



SPATIAL AND TEMPORAL VARIATION OF WATER TEMPERATURE REGIMES ON THE SNOQUALMIE RIVER NETWORK¹

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ABSTRACT: Although mean temperatures change annually and are highly correlated with elevation, the entire thermal regime on the Snoqualmie River, Washington, USA does not simply shift with elevation or season. Particular facets of the thermal regime have unique spatial patterns on the river network and at particular times of the year. We used a spatially and temporally dense temperature dataset to generate 13 temperature metrics representing popular summary measures (e.g., minimum, mean, or maximum temperature) and wavelet variances over each of seven time windows. Spatial stream-network models which account for within-network dependence were fit using three commonly used predictors of riverine thermal regime (elevation, mean annual discharge, and percent commercial area) to each temperature metric in each time window. Predictors were strongly related ($r^2 > 0.6$) to common summaries of the thermal regime but were less effective at describing other facets of the thermal regime. Relationships shifted with season and across facets. Summer mean temperatures decreased strongly with increasing elevation but this relationship was weaker for winter mean temperatures and winter minimum temperatures; it was reversed for mean daily range and there was no relationship between elevation and wavelet variances. We provide examples of how enriched information about the spatial and temporal complexities of natural thermal regimes can improve management and monitoring of aquatic resources.

(KEY TERMS: river network; time series analysis; spatial modeling; thermal regime; wavelet decomposition; metric.)

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INTRODUCTION

Water temperatures fluctuate over time (Arismendi *et al.*, 2013) and along river networks (Fullerton *et al.*, 2015), playing critical roles as both drivers and indicators of riverine health. Conceptualizing a

unique time series of water temperature data at every point on a river network is a challenge; measuring or modeling the full suite of spatially and temporally variable data across a river network is daunting. One year of river temperature data from a single sensor measured every hour yields over 8,700 observations. Instead of directly analyzing a time

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series of this magnitude, it is common to aggregate each series into one or more summary metrics such as mean annual temperature, maximum summer temperature, or mean daily range during a particular period of interest. These metrics are theoretically chosen because they represent facets of the thermal regime that are known to have biological implications. For example, maximum temperatures induce lethal effects in fishes and other organisms (Brett, 1952). However, there are many other facets of the thermal regime that might also be ecologically important, for example, sudden increases in temperature that trigger juvenile outmigration from mainstems to cooler tributaries or sublethal thresholds that limit growth potential. We often make the implicit assumptions that we can infer (1) information about multiple biologically relevant facets of the thermal regime from one or two summary metrics; (2) details about the thermal regime in one part of the network from observations in another part of the network; and (3) relationships about key drivers of temperature observed in one time period or for one summary metric from observations in another time period or from models built on a different summary metric. Our goal is to explore the validity of these assumptions and the subsequent ramifications on management and monitoring of riverine thermal regimes.

The distribution of thermal regimes on the river network has clear biological relevance because organisms live in specific thermal niches (Magnuson and Destasio, 1996). Water temperature regulates the physiological processes of metabolism and growth that ultimately drive food webs, aquatic communities, and population dynamics. For example, increased water temperatures speed up metabolic rates of aquatic organisms and, therefore, alter the timing of life-history transitions (Beacham and Murray, 1990). Many species also have lethal thermal thresholds (Richter and Kolmes, 2005) which may vary over their life cycle; thus, a specific spatiotemporal thermal niche may be required to support some species. For example, imperiled freshwater mussels have upper thermal tolerance thresholds that limit, in particular, larval and juvenile life stages (Daraio and Bales, 2014). It is not only facets involving magnitudes, such as means and maximums, which have ecological relevance. A biological response to thermal variability (e.g., diel variation and seasonality) might be expected from first principles, but research is in the early stages (Arismendi *et al.*, 2013). Degree-day accumulation has been shown to drive the phenology of emergence and migration in many species, from aquatic insects to fishes (Ward and Stanford, 1982; McCullough *et al.*, 2009) and there are indications that thermal variance may impact the timing of life-history transitions (Steel *et al.*, 2012). Given the

spatiotemporal complexity of the thermal regime and the potential of biological responses to a variety of thermal cues, it is useful to understand the distribution of multiple facets of water temperature, for example, means, quick fluctuations in water temperature, winter minimums, or seasonal daily range, on river networks.

