Impacts of network structure and landscape complexity on the cumulative thermal exposure of migrating salmon

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#Abstract

Warming water temperatures may challenge migrating adult salmon. Elevated and persistent thermal stress during upstream migration is linked to a variety of negative effects on salmon survival including increased disease, lower energy density and curtailed aerobic scope. Yet linking landscape controls to temperature dynamics across space and time and quantifying the migratory thermal exposure of salmon remains a challenge. In this study we combine a large in-stream temperature collection effort with improved analytical approaches to assess how landscape features control temperature regimes and vary cumulative levels of thermal exposure experienced by salmon migrating throughout the large and diverse Thompson River watershed in central British Columbia Canada. We used temperature data collected continuously between 2014 and 2017 at major river confluences in two neighboring and topographically distinct sub-basins to describe annual temperature dynamics resulting in 290 unique site-year observations. By quantifying landscape and climate contributions to temporal stream temperature dynamics, we demonstrate the importance of landscape and network interactions that lead to remarkably different temperature dynamics in the two neighboring sub-basins. For instance, high elevation lakes and glaciers were associated with cooler stream temperatures and low thermal exposure probability while low elevation lakes and wildfire exhibited the inverse. Integrated by the river network, dominant warming features were shown to lead to higher exposure potential along common migratory corridors (i.e., mainstem), leading to higher thermal exposure for populations with longer migrations. Importantly, in the four years of observation, high inter-annual variation in migratory thermal exposure was observed, suggesting systems like the Thompson River watershed, which are currently exhibiting near prohibitive temperatures for migrating salmon, may become more persistently troublesome as global temperatures rise. By linking watershed attributes to the thermal challenges of upstream migration, our study identifies differential exposure potentials among salmon populations that may be useful to conservation assessment and improve management prioritization.

#Introduction

Freshwater temperatures reflect climate and landscape interactions (Webb, Hannah, Moore, Brown, & Nobilis, 2008) and control ecological processes (Angilletta, 2009). Freshwater temperatures and their impacts on biota are of increasing concern with rising global temperatures (Comte & Olden, 2017). A filtered manifestation of climate (Griffiths, Schindler, Ruggerone, & Bumgarner, 2014), the contribution of climate change to shifting freshwater temperatures is complexified by landscape dynamics (e.g., Lisi, Schindler, Bentley, & Pess, 2013; MacDonald, Herunter, & Moore, 2003). Moreover, as catchment area increases, a greater variety of landscape features contribute to water’s thermal profile and their relative importance shift in magnitude. The hierarchical structuring of the river’s diverse and changing thermalscape organizes the freshwater ecosystem (Brown & Hannah, 2008), dampening variation (Moore et al., 2015; Steel, Sowder, & Peterson, 2016) and buffering against the changing climate (Chezik, Anderson, & Moore, 2017). As a result, thermal extremes and the associated stress on organisms will vary depending on network location and the composition of the upslope landscape.

Different landscape features and land-uses influence river temperatures. For example, lakes are known to act as heat sinks, warming and stabilize the thermal regimes of downstream rivers (Moore, 2006; Wetzel, 2001), while glaciers and steep slopes often contribute to stream cooling during the summer through the contribution of melt- and groundwater (Cadbury, Hannah, Milner, Pearson, & Brown, 2008; Lisi, Schindler, Cline, Scheuerell, & Walsh, 2015; Stahl & Moore, 2006). Human interventions such as urbanization (Nelson & Palmer, 2007), logging (MacDonald et al., 2003) and stream regulation (Moore, 2006) generally warm riverine temperatures although dams exhibit distinctively mixed effects (Moore, 2006; Todd, Ryan, Nicol, & Bearlin, 2005). Thus, different landscape features will impact downstream water temperatures differently with relative influences shifting seasonally. Accordingly, downstream water temperature regimes are a hierarchical aggregate of the contributing watershed (Isaak et al., 2014; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Tributaries that drain basins of different composition and size will add their distinct thermal signature resulting in a constantly shifting thermal mosaic over space and time (Palmer et al., 2009; Peterson, Theobald, & Hoef, 2007).

Organisms that migrate through river networks to access essential habitat may experience temperatures that at times exceed their thermal limits depending on their timing and route through the network (Matthew L Keefer et al., 2015; Steel et al., 2016). Renowned for their extraordinary migrations from the Pacific Ocean to the interior of Western North America, adult Pacific Salmon (*Oncorhynchus spp.*) may transit diverse habitats of varied temperatures in order to reproduce in their natal streams (Quinn, 2011). A coldwater species, adult salmon may be close to or beyond their thermal optimum during their migration (Isaak, Young, Nagel, Horan, & Groce, 2015; Keefer et al., 2018; Keefer, Peery, & Heinrich, 2008) leading to thermal stress that can result in pre-spawn mortality (e.g., Hinch et al., 2012). For instance, in especially warm years en route mortality has exceeded 90% in some stocks of Fraser River sockeye (*O. nerka*) (Cooke et al., 2004; Macdonald, 2000). Spawning throughout river systems west of the Rocky Mountain Range at different times throughout the year, salmon species and populations experience varied levels of thermal exposure depending on their migration timing and route (Matthew L Keefer & Caudill, 2015). If water temperatures increase as expected under climate change, adult migration may become increasingly strenuous, possibly leading to loss of suitable habitat (Ruesch et al., 2012) or abundance declines (Hague et al., 2011; Rand et al., 2006) if rapid evolution can’t keep pace with climate chnage (Reed et al., 2011).

