	224	2.63	0.88	3	6.0	0.45	0.47 \pm 0.36	0.32	C (P)
Little Deschutes (3)	24 Jul 2001	144	1.80 ³	1.00	4	3.5	0.50	0.43 \pm 0.05	NA	A
Whychus (4)	28 Jul 2000	58	0.90	0.75	4	3.0	0.62	0.36 \pm 0.21	NA	C (L)
<i>John Day</i>										
John Day ¹ (5)	29 Aug 2004 ²	446	6.42 ^{3,4}	1.00	5	5.5	0.50	0.32 \pm 0.2	0.54	A (L)
Middle Fork John Day (6)	5 Aug 1998	74	0.76	0.59	2	4.5	0.62	0.35 \pm 0.51	0.88	L (C)
Middle Fork John Day (7)	16 Aug 2003	76	1.16	0.64	2	4.5	0.61	0.48 \pm 0.12	0.57	L (C)
North Fork John Day (8)	11 Aug 2002	139	2.42 ³	0.79	2	5.6	0.40	0.62 \pm 0.57	0.26	A (L)
South Fork John Day (9)	15 Aug 2003	83	1.41	0.67	3	3.8	0.66	0.38 \pm 0.15	NA	C (L)
<i>Klamath</i>										
Scott ¹ (10)	25 Jul 2003	116	1.64	1.00	4	4.2	0.50	0.31 \pm 0.22	0.65	C (L)
Scott (11)	10 Aug 2006	92	1.28	0.80	2	4.6	0.40	0.11 \pm 0.11	0.46	U (C)
Shasta (12)	26 Jul 2003	65	1.19	0.74	3	4.4	0.37	0.4 \pm 0.32	0.80	L
Sprague ¹ (13)	12 Aug 1999	169	1.50	0.97	4	5.3	0.48	0.49 \pm 0.31	0.50	A
Sprague ¹ (14)	31 Jul 2007 ²	172	2.78 ⁴	0.94	4	5.4	0.47	0.34 \pm 0.39	0.11	A (C)
Williamson (15)	4 Aug 1999	139	1.08	1.00	4	4.4	0.50	0.62 \pm 0.36	0.62	C (U)
<i>Lower Columbia</i>										
Sandy (16)	8 Aug 2001	86	1.21	1.00	4	4.3	0.50	0.38 \pm 0.26	0.26	A (C)
<i>Lower Snake</i>										
Clearwater ¹ (17)	3 Aug 2000	151	1.47 ³	0.57	2	5.4	0.54	2.65 \pm 3.04	0.45	L (C)
Grande Ronde ¹ (18)	19 Aug 1999 ²	273	2.43	0.98	4	5.6	0.49	0.48 \pm 0.19	NA	C (L)
Joseph ¹ (19)	22 Aug 1999	118	1.07	0.96	5	4.3	0.52	0.4 \pm 0.35	NA	C (A)

Basin/River (Map Reference)	First day of survey	Total length surveyed (km)	Flight duration (h)	Proportion of river surveyed	Strahler stream orders (n)	Distance- weighted mean Strahler order ⁵	Survey midpoint (km from mouth / total km)	TIR Accuracy (mean ± sd, °C) ⁶	Discharge in survey year (percentile) ⁷	Profile class (second choice)
Lochsa ¹ (20)	4 Aug 2000 ²	153	1.20	0.80	2	5.4	0.40	1.15±0.83	0.16	L
Minam (21)	21 Aug 1999	73	0.59	0.85	4	3.5	0.57	0.75±0.78	0.77	L
Salmon ¹ (22)	8 Aug 2001 ²	645	5.74 ^{3,4}	0.96	3	6.3	0.48	0.5±	0.02	A (C)
Selway ¹ (23)	4 Aug 2000 ²	153	1.58 ³	0.75	2	5.6	0.37	1.4±0.6	0.15	A (L)
Wallowa (24)	23 Aug 1999	80	0.81	0.78	3	3.9	0.39	0.43±0.5	0.84	L (C)
<i>Middle Columbia</i>										
Eightmile (25)	3 Aug 2002	54	1.38	0.92	3	2.5	0.54	0.58±0.34	NA	P (A)
Fifteenmile (26)	1 Aug 2002	83	1.64	1.00	4	3.6	0.50	0.49±0.26	NA	P (A)
Touchet ¹ (27)	8 Aug 2002 ²	119	2.08	0.82	5	5.1	0.51	0.29±0.13	NA	A
Walla Walla ¹ (28)	15 Aug 2000	109	2.20	0.92	5	5.0	0.46	0.4±0.42	0.47	P (A)
Walla Walla ¹ (29)	13 Aug 2003	97	1.76	0.85	5	5.2	0.43	0.39±0.17	0.44	P (A)
<i>N California Coastal</i>										
Eel ¹ (30)	11 Aug 2005 ²	186	2.33 ^{3,4}	0.60	2	7.0	0.33	0.32±0.29	0.78	P
Mattole (31)	19 Jul 2001	111	1.67	0.97	3	3.7	0.51	0.4±0.3	0.28	P
Redwood (32)	29 Jul 2003	95	1.60 ³	0.93	3	3.5	0.47	0.35±0.21	0.38	P
Russian ¹ (33)	23 Jul 2004 ²	157	2.69 ^{3,4}	0.79	2	5.0	0.45	0.32±0.25	0.54	A
<i>N Oregon Coastal</i>										
Nehalem (34)	5 Aug 2000	179	3.04	0.91	4	4.1	0.49	0.36±0.28	0.29	P (C)
Siletz ¹ (35)	5 Aug 2001	103	1.54	0.84	4	4.4	0.58	0.2±0.14	0.74	A
<i>Puget Sound</i>										
Deschutes (36)	19 Aug 2003	68	1.16	0.83	2	3.0	0.44	0.14±0.09	0.02	U (P)
Nooksack ¹ (37)	20 Aug 2001	120	1.46	1.00	4	3.9	0.50	0.64±0.6	0.67	C (A)
Snoqualmie ¹ (38)	13 Aug 2006	103	3.47 ^{3,4}	0.79	2	4.6	0.39	0.08±0.04	0.23	L (C)
NF Stillaguamish ¹ (39)	7 Sep 2001	93	1.65 ⁴	0.89	4	3.6	0.45	0.23±0.21	0.81	A
SF Stillaguamish ¹ (40)	8 Sep 2001	100	1.45	0.93	3	3.4	0.47	0.17±0.15	NA	A (L)

(Table 3.1 continued)

Basin/River (Map Reference)	First day of survey	Total length surveyed (km)	Flight duration (h)	Proportion of river surveyed	Strahler stream orders (n)	Distance- weighted mean Strahler order ⁵	Survey midpoint (km from mouth / total km)	TIR Accuracy (mean ± sd, °C) ⁶	Discharge in survey year (percentile) ⁷	Profile class (second choice)
<i>S Oregon Coastal</i>										
Applegate (41)	18 Aug 1998	75	0.64	0.78	2	4.8	0.39	0.24±0.12	0.94	A (L)
Applegate (42)	19 Jul 1999	75	0.66	0.79	2	4.7	0.39	0.15±0.14	0.96	A
Cow (43)	25 Jul 2000	96	1.31	0.51	2	4.0	0.61	0.54±0.48	0.86	A
Evans ¹ (44)	1 Aug 2003	56	0.98	0.69	3	3.5	0.65	0.46±0.21	NA	A
Little Butte ¹ (45)	13 Jul 2001	62	1.05	0.94	3	3.3	0.47	0.26±0.26	NA	C (A)
North Umpqua (46)	25 Jul 2002	85	1.33 ³	0.71	3	4.7	0.36	0.33±0.31	0.14	L
Rogue ¹ (47)	30 Jul 2003 ²	261	2.62	0.72	2	5.6	0.37	0.32±0.25	0.45	A
Umpqua ¹ (48)	23 Jul 2002 ²	289	5.16 ³	0.81	5	5.4	0.50	0.47±0.42	0.10	A
<i>Upper Columbia</i>										
Entiat (49)	11 Aug 2001	78	1.95	0.98	7	3.9	0.49	0.17±0.06	NA	A
Wenatchee ¹ (50)	13 Aug 2001 ²	89	1.15	0.70	4	4.4	0.65	0.2±0.16	0.12	A (P)
<i>Washington Coastal</i>										
Hoh (51)	25 Sep 2000	60	0.70	0.67	2	3.8	0.34	0.5±0.31	0.67	A (L)
Willapa (52)	30 Aug 2001	61	1.56	0.85	4	3.8	0.55	0.83±0.32	1.00	A
<i>Willamette</i>										
Molalla (53)	26 Jul 2004	76	1.44 ³	0.99	5	4.0	0.49	0.4±0.2	0.26	A
Pudding ¹ (54)	11 Aug 2004 ²	107	2.97 ^{3,4}	0.97	4	4.5	0.52	0.08±0.08	0.72	U
Thomas (55)	3 Aug 2000	50	0.87	0.81	3	3.5	0.47	0.33±0.15	NA	A (L)
Tualatin ¹ (56)	27 Jul 1999	129	1.38 ⁴	1.00	4	4.2	0.50	0.36±0.27	0.90	C (L)
Yamhill (57)	27 Jul 2005	103	1.93	0.90	3	5.0	0.45	0.38±0.29	0.83	A
<i>Yakima</i>										
Naches (58)	14 Aug 2004	72	1.28 ³	0.76	3	5.3	0.38	0.27±0.21	NA	U (C)
MEAN		127	1.41	0.85	3.3	4.5	0.48	0.44	0.51	
SD		98	0.58	0.13	1.1	0.9	0.08	0.37	0.29	

(Table 3.1 continued)

¹ Adjacent surveys were combined; ² Survey was conducted over 2 days; ³ Survey occurred in a downstream direction; ⁴ Upstream section of a combined survey was surveyed first

⁵ Weighted average stream order, calculated as $\sum_n^1 (S_j * L_j) / \sum_n^1 L_j$ where S_j = Strahler stream order in reach j , L_j = length (km) of reach j , and n = all reaches in the survey (reach data from NHDPlusV2 hydrography dataset [McKay *et al.* 2012])

⁶ Absolute deviation between radiant temperature (from TIR) and instream temperature measured with Onset loggers at a variety of locations throughout the river (source: project completion reports, available on request)

⁷ Percentile of discharge in survey year relative to period of record for gages located on, upstream of, or downstream of thermal infrared surveys (mean of 2 gages per survey; range 1-6) and for the month in which the TIR survey was conducted. NA: Data were not available for all surveys. Source: USGS (<http://waterdata.usgs.gov/nwis>). We computed statistics only when a complete monthly record was available.

Table 3.2. Rivers with a large dam (≥ 15 m tall) near the reach surveyed.

Profile	Dam name ¹	Height (m)	Position of dam relative to survey	Profile class	Predicted shape if dam were absent
Applegate 1998, 1999	Applegate	73.8	Upstream end	asymptotic	Remain asymptotic, possibly linear
Cow 2000	Galesville	50.9	Upstream end	asymptotic	Remain asymptotic, possibly linear
Crooked 2005	Arthur R. Bowman	74.7	Middle, near Prineville	complex	Complex regardless due to other factors
Rogue 2003	William L. Jess	105.2	Upstream end	asymptotic	Remain asymptotic
Russian 2004	Coyote Valley	54.9	Upstream end	asymptotic	Remain asymptotic, possibly linear
Shasta 2003	Shasta River	29.3	Upstream end	linear	Remain linear, possibly asymptotic
Tualatin 1999	Scoggins	151.0	In Scoggins Creek (tributary in middle of profile)	complex	Asymptotic or linear

¹ Source: 2013 National Inventory of Dams dataset (<http://nid.usace.army.mil>)

Table 3.3. Summary characteristics of surveys in each thermal profile class.

Profile class	Survey		Median (95% confidence interval)				Weighted average Strahler order ²
	(n)	No. less certain (n) ¹	Profile length (km)	Proportion of river surveyed	Midpoint of profile in river	Strahler orders (n)	
Asymptotic	27	12	100 (54-516)	0.83 (0.61-1.0)	0.48 (0.36-0.65)	3.0 (2.0-5.7)	4.7 (3.4-6.1)
Linear	9	5	80 (67-153)	0.74 (0.58-0.84)	0.40 (0.36-0.62)	2.0 (2.0-3.8)	4.5 (3.6-5.4)
Parabolic							
Inland	4	2	90 (56-108)	0.92 (0.86-0.99)	0.48 (0.43-0.53)	4.5 (3.1-5.0)	4.3 (2.6-5.2)
Coastal	4	1	152 (96-185)	0.92 (0.62-0.97)	0.48 (0.34-0.51)	3.0 (2.1-3.9)	3.9 (3.5-6.8)
Uniform	4	3	82 (68-106)	0.81 (0.77-0.96)	0.42 (0.38-0.51)	2.5 (2.0-3.9)	4.5 (3.1-5.2)
Complex	10	0	119 (58-262)	0.97 (0.70-1.0)	0.50 (0.46-0.65)	4 (3.0-4.8)	4.2 (3.4-5.6)

¹ Surveys for which classification was less certain based on goodness of fit diagnostics

² See footnote 5 in **Table 3.1**

Table 3.4. Mean of partial correlation coefficients describing relationships between river temperature and hydroclimatic variables for each thermal profile class.

Profile class	Elevation	Mean August air temperature	Mean August precipitation	Discharge	Velocity	Gradient	Tributary temperature	Distance upstream
Asymptotic	-0.49	0.37	-0.29	0.00	0.14	-0.27	0.50	-0.78
Linear	0.02	-0.03	-0.11	-0.08	0.00	-0.03	0.13	-0.83
Parabolic								
Inland	-0.83	0.82	-0.60	-0.33	0.25	-0.47	0.78	-0.85
Coastal	-0.53	0.78	-0.09	-0.69	-0.04	-0.23	0.25	0.01
Uniform	-0.10	-0.07	0.10	-0.13	-0.22	-0.42	0.58	0.17
Complex	-0.21	0.10	-0.05	-0.11	-0.08	-0.24	0.69	-0.27

Table 3.5. Median (95% confidence interval) of network metrics for each profile class.

Profile class	Basin shape	Stream density	Significant confluence density
Asymptotic	0.12 (0.04-0.23)	0.69 (0.44-0.86)	0.04 (0.02-0.12)
Linear	0.21 (0.08-0.31)	0.70 (0.43-0.80)	0.05 (0.03-0.08)
Parabolic			
Inland	0.22 (0.10-0.35)	0.82 (0.74-1.01)	0.07 (0.04-0.08)
Coastal	0.07 (0.06-0.09)	0.79 (0.68-0.89)	0.09 (0.02-0.12)
Uniform	0.16 (0.07-0.27)	0.71 (0.59-0.77)	0.08 (0.05-0.09)
Complex	0.13 (0.09-0.33)	0.63 (0.31-0.77)	0.07 (0.02-0.11)

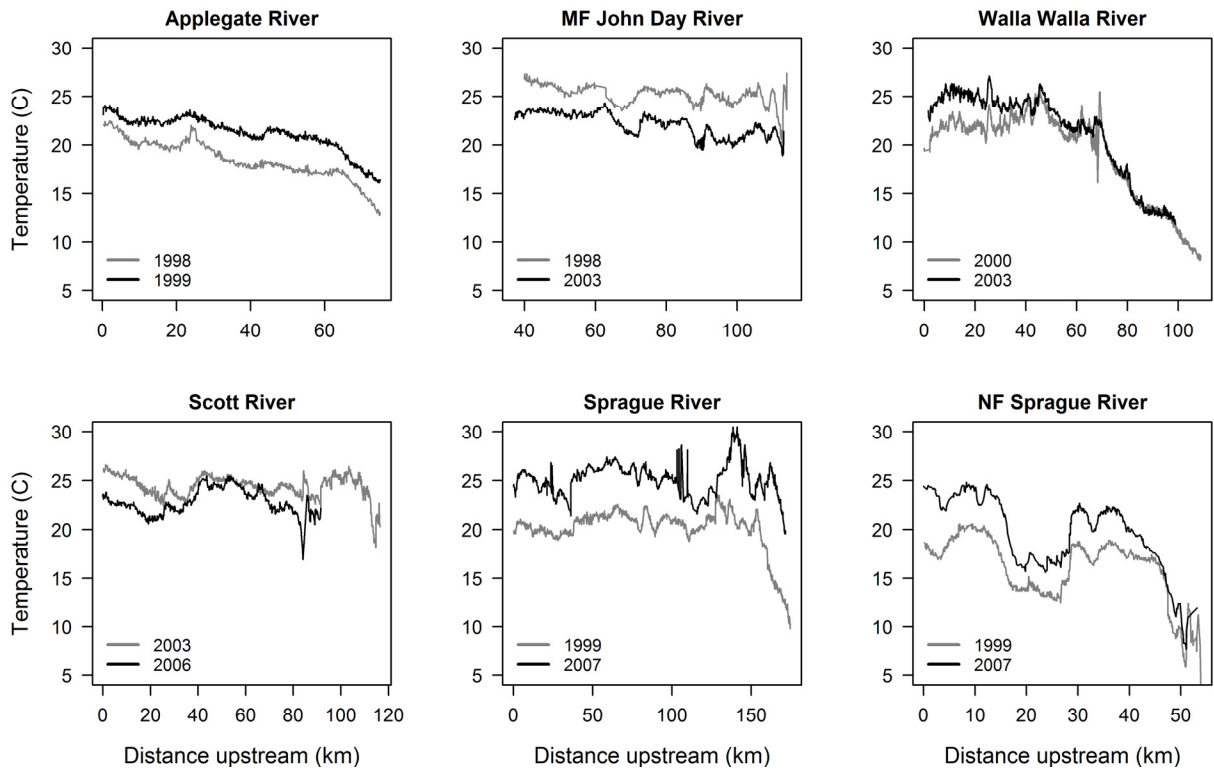


Figure 3.1. Longitudinal profiles for rivers in which surveys were flown in two years, illustrating similar spatial variance patterns. The NF Sprague River did not meet analysis criteria, but we included it here to illustrate consistency among years.

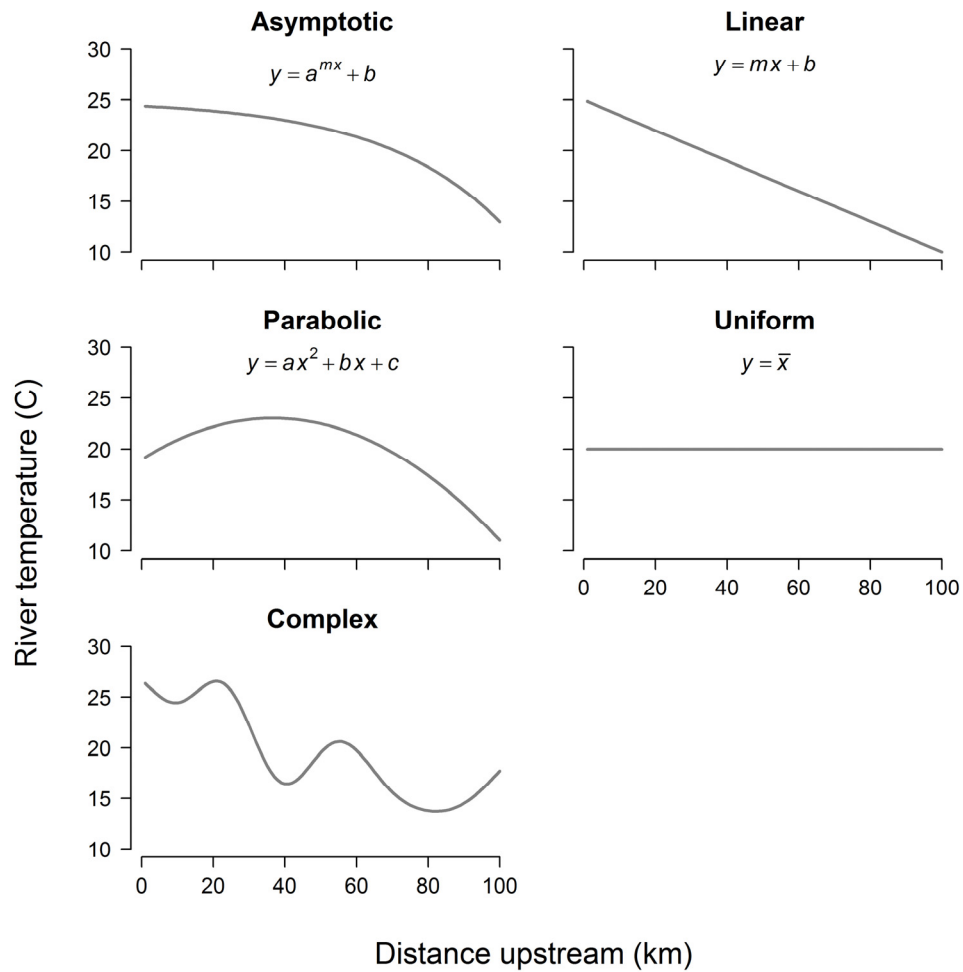


Figure 3.2. Theoretical representations and model equations for the five thermal profile classes, where y is river temperature ($^{\circ}\text{C}$), x is the distance upstream from the downstream terminus of the profile (km), and a , b , c , and m are constants.

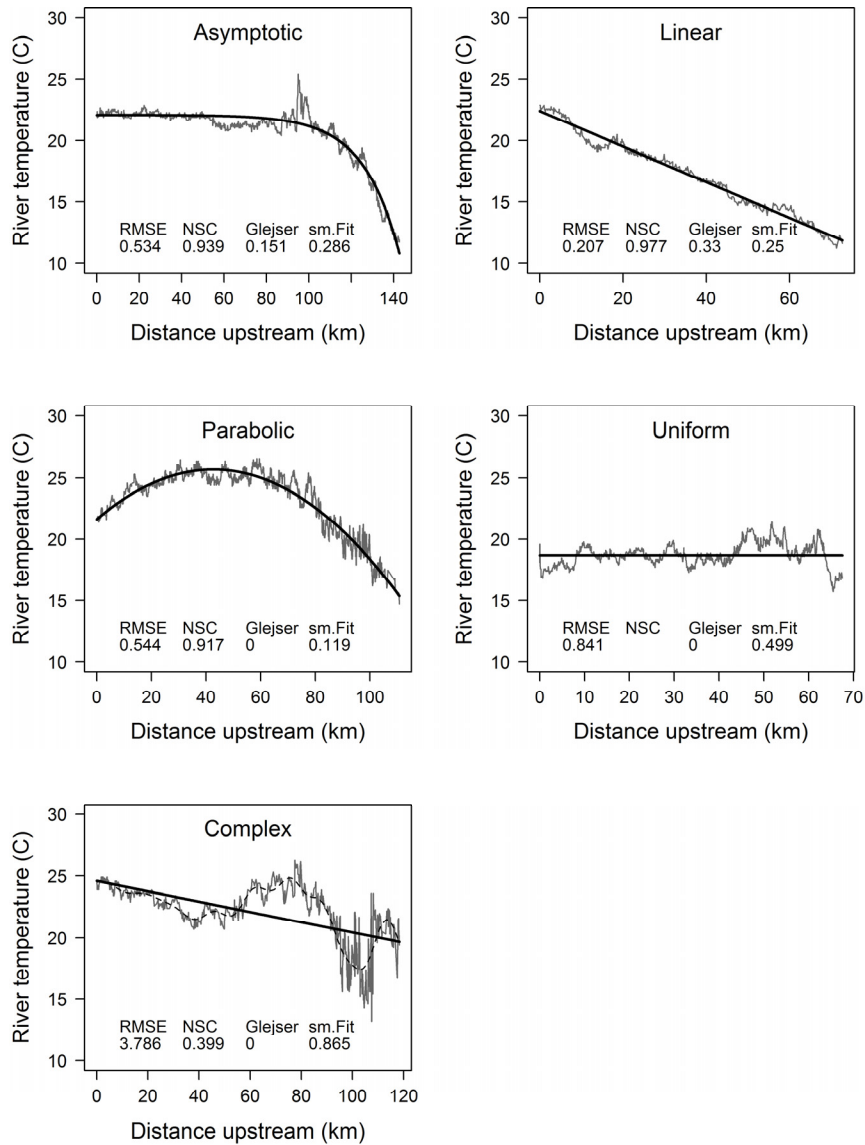


Figure 3.3. Examples of profile classification and diagnostics for *asymptotic*, *linear*, *parabolic*, *uniform*, and *complex* profiles. For each example, the plot shows river temperature vs. distance surveyed in gray and fitted values for the best model selected from the candidate set in black. Diagnostic goodness of fit metrics root mean square error (RMSE), Nash-Sutcliffe Coefficient (NSC), p-value from a Glejser test for homoscedasticity (Glejser), and the difference in RMSE between the best model and a smoothed trend (20-knot GAM; sm.Fit) are shown on each plot. For the *complex* profile example, diagnostic values refer to the *linear* fit (solid line); the smoothed fit (dotted line) is also presented to illustrate the trend. The rivers shown are Asymptotic: Little Deschutes River (2001); Linear: Minam River (1999); Parabolic: Mattole River (2001); Uniform: Deschutes River (Puget Sound) (2003); and Complex: Joseph Creek (1999). Plots of other profiles are provided in **Figure S 3.2**.

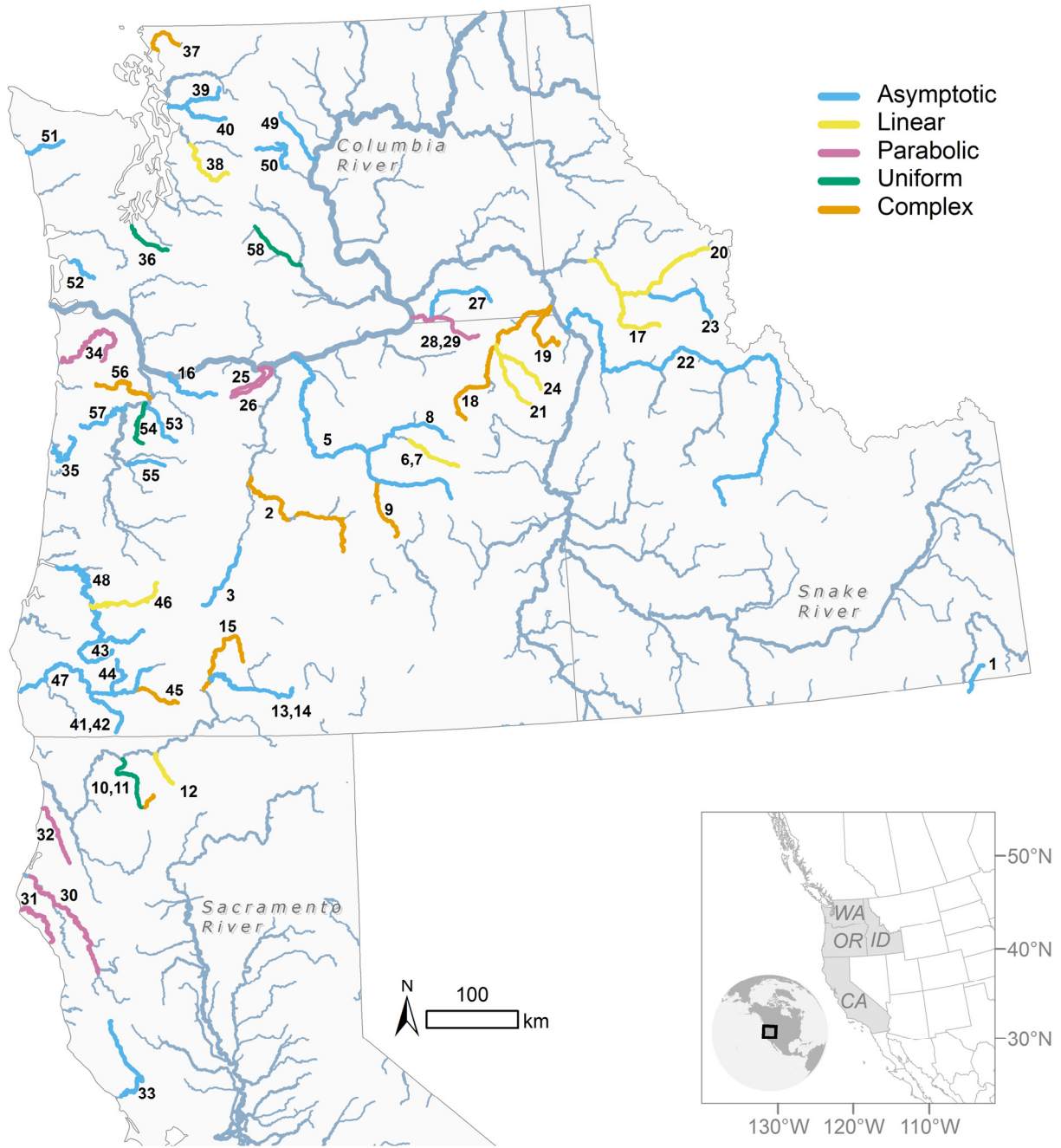


Figure 3.4. Geographic locations of rivers in each profile class.

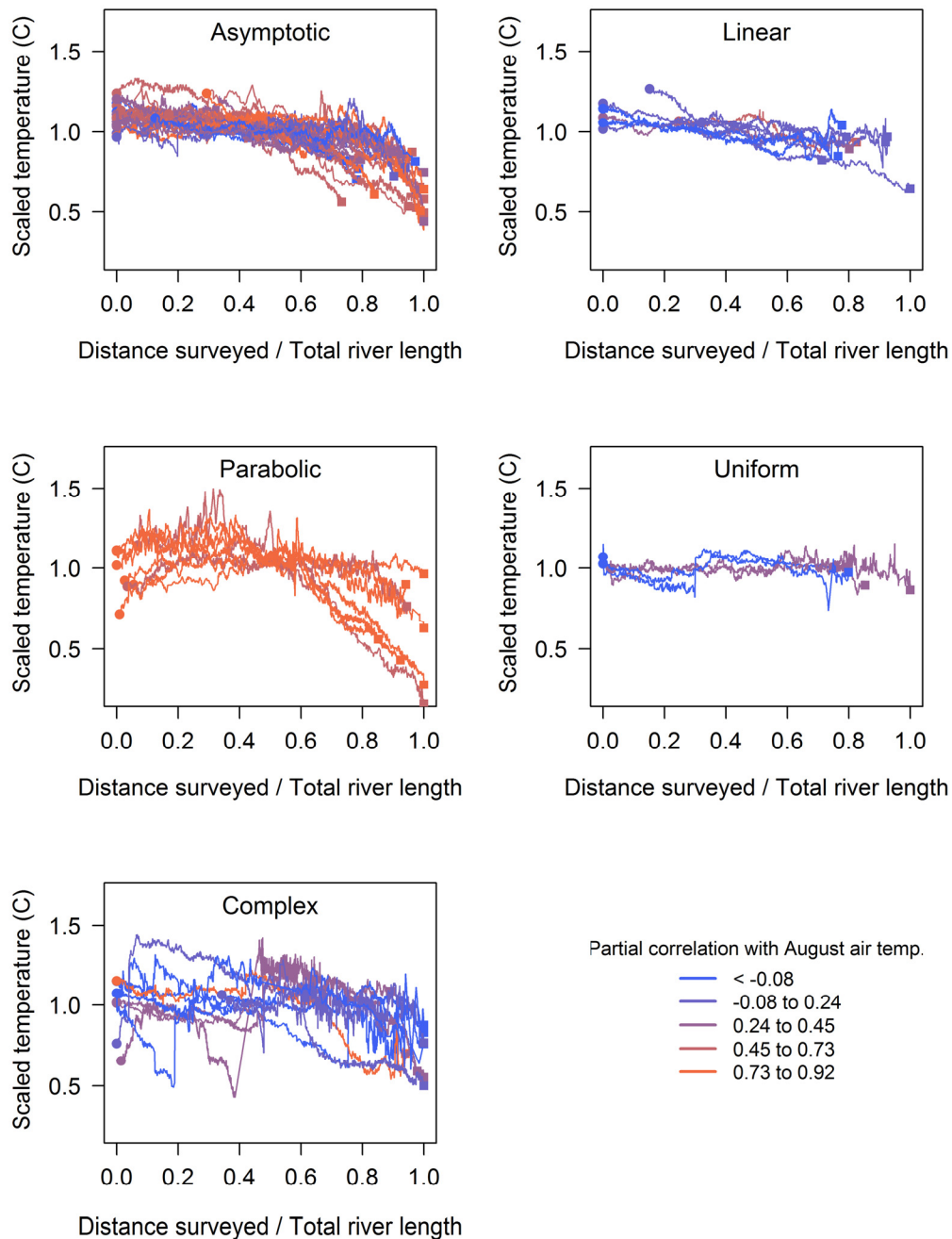


Figure 3.5. Partial correlations between river temperature and mean August air temperature for longitudinal profiles assigned to each class (*asymptotic*, *linear*, *parabolic*, *uniform*, and *complex*). The longitudinal profiles within each class are standardized on both axes to facilitate comparison of partial correlations among profiles. The downstream (circles) and upstream (squares) end points of individual surveys are demarcated to indicate the extent of the river included in each survey. Non-standardized plots of longitudinal profiles for all rivers assigned to each profile class are provided in **Figure S 3.2**.

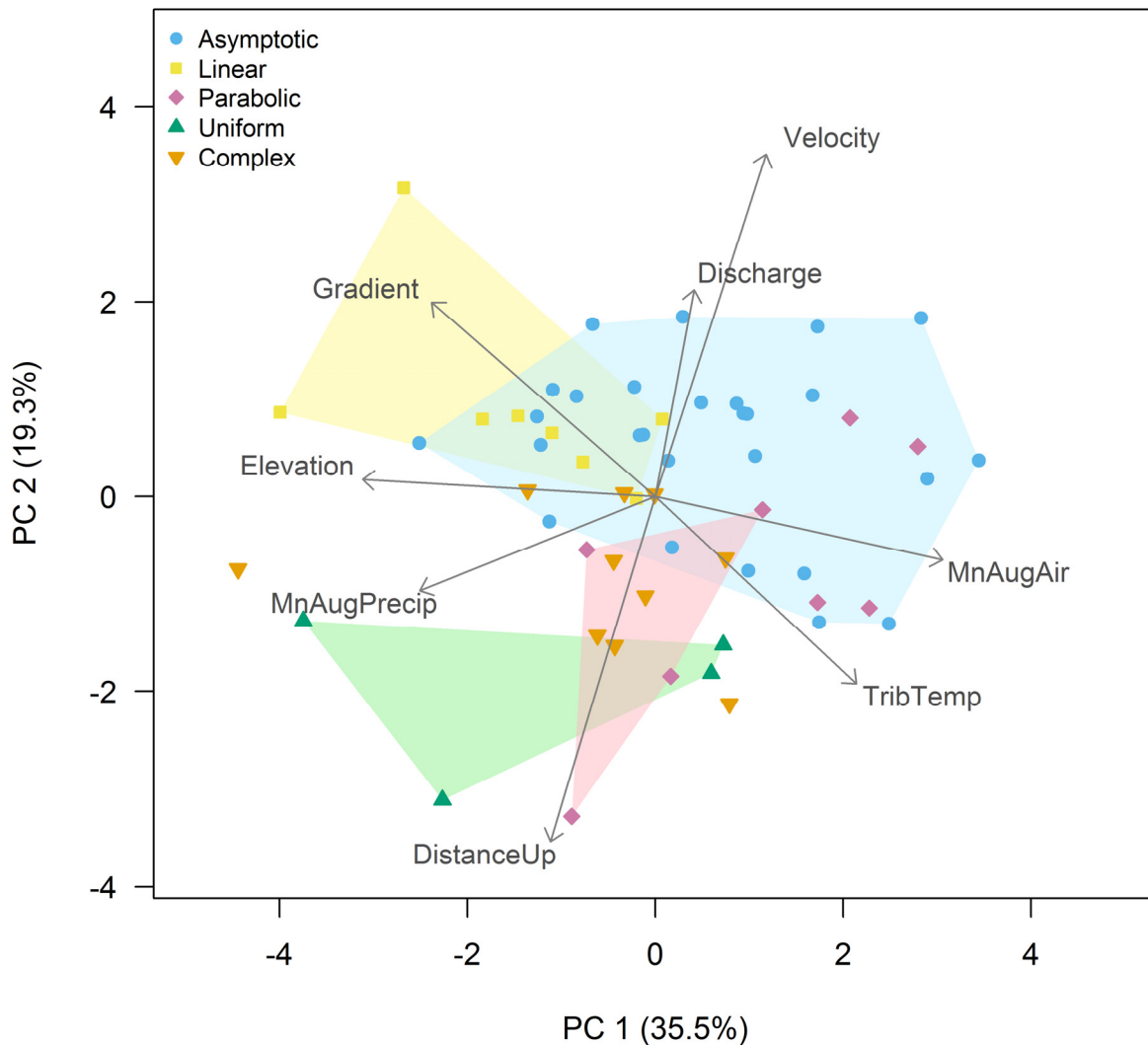


Figure 3.6. Principal components analysis (PCA) biplot showing the relationship in multivariate space of river temperature profiles (symbols) with respect to the strength and direction of partial correlations between water temperature and hydroclimatic variables (arrows). Note that the ordination is of partial correlation coefficients. Symbols indicate the class to which each profile was assigned. Colored polygons enclose symbols of the same color, with blue for *asymptotic*, yellow for *linear*, green for *uniform*, and pink for coastal *parabolic* profiles. Inland *parabolic* profiles are pink symbols within the blue polygon. Abbreviations: MnAugAir, mean August air temperature; MnAugPpt, mean August precipitation; TribTemp, temperature of tributaries; and DistanceUp, distance upstream.

3.8. Supplementary Information

Table S 3.1. Data specifications for combined adjacent surveys conducted on the **same day**.

Adjacent Mainstem Sections

Rivers: lower (black) and upper (red) Tualatin

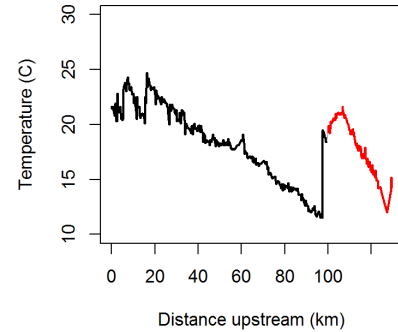
Date/time: 27 July 1999 14:58-16:04 and 17:19-17:35

Duration: 1.38 h

Delay between surveys: 45 min

Flight direction: upstream

Notes: The thermal discontinuity at 100 km was not caused by joining the two surveys. This temperature difference was due to the influence of Scoggins Creek.



Adjacent Mainstem and Major Fork

Rivers: Clearwater (black), SF Clearwater (red)

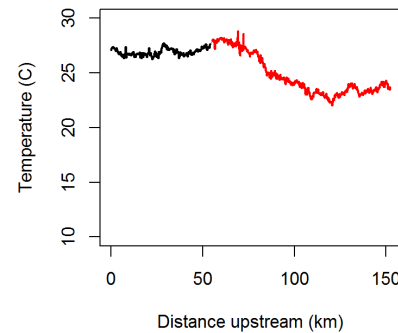
Date/time: 3 Aug 2000 17:50-18:12 and 19:00-20:06

Duration: 1.47 h

Delay between surveys: 45 min

Flight direction: upstream

Notes: Survey was conducted by IRZ Consulting for ID DEQ.



Rivers: Walla Walla (black), SF Walla Walla (red)

Date/time: 15 Aug 2000 14:07-16:20

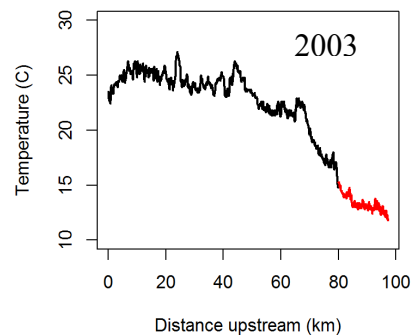
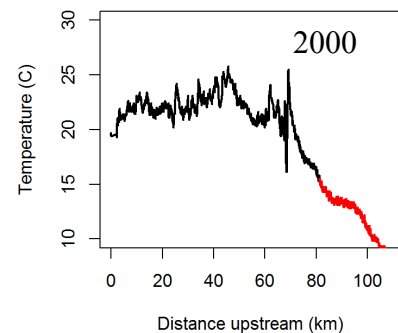
and 13 Aug 2003 13:59-15:45

Duration: 2:20 (2000) and 1.76 h (2003)

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: Temperatures may have been elevated in middle reaches by irrigation withdrawals.



Rivers: Joseph Cr (black), Chesnimnus Cr (red)

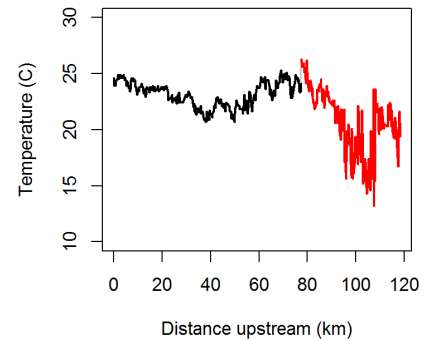
Date/time: 22 Aug 1999 14:31-15:36

Duration: 1.07 h

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: None



Rivers: Nooksack (black), SF Nooksack (red)

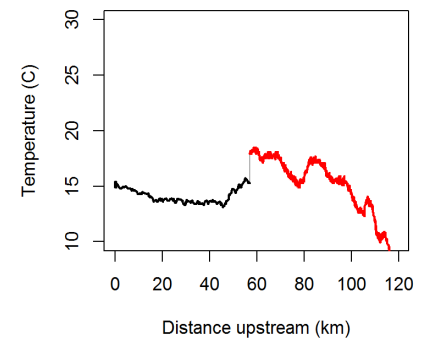
Date/time: 20 Aug 2001 13:51-14:24 and 16:46-17:43

Duration: 1.46 h

Delay between surveys: 2.5 h

Flight direction: upstream

Notes: Water temperature in the Nooksack decreased in a downstream direction below the confluence with its north and south forks (60 km). The south fork was 4 °C warmer than the north fork at their confluence; thus, the drop in temperature was likely caused by the colder north fork. However, air temperature reportedly increased 1 °C during the delay between surveys. This profile was classified as *complex*. It is possible, however, that this profile may be *asymptotic*.