We distinguish here between facets, which describe the conceptual elements of the thermal regime that are of biological importance, and metrics, which are an attempt to quantify a particular facet. The distinction is necessary for two reasons. First, it forces clarity of thinking. For example, when we calculate mean temperature, what biologically important facet of the thermal regime are we trying to capture and is this the best metric to capture that facet? Or, if we are worried about juvenile Chinook salmon growth, what are the facets most closely related to food sources and growth? And second, we often do not know the exact threshold or the exact time frame linking temperature and biological response and so multiple metrics for a given facet are possible.

The natural and anthropogenic mechanisms driving many facets of temperature regimes are well understood and provide an explanation for how thermal regimes might vary over time and space (Caissie, 2006; Webb *et al.*, 2008). Climatic drivers, stream morphology, groundwater influences, and riparian canopy conditions, all affect stream thermal regimes (Caissie, 2006; Webb *et al.*, 2008). For example, smaller channels with greater groundwater flow may have similar springtime mean temperatures as compared to channels with little or no groundwater flow, but less daily variation (Arrigoni *et al.*, 2008). Small channels are also most sensitive to riparian shading, which decreases direct radiation and, through cooler air temperatures, reduces convective heat exchange (Johnson, 2004; Jones *et al.*, 2006). Larger channels have greater thermal inertia, both through the larger amount of water in the channel and through greater mixing with the alluvial aquifer (Poole and Berman, 2001). Human impacts such as agriculture, timber harvest, dams, urbanization, channelization, water withdrawals, and climate change along with a variety of natural disturbances threaten to alter not only mean temperatures but also the thermal structure of river networks (Schär *et al.*, 2004; Webb *et al.*, 2008). Dams may mute daily variation or shift seasonal patterns (Steel and Lange, 2007; Olden and Naiman, 2010), fires can increase the sunlight a channel receives and warm temperatures (Isaak *et al.*, 2010), and climate change is predicted to shift thermal regimes unevenly across river networks (Isaak *et al.*, 2010; Arismendi *et al.*, 2013). In fact, thermal disturbances rarely occur evenly across the river network or over time.

Mitigating anthropogenic and natural disturbances, managing aquatic species, and monitoring changing conditions across whole watersheds requires an improved understanding of thermal regimes on river networks, including biologically important facets of stream temperature such as variability during egg incubation or extreme events during migration periods. Commonly used predictors of mean annual temperatures and, occasionally, maximum temperatures include landform, elevation, channel slope, drainage area, mean annual flow, and annual summaries of air temperature regimes, as well as indications of human land use (Webb *et al.*, 2008; Mayer, 2012). These predictors often adequately describe mean annual temperature or summer temperature patterns (Isaak *et al.*, 2010; Ruesch *et al.*, 2012). However, their usefulness for predicting other facets of water temperature regimes has yet to be fully evaluated.

Capturing fine-scale temporal variability in temperature at discrete locations is possible using instream sensors; however, capturing the spatial variability in the full thermal regime at biologically relevant spatial scales (1-100 km; Fausch *et al.*, 2002) is much more costly to collect in terms of time and funding (e.g., Torgersen *et al.*, 2001). Thus, models are often fit to site-based measurements and used to extrapolate particular metrics, for example, mean summer temperature, to unsampled parts of the network (Benyahya *et al.*, 2007). The difficulty is that temperature measurements within a watershed are often spatially correlated. Sites may be longitudinally connected by flow or their watersheds and riparian areas may have similar climatic, topographic, land use, or land cover characteristics (e.g., Peterson *et al.*, 2006; Isaak *et al.*, 2010; Ruesch *et al.*, 2012). When data exhibit spatial autocorrelation, the assumption of independence is violated and spatial statistical methods must be used to make valid inferences and predictions on the river network. Traditionally, these methods were based on Euclidean distance (Cressie, 1993), which does not capture the unique branching structure of the river network, longitudinal connectivity, or streamflow volume and directionality. More recently, spatial stream-network models (SSNMs; Ver Hoef and Peterson, 2010) that use hydrologic distance (i.e., distance along the river network) have been developed, which account for flow connectivity (i.e., water flows from one site to another) as well as discontinuities that often occur in tributaries just upstream from river confluences (Cressie *et al.*, 2006; Ver Hoef *et al.*, 2006). SSNMs have been applied to single metrics of stream temperature in a handful of studies and, in these cases, accounting for spatial correlation in the data has substantially improved the accuracy of predictions at unsampled locations

throughout the entire watershed (Isaak *et al.*, 2010; Ruesch *et al.*, 2012). To the best of our knowledge, an investigation of the similarities and differences in spatial pattern for a suite of stream temperature metrics has not been undertaken.