Estimating salmon migratory thermal exposure is challenging as the river thermalscape is quite variable over space and time (Fullerton et al., 2018). Historically, the thermal challenge of migration has typically been assessed low in the watershed (e.g., Wild Fish Conservancy, 2015). Such an approach is pragmatic because temperatures lower in the basin are typically warmer (Steel et al., 2016) and constitute a common migratory corridor to many populations, thereby greatly simplifying the monitoring effort. However, the accumulation of migratory sub-lethal effects on salmon survival has become increasingly concerning (Healey & Bradford, 2011), necessitating improved broad-scale temperature monitoring and modeling (e.g., Isaak et al., 2015). Statistical inference facilitates prediction at unobserved locations, improving estimation of network-wide thermal exposure. To date, these approaches have often greatly simplified temporal (e.g., Isaak et al., 2015) or spatial (e.g., Quinn, Hodgson, & Peven, 1997) thermal exposure contributions. However, studies that have placed internal tags in salmon have found that thermal exposure is dependent on migration timing and route along the network (Matthew L Keefer et al., 2015). Thus, there is a need for further incorporation of temperature dynamics aross space and time towards understanding thermal exposure of migratory salmon.

The Thompson River watershed in central British Columbia Canada is an important salmon catchment where temperatures may be challenging these migratory fishes. The Thompson is a tributary to the greater Fraser River, a system which has exhibited substantial warming over the last half century (Ferrari, Miller, & Russell, 2007; Morrison, Quick, & Foreman, 2002). The Thompson River is home to steelhead (*Oncorhynchus. mykiss*), pink (*O. gorbuscha*), Chinook (*O. tshawytscha*), coho (*O. kisutch*) and sockeye (*O. nerka*) salmon, including the Adams River migration of sockeye salmon. Yet, the Thompson River has exhibited many population declines across species due to degraded ocean conditions and freshwater habitat (Labelle, 2009). Sockeye salmon migrating to the South Thompson River watershed have exhibited an increase in pre-spawn mortality (Hinch et al., 2012; Young et al., 2006). Linked to a shift towards earlier adult migration, energy depletion has been cited as a cause of decreased survival with warmer migration temperatures speculated to be a fundamental contributor (Crossin et al., 2008). Similarly, increasing temperatures is believed to be contributing to the decline of coho, steelhead and Chinook abundances (Bradford & Irvine, 2000). Although direct links of temperature on these species is to date unclear, sub-lethal effects have been shown to exacerbate the impacts of disease and parasites (Gilhousen, 1992) on energy density and curtail aerobic scope (Eliason et al., 2011), making migration more strenuous and survival less likely (Martins et al., 2011). These findings suggest that as water temperatures warm, persistent thermal stress during migration is likely to increase mortality rates through multiple ultimate mechanisms.

Thermal exposure depends on salmon river entry timing and migration rate in concert with the aforementioned climate and landscape spatial controls on the migratory river thermalscape. Here we ask: 1. In what capacity do climate and landscape features contribute to the dynamics of the thermalscape of the Thompson River system? 2. What is the thermal exposure posed to salmon with different migration timing and routes? To address these questions we model climate and landscape effects on seasonal water temperature dynamics using a statistical stream network framework (Hoef & Peterson, 2010; Peterson et al., 2013). Previous work has generally used such network models to predict average mean August water temperature or some other summary statistic as a function of watershed characteristics (e.g., Isaak et al., 2015): here we use these spatial models to actually model the temporal dynamics of water temperatures. This modeling advance allows for the re-creation of thermal dynamics along any migratory route while accounting for changing seasonal dynamics and upslope landscape effects. Understanding the various contributors to stream temperature during migration should inform routes and populations at greater risk of thermal stress and inform how watershed landuse and climate change alter such risks.

#Methods

###Data

*Thompson River Watershed*

To capture the thermal heterogeneity of the Thompson River watershed, Hobo Pendant data loggers were deployed at 103 locations between 2014 and 2017, with the goal of capturing confluence interactions and specific landscape effects (Fig. $\ref{fig:1}$). By placing loggers in triads, upstream and downstream of major confluences, we aimed to capture the relative contribution of each stream to the subsequent downstream temperatures (e.g., Marsha, Steel, Fullerton, & Sowder, 2018). We focused logger deployment in the North Thompson River watershed because the basin contains more distinct regions where the contributions of specific landscape features may be more pronounced. In its northern reaches, the North Thompson River watershed is dominated by steep slopes, snow-capped mountains and small glaciers. The west side of the watershed is perched on a high plateau, is relatively flat and dominated by lakes connected by relatively slow-moving steams. In the transition between the northern and western regions is a large inactive, volcanic field, largely captured within Wells Grey Provincial Park, and distinguished by canyons, rapid flows and dramatic waterfalls. The southern portion of the North Thompson River watershed is narrow, largely composed of the mainstem with many small creeks and streams flowing out of increasingly arid hills. The South Thompson River watershed is dominated by lakes, which are fed by small streams tumbling out of the Canadian Rocky Mountains. The north and south basins of the Thompson River merge in the southwest before continuing to the mainstem of the Fraser River and ultimately to the Pacific Ocean. The Thompson River region is dominated by conifers, is actively logged and frequently experiences wildfires. Agriculture and ranching occur in the watershed but the topology of the region limit these industries largely to the floodplain along the mainstem with the exception of some more extensive orchard agriculture in the South Thompson River watershed’s Okanagan Valley and low density ranching in the western portion of the North Thompson River watershed.