Rivers: Stillaguamish (black), SF Stillaguamish (red)

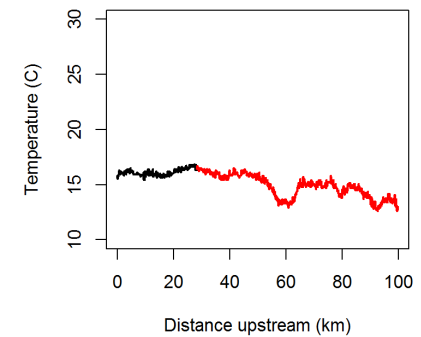
Date/time: 8 Sept 2001 15:03-16:30

Duration: 1.45 h

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: None



Rivers: Stillaguamish (black), NF Stillaguamish (red)

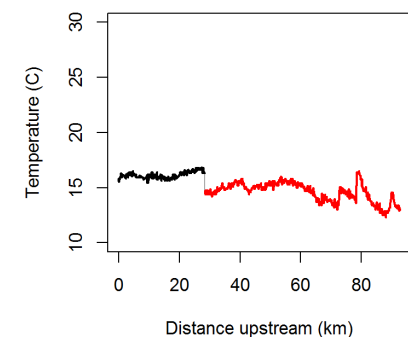
Date/time: 7 Sept 2001 16:52-17:23 and 14:50-15:58

Duration: 1.65 h

Delay between surveys: 1 h

Flight direction: upstream

Notes: The north fork was flown before the mainstem. The peak in temperature at the confluence may have been caused by flight direction and timing but likely shows the influence of the warmer south fork entering. The discrepancy did not affect the profile shape.



Rivers: Snoqualmie (black), MF Snoqualmie (red)

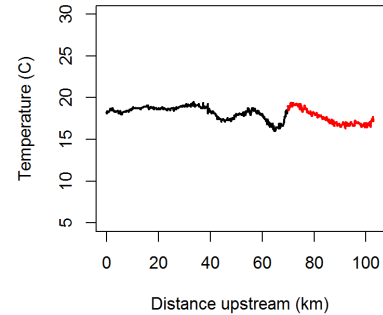
Date/time: 13 Aug 2006 14:14-17:42

Duration: 3.47 h

Delay between surveys: none; temporally contiguous

Flight direction: downstream

Notes: None



Rivers: Siletz (black), NF Siletz (red)

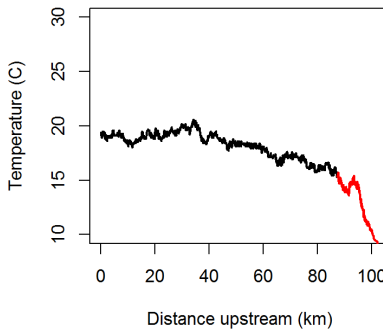
Date/time: 5 Aug 2001 13:46-15:20

Duration: 1.54 h

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: None



Rivers: Evans Cr (black), WF Evans Cr (red)

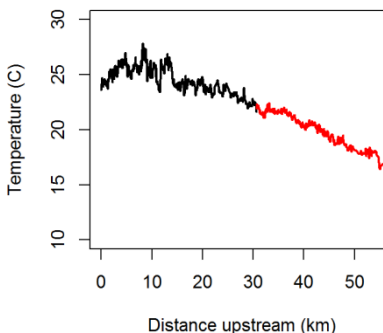
Date/time: 1 Aug 2003 13:50-14:22 and 15:10-15:41

Duration: 0.98 h

Delay between surveys: 45 min

Flight direction: upstream

Notes: None



Rivers: Little Butte Cr (black), SF Little Butte Cr (red)

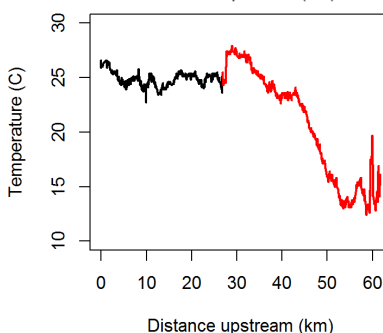
Date/time: 13 July 2001 14:04-15:07

Duration: 1.05 h

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: None



Rivers: Sprague (black), SF Sprague (red)

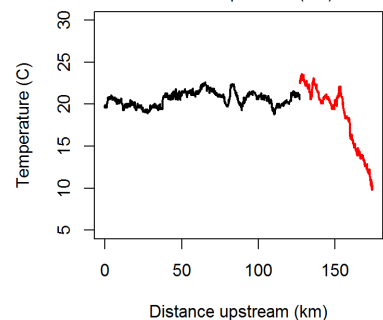
Date/time: 12 Aug 1999 14:16-15:20 and 16:04-16:31

Duration: 1.5 h

Delay between surveys: 45 min

Flight direction: upstream

Notes: This river was also surveyed in 2007 (**Table S 3.2**).



Rivers: Scott (black), EF Scott (red)

Date/time: 25 July 2003 14:00-15:39

Duration: 1.64 h

Delay between surveys: none; temporally contiguous

Flight direction: upstream

Notes: This river was also surveyed in 2006 (as a single survey).

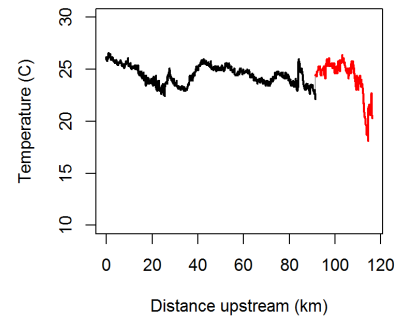


Table S 3.2. Data specifications for combined adjacent surveys conducted on **different days**.

Adjacent Mainstem Sections

Rivers: Salmon (colors denote 4 surveyed sections)

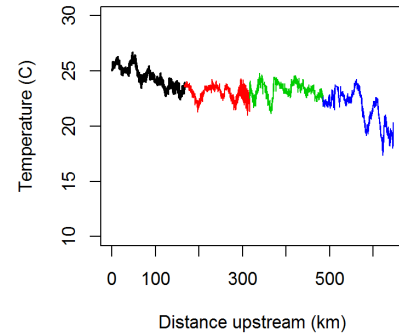
Date/time: 8, 9, 11, and 12 Aug 2001, each between 16:00 and 18:00

Duration: 5.74 h (each survey < 2h)

Flight direction: downstream

Air temperature: not reported

Notes: Differences at junctions (lower part of upstream section and upper part of downstream section) were only 0.5, 0.2, and 0.1 °C °C; thus, it was appropriate to combine these surveys in one profile. Surveys were conducted by IRZ Consulting for ID DEQ.



Rivers: lower (black) and upper (red) Grande Ronde

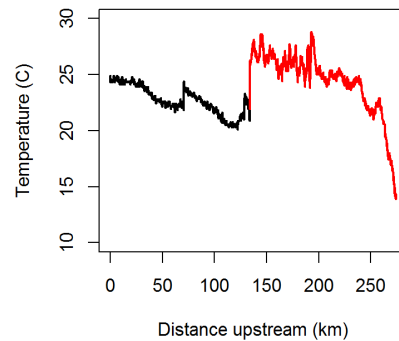
Date/time: 19 Aug 1999 14:33-15:38 and 20 Aug 14:51-16:12

Duration: 2.43 h

Flight direction: upstream

Air temperature: not reported

Notes: The survey report concluded the surveys can be combined because a comparison of images from both days at the junction revealed only a 0.3 °C difference. The pronounced increase in the profile at 150 km was due to the influence of Lookingglass Creek, which was much colder than the mainstem, causing a 4.4 °C decrease in mainstem temperature in a downstream direction. This decrease in temperature was part of the upper survey and was not caused by combining the two surveys. Subsequent decreases in temperature downstream were caused by the Wallowa and the Wenaha rivers.



Rivers: lower (black) and upper (red) John Day

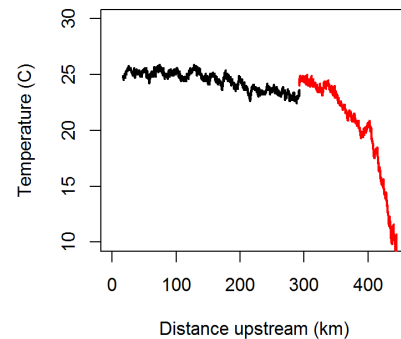
Date/time: 30 Aug 2004 13:36-17:35 and 29 Aug 13:31-15:55

Duration: 6.42 h

Flight direction: downstream

Air temperature: 33.8 °C at km 172 (30 Aug) and 30.7 °C at km 322 and 21.2 °C near the headwaters (29 Aug)

Notes: The decrease in temperature at the junction of the two surveys was likely caused by lower temperatures of the NF John Day, but it could have been due to timing because temperature at the start of the second day was 1.1 °C cooler than the end of previous day. The differences in temperature, duration, and flight direction between the two surveys would not have changed our classification of this profile as *asymptotic*.



Rivers: lower (black) and upper (red) Crooked and SF Crooked (green)

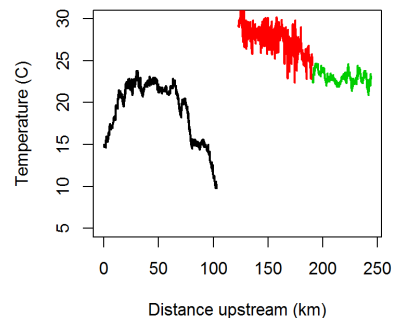
Date/time: 6 Aug 2005 14:30-15:06, 6 Aug 16:16-17:17, and 7 Aug 13:13-14:14

Duration: 2.63 h

Flight direction: upstream

Air temperature: 34.9 °C (6 Aug) and 32.2 °C (7 Aug)

Notes: The large temperature difference between the two surveys was caused by cold water released from the Prineville Reservoir, not the difference between survey dates and times. The upper section was surveyed directly after the lower section on the same day. The complexity of this profile was most likely caused by the dam and cold-water inputs near the mouth; these differences were much larger than any influences attributable to different survey dates.



Rivers: lower (black) and upper (red) Pudding

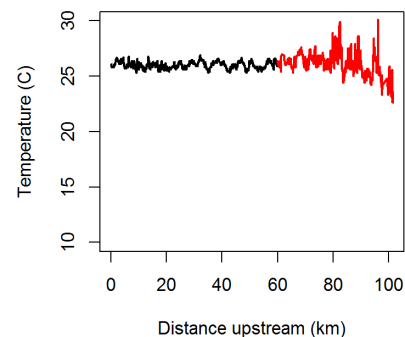
Date/time: 12 Aug 2004 14:07-15:48 and 11 Aug 16:01-17:59

Duration: 2.97 h

Flight direction: downstream

Air temperature: 33.1 °C (12 Aug) and 33.5 °C (11 Aug)

Notes: The similar temperatures and weather conditions for the surveys made it appropriate to combine these surveys. If the upper section had been surveyed later in the day (like the lower section), the upper section would have been very similar in shape to the lower section.



Rivers: lower (black) and upper (red) Rogue

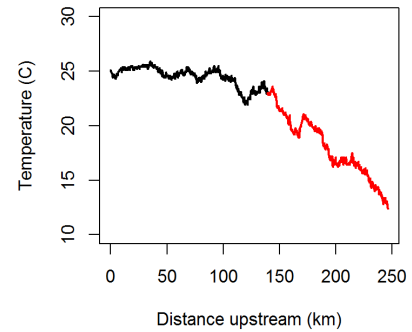
Date/time: 30 July 2003 14:30-15:59 and 31 July 14:20-15:29

Duration: 2.62 h

Flight direction: upstream

Air temperature: 39.1 °C (30 July) and 36.6 °C (31 July)

Notes: The similar temperatures and timing made it appropriate to combine these surveys.



Rivers: lower (black) and upper (red) Russian

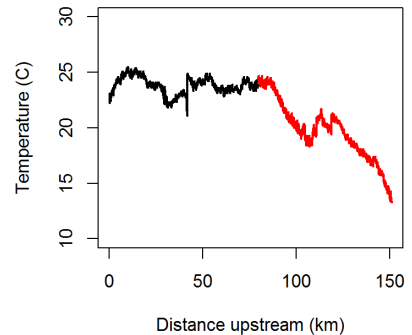
Date/time: 24 July 2004 14:27-15:36 and 23 July 14:08-15:46

Duration: 2.69 h

Flight direction: downstream

Air temperature: 22.6 °C (24 July) and 23.7 °C (23 July)

Notes: The similar temperatures and timing made it appropriate to combine these surveys.



Rivers: lower (black) and upper (red) Eel

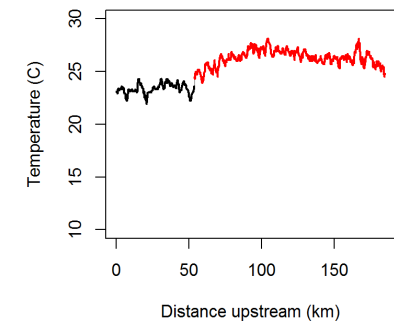
Date/time: 12 Aug 2005 13:50-15:37 and 11 Aug 14:51-15:24

Duration: 2.33 h

Flight direction: downstream

Air temperature: 34.8 °C (12 Aug) and 34.3 °C (11 Aug)

Notes: Profile shape was not influenced by the minimal difference in temperature at the junction between surveys.



Adjacent Mainstem and Major Fork

Rivers: MF Clearwater (black) and Lochsa (red)

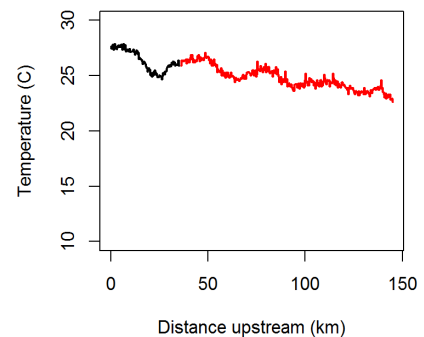
Date/time: 3 Aug 2000 18:12-18:30 and 4 Aug 19:23-20:17

Duration: 1.2 h

Flight direction: upstream

Air temperature: not reported

Notes: Profile shape was not influenced by combining the two surveys. Surveys were conducted by IRZ Consulting.



Rivers: MF Clearwater (black) and Selway (red)

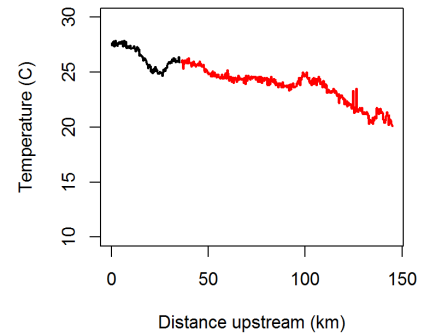
Date/time: 3 Aug 2000 18:12-18:30 and 4 Aug 18:05-19:22

Duration: 1.58 h

Flight direction: The Selway survey was flown in downstream direction, whereas the MF Clearwater was flown in an upstream direction.

Air temperature: not reported

Notes: Profile shape was not influenced by combining the two surveys. Surveys were conducted by IRZ Consulting.



Rivers: Touchet (black) and NF Touchet (red)

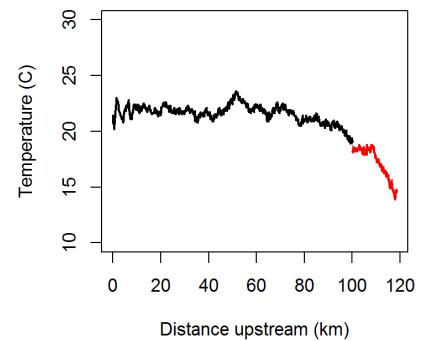
Date/time: 8 Aug 2002 13:37-15:22 and 9 Aug 13:38-14:03

Duration: 2.07 h

Flight direction: upstream

Air temperature: 28.0 (8 Aug) and 23.2 °C (9 Aug)

Notes: There was a 1 °C difference in water temperature at the junction of the two surveys. However, the profile shape was strongly asymptotic and not influenced by this difference.



Rivers: Wenatchee (black) and Nason Cr (red)

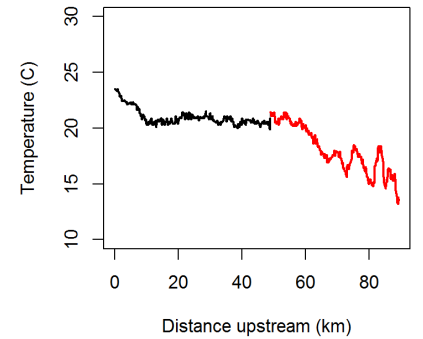
Date/time: 13 Aug 2001 14:41-15:17 and 14 Aug 14:37-15:30

Duration: 1.15 h

Flight direction: upstream

Air temperature: 28.6 (13 Aug) and 31.1 °C (14 Aug)

Notes: The minimal difference in water temperature at the junction of surveys was likely due to the confluence with the Chiwawa River. This difference also may have been influenced by meteorological conditions. However, this difference did not affect the profile shape.



Rivers: Umpqua (black) and South Umpqua (red)

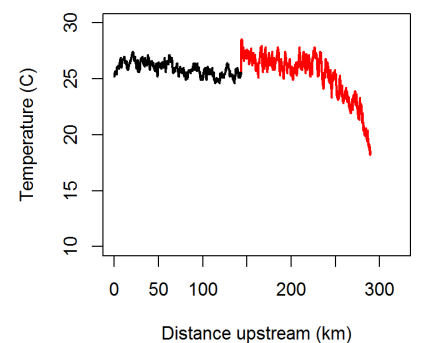
Date/time: 23 July 2002 14:33-16:07 and 28 July 14:10-17:26

Duration: 5.16 h

Flight direction: downstream

Air temperature: 33.6 (23 Jul) and 31.4 °C (28 Jul)

Notes: At their confluence, the North Umpqua was ~1.7 °C cooler than the South Umpqua; thus the change in temperature at the junction of combined surveys was likely caused by the confluence with the North Umpqua. This difference did not affect the profile shape.



Rivers: Sprague (black) and SF Sprague (red)

Date/time: 2 Aug 2007 14:33-16:32 and 31 July 15:38-16:26

Duration: 2.78 h

Flight direction: upstream

Air temperature: 29.3 (2 Aug) and 29.9 °C (31 Jul)

Notes: There was no noticeable difference in water temperature at the junction between surveys. The upper section was surveyed later in the day on a slightly warmer day; therefore, it is possible that this profile shape may be more strongly asymptotic (i.e., if the upper survey were shifted downward).

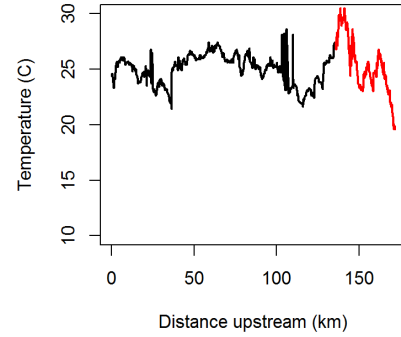


Table S 3.3. Potential implications of flight direction on profile classification.

Actual Profile Shape	<u>Downstream direction:</u> Expected bias: stronger cooling trend in headwaters	<u>Upstream direction:</u> Expected bias: weaker cooling trend in headwaters
<i>Asymptotic</i>	No effect	No effect; but if slope levels out, it may be misclassified as <i>linear</i> or <i>uniform</i>
<i>Linear</i>	May be misclassified as <i>asymptotic</i>	No effect; but if slope levels out, it may be misclassified as <i>uniform</i>
<i>Parabolic</i>	No effect	No effect; we did not observe <i>asymptotic</i> profiles where temperature increased in an upstream direction
<i>Uniform</i>	May be misclassified as <i>asymptotic</i>	No effect; water temperatures are unlikely to be warmer upstream

Table S 3.4. Attributes of remotely sensed profiles of summertime river temperature that met relaxed filter criteria (i.e., no stream order criterion and survey midpoint in middle half of river) and which were used only in supplementary analyses.

Basin/River (Map Reference)	First day of survey	Total length surveyed (km)	Flight duration (h)	Proportion of river surveyed	Strahler stream orders (n)	Distance- weighted mean Strahler order ⁵	Survey midpoint (km from mouth / total km)	TIR accuracy (mean ± sd, °C) ⁶	Discharge in survey year (percentile) ⁷	Profile class (second choice)
<i>Bear</i>										
Smiths Fork (59)	26-Jul-06	63	1.06	0.74	1	4.0	0.37	0.24±0.09	0.37	L
<i>Deschutes</i>										
North Fork Crooked (60)	8-Aug-05	66	1.31	0.53	5	4.5	0.73	0.68±0.86	NA	U (L)
<i>Klamath</i>										
Sycan (61)	16-Aug-99	112	0.83	0.51	5	4.2	0.75	0.3±0.16	NA	A (L)
<i>Lower Snake</i>										
Catherine ¹ (62)	21-Aug-99	102	0.73 ³	0.64	4	3.7	0.68	1.52±1.16	NA	A
Lemhi (63)	9-Aug-01	65	0.50	0.55	2	4.1	0.27	1.52±0.57	0.21	L
Little Salmon (64)	31-Aug-04	52	1.12	0.64	4	4.0	0.68	0.38±0.25	0.50	C (A)
Middle Fork Salmon (65)	10-Aug-01	168	1.20	0.77	1	6.0	0.40	1.15±0.38	0.23	A (P)
<i>Middle Snake</i>										
North Fork Malheur (66)	6-Aug-98	60	0.53	0.64	4	3.6	0.68	0.28±0.17	0.73	C (A)
<i>N Oregon Coastal</i>										
Siuslaw ¹ (67)	22-Aug-02	104	3.29 ³	0.58	4	3.4	0.67	0.34±0.24	0.16	A
<i>Upper Columbia</i>										
Wenatchee (67)	16-Aug-02	86	1.02	0.68	1	5.0	0.34	0.3±0.1	0.59	L

¹ Adjacent surveys were combined; ² Survey was conducted over 2 days; ³ Survey occurred in a downstream direction; ⁴ Upstream section of a combined survey was surveyed first

⁵ Weighted average stream order, calculated as $\frac{\sum_n^1(S_j * L_j)}{\sum_n^1 L_j}$ where S_j = Strahler stream order in reach j , L_j = length (km) of reach j , and n = all reaches in the survey (reach data from NHDPlusV2 hydrography dataset [McKay et al. 2012])

⁶ Absolute deviation between radiant temperature (from TIR) and instream temperature measured with Onset loggers at a variety of locations throughout the river (source: project completion reports)

⁷ Percentile of discharge in survey year relative to period of record for each gage located on, just upstream, or just downstream of thermal infrared surveys (2 gages per survey; range 1-6) and for the month in which the TIR survey was conducted. NA=Data were not available for all surveys. Source: USGS (<http://waterdata.usgs.gov/nwis>). We computed statistics only when a complete monthly record was available.

Table S 3.5. Hydroclimatic variables¹ summarized over all reaches in each profile of remotely sensed summertime water temperature.

River and year of survey	Mean elevation ²	Mean August air temp. ³	Mean August precip. ⁴	Discharge ⁵ at base of survey (m ³ /s)	Mean velocity ⁶	Mean gradient ⁷	Cumulative drainage area (km ²) ⁸	Mean tributary temp. ⁹
Surveys that met strict filter criteria								
<i>Bear</i>								
Cub 2006	211	20.4	29.6	1	1.12	0.010	550	21.9
<i>Deschutes</i>								
Crooked 2005	166	18.0	18.0	14	1.71	0.002	10263	18.9
Little Deschutes 2001	133	15.7	19.1	10	1.28	0.001	2299	22.3
Whychus 2000	456	16.5	16.6	4	1.65	0.022	601	13.2
<i>John Day</i>								
John Day 2004	402	20.5	17.5	34	1.90	0.004	20526	20.6
MF John Day 1998	236	17.5	23.2	5	1.52	0.006	1291	21.2
MF John Day 2003	236	17.5	23.2	5	1.52	0.006	1291	21.2
NF John Day 2002	341	18.9	20.6	21	1.82	0.005	6839	22.1
SF John Day 2003	450	18.2	18.8	2	1.47	0.010	1570	22.4
<i>Klamath</i>								
Scott 2003	497	21.1	11.2	14	1.69	0.009	2109	21.7
Scott 2006	252	21.4	11.3	17	1.76	0.007	2109	19.8
Shasta 2003	120	21.4	14.6	11	1.54	0.003	1934	22.6
Sprague 1999	274	17.2	15.9	10	1.23	0.002	4169	19.0
Sprague 2007	223	17.3	15.8	10	1.21	0.002	4169	25.5
Williamson 1999	68	16.2	15.7	9	1.09	0.000	6970	18.7
<i>Lower Columbia</i>								
Sandy 2001	959	18.2	39.9	44	1.72	0.017	1297	16.4
<i>Lower Snake</i>								
Clearwater 2000	450	19.8	30.1	114	1.91	0.006	14301	24.1
Grande Ronde 1999	319	19.6	23.1	48	2.07	0.007	10471	22.9
Joseph 1999	570	19.2	30.5	1	1.48	0.008	1428	21.1
Lochsa 2000	338	19.5	32.1	109	2.00	0.004	8834	28.4
Minam 1999	534	16.1	31.7	7	1.54	0.013	619	15.4
Salmon 2001	226	19.2	25.4	173	2.14	0.003	34913	22.6
Selway 2000	256	19.3	32.6	76	1.81	0.005	8834	22.7

River and year of survey	Mean elevation ²	Mean August air temp. ³	Mean August precip. ⁴	Discharge ⁵ at base of survey (m ³ /s)	Mean velocity ⁶	Mean gradient ⁷	Cumulative drainage area (km ²) ⁸	Mean tributary temp. ⁹
Wallowa 1999	316	17.5	29.7	12	1.74	0.009	2367	17.4
<i>Middle Columbia</i>								
Eightmile 2002	797	19.6	11.4	1	1.30	0.017	306	19.2
Fifteenmile 2002	920	19.4	11.6	1	1.38	0.017	649	18.5
Touchet 2002	374	22.0	18.0	11	1.57	0.005	1922	17.4
Walla Walla 2000	398	21.6	18.7	10	1.50	0.006	4577	19.2
Walla Walla 2003	302	22.3	16.4	11	1.50	0.004	4577	20.7
<i>N California Coastal</i>								
Eel 2005	147	20.1	9.7	143	1.58	0.002	9364	24.5
Mattole 2001	179	18.8	15.9	14	1.24	0.004	764	22.8
Redwood 2003	290	19.6	14.8	13	1.41	0.007	724	21.1
Russian 2004	112	21.1	4.1	34	1.45	0.002	3793	22.1
<i>N Oregon Coastal</i>								
Nehalem 2000	164	17.0	34.8	47	1.45	0.002	2179	18.1
Siletz 2001	411	17.0	38.4	29	1.32	0.010	744	15.1
<i>Puget Sound</i>								
Deschutes 2003	133	18.1	31.1	6	1.36	0.006	412	15.9
Nooksack 2001	184	17.5	47.5	70	1.59	0.003	2047	13.2
Snoqualmie 2006	162	17.8	45.8	77	1.49	0.003	1793	16.7
NF Stillaguamish 2001	195	17.7	44.7	62	1.31	0.004	1723	14.0
SF Stillaguamish 2001	245	17.2	55.6	30	1.50	0.006	657	14.0
<i>S Oregon Coastal</i>								
Applegate 1998	169	20.9	14.0	21	1.72	0.004	1991	18.9
Applegate 1999	167	20.9	14.1	19	1.70	0.004	1994	21.0
Cow 2000	186	20.4	16.7	14	1.43	0.005	1291	20.0
Evans 2003	506	20.5	15.0	4	1.36	0.011	581	19.7
Little Butte 2001	565	20.0	18.1	8	1.65	0.015	967	22.1
North Umpqua 2002	176	20.4	18.7	48	1.73	0.005	3529	24.4
Rogue 2003	286	20.8	17.2	152	2.07	0.002	13336	23.0
Umpqua 2002	115	19.8	19.5	138	1.81	0.003	10907	25.1

(Table S3.5 continued)

River and year of survey	Mean elevation ²	Mean August air temp. ³	Mean August precip. ⁴	Discharge ⁵ at base of survey (m ³ /s)	Mean velocity ⁶	Mean gradient ⁷	Cumulative drainage area (km ²) ⁸	Mean tributary temp. ⁹
<i>Upper Columbia</i>								
Entiat 2001	620	18.1	16.9	10	1.73	0.011	1079	17.3
Wenatchee 2001	379	18.4	19.4	45	1.70	0.007	2374	19.6
<i>Washington Coastal</i>								
Hoh 2000	97	16.4	74.3	57	1.59	0.004	772	14.6
Willapa 2001	86	16.8	43.6	14	1.10	0.002	616	17.0
Molalla 2004	318	18.2	30.1	26	1.57	0.009	892	19.7
Pudding 2004	101	19.4	21.9	19	1.10	0.001	1373	26.0
Thomas 2000	202	18.1	30.4	10	1.43	0.009	372	20.4
Tualatin 1999	278	19.3	22.6	27	1.21	0.003	1836	15.3
Yamhill 2005	41	19.4	15.2	60	1.28	0.001	2000	21.8
<i>Yakima</i>								
Naches 2004	251	19.2	13.5	48	2.03	0.009	2852	17.1
Surveys that met relaxed filter criteria								
<i>Bear</i>								
Smiths Fork 2006	154	15.8	28.0	5	1.50	0.005	710	14.0
<i>Deschutes</i>								
North Fork Crooked 2005	195	16.7	20.4	3	1.45	0.006	837	23.6
<i>Klamath</i>								
Sycan 1999	418	16.2	16.8	3	1.21	0.005	1446	14.4
<i>Lower Snake</i>								
Catherine 1999	710	18.2	28.2	3	1.30	0.018	809	16.4
Lemhi 2001	244	18.1	23.8	8	2.05	0.008	2903	19.1
Little Salmon 2004	432	18.1	22.8	5	1.06	0.007	897	19.3
Middle Fork Salmon 2001	475	17.3	23.9	62	1.93	0.007	7420	19.6
<i>Middle Snake</i>								
North Fork Malheur 1998	526	17.2	18.8	3	1.43	0.012	1125	20.0
<i>N Oregon Coastal</i>								
Siuslaw 2002	59	18.9	21.0	9	1.23	0.002	820	17.6

(Table S3.5 continued)

River and year of survey	Mean elevation ²	Mean August air temp. ³	Mean August precip. ⁴	Discharge ⁵ at base of survey (m ³ /s)	Mean velocity ⁶	Mean gradient ⁷	Cumulative drainage area (km ²) ⁸	Mean tributary temp. ⁹
<i>Upper Columbia</i>								
Wenatchee 2002	192	20.5	13.0	77	1.88	0.004	3442	17.0

(Table S3.5 continued)

¹ Source: Attributes of 1:100,000-scale stream reaches in the NHDPlusV2 hydrography dataset [McKay et al. 2012]

² elevslope table (mean of MAXELEVSMO and MINELEVSMO)

³ IncrTempMM08.txt (V) over the period of record; ⁴ IncrPrecipMM08.txt (V) over the period of record

⁵ EROM model (Q0001E); ⁶ EROM model (V0001E); ⁷ elevslope table (SLOPE); ⁸ PlusFlowlineVAA table (TotDASqKM, km² at the lowest point in the survey)

⁹ From TIR surveys; ¹⁰ Surveys that met strict filter criteria were included in analyses reported in the main text

Table S 3.6. The number (and percent) of longitudinal profiles in to each profile class under strict versus relaxed inclusion criteria (top), and comparing first and second best profile classes (bottom).

	Asymptotic	Linear	Parabolic	Uniform	Complex	Total	
						n	(%)
Classification based on best model fit							
Strict criteria ¹	27	9	8	4	10	58	85%
Relaxed stream order	1	2	0	0	0	3	4%
Relaxed mid-point	3	1	0	1	2	7	10%
Total	31	12	8	5	12	68	
Strict criteria (%)	46.6%	15.5%	13.8%	6.9%	17.2%		
Relaxed criteria (%)	45.6%	17.6%	11.7%	7.4%	17.6%		
Classification based on second best fit							
Strict criteria	22	15	6	2	13	58	85%
Relaxed stream order	0	2	1	0	0	3	4%
Relaxed mid-point	4	3	0	0	0	7	10%
Total	26	20	7	2	13	68	
Strict criteria (%)	37.9%	25.9%	10.3%	3.4%	22.4%		
Relaxed criteria (%)	38.2%	29.4%	10.3%	2.9%	19.1%		

¹ Results reported in the main text

Table S 3.7. Hydroclimatic and network variables associated with each profile.

River and year of survey	Partial correlation coefficients (r) between variable and TIR water temperature ¹								Significant confluence density ²	Tributary density ³	Basin shape ⁴
	Elevation	Mean August air temp.	Mean August precip.	Discharge	Velocity	Gradient	Tributary temp.	Distance upstream			
Surveys that met strict filter criteria											
<i>Bear</i>											
Cub 2006	-0.78	0.72	-0.72	-0.16	-0.26	-0.85	0.78	-0.85	0.01	0.73	0.20
<i>Deschutes</i>											
Crooked 2005	-0.03	0.25	-0.60	0.56	-0.01	0.00	0.74	0.46	0.01	0.50	0.13
Little Deschutes 2001	-0.73	0.48	-0.48	0.21	0.41	-0.32	0.72	-0.71	0.03	0.24	0.11
Whychus 2000	-0.14	0.24	-0.44	0.36	-0.31	-0.16	0.71	-0.87	0.05	0.27	0.10
<i>John Day</i>											
John Day 2004	-0.92	0.78	-0.57	0.21	0.32	-0.72	0.83	-0.68	0.03	0.73	0.10
MF John Day 1998	0.12	-0.05	-0.40	0.05	-0.11	-0.09	0.61	-0.82	0.08	0.79	0.09
MF John Day 2003	0.12	-0.05	-0.40	0.05	-0.11	-0.09	0.61	-0.82	0.08	0.79	0.09
NF John Day 2002	-0.51	0.43	-0.62	-0.20	0.10	0.01	0.42	-0.92	0.04	0.78	0.23
SF John Day 2003	-0.23	0.14	-0.08	0.04	-0.07	-0.31	0.89	-0.26	0.11	0.75	0.09
<i>Klamath</i>											
Scott 2003	-0.39	-0.38	-0.05	-0.33	-0.15	-0.50	0.66	-0.28	0.11	0.66	0.16
Scott 2006	0.35	-0.40	0.55	-0.57	-0.51	-0.62	0.72	-0.09	0.07	0.66	0.16
Shasta 2003	-0.02	-0.70	-0.49	0.07	0.29	0.29	-0.56	-0.91	0.05	0.39	0.32
Sprague 1999	-0.91	0.83	-0.10	0.11	-0.10	-0.63	0.73	-0.36	0.02	0.55	0.14
Sprague 2007	-0.13	0.16	0.34	-0.05	0.24	-0.08	0.57	-0.05	0.04	0.55	0.14
Williamson 1999	0.84	-0.79	0.80	-0.19	-0.03	0.16	0.50	0.10	0.07	0.45	0.36
<i>Lower Columbia</i>											
Sandy 2001	-0.53	0.33	-0.13	0.16	0.30	-0.60	0.43	-0.89	0.09	0.83	0.17
<i>Lower Snake</i>											
Clearwater 2000	-0.35	0.48	0.09	-0.28	-0.02	-0.10	0.55	-0.83	0.05	0.80	0.20
Grande Ronde 1999	-0.56	0.44	-0.51	-0.81	-0.09	-0.52	0.66	-0.03	0.04	0.69	0.13
Joseph 1999	-0.07	-0.13	-0.20	-0.05	0.15	-0.33	0.73	-0.56	0.07	0.69	0.09
Lochsa 2000	-0.02	0.36	-0.03	-0.37	0.02	-0.06	0.09	-0.90	0.02	0.77	0.27
Minam 1999	0.02	-0.04	-0.08	-0.33	-0.13	-0.07	-0.14	-0.99	0.05	0.63	0.08
Salmon 2001	-0.13	0.50	-0.33	-0.52	-0.03	-0.10	0.81	-0.72	0.02	0.72	0.08
Selway 2000	0.59	-0.17	-0.07	-0.44	-0.12	-0.06	0.02	-0.94	0.04	0.77	0.23

River and year of survey	Partial correlation coefficients (r) between variable and TIR water temperature ¹								Significant confluence density ²	Tributary density ³	Basin shape ⁴
	Elevation	Mean August air temp.	Mean August precip.	Discharge	Velocity	Gradient	Tributary temp.	Distance upstream			
Wallowa 1999	0.67	-0.48	0.67	0.36	-0.14	-0.09	-0.29	-0.58	0.06	0.61	0.22
<i>Middle Columbia</i>											
Eightmile 20025	-0.72	0.72	-0.49	-0.26	-0.29	-0.73	0.53	-0.92	0.07	1.02	0.17
Fifteenmile 2002	-0.72	0.81	-0.46	-0.32	-0.11	-0.66	0.95	-0.87	0.04	0.91	0.10
Touchet 2002	-0.92	0.92	-0.85	0.89	0.11	-0.77	0.91	-0.73	0.05	0.80	0.09
Walla Walla 2000	-0.90	0.86	-0.76	-0.40	0.47	-0.45	0.80	-0.81	0.08	0.74	0.35
Walla Walla 2003	-0.87	0.78	-0.59	-0.28	0.38	-0.32	0.60	-0.88	0.06	0.74	0.35
<i>N California Coastal</i>											
Eel 2005	-0.75	0.80	0.49	-0.61	-0.32	-0.12	0.40	0.76	0.02	0.87	0.10
Mattole 2001	-0.89	0.89	-0.33	-0.86	0.22	-0.19	0.32	-0.65	0.12	0.89	0.07
Redwood 2003	-0.86	0.74	-0.31	-0.72	-0.20	-0.42	-0.10	0.14	0.11	0.72	0.07
Russian 2004	-0.63	0.73	-0.34	-0.54	0.39	0.14	0.64	-0.85	0.04	0.78	0.10
<i>N Oregon Coastal</i>											
Nehalem 2000	0.37	0.71	-0.23	-0.57	0.16	-0.18	0.38	-0.20	0.07	0.68	0.06
Siletz 2001	-0.90	0.70	-0.68	0.78	0.53	-0.71	0.48	-0.83	0.06	0.94	0.05
<i>Puget Sound</i>											
Deschutes 2003	-0.54	0.32	-0.46	0.12	-0.19	-0.62	0.55	0.24	0.05	0.58	0.06
Nooksack 2001	-0.53	0.31	-0.29	-0.50	-0.30	0.07	0.67	-0.16	0.03	0.60	0.14
Snoqualmie 2006	-0.19	-0.03	-0.04	-0.21	0.09	-0.03	0.02	-0.65	0.05	0.70	0.11
NF Stillaguamish 2001	-0.18	0.07	0.06	0.08	0.16	-0.17	0.25	-0.80	0.04	0.69	0.14
SF Stillaguamish 2001	-0.41	0.30	-0.10	-0.07	0.33	0.38	0.39	-0.81	0.05	0.62	0.05
<i>S Oregon Coastal</i>											
Applegate 1998	-0.34	-0.19	-0.01	0.13	0.01	0.07	0.40	-0.94	0.04	0.63	0.22
Applegate 1999	-0.78	-0.43	-0.28	0.23	-0.08	-0.31	0.40	-0.89	0.04	0.63	0.22
Cow 2000	0.12	0.29	-0.64	-0.22	0.04	-0.21	0.38	-0.88	0.06	0.66	0.03
Evans 2003	-0.47	0.42	-0.16	-0.01	0.19	-0.28	0.93	-0.97	0.11	0.66	0.09
Little Butte 2001	-0.81	0.78	0.88	-0.10	0.12	-0.58	0.63	-0.79	0.10	0.54	0.24
North Umpqua 2002	-0.08	0.21	-0.57	0.05	0.00	-0.02	0.72	-0.98	0.08	0.62	0.25
Rogue 2003	-0.17	0.66	-0.74	-0.47	-0.10	-0.04	0.25	-0.92	0.02	0.62	0.11
Umpqua 2002	-0.84	0.21	-0.44	-0.38	-0.02	-0.40	0.67	-0.53	0.03	0.64	0.09

(Table S 3.7 continued)

River and year of survey	Partial correlation coefficients (r) between variable and TIR water temperature ¹								Significant confluence density ²	Tributary density ³	Basin shape ⁴
	Elevation	Mean August air temp.	Mean August precip.	Discharge	Velocity	Gradient	Tributary temp.	Distance upstream			
<i>Upper Columbia</i>											
Entiat 2001	-0.63	0.62	-0.49	0.09	0.02	-0.14	0.44	-0.98	0.06	0.77	0.15
Wenatchee 2001	-0.59	0.82	-0.63	-0.21	-0.26	-0.49	0.59	-0.87	0.07	0.68	0.15
<i>Washington Coastal</i>											
Hoh 2000	-0.25	0.03	0.17	0.10	-0.07	0.05	0.41	-0.77	0.02	0.57	0.10
Willapa 2001	-0.50	-0.51	-0.09	0.05	0.01	-0.45	-0.23	-0.69	0.15	0.80	0.12
<i>Willamette</i>											
Molalla 2004	-0.75	0.50	-0.45	-0.16	0.68	-0.34	0.52	-0.92	0.11	0.69	0.17
Pudding 2004	-0.49	0.44	-0.36	-0.13	-0.08	-0.43	0.79	-0.04	0.09	0.77	0.15
Thomas 2000	-0.55	0.52	0.23	0.15	0.57	-0.13	0.34	-0.84	0.06	0.63	0.09
Tualatin 19995	0.00	-0.11	0.00	-0.32	-0.02	-0.01	0.53	-0.70	0.06	0.78	0.12
Yamhill 2005	-0.48	0.38	0.23	0.20	0.34	-0.03	0.43	-0.62	0.08	0.78	0.15
<i>Yakima</i>											
Naches 2004	0.29	-0.65	0.68	0.07	-0.10	-0.04	0.24	0.55	0.08	0.77	0.28
Surveys that met relaxed filter criteria											
<i>Bear</i>											
Smiths Fork 2006	0.06	0.07	-0.15	-0.09	-0.11	-0.10	0.27	-0.81	0.06	0.80	0.12
<i>Deschutes</i>											
NF Crooked 2005	0.05	-0.14	0.00	0.18	-0.22	-0.25	NA	-0.27	0.06	0.76	0.05
<i>Klamath</i>											
Sycan 1999	-0.56	0.49	0.18	-0.09	-0.04	-0.17	0.57	-0.76	0.06	0.63	0.03
<i>Lower Snake</i>											
Catherine 1999	-0.30	0.36	0.28	0.53	0.10	-0.28	0.90	-0.92	0.08	0.61	0.04
Lemhi 2001	0.14	-0.01	-0.27	-0.22	-0.19	-0.38	NA	-0.94	0.02	0.54	0.20
Little Salmon 2004	-0.69	0.59	-0.60	-0.18	0.00	-0.61	-0.07	0.04	0.14	0.79	0.18
MF Salmon 2001	-0.82	0.72	-0.56	-0.77	-0.16	-0.21	NA	-0.86	0.04	0.77	0.16
<i>Middle Snake</i>											
NF Malheur 1998	-0.49	-0.57	-0.12	0.30	0.28	-0.43	0.28	-0.94	0.10	0.75	0.13
<i>N Oregon Coastal</i>											
Siuslaw 2002	0.38	0.38	-0.33	-0.32	-0.08	0.19	0.48	-0.94	0.05	0.80	0.03

(Table S 3.7 continued)

River and year of survey	Partial correlation coefficients (r) between variable and TIR water temperature ¹								Significant confluence density ²	Tributary density ³	Basin shape ⁴
	Elevation	Mean August air temp.	Mean August precip.	Discharge	Velocity	Gradient	Tributary temp.	Distance upstream			
<i>Upper Columbia</i>											
Wenatchee 2002	0.22	0.10	0.29	-0.22	-0.19	-0.35	0.21	-0.85	0.04	0.72	0.21

(Table S 3.7 continued)

¹ the partial correlation between remotely sensed river temperature and hydroclimatic variables discretized at 1-km intervals over the length of each profile; bold values indicate significance at p<0.05.