We analyzed a spatiotemporal dataset collected in the Snoqualmie River, Washington, USA using SSNMs. We quantified the degree to which particular metrics could be explained by a constant set of landscape predictors, the relationships with those predictors, and the degree of additional spatial pattern in the metric. We explored the thermal regime within this watershed through two unique lenses: (a) metrics that describe biologically relevant facets of the thermal signal, and (b) a set of temporal windows that focus on both traditional seasons and also on salmonid life stages. Our analysis aimed to answer three questions:

1. Are there unique relationships between traditional predictors (elevation, mean annual discharge, and land development) and particular facets of the thermal regime?
2. How much of each facet of the water temperature regime can be explained by these traditional predictors and how much can be explained by spatial correlation with neighboring sites?
3. How do facets of the thermal regime vary during the year? Are relationships between facets of the thermal regime and traditional predictors consistent across time windows?

We conclude by exploring how our results increase our understanding of the structure and drivers of riverine thermal regimes, and by describing implications for management and monitoring.

METHODS

Study Area

Three main forks of the Snoqualmie River drain a 2,400 km² watershed on the west side of the Cascade Range, Washington (Figure 1). The three forks run through mostly forested public land owned by the Department of Washington Natural Resources and the United States Forest Service. Elevation decreases rapidly until the forks converge at the Three Forks Natural Area in Snoqualmie, Washington. Snoqualmie Falls, downstream on the mainstem, signals a transition toward greater human development including agricultural, residential, and commercial land use. Much of the Snoqualmie River floodplain

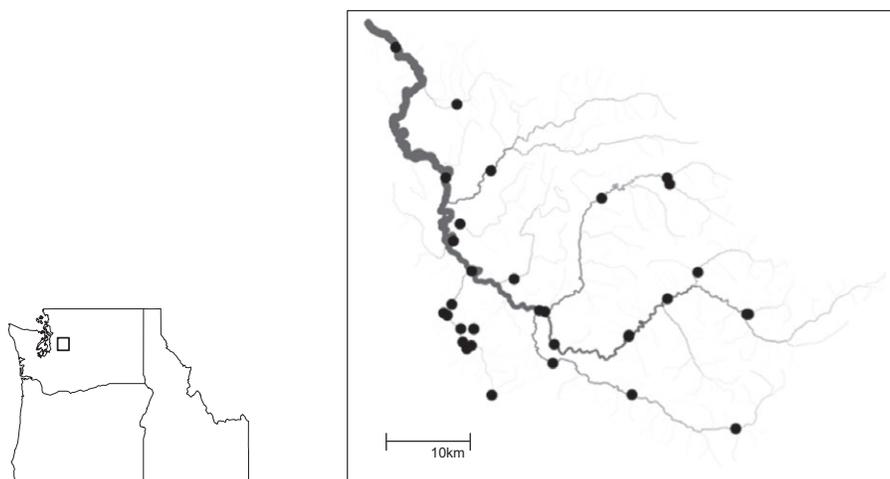


FIGURE 1. The Snoqualmie River, Washington, USA and Monitoring Locations (black circles). Streamflow is from east to west with the outlet into the Snohomish River in the northwest. River thickness is proportional to mean annual discharge, as estimated from drainage area.

lies within one of King County’s agricultural protection districts. Development gradually increases until the Snoqualmie River merges with the Snohomish River near Monroe, Washington. The Snoqualmie River is home to stocks of Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and winter steelhead (*O. mykiss*) salmon. In 2002, both Chinook and winter steelhead stocks in the Snoqualmie River were classified as “depressed” (Washington Department of Fisheries, 1993). Presently, Puget Sound Chinook and Puget Sound steelhead are listed as threatened under the Endangered Species Act.

Thirty-four temperature-monitoring sites (Figure 1) were chosen within the watershed, including multiple sites along the mainstem and in all major tributaries. Practical limitations of accessibility meant that sites had to be publicly accessible and within 1 km of a road. We note that the Raging River, a major tributary in the lower watershed, was intentionally oversampled, with 10 of the 32 observation sites chosen along the river and its tributaries, to enable analyses of the effects of scale on monitoring designs in future studies.

Data

Tidbit loggers by Onset (Bourne, Massachusetts) were installed in July 2011. Each logger was protected by a black PVC solar shield, anchored with rocks so as to remain underwater at low flows and to remain in the channel during high flows, and cabled to a nearby rock or tree via steel cable. Water temperature was recorded in degrees Celsius at each location every 30 min with an accuracy of $\pm 0.2^{\circ}\text{C}$.