*Stream Temperature Data Collection*

We monitored stream temperatures at two-hour intervals from July of 2014 to August of 2017, with routine annual data collection and redeployment. By returning each year we ensured the loggers remained in the water column and that depleted batteries and lost loggers were replaced. We affixed the loggers to the landscape by attaching cable to boulders, bridge pylons or large trees expected to remain constant and unyielding to extreme river flows. White PVC shields were attached to the cable to protect the loggers from debris and solar radiation that may bias temperature readings (e.g., Isaak & Horan, 2011). To prevent de-watering events, we sunk loggers attached to weights in deep pools protected from the direct influence of the rivers thalweg when possible. We cleaned the temperature data via manual inspection and flagged data believed to be associated with de-watering events (e.g., Sowder & Steel, 2012). Concerned with the most likely thermal experience, we averaged raw temperature readings to the daily level.

###Statistical Models

Interested in how temperatures change during adult salmon migration we require linked spatial and temporal models that describe thermal conditions in any given place at any given time on the river network. To do this we first characterize temperature’s temporal pattern and then subsequently model those descriptive coefficients given climatic and landscape covariates in a spatial statistical stream network model (SSNM). Combining process and statistical approaches this unique methodology parses landscape, network and seasonal dynamics that then allow for prediction of temperatures across time at any place on the network.

*Temporal Stream Temperature Model*

To characterize the seasonal dynamics of stream temperatures we used two cyclical models in linear combination,

where mean daily () temperatures () at each site () are described primarily by broad seasonal dynamics () and modified by local seasonal conditions (). The remaining variance () not captured by these models is assumed to be independent and random (i.e. *i.i.d*).

Dominated by seasonal shifts in solar radiation due to the tilt of the earth’s axis and its orbit around the sun, we describe the primary periodic dynamics of stream temperature using a cyclical model (e.g., Shumway & Stoffer, 2000),

where the annual oscillation of temperature is described by a modified cosine curve. Shifting the cosine curve vertically captures the mean annual water temperature () while amplifying the curve captures the annual range of temperatures around the mean (). The frequency of the temperature cycle is captured in () and described by,

where is the number of observations per year and is the integer location of observation in the year. Because we averaged our data to the daily level, we used the day of year as a common value of across sites, and set to 365 (or 366 in leap years). Although the solstices should vaguely coincide with the extremes in annual temperature, shifts due to local climatic variation are allowed in . Because is equivalent to January 1st, is approximately described by a value of 1 in the Northern Hemisphere or a shift in the cosine curve of such that the cosine curve begins near its lowest point.

Hysteresis is a common feature of annual stream temperatures, where rising spring and declining fall temperatures are not symmetrical around summer’s peak temperature (Letcher et al., 2016), rendering a simple cosine curve a poor descriptive model on its own. Divergences from the expected pattern of temperature given changing levels of solar radiation are typically a result of seasonal precipitation, where higher stream flows depress stream temperatures (Lisi et al., 2015). In the northern hemisphere this is commonly observed in the spring when snow melt drives a basin-wide freshet. To account for seasonal patterns in stream temperature driven by local climate, we include a double cycle cosine curve that acts to modulate the annual curve (eq. $\ref{eq2}$),

where is an expansion factor that alters the strength of the hysteresis and just as in equation $\ref{eq2}$, shifts the curve to align with local seasonal effects. In the Thompson River watershed, typically corresponds with a value of 1.5 which results in warmer winter and summer stream temperatures and cooler spring and fall temperatures. This is because low flows in the summer and winter lead to a greater influence of solar radiation and ground water respectively, while snow-melt and rain dominate in the spring and fall in the Thompson River region.

Implementing this model in the probabilistic programming language Stan (Stan Development Team, 2017) allowed us to explore the entire probability space of these parameters and propagate that variability to the subsequent spatial model. Furthermore, using a Bayesian framework allowed us to provide reasonable prior estimates and limit the parameter space over which the model must search. For instance, and parameters are not reasonably expected to go below 0$\text{\textdegree}$C, therefore we limited those parameters to above zero and provided weak lognormal priors centered on 2 with a variance of 1. Similarly, given the cyclical nature of our model, values can take on reasonable estimates at regular intervals *ad infinitum*. Running a multi-chain (MCMC) analysis requires the chains agree on an estimate which can be difficult when multiple values lead to the same fit. To avoid disagreement, we limited to positive values and provided weakly normal priors with a variance of 0.25 centered on 0.9 for and 1.5 for . The expansion factor was limited to between 0 and 3, maximizing the hysteresis adjustment to no more than 3$\text{\textdegree}$C in either direction thereby limiting the models flexibility and influence. After fitting equation $\ref{eq1}$ to the data, we visually inspected the fits at each site and year and consulted diagnostic statistics accepting value less than 1.1 and effective sampling size ratios of greater than 0.001 (Gelman et al., 2013). We excluded sites and years that had poor visual fits even when other diagnostics were not problematic. Strict data requirement cut-offs were not used as data near the seasonal extremes play a disproportionate role in fitting equation $\ref{eq1}$ parameters. Using a more subjective approach allowed us to include more sites despite varying degrees of missing data.

*Spatial Stream Network Model*

Advances in stream network modeling, that account for branching architecture, directed flow, longitudinal connectivity and weighted confluence contributions, have greatly enhanced our ability to account for network spatial relationships and proportion landscape and climate contributions to observations on the network (Hoef & Peterson, 2010; Isaak et al., 2014; Peterson et al., 2013, 2007). Applications of these models to stream temperature data have largely been limited to temporally static summary statistics – for example, mean summer temperature – that attempt to understand network mediated landscape contributions to biologically meaningful thresholds (Isaak et al., 2010). Here we advance this approach by using these spatial statistical stream network models on the actual parameters that describe the entire seasonal dynamics. This approach allowed us to deconstruct how different watershed features affect the dynamics of temperature regions – for example, watershed features may differently affect the average temperature or the amplitude or seasonality of the streams annual temperature profile.