² the number of confluences contributing >10% of the flow divided by the length of the survey

³ the total length of all tributaries in the contributing drainage divided by the drainage area (km/km²) at the base of the survey

⁴ the drainage area divided by the square of the length of the mainstem (Benda et al. 2004)

⁵ there was only 1 tributary for this river so correlations could not be computed; the value listed is the mean of other surveys

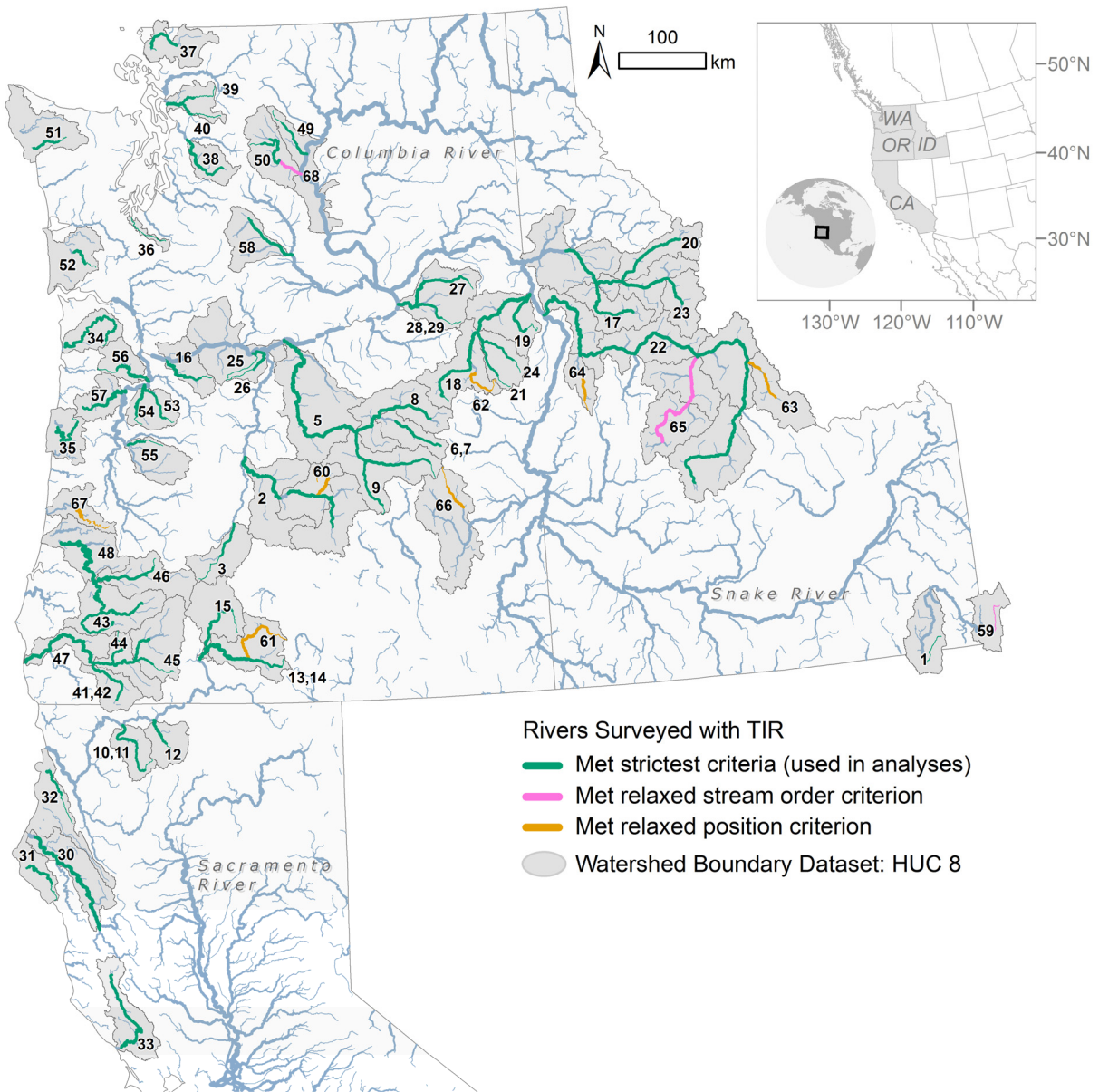


Figure S 3.1. Spatial extents of thermal infrared surveys (TIR) used to evaluate shapes of thermal profiles. Information about each profile (river name, characteristics) is presented in **Table 3.1** and can be referenced using the values on the map. Surveys meeting strict criteria (survey length >50 km; covering >50% of river length; crossing >1 Strahler stream order, and centered in the middle 3rd of the river), shown in green, were used in analyses. Surveys without a stream order criterion (pink) or meeting a relaxed position criterion (centered in the middle half of the river; orange) were used in supplementary analyses only. Stream order is represented by line thickness.

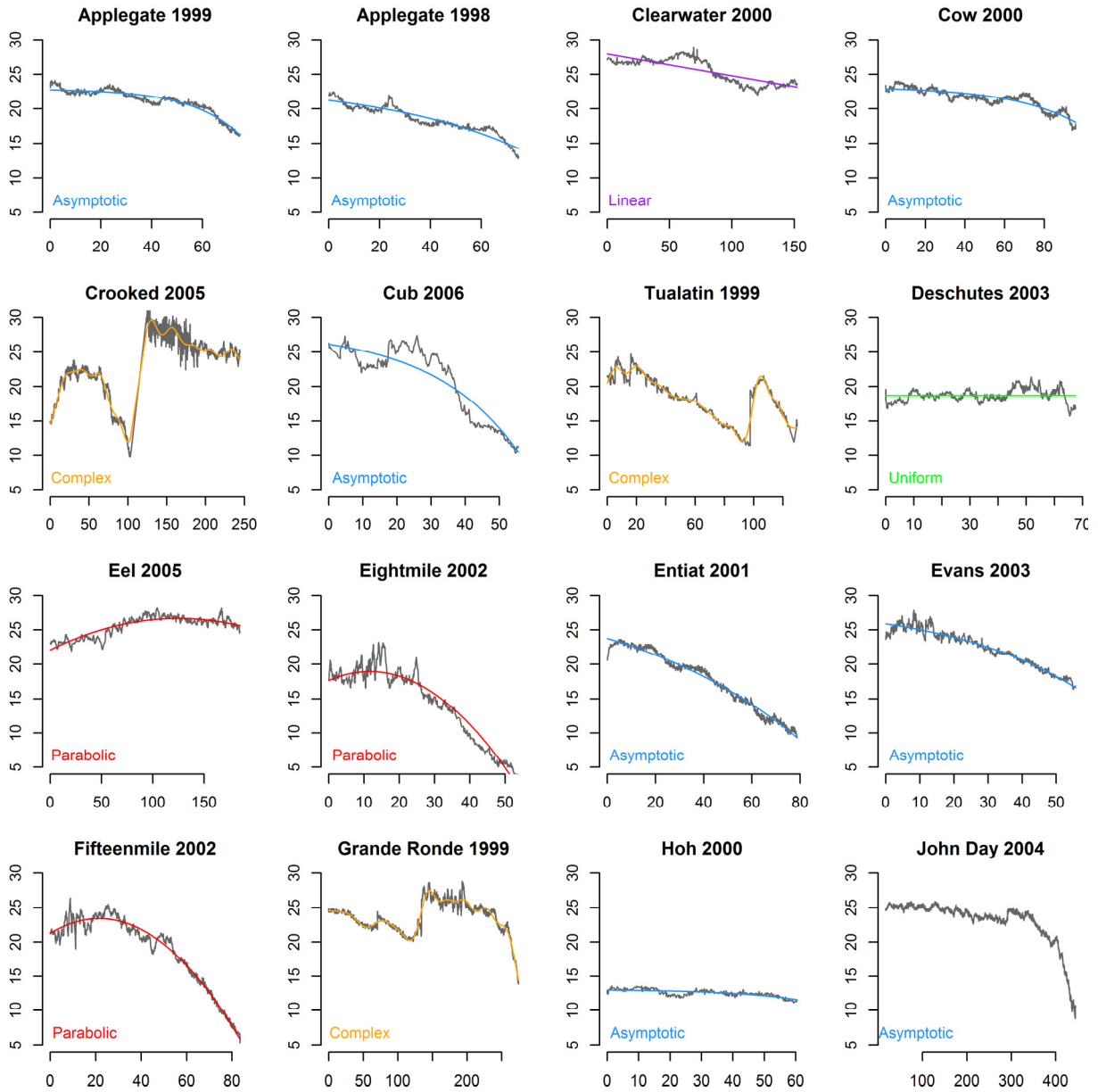


Figure S 3.2. Longitudinal profiles of river temperature ($^{\circ}\text{C}$) (ordinate) versus distance upstream (km) (abscissa) for each river that met strict criteria for inclusion in analyses. In each panel, water temperature from remotely sensed thermal infrared surveys is plotted in gray. Shape for the best-fitting profile class is plotted in color, where blue = asymptotic; purple = linear; red = parabolic; green = uniform; and orange = complex. The asymptotic model did not converge for the John Day 2004 and North Fork John Day 2002 surveys; model fits for other shape classes were poor. Therefore, we classified these profiles as asymptotic because visual assessments by 4 coauthors unanimously agreed that this profile shape was appropriate. Continued on next page.

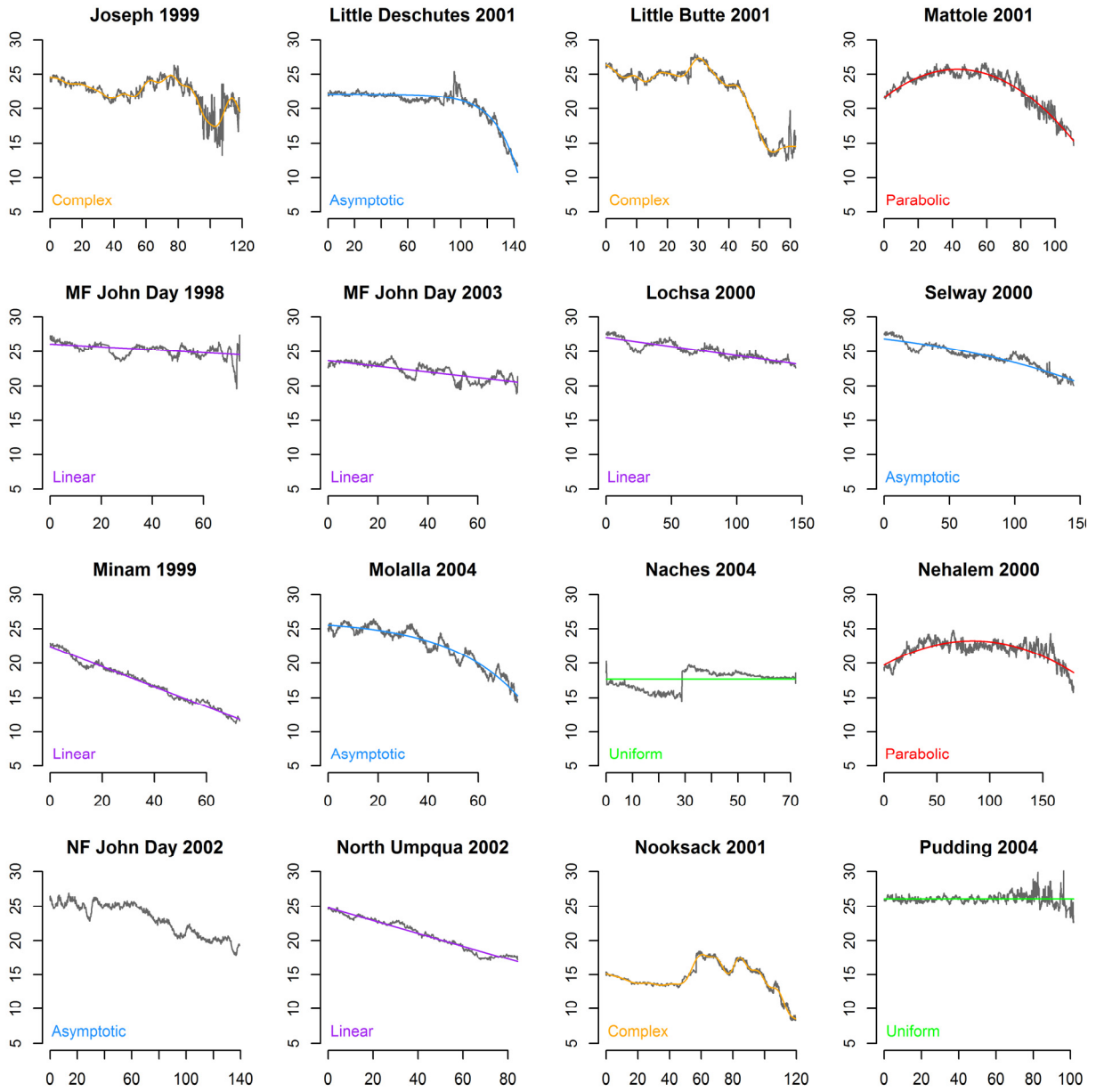


Figure S 3.2 (continued).

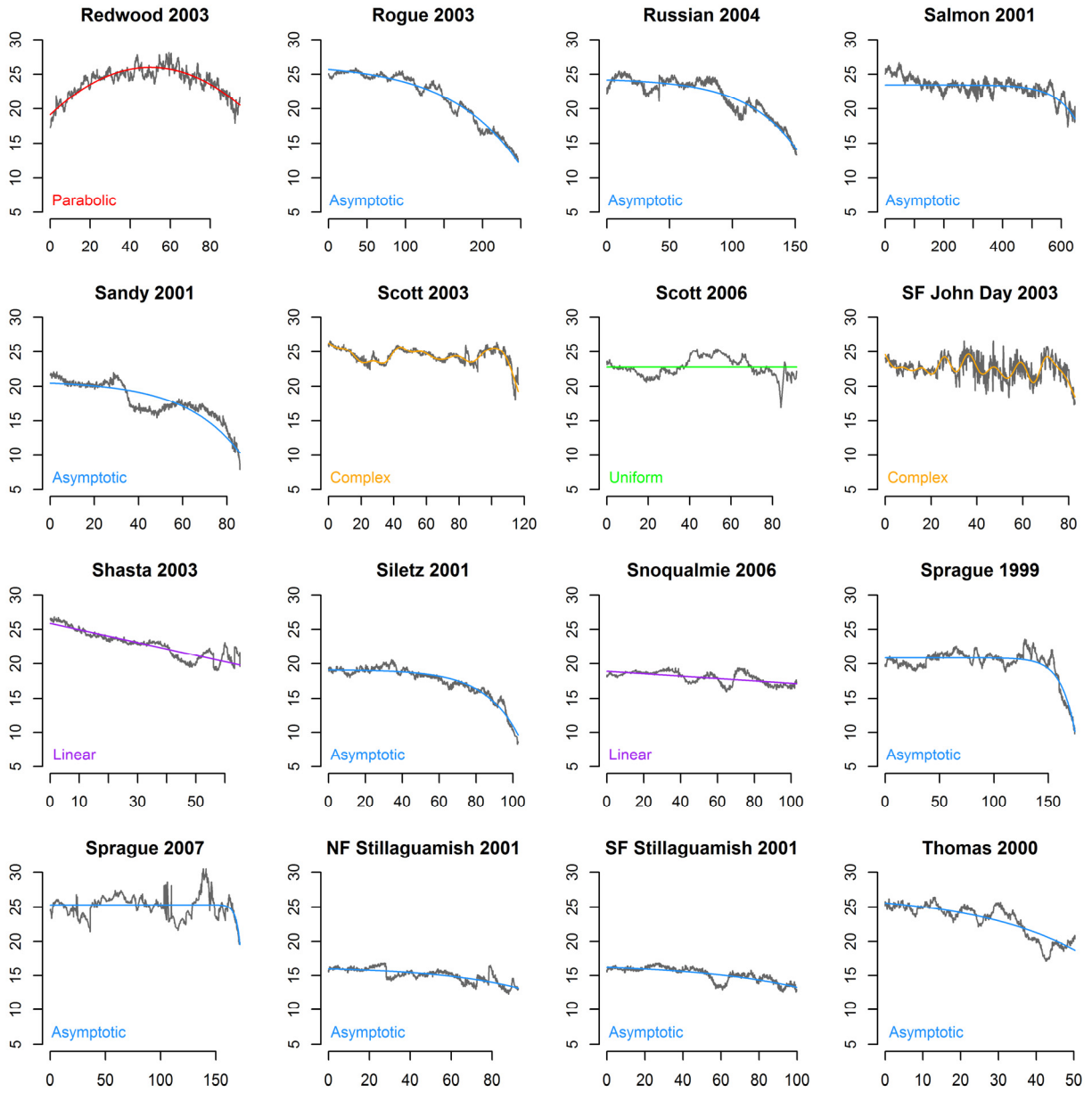


Figure S 3.2 (continued).

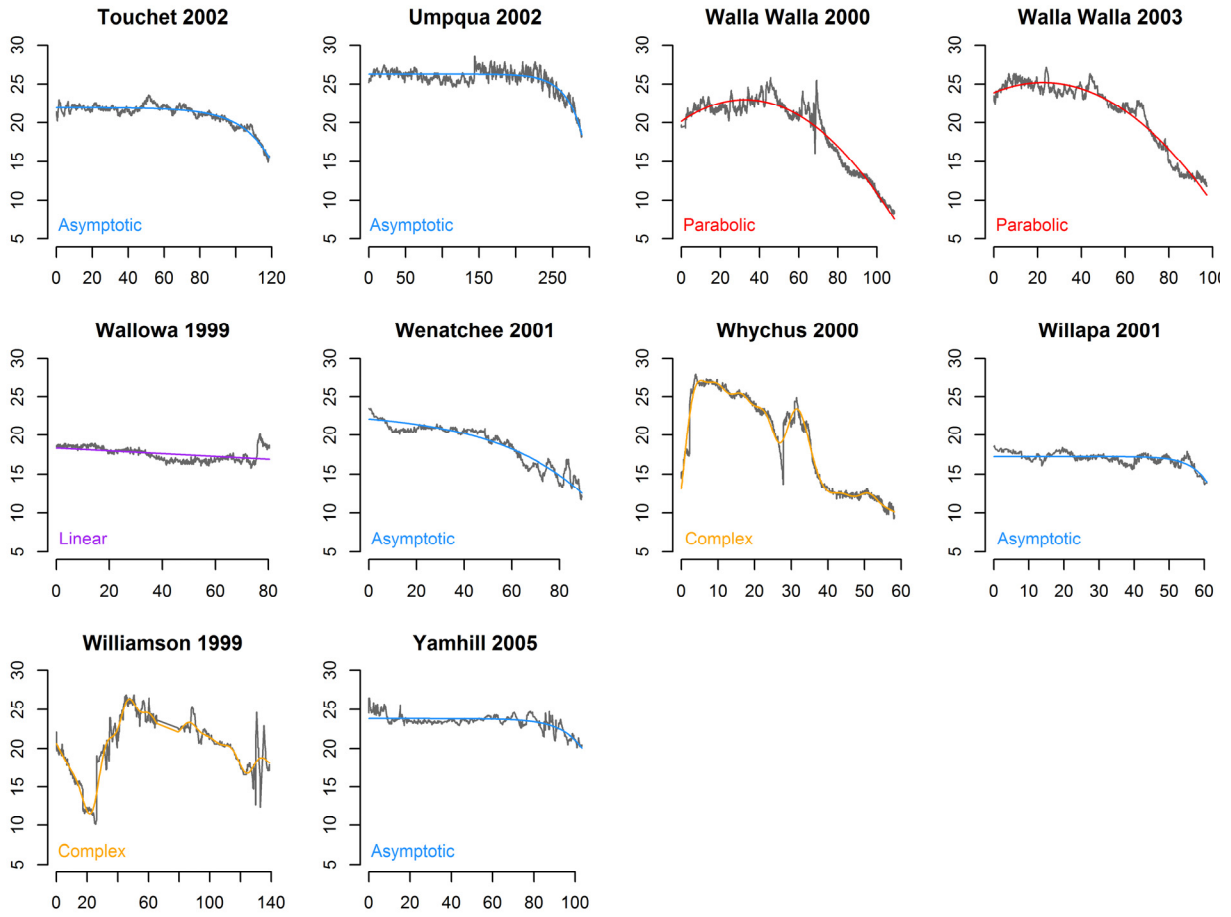


Figure S 3.2 (continued).

Chapter 4. Thermal heterogeneity may support Pacific salmon in many rivers as waters warm

4.1. Abstract

Cold water is an essential component of suitable habitat for Pacific salmon (*Oncorhynchus* spp.). However, many rivers through which these fish migrate as both smolts and again as adults can be warmer than physiological preferences or even tolerances. Fish are known to make use of cold water “refuges” within an otherwise too-warm stream environment. The ability of salmon to contend with warming water due to climate change will depend on whether patches of cold water remain prevalent, large enough, and sufficiently distributed for fish to move among essential habitats. I quantified summer thermal heterogeneity patterns for over 12,000 km of 2nd to 7th-order rivers throughout the Pacific Northwest and California using high-resolution remotely sensed water temperature data. I evaluated: (1) the frequency, size and spacing of cold water patches, (2) potential influences of climate change on thermal heterogeneity patterns, and (3) the ability to resolve spatial patterns at decreasing spatial resolution of water temperature data. Across all rivers, median size and spacing of cool patches <15 °C were both around 250 m. Patches of this size are large enough for juvenile rearing and for resting during migration, and the distance between patches is well within the movement capabilities of both juvenile and adult salmon. However, thermal heterogeneity patterns were highly river-specific, with some rivers having very long stretches of warm habitat with few cool patches. I used two approaches for predicting potential future thermal heterogeneity patterns. In one, I considered how thermal heterogeneity would change if longitudinal profiles (water temperature versus distance upstream) retained their existing shape but warmed by 0.5 to 3°C. In the second, I used three variables from downscaled global climate model projections, August air temperature, mean annual precipitation, and the probability that winter precipitation will fall as snow, in random forest models to predict future thermal heterogeneity patterns. In both cases, I found little change overall, but large change in individual rivers or in portions of rivers. Metrics describing the density, size, and spacing of patches were nonlinearly related to the resolution of water temperature. Heterogeneity apparent at fine scales (<1 km) may be important to fish; this level of detail may be difficult to quantify without spatially continuous empirical data. Results from this research can inform monitoring strategies as well as near-term climate-ready conservation priorities.

4.2. Introduction

Regional climate models suggest that the Pacific Northwest (USA) will see warmer drier summers and wetter winters, and in many mid-elevation areas, winter precipitation that previously fell as snow will fall as rain (Dalton et al. 2013, Hamlet et al. 2013, Mote et al. 2013). Summer flows are projected to decrease across most of the Pacific Northwest due to decreased snowpack, reduced summer precipitation, and higher evaporation caused by warmer summer temperatures (Jefferson 2011, Leibowitz et al. 2012, Tohver et al. 2014). Lower flows will enhance stream warming during summer because of lower water volumes (i.e., reduced thermal inertia). River temperatures have already increased (Arismendi et al. 2012, Isaak et al. 2012) and will continue to do so. For instance, Wu et al. (2012) predicted an increase of 0.55 and 1.68 °C in mean annual stream temperatures for 12 Pacific Northwest rivers by the 2020s and 2080s, respectively. Effects are expected to be greatest in rain-dominated and transitional (i.e., rain-on-snow hydrology) basins, mainly because the most arid regions are already very dry.

Conservation and management of freshwater habitat for cold-water species will increasingly require ways to assess and maintain suitable thermal landscapes. Pacific salmonids (*Oncorhynchus* spp.) have evolved in freshwater systems with abundant cold water, and are adapted to thermal regimes that naturally vary over time and across space (Waples et al. 2008, McCullough et al. 2009, Beechie et al. 2012). Rising air temperature and changes in hydrology were correlated with salmon extinctions in California (Zeug et al. 2011) and Japan (Fukushima et al. 2011). Vulnerability analyses for extant populations of Pacific salmon have predicted that large portions of species ranges within freshwater environments will become unsuitable in the future (Mantua et al. 2010, Wenger et al. 2011, Isaak and Rieman 2013, Wade et al. 2013). Risk is expected to increase as changes to thermal and hydrologic conditions negatively influence growth and survival (Crozier et al. 2010, Xu et al. 2010, Walters et al. 2013, Lawrence et al. 2014) and alter phenology (Kovach et al. 2013, Crozier and Hutchings 2014, Otero et al. 2014).

A large body of research has evaluated temporal patterns in water temperature and how salmon respond to natural and altered thermal regimes (Steel et al. 2012, Arismendi et al. 2013, Penaluna et al. 2015). However, far fewer studies have attempted to describe *spatial* patterns in water temperature and to consider potential consequences for salmon of changes in thermal heterogeneity due to climate change. Thermal regimes can be quite diverse at broad spatial scales (e.g., among rivers) (Lisi et al. 2013, Chapter 2) and at fine spatial scales (e.g., 1-100 m)

(Dugdale et al. 2015), but we know little about patterns of thermal heterogeneity at intermediate scales (e.g., 10s to 100s of m). Sensitivity of water temperature to climate change will differ across space (van Vliet et al. 2011, Arismendi et al. 2012). The ability of salmon to contend with warmer future summer water temperature will depend on whether patches of cold water remain prevalent, large enough, and sufficiently distributed for fish to move among essential habitats.

I used remotely sensed spatially continuous water temperature data to explore within-river thermal heterogeneity throughout the Pacific Northwest. I characterized existing and potential future patterns of summertime thermal heterogeneity in terms of cold-water patches available to Pacific salmon at an intermediate scale (i.e., patches 10s to 100s of m long). Specifically, my research addressed three questions: (1) Are the frequency, size and spacing of cold water patches in Pacific Northwest rivers sufficient to meet needs of salmon during summer?, (2) How might climate change influence thermal heterogeneity patterns?, and (3) What spatial resolution of water temperature data is sufficient to resolve biologically relevant thermal heterogeneity?

4.3. Methods

4.3.1. Study Area

We considered a sample of watersheds across Washington, Oregon, Idaho, and northern California (USA). Precipitation in the region occurs predominantly from October to March and falls as snow or rain, depending mainly on elevation and proximity to the Pacific Ocean. Snowmelt contributes significantly to stream flow from April to September in snowmelt dominated and transitional watersheds (Hamlet 2010). Human population density in the study watersheds ranges from low (e.g., roadless areas in Idaho) to high (e.g., near major cities). Human influences on processes controlling hydrology and temperature include major hydropower facilities, water diversion for irrigation, forest management, and altered riparian vegetation associated with agriculture and urban development.

4.3.2. Water Temperature Data

River temperature surveys were conducted using airborne thermal infrared (TIR) remote sensing, as described in Chapter 3. All surveys occurred during the afternoon in July or August between 1994 and 2007, when water temperatures were expected to be near the daily and annual maximum and likely to be most limiting to aquatic biota. Instream thermal sensors were used to

ground-truth remotely sensed temperatures; mean accuracy was generally within 0.5 °C. Thermal image data were georeferenced and water temperatures were subsampled from images at approximately 150- to 200-m intervals along the thalweg of each river. We created longitudinal profiles for each river using plots of water temperature versus distance from the downstream end of the survey.

Unlike the profile trend analysis described in the preceding chapter which only used data representative of whole rivers, this analysis included all datasets that were at least 20 km long and which was considered habitat for anadromous salmon (i.e., as identified in state geodatabases). I chose the length criterion to minimize edge effects associated with smoothing used in some analyses (described later). This resulted in a total of 12,341 km of surveyed thermal habitat (reduced from a total >16,000 km) throughout the Pacific Northwest and northern California (**Figure 4.1**).

The water temperature data were not a random sample of rivers in the region (i.e., surveys were originally commissioned for other projects). Surveys generally occurred in mid to large-order streams (**Table 4.1**); tributary habitat was not well represented because vegetation obscures narrower waterways making collection of remotely sensed water temperatures less feasible. Surveys covered up to about 30% of the geographic distribution of many anadromous salmonids, but were more representative for mainstem spawners like Chinook salmon (*O. tshawytscha*) than for tributary spawners like coho (*O. kisutch*) and steelhead (*O. mykiss*). Surveys occurred predominantly in forested areas, but also occurred in open natural areas and some developed areas. Ranges in values were large among surveys for discharge, velocity, elevation, slope, air temperature, and precipitation amount and timing (**Table 4.2**). Collectively, surveys encompassed a diverse suite of habitat conditions throughout the Pacific Northwest and northern California.

4.3.3. Characterizing Thermal Heterogeneity

4.3.3.1. Threshold-based Metrics

Water temperatures to which salmonids are sensitive depend on species, life stage, geographic location, acclimation history and a variety of other factors (McCullough et al. 2009). Here, I classified thermal riverine habitat into three zones generally considered to be optimal, tolerable, and stressful for Pacific salmon and trout. These zones correspond to EPA criteria for 7 day average of daily maxima; see Table 3 in Palmer et al. (2003). The optimal or “cool” zone

encompasses anything below 15 °C, a summer temperature below which many salmonids can thrive. The “tolerable” zone consists of water temperatures between 15 and 20 °C, and the unsuitable or “warm” zone comprises temperatures above 20 °C. The 20 °C threshold denotes temperatures above which survival and fitness of adults migrating upstream may be decreased and growth and survival of juveniles may be depressed (i.e., due to increased metabolic costs, susceptibility to pathogens, decreased ability to successfully compete or evade predators, impaired smoltification, etc.) (Palmer et al. 2003).

To describe thermal habitats available to salmon in rivers for which TIR data were available, I first allocated each longitudinal thermal profile into the three thermal zones. Specifically, I recorded each location along the longitudinal profile where temperature crossed a threshold into a new thermal zone. The result was a series of river segments, classified as belonging to one of three thermal zones. Hereafter, I refer to these as *cool*, *tolerable*, and *warm* patches (**Figure S 4.1**, top panel).

Next, I used summary metrics to quantify the density, length, and spacing of thermal patches in each river, and summarized pooled metrics across the suite of rivers considered (**Table 4.3**). All analyses were conducted in R (R Development Core Team 2015).

4.3.3.2. Peak-valley Metrics

Fish can acclimate to water temperature over time, and previous experience can influence how they perceive water temperature as they move through rivers. Areas that are cooler relative to surrounding habitat may represent relative reprieve compared to what fish recently experienced in adjacent reaches, even though the cooler temperature is still suboptimal. This way of thinking about thermal heterogeneity is complementary to the threshold-based analysis described above that simply treats everything above a 20 °C threshold as too warm for salmon. Here, I explored patches of relatively cooler (warmer) habitat within the *warm* zone (i.e., within reaches above the 20 °C threshold).

My approach was to overlay a smoothed trend on each longitudinal thermal profile (i.e., raw TIR data), and use the intersection of these lines to identify valleys (and peaks) that may be perceived as thermal refuges (or barriers) by fish (**Figure S 4.1**, bottom panel). Stretches of the trend that dipped below 20 °C were replaced with a line at 20 °C (i.e., I did not investigate relative peaks and valleys below this threshold). I computed the trend as a 10-km moving average so that results would be comparable across rivers of different length. The degree of

smoothing using other common smoothing techniques depends on the length of river analyzed. I chose this level of smoothing to balance simplicity with the need to have a trend that is sinuous enough to reflect temperatures experienced by fish as they are moving upstream or downstream. Even though a sinuous curve may seem overly complex for describing the dominant trend in longitudinal temperatures (Chapter 3), it is likely more congruous with how fish experience water temperature. Moving average computation shortens the length of a dataset (i.e., a centered 10-km moving average on a 50-km dataset yields a 40-km trend). To offset this loss of information, I duplicated the first and last 5 km of a dataset before smoothing. To evaluate the effect of this decision, I chopped long profiles into shorter segments and compared the trends on these segments to the real (known) data. Differences were typically very small (not shown).

I used three criteria to identify valleys (peaks) having potential to influence fish behavior, hereafter, *key* valleys (peaks): (1) a height criterion; (2) a length criterion, km; and (3) an area criterion, km-C. These criteria described minimum characteristics of valleys (peaks) relative to the adjusted trend line (i.e., for regions where temperatures exceeded 20 °C). The height criterion was set to 2°C, the standard regulatory amount by which a refuge must differ from surrounding mixed water (Torgersen et al. 2012). The area criterion, set to 0.5 km-C, conceptually represented the amount of habitat where temperatures were lower, for valleys, or higher, for peaks, than surrounding temperatures. The area of each valley (peak) was calculated as the area of a polygon with x values of length and y values of water temperature, appended to water temperature values from the adjusted trend over the same distance and location. I also imposed a length criterion to identify biologically useful valleys (peaks). For instance, both a very long valley with marginally lower temperature and a very short valley with a large drop in temperature may fulfill the area criterion but are unlikely to be useable as habitats by fish. The height criterion specified that the difference in temperature between the trend and a valley (peak) had to exceed 2 °C. The length criterion specified that a valley (peak) was at least 500 m long.

I quantified spatial pattern metrics for peaks and valleys in each river, and summarized pooled metrics across the suite of rivers considered (**Table 4.3**). For consistency, I computed patch density, although this metric is really not informative because the smoothing technique forces the number of peaks and valleys to be similar (an equal number above and below the trend line). Truncating the trend line at 20 °C could alter this equality because relative peaks and valleys below the threshold were not counted.

4.3.3.3. *Physiographic and Species Lenses*

Thermal heterogeneity patterns may differ in different parts of the region. For instance, in places where groundwater strongly influences water temperature, we might expect to see increased prevalence of cold water patches. Patterns may also differ for species having different thermal requirements. To get a sense for how responsive thermal heterogeneity patterns are to such factors, I (1) plotted patch metrics versus stream order, elevation, and drainage area; and (2) repeated the analysis using lower temperature thresholds (12 and 18 °C) to characterize patterns available to species with cooler thermal requirements.

4.3.4. Thermal Heterogeneity Given Climate Change

Thermal regimes in rivers will be influenced by climate change. Means, maxima and minima are expected to increase across many temporal scales (e.g., annually, seasonally, daily), and variability in thermal extremes is also likely to increase. However, less is known about how patchiness in space will change. For instance, will cold water patches remain accessible to fish navigating a river or will they become fewer in number and farther apart?

4.3.4.1. *Projecting Future Water Temperature Patterns: a Simple Approach*

One approach to estimating how thermal heterogeneity patterns may look in the future is to increase the entire longitudinal profile by a given amount (**Figure S 4.2**, top panel). This approach is supported by the temporal consistency of spatial patterns for surveys that were conducted in both cool and warm years (**Figure 3.1**). I represented future climate scenarios as increases in water temperature of 0.5, 1, 1.5, 2, 2.5, and 3 °C. No specific time periods were assumed. I then computed pattern metrics summarizing size, spacing, and density of patches for rivers in each climate scenario, as described above.

This approach was a simplification and requires several caveats. We know that some rivers are likely to be more sensitive to climate change than others (Arismendi et al. 2012, Isaak et al. 2012, Luce et al. 2014). For instance, correlations between air and water temperature differ among streams (**Figure S 4.3**), which may reflect differential contribution of groundwater or other controls on stream temperature over space. Moreover, climate change may alter covariates of water temperature differently across space (**Figure S 4.4**). Change may be slower in streams that are groundwater-fed, whereas change may be faster in snow-fed streams where snowpack is expected to decrease or disappear. This approach also did not incorporate projected changes in precipitation amount and timing, which are known to influence water temperature patterns.

4.3.4.2. Projecting Future Water Temperature Patterns Using Climate Covariates

I took steps toward addressing several of these concerns by also predicting potential future thermal heterogeneity patterns using a second approach. I used random forest regression (Breiman 2001, Cutler et al. 2007) to construct relationships between water temperature and three climate covariates suspected to be both highly related to water temperature and responsive to climate change: (1) maximum weekly air temperature between 16 July and 31 August, (2) mean annual precipitation, and (3) the proportion of precipitation that falls as snow during winter (Dec, Jan, Feb). I also included distance upstream (km) as a covariate. I chose random forest regression instead of other common techniques (e.g., generalized linear mixed models) because it is robust to anisotropy (data that are not stationary over space) and spatial autocorrelation (Cutler et al. 2007). Therefore, it accounts for spatial relationships between water temperature and covariates that differ over space. Moreover, data transformations are unnecessary and this approach is good for making predictions (as compared to identifying causal relationships, which was not my intent). All analyses were conducted in R (R Development Core Team 2015).

Fitted values for these models represented the portion of longitudinal trends that were explained by the three climate covariates (data sources and climate scenarios are described below). Residuals were assumed to be patchiness in longitudinal profiles not controlled by climate covariates. Rather, this finer scale heterogeneity is likely controlled by processes not included in models, such as local groundwater inputs, anomalies in adjacent landscape features or land use, network geometry or stream geomorphology. I predicted future longitudinal trends by substituting future values of the three climate covariates. I summed future trend profiles and residuals from the fitted model to get potential future longitudinal profiles (**Figure S 4.2**, bottom panel). Finally, I computed thermal heterogeneity metrics (patch density, size, and spacing) for the future scenario, and compared resulting patterns to the original spatial patterns computed using TIR data.

I considered covariate data from historical and future periods, where future values are representative of expectations under a greenhouse gas concentration scenario that is currently considered to be most realistic: representative concentration pathway (RCP) 8.5, a high emissions scenario (Taylor et al. 2012). Data were derived from downscaled projections from the 10 General Circulation Models (GCM) described in the fifth phase of the Coupled Model Intercomparison Project (CMIP5) (Taylor et al. 2012). GCMs were statistically downscaled to

1/16th degree resolution (about 5 x 7 km²) for the western US using the Multivariate Adaptive Constructed Analogs (MACA) method (Abatzoglou and Brown 2012). The same historical (1970-1999) and future (2070-2099) periods were used for air temperature and precipitation; time periods for the probability of winter precipitation falling as snow differed slightly: 1979-2012 and 2035-2065. Thus, estimates of this covariate are likely conservative for the 2080s.

Gridded air temperature and precipitation data for the region were provided by S. Lee, Climate Impacts Group, University of Washington. Maximum weekly air temperature for each week during 16 July – 31 Aug was calculated from downscaled daily maximum and minimum values for a given 30-year period (historical and future). Mean annual precipitation was calculated for entire years within each 30-year period. Future values were the median of projections by the 10 GCM models. Gridded data for the probability of winter precipitation falling as snow were obtained from Klos et al. (2014). Using a geographic information system (GIS), I attributed rivers having TIR data with values from the gridded air temperature, precipitation, and snow probability datasets. For each reach in the National Hydrography Dataset (version 2), I used a distance-weighted average of the nearest gridded value for use in random forest models.

4.3.5. Influence of Spatial Grain

I was interested in how characterization of thermal heterogeneity would differ across spatial resolution of water temperature data. Specifically, what biologically relevant patches might be missed or mischaracterized at coarser resolutions, given that we know the true distribution of patches at the finest resolution (i.e., the raw data)?

Using empirical TIR data, I binned mean water temperature at resolutions of 0.25, 0.5, 1, 2, 3, 4, and 5 km using the approach of Welty (2015). Binning data had a smoothing effect on the resulting patterns (**Figure S 4.5**). For data at each resolution, I computed the pattern metrics as described above.

4.4. Results

4.4.1. Thermal Heterogeneity is Prevalent and Complex

Water temperature was very warm during summer afternoons in many rivers throughout the region. Over 60% of the pooled length of rivers for which I had data was >20 °C, a

temperature above which conditions are thermally stressful for salmon (**Figure 4.2**, top panels). However, I found substantial thermal heterogeneity within rivers.

System-wide, the density of *cool* (<15 °C) and *tolerable* (15-20 °C) patches was higher than the density of *warm* patches (>20 °C) when I characterized patches using thermal zones (**Figure 4.2**). Cool patch densities were within the range observed by Dugdale et al. (2015). The density of relative peaks was similar to the density of valleys; however, this metric was influenced by the approach and is uninformative.

Warm patches were slightly longer than *cool* or *tolerable* patches, in general (**Figure 4.2**, third row, left). The median length of *cool* patches was about 250 m. However, there was considerable variance, wherein some rivers had very short patches and others had very long patches. Within habitat >20 °C, the length of peaks and valleys was similar (**Figure 4.2**, third row, right). Key peaks (2 °C warmer than the trend line) were slightly longer than key valleys (2 °C cooler than the trend line), but high variability obscured this pattern.

The median spacing between *cool* patches was about 250 m (**Figure 4.2**, bottom, left). This is well within the distance that fish can swim, both as juveniles and as adults. However, there was again considerable variance, suggesting that cold patches were closely spaced in some rivers but very distantly spaced in others. Within habitat >20 °C, the spacing between peaks and between valleys was similar (**Figure 4.2**, bottom, right). Key valleys were slightly farther apart than key peaks, but variability was very high.

Together, these results suggested an intuitive portrait of thermal heterogeneity in mid to large-order rivers. Density of *cool* patches was highest in downstream portions of rivers, as indicated by relationships with stream order, drainage area, and elevation (**Figure 4.3**). Size of *cool* patches did not show strong relationships with stream order or drainage area, but increased with elevation and with longitudinal position within a river (**Figure 4.4**). Trends across stream order and drainage area (but not elevation) suggested that density of *warm* patches increased and patch size decreased in an upstream direction. Spacing between *cool* patches did not show strong patterns with longitudinal position (**Figure 4.3**, **Figure 4.4**). Patterns were river-specific, with some rivers having many *cool* patches and some having few. Moreover, the first *cool* patch was a short distance from the mouth in some rivers but was far upstream in others (**Figure 4.4**).

Results also depended on species-specific thermal requirements. For instance, when I characterized thermal heterogeneity for a species having lower temperature thresholds of 12 and

18 °C (instead of 15 and 20 °C), I found a higher density of *cool* patches, *warm* patches that were longer but also more variable in length, and an increased variance in patch spacing (**Figure 4.5**). Characteristics of peaks and valleys >18 °C were similar to characteristics for peaks and valleys >20 °C (**Figure 4.6**).