Data for this analysis were retrieved in September 2012 but the network remains intact. During the 2014 data recovery, the water temperature at each site was also measured using an AquaTuff (Cooper-Atkins, Middlefield, Connecticut) instantaneous temperature sensor ($\pm 0.3^{\circ}\text{C}$) at the logger, along a 2 m radius from the logger, and in deeper areas within that 2 m radius.

Data were cleaned according to Sowder and Steel (2012) and the full-year dataset was summarized as thirteen metrics, describing several facets of the thermal regime (Table 1). The first six metrics are commonly found in the literature and capture mean temperatures, maximums, minimums, and variability.

TABLE 1. Stream Temperature Metrics Used in Our Analysis. The wavelet variance metrics decompose the variability of a time series into increasing temporal scales.

Metric Name	Description	Facet
AWAT	Average of all average weekly temperatures	Mean
MWAT	Maximum of all average weekly temperatures	Maximum
MWMT	Maximum of all weekly maximum temperatures	Maximum
mWAT	Minimum of all average weekly temperatures	Minimum
VAR	Empirical variance of the time series	Across-day variance
AvgDelT	Average daily temperature range	Within-day variance
Wv1.5 h	1.5 h wavelet variance	Within-day variance
Wv3 h	3 h wavelet variance	Within-day variance
Wv6 h	6 h wavelet variance	Within-day variance
Wv12 h	12 h wavelet variance	Within-day variance
Wv1 day	1 day wavelet variance	Across-day variance
Wv2 day	2 day wavelet variance	Across-day variance
Wv4 day	4 day wavelet variance	Across-day variance

We retain the most commonly used terminology for these metrics which reflects a history of first summarizing data at the weekly scale. In our analysis, data were first summarized within each day to provide a daily average and range. The seven daily averages within each week were then combined as the average weekly average temperature (AWAT) and averaged across the time window of interest. We note that this is equivalent to the average of the raw values within that time window except where there are missing data. Within a time window, the maximum of all weekly average temperatures (MWAT) and the minimum of all weekly average temperatures (mWAT) were retained as indications of high and low temperature patterns occurring over multiple days. Maximum weekly maximum temperature (MwMT), where the weekly maximum was calculated as the average of the seven daily maximum temperatures, was kept as a metric to describe extreme, possibly lethal, high temperatures. All observations were used to calculate the empirical variance (VAR) and the average of all daily ranges within the time window of interest (AvgDelT) was calculated as a second metric describing variability in water temperature.

Wavelet analysis was also used to decompose the temperature time series into the variability occurring at each of several time scales independently. A discrete wavelet transform is an orthonormal square matrix of filters that is pre-multiplied by a time series of data (Torrence and Compo, 1998; Percival and Walden, 2000). Wavelet variance decomposition can be thought of as describing the energy being put into each time scale of the time series. In this case, higher wavelet variances would be indicative of greater thermal fluctuations at particular time scales. Wavelet decomposition and a statistically similar procedure, Fourier transformation, have been used successfully in other studies to describe the complexities of riverine thermal regimes (Steel and Lange, 2007; Webb *et al.*, 2008; Maheur *et al.* 2015). We calculated the wavelet variance of our temperature series at 1.5 h, 3 h, 6 h, 12 h, 1 day, 2 days, and 4 days using the *wmtsa* package (Constantine and Percival, 2011) in R statistical software (R Core Team, 2012).

Full-year temperature metrics describe the annual thermal profile of sites on the river network, but organisms are known to respond to biologically important cues in different seasons. We examined seasonal differences in the thermal regime by comparing thermal patterns in summer, when most monitoring occurs, to those found in winter. Biologically relevant thermal cues may also occur at different times for different species; therefore, we subset the data for additional times to model temperature patterns during particular salmonid life stages. Altogether, we considered seven time windows: the full-year, summer and

winter seasonal-time windows, and the spawning and egg incubation time windows for winter steelhead and for coho salmon (Table 2). Spawning seasons were estimated based on expertise of local fisheries, biologists and the most recent available published descriptions (Washington Department of Fisheries 1993). The egg incubation season began at the midpoint of the respective spawning season and extended until, on average across all sites, 1,150 degree days (Steel *et al.*, 2012) had been accumulated. Given year-to-year variation in migration timing and variability across the network, these biological time windows (Table 2) are not intended to predict exactly when spawning and egg incubation are happening but, rather, to estimate a general time frame in which particular biological activities are likely to occur. For simplicity, we refer to winter steelhead as steelhead when defining spawning and egg incubation time windows.