Currently, multi-variate methods that link predictors to a variety of responses simultaneously are not available within the stream-network framework. Therefore, we built individual models for each parameter resulting in five stream network models with the general construction,

where standardized equation $\ref{eq1}$ coefficients (, see Table $\ref{tbl1}$) at site in year are predicted by a matrix of climate and landscape variables , where the relationship between the temporal model’s coefficients and these predictors are described by a vector of coefficients. The error term is decomposed into random effects () accounting for basin wide year effects (), site effects (), exponentially weighted flow connected autocovariance () and residual *i.i.d* error () (Hoef & Peterson, 2010).

In order to calculate predictor variables at each site, we first built a landscape network describing the branching architecture of our streams (Theobald et al., 2006) and delineated reach contributing areas (RCA) for each downstream confluence in the network (Peterson & Hoef, 2014). Geo-referenced stream data were gathered from the British Columbia Data Catalogue made available by the Ministry of Citizens Services. Streams were subset to greater than second order, cleaned of network braiding, complex confluences, pseudo-nodes and all vectors were directed towards the outlet. Sites were snapped to the network (Fig. $\ref{fig:1}$) and center-points of each stream segment were used as prediction locations. Reach contributing areas were delineated using a 25 metre digital elevation model (DEM). Prior to delineation, the DEM was cleaned of topological errors and the known stream network was burned into the DEM at a 5 metre depth. All predictor variables were summarized by RCA using the *‘zonal\_stats’* tool in the Python package *‘rasterstats’*.

Climate and landscape predictor variables known to significantly contribute to stream temperatures (e.g., Isaak et al., 2010), were gathered from multiple sources. Climate data were calculated using the open source tool ClimateBC (Wang, Hamann, Spittlehouse, & Carroll, 2016), which extracts and downscales PRISM climate normal data and extrapolates to any location within British Columbia (Daly et al., 2008). Sampling at 1 km resolution across the Thompson River watershed, we used ClimateBC to estimate the mean annual air temperature in each year between 2014 and 2017. We calculated the amplitude around the mean as the difference between the average maximum summer air temperature (June-Aug.) and the average minimum winter air temperature (Dec.-Feb.). Static landscape variables included glacial coverage gathered from the Rudolph Glacier Inventory (v5.0) (Arendt et al., 2015), lake area calculated from polygons in the BC Freshwater Atlas and elevation extracted from the aforementioned DEM. To characterize dominant changes to the landscape in recent decades, we extracted high resolution forest change data from the National Forest Information System. Derived from Landsat images, these data identify logging and wildfire for each year between 1985 and 2010 at a 30 metre resolution (White, Wulder, Hermosilla, Coops, & Hobart, 2017). Summing these data within each RCA, we determined the total loss of forest in each category over the 25 year period as a general measure of impact. Climate and elevation data were averaged by RCA whereas landscape variables were summarized by total km2 in each RCA.

Ultimately, we are interested in the contribution of each predictor variable from the entire watershed to each observation and prediction site. Using the spatial relationships defined in our landscape network, we calculated the upslope area average of each predictor for each site. To characterize the contribution of glaciers, lakes and forest-change relative to the size of each sites catchment, we divided these variables by their catchment area, thereby calculating their proportional area coverage. Visual inspection suggested a logit transformation of these percentages in order to spread the data more evenly and limit the influence of extreme data points. Climate, elevation and catchment area were all centered and scaled in order to limit the influence of the y-intercept and allow effect size comparison across variables (Table $\ref{tbl1}$).

Not all predictor variables display strong relationships with each temporal coefficient, therefore we limited predictors and interactions in each model to those that resulted in lower Akaike Information Criterion (AIC), significant gains in explained variance and improved leave one out cross validation results. Once SSNM models were constructed for each parameter, we iteratively sampled coefficient estimates from the posteriors of equation $\ref{eq1}$, fit our SSNM models to those estimates and predicted temporal coefficients at our prediction sites. This process resulted in 250 estimates of each coefficient for each year (2014-2017) at 4376 prediction locations throughout the Thompson River watershed.

To approximate the thermal exposure of migrating salmon, we need to define when salmon might arrive in the Thompson River, how quickly they might move through the river network, and what temperatures are considered stressful. Previously, migration timing of Chinook populations throughout the Thompson River watershed were estimated in 2000 and 2001 by Parken, Candy, Irvine, & Beacham (2008) using coded wire tags and genetic sampling. Measured at the Albion Test Fishery, approximately 50 km upstream from the Fraser River mouth, populations occurred in three run-timing groups, early (June), mid (July) and late (August) summer. Using an estimated migration rate of 36 km per day (Salinger & Anderson, 2006), we calculated the number of days (~13 days) required to travel the 447 km between the Albion Test Fishery and the confluence of the North and South Thompson Rivers. Although we do not account for temperature-driven changes in migration speed (e.g., Salinger & Anderson, 2006), we do sample migration dates uniformly across the migration windows which should consume individual variation and generalize our findings more widely. Moreover, although we are using migration timing data for Chinook salmon, we note that these different run-timing groups also apply to sockeye salmon and were chosen by Parken et al. (2008) to correspond with contemporary conservation requirements for salmon more broadly (Bailey & Canadian Science Advisory Secretariat, 2001).