4.4.2. Warmer Water but Similar Thermal Heterogeneity in Future

When I assumed future longitudinal profiles will become warmer versions of existing profiles, I found, as expected, that the total amount of *warm* habitat (>20 °C) increased whereas *tolerable* and *cool* habitat decreased (**Figure 4.6**). Density of *cool* patches increased some with increasing water temperature, whereas the length and spacing of *cool* patches did not change appreciably. Conversely, the density of *warm* patches decreased marginally, and at least some patches became longer. It is uninformative to consider how warming existing thermal profiles influences peaks and valleys from the trend line, as these shapes did not change.

Expected changes in climate covariates were stronger for certain covariates, and differed by river. For instance, in Joseph Creek, a tributary to the lower Grande Ronde River in Oregon, there was a clear increase in future summer air temperature and a decrease in the probability of winter precipitation falling as snow, but not much change in mean annual precipitation (**Figure S 4.7**). Moreover, both the magnitude of covariates (**Figure 4.7**, middle column) and the amount of change expected (**Figure 4.7**, right column) differed over the length of the river. Relationships were river-specific, with some future longitudinal trends predicted largely from changes in air temperature, and others more strongly related to different or multiple covariates.

The total length of river falling into *cool*, *tolerable*, and *warm* habitat zones shifted slightly toward more warm habitat overall in the 2080s (**Figure 4.8**). The mean increase in water temperature across all locations was 0.37 °C. Locations with the lowest temperatures warmed more than locations with the highest temperatures (5th and 95th percentiles increased by 2.02 and effectively 0 °C) (**Figure S 4.8**). Density of *tolerable* and *warm* patches decreased whereas density of *cool* patches remained similar. Both median length and variance in patch length increased slightly for all three thermal zones, but variance became especially high for *warm* patch length. Spacing of *cool* patches increased, but so did variance in this metric. Future peak and valley patterns were remarkably similar to historical patterns (**Figure S 4.9**).

4.4.3. Metrics Sensitive to Spatial Grain of Water Temperature Data

Not surprisingly, coarsening the resolution of water temperature data altered thermal heterogeneity metrics. As resolution decreased (i.e., bin size increased), patch size and spacing increased and patch density decreased (**Figure 4.9**). The same occurred for valley and peak metrics (**Figure S 4.10**). What is notable is how strongly nonlinear these relationships were, especially at resolutions below 1 km. Thus, there was spatial structure below the 1-km resolution that could be observed and quantified in the spatially continuous TIR data that may be missed if data were sampled or modeled at coarser resolutions.

4.5. Discussion

Conservation and management of freshwater habitat for cold-water species will increasingly require ways to assess and maintain suitable thermal landscapes. Concern about cold water habitat for Pacific salmon in rivers has featured in the news, particularly after conditions were warmer and drier than usual in the summer of 2015. Managers have struggled with how to define aspects of thermal habitat needed by cold water species and how to implement regulations required by federal legislation (e.g., the Clean Water and Endangered Species Acts in the U.S.A.) that are robust to climate change effects. In particular, managers seek ways to understand and implement the concept of “sufficiently distributed cold water refuges”.

My research contributes to this dialogue by providing some approaches for characterizing thermal heterogeneity at intermediate spatial scales and by illustrating the substantial spatial variation in summertime river temperature (e.g., reaches of 10s to 100s of km) within and among hundreds of rivers throughout the Pacific Northwest. As expected, cooler patches were shorter and farther apart toward river mouths and longer and closer together toward their source. The size and spacing of existing cool patches may be sufficient for salmon in many rivers. However, there were long stretches considered stressfully warm to salmon in some rivers. I predicted minor changes in density, spacing, and size of cool patches in warmer climate conditions overall, but cool patches were arranged differently. Notably, my analyses illustrated the presence of thermal heterogeneity which may be important to fish at scales below a 1-km resolution. This suggests that predictions of thermal heterogeneity in places or times where data are sparse should be interpreted cautiously. Below, I discuss my results in the context of (a) how cold water refuges are defined and quantified, (b) the adequacy of thermal heterogeneity for salmon, and (c) guidance for managing thermal diversity in a changing climate.

4.5.1. Defining Thermal Refuges in Space and Time

Identification and management of cold water refuges is challenging because they vary over space and time and their use differs among species and life stages (Torgersen et al. 2012). In this study, I have presented one way to resolve spatial patterns of water temperature during summer that may be a good “first pass” for identifying areas of potential management concern at intermediate spatial scales. Analysis at intermediate scales facilitates identification of habitats suitable for temporary holding during migration (e.g., cold tributary plumes; Keefer et al. 2009), spawning (e.g., regions of significant subsurface upwelling), and spatial juxtaposition of thermally suitable habitats needed for feeding, growing, and sheltering (Schlosser 1995, Flitcroft et al. 2012). The data used in my analysis were one-dimensional (i.e., longitudinal patterns of temperature) and did not capture patterns across the width of the stream. I therefore interpret my findings as longitudinal distributions of “thermal patches” along the course of a stream. There may be thermal refuge at depth in larger pools that I could not resolve with these data, although vertical stratification is generally not a concern for interpreting patterns in these well-mixed rivers. There may also be thermal refuge at different times that these data did not capture (Dugdale et al. 2013, Ebersole et al. 2015, Wawrzyniak et al. 2016). Because fish are mobile, they may use refuges differently at various times (Sutton et al. 2007, Brewitt and Danner 2014), optimizing use of thermal habitats by swimming small distances throughout the day (Torgersen et al. 2012, Armstrong and Schindler 2013). When areas of concern are identified at an intermediate scale, managers can then more comprehensively investigate patterns at finer spatial scales using remotely sensed data, placement of additional sensors, and field surveys to determine adequacy for fish (Torgersen et al. 1999, Ebersole et al. 2003, Monk et al. 2013, Dugdale et al. 2015).

The spatially continuous dataset was uniquely suited for evaluating what might have been missed had I used sparser data to evaluate spatial patterns. When longitudinal thermal profiles were constructed from coarsened data, I was less likely to detect thermal patches that might be important to fish. The strong nonlinear response in thermal heterogeneity metrics that I found suggests that substantial complexity exists at spatial scales < 1 km. Often, researchers deploy monitoring sensors at a discrete set of stationary points. Understanding spatial water temperature patterns between these points is then inferred, interpolated, or modeled. My analysis suggests that these approaches are unlikely to detect fine scale and potentially biologically relevant

thermal heterogeneity present between established monitoring sensor locations. Existing spatially-explicit water temperature models typically do not make predictions at scales finer than 1 km. Predictions from these models may be very useful for some questions (e.g., range shifts and broad scale spatial patterns) but not others (identifying thermal refuges). It is easy to envision very different management decisions if one was unaware of biologically important fine scale thermal heterogeneity. For example, migrating fish may be trapped and transported around a stream reach believed to be too warm if existing thermal refuges were not detected using available stream temperature information.

Despite the spatiotemporal variability of thermal refuges and different needs of species and life stages, regulations typically specify simplified metrics for temperature standards. For instance, the U.S. Environmental Protection Agency defines cold-water refuges as “waters that are 2 °C colder than the surrounding water”. This necessarily vague definition allows flexibility in determining what is sufficient given a river’s context and the species living there. The challenge will be to match the scale of measurement to the scale of the management question, and to ensure that metrics used to characterize thermal refuges capture the ecological facet(s) of interest (Steel et al. 2016). For example, an ecological facet of interest may be the distance between cool patches available to adult summer Chinook salmon as they migrate upstream. This requires further definition of what constitutes a “cool patch”. I used two complementary definitions: (1) the contiguous length of river where maximum temperature is below an absolute biologically-relevant thermal criterion (e.g., 15 °C), and (2) the contiguous length of river within a warm stretch (e.g., > 20 °C) where temperature was relatively cooler (e.g., <2 °C) than in adjacent stretches. These generic definitions can easily be tailored for a particular species or life stage. For instance, I found a greater number of smaller, more isolated cool patches when I used lower thermal tolerance thresholds of 12 and 18 °C.

4.5.2. Adequacy of Cold Patches for Salmon During Summer

Given a well-defined ecological facet (e.g., upstream migration for species X in river Y) and species-specific metrics, one can characterize the size, spacing, and density of cold patches available to fish, as I have done. Evaluating whether such patches are sufficient for meeting fish needs will also require consideration of whether patches are big enough, spaced within distances that fish can swim, and numerous enough for fish to actually use.

The size a cold water patch needs to be in order to provide benefit is not well understood. The majority I quantified were large enough (~250 m) for at least temporary use by salmon, which have been observed using territories as small as 0.13 m² at high densities (Lindeman et al. 2015). The minimum patch size almost certainly depends on fish age and ecological conditions within the patch, such as density of other fish using the refuge, and whether habitat conditions therein are suitable (Breau et al. 2007, Woolnough et al. 2009, Breau et al. 2011). Elevated densities can further suppress growth and survival for juveniles already stressed by high water temperatures (Harvey and Nakamoto 1996, Crozier et al. 2010). Use of a thermal refuge may reduce metabolic costs and susceptibility to pathogens or toxins, but may increase competition and vulnerability to predators or anglers (Torgersen et al. 2012).

The extent to which connectivity among cold water patches limits salmon depends on many things including species, life stage, and environmental characteristics in a given river at a particular time. Research on in-stream fish behavior is amassing yet we still have much to learn about how and when fish decide to move to seek refuge in cooler habitats. Both juvenile and adult salmon are capable of swimming the distances (~250 m) between cold water patches in most Pacific Northwest rivers. However, the fact that fish can swim long distances and can move fast enough to quickly cover the distance between cool patches does not mean that they will choose to move through a warm section of river. Migration may be delayed (Keefer et al. 2009) or may cease altogether at high temperatures (Richter and Kolmes 2005, Hasler et al. 2012). Fish that do swim through thermally stressful waters may experience latent sublethal and cumulative effects caused by increased susceptibility to pathogens, toxins, predation or other heat-related stressors (Marcos-Lopez et al. 2010, Dietrich et al. 2014, Fenkes et al. 2016).

Patch density is inextricably linked to the size and connectivity of patches. For instance, there may be a large number of closely spaced but very small patches. Whether this group of small patches is equivalent to a single large patch (e.g., Simberloff and Abele 1982, Kingsland 2002) with respect to fish needs is unknown, and will amount to a political decision until better science is available. Additional behavioral observations, archival tag studies, and experiments are needed to resolve this issue.

4.5.3. Managing Thermal Heterogeneity in a Changing Climate

I have demonstrated that there is substantial thermal heterogeneity at an intermediate spatial scale within and among rivers throughout the Pacific Northwest during summer. These

patterns should prove invaluable as a measure of baseline conditions to which future patterns can be compared. As the climate continues to warm, important questions remain about how existing thermal heterogeneity patterns will change and how species will respond. I predicted increased water temperatures overall, and cold patches that were slightly fewer, smaller, and less well connected. Although patterns summarized over all rivers changed only a little, it is likely that the arrangement of patches within a river will change. For instance, a small cool patch between two warm patches may disappear, resulting in a single larger warm patch.

Several aspects of our approach for estimating future water temperatures may have under-represented potential changes. For one, the estimates of air temperature that I used as covariates were likely too coarse to detect real spatial heterogeneity in air temperature values, especially in complex terrains (Minder et al. 2010). Second, neither of my approaches included responses of hydrology to changes in climate. The amount and timing of discharge can influence spatial thermal heterogeneity patterns. When discharge is high, spatial variability will be dampened due to increased mixing whereas times of low discharge may increase spatial variability by allowing smaller volumes to respond more quickly to radiative forces. Although the random-forest modeling included covariates describing the magnitude of annual precipitation and the form of winter precipitation (i.e., rain or snow), it was unable to translate these effects into magnitude or timing of future stream discharge. In rivers that were historically fed by glaciers or those that had snowmelt-driven hydrographs, future thermal regimes may be expected to change substantially. In the near future, summertime water temperature may actually decrease as glaciers and snow melt. Eventually, these rivers may warm earlier and to a greater extent without the moderating influence of meltwater during spring and summer. It is likely that change will be smallest in rivers strongly influenced by ground water, because ground water will respond slowly to climate change (Mayer 2012, Luce et al. 2014). Third, these models did not include estimates of fine-scale controls on thermal heterogeneity such as groundwater influence, riparian shading, land use features, or geomorphology; climate scenarios modeled only changes in trends. In both approaches, I assumed that existing fine scale heterogeneity would persist, as it did between warm and cool years in the few rivers where repeat aerial thermal infrared surveys were conducted. Models capturing mechanistic relationships between thermal heterogeneity and potential drivers could be used to predict locations of thermal refuges in places where no empirical data exist, and for future climate conditions.

As an example of how my analyses could inform conservation of thermal habitat for salmon in one watershed, consider the coastal Siletz River basin in Oregon. This watershed hosts threatened populations of coho and steelhead, coastal cutthroat populations that are candidates for ESA listing, the only native population of summer steelhead in the coast region, and healthy populations of Chinook and chum. By characterizing water temperature in terms of thermal suitability zones, managers can locate reaches that may be least likely to change in a warmer climate (**Figure 4.10**, left). These reaches may represent opportunities for conserving potential strongholds. Comparison of size and spacing of thermal patches in historical and future scenarios can highlight locations likely to remain cool in the future as well as areas where more intensive intervention may be necessary (**Figure 4.10**, right). Management of the thermal landscape in a particular river will depend on local conditions, species of interest, and on sociopolitical goals. Approaches used to protect, restore, or create cold water patches should carefully consider their spatiotemporal context and applicability to species of concern. A focus on additional spatially-continuous monitoring, protecting the processes likely to promote thermal diversity, reducing known threats and impacts, and building resilience will continue to be important.

4.6. Acknowledgements

Individual river temperature surveys and image processing were conducted by R. Faux, Watershed Sciences Inc., except for rivers in the Salmon and Clearwater basins in Idaho, the data for which were provided by D. Essig of the Idaho Department of Environmental Quality. I am grateful to the many local, state, federal, tribal and nongovernmental organizations that funded the collection of these data for water quality monitoring and assessment. The North Pacific Landscape Conservation Cooperative provided funding that supported this work. I thank Christian Torgersen, Josh Lawler, Ashley Steel, Joe Ebersole, Dan Miller, Se-Yeun Lee, Lisa Crozier, and Tim Beechie for helpful discussions while I was developing this research, and for support from Beth Sanderson to pursue this topic.

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Table 4.1. Length of rivers surveyed with remotely-sensed thermal infrared as a percent of total length (species, stream order) or watershed area (land use/land cover, ecoregion) in each class. For example, surveyed rivers represented 24% of all sixth-order rivers in the Pacific Northwest and northern California. See **Table S 4.1 - Table S 4.4** for more information.

Salmon	%	Stream Order	%	Land Use / Land Cover	%	Level II Ecoregion	%
Anadromous	15	Second	1	Evergreen forest	6.8	Forested Mountains	8.9
Steelhead: summer	23	Third	3	Shrub/scrub	2.3	Coastal Forests	10.4
Steelhead: winter	10	Fourth	8	Grassland/herbaceous	3.7	Western Deserts	2.8
Chinook: fall	19	Fifth	15	Cultivated crops	4.8	Mediterranean California	0.3
Chinook: spring	33	Sixth	24	Pasture/hay	7.4		
Chinook: summer	27	Seventh	13	Mixed forest	7.5		
Coho	13	Eighth+	8	Developed, open space	5.2		
Chum	9			Developed, low intensity	5.7		
Pink	13			Open water	1.3		
Sockeye	27			Emergent herbaceous wetlands	7.1		
				Deciduous forest	3.3		
				Barren land (rock/sand/clay)	1.0		
				Woody wetlands	6.2		
				Developed, medium intensity	3.6		
				Developed, high intensity	4.0		
				Perennial ice/snow	2.6		

Table 4.2. Distributions (quantiles) of conditions for each reach¹ surveyed with remotely-sensed thermal infrared.

Quantile	Cumulative drainage area ² (km ²)	Discharge ³ (cfs)	Velocity ⁴ (m/s)	Elevation ⁵ (m)	Slope ⁶ (%)	Max weekly summer air temperature ⁷ (°C)	Mean annual precipitation ⁸ (mm)	Probability of winter precipitation as snow ⁹
0%	0	0	0.3	0	0	10.0	156	0
5%	19	13	0.8	38	0	13.9	289	0.01
25%	181	111	1.2	268	0	16.2	449	0.01
50%	907	456	1.5	631	3e-3	17.7	645	0.65
75%	3,993	2,060	1.9	1,168	0.01	19.4	1,131	0.95
95%	20,500	8,537	2.8	1,678	0.03	21.7	2,134	0.97
100%	575,519	190,859	8.3	2,273	0.94	23.6	4,690	0.97

¹ TIR data were linked to reaches in the National Hydrography Dataset (nhd.usgs.gov) at a resolution of 1:100,000

² TotDASqKM, PlusFlowlineVAA table, attributes of NHDPlusV2 (www.horizon-systems.com/nhdplus; McKay et al. 2012)

³ Q0001E, EROM model, attributes of NHDPlusV2

⁴ V0001E, EROM model, attributes of NHDPlusV2

⁵ mean of MAXELEVSMO and MINELEVSMO, elevslope table, attributes of NHDPlusV2

⁶ SLOPE, elevslope table, attributes of NHDPlusV2

⁷ Mean of the maximum weekly air temperature, JA, 1970-1999 (Wigmosta et al. 1994)

⁸ V, IncrPrecipMA.txt, attributes of NHDPlusV2

⁹ Climatic snow likelihood, DJF, 1979-2012 (zionklos.com/rain-snow_maps/; Klos et al. 2014)

Table 4.3. Metrics characterizing thermal habitat within rivers.

Metric name	Description (units)	Summary	Approach
Patch density	total number per km (#/km)	count per km	Threshold-based
Patch length	distance from start to end (km)	quantiles, 5, 95% CI	Both
Patch spacing	distance between patches (km)	quantiles, 5, 95% CI	Both
Patch height	temperature change (°C)	quantiles, 5, 95% CI	Peak-valley
Patch area	area (km-°C)	quantiles, 5, 95% CI	Peak-valley

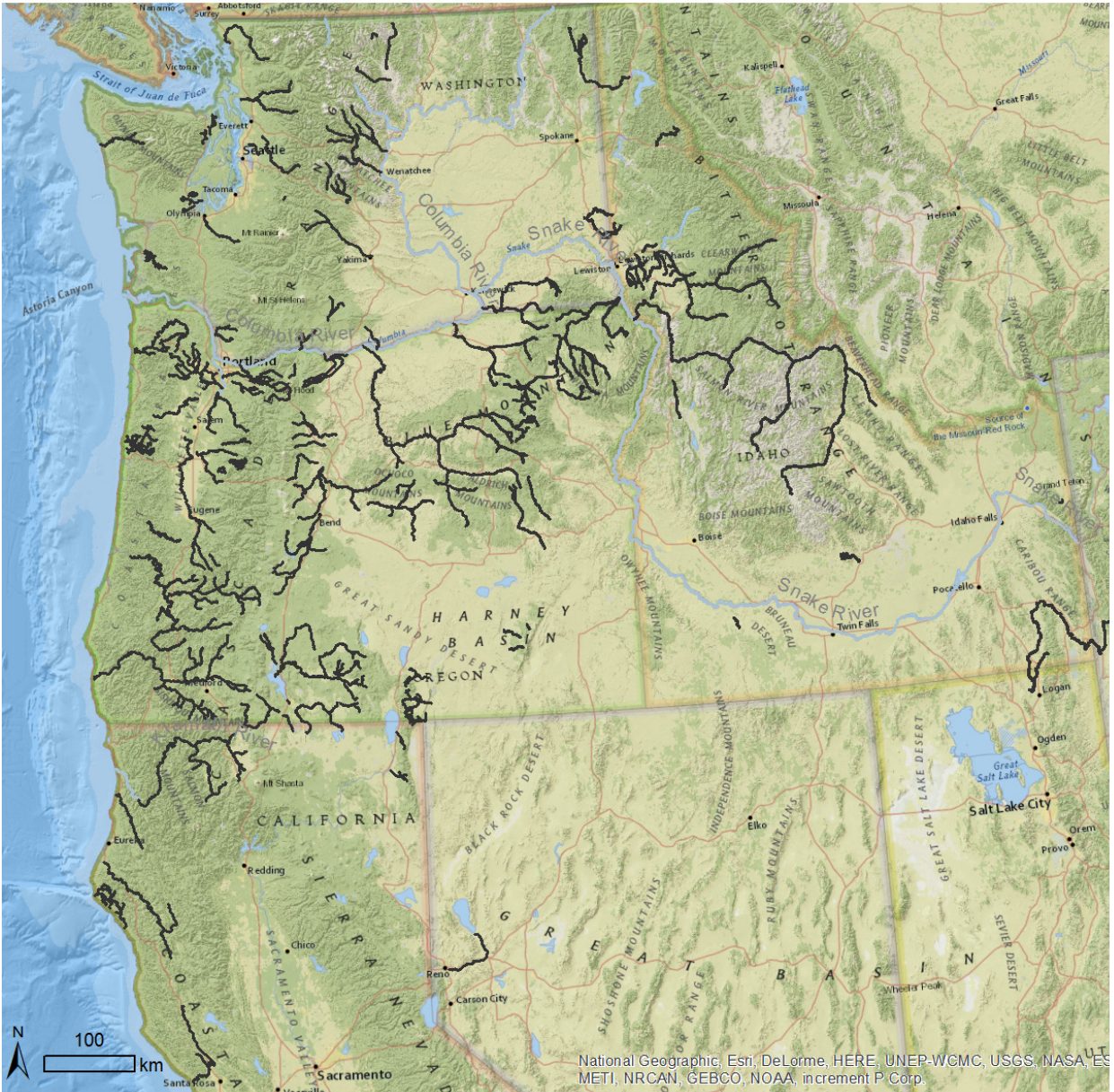


Figure 4.1. Map of rivers for which thermal infrared (TIR) surveys of water temperature were available.

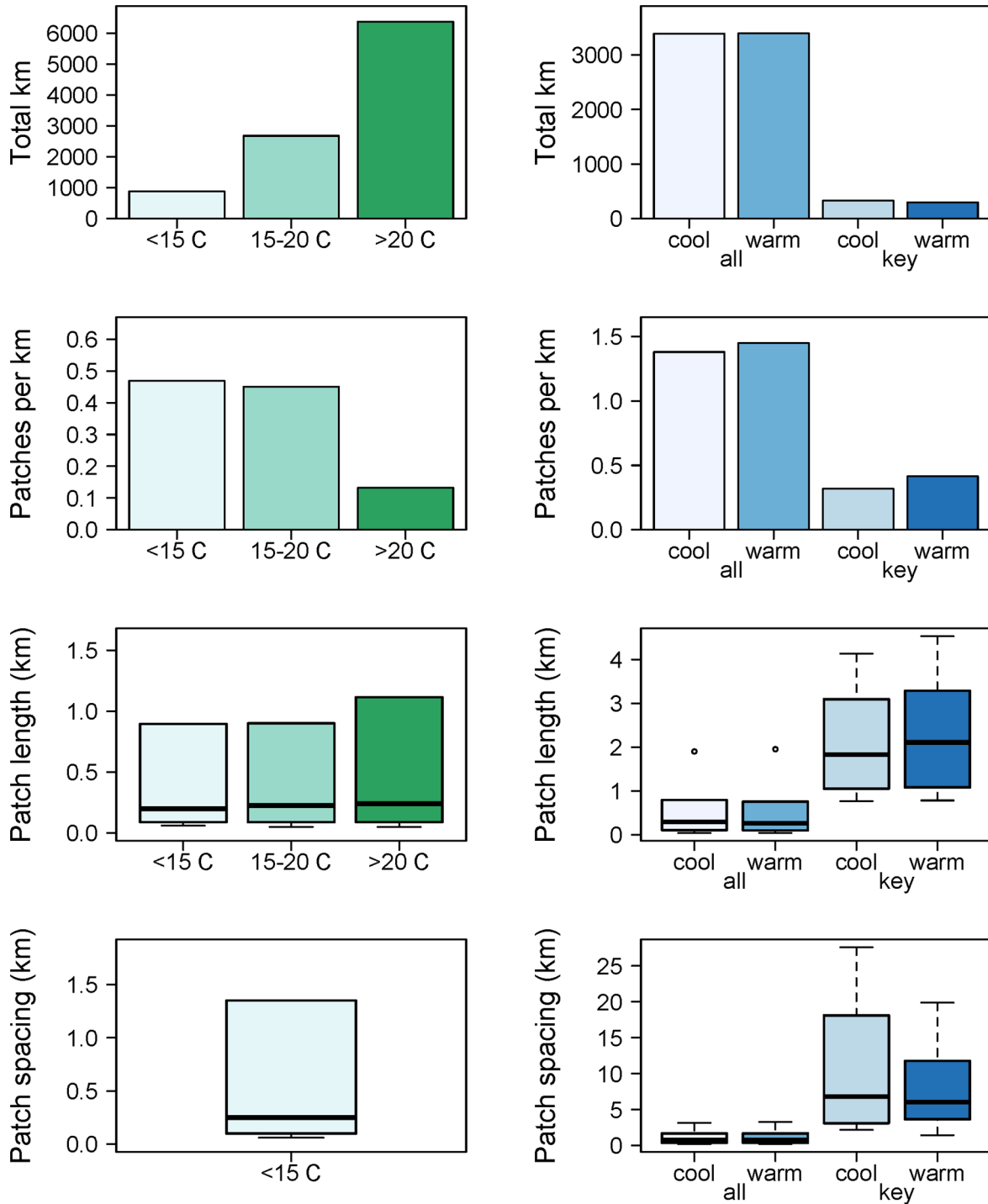


Figure 4.2. Metrics of thermal heterogeneity, summarizing all anadromous habitat in rivers for which TIR data were available (12,341 km). **Left:** Thermal heterogeneity quantified by slicing longitudinal profiles into three thermal zones. **Right:** Thermal heterogeneity within portions of rivers exceeding 20 °C, quantified as peaks (warm patches) and valleys (cool patches) from a moving average trend. Key patches were at least 500 m long and had temperature differentials of 2 °C or greater.

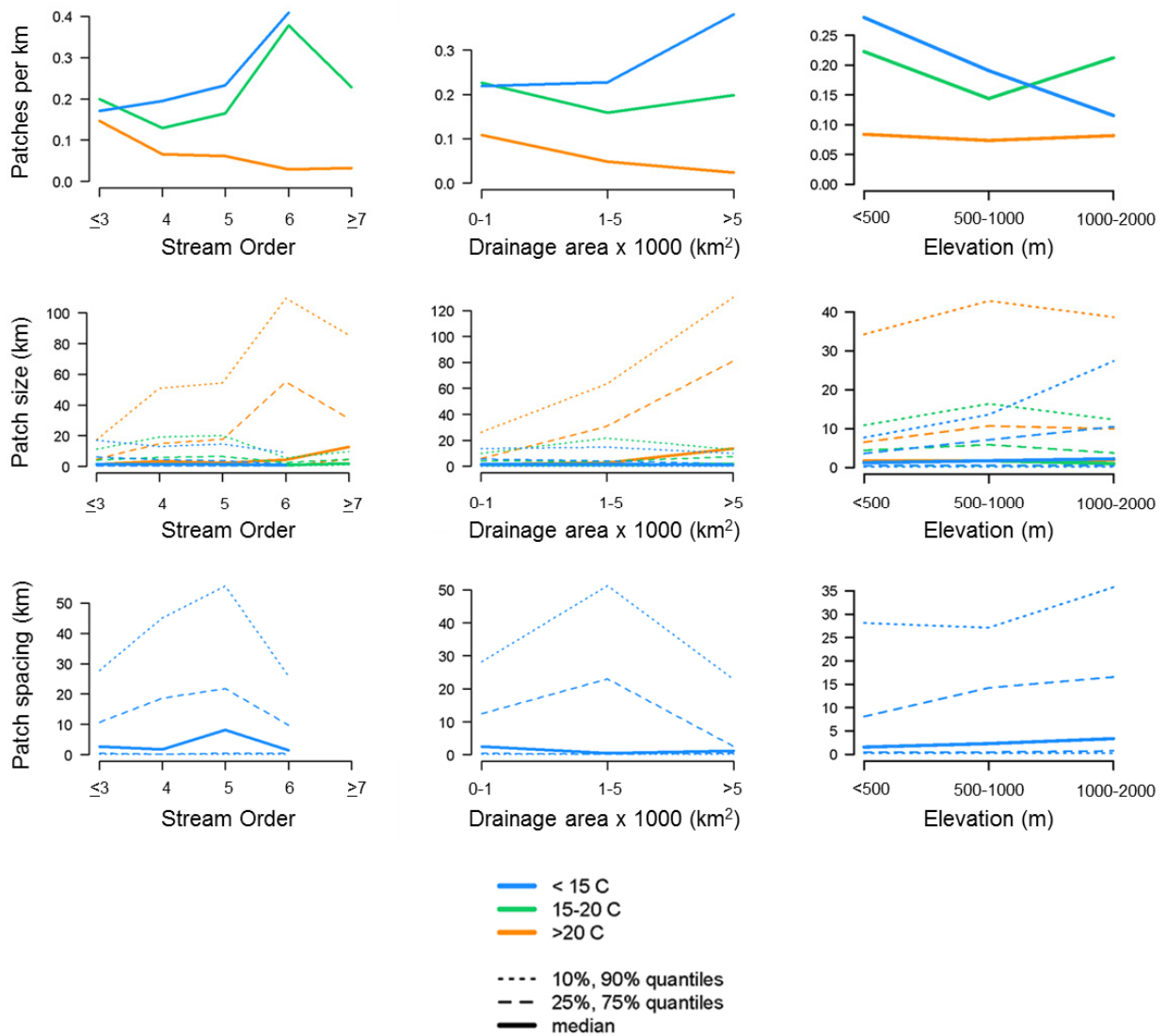


Figure 4.3. Thermal heterogeneity metrics (y axes), quantified by slicing longitudinal profiles into three thermal zones, plotted against stream order (left column; x axes), drainage area (middle column), and elevation (right column). Data included all anadromous habitat in rivers for which TIR data were available (12,341 km).

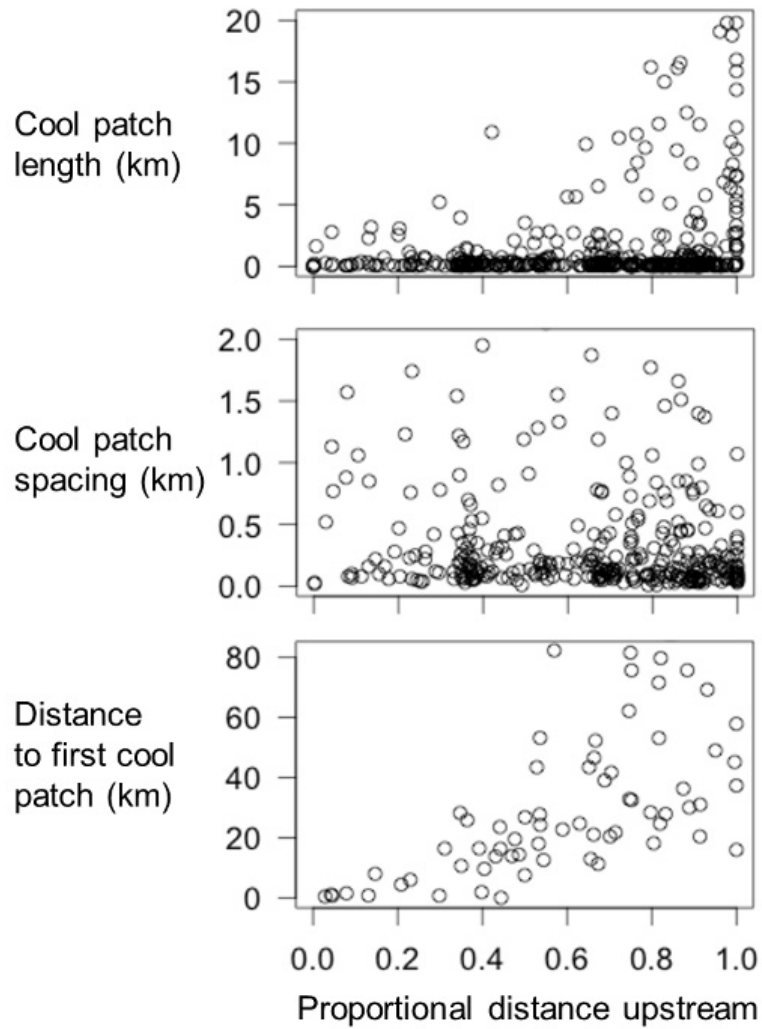


Figure 4.4. Metrics describing the size, spacing and first location of cool patches versus longitudinal position within a river (scaled between 0 and 1, where 0 is the bottom end of a survey and 1 is the top). Data included all anadromous habitat in rivers for which TIR data were available (12,341 km).

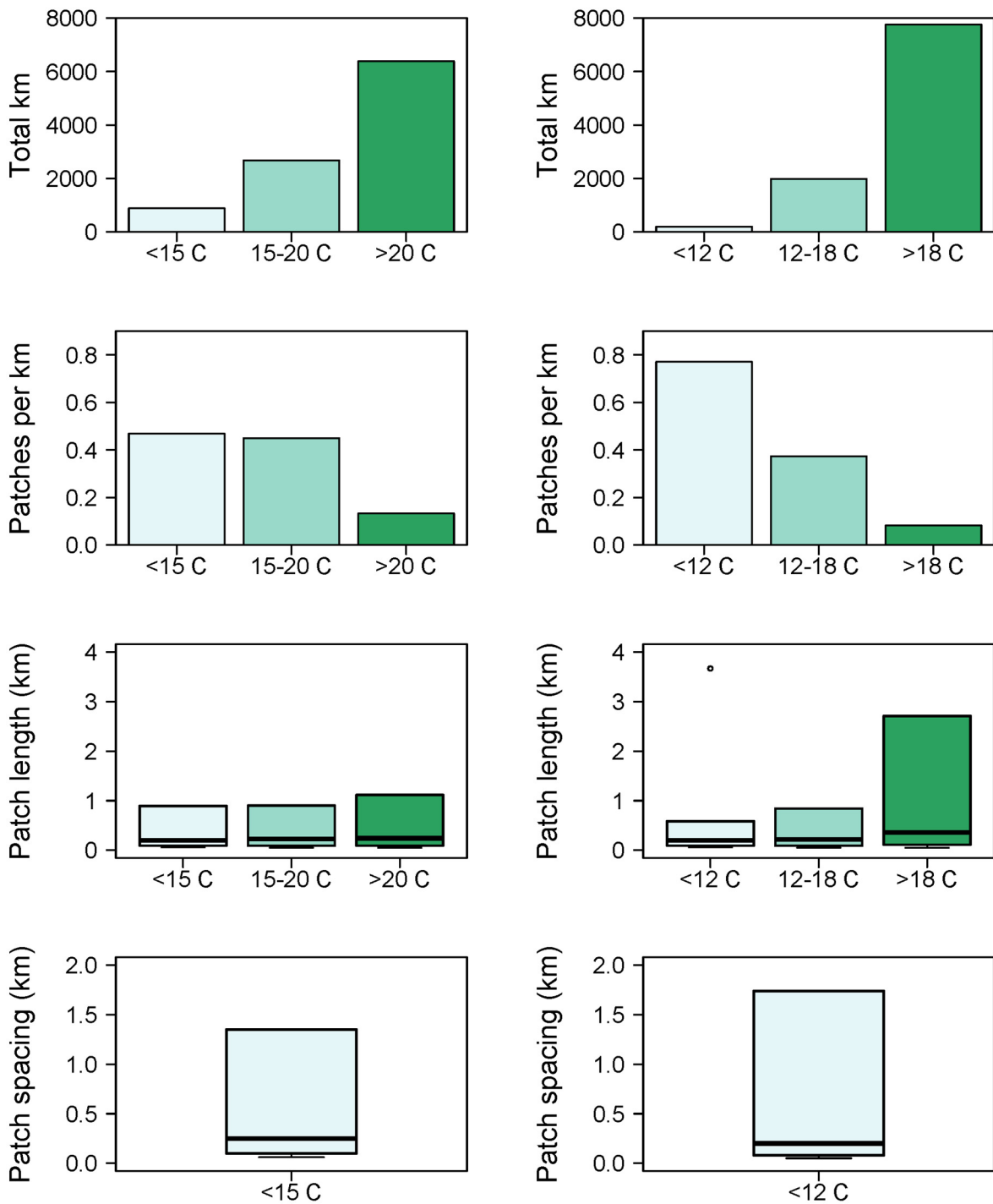


Figure 4.5. Metrics of thermal heterogeneity, quantified by slicing longitudinal profiles into three thermal zones. Data included all anadromous habitat in rivers for which TIR data were available (12,341 km). **Left:** Original zones denoted by thresholds of 15 and 20 °C. **Right:** Zones denoted by lower temperature thresholds of 12 and 18 °C.

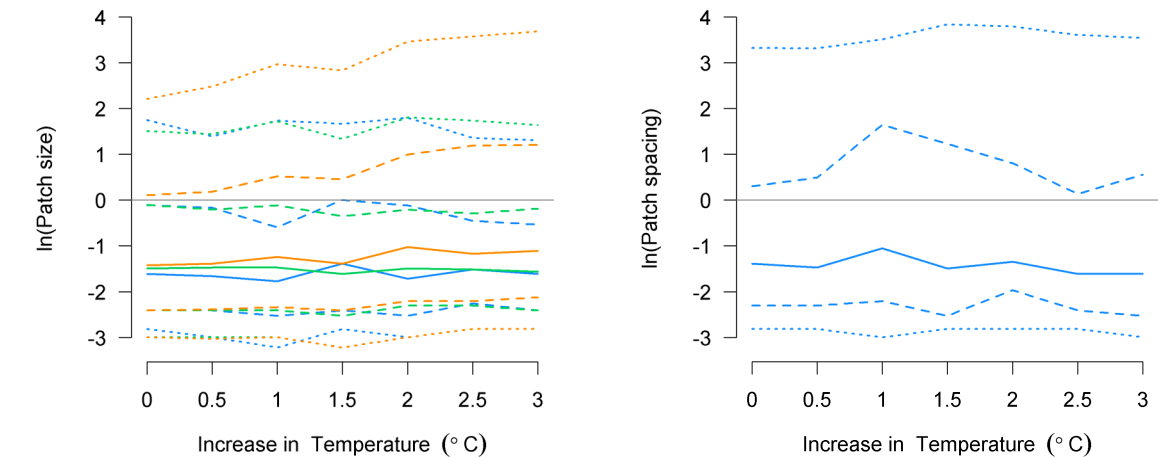
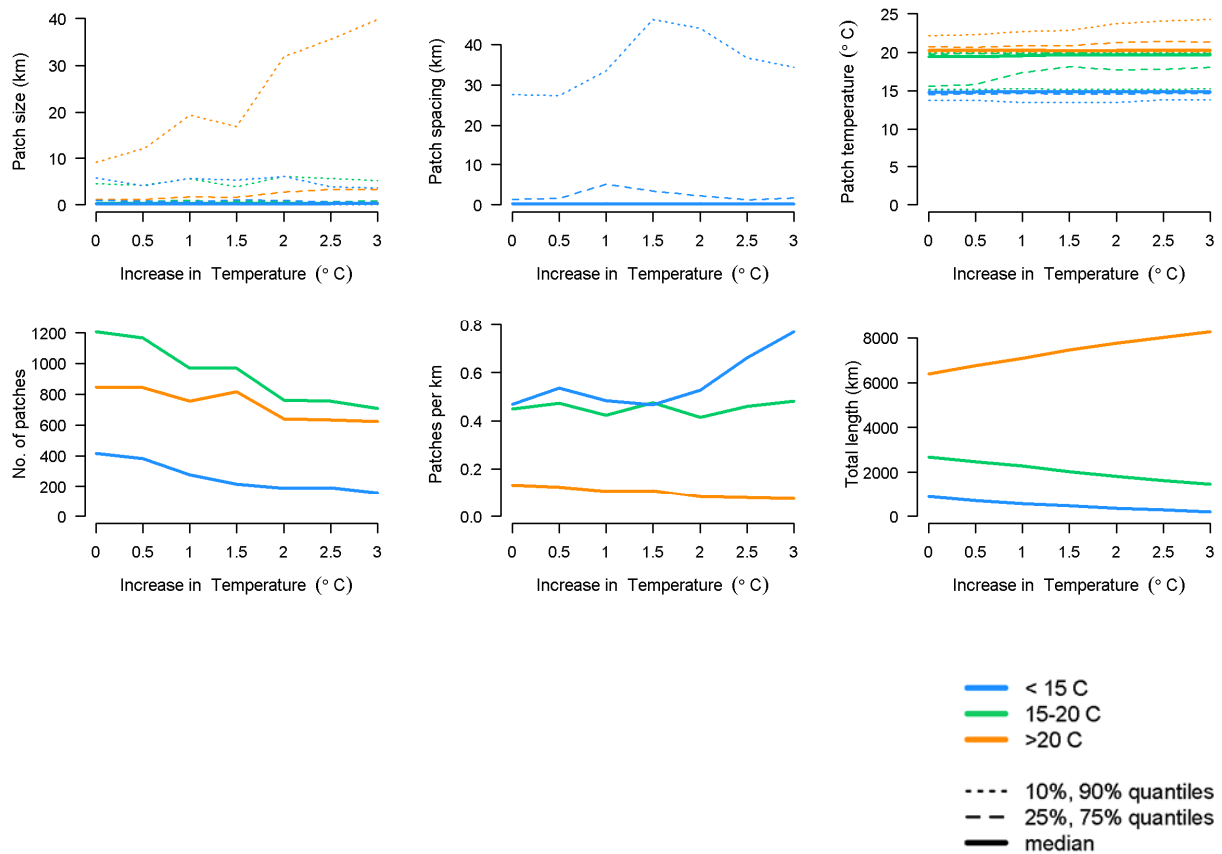


Figure 4.6. Top: Thermal heterogeneity metrics (y axes), quantified by slicing longitudinal profiles into three thermal zones, plotted across scenarios of homogeneously increasing water temperature (x axes). Data included all anadromous habitat in rivers for which TIR data were available (12,341 km). **Bottom:** patch size and spacing plotted on the log scale to illustrate the relative lack of change with increasing temperature.