Information describing connectivity, proximity, and directionality of river temperature sensors was needed to fit a SSNM. River network data from the NHDPlus database (Horizon Systems Corporation, 2007) were prepared using the Spatial Tools for the Analysis of River Systems (Peterson and Ver Hoef, 2014) and Functional Linkages of Water basins and Streams (Theobald *et al.*, 2005) custom toolsets for ArcGIS v9.3.1 (ESRI, 2008). Data preparation involved topologically correcting the river dataset and ensuring that all segments were digitized in the downstream direction. In addition, we “snapped” sampling and prediction points to the correct river segment. This ensured that routing occurred correctly along the network and that sampling sites coincided with the geographic information system dataset used to represent rivers. Landscape attributes for each reach were also obtained from the NHDPlus database (Horizon Systems Corporation, 2007) and assigned to each sampling and prediction point. We considered three traditional predictors of water temperature that

TABLE 2. Time Windows Considered in Our Study. Spawning windows are from the Washington Department of Fish and Wildlife Salmon Stock Inventory. Incubation windows were calculated from the midpoint of the spawning window until approximately 1,150 degree days had been accumulated.

Type	Time Window	Date Range
Seasonal	Full-year	August 20, 2011- August 19, 2012
	Summer	May 1, 2012-August 31, 2012
	Winter	November 1, 2011- March 31, 2012
Biological	Coho spawning	November 1, 2011- January 31, 2012
	Steelhead spawning	March 1, 2012-June 1, 2012
	Coho egg incubation	December 15, 2011-July 1, 2012
	Steelhead egg incubation	April 15, 2012-August 15, 2012

capture a range of information: elevation, which is highly correlated with both mean air temperature and precipitation in the Pacific Northwest; mean annual discharge, which represents the size of the stream and its ability to be influenced by solar radiation or shading and which is highly correlated with stream width and stream order; and percent commercial land use in the catchment area draining to the sample reach, which is associated with impermeable surfaces that alter runoff pathways and is highly correlated with other aspects of human development. We did not use air temperature directly which was available only as modeled estimates across the full spatial domain of our model.

Exploratory Data Analysis

We plotted each time series and visually inspected natural thermal regimes in each part of the river network for similarities and differences. We also explored correlations between metrics across the entire time series and within time windows of interest in order to (1) understand how our metrics of stream temperature were related to one another, and (2) determine whether any metrics capture all of the information about a thermal regime during a particular time window. High correlations would indicate that information is shared between metrics and that they are therefore somewhat redundant. Low correlations indicate that each metric contains relatively independent information about a particular facet of the thermal regime and one metric cannot be well estimated from the other. Correlations were calculated as simple Pearson correlation coefficients, and visualized using the R package *corrplot* (Wei, 2013).

Model

In traditional, nonspatial linear models the random errors are assumed to be independent. In a spatial statistical model, this assumption is relaxed and a covariance model is used to account for spatial correlation in the errors. Conventional covariance models represent the proximity between locations based on Euclidean distance. Such models may be inappropriate for data collected on river networks because they do not represent the branching structure of the network, longitudinal connectivity, streamflow volume, or flow direction. As an alternative, tail-up autocovariance models have been specifically designed for modeling river network data (Ver Hoef *et al.*, 2006; Ver Hoef and Peterson, 2010) and account for the unique characteristics of a river network.

The SSNM described in Ver Hoef and Peterson (2010) extends the standard linear model as:

$$Y = X\beta + z_u + \varepsilon, \quad (1)$$

where Y is a vector of the response (i.e., temperature metric), X is a matrix of predictors (for our models, these included elevation, mean annual discharge, and percent commercial area in the catchment), β is a vector of estimated coefficients, ε is a vector of independent normally distributed random errors, and z_u is the tail-up covariance model. A tail-up model is based on hydrologic rather than Euclidean distance, where spatial correlation is restricted to flow-connected locations (i.e., water flows from an upstream location to a downstream location). These types of models also include a spatial-weighting scheme to represent the disproportionate influence that upstream tributaries can have on downstream conditions, as well as discontinuities upstream of confluences. In this study, the spatial-weighting scheme was based on mean annual discharge provided in the NHDPlus dataset.