Upon estimating salmon arrival in the Thompson River system, we used our predicted SSNM model estimates of equation $\ref{eq1}$ parameters to calculate expected daily temperature probability distributions at each prediction site on the expected day of passage. To do this we calculated the day of passage by dividing the upstream distance of any prediction site by the migration speed (36 km/day) and added the result to the date of arrival at the outlet, giving the expected value at each prediction site in the network, dependent on the day of passage through the Albion Test Fishery. Using the expected value in combination with all 250 site predicted coefficient estimates we calculated the full distribution of mean temperature and standard deviation estimates at each prediction point (e.g. Fig. $\ref{fig:2}$). These distributions were then used to calculate three metrics of thermal exposure that describe the difficulty of migrating to and spawning at any location on the network.

*Thermal Exposure Probability*: Temperature sensors capture a single point estimate within a thermally heterogeneous environment. We are interested in the most likely (i.e., mean) thermal experience and the probability of experiencing stressful temperatures above a known threshold at a given place and time. Assuming thermal heterogeneity of the environment is normally distributed around the mean temperature estimate, we can calculate the area under the curve equal to or exceeding any threshold temperature that may be stressful to salmon and divided this value by the total area, returning the probability of experiencing temperatures as warm or warmer than the given threshold at that point in time. For example, if our mean temperature estimate was 17$\text{\textdegree}$C with a standard deviation estimate of 2, the probability of a temperature above 19$\text{\textdegree}$C would be 0.16. Using all 250 mean and standard deviation estimates at a given site, we calculate a distribution of probabilities and return the median probability of experiencing an above threshold temperature at that location. Thus, the thermal exposure probability is the median probability of experiencing a temperature greater than the given threshold at a given site.

*Cumulative Migratory Thermal Exposure*: Following the flow connected path from each site to the outlet, we summed all above threshold mean temperature estimates. These values indicate temperatures with at least 50% probability of exceeding a given threshold. A greater number of these high thermal exposure probability estimates result in greater cumulative migratory thermal exposure, indicating persistent or acute thermal challenges during migration. For instance, locations with extremely high thermal exposure probability will result in a greater proportion of the 250 mean temperature estimates being above the threshold temperature, resulting in an acute increase in cumulative migratory thermal exposure. Whereas persistent thermal exposure would occur when many locations along the migratory route have mean estimates above threshold. Thus, higher cumulative thermal exposures indicate fish migration routes with greater potential of experiencing deleterious temperatures overall. We reported the median value for each run-timing group to capture the typical cumulative thermal exposure throughout the migration window.

*Average Migratory Thermal Exposure Probability*: Finally, we divided the cumulative migratory thermal exposure by the total number of temperature estimates along the migration route (*n* = #sites 250), giving the average migratory thermal exposure probability. While the migratory exposure strictly increases during upstream migration, the exposure probability can both increase and decrease, thereby depicting changing temporal and landscape effects on temperature during migration and seperating persistent and acute thermal challenges on the network. This metric can also be thought of as the proportion of temperature estimates with a greater than 50% chance of exceeding the temperature threshold, over the course of the migration. We again reported the median value for each run-timing group to characterize the typical cumulative migratory thermal exposure probability.

This flexible analytical approach can calculate thermal exposure at a variety of thresholds and spatial extents as determined by species thermal limits and behaviours. Here we use a lower threshold of 19$\text{\textdegree}$C to indicate significant but manageable stress and a value of 22$\text{\textdegree}$C to indicate temperatures blocking migration per values identified for sockeye, steelhead and Chinook salmon (Richter & Kolmes, 2005). We emphasize that these temperature thresholds are for considering temperature – in order to consider risk we would also need to consider the sensitivities of different populations, which can vary due to different local adaptations (e.g., Eliason et al., 2011; Anttila, Farrell, Patterson, Hinch, & Eliason, 2018). Ultimately, this process produces median thermal exposure probabilities by migration group, in any year and at any temperature threshold of interest, at any point in the network. As such, we calculated the median cumulative migratory thermal exposure and median spawn site thermal exposure probability for the 16 populations of Chinook salmon identified by Parken et al. (2008) in the Thompson River watershed (Fig. $\ref{fig:1}$) per each populations migration route and run-timing.

#Results

*Temporal Stream Temperature Model*

Of the 408 unique site-year combinations, we selected 290 that displayed strong fits, capturing the maximum temperatures and hysteresis present in the data (e.g., Fig. $\ref{fig:2}$). Of those the data were spread fairly evenly between years with 61 estimates in 2014, 91 in 2015, 67 in 2016 and 71 in 2017. Many sites displayed poor fits when temperature data near the annual extremes were limited and thus were eliminated from the spatial analysis. Frequently, data were limited due to dewatering events, late (i.e., fall) deployment in 2014 or logger loss. The selected sites in Fig. $\ref{fig:2}$ exhibit many of the characteristics that either constituted acceptance or rejection. For instance, the North Thompson (NT) Headwaters and Barri$\`e$r River lower in the North Thompson River watershed displayed four quality years of data and acceptable fits. Meanwhile, Bridge Creek and the Shuswap River each exhibited one year, 2014 (late deployment) and 2016 (logger loss) respectively, that did not capture enough data to constitute convincing estimates of all parameters. Thus, these site-years were removed from the spatial analysis. Overall fits were strong with no apparent bias seasonally except for when peak summer temperatures were extremely ‘sharp’ but our estimates of variance largely captured these values at 95% confidence (e.g., Bridge Creek, 2015 Fig. $\ref{fig:2}$).