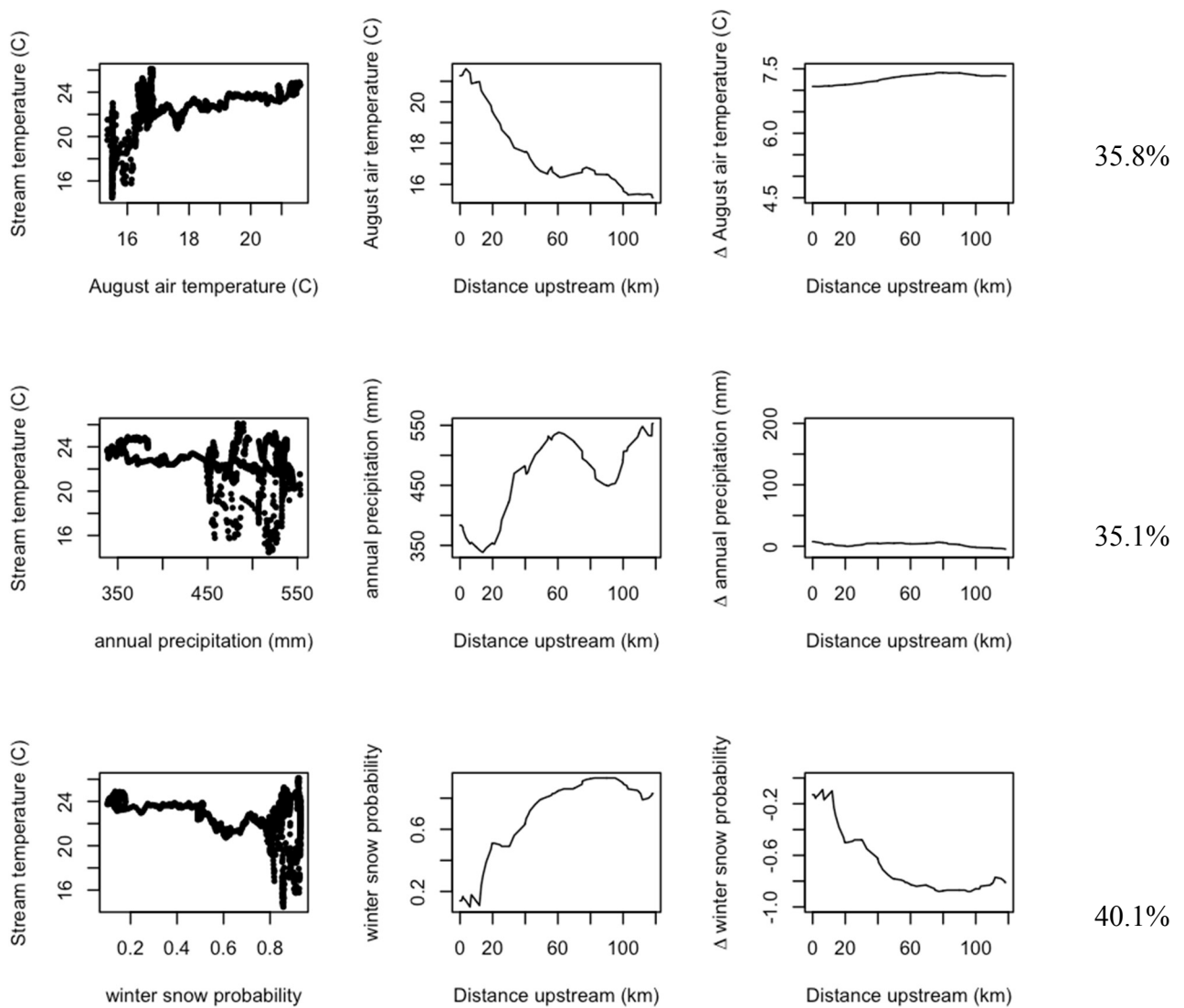


Figure 4.7. Covariates used to predict future trends in water temperature, illustrating relationships with water temperature (left column), over the length of a river (middle column), and expected change (i.e., future minus historical values) over the length of a river (right column). Percentages on the right are the amount that mean standard error would increase if the model did not include the covariate. Data shown are for Joseph Creek, a tributary to the lower Grande Ronde River, Oregon.

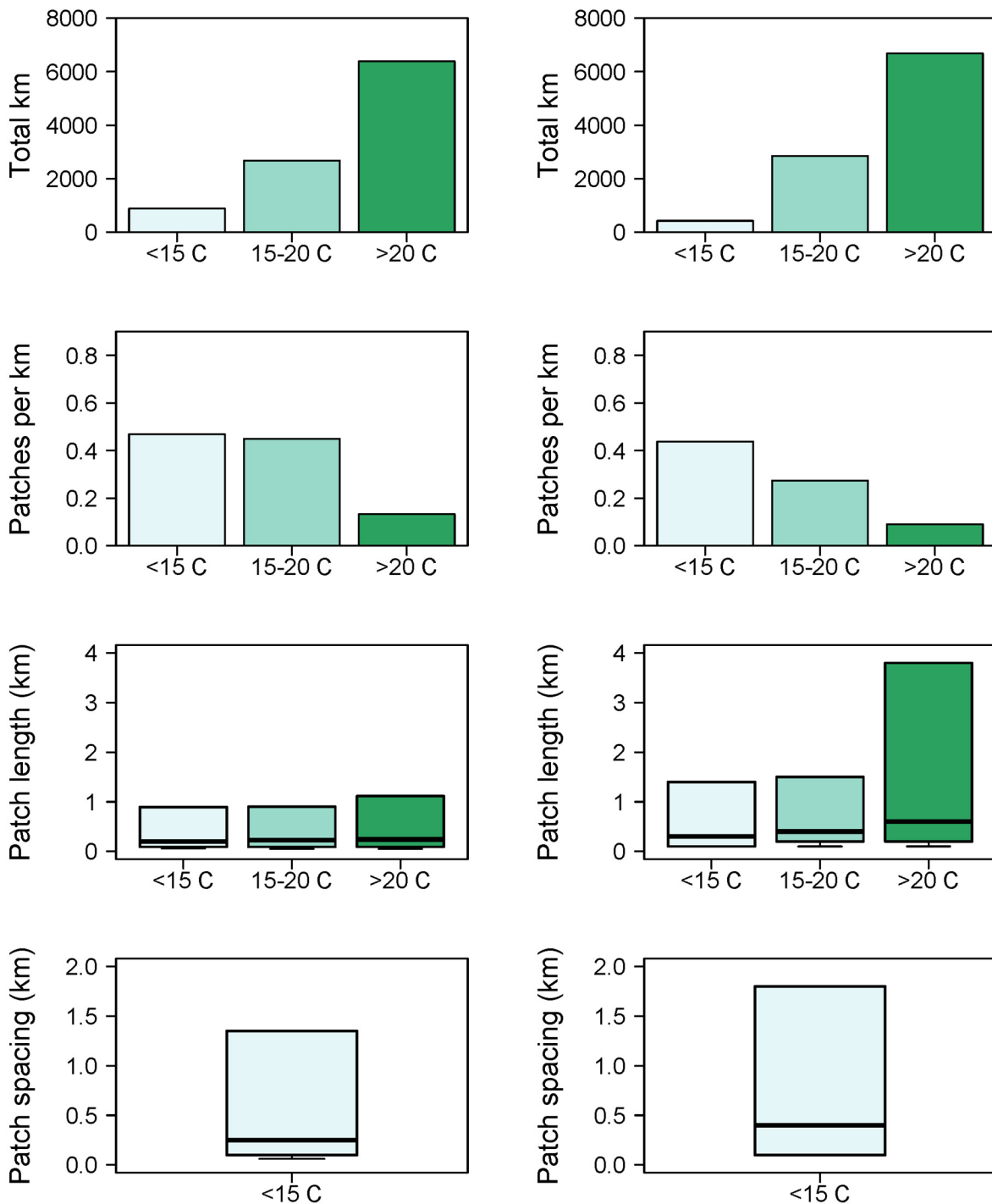


Figure 4.8. Metrics of thermal heterogeneity, quantified by slicing longitudinal profiles into three thermal zones. Data included all anadromous habitat in rivers for which TIR data were available (12,341 km). **Left:** Original TIR data. **Right:** Projected patterns in the 2080s assuming the RCP 8.5 climate change scenario.

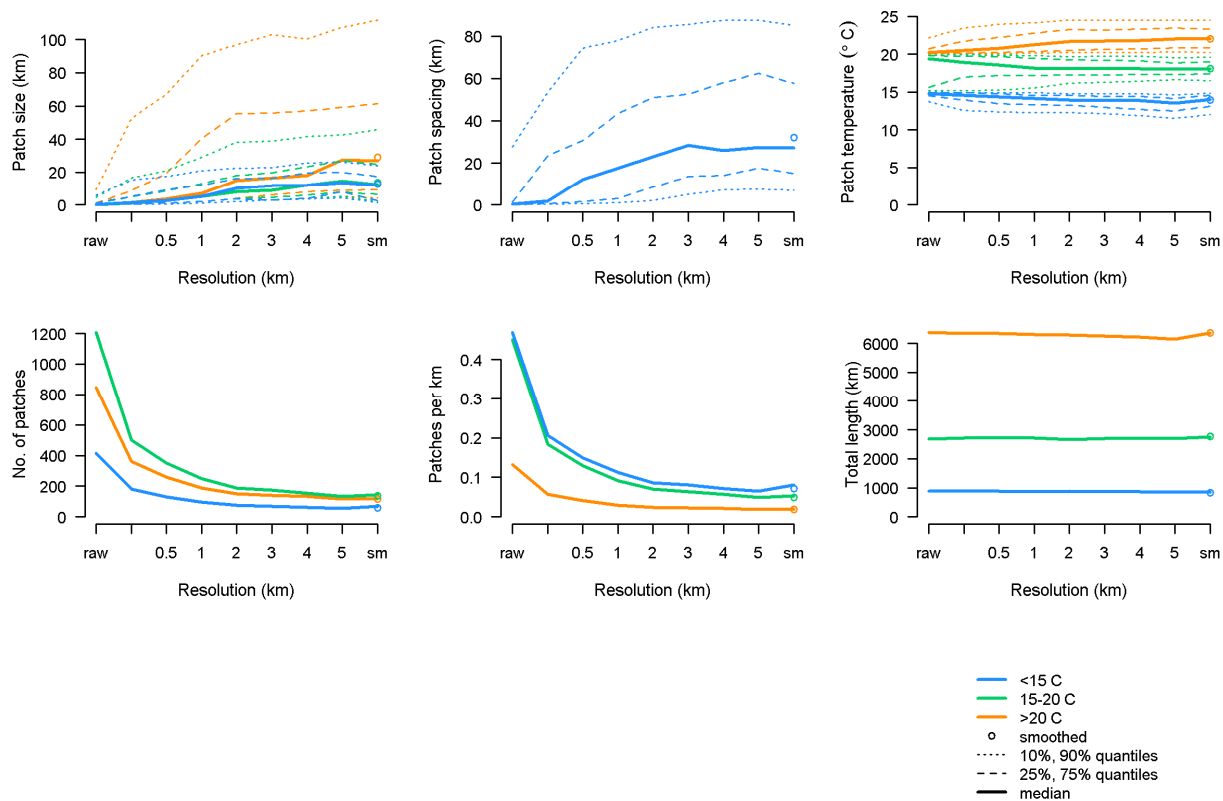


Figure 4.9. Thermal heterogeneity metrics (y axes), quantified by slicing longitudinal profiles into three thermal zones, plotted across decreasing resolution of water temperature data (x axes). Data included all anadromous habitat in rivers for which TIR data were available (12,341 km). Raw = original TIR data resolution; sm = smoothed.

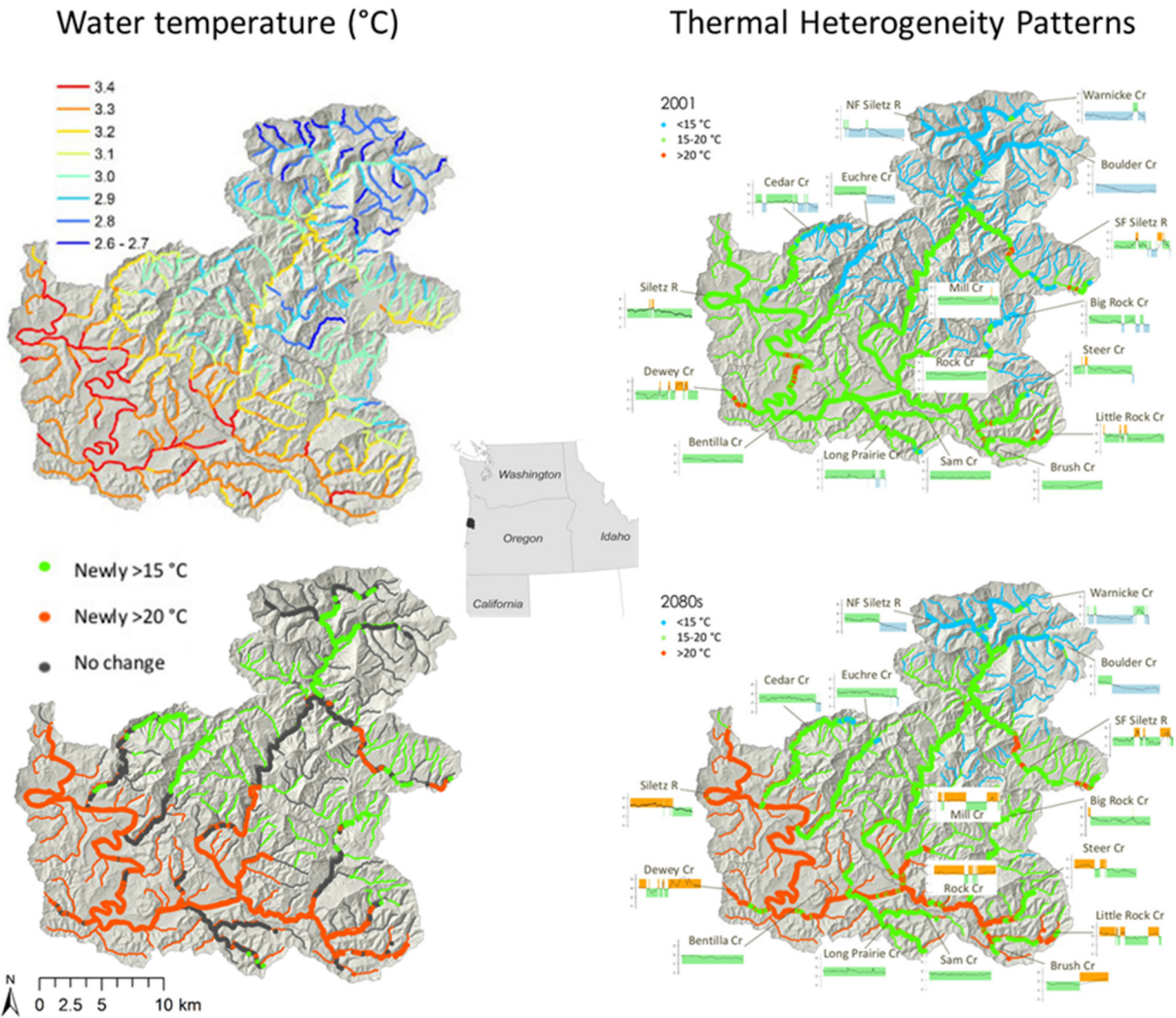


Figure 4.10. Left: Change in water temperature in the Siletz River, Oregon, expected in the 2080s as predicted by NorWeST (Isaak et al. 2014) (top), and showing change in thermally suitable zones for general salmonids (bottom). Right: patches of cool (blue), tolerable (green), and warm (orange) distributed throughout streams and based on TIR data (collected 5-7 August 2001) (top) and potential distribution of future patches if water temperature increased homogeneously by 3 °C (bottom). Inset plots are longitudinal profiles of water temperature for each stream where we had TIR data (y-axis: water temperature, x-axis: distance upstream).

4.8. Supplementary Information

Table S 4.1. Length of rivers surveyed with remotely-sensed thermal infrared that are used by each species of Pacific salmon (TIR_{sp}) as a percentage of total length¹ of all rivers surveyed (TIR_{all}) and as a percentage of habitat^{2,3} for the same species (Hab_{sp}), and the length of habitat for a given species as a percentage of the total length of all anadromous salmon habitat (Hab_{all}).

Species	TIR_{sp} / TIR_{all} (%)	TIR_{sp} / Hab_{sp} (%)	Hab_{sp} / Hab_{all} (%)
Anadromous	72	15	100
Steelhead: summer	54	23	48
Steelhead: winter	34	10	68
Chinook: fall	22	19	25
Chinook: spring	47	33	29
Chinook: summer	8	27	6
Coho	33	13	34
Chum	4	9	9
Pink	2	13	4
Sockeye	8	27	6

¹ TIR data were linked to reaches in the National Hydrography Dataset (nhd.usgs.gov) at a resolution of 1:100,000

² Pacific Northwest: www.streamnet.org/data/interactive-maps-and-gis-data (referenced to StreamNet's "best available mixed-scale routed hydrography" as of January 2012 (MSHv3) on the LLID-based stream routing system)

³ California: www.calfish.org/ProgramsData/Species/AnadromousFishDistribution.aspx (steelhead and coho are 1:24,000 resolution; Chinook are 1:100,000)

Table S 4.2. Length of rivers surveyed with remotely-sensed thermal infrared in each stream order class (TIR_{SO}) as a percentage of total length¹ of all rivers surveyed (TIR_{all}) and as a percentage of all reaches in the same stream order class (NHD_{SO}), and the length of reaches in a given stream order class as a percentage of the total length of all NHD reaches excluding first order streams (NHD_{all}). Weighted average stream order is 4.44 and 4.26 for reaches used by Pacific salmon and for all TIR reaches, respectively (and 2.99 for all NHD reaches).

Strahler stream order	TIR_{SO} / TIR_{all} (%)	TIR_{SO} / NHD_{SO} (%)	NHD_{SO} / NHD_{all} (%)
2	8	1	50
3	18	3	25
4	22	8	12
5	24	15	7
6	18	24	4
7	4	13	0.1
7-9	1	8	<0.1

¹ TIR data were linked to reaches in the National Hydrography Dataset (nhd.usgs.gov) at a resolution of 1:100,000

Table S 4.3. Area of 10-digit watershed boundary dataset¹ units containing rivers surveyed with remotely-sensed thermal infrared containing each land use/land cover class² (TIR_{CL}) as a percentage of total area of all watersheds containing surveyed rivers (TIR_{all}) and as a percentage of area in a given class for all watersheds in the Pacific Northwest, northern California and Great Basin (TIR_{CL}), and the area of watersheds in each class as a percentage of the total area of all watersheds in the region (WBD_{all}).

Land use/land cover class	TIR _{CL} / TIR _{all} (%)	TIR _{CL} /WBD _{CL} (%)	WBD _{CL} / WBD _{all} (%)
Evergreen forest (42)	44.7	6.8	25.5
Shrub/scrub (52)	25.3	2.3	41.4
Grassland/herbaceous (71)	7.7	3.7	8.1
Cultivated crops (82)	7.4	4.8	6.0
Pasture/hay (81)	3.6	7.4	1.9
Mixed forest (43)	2.6	7.5	1.4
Developed, open space (21)	2.2	5.2	1.7
Developed, low intensity (22)	1.3	5.7	0.9
Open water (11)	1.0	1.3	2.9
Emergent herbaceous wetlands (95)	1.0	7.1	0.5
Deciduous forest (41)	0.9	3.3	1.1
Barren land (rock/sand/clay) (31)	0.8	1.0	3.2
Woody wetlands (90)	0.7	6.2	0.4
Developed, medium intensity (23)	0.5	3.6	0.6
Developed, high intensity (24)	0.2	4.0	0.2
Perennial ice/snow (12)	<0.1	2.6	<0.1

¹ Watershed Boundary Dataset: <http://nhd.usgs.gov/wbd.html>

² Land use/land cover, 2011: <http://www.mrlc.gov/nlcd2011.php>

Table S 4.4. Length of rivers surveyed with remotely-sensed thermal infrared in each ecoregion (TIR_{ER}) as a percentage of total length¹ of all rivers surveyed (TIR_{all}) and as a percentage of all reaches in the same ecoregion² (NHD_{ER}), and the length of reaches in a given ecoregion as a percentage of the total length of all NHD reaches in Washington, Oregon, Idaho, and California, excluding first order streams (NHD_{all}).

Ecoregion	TIR _{ER} / TIR _{all} (%)	TIR _{ER} /NHD _{ER} (%)	NHD _{ER} / NHD _{all} (%)
Level II			
Western Forested Mountains (6.2)	69.4	8.9	42.3
Coastal Forests (7.1)	18.2	10.4	9.5
Western Deserts (10.1)	11.4	2.8	21.9
Mediterranean California (11.1)	0.9	0.3	18.9
Other	0	0	7.4
Level III			
Blue Mountains (11)	21.1	16.9	6.8
Eastern Cascades Slopes and Foothills (9)	14.9	18.0	4.5
Klamath Mountains/California High North Coast Range (78)	11.4	13.2	4.7
Coast Range (1)	8.8	8.2	5.8
Columbia Plateau (10)	7.3	5.0	7.9
Willamette Valley (3)	6.7	16.8	2.2
Cascades (4)	6.4	7.5	4.6
Idaho Batholith (16)	5.6	5.9	5.2
North Cascades (77)	4.9	9.5	2.8
Northern Rockies (15)	3.5	3.8	5.0
Puget Lowland (2)	2.7	9.6	1.5
Northern Basin and Range (80)	2.5	1.5	8.7
Middle Rockies (17)	1.5	3.0	2.7
Central California Foothills and Coastal Mountains (6)	0.9	0.5	9.9
Snake River Plain (12)	0.7	1.0	3.6
Wyoming Basin (18)	0.6	15.7	0.2
Central Basin and Range (13)	0.4	1.2	1.6
Wasatch and Uinta Mountains (19)	0.2	6.0	0.2
Other	0	0	22.2

¹ TIR data were linked to reaches in the National Hydrography Dataset (nhd.usgs.gov) at a resolution of 1:100,000

² Ecoregions (Omernik 1987): www.epa.gov/naaujydh/pages/ecoregions.htm

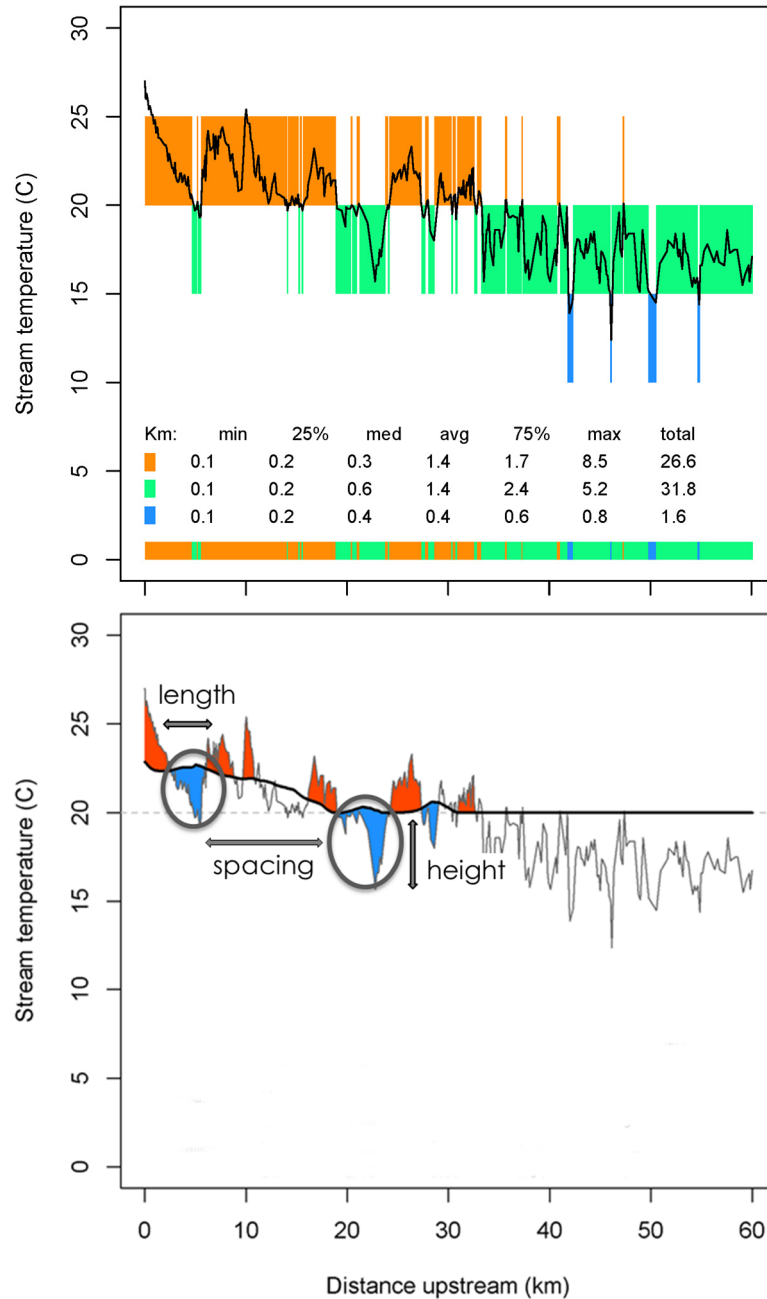


Figure S 4.1. Top: Stream temperature falling into cool (<15 °C; blue), tolerable (15-20 °C; green) and warm (>20 °C; orange) thermal zones for salmon in Lawyer Creek, a tributary to the Clearwater River, ID (TIR data collected 3 Aug 2005). Table values describe mean and quantiles of river length within each thermal zone. The colored bar at the bottom of the plot provides a linear view of the thermal zones. **Bottom:** Key peaks (red) and valleys (blue), identified as deviations from the 10-km moving average (thick black trend line). Anything below 20 °C was not analyzed. Key patches were at least 500 m long with a temperature difference of at least 2 °C. Annotations illustrate patch length, spacing, and height metrics (Table 4.3).

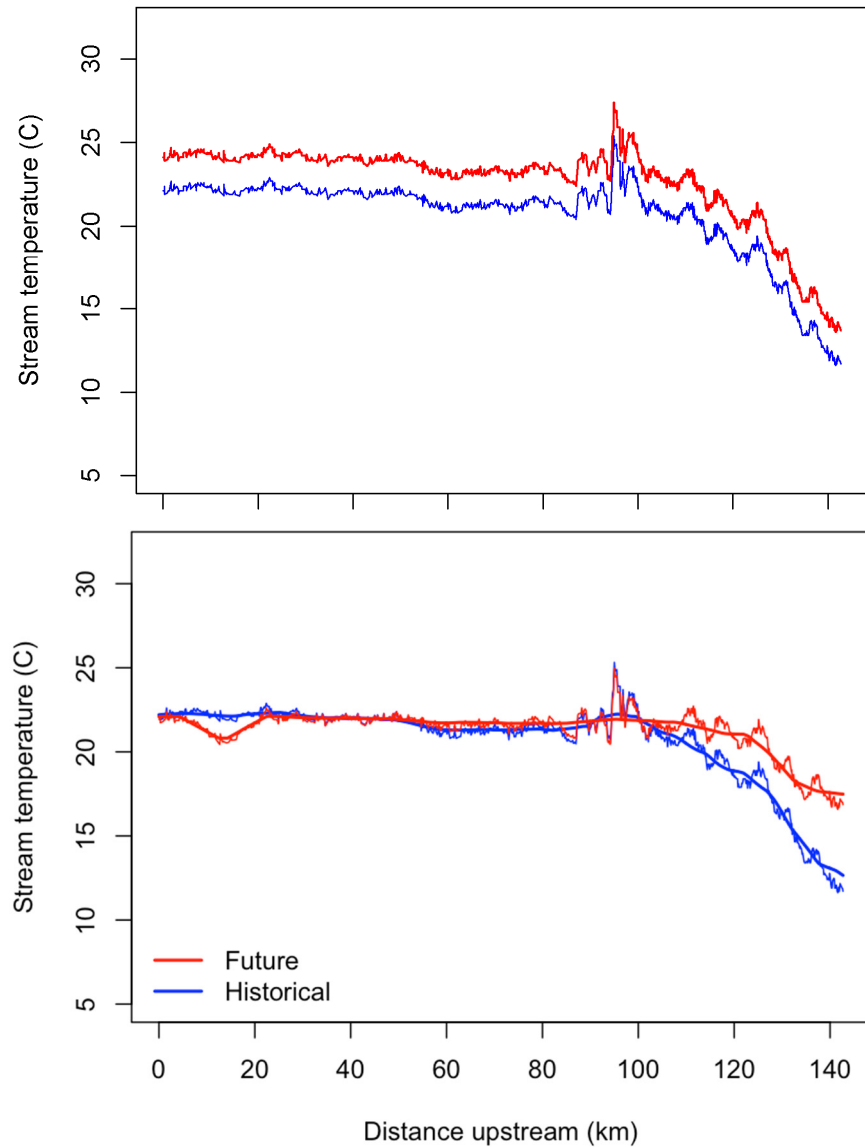


Figure S 4.2. Top: historical (blue) and future (red) longitudinal profile patterns assuming a homogeneous increase in water temperature of 2 °C in the future. **Bottom:** longitudinal trend (thick blue line) fit to raw TIR data (thin blue line) and three covariates: air temperature, mean annual precipitation, and the proportion of winter precipitation falling as snow. The predicted future longitudinal profile (thin red line) was calculated by summing residuals from the fitted model and the predicted future longitudinal trend (thick red line), which used covariates from a climate scenario representative of conditions in the 2080s (RCP 8.5). Data shown are for the Little Deschutes River (TIR survey occurred on 24 July 2001).

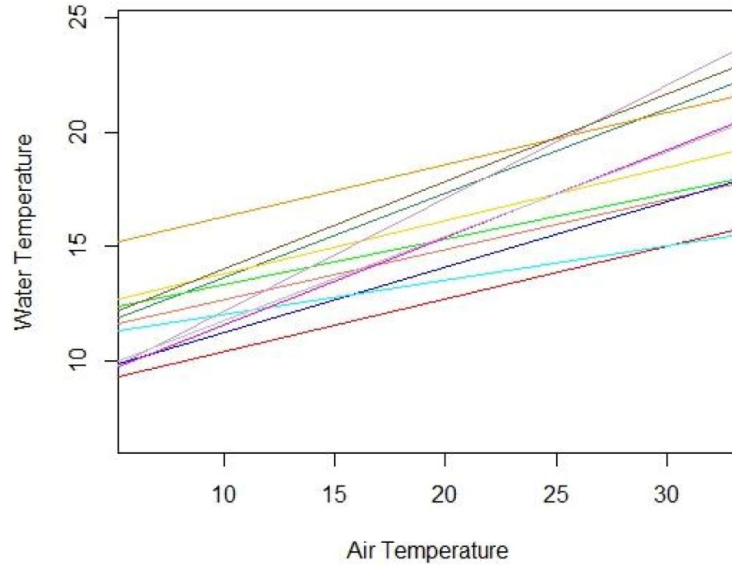
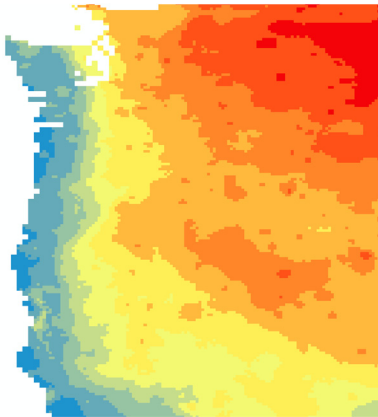
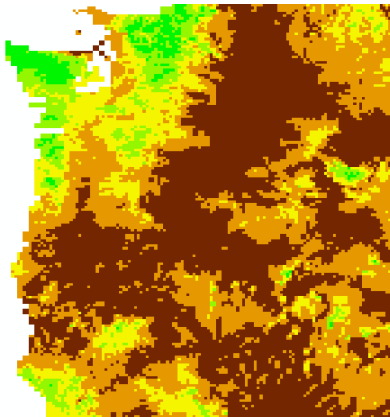


Figure S 4.3. Relationships between water and air temperature (°C) measured at 12 concurrent locations throughout the Snoqualmie watershed, WA. Source: Akida Ferguson, unpublished data.

Δ Summer air temperature



Δ Mean annual precipitation



Δ Probability of winter precipitation as snow

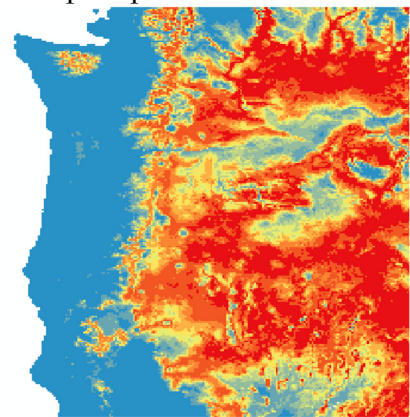


Figure S 4.4. Left: Change in weekly maximum air temperature (°C) during summer (Jul, Aug) from historical (1970-1999) to future (2070-2099) periods as projected using climate scenario RCP 8.5. Blue = small increase, red = large increase. Source: S. Lee, Climate Impacts Group, University of Washington. **Middle:** Change in mean annual precipitation (mm) from historical (1970-1999) to future (2070-2099) periods as projected using climate scenario RCP 8.5. Brown = decrease; green = increase. Source: same as left. **Right:** Change in the probability of winter precipitation falling as snow from historical (1979-2012) to future (2035-2065) periods as projected using climate scenario RCP 8.5. Blue = no change; red = decrease. Source: Klos et al. 2014.

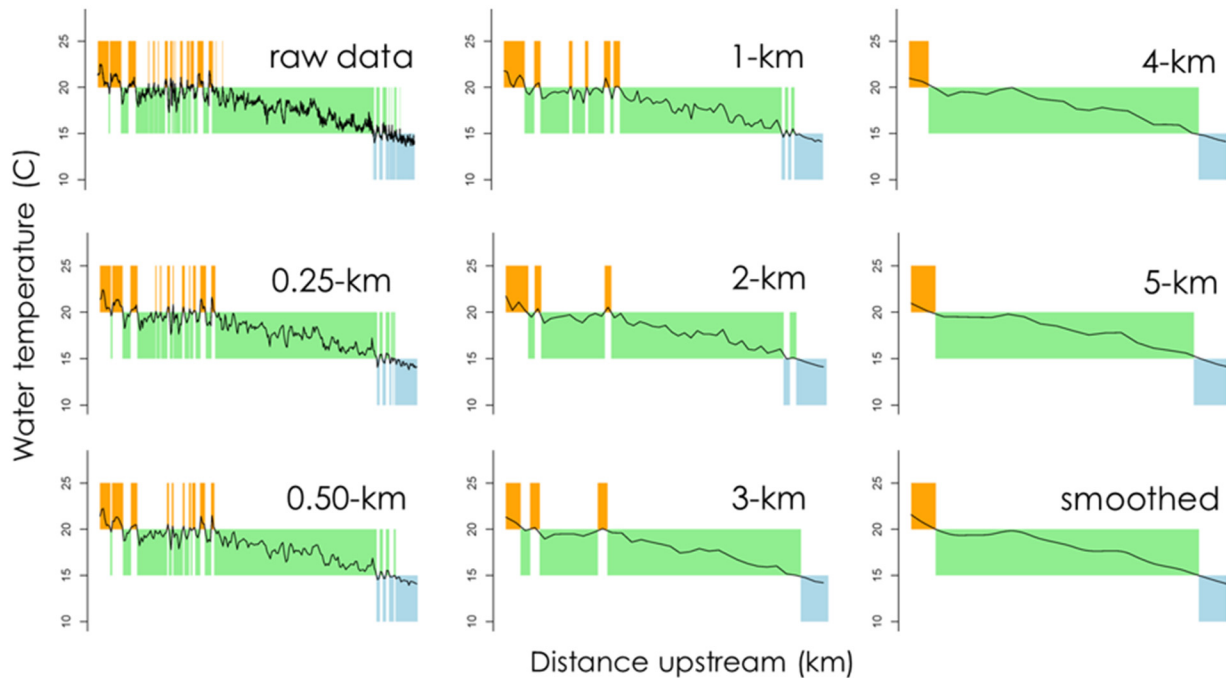


Figure S 4.5. Longitudinal profiles of raw stream temperature (from TIR) and temperature binned at decreasing resolutions (i.e., increasing bin sizes). Data shown are for Lawyer Creek, a tributary to the Clearwater River, ID (TIR data collected 3 Aug 2005). At each resolution, profiles are sliced into warm (orange), tolerable (green), and cool (blue) patches using temperature thresholds of 15 and 20 °C.

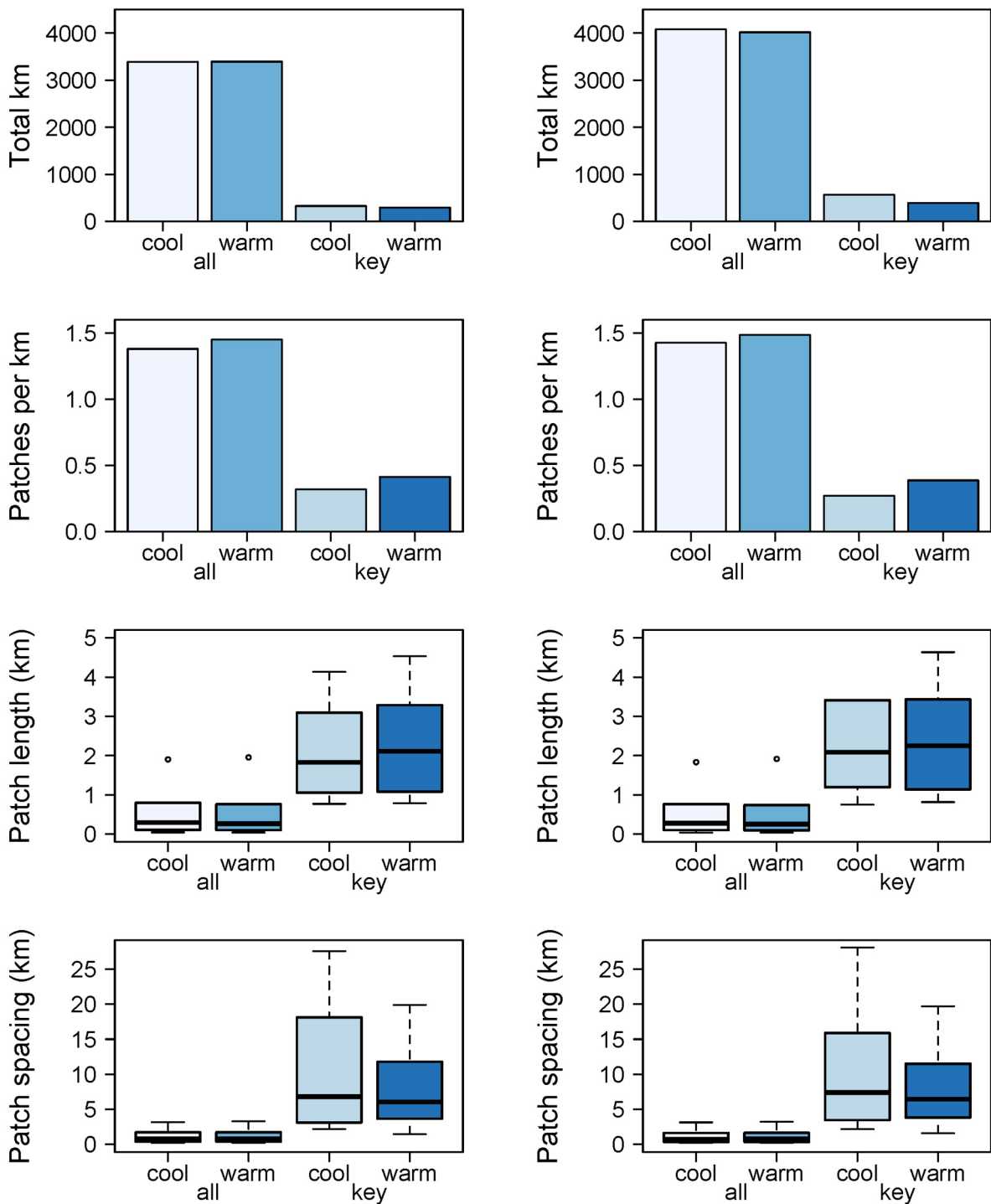


Figure S 4.6. Metrics of thermal heterogeneity, summarizing all anadromous habitat in rivers for which TIR data were available (12,341 km), quantified as peaks (warm patches) and valleys (cool patches) from a moving average trend. Key patches were at least 500-m long and had temperature differentials of 2 °C or greater. **Left:** Thermal heterogeneity within portions of rivers exceeding 20 °C. **Right:** Thermal heterogeneity within portions of rivers exceeding 18 °C.

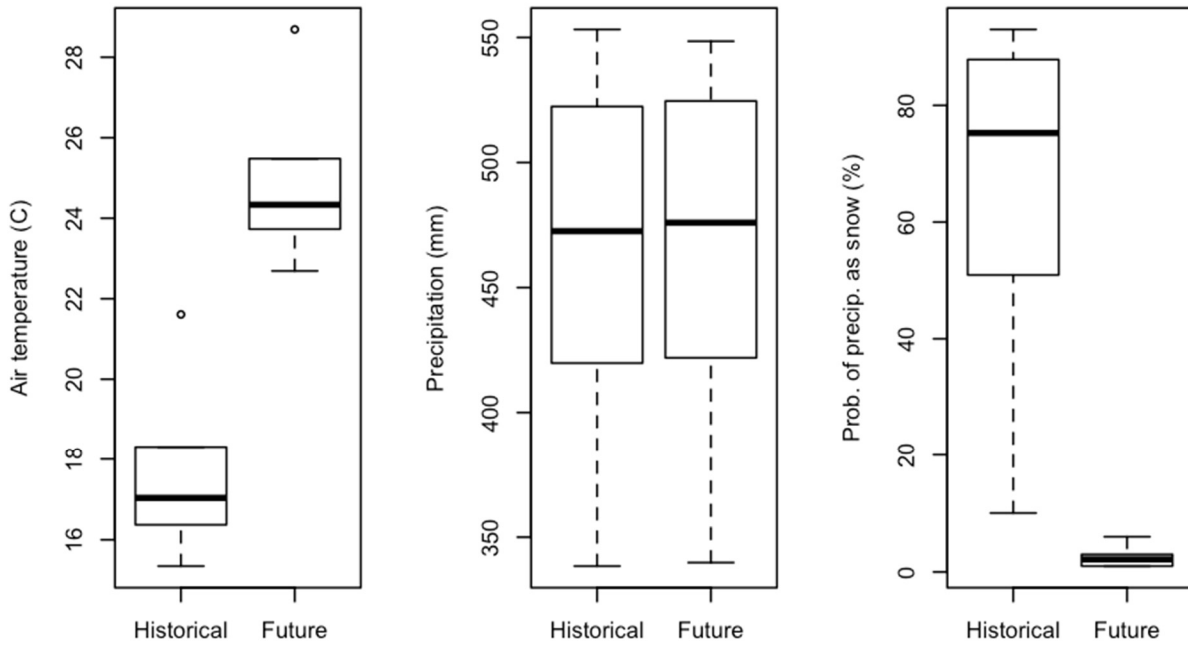


Figure S 4.7. Covariates used to fit historical (1970-1999) and predict future (2070-2099) trends in water temperature. Data shown are for Joseph Creek, a tributary to the lower Grande Ronde River, Oregon.