While the SSNM is flexible enough to include a mixture of covariances based on both hydrologic and Euclidean distance (e.g., Peterson and Ver Hoef, 2010), additional parameters must be estimated, and in this case it would require an additional two degrees of freedom. Isaak *et al.* (2014) recommend that at least 50 observation sites are needed to estimate the parameters for a full covariance mixture. We had a large number of measurements in our dataset, but were limited to 34 sites; as such, we decided to include only the tail-up covariance model, which has been shown to describe spatial dependency in other stream temperature studies (Ruesch *et al.*, 2012; Isaak *et al.*, 2014). An introduction to the use of spatial statistics and SSNMs for river management can be found in Isaak *et al.* (2014); a more technical description of the models can be found in Ver Hoef and Peterson (2010) and in Peterson and Ver Hoef (2010).

A SSNM was fit to each temperature metric and temporal window for a total of 91 (13 temperature metrics \times 7 time windows) independent models, each of which contained the same three predictors: elevation, mean annual discharge, and percent commercial area in the watershed draining to that reach. Again, these three predictors were chosen because they are commonly used in water temperature models and their mechanistic effects on at least some facets of the thermal regime are well understood. We used the same set of predictor variables in each of the SSNMs so that we could compare parameter estimates, model fit, predictive accuracy, and percent variance explained across metrics and time windows. Note that

our goal was not to identify the best model for each of the 91 temperature metrics. Instead, our intention was to determine whether a traditional model, that explains a large amount of variability in mean temperature over the full-year and which is expected to have a relatively strong predictive accuracy for mean temperature, can also be used to predict other facets of the thermal regime across multiple time windows of interest. Parameter estimates, standard errors, and variance components were estimated using restricted maximum likelihood and recorded. Predictions were generated at unsampled prediction sites to provide a semi-continuous view of stream temperature over the entire watershed and used for visualization purposes only. Standardized mean squared prediction errors and standardized bias were calculated using leave-one-out cross-validation (LOOCV), where each observation is withheld, a model is fit to the remaining data, and a prediction generated for the withheld observation. This provides a way to evaluate the standardized bias ($\text{mean}((\text{obs} - \text{pred})/\text{predSE})$) of the predictions and the mean squared prediction error ($\text{mean}(((\text{obs} - \text{pred})/\text{predSE})^2)$). All models and visualizations of predicted values were generated using the SSN package (Ver Hoef *et al.*, 2014) in R statistical software (R Core Team, 2012).

We compared parameter estimates to look for differences in the relationships between water temperature and traditional predictors across temperature metrics and across time windows. A 95% confidence interval was estimated for each predictor parameter and we explored whether or not these intervals overlapped in models of the same metric in different seasons. Finally, we decomposed the variability in each model into the percentage of variability explained by the predictors, the tail-up spatial correlation structure, and the residual variance (i.e., remaining unexplained variability); a process analogous to ANOVA in ordinary least squares regression.

RESULTS

Summarizing the Complexity of Natural Thermal Regimes

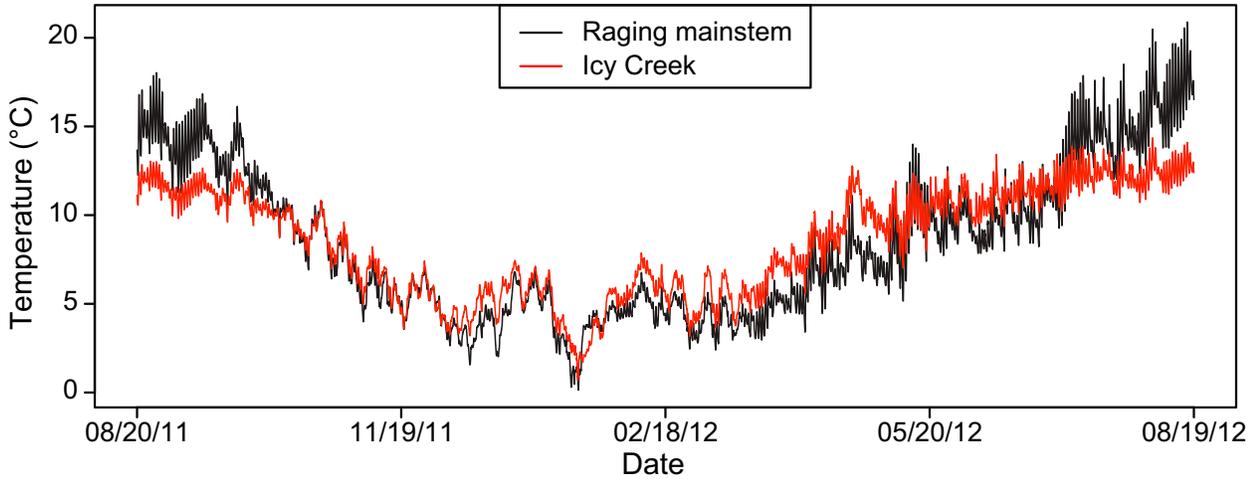
Observations of water temperature at locations near sensors indicated that the thermal regimes we measured were representative of the local area. Measurements taken 2 m upstream and downstream as well as those taken up to 2 m toward the center of the channel or at greater depths where possible never differed more than the accuracy of the sensor.