*Spatial Stream Network Models*

Stream network (SSNM) model selection resulted in primarily strong fits that accounted for much of the variance in the temporal model parameters (eq. $\ref{eq1}$). Leave-one-out cross validation demonstrates the predictive capability of our models with largely strong 1:1 relationships between observed and predicted parameter values (Fig. $\ref{fig:3}$). Variance () and timing () coefficient models exhibited particularly strong predictive relationships with limited exception, likely due to their minimal variance among sites and shared values across years (i.e., eq. $\ref{eq2}$). Elevation was the only covariate included in these three SSNM models (i.e., and ), with higher average catchments leading to lower values across parameters. In other words, higher elevation was associated with less thermal variation (), a later onset of spring () and delayed seasonal effects of snow and rain (). A key difference between these three models is the contribution of the covariate relative to the correlation structures. Elevation dominated in the model (46%), while only capturing 10% of the variation in the models. Site-level correlation () accounted for much of the remaining variance in all three models but demonstrated a particularly strong effect of site (62%) while variance in the parameter was primarily captured through autocorrelation () along the flow connected network (52%). All three of these SSNM models had very little unaccounted for residual variance ( 1%) (Fig. $\ref{fig:3}$).

Covariates that contributed to the efficacy of , and SSNM models varied with the exception of mean annual air temperature which was the dominant predictor across models (Fig. $\ref{fig:4}$). Water’s mean annual temperature () was additionally positively affected by the annual range of temperatures averaged across the contributing area (Air Amplitude), the percent catchment burned (WildFire), the catchment’s mean elevation (Elevation) and the percentage of lake area (Lakes). The interaction of elevation and lake predictors was notably the only cooling influence on while counter-intuitively elevation alone had a slight warming effect. Overall, these covariates captured on average 37% of the variation in the observed values while auto-correlation along the flow connected network captured 29%. Much of the remainder was accounted for by correlation within years (25%) and within sites (4%) with 5% of the variance in remaining unaccounted.

The SSNM describing the amplitude (*A*) of water temperatures around the mean showed positive relationships with the contributing basins mean air amplitude, the catchment area, its percentage lake area and glacial coverage. The percent catchment area covered by glaciers reduced the range of annual temperatures around the mean (center, Fig. $\ref{fig:4}$). Thus, glaciers dampen temperature variation. The covariates in this SSNM captured the largest amount of variance in the data (46%) compared with covariates in all other SSNMs. The remainder was largely evenly distributed between the flow connected correlation structure ( = 19%) and correlation within sites ( = 18%).

The parameter controlling the strength of seasonal hysteresis was notably under-estimated by the SSNM at high values and over-estimated at low values, resulting in relatively even attribution of this parameter across sites (Fig. $\ref{fig:3}$). Neither the covariates (10%) nor the autocorrelation structures (,,) dominated in accounting for variance in this parameter (20,25 and 7% respectively). The little variance captured by covariates included negative effects of mean annual air temperatures, mean catchment elevation and percent catchment area covered by glaciers (Fig. $\ref{fig:4}$). In other words, seasonal hysteresis is reduced in colder regions, a characteristic typical of higher elevations, and further dampened by the presence of glaciers at high elevations.

*Projected Network Thermal Exposure*

Spatial projections of thermal exposure probabilities highlight the thermal challenge of the South Thompson River’s mainstem and the North Thompson River’s western high plateau (Figs. $\ref{fig:5}$, S1). The potential for stressful conditions above 19$\text{\textdegree}$C were relatively elevated during the mid-summer migration and least likely during the late-summer migration (Fig. S1). Furthermore, the likelihood of stressful conditions varied across years with a general decline between 2014 and 2017 across migratory periods. Thermal exposure at 22$\text{\textdegree}$C was extremely unlikely across migrations and years (Fig. S2). Of those regions that had elevated stress potentials above 19$\text{\textdegree}$C, large lakes in low elevation basins constituted the most common landscape characteristic, such as in the Okanagan Valley region of the South Thompson River watershed.

Reflecting regionally elevated thermal exposure probabilities, cumulative migratory thermal exposure generally increased with migratory distance and was much higher in the South Thompson River watershed (Figs. $\ref{fig:5}$, $\ref{fig:6}$, S3). In other words, South Thompson River watershed residents are more likely to experience stressful temperature than those in the North Thompson River watershed, and the opportunity of experiencing these temperatures grows the further these southern populations migrate. This finding was particularly true in 2014, early and mid-summer of 2015 and mid-summer of 2016, while elevated thermal exposure was relatively unlikely in 2017. Cumulative migratory thermal exposure above 22$\text{\textdegree}$C, was nearly non-existent in either basin across sites, years and migratory periods (Fig. S4).

Contrary to the cumulative thermal exposure, the average thermal exposure probability declined with migratory distance in the South Thompson River watershed (Figs. $\ref{fig:5}$, S5). In the North Thompson River watershed, the probability of thermal stress was notably highest in the western portion of the watershed and did not follow the migratory distance patterns of the South Thompson. These findings also reflect the thermal exposure probability dynamics of the mainstem versus the tributaries (Figs. $\ref{fig:5}$, S5). Moving further up the watershed and away from the mainstem reduces the local probability of thermal stress leading to an overal decline in the migratory probabilities of thermal stress. Thus, once migratory salmon make it through the warm lower mainstem portions of these rivers, they will generally encounter lower temperatures. There was little to no evidence that the 22$\text{\textdegree}$C threshold is likely among any migration route (Fig. S6).