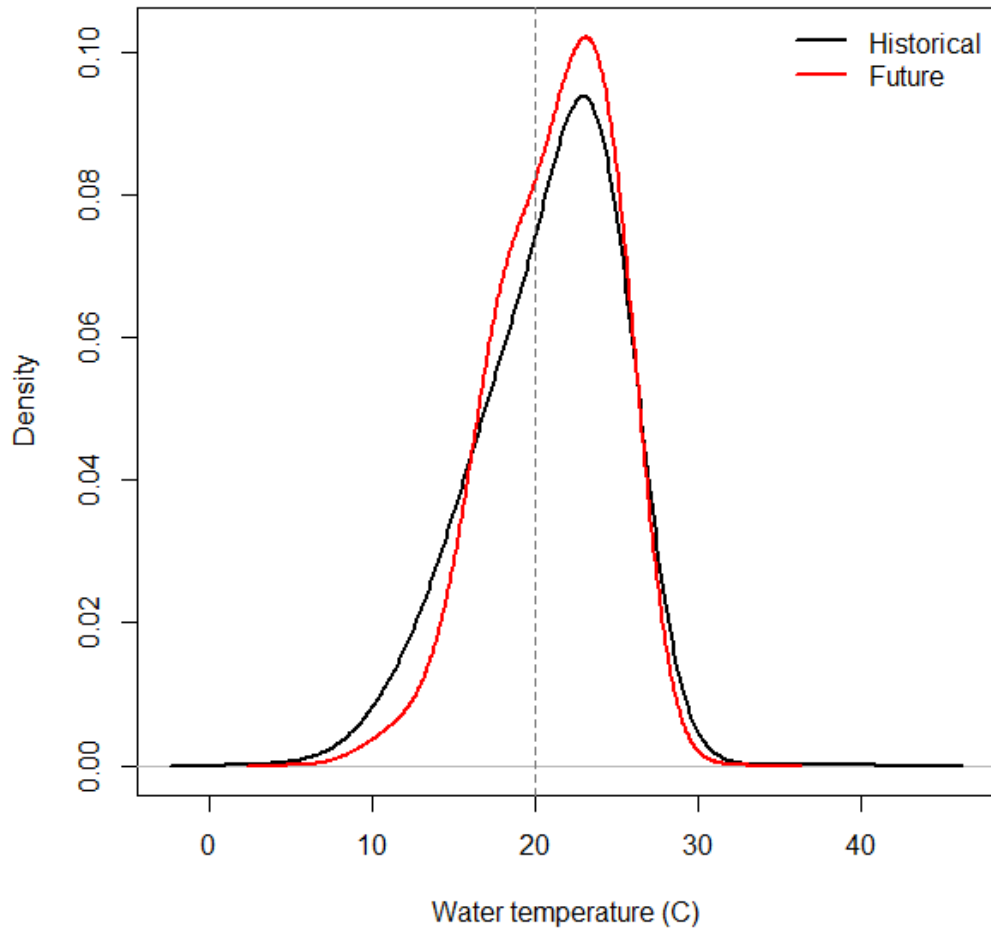


Figure S 4.8. Distribution of water temperature values across all reaches for the historical scenario (computed using TIR data) and a future scenario (predicted using random forest models).

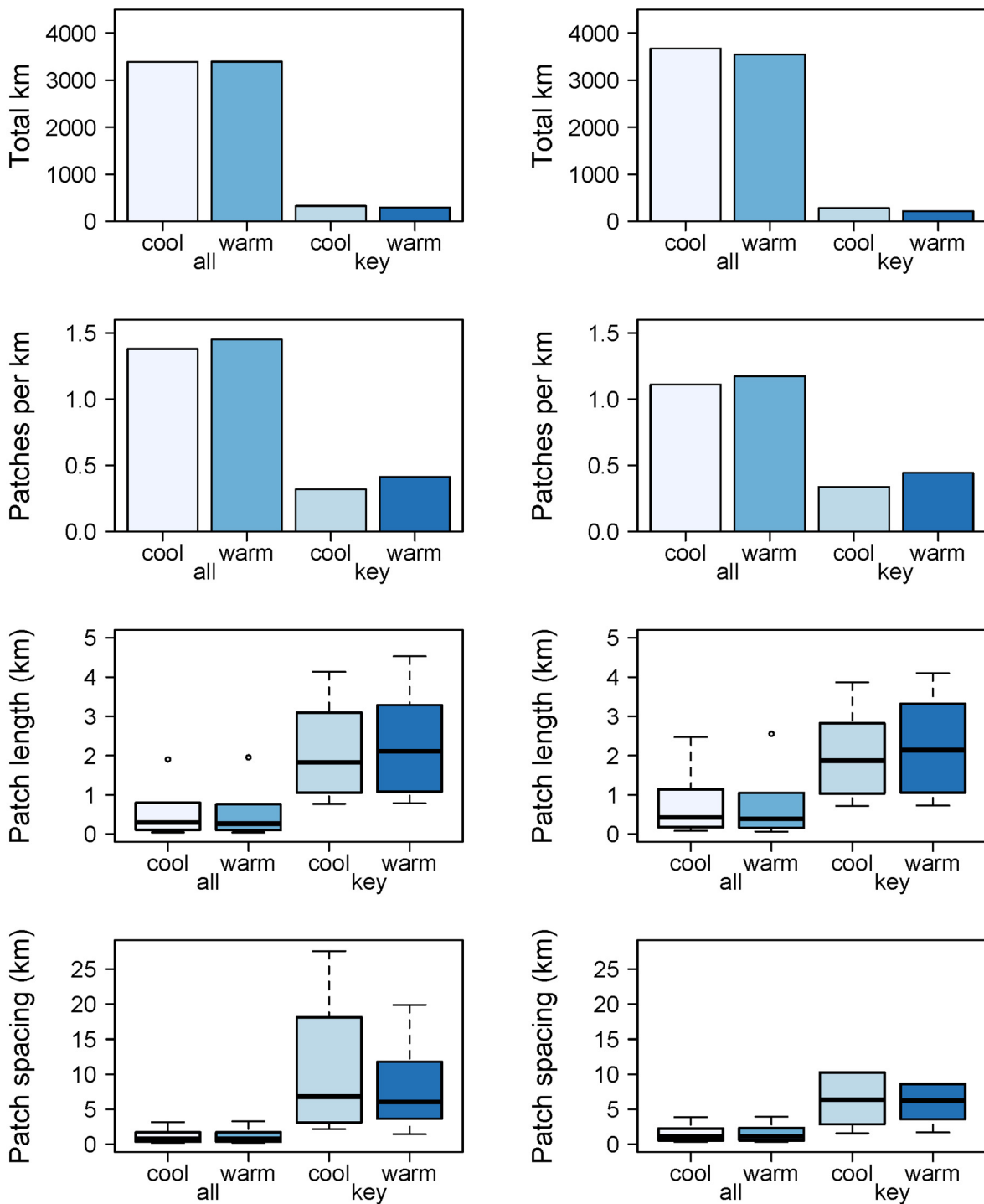


Figure S 4.9. Metrics of thermal heterogeneity, summarizing all anadromous habitat in rivers for which TIR data were available (12,341 km), quantified as peaks (warm patches) and valleys (cool patches) from a moving average trend. Key patches were at least 500-m long and had temperature differentials of 2 °C or greater. **Left:** Original TIR data. **Right:** Projected patterns in the 2080s assuming the RCP 8.5 climate change scenario.

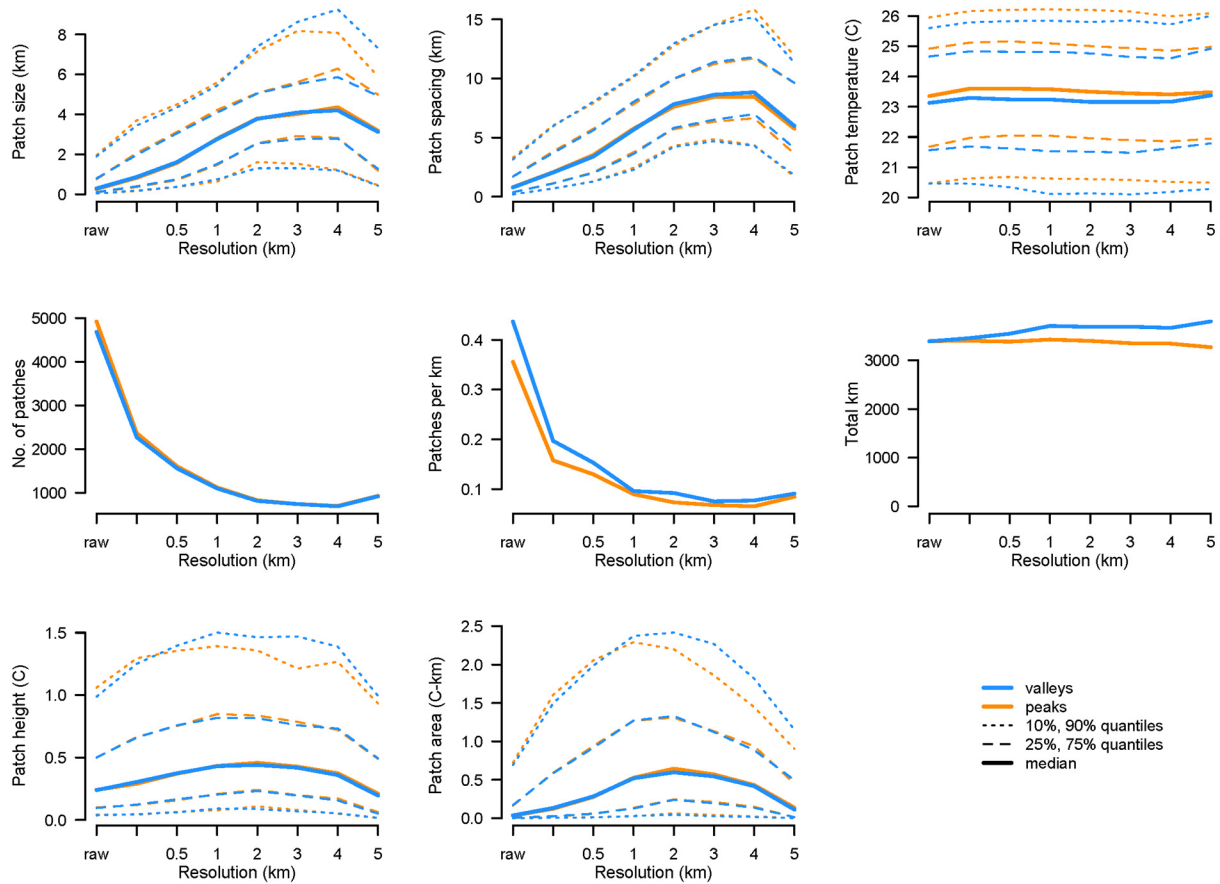


Figure S 4.10. Thermal heterogeneity metrics (y axes), quantified as peaks (warm patches) and valleys (cool patches) from a moving average trend, plotted across decreasing resolution of water temperature data (x axes). Data included all anadromous habitat in rivers for which TIR data were available (12,341 km). Raw = original TIR data resolution.

Chapter 5. Stream network shape influences the strength of growth and phenological responses to climate change in juvenile salmon

5.1. Abstract

The diversity of freshwater habitats to which fish are adapted may afford some protection from climate change. However, it is unclear what role the spatial properties of river networks will play in determining risk. Patchiness in water temperature may provide opportunities for fish to behaviorally optimize their growing conditions. I hypothesized that climate change will alter growth (positively or negatively depending on initial conditions and physiological optima) and timing of fry emergence and smolt outmigration (shifting them to be earlier or later, depending on growth rate); but that these changes will be smaller in more spatially complex stream networks. To address these questions, I developed a spatially-structured, individual-based model in which fish movement decisions and growth were governed by water temperature and conspecific density. I evaluated growth and phenology of Chinook salmon (*Oncorhynchus tshawytscha*) under six climate scenarios in each of three network shapes of increasing spatial complexity. Under cool (current-day) climate conditions, salmon grew best and were ready to smolt earliest in the network having the lowest spatial complexity. However, in warmer climate scenarios, fish grew best and were capable of smolting earliest in the most spatially complex network. Across networks, some fish grew poorly in warmer climate scenarios; however, the vast majority grew bigger and were capable of smolting earlier because water temperatures experienced by fish were ~ 2 °C closer to optimal temperatures for growing. An increased summer maximum temperature and earlier spring warming both yielded increased growth and earlier smolting; the magnitude of responses to increased temporal variability in water temperature were smaller but in the opposite direction (i.e., negative growth and later smolting). My results demonstrate that network topology may influence how fish respond to future thermal landscapes, and should help conservation planners incorporate a spatiotemporal context into decisions that will best promote thermal diversity.

5.2. Introduction

Pacific salmonids (*Oncorhynchus* spp.) are expected to be vulnerable to changes in hydrologic and thermal regimes caused by climate change (Isaak et al. 2010, Crozier and McClure 2015, Falke et al. 2015). As environmental conditions become less tolerable (Mantua et

al. 2010, Arismendi et al. 2012), salmon can either adapt (Reed et al. 2011, Crozier and Hutchings 2014), shift their spatial distribution (Wenger et al. 2011, Isaak and Rieman 2013), or bear the potential consequences. In the future, incubating eggs may be more prone to scour from increased winter storm activity, and timing of migrations may reflect altered hydrology (Leppi et al. 2013, Shanley and Albert 2014). Future thermal landscapes will likely alter growth, survival, and phenology in multiple life stages (Crozier et al. 2010, Kovach et al. 2013). Altered phenology may be problematic if it results in mismatches between evolved life history strategies and environmental conditions. For instance, fish emerging earlier, growing faster, and migrating to sea earlier may find inadequate food resources or increased susceptibility to predators in the marine environment.

Although it is clear that future climate will challenge salmon, we do not know how spatial properties of thermal habitat will influence expected salmon responses. Diverse thermal habitats should afford more opportunities for salmon to find optimal growing conditions, promote life history diversity, and reduce long-term risk (Waples et al. 2008, Lisi et al. 2013, Griffiths et al. 2014, Anderson et al. 2015). Complex network shapes provide diverse and heterogeneous habitats (Benda et al. 2004, Torgersen et al. 2008). Olden and Naiman (2010) state: “The management of riverine landscapes for thermal integrity will require a broad perspective that recognises the heterogeneous nature in which the topology of the drainage network controls the physical processes shaping spatial and temporal variability in stream temperatures.” Network topology has been shown to influence colonization and distribution patterns (Martin and Petty 2009, Della Croce et al. 2014) and may be important for other aspects of population ecology. Understanding whether network shape influences fish response to climate-altered thermal regimes should enable smart conservation planning.

I hypothesized that (1) changes in water temperature associated with climate change will alter growth and shift timing of fry emergence and smolt outmigration; but that (2) effects of climate change on salmon will be smaller in networks having more spatial structure (e.g., dense tributary junctions). Warmer water temperature accelerates physiological processes and development rates. If current water temperatures are below physiological optima, warmer future water temperatures should increase growth rates; whereas if water temperatures are already optimal, warmer future water temperatures may depress growth due to increased metabolic costs, decreased resistance to disease, or increased ecological interactions. If fish grow more rapidly,

they may be ready to head to sea at an earlier date. However, if the size fish can attain is compromised by stressfully high water temperature, outmigration may be delayed. Under suitable thermal conditions, growth may be higher and outmigration earlier in networks of low spatial complexity due to more consistent access to reaches with optimal growth temperatures. Under thermally stressful conditions, decreases in growth and changes in phenology may be smallest in networks having more spatial discontinuities and shorter distances to cool water refuges.

These hypotheses would be difficult to test empirically, given the broad spatiotemporal extent considered, the complexity of variables involved, the difficulty of experimentally controlling water temperature in situ, and the number of Endangered Species Act-listed salmon that would be needed. The role of network topology was investigated by Leibowitz and White (2009) in a life cycle model to better understand coho salmon (*O. kisutch*) populations dynamics. Individual-based models (IBM) are well suited to evaluating how fish may respond to potential future climates and associated thermal heterogeneity because interacting processes can result in emergent properties not observable with models that do not track individuals. Many IBMs have been developed for evaluating consequences for fish of the environmental conditions they experience in one or several stream reaches (Van Winkle et al. 1998, Railsback and Harvey 2002, Charles et al. 2008, Piou and Prévost 2012, Penaluna et al. 2015). However, I am not aware of any models that have explicitly considered simultaneously the response of individual fish to different aspects of altered thermal regimes and to spatial variance in thermal habitat across a whole stream network.

Here, I present a simple individual-based model to theoretically evaluate: (1) how juvenile salmon growth and phenology might respond to altered thermal regimes, and (2) whether responses would differ among stream networks with different shapes. Answers to these questions will improve climate adaptation plans by providing guidance on prioritization of locations for conservation activities that will maximize thermal diversity.

5.3. Methods

I used a simulation approach to consider potential responses by subyearling Chinook salmon (*O. tshawytscha*) to climate and network scenarios. I ran virtual experiments exploring six climate scenarios as applied to each of three stream network shapes.

5.3.1. Climate Scenarios and Network Shapes

I created six climate scenarios, including one contemporary (current-day) scenario and five scenarios representing fundamental aspects of future thermal regimes expected given climate change (**Figure 5.1**). The climate scenarios differed based on (1) the rate at which water temperature warmed during spring (slow versus rapid), (2) the maximum temperature reached during summer (cool versus warm), and (3) the temporal pattern in progression of water temperature from day to day (stable versus variable). Values in **Figure 5.1** represent water temperature at the river's mouth (its warmest location) over the course of a year beginning on 1 October. The median increase in water temperature across all locations in a network on the hottest day of the year was 2.2 °C for the rapid-warm-stable climate scenario, and marginally more for the rapid-warm-variable scenario, compared to the contemporary climate scenario. Headwater reaches warmed the least (minimum increase of 0.45 °C) and the mouth warmed the most (maximum increase of 6.92 °C). The rate of warming in the Pacific Northwest has been about 0.22 °C per decade between 1980 and 2009 (Isaak et al. 2012). My scenarios therefore represent climate conditions that could occur approximately 100 years into the future.

I chose three hypothetical dendritic network configurations to represent the variety of stream network shapes observed in the Pacific Northwest: a long network, a more typical pear-shaped network, and a compact network as described by (Benda et al. 2004) (**Figure 5.2**). These three network shapes were computer-generated using topological rules governing where tributaries were added as the network was grown (e.g., biased toward the base or tips of the network) (Som et al. 2014). Each network had 101 tributary-to-tributary reaches; the length of each reach was drawn from a uniform distribution (0.5, 4 km). Total stream length and the number of reaches in each stream order class (1st through 5th) was similar across the three networks. However, each network had different spatial properties such as mainstem length, watershed area, and the density of tributaries and confluences (**Figure 5.2**). I hypothesized that these properties would provide fundamentally different thermal landscapes, with the compact network providing more thermal heterogeneity because of its high density of tributary junctions. I used the same three networks for all simulations.

5.3.2. Individual-Based Model

5.3.2.1. Overview

Each simulation began with 250 eggs deposited throughout the reaches in a network (see “Initial Conditions” below) during a spawning event on 1 October. For each 12-h time step, water temperature at each location was updated according to the climate scenario, and fish eggs were incubated at the temperature corresponding to their location. Temperatures were decreased at night; diel temperature fluctuation in mid-order reaches was twice as large as in high and low-order reaches (Caissie 2006).

After sufficient thermal units (i.e., degree-days) had accumulated, fish emerged as alevins capable of moving and growing. I used the median values of accumulated thermal units from Steel et al. (2012) for stable and naturally varying thermal regimes (**Table 5.1**). Once a fish emerged as a 0.4-g fry, the next time step began as before by updating water temperatures (**Figure S 5.1**). Fish then “decided” whether to move, how far, and in what direction (see movement submodel, below). Finally, fish grew according to the conditions they experienced (see growth submodel, below). The experiment was terminated on 30 September of the same water year, and I evaluated growth and potential outmigration date as primary responses.

Environmental variables influencing salmon included water temperature and density of fish. Both are known to directly affect fish growth (Crozier et al. 2010, Parra et al. 2012, Baerum et al. 2013). Water temperature was represented as multiple (typically around 4) discrete point locations within each reach; fish could be located anywhere in a reach, but responded to the nearest water temperature. Fish density in each reach was an emergent property arising from the distribution of fish as they moved around the network.

5.3.2.2. Design Concepts

The IBM comprised several modules, and ran within the platform for Spatial Modeling on Stream Networks package in R (Ver Hoef et al. 2014). Code to generate networks having different spatial properties was provided by N. Som, US Fish and Wildlife Service (Som et al. 2014). Code implementing the Wisconsin Bioenergetics Growth model was provided by M. Nahorniak, South Fork Research (Nahorniak 2015). All parameters used in the model are listed in **Table 5.1**.

My artificial stream networks allowed us to compare outcomes across network shapes while controlling for natural variation present in real stream datasets that could occlude patterns.

Similarly, my simple caricatures of climate scenarios allowed us to evaluate separately how warming rate, summer maximum, and variability influenced fish. I considered only water temperature, conspecific density and size of fish from the same cohort as controls on fish movement and growth. I did not include variables such as food supply, substrate, cover, predation, competition with other species or ages, pathogens, or other environmental conditions such as flow, which are known to influence growth and survival in nature.

Fish movement was designed to represent decisions made by fish without complete knowledge about the whole network. Fish “knew” only about water temperatures and the relative density of fish they were presently experiencing but did not know what conditions existed beyond their immediate vicinity.

Stochastic elements of the model included the initial spatial pattern of water temperature in a network, the initial distribution of eggs, and the distance fish moved in each time step. Each of these is described below. Differences among simulations therefore represent natural variability and uncertainty in stochastic processes. To capture the response to these stochastic elements, I ran 100 simulations per network and climate scenario. Conceptually, it may be useful to think of each simulation as one of 100 years in a given network or as one realization of that particular network out of 100 possible realizations (i.e., the topology remains the same but the geology and topography governing water temperature processes differ).

5.3.2.3. *Initial Conditions*

For each simulation, I generated spatially-explicit water temperatures for each time step in a given climate scenario. First, I mapped plausible spatial patterns of water temperature, assuming that headwater reaches were coolest and that temperature warmed as it progressed downstream toward the mouth (Eq. 5.1 below). This represented a common pattern where downstream temperatures were strongly autocorrelated with upstream temperatures (Fullerton et al. 2015). Second, I stochastically added spatial variance to this initial pattern at multiple spatial scales. Third, I scaled the result to range between 0 and 1 (Eq. 5.2 below). This represented the spatially-explicit pattern of *relative* water temperatures across all network locations that was maintained throughout a simulation. Finally, at each time step, I multiplied all of the scaled, spatially-explicit values by the temperature for that time step extracted from the annual pattern associated with a given climate scenario (Eq. 5.3 below).

Water temperature at a given location i (WT_i , in °C) was initially generated based on Shreve stream order (SO):

$$WT_i = r * \frac{\ln(SO_i) + 0.1}{\max(\ln(SO))} + 8 \quad [Eq. 5.1]$$

where r is a random sample drawn from a uniform distribution (15, 20 °C) from the population of water temperature locations in a network (~400). The fractional portion of the equation (relative stream order) ranged between 0 and 1. Addition of the scalar (value of 8) yielded water temperatures that ranged across the network from 8 to 28 °C.

I added spatial heterogeneity to this process by randomly increasing or decreasing the temperature in both whole tributary watersheds and at individual locations at the beginning of each simulation. Spatial heterogeneity in water temperature patterns at the tributary watershed level represented the potential effect of differing geology and topography on tributary water temperature (Lisi et al. 2013). I selected a random sample of three mid-order reaches (Shreve orders between 2 and 40), traced upstream pathways, and increased temperatures for all selected reaches by 3 °C. I decreased temperature for a second random sample of three mid-order tributary watersheds in the same manner. It was possible for temperature in a tributary to be both increased and decreased, resulting in no net change. I added site-level heterogeneity by randomly sampling 35 points within a network and either increasing or decreasing temperature by 3 °C. These points were representative of localized cold or warm water patches.

I then scaled the resulting values between 0 and 1 to get a vector WT_{scaled} of spatially-explicit *relative* values of water temperature across the network. For a given location i :

$$WT_{scaled,i} = \frac{WT_i - \min(WT_{sh})}{\max(WT_{sh}) - \min(WT_{sh})} \quad [Eq. 5.2]$$

where WT_{sh} = the vector of water temperatures from Eq. 5.1 to which I had added spatial heterogeneity. This can be thought of as the spatial scaffolding upon which I draped temporal patterns. Scaled temperatures (temperature at a location relative to other locations in the network) were maintained throughout a simulation.

The spatially-explicit vector of water temperatures for time step t in climate scenario c was calculated as:

$$WT_{t,c} = (p_{t,c} - \min(WT_{sh})) * WT_{scaled} + \min(WT_{sh}) \quad [Eq. 5.3]$$

where $p_{t,c}$ = the water temperature at the mouth predicted for time step t from climate scenario c (i.e., from one of the curves in **Figure 5.1**), WT_{sh} = the vector of water temperatures from Eq. 5.1 to which I had added spatial heterogeneity, and WT_{scaled} = the set of scaled water temperatures for all locations in the network from Eq. 5.2. $WT_{t,c}$ values ranged across the network from $\min(WT_{sh})$ to $p_{t,c}$.

The amount of change in temperature throughout the year depended on spatial location; I modeled temperatures increases to be greatest in downstream reaches, which may be expected to occur in at least some watersheds, especially during summer (Steel et al. 2016) (**Figure S 5.2**). The coldest location remained cold throughout the year (WT_{scaled} value of 0) and the warmest location followed the climate scenario trajectory exactly (WT_{scaled} value of 1). Thus, as water temperature warmed through the season, the warmth spread up from the base of the network like a tide.

Diel variation in water temperature was proportional to the median temperature in a network for a given time step and was twice as large in mid-order reaches (Caissie 2006). For example, if the median temperature across locations in a network on 20 October (from Eq. 5.3) was 11 °C, the day and night time temperatures in mid-order reaches for that date were $x_i + 0.3(11 \text{ °C})$ and $x_i - 0.3(11 \text{ °C})$, respectively, where x_i = temperature for location i on that date (from Eq. 5.3). Daytime and nighttime temperatures in other reaches were $x_i + 0.15(11 \text{ °C})$ and $x_i - 0.15(11 \text{ °C})$, respectively.

I systematically placed 250 fish eggs (one egg per location) in the coldest locations within mid-order reaches of a network (Shreve orders between 2 and 40) (**Figure S 5.3**). Eggs were then “jittered” in space. That is, eggs were moved randomly upstream or downstream by running the movement submodel for one time step. Because water temperature influenced movement and water temperature was distributed differently throughout the network each time the model was run, the locations of eggs also differed. Varying initial conditions ensured that there were no systematic biases in fish response due to the temperature in reaches into which fish were initially placed.

5.3.2.4. Movement Submodel

Movement of individual fish was determined by conspecific density, fish size, and water temperature. For the first time step after it had emerged, a fish swam upstream. For subsequent time steps, it continued to move in the same direction as long as it was in the same reach. At the

beginning of each time step, a fish first decided how far to move based on the density it currently experienced (farther if conditions were crowded; Eq. 5.4, below) and its own size (further as it grew larger; Eq. 5.5, below). As it encountered tributary junctions, a fish had the option of changing course based on its assessment of the growing conditions in each branch. The fish continued moving until it had moved the pre-determined distance (i.e., it did not abort movement if it encountered suitable habitat along the way).

Move distance (k , in m) was drawn from a lognormal distribution with the following properties:

$$\ln(\mu) = \ln(m_{min}) + \frac{\ln(m_{max}) - \ln(m_{min})}{D_m} * \min(d, D_m); \quad \ln(\sigma) = 0.5 \quad [Eq. 5.4]$$

where m_{min} = lower bound of move distance (m), m_{max} = upper bound of move distance (m), d = conspecific density (fish per linear km), and D_m = upper threshold of conspecific density past which move distance did not increase (**Table 5.1**). This value was then scaled to fish size:

$$k = k * \left(1 + \min \left(1, \frac{w}{W} \right) \right) \quad [Eq. 5.5]$$

where k = movement distance (m) drawn from the lognormal distribution described in Eq. 5.4, w = fish weight (g), and W = upper threshold of weight (g) beyond which movement distance did not increase (**Table 5.1**). For example, when a 1-g fish was alone it moved ≈ 75 m on average (range: 0 to 600 m); if density reached 30 fish, movement distance ≈ 250 m (range: 0 to 1.5 km). Mean movement ranges for a 10g and 20g fish were ≈ 100 and 125 m when alone, and up to 2 and 2.5 km at high densities (**Table 5.1**).

As fish encountered a tributary junction, they chose to move into one of three positions: upstream into the left or right tributary or downstream within the same reach. At a confluence, fish “sensed” temperatures in each of the three reaches, and then moved into the reach where its growth would be highest (growth model, below) (Railsback and Harvey 2002). Fish density did not influence this decision because a fish presumably could not sense densities in each of the three reaches. This process was repeated for multiple tributary junctions encountered until the fish had moved its allocated distance for that time step.

5.3.2.5. *Growth Submodel*

At a fish’s final position for a given time step, it grew according to water temperature and fish densities experienced. Growth was estimated using the Wisconsin Bioenergetics model

(Hanson et al. 1997). I used consumption equation 3, respiration equation 1, and excretion equation 3 from that model, which are commonly used for salmon. I used original values for most parameters, but updated temperature-dependent consumption parameters as defined in recent experiments for subyearling Chinook salmon (Perry et al. 2015, Plumb and Moffitt 2015) (**Table 5.1**). I also increased the prey energy density parameter from the default value of 2500 J·g⁻¹ to 3500 J·g⁻¹ to more reasonably match salmon prey (Gonzales 2006, Beauchamp et al. 2007).

Conspecific fish density influenced consumption via a linear relationship with an upper threshold. The proportion of maximum consumption (p-value) for a fish was reduced as the density of conspecifics increased up to a maximum density:

$$p = \begin{cases} 1 - \frac{d}{D_g} & \text{for } d < D_g, \\ p_{min} & \text{otherwise} \end{cases} \quad [Eq. 5.6]$$

where p = p-value used in bioenergetics consumption equations, d = conspecific density (fish per linear km), and D_g = upper threshold of fish density past which p-value did not decrease. At a density of 1 fish, p-value was maximized at 0.97, and linearly decreased to $p_{min}=0.2$ as fish density approached D_g (**Table 5.1**).

Fish were assumed to survive as long as their final size exceeded 3g. I did not explicitly model mortality otherwise.

5.3.3. Quantifying Outputs

For each scenario, I quantified distributions of (1) date fish emerged, (2) mean daily fish densities experienced, (3) daily movement distances, (4) daily and cumulative consumption rates, (5) daily growth rates, (6) final fish weights, and (7) the date at which fish were large enough to smolt. Many factors are believed to play into the date at which fish begin smoltification (e.g., size, daylight, temperature, water quality cues, etc. (Sykes et al. 2009, Finstad and Hein 2012, Spence et al. 2014). Mangel and Satterthwaite (2008) proposed thresholds for optimal sizes at which coho salmon and steelhead (*O. mykiss*) smolt that balance the risks and benefits of remaining in freshwater versus heading to sea. Widener (2012) used threshold sizes of between 7 and 11 g (~80-100mm) for age-0 Chinook to become smolts. For this analysis, I assumed that fish were capable of initiating smolting when they reached a weight of at least 5 g.

The model was not dependent on empirical data, thus replication was limited only by computing power and time. Because large sample sizes can yield statistically significant results that are not biologically meaningful, I did not rely on typical p-value thresholds, but rather on weight of evidence. I report model outcomes as probability distributions, so that inferences can be drawn from the whole dataset, rather than from potentially misleading statistics.

Variance and median of final fish weight stabilized at about 20 simulations per scenario (results from as few as 10 simulations were similar) (**Figure S 5.4**, top). The amount of variance contributed by different responses among 250 fish in a typical simulation (“year”) was similar to the amount of variance contributed by different initial conditions among the 100 simulations (“years”) for a typical fish (**Figure S 5.4**, bottom). Henceforth, I report pooled data for 25,000 fish and present distributions in boxplots. That is, 250 fish per simulation for each of 100 simulations were combined for each network and climate scenario combination. I also report the percent of simulations in which a particular comparison met criteria (e.g., in 60% of simulations, median growth was higher for fish in network A than in network B).

5.3.4. Sensitivity Analysis

To assess sensitivity of results to nominal parameter values, I conducted a basic sensitivity analysis. I selected six parameters that I believed would be most influential: two that acted on the egg stage, two that influenced movement, and two that influenced growth (**Table 5.2**). I perturbed the values of each of these parameters individually +/- 10% in each of the three networks for the contemporary climate scenario (slow-cool-stable) and for one representation of future climate (rapid-warm-stable). For each case, I evaluated the effect of parameter perturbation on four metrics: date emerged, growth rate, final fish weight, and date a fish can smolt.

I also conducted a suite of exploratory evaluations: increasing or decreasing the whole thermal regime (not just the summer max) by 3 °C; restricting spawning to 3rd order or larger reaches (instead of 2nd order or larger); and using the original set of published bioenergetics parameters for adult Chinook salmon that have typically been used because data were not previously available for juveniles: CQ=5; CTO=15; CTM=18; CTL=24; CK1=0.36; CK4=0.01 (Hanson et al. 1997).

5.4. Results

Metrics of fish performance were reasonable for subyearling Chinook salmon (**Figure S 5.5**). Predictions of emergence timing, conspecific densities experienced, daily consumption and growth rates, final weight and outmigration date were all within ranges observed in the field (**Table 5.3**). Temperatures available were well within the range of temperatures available in Pacific Northwest rivers. Incubating eggs experienced temperatures around 7-9 °C, and mobile fish sought out temperatures of 11-13 °C during spring and summer (warmer than were generally available), very infrequently experiencing temperatures near the growth optimum ~21 °C, but similar to temperatures selected behaviorally by juvenile subyearling Chinook salmon (Richter and Kolmes 2005, Tiffan et al. 2009) (**Figure S 5.6**). The higher growth rates produced by my model compared to field observations likely reflect constraints on growth that my model did not capture, such as competition, food availability, predation, and other stressors. Moreover, the final weight of modeled fish would have been lower had I allowed fish to leave the system after they had reached the threshold size needed to smolt.

5.4.1. Responses Across Network Shapes

Water temperatures seasonally available to fish were similar across network shapes (**Figure S 5.6**). Diel temperature fluctuations were also similar across networks. Median diel variance across locations and time steps was 3.0, 3.1, and 3.0 °C in the long, typical, and compact networks (range: 2.1 to 7.4 °C) under the slow-cool-stable climate scenario, and slightly higher in the rapid-warm-stable climate scenario, at 3.6, 3.7, and 3.7 °C (range: 2.2 to 8.7 °C). Fish in all three networks experienced similar temperatures during egg incubation, but once mobile, fish in the long network experienced the warmest temperatures whereas fish in the compact network experienced the coolest temperatures. Differences among networks were most noticeable during spring and summer.

There was considerable variance in fish responses across individuals and simulations within a network and climate scenario. Nonetheless, fish in the long network generally consumed more, grew faster, weighed more, and could smolt earlier than fish in other networks under the contemporary climate scenario (**Figure 5.3**). Median final fish weight was higher in the long network than in the typical and compact networks in 72% and 75% of simulations, respectively. Fish weight was essentially the same between the typical and compact networks (weight in the typical network exceeded that in the compact network in 51% of simulations). Under future

climate scenarios, median temperatures experienced in warmer climates were >2 °C closer to optimal growing conditions. Correspondingly, fish generally grew better and outmigrated earlier in all networks. However, patterns among networks were reversed under future climate conditions. In the rapid-warm-stable climate scenario, fish growth increased the most in the compact network and the least in the long network (**Figure 5.4**). Median final fish weight was higher in the compact network than in the typical and long networks in 65% and 70% of simulations, respectively. Final weight in the typical network exceeded weight in the long network in 58% of simulations. Correspondingly, shifts toward earlier smolting were largest in the compact network and smallest in the long network.

5.4.2. Responses to Aspects of Climate-Altered Thermal Regimes

Fish growth increased the most when temperatures reached a warmer maximum during summer, whereas gains about half as large resulted when warming began earlier in the spring, regardless of whether or not summer maxima were higher (**Figure 5.5**). Adding daily variability to thermal regimes had a much less noticeable effect but usually caused decreased growth. The degree of change associated with each of these aspects of altered future thermal regimes also differed among networks (**Figure 5.5**). The degree of separation in response among networks was largest when summer maxima increased; networks responded more similarly with increases in spring warming or variability.

5.4.3. Sensitivity Analysis

Responses were most sensitive to changes in parameters controlling egg incubation (spawn date and ATU_{crit} , the threshold of accumulated thermal units necessary for emergence) and those controlling fish growth (prey caloric density and the density of conspecifics above which consumption was limited, D_g) (**Figure S 5.7**). Results were largely insensitive to parameters controlling fish movement; possibly, a 10% perturbation may not have been sufficient to detect an effect. Date emerged was most responsive to changes in spawn date and secondarily to ATU_{crit} . Growth rate was sensitive to changes in all four parameters. Final fish weight was most responsive to changes in prey caloric density, followed by changes in D_g and spawn date. Date a fish was capable of smolting was most responsive to changes in spawn date and to prey caloric density.

Sensitivities were similar among networks and between the two climate scenarios tested. A notable exception was that fish emerged much earlier in the future climate scenario. Trends

across networks were noticeable in some cases, particularly for growth and weight. Of the four parameters to which results were sensitive, prey caloric density and D_g had the greatest potential to influence my conclusions about climate scenarios and network shapes because these parameters were called repeatedly throughout a simulation; spawn date and ATU^{crit} affected all individuals equally at the beginning of each simulation.

In exploratory simulations in which I adjusted the entire thermal regime or restricted spawning to 3rd-order or larger reaches, median final weight increased or decreased marginally, but overall among-network patterns remained unchanged across climate scenarios. Notably, when I used the originally-published values of bioenergetics parameters for adult Chinook salmon which had a lower optimal growth temperature, growth and final weights were an order of magnitude larger than when I used the updated set of parameters calibrated for juvenile subyearling Chinook salmon. The relatively cool temperatures (~11-13 °C) experienced by fish in my simulations promoted better growth under the original parameterization.

5.5. Discussion

5.5.1. Response to Climate Change Likely Idiosyncratic

The consequences of climate change for salmon are expected to be generally negative (Jonsson and Jonsson 2009, Arismendi et al. 2012). However, the way that fish will respond are likely to be complex and case specific, varying by species, life stage, and the extent to which and times at which environmental conditions change. Growth rates of modeled subyearling Chinook salmon generally increased in all five of the future climate scenarios that I tested, suggesting that temperatures experienced by fish in the contemporary climate scenario were below optimal growing conditions and that the future climate scenarios were not thermally stressful enough to suppress growth. Enhanced growth under warmer conditions is not unexpected if fish had been limited by temperatures that were below their physiological optimum. For instance, using a bioenergetics approach, Beer and Anderson (2011) found that in streams where water temperature was cool during summer, warming air temperature and loss of snow were likely to translate into increased growth rates for Chinook and steelhead, whereas growth decreased in streams where summertime water temperature was already warm. Although growth was positive for most fish in my virtual experiment, I found reduced and even negative growth for some fish that experienced especially warm temperatures during late summer (**Figure S 5.8**). Depressed growth might be expected to occur in places or at times where water temperature warms

substantially, for species that have lower thermal requirements such as bull trout (*Salvelinus confluentus*), or in the presence of other stressors. Growth in the field may also be reduced further by factors not considered by my modeling.

5.5.1.1. Unexpected Network Influence

One of my primary objectives was to consider whether network topology could influence how salmon responded to climate change. It was unsurprising that responses differed among networks because thermal landscapes are strongly linked to localized controls and water temperature drives biological processes. What was surprising was which networks yielded the largest response to future climates.

Initially, fish grew the most and were ready to smolt earliest in the long network commensurate with expectations. This pattern was not established during the incubation period; rather, results stem from growth of mobile fish in differently shaped networks. In the compact and typical networks, it was possible for fish to move from one cool branch to another without ever encountering intervening warm habitat (i.e., not intentionally avoiding it, but not finding it either). Whereas, in the long network, fish could not avoid warm intervening mainstem habitat when moving among tributaries (**Figure 5.6**). Smoother gradations in water temperature in the long network may also have allowed fish to more quickly find optimal thermal habitat. Whereas in the typical and compact networks, higher thermal heterogeneity may have caused more fish to become “stuck” in local maxima rather than continuing on to a global maximum.

I expected that the compact network would provide a moderating influence to increasing temperature because its more complex topology provided higher spatial diversity in water temperature. Contrary to expectations, changes were greatest in the compact network, suggesting that this shape may be most sensitive to climate change. Tributaries that previously had been connected by stretches of cool water in the contemporary climate scenario were separated by stretches of warm water in future climate scenarios (**Figure 5.6**). Fish moving within these networks more frequently encountered newly warm habitat and therefore grew more than they had in the cooler climate scenario.

5.5.1.2. Life Cycle Consequences of Elevated Growth

There are advantages to higher growth rates. A larger fish has lower relative metabolic costs and therefore more cushion in the amount of weight loss it can sustain (Hanson et al. 1997, Beauchamp et al. 2007), and size confers benefits in competitive ability (Fausch and White

1986), protection from predators (Peterson and Kitchell 2001), and survival and fitness advantages (Duffy and Beauchamp 2011, Thompson and Beauchamp 2014). However, enhanced growth during freshwater life stages does not imply that climate change will have a net positive effect on fish because altered growth can result in subsequent effects throughout the life cycle. Conditions experienced early in life can influence the decision to smolt (Beakes et al. 2011), smolt timing (Roper and Scarnecchia 1999), and survival to adulthood (Thompson and Beauchamp 2014). For instance, Reed et al. (2010) observed that sockeye salmon (*O. nerka*) in Alaska reared in a warmer lake than other fish from the same genetic lineage grew larger and smolted slightly earlier. Because fish grew larger in my modeled future climate scenarios, they were therefore assumed ready to smolt at an earlier date. If higher growth does result in earlier outmigration, phenological asynchrony may ensue whereby smolts entering seawater may find insufficient food resources or may experience altered susceptibility to size-selective mortality. Fish size and timing of ocean entry may affect early marine growth (Weitkamp et al. 2015) and subsequent age structure (Tattam et al. 2015). Conversely, fish not growing well during early freshwater rearing may delay or abandon smolting (Perkins and Jager 2011). For instance, some fall Chinook migrating out of the Snake River choose to spend the winter in the reservoirs and re-initiate smolting the subsequent spring (Widener 2012).