The thermal regime across our study sites showed strong seasonality; mean temperatures and daily variability in temperature were both smaller in winter than in the summer. Mean annual temperature did not capture the complexity of the thermal regimes observed on the network. For example, sites on the Raging River and its nearby tributary Icy Creek had similar annual mean temperatures at 8.4°C and 8.5°C, but summer temperatures on the Raging River were consistently higher and more variable than those observed for the aptly named Icy Creek (Figure 2a). Many such subtle differences were observed and no single metric, or pair of metrics captured all of the potentially biologically relevant complexity. Some pairs of metrics were highly correlated with one another; for example, there was a strong relationship between MWAT and MWMT ($r = 0.96$ in summer and 0.99 in winter) and the 6 and 12-h wavelet variance (1.00 in summer and 0.99 in winter). However, no one metric was so strongly correlated ($|r| > 0.5$) with all of the other metrics that we could assume it captured all of the information encoded in the suite of metrics (Figures 2b and 2c). In addition, the strength and direction of the correlation between metrics was not necessarily consistent across seasons. For example, VAR and AWAT were negatively associated in the summer (-0.71 ; Figure 2b) and positively associated in the winter (0.44; Figure 2c). This was also the case for MWMT and Wv1.5 h, which had a relatively strong correlation in summer (0.50), but only a weak negative correlation (-0.20) in winter.

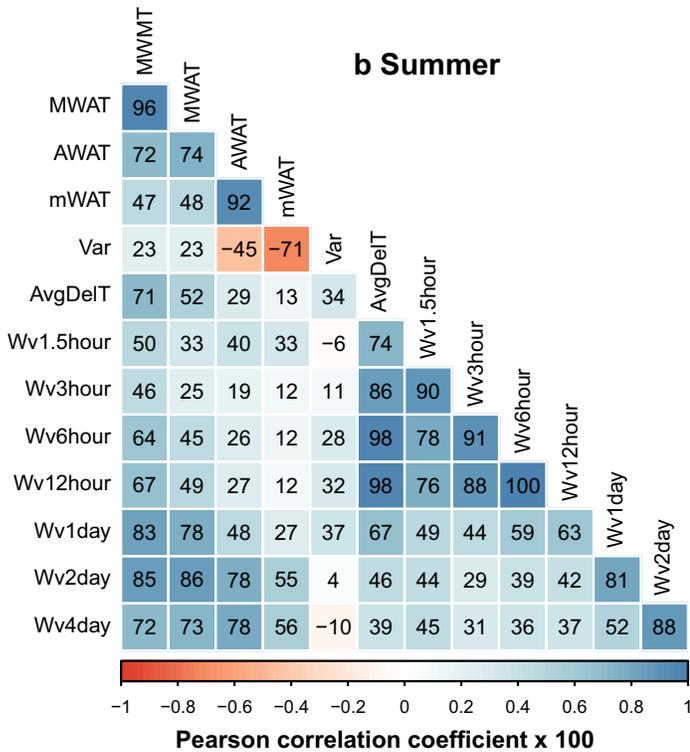
Spatial Stream-Network Model Evaluation

We built 91 models (7 time windows \times 13 metrics) using the same set of three traditional predictors of water temperature in order to compare models across facets of the thermal regime and across time windows; we evaluated models using LOOCV to estimate prediction bias and accuracy of the prediction standard errors. Standardized bias was small for all models, ranging from -0.045 to 0.062 (results not shown). The largest bias was observed for the variance metric (VAR), while the smallest bias for the traditional metrics was observed for AWAT and mWAT. All bias estimates for the wavelet metrics were very small (-0.008 , 0.12). Mean squared prediction errors were generally close to 1 for all metrics in all time windows (0.79, 1.09) (Table 3). Mean squared prediction standard errors for VAR ranged from 0.98 to 1.05. Again, AWAT performed particularly well in all seasons as might be expected.