*Chinook Salmon Thermal Exposure*

Different Chinook salmon populations with different migration timing and routes had different exposure to excessively high temperatures. South Thompson River watershed populations are much more likely to experience thermal exposure than those in the North Thompson River watershed (Fig. $\ref{fig:6}$, S7). In many years the potential for thermal exposure (>19$\text{\textdegree}$C) among southern populations persisted after diverging off the mainstem and arriving on the spawning grounds but rarely above 50% probability. At the 22$\text{\textdegree}$C threshold, only the mid-summer migrants in the South Thompson River watershed exhibited any chance (>50%) of experiencing these temperatures during migration and they were extremely unlikely across populations on the spawning grounds (Fig. $\ref{fig:6}$). Notably, longer distance migrations were exposed to a greater number of likely stressful temperatures in the southern watershed. Broadly, thermal exposure was consistent across run-timing groups and years within watersheds though fewer populations are observed during the more stressful mid-summer migration window in the South Thompson (Fig. S7). Across populations, thermal exposure potential declined from 2014 to 2017.

#Discussion

This study linked a large field temperature collection effort with new analytical approaches to model stream temperatures throughout a large watershed towards predicting thermal exposure of different migratory salmon populations. We focused on the 38,000 km2 Thompson River watershed of British Columbia, a climatically-diverse watershed of significant topological complexity, home to imperiled salmon populations. We decomposed the different ways that climate, land-use, and watershed features contribute to the temperature regimes of this region – for example, wildfire and lakes lower in the watershed were associated with warmer average temperatures, whereas glaciers dampened temperature variation. Accordingly, there was great spatial variation in river temperatures yet this heterogenity demonstrated significant spatial organization by the river network. Spatial and temporal thermal variation along migratory corridors result in different degrees of thermal exposure among migrating Chinook salmon populations, destined for locations throughout the basin and returning at varied times throughout the summer.

Watershed features and their interactions demonstrated diverse controls on the different aspects of temperature regimes. Lakes were a particularly dominant landscape feature contributing strongly to stream temperatures (Fig. $\ref{fig:4}$). Although the North and South Thompson River watersheds share nearly the same total lake area (726 and 756 km2 respectively), these two basins exhibit dramatically different lake effects on temperature. Unlike the North Thompson River watershed, 47% of the South Thompson River’s two longest and largest rivers’ are consumed by large lakes. The impoundment of tributary waters in these lakes allows for surface waters to warm from increased solar radiation over the summer. The subsequent outflow is then dominated by these warm surface temperatures which do not reflect colder inputs from upstream (Wetzel, 2001). In contrast the North Thompson River watershed exhibits a cooling effect of lakes due to the mediating effect of elevation. In this watershed many of the lakes are found at high elevation and near the headwaters where snow and glacial melt dominate, leading to a cooling of downstream temperatures (Fig. $\ref{fig:4}$). Although this pattern is somewhat confounded by a strong latitudinal gradient, the western portion of the North Thompson stands in contrast with greater thermal exposure potential despite its northern location. In this western region, lakes are characteristically more similar to the South Thompson River basin in network location and size, exerting a similar, albeit milder, influence. Together these findings demonstrate the complex mixture of landscape interactions filtering the climate and leading to heterogeneous stream temperature dynamics, organized by the network.

Warming global temperatures could alter the effects of current landscape features. As we found lakes at higher elevation were associated with cooler stream temperatures, possibly due to short residence times and the water’s cyrospheric origin, making these lakes cooling features for downstream habitat conditions (Dorava & Milner, 2000; Slemmons, Saros, & Simon, 2013). As global temperatures rise, the greater Fraser River basin is transitioning away from a snow-dominated precipitation regime towards an increasingly snow-rain hybrid (Kang, Gao, Shi, Siraj-ul-Islam, & Déry, 2016), common to similarly temperate regions around the globe (Hartmann et al., 2013). With less snow and ice on the landscape, our models suggest the thermal character of many locations will become warmer as the cooling effect of high elevation lakes are lost (Fig. $\ref{fig:4}$). Moreover, just as these cool-water reservoirs are depleting, climate change is producing hotter and persistently dry periods that are encouraging a greater risk of wildfire (Jolly et al., 2015). The loss of canopy cover along stream banks allows a greater degree of direct solar radiation on the waters surface, increasing stream temperatures (Pettit & Naiman, 2007). Although our study already identifies wildfire’s warming contribution to stream temperatures, we might expect an increasing degree of influence as wildfires become larger and more frequent on the landscape (Heyck-Williams, Anderson, & Stein, 2017), leading to a greater impact of fire on stream temperature and thus cold-water fishes (Williams, Isaak, Imhof, Hendrickson, & McMillan, 2015).

The analytical approach we employed advances the application of spatial stream network models so that they recreate the seasonal dynamics of temperatures on the river network, rather than just time-invariant summary statistics of temperature. Complimentary temporal and spatial models may correct for poor fits and result in more accurate and precise estimates in unknown locations. It’s largely understood that considering the spatial linkages between observations in a stream network improves prediction in unknown locations (Hoef & Peterson, 2010; Peterson et al., 2013). By leveraging shared information between estimates along the network and by refitting the model to all posterior values, we not only explore the full range of possible values at a given site but also draw more extreme values towards the mean. As a result, spurious temporal model estimates are properly down-weighted towards a broader consensus among data points, improving temperature estimates and subsequently migratory thermal exposure estimates. In this way, we not only provide fully probabilistic estimates of thermal exposure to extreme temperatures but also narrow the variance and improve certainty. Unfortunately, we build these models separately and were required to eliminate temporal parameter estimates in years where data was limited, but uncertainty was propagated across modeling steps. To avoid data loss, it might be possible to fit the temporal model simultaneously under a hierarchical spatial model, such that data informing temporal model parameters could be shared along the network, leading to better temporal fits and estimates in data poor years. Ultimately, our data collection and statistical methodology generalize the spatial heterogeneity of the thermalscape, providing insights into the most likely thermal experience and the relative challenge of different migratory routes. More spatially resolved data might improve the accuracy and precision of the model but would still not capture distinct cold-water refuges (e.g. ground water seeps), that salmon might use as thermal oases, leap-frogging through challenging areas to more suitable habitat (Fullerton et al., 2018). More complex models with much greater geomorphic resolution or direct observation studies utilizing internal tagging methodologies (e.g., Matthew L Keefer & Caudill, 2015) could be useful for identifying these habitat features.