5.5.1.3. Timing and Variability

The timing of thermal exposure may have important consequences for fish. When my modeled fish experienced earlier spring warming, fry emerged earlier, and their growth and final size increased enough to shift smolt date earlier by 5 to 18 days, depending on the network and climate scenario. I also found earlier emergence and smolting in my sensitivity analysis when I used an earlier spawn date or a lower threshold for accumulated thermal exposure needed to emerge. However, only the earlier spawning caused decreases in growth and final size, likely because fish emerged too early when temperatures were suboptimal for growing. Finstad and Jonsson (2012) found that Atlantic salmon (*Salmo salar*) eggs incubated at cooler temperatures resulted in fish that later grew less in warm environments than fish that had incubated at warmer temperatures. When ecological interactions and variation in spawn timing also occur, warmer springs could lead to bigger gaps between small and large fish by the end of the growing season, and to a variety of life history strategies depending on size/fitness tradeoffs (Lisi et al. 2013).

Although I found that fish responses to temporal variability in water temperature from day to day were smaller than responses to changes in summer maxima or to rate of spring warming, temporal variability may have important biological consequences. For instance, emergence timing of Chinook salmon was related to variability in water temperature in an experiment (Steel et al. 2012). My model could be improved by linking to a thermal exposure-based emergence model such as the one presented in Beer and Anderson (2001) and in Beer and Anderson (2011). I found differences between stable and variable thermal regimes in post-emergence responses in later life stages. Fish that had experienced variable thermal regimes grew less well; median fish sizes were smaller but some individuals did respond positively. Geist et al. (2010) found that temperature delivery had important consequences for survival of juvenile Snake River fall Chinook salmon, where growth of fish experiencing fluctuating temperatures was approximately half as large as growth of fish experiencing stable regimes, even when mean temperatures were similar.

5.5.2. Strengths and Limitations of the IBM

My model provides a novel contribution to the suite of existing tools for predicting the effects of climate change on Pacific salmon in several ways. To my knowledge this is the first implementation of an IBM that evaluated spatially explicit responses across an entire stream network. The role of network topology on the response of whole populations has been explored for coho salmon, but individual responses were not considered (Leibowitz and White 2009). Bioenergetics and growth are typically evaluated on a daily basis; however, this temporal scale may be too coarse to capture important dynamics (Holsman and Danner 2016). I modeled bioenergetics at a sub-daily time step because thermal regimes can differ enormously between night and day.

Primary assumptions in the IBM were that: (1) water temperature, conspecific density, and fish size were primary drivers of fish movement and growth; (2) egg size, size of fry at emergence, intrinsic metabolic rate, and competitive ability were constant across individuals; (3) resource availability; interactions with predators, pathogens, or competitors other than members of the same cohort; and flow, physical habitat, or water quality did not influence individuals differently; and (4) biological interactions, physical stream habitat, and landscape features (e.g., allochthonous inputs, elevation, land use) did not differ among network shapes or with changing climate conditions. Additionally, I assumed that climate scenarios and thermal heterogeneity

patterns were realistic. Despite these limitations, my simple IBM provided results that matched field observations reasonably well, and yields insight into the potential mechanistic influence of spatiotemporal temperature patterns during critical early life history stages.

There may be countervailing or synergistic pressures associated with climate change that were not captured in my model. For example, if increased winter flooding causes fewer fry to emerge (i.e., because more redds were scoured), the surviving fish may enjoy higher per capita food availability and reduced competition. Even though fewer fish would survive to the smolt stage, these fish may grow large and exhibit higher survival in later life stages. This effect on growth could be exacerbated or nullified depending on how fish respond to future thermal landscapes. Crozier and Zabel (2006) found a negative relationship between water temperature and survival for some but not all populations of spring Chinook in the Snake River, Idaho. Other populations responded more strongly to flow and density, suggesting that climate change will likely have different impacts on different populations in this metapopulation. Similarly, Xu et al. (2010), found that growth of brook trout (*Salvelinus fontinalis*) in Massachusetts differed seasonally and depended on water temperature, flow, and fish density. Moreover, unforeseen changes in predator and prey communities as a result of climate change will influence the accuracy of model results.

5.5.3. Informing Spatial Conservation Priorities

These virtual experiments can immediately inform management decisions during the recovery-planning process and during population-status reviews for ESA-listed salmonids. For example, given a set of watersheds of varying topology, managers can consider which network might afford more protection from expected effects of altered thermal regimes. This information can be used to help characterize which salmon populations are most at-risk, and to prioritize conservation and restoration activities accordingly. More broadly, my research suggests that different spatial patterns of water temperature within and among networks may elicit a diversity of responses by salmon to altered thermal regimes. Penaluna et al. (2015) found that variability in habitat conditions mediated the response of cutthroat trout (*O. clarkii*) to climate change in several watersheds in northwestern Oregon. Boughton et al. (2007) showed experimentally that temperature heterogeneity at local scales influenced growth of steelhead in California. Although it is possible that some fish will capably adapt to changing conditions (Reed et al. 2011), higher habitat diversity both within and across networks should translate to higher resilience of fish to

stressors (Schindler and Hilborn 2015). For example, Armstrong et al. (2010) found that juvenile coho in the Wood River, Alaska were able to capitalize on growing opportunities by moving among thermally diverse habitats. Conservation of thermal complexity will best be accomplished through conservation of watershed processes that promote diverse and complex stream habitats (Beechie et al. 2012). My work adds to a growing body of literature demonstrating that spatiotemporal context (Steel et al. 2016) and network relationships (Flitcroft et al. 2012, Mari et al. 2014, Yeakel et al. 2014) are important to salmon and should be explicitly considered during conservation and climate adaptation planning.

5.6. Acknowledgements

I am grateful for discussions with Brian Burke, Josh Lawler, Christian Torgersen, Joe Ebersole, Scott Leibowitz, Ashley Steel, Nate Mantua, Lisa Crozier, and David Boughton while developing the individual based model and its hypothetical framework. I thank Brian Burke, Nick Som, and Matt Nahorniak for sharing their code. I thank Brian Burke, Josh Lawler, and Scott Leibowitz for constructive feedback on earlier versions of this chapter, and for support from Beth Sanderson to pursue this research.

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Table 5.1. Parameters defining fish characteristics and behaviors in the individual-based model.

Parameter	Value	Description	Reference
General			
Spawn date	1 Oct	Date at which eggs are laid (over the last decade, the median date fall Chinook in the Columbia River pass Bonneville dam is ~ 10 September)	www.fpc.org/adultsalmon / adultqueries/ Adult_Table_Species_Graph_2015.html
No. Fish	250	Number of virtual fish in each network per simulation. Assuming each virtual fish represents 1000 real fish, overall mean density would be ~ 0.18 fish· m ⁻² assuming an average stream width of 7m and total network length=200km	Bjornn and Reiser 1991; Jonasson et al. 1998
Initial weight	0.4	Mass of emerged alevin (g)	Beacham and Murray 1993; Geist et al. 2006
ATU _{crit}	1160; 1140	Accumulated thermal units (°C-d) required to emerge as alevins for ‘stable’ and ‘variable’ climate scenarios	Steel et al. 2012
SO _{lo}	2	Lowest Shreve order fish eggs could be deposited in	Quinn 2005; Isaak and Thurow 2006
SO _{hi}	40	Highest Shreve order fish eggs could be deposited in	Quinn 2005; Isaak and Thurow 2006
Size to smolt	5	Size (g) needed to smolt; ~78 mm	Denny et al. 2012; Widener 2012
Size of survivor	3	Size (g) needed to be counted as a survivor; ~50 mm	Widener 2012; Roper and Scarnecchia 1999
Movement			
m_{min} in Eq. 5.4	75	Lower bound of movement distance (m)	Beall et al. 1992; Rodriguez 2002
m_{max} in Eq. 5.4	250	Upper bound of movement distance (m)	Beall et al. 1992; Rodriguez 2002
W in Eq. 5.5	30	Fish weight (g) beyond which movement distance does not increase (Chinook smolts in the Columbia River migrating past Bonneville dam are all smaller than this)	www.fpc.org/smolt/ forklengthqueries/ forklength_query_12.html
D_m in Eq. 5.4	30	Upper threshold of fish density (virtual fish per linear m) above which movement distance does not increase; equates to ~4.29 fish·m ⁻²	Unknown, but see ISAB 2015

Parameter	Value	Description	Reference
<i>Growth</i>			
D_g in Eq. 5.6	10	Upper threshold of fish density (virtual fish per linear m) above which Bioenergetics p-value does not decrease; equates to $\sim 1.43 \text{ fish}\cdot\text{m}^{-2}$	Unknown, but see ISAB 2015
p_{min} in Eq. 5.6	0.2	Lowest value of Bioenergetics p-value possible, even at high fish densities	Arbitrary, to match lower p-values used in Beauchamp et al. 2007
<i>Bioenergetics</i> ¹			
CQ	4.97	Lower temperature ($^{\circ}\text{C}$) for C_{max} ²	Plumb and Moffitt 2015
CTO	20.93	Optimum temp. ($^{\circ}\text{C}$) for C_{max}	Plumb and Moffitt 2015
CTM	20.93	Maximum temp. ($^{\circ}\text{C}$) for C_{max}	Plumb and Moffitt 2015
CTL	24.05	Upper temperature ($^{\circ}\text{C}$) for C_{max}	Plumb and Moffitt 2015
CK1	0.09	Proportion of C_{max} at CQ	Plumb and Moffitt 2015
CK4	0.53	Proportion of C_{max} at CTL	Plumb and Moffitt 2015
Predator caloric density	5900	Energy density of fish being modeled ($\text{J}\cdot\text{g}^{-1}$ body weight)	Van Winkle et al. 1998; Railsback and Rose 1999
Prey caloric density	3500	Prey energy density ($\text{J}\cdot\text{g}^{-1}$ body weight)	Railsback and Rose 1999; Gonzales 2006; Beauchamp et al. 2007
PFF	0.1	Proportion of indigestible prey	Nahorniak 2015; Hanson et al. 1997
Oxygen	13560	Converts predator mass ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) to energy ($\text{J}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) lost to respiration	Elliott and Davidson 1975 (cited in Hanson et al. 1997)

¹ Default values for Chinook salmon were used for the remaining bioenergetics parameters not defined here (Stewart and Ibarra 1991, Hanson et al. 1997). Consumption: CA=0.338, CB=-0.275; Respiration: RA=0.00264, RB=-0.217, RQ=0.06818, RTO=0.0234, RTM=0, RTL=25, RK1=1, RK4=0.13, ACT=9.7, BACT=0.0405, SDA=0.172; Egestion/Excretion: FA=0.212, FB=-0.222, FG=0.631, UA=0.0314, UB=0.58, UG=-0.299.

² Maximum consumption rate

(Table 5.1 continued)

Table 5.2. Sensitivity analysis (+/- 10% of nominal values).

Stage	Parameter	nominal	-10%	10%
egg	spawn date	1 Oct	4 Sep	28 Oct
egg	ATU _{crit}	1160	1044	1276
movement	D _m	30	27	33
movement	W	30	27	33
growth	D _g	10	9	11
growth	prey caloric density	3500	3150	3850

Table 5.3. Comparison of model predictions with values observed in field studies.

Fish response	Modeled values	Field values	References
Date eggs emerged as alevins	Median = 19 February; 5 th , 25 th , 75 th and 95 th percentiles = 10 Feb, 16 Feb, 22 Feb and 4 Mar	<ul style="list-style-type: none"> • 83% of fish emerged by 4 Mar (laboratory) • Late Nov to early Mar (Willamette R tributaries) 	Steel et al. 2012 Schroeder et al. 2015
Daily movement rate	Median < 300 m, max ~800 m; mean highest in summer; variance highest in winter	<50 m to several km, depending on life stage and life history strategy	Bradford and Taylor 1997, Petty et al. 2012, Dugdale et al. 2015
Conspecific density	From 0.01 to 9 virtual fish per linear km; equates to ~0.4 to 1.3 fish·m ⁻² assuming stream width = 7 m and 1000 real fish ~ 1 virtual fish	From 0 to >2 fish·m ⁻² ; means < 1 fish·m ⁻² for Chinook salmon, coho salmon, and steelhead	Bjornn and Reiser 1991, Ebersole et al. 2006, Myrvold and Kennedy 2015
Specific consumption rate (daily amount of food consumed)	Between 0.04 and 0.20 g·g ⁻¹ ·d ⁻¹ ; median = 0.11 during spring (Apr-Jun); median = 0.09 during winter (Jan-Mar) and summer (Jul-Sep)	<ul style="list-style-type: none"> • Mean = 0.11 and 0.07 g·g⁻¹·d⁻¹ in mid- and late summer for Chinook in Snake R tributaries; differed among streams • 0.10 g·g⁻¹·d⁻¹ for a 50-g sockeye; higher for smaller sizes 	Chittaro et al. 2014 Beauchamp et al. 2007
Specific growth rate (daily growth)	Between 0 and 0.35 g·g ⁻¹ ·d ⁻¹ ; medians of 0.025 and 0.12 g·g ⁻¹ ·d ⁻¹ during spring and summer	<ul style="list-style-type: none"> • 0.003 to 0.029 g·g⁻¹·d⁻¹ for spring Chinook salmon during summer • 0.05 and 0.07 g·g⁻¹·d⁻¹ for coho during winter and spring 	Chittaro et al. 2014 Ebersole et al. 2006
Final weight	0.4 g newly emerged; medians of 1.5 and 15 g by spring and last day of simulation	From 3.5 to 10.5 g for spring Chinook leaving Snake R tribs; estimated weights passing lowest mainstem dam ~ 8 to 45 g	Achord et al. 2007 www.fpc.org/smolt/forklengthqueries/forklength_query_12.html
Date large enough (>5g) to smolt	Median = 11 Jul; 5 th , 25 th , 75 th and 95 th percentiles = 26 May, 22 Jun, 29 Jul and 25 Aug	Subyearling Chinook generally emigrate between Apr and June; prevalence and timing differ among rivers	Roper and Scarnecchia 1999, Sykes et al. 2009, Schroeder et al. 2015

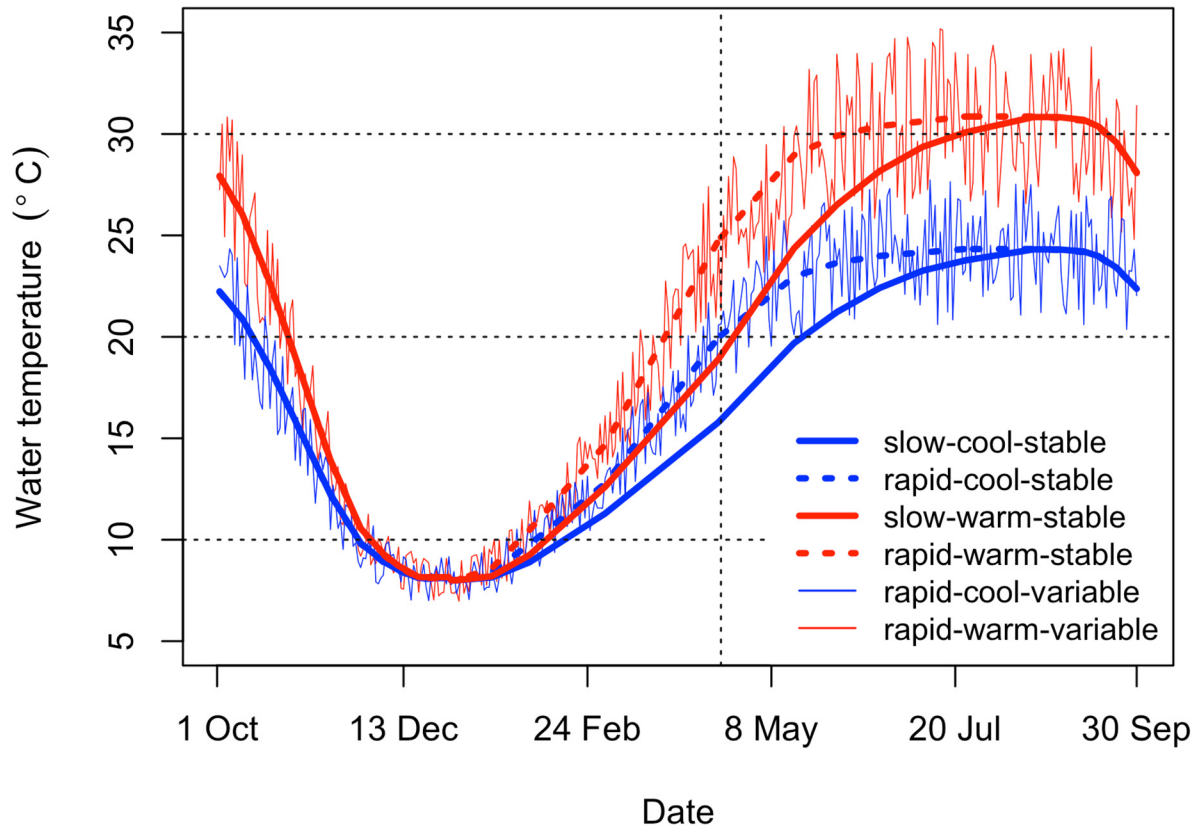


Figure 5.1. Annual riverine thermal regimes for six hypothetical climate scenarios used in simulations; pictured is the lowest mainstem location (warmest location and also the location where change is greatest). Scenarios incorporated simplifications of three anticipated changes to future thermal regimes: (1) increased rate at which water temperature rises in the spring (rapid vs. slow); (2) increased maximum summer temperature (warm vs. cool); and (3) increased variability (variable vs. stable).

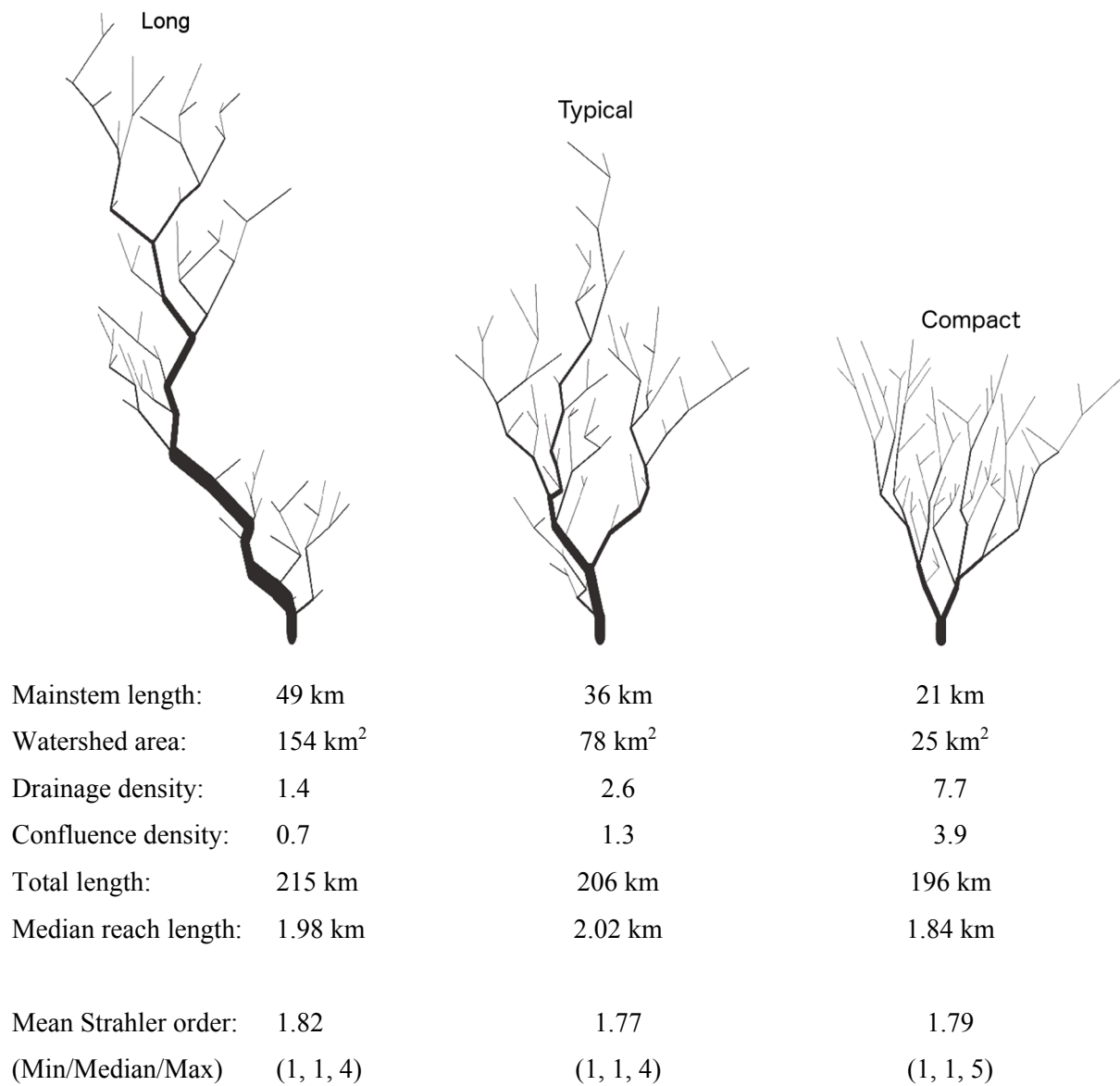


Figure 5.2. Three hypothetical networks used in simulations, and their characteristics (n=101 reaches per network).

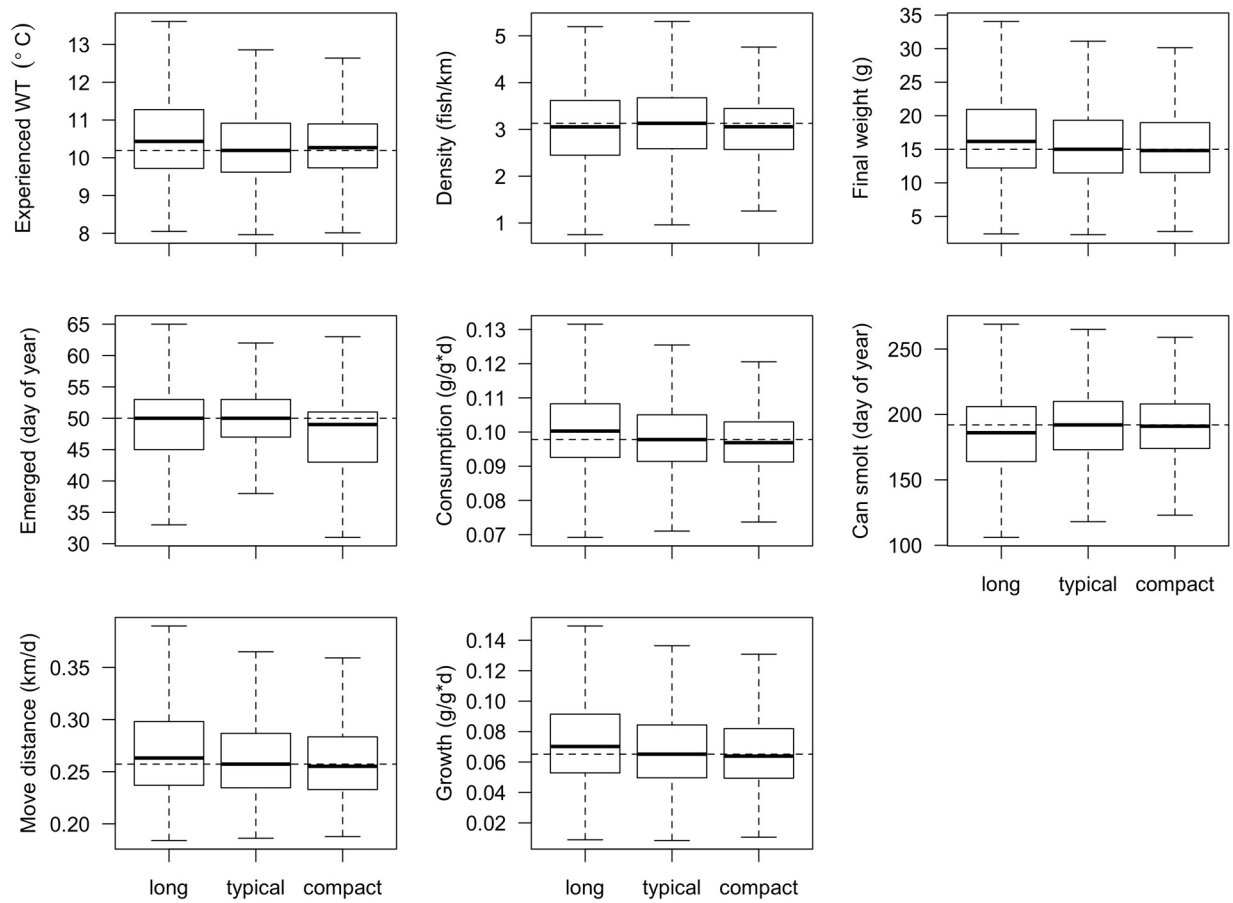


Figure 5.3. Metrics of fish response across three network shapes (x-axis) for the slow-cool-stable climate scenario. Each boxplot summarizes distributions of the response across 25,000 fish (250 fish per simulation, pooled across 100 simulations). *Emerged*, *Final weight*, and *Can smolt* are responses at a specific point in time; other responses are means across time once fish emerged (*experienced water temperature* included all time steps). Horizontal dotted lines, set to the median of the typical network in each panel, are intended to aid comparison within a panel.

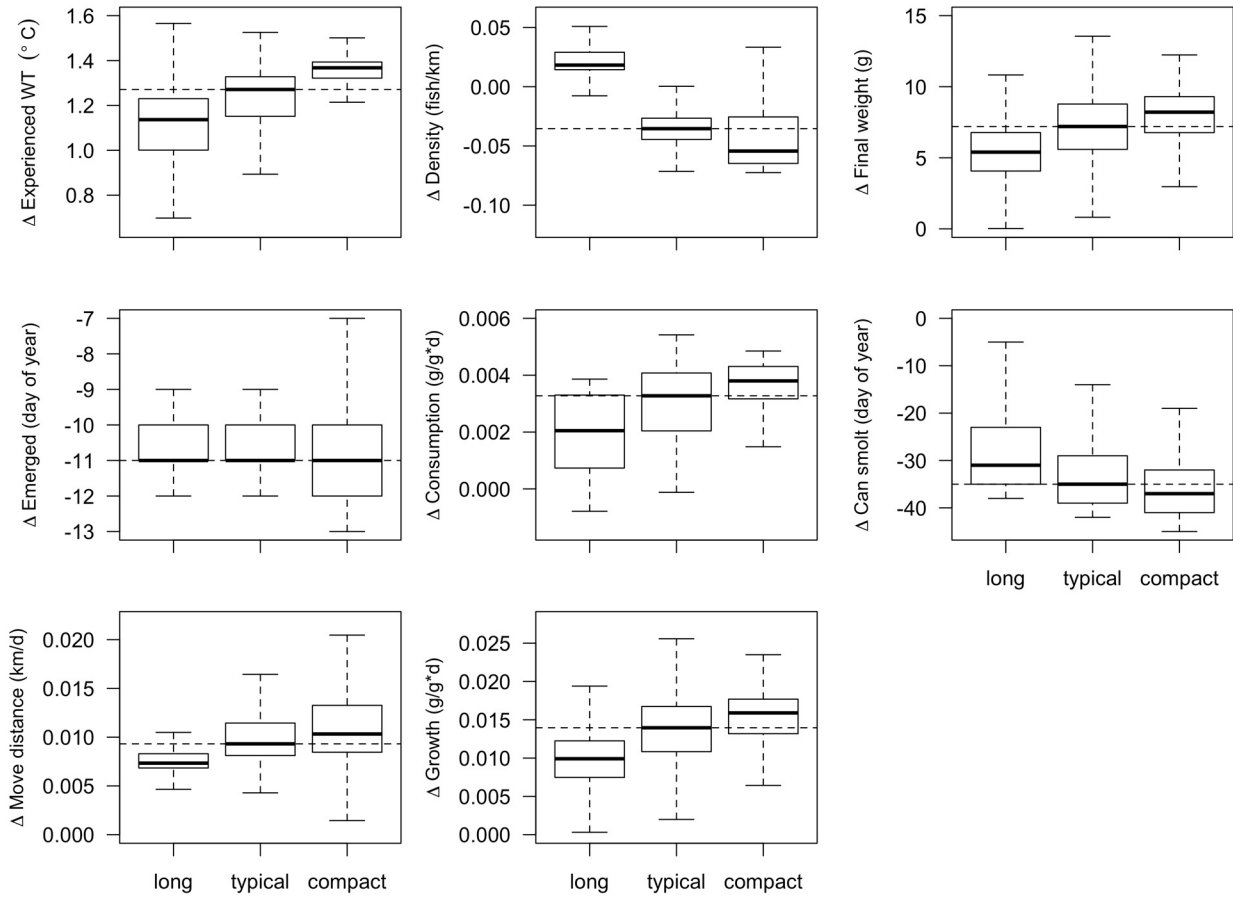


Figure 5.4. Differences in fish responses between the current-day climate scenario (slow-cool-stable) and a future climate scenario (rapid-warm-stable) across three network shapes (x-axes). *Emerged*, *Final weight*, and *Can smolt* are responses at a specific point in time; other responses are means across time once fish emerged (*experienced water temperature* included all time steps). Horizontal dotted lines, set to the median of the typical network in each panel, are intended to aid comparison within a panel.

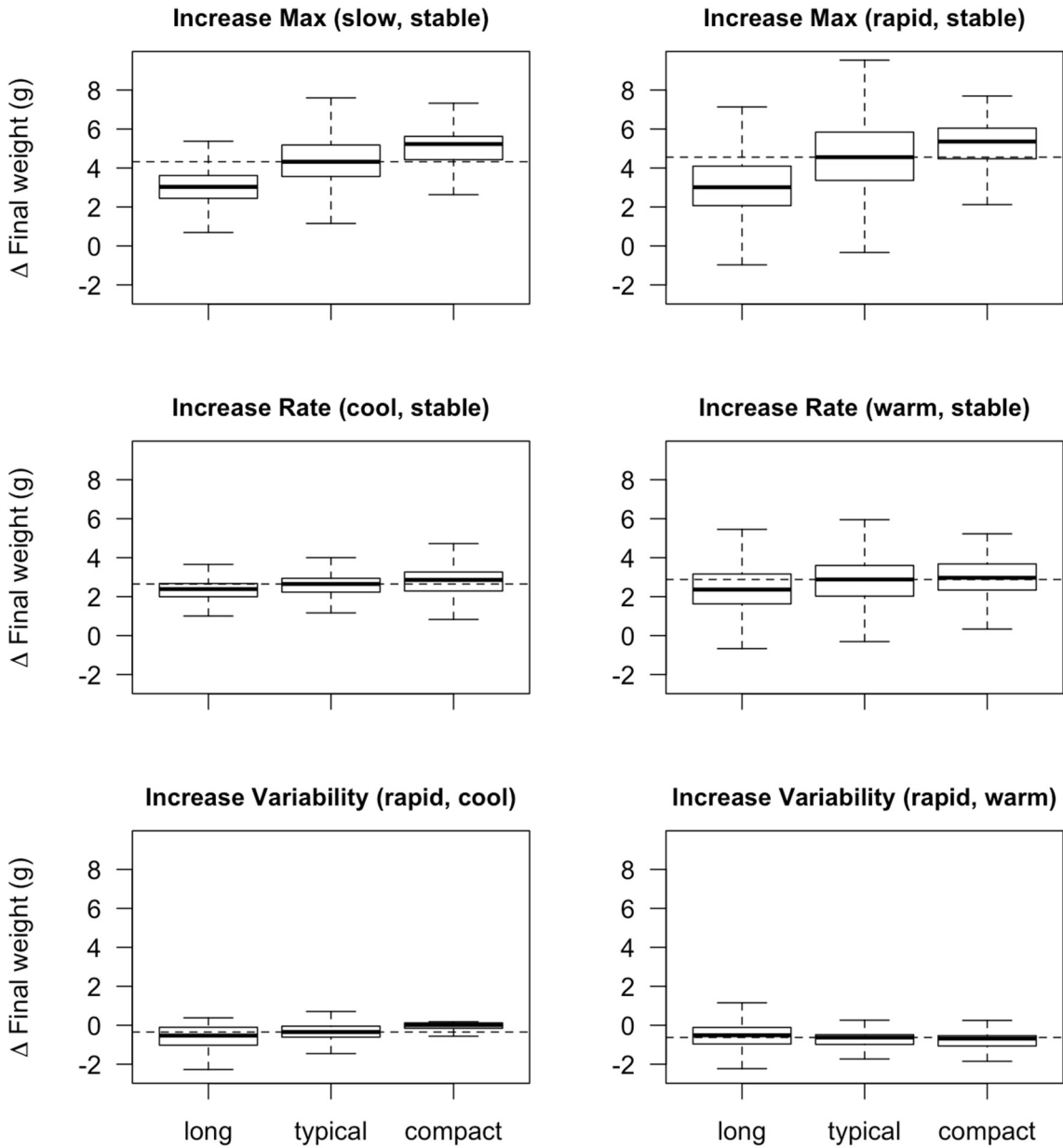


Figure 5.5. Differences in final weight (g) of fish across three network shapes (x-axis) that are attributable to increased summer maximum water temperature (top row), increased rate of spring warming (middle row), or increased variability (bottom row) in climate scenarios. Parentheses in headings describe the aspects of climate scenarios that were held constant for that particular comparison (e.g., top, left panel: the two climate scenarios compared both had a slow rising limb and stable variance; top, right panel: the two climate scenarios compared both had a rapid rising limb and stable variance). Horizontal dotted lines, set to the median of the typical network in each panel, are intended to aid comparison within a panel.

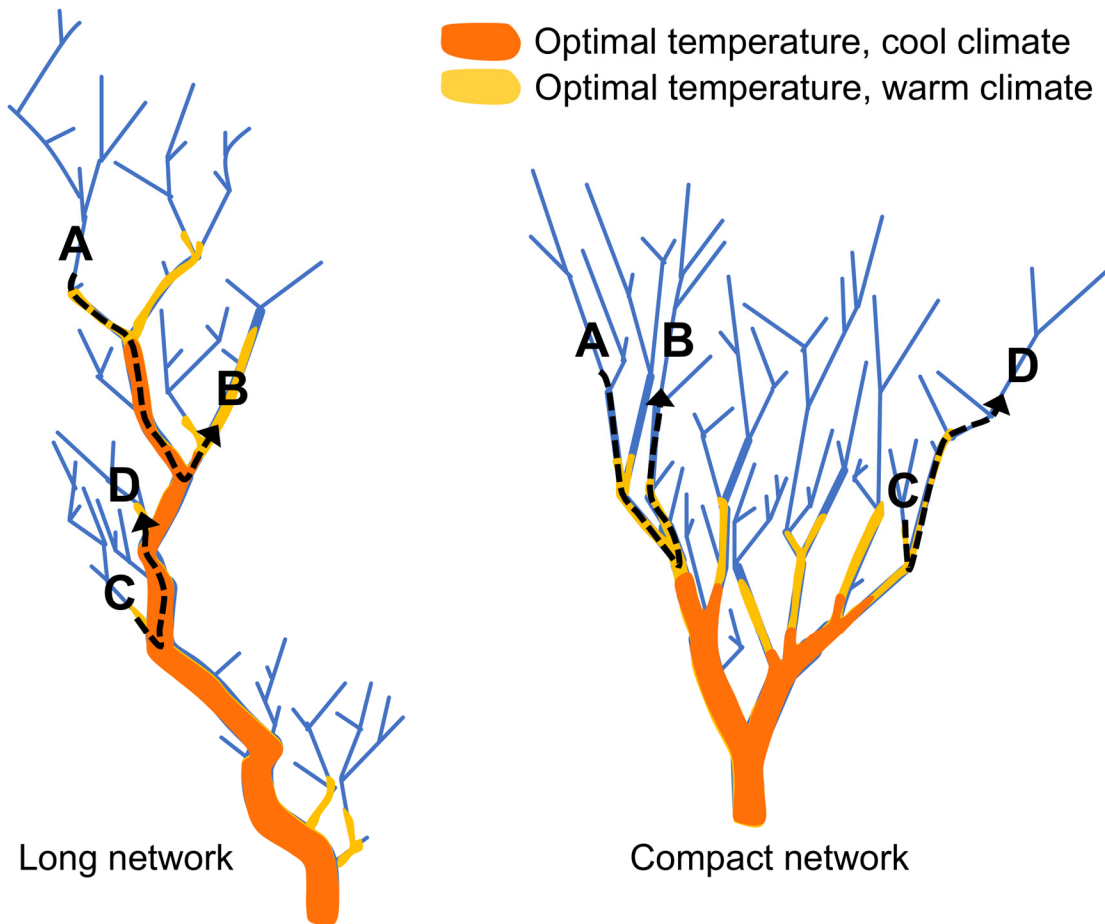


Figure 5.6. Schematic illustrating how fish in the compact network moving from A to B or from C to D could miss optimal thermal habitat in a cool climate but not in a warm climate, whereas fish in the long network encountered optimal habitat under both climate scenarios.

5.8. Supplementary Information

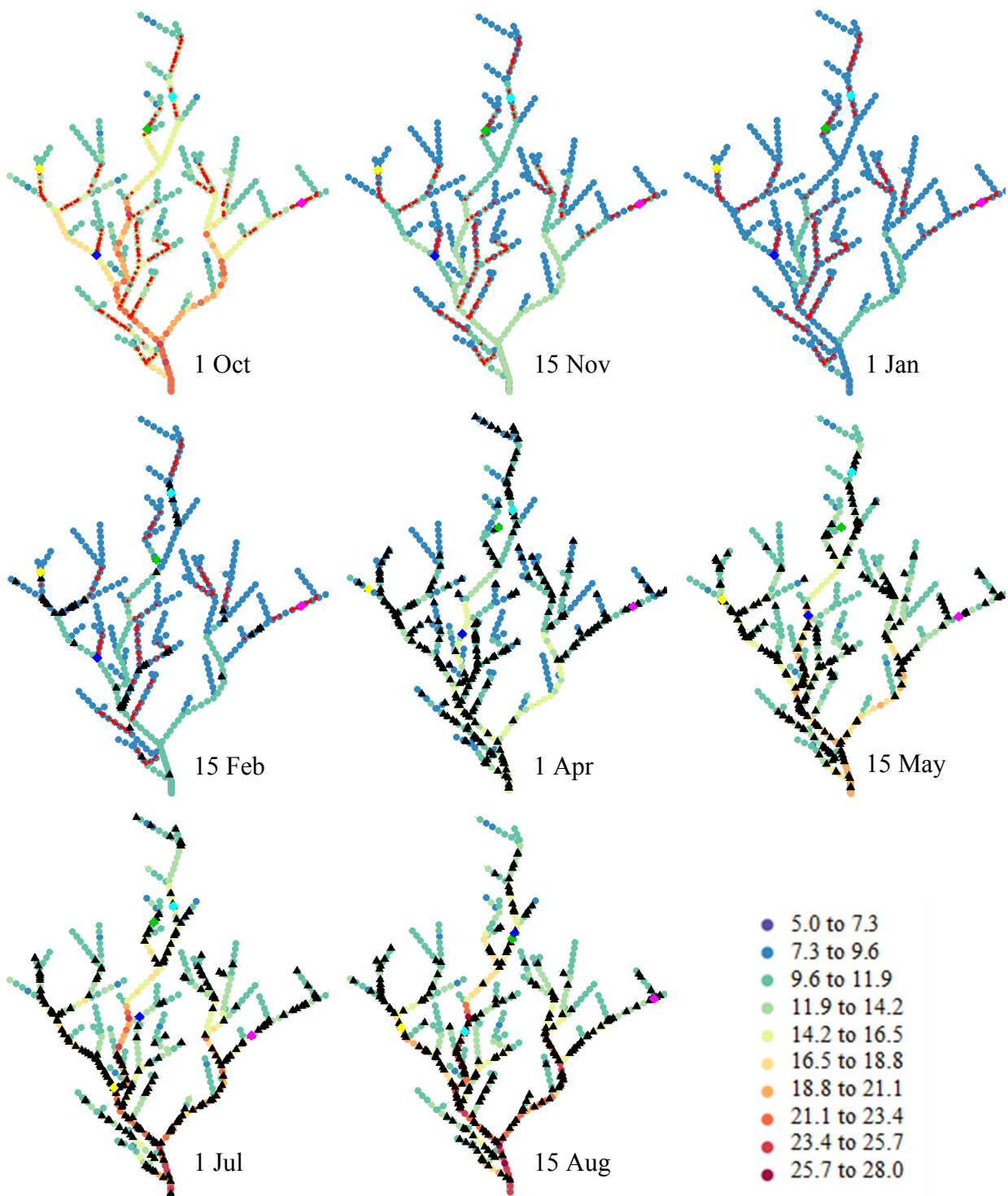


Figure S 5.1. Daytime snapshots of water temperature and fish location for one simulation in the typical network and the slow-cool-stable climate scenario. Colors denote water temperature (°C); red dots are fish eggs; black triangles are emerged fish. Larger bright dots (yellow, green, pink, aqua, and blue) are 5 individual fish highlighted for reference.

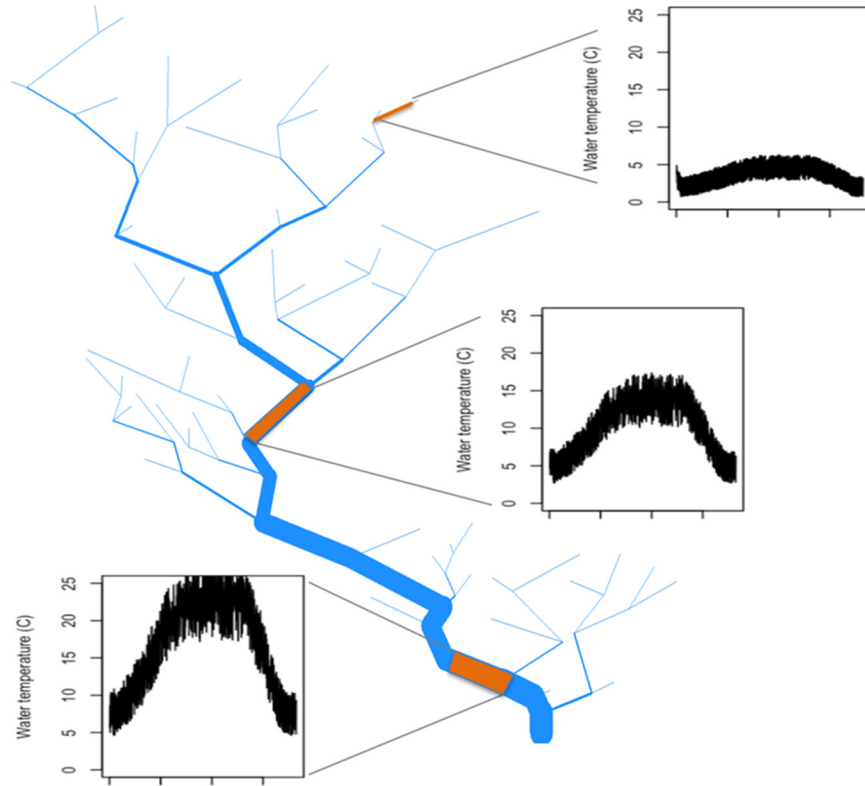


Figure S 5.2. Temporal patterns of water temperature differed throughout the network. Although each location followed the trajectory dictated by a climate scenario (i.e., the relative shape), the magnitude of change depended on spatial position.

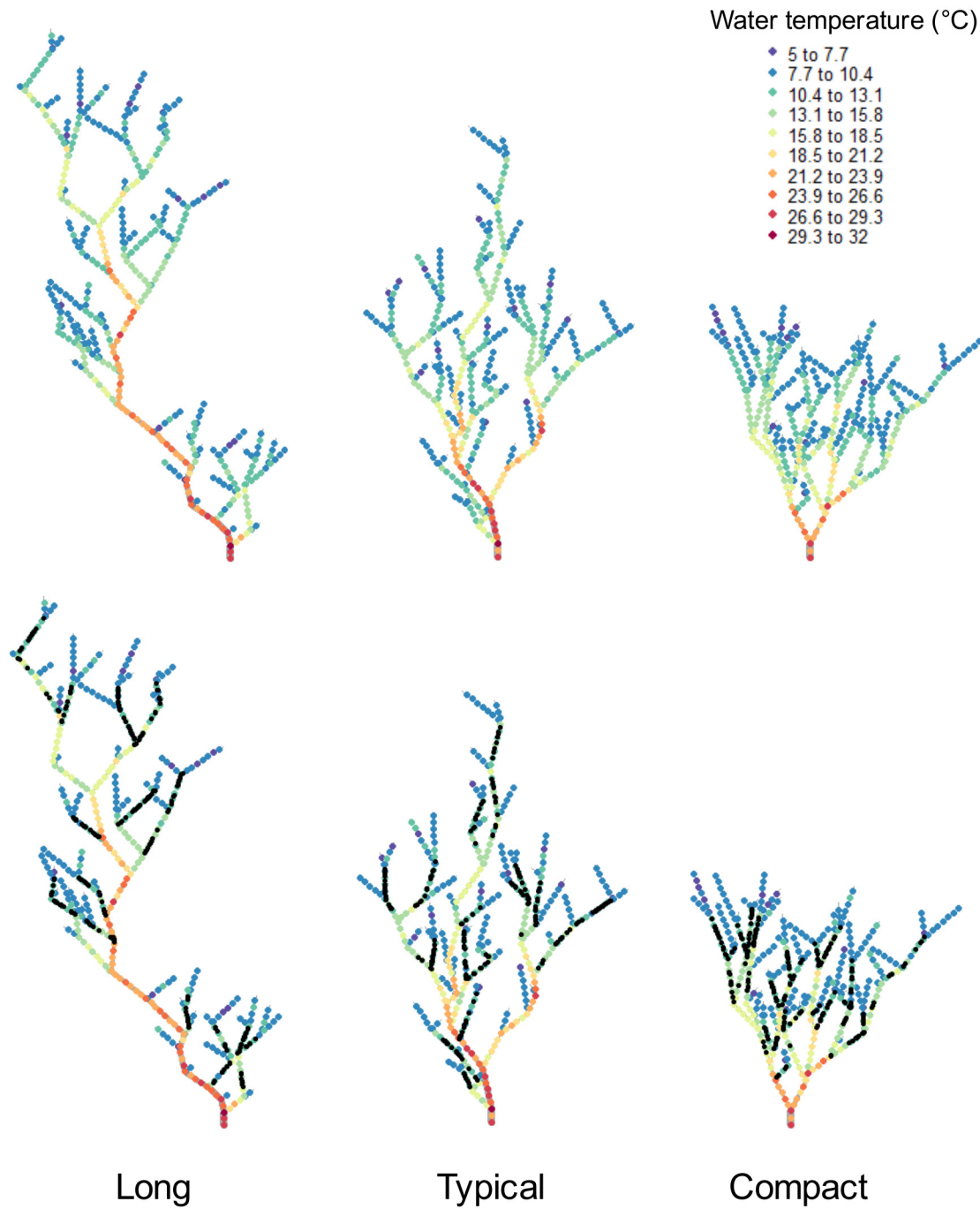


Figure S 5.3. One example illustrating initial spatial patterns of water temperature (**top**) and the location of fish eggs (black dots, **bottom**) in each network.

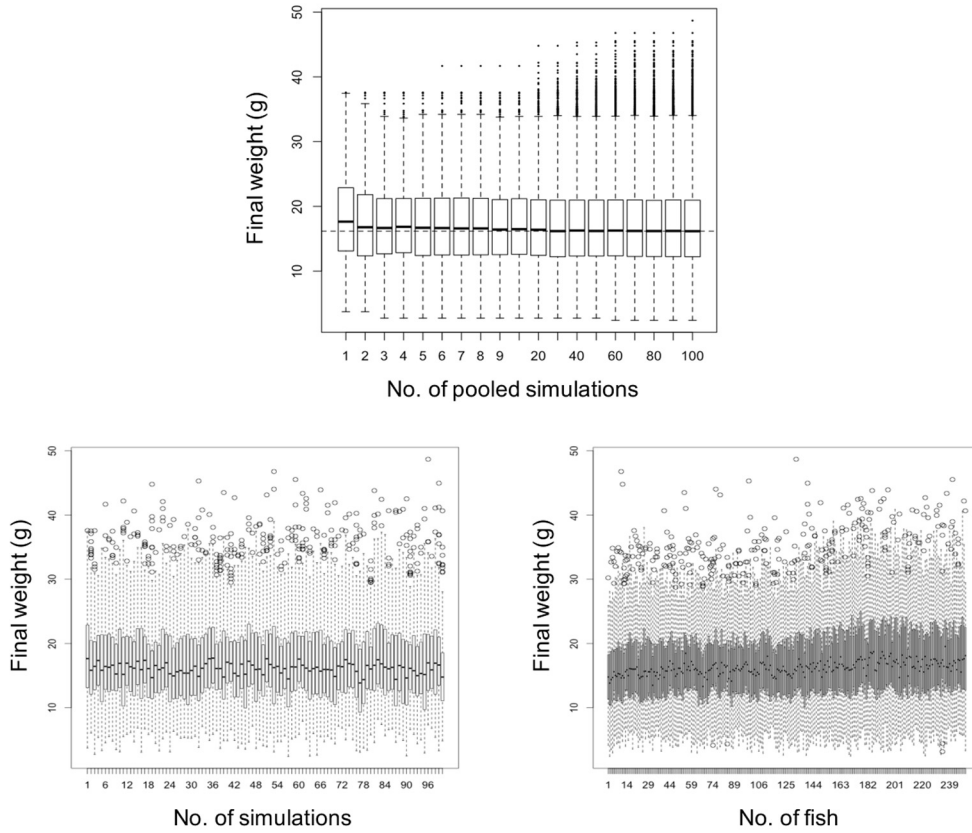


Figure S 5.4. Distributions of final fish weight (g) across an increasing number of pooled simulations (top), for 250 fish within each of 100 simulations (bottom left), and for 1 fish across 100 simulations for each of 250 individual fish (bottom right). Results are shown for the typical network in the slow-cool-stable climate scenario.

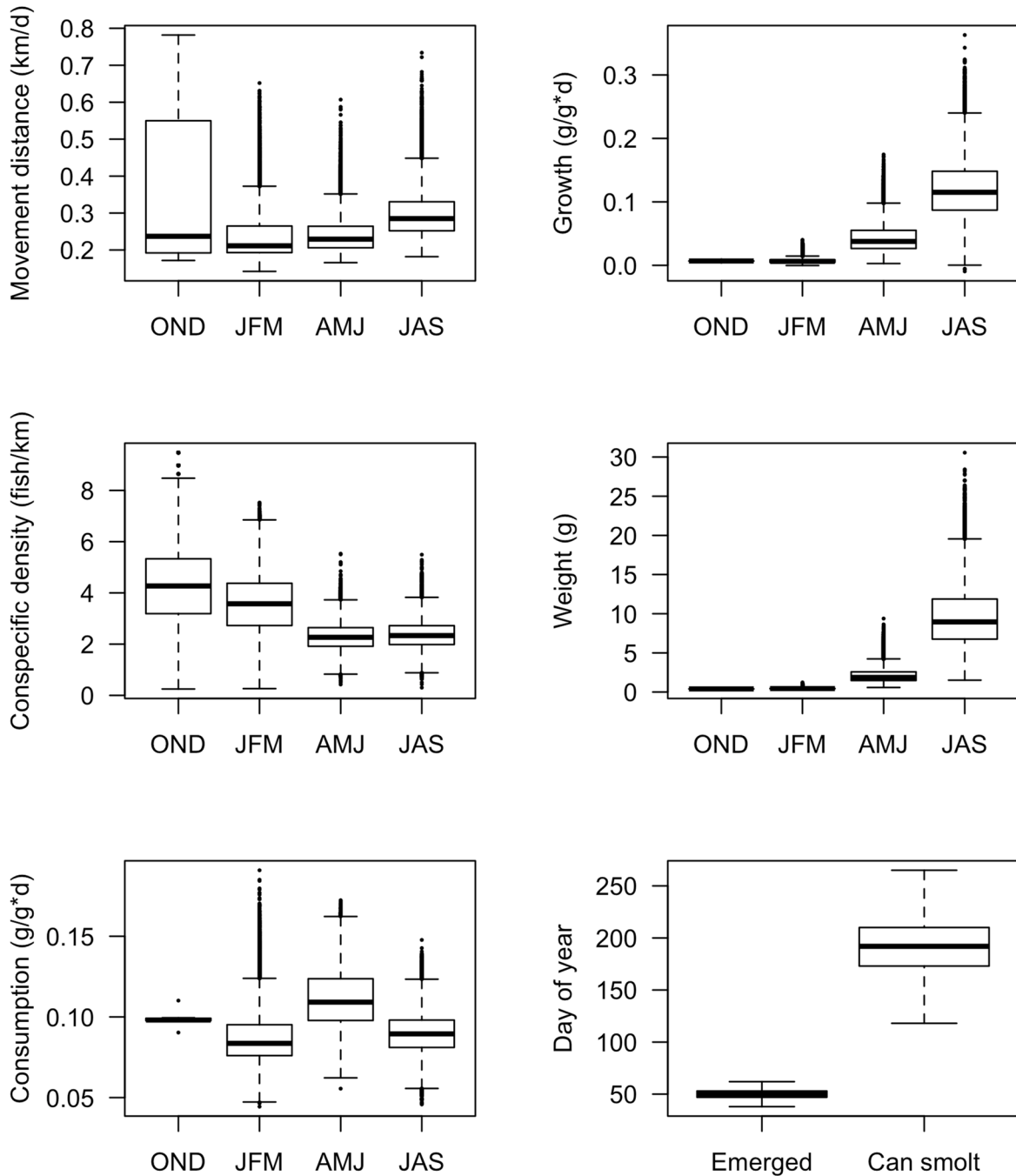


Figure S 5.5. Metrics of fish responses across seasons in the typical network for the slow-cool-stable climate scenario. Each boxplot summarizes distributions of the mean daily response (i.e., averaged over all 12-h time steps after fish emerged within each season) for 25,000 fish (250 fish per simulation, pooled across 100 simulations). Day of year represents one point in time (i.e., not averages over time). Lines are medians; box edges are quartiles, and whiskers are the greater of max or $1.5 \times$ the interquartile range. Letters in the x-axis are calendar months.

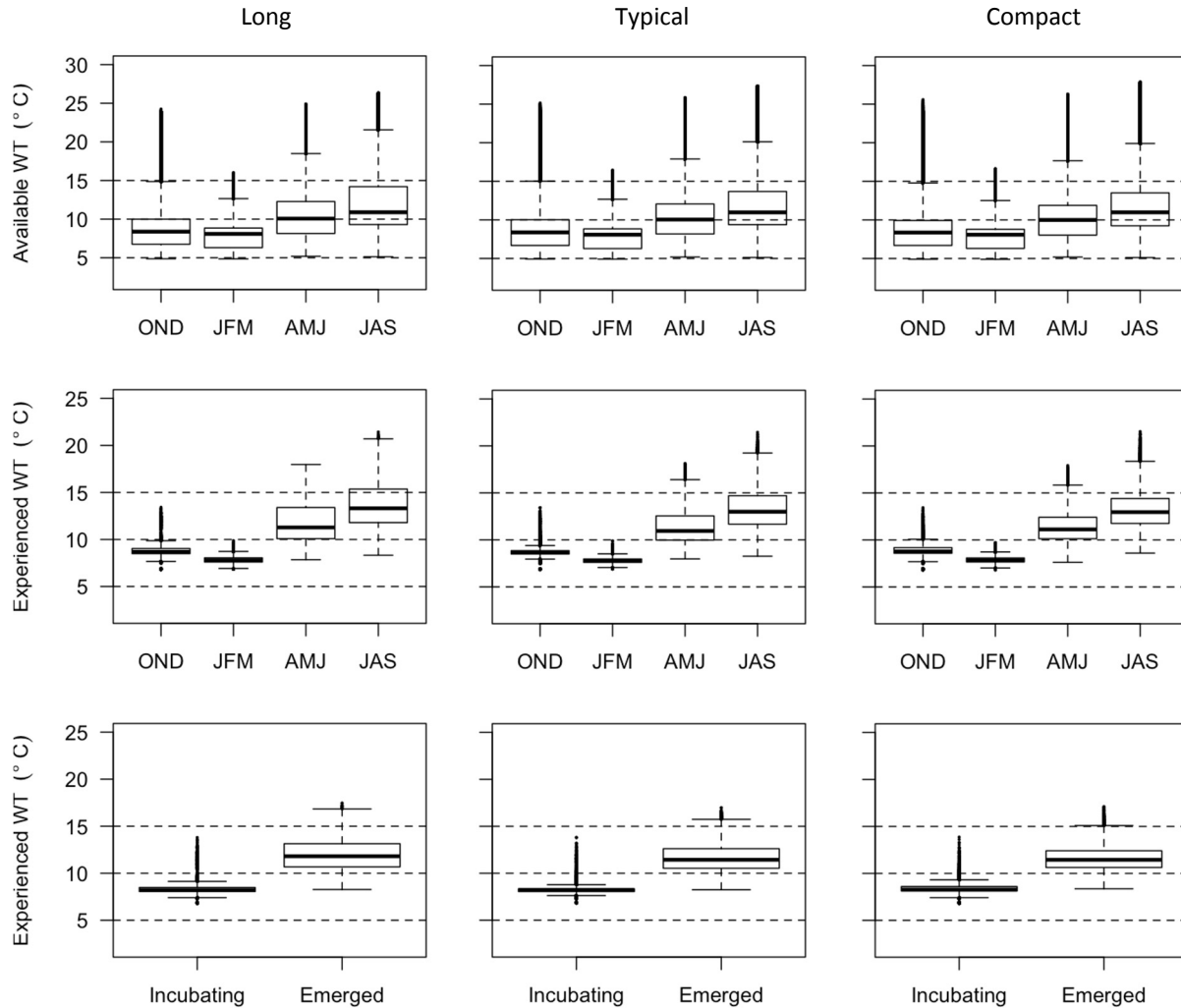


Figure S 5.6. Water temperature (WT) available to fish (i.e., across all locations) in each season (top row; $n \sim 400$ sites per network \times 100 simulations), water temperature actually experienced by fish in each season (middle row; $n = 250$ fish \times 100 simulations), and water temperature experienced during each life stage (bottom row; $n = 250$ fish \times 100 simulations) in each network (columns) for the slow-cool-stable climate scenario. Each boxplot summarizes distributions of the mean temperature value over all 12-h time steps within each time period. Letters in the x-axes of the top and middle rows are calendar months. Horizontal dotted lines are intended to aid comparison across panels.

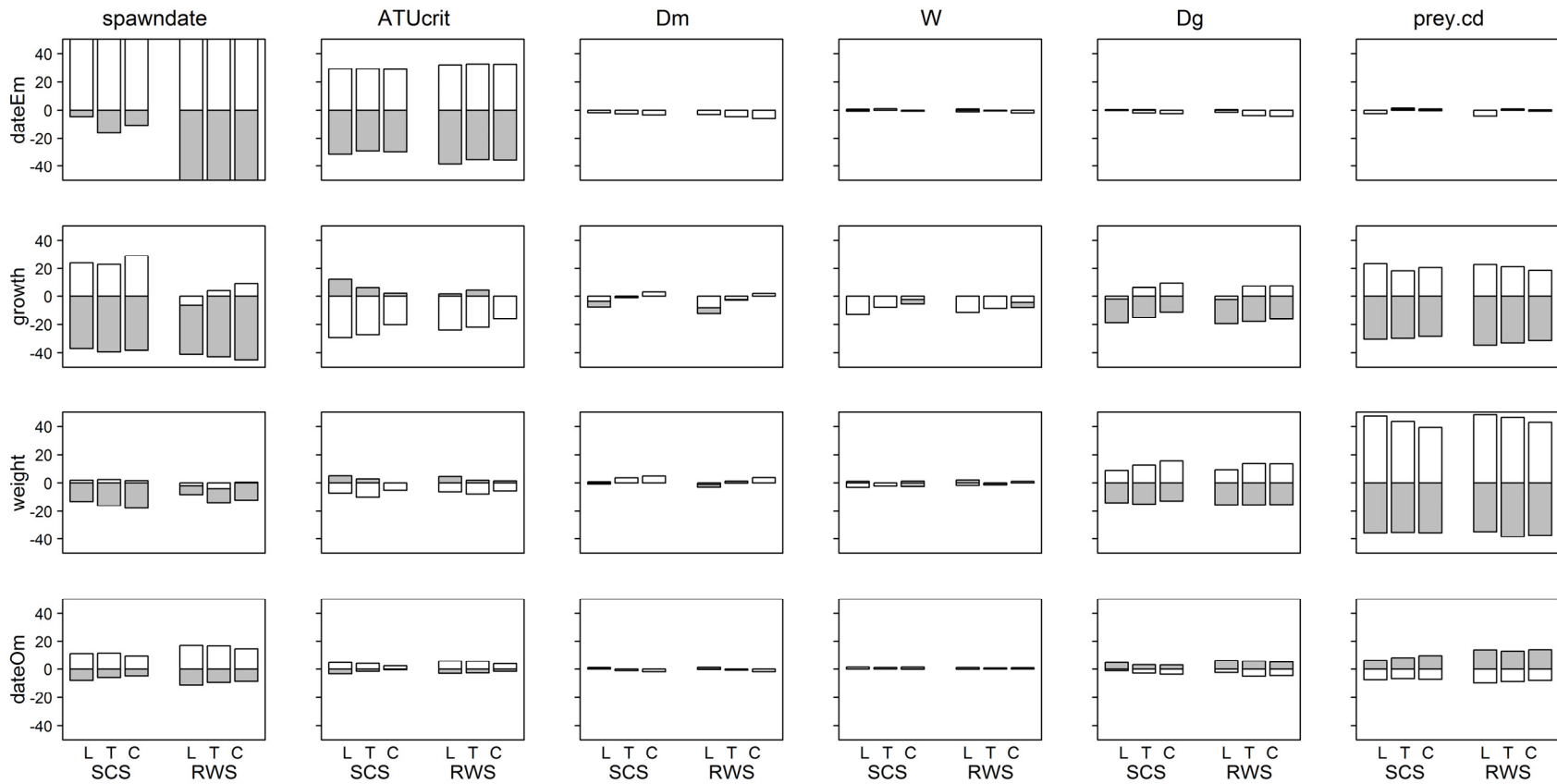


Figure S 5.7. Findings from a sensitivity analysis illustrating the effect on date emerged (dateEm), growth rate (growth), final weight (weight), and date can smolt (dateOm) (rows) to perturbations of +10% (open bars) and -10% (filled bars) in each of six parameters expected to exert the most influence on results (columns). The first two parameters, spawndate and ATU_{crit} , act on the egg stage; the second two parameters, D_m and W , act on fish movement; and the last two parameters, D_g and prey caloric density, act on fish growth. Bars show the percent increase or decrease in median response values (across 250 fish x 10 simulations). Results are shown for the long (L), typical (T), and compact (C) networks within the slow-cool-stable (SCS) and rapid-warm-stable (RWS) climate scenarios (x-axis labels). See **Table 5.1** for parameter definitions and **Table 5.2** for nominal and adjusted values tested.

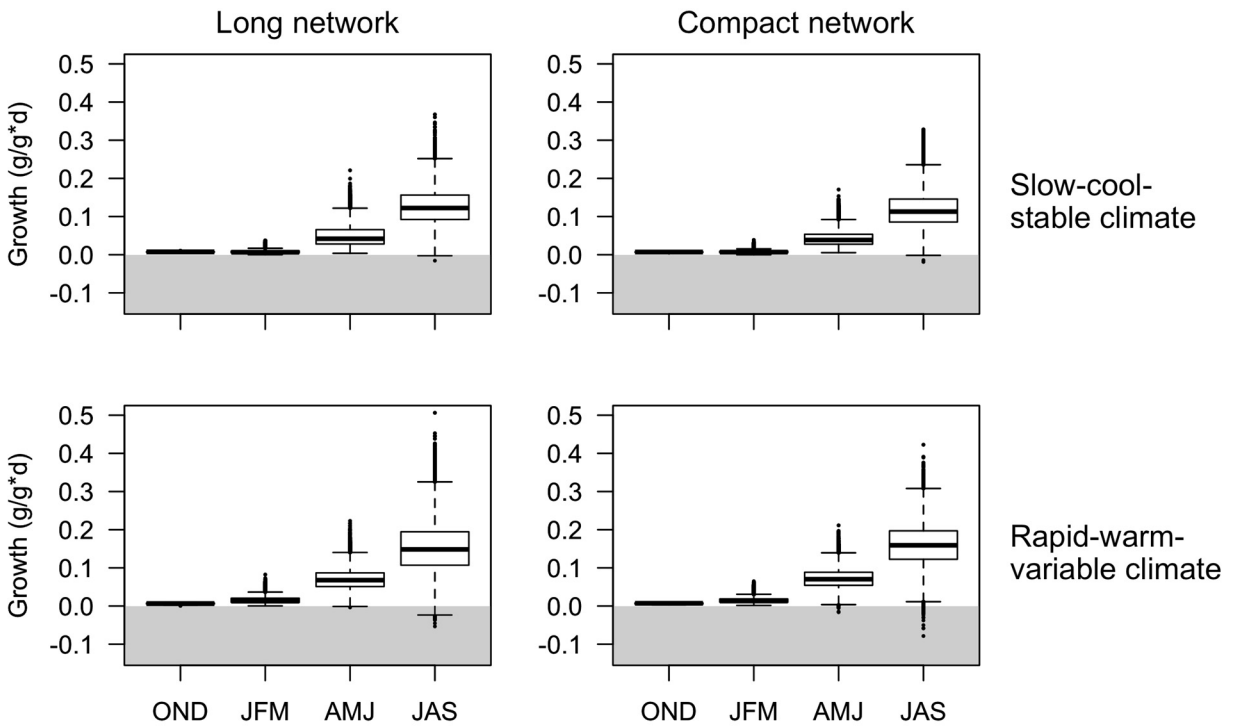


Figure S 5.8. Seasonal growth of fish in the long and compact networks for the current-day climate scenario (slow-cool-stable) and a warm climate scenario (rapid-warm-variable). Shaded boxes denote the region of negative growth in each plot. Note different y-axis magnitudes. Letters in the x-axis are calendar months.

Chapter 6. Synthesis and Future Directions

In addition to enriching our understanding of how Pacific salmon may respond to changing thermal landscapes, the topics of my research have direct relevance to numerous environmental regulations and associated conservation and management issues. For instance, the Clean Water Act (1972) dictates regulation of water temperature as a component of water quality. West Coast federal, state, and local agencies tasked with implementing these policies need to ensure that they also comply with needs established by the Endangered Species Act (1973) for Pacific salmon and other biota and with Native American Treaty Rights. Given the numerous (and sometimes fiercely) competing entities involved, litigation is not uncommon. In addition, conservation and management plans need to have the capacity to adapt to a changing climate.

It may, at times, be tempting to seek a suite of “one-size-fits-all” constructs for guiding the monitoring and conservation of thermal regimes. However, ecological systems are complex and we therefore need to embrace complexity in our management schemes. In characterizing spatial patterns of water temperature at multiple spatial scales, I found more complexity than generality. And in evaluating what climate-altered thermal regimes may mean for Pacific salmon, I continually realized that an answer to any question would necessarily depend on its specific context. For instance, understanding whether patches of cold water are likely to be adequate for salmon in the future is tightly linked to one’s definition of cold water patch and to which species and life stage are of concern. Similarly, finding that juvenile fish may actually grow better in warmer climates but that there may still be unforeseen consequences to later life stages suggests that responses will be uncertain and variable and that management will need to be case-specific. Below, I list key insights from my research and their potential implications. I do not see these as final answers, but instead hope that they will add to a growing complement of ideas that can guide future questions and better-informed management applications. I end by describing next steps that should make this research even more useful.

6.1. Major Findings

6.1.1 Whole-River Spatial Patterns in Water Temperature

- Many longitudinal river temperature patterns did not fit theoretical expectations
- Longitudinal river temperature patterns were diverse and varied geographically
- Correlations with common predictors of water temperature varied among rivers

The diversity of thermal profile shapes that I observed suggests that there currently exists a variety of thermal habitats available to fish throughout the Pacific Northwest. Given that habitat diversity promotes structure and long-term viability in populations, metapopulations, communities, and species, the observed diversity in thermal landscapes may afford salmon opportunities to adapt to changing climate conditions. The patterns compiled here should serve as useful historical records to which future patterns can be compared. Meanwhile, it may help practitioners identify unique rivers needing protection and can help guide restoration activities by framing what is possible in a given river. Knowing that profile shapes other than the asymptotically-downstream warming pattern exist may improve development of water temperature models.

6.1.2 Within-River Spatial Patterns in Water Temperature

- Within-river thermal heterogeneity was prevalent and complex
- Median size and spacing of cold water patches was sufficient for salmon overall but patterns differed substantially across rivers
- Water temperature will be warmer overall in the future, but thermal heterogeneity patterns may remain similar
- Characterization of thermal heterogeneity was nonlinearly related to spatial grain of water temperature data

My research illustrated substantial spatial variation in summertime river temperature at intermediate spatial scales (e.g., reaches of 10s to 100s of km), both within and among hundreds of rivers throughout the Pacific Northwest. These analyses focused at an intermediate spatial scale that was conducive to identification of habitats suitable for temporary holding during migration and for identifying spatial juxtaposition of thermally suitable habitats needed during different life stages. These analyses can be used to identify locations where evaluation of thermal heterogeneity at finer spatial scales may be warranted. I found that using spatially continuous

data may be more appropriate for this purpose than using water temperature predicted at a coarser grain because it is more likely to identify ecologically important spatial variability at scales <1 km. Managers and ecologists interested in characterizing thermal refuges (or barriers) may be able to adapt my metric-based approach to their specific needs.

6.1.3 Juvenile Salmon Response to Climate-Altered Thermal Regimes

- Salmon grew best and were ready to smolt earliest in a topologically simple stream network under current-day climate conditions; given warmer future thermal regimes, growth increased most and outmigration timing occurred earliest in a complex network
- Median fish growth increased in all network shapes when experiencing climate-altered thermal regimes, but individual fish responses were extremely variable
- Fish growth was most influenced by increases to the summer mean, about half as much by increases in the rate of spring warming, and least but negatively by increases in day-to-day variance

Results from this model suggested that salmon response to climate change will be complicated. In certain stream networks, growth may increase in warmer climates, potentially causing earlier outmigration of smolts that could lead to mismatches in ecology in later life stages. If realistic, these results could inform prioritization of conservation and restoration actions. For example, if topology influences the way that climate change will alter future water temperature regimes (either directly or indirectly via its influence on other factors), then change may be slower in certain networks, allowing fish more time to adapt. This model should be easily adaptable to a variety of management questions, and is capable of estimating water temperature in real stream networks given a sufficient array of sensors.

6.2. Anticipated Research Needs and Next Steps

6.2.1. Characterizing Thermal Heterogeneity

A number of extensions could be made to the approach I outlined for characterizing thermal heterogeneity within rivers. In some rivers, managers may be more interested in potential thermal barriers (as opposed to thermal refuges). For instance, there may be warm water barriers in lower mainstems that adult salmon migrate through during upstream spawning migrations or that smolts pass through on their way out to sea. The approach I described should work equally well for identifying potential barriers. For particular situations and species, it will

be important to carefully define what is considered a ‘barrier’ or a ‘refuge’ before quantifying patch metrics. Specifically tying the definition of a thermal patch to an ecological or management question of interest will improve the utility of this approach.

6.2.2. Integrating Thermal Patterns Across Spatial Scales

A fruitful next step could be to evaluate whether longitudinal profile shapes are related to hydrologic regions classified as rain-dominated, transitional, or snow-dominated. This could influence the extent to which each shape might be expected to change as the climate warms. For instance, if a shape is controlled by cool water contributed by glaciers or snowmelt, then the lack of these inputs in the future may cause new longitudinal patterns to emerge. It may also be useful to consider whether within-river thermal heterogeneity differs among classes of rivers. For example, are cold water patches distributed differently within rivers classified as having parabolic longitudinal profiles than in rivers having asymptotic profile patterns?

Using spatially continuous data, I found substantial heterogeneity at scales finer than 1 km. Whole-river patterns derived from TIR data and from NorWeST models appear to be similar. It would be informative to also compute within-river pattern metrics on the modeled data to learn what we might be missing when using modeled data. If information loss is minimal, then data such as those predicted by the NorWeST project could be used for making informed management decisions in many areas where other data do not yet exist. If fine-scale variability is not easily identified from coarser modeled products, there exists a treasure trove of information in the two-dimensional image data from the TIR surveys that has yet to be fully mined. Research using TIR in other systems has demonstrated that thermal refuges can be both small in space and that their temporal consistency can vary, depending on the refuge type. It was beyond the scope of my objectives to evaluate thermal heterogeneity at a fine resolution. Such an exercise could prove invaluable on a case-by-case basis as needed for particular management objectives (and indeed is why most data were collected in the first place).

6.2.3. Spatial Patterns Over Time

An important next step will be to collect and evaluate data for the same locations but for other times (repeat summer surveys, different dates, different times of day, different seasons) and under different flow conditions to see how much thermal heterogeneity patterns change. Although we do have repeat surveys for several rivers that indicate persistence of patterns during summer afternoons, it would be good to have a larger sample. Comparisons between warm and

cool years could suggest whether patterns are likely to hold in warmer climates and whether different rivers might be more or less responsive. For example, one might expect spatial patterns in groundwater-driven streams to remain similar whereas patterns could change a lot in rivers currently fed by glaciers or snowmelt if those cold water sources disappear in the future. Others have evaluated longitudinal patterns at finer time scales (hours, days) and found that they are not stable over time in all locations. In fact, locations that were colder than surrounding water at one time of day (e.g., 3 pm) were warmer than surrounding water at other times (e.g., 3 am), suggesting that these locations may be influenced by inputs of ground water which has a more constant temperature. It would be instructive to see which locations are more temporally stable and which fluctuate daily in order to think about what might be driving these patterns.

6.2.4. Drivers of Cold Water Patches

Research to identify factors that govern the formation and maintenance of thermal refuges within rivers is needed for conservation of cold water habitat for fishes. In a separate project, I am collaborating with hydrologists, geomorphologists, and climatologists on this question.

For associating potential drivers and cold water patches, it makes sense to characterize the locations of cold water patches differently than described in Chapter 4. Specifically, it will be important to locate places where the longitudinal profile begins to cool in a downstream direction because this is where the influence of the driver is first noticed. This could be achieved by computing first and second derivatives on longitudinal thermal profiles (**Figure 6.1**). Derivatives could also be used to assess complexity of thermal profiles.

Understanding how the myriad potential influences interact to form cold water patches will likely best be addressed using a hierarchical approach. Water temperature is predominantly governed by climate forcing at large scales and by local conditions at fine scales. Landscape features such as tributary confluences directly influence the presence, size, and permanence of discrete thermal refuges whereas more diffuse processes (e.g., network topology, geomorphology, hydrology) indirectly influence thermal refuge patterns. An important reason for gaining a mechanistic understanding of what is driving the presence and duration of cold water patches is to predict where and when they might occur in future climates or in unsampled locations, and so that formative processes can be conserved. Because of limitations in different

approaches, it is likely that a hybrid of process-based models and empirical data will be most useful for predicting future cold water patches.

6.2.5. Predicting Future Thermal Landscapes

Representations of future thermal regimes should include effects of all aspects of climate change expected to be important. For instance, glacier melt and changes in discharge amount and timing associated with shifting hydrologic regimes (e.g., snow-dominated versus rain-dominated) can alter the availability and temperature of water. I was unable to incorporate expected changes in hydrology in my analyses. The Distributed Hydrology Soil Vegetation Model and its associated water temperature model are a promising option for producing estimates of future thermal regimes that incorporate these processes.

In my assessment of how thermal heterogeneity patterns will change in the future, I assumed that the residuals from a model fitting climate variables to the TIR data represented components of thermal heterogeneity that were less likely to be influenced by climate change. I suggested that this residual variation in spatial pattern might be controlled by local processes such as shade provided by riparian vegetation or topography, or by interactions with subsurface water. It would be interesting to relate these residuals to a metric of the human footprint to see how much could be explained by the ways that we have modified rivers and their surrounding landscapes.

Finally, we often focus on expected increases in water temperature associated with climate change during the warm season. A useful addition to the climate scenarios that I used in the individual-based model will be to also consider how winter temperatures will change. Warming winter temperatures may influence salmon by causing a shorter window for eggs to incubate before emerging. This may have a bigger effect on altered phenology than changes during spring, summer and fall for many species.

6.2.6. Advancing and Applying the Individual-Based Model

There are many advances and applications of the individual-based model that I can envision. It is novel in many ways (e.g., spatially explicit, network-wide), but naive in others. For instance, there are much more sophisticated models in existence for evaluating fish ecology in a single river reach (e.g., InStream) that could be combined with this network framework. The IBM could also be linked with models that focus on other life stages, such as the egg-to-fry stage modeled by Beer and Anderson (2001, 2011) and could inform life-cycle modeling efforts. In my

model, I made some simplifying assumptions about thresholds for accumulated thermal exposure needed in order for eggs to emerge from the gravel. By modeling this dynamically, we could see more dramatic effects in later life stages.

Certain additions describing the riverscape environment or modifications to fish behavior could make the IBM more realistic. The model would be improved by incorporating discharge and other features (e.g., dams, riparian, channelization, land use). Possibly, elevation could be used as a surrogate to represent gradients in precipitation, air temperature, hydrologic regime (snow- or rain-dominated), and discharge. Improvements to fish behavior include allowing spawn timing to respond to how rapidly water temperature decreases (as opposed to all fish spawning on the same day), allowing juveniles to sense conditions upstream a short distance as might be expected if they can sense cues floating downstream, and adding a downstream bias to ensure that some fish begin to head toward the ocean. I parameterized the IBM for Chinook salmon that predominantly smolt during their first year. It would be easy to parameterize the model for other species, especially those that spend the winter in freshwater.

The most basic next steps will entail more extensive sensitivity analyses to consider possible consequences of mis-parameterizing the model and to highlight key uncertainties. For instance, a closer look at the parameters characterizing movement is warranted as these would be expected to influence results more than they did in my simple sensitivity analysis. As well, it is possible and even likely that other aspects of a fish's ecology will also be influenced by a changing climate. Prey may grow at different rates and be more or less available at different times, and competitors and predators will also be influenced. There are many ecological components that I omitted in order to focus on my particular research questions. Inclusion of any of these (e.g., predation, variety in the prey base) could improve the realism of results. This would also help to clarify whether results could be influenced by ignoring potential changes in the ecological community associated with climate change. I tested only one instantiation of a long, typical, and compact network. The code exists to create other examples of networks classified into one of these three shapes or additional shapes, and to run the same experiment across a suite of them.

Questions about spatial and temporal patterns in water temperature could be asked. For example, in my experiment, I assumed that water temperature correlated with stream order (i.e., the classic downstream warming paradigm). However, it would be interesting (and easy) to test

how fish respond to other whole-river patterns of downstream warming (e.g., parabolic, linear, etc.), using the TIR data to inform the model. Relationships between thermal heterogeneity patterns and network topology have not been well studied. Other fine-scale patterns of thermal landscapes could be explored, ranging from smooth gradients in water temperature to completely random or highly patchy patterns. The model could also be used to consider how temporal patterns in water temperature influence fish. For instance, would fish seek out cooler habitats during summer if they did not experience respite from warm temperatures at night? I modeled fish growth at night and during the day. It would be interesting to compare these results to a more standard approach in which fish grow on a daily time step. More broadly, how variable is the fish response over multiple years in the same network?

Several additional ideas come to mind for considering whether network topology can influence fish response to climate change. One idea is to examine how shifting ranges of natives and non-natives will change the degree to which they may overlap in the future and whether risk to native species is greater in networks having specific shapes. Another idea is to evaluate the role of topology on fish survival in the presence of disease – for instance, do fish congregating in thermal refuges suffer elevated risk of coming in contact with pathogens? A third idea is to evaluate population-level response to temporary thermal barriers or to loss of tributary habitat as tributaries temporarily dry up more frequently with loss of snow (i.e., changing the shape of the network that remains accessible).

I intend to explore how theoretical outcomes compare to empirical observations by applying the model in the Snoqualmie River watershed in western Washington. We (A. Steel, USFS, others) have semi-continuous spatial and temporal water temperature predictions made using a spatial stream network model and 4 years of empirical data from a suite of over 30 loggers. We also have access to fish data collected by the Washington Department of Fish and Wildlife for the upper watershed. Although the years of water temperature and fish data do not overlap, we may be able to choose the water temperature year most similar to conditions during fish surveys. One of the years of water temperature, 2015, was anomalously warm and modeling how fish would respond in this year may lend insight into how fish could respond to altered thermal regimes in a warmer future. We (NOAA Fisheries) also have a substantial dataset of juvenile salmon and a limited water temperature dataset (loggers in a few streams) in the Snake

River basin, Idaho. Applying the IBM in these streams may yield management insights and could inform ongoing life cycle modeling for an important metapopulation.

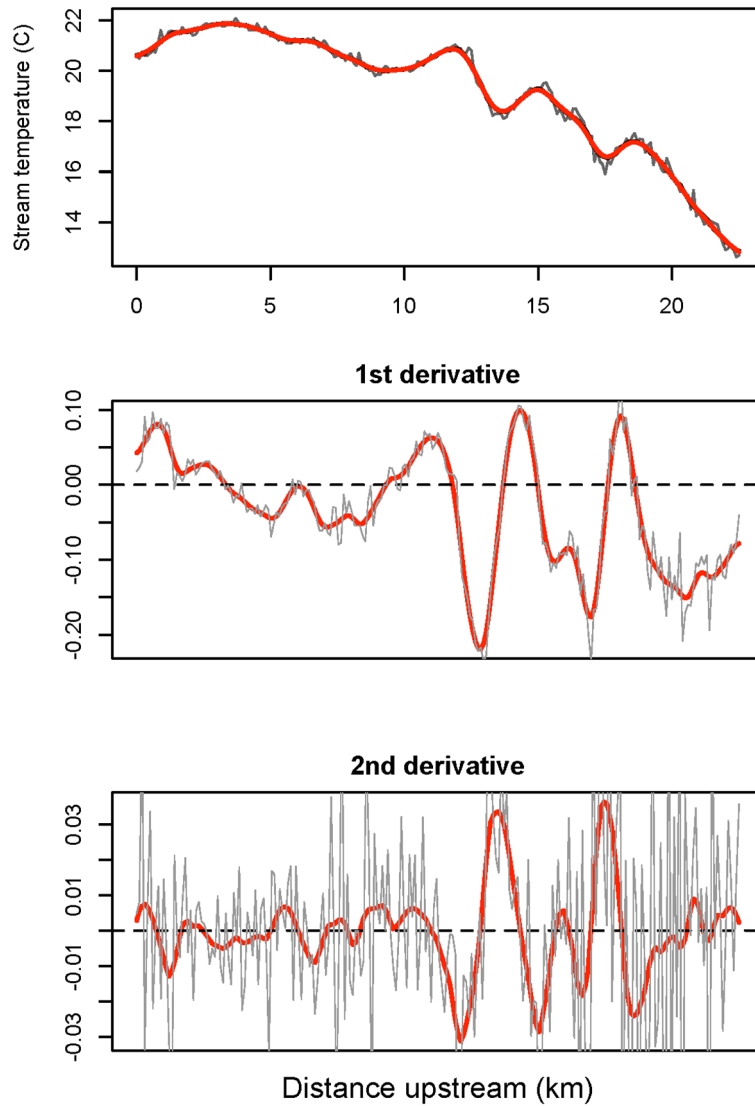


Figure 6.1. Longitudinal profiles of stream temperature from TIR (top panel) for Granite Creek, a tributary to the North Fork John Day, OR (collected on 20 August 2004). The first and second derivatives (approximated using differencing) are shown in the middle and bottom panels, respectively. Raw data are displayed as thin gray lines and smoothed trends are shown as thick red lines. Derivatives shown here were computed in an upstream direction. Therefore, negative first derivatives indicate cooling in an upstream direction.

VITA

EDUCATION

M.S., Aquatic Ecology, University of Notre Dame, Notre Dame, IN, 1998 (G.A. Lamberti)
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PROFESSIONAL EXPERIENCE

Fisheries Research Scientist, 2002 to present

Northwest Fisheries Science Center, NOAA Fisheries, Seattle, WA

Aquatic Biologist, 1998 to 2002

Nongame and Endangered Wildlife Program, NC Wildlife Resources Commission, Raleigh, NC

RESEARCH INTERESTS

Spatial structure of aquatic populations, especially those living in stream networks; relationship between spatiotemporal scale and ecological patterns and processes; climate change impacts to aquatic systems; influence of nonindigenous species on native aquatic fauna; and ways that science can contribute to improved decision-making.

Recent projects have focused on the spatial structure of threatened and endangered Pacific salmon metapopulations and effects of altered thermal regimes on salmon. Prior NWFSC projects included habitat analyses to support policy decisions, development and application of a watershed restoration planning decision support system, evaluation of riparian conditions in the Columbia River basin, and life history diversity of salmon in Puget Sound. Prior work involved aquatic nongame and endangered wildlife issues in North Carolina, especially conservation of native crayfishes. Thesis research at Notre Dame focused on interactions between a nonindigenous fish and the Great Lakes ecosystem. Undergraduate research at Ohio State investigated factors controlling growth and overwinter survival of juvenile largemouth bass.