We discovered that different Chinook salmon populations with different migration routes and timing had different thermal exposures. Many locations were consistently likely to reach 19$\text{\textdegree}$C, a temperature that can cause stress, and some locations and times exhibited elevated probabilities of 22$\text{\textdegree}$C, which can cause mortality in some populations (Richter & Kolmes, 2005). Salmon migrating through different parts of the watersheds were exposed to greatly different water temperatures. In the southern watershed, the downstream rivers that salmon must migrate through reached the highest temperatures of the whole watershed, such that these migratory corridors present one of the biggest thermal challenges to these adult salmon. In contrast populations in the northern watershed exhibited limited and localized thermal challenges most broadly isolated to the watersheds uninhabited western region (Fig. $\ref{fig:6}$). In addition, different run-timing groups of salmon were also exposed to different water temperatures with the mid-summer run in the South Thompson River watershed demonstrating the greatest exposure (Figs. $\ref{fig:6}$, S7). These data are a key step in understanding the thermal risks posed to different salmon populations at present day and the future. It is important to acknowledge that different populations of salmon have different thermal tolerances due to local adaptation (e.g., Eliason et al., 2011). It is also possible that rapid evolution or phenotypic plasticity in run-timing may allow salmon to keep up with climate change (Reed et al., 2011). Migrating salmon also may behaviorally thermoregulate by using coldwater refuges not capture in this study. Regardless, these systems appear extremely close to upper thermal thresholds for salmon suggesting small increases in summer temperature could lead to much higher thermal stress and poorer outcomes for these populations. Currently, thermal stress is primarily considered at the common migration corridor near the ocean outlet and on the spawning grounds as this is a particularly sensitive life history (Richter & Kolmes, 2005), but our work shows that thermal challenges exist in many locations of the river network. By considering the cumulative thermal challenge of migration, now and in the future, we may more effectively identify populations of greater thermal exposure and associated conservation concern than previously recognized.

The observed inter-annual variation of thermal exposure in the Thompson River basin suggest limited climatic shifts could result in increasingly persistently challenging stream temperature conditions for salmon in the future. Climate projections in the Fraser River basin predict a shift in precipitation from a snow to rain dominated regime, leading to earlier spring run-off and lower summer flows (Shrestha, Schnorbus, Werner, & Berland, 2012). Warming stream temperatures and reduced river flows have already been observed in the Fraser Basin (Morrison et al., 2002). During this study, the particularly dry winter of 2014 produced at least 100" less snow pack than the subsequent three years according to local ski resort records, and exhibited the warmest stream temperatures and the greatest probability of >22$\text{\textdegree}$C exposure (see Supp. Figs.). Meanwhile increased snowfall in 2015 and 2016 exhibited lower stream thermal exposure despite approximately 1.5$\text{\textdegree}$C warmer basin wide mean annual air temperatures. In combination, cool climates and normal winter snow fall in 2017 resulted in the lowest thermal exposure in this study. These observations suggest that punctuated climate extremes from inter-annual variation, driven by regional climate processes such as the Pacific Decadal Oscillation or El Nio, will drive inter-annual variation in thermal exposure conditions. As climate change progresses, rising mean annual air temperatures will reduce snowpack and increase glacial retreat thereby weakening the thermal buffering capacity of the watershed. Under such conditions it is reasonable to expect variability will lead to particularly acute stressful conditions in some years (Hague et al., 2011) that will systematically and abruptly act on some salmon populations more than than others, possibly negatively effecting diversity in the watershed (Beechie, Buhle, Ruckelshaus, Fullerton, & Holsinger, 2006; Ward, Anderson, Beechie, Pess, & Ford, 2015).

Our study has two main implications for the management of salmon. First, we identify populations that have higher exposure to potentially dangerously high, water temperatures. Such information can inform on-going risk assessment processes and conservation prioritization. For example, 7 Chinook salmon populations in the South Thompson River watershed were likely to experience persistent temperatures at or above 19$\text{\textdegree}$C during migration in some years (Fig. S7), with stressful conditions continuing onto the spawning grounds for 5 of those population (Fig. $\ref{fig:6}$). Potential management actions include precautionary intervention in both commercial and recreational fisheries for stocks that may be suffering from high thermal exposure (e.g., Macdonald, Patterson, Hague, & Guthrie, 2010). Second, we develop a predictive framework that connects watershed characteristics to temperature regimes. Thus, information such as this can help identify watershed features that may predispose systems to thermal risk. For example, while lakes are foundationally important habitats to salmon (e.g., sockeye salmon), they may render watersheds more vulnerable to excessively high temperatures. Moreover, it may illuminate regions where climate affects could exacerbate thermal exposure such as forests with increasing wildfire risk or the loss of glacial effects.

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