a Example thermal regimes



b Summer



c Winter

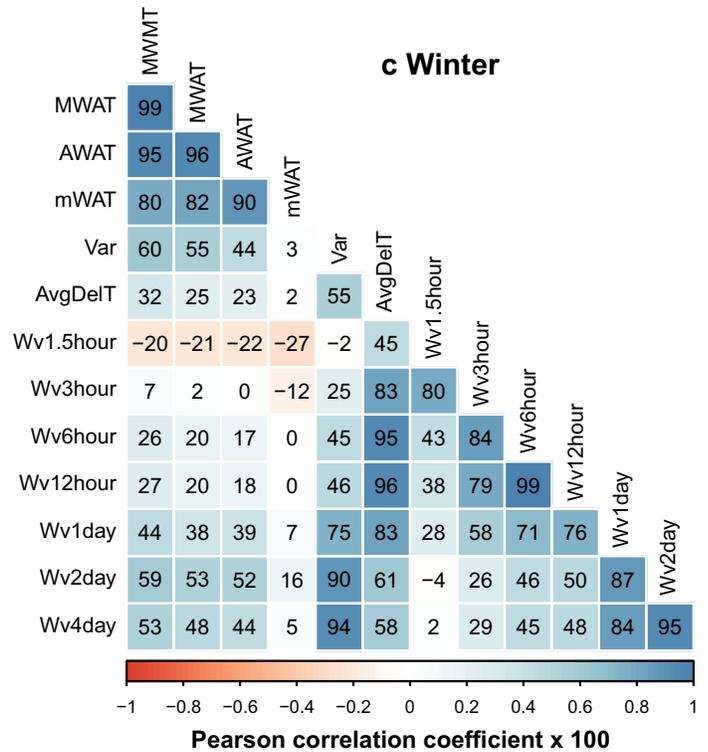


FIGURE 2. Variation in Multiple Facets of Stream Temperature Regimes across Seasons. (a) Thermal regimes for two nearby sites, the Raging Mainstem (black) and Icy Creek (red) that have similar full-year means, 8.4°C and 8.5°C, but different thermal profiles over the year. Correlations among the thirteen metrics for all sites for (b) summer and (c) winter. Numbers are Pearson correlation coefficients × 100. Color shading highlights the patterns in those values. Metric acronyms are defined in Table 1.

We also note that our models assumed normality of errors and applied a linear model to all temperature metrics. The models performed well despite this limitation. The standardized bias in predictions was low and the predictive standard errors were reasonably well estimated. There were no consistent departures from normality in the residuals of our models, except in the models of within-day wavelet variance where the largest residuals fell outside of what would be expected, given a normal distribution.

Spatial Patterns of Thermal Regime across Time Windows and Metrics

Our predictors are inherently spatial; therefore, differences in predictor coefficient estimates across time windows are indicative of variation in the spatial patterns of the thermal regime across these same time windows. We compared parameter estimates describing the relationship between temperature metrics and elevation, mean annual discharge, and

TABLE 3. Standardized Mean Squared Prediction Errors for (a) Traditional Temperature Metrics, and (b) Wavelet Variances Calculated Using Leave-One-Out Cross-Validation. When prediction standard errors are well estimated for a given season and time window, the standardized mean squared prediction error will be close to 1.

(a) Traditional Metrics							
	MWMT	MWAT	AWAT	mWAT	AvgDeLT	VAR	
Summer	0.99	0.95	0.94	1.06	1.03	1.01	
Winter	1.09	1.08	0.99	0.98	1.01	1.03	
Full	0.95	0.96	0.97	0.94	0.89	1.00	
Coho Egg Incubation	0.94	0.93	0.99	0.99	0.96	1.05	
Coho Spawning	1.03	1.04	0.99	0.98	1.04	1.01	
Steelhead Egg Incubation	0.98	0.98	0.94	1.01	0.92	0.98	
Steelhead Spawning	0.95	0.93	0.99	1.06	0.97	1.01	
(b) Wavelet Variances							
	Wv1.5 h	Wv3 h	Wv6 h	Wv12 h	Wv1 day	Wv2 day	Wv4 day
Summer	0.99	1.04	1.04	1.04	1.02	0.99	1.03
Winter	0.96	0.96	0.99	0.97	0.94	1.03	0.98
Full	0.91	0.80	0.87	0.89	0.96	1.01	1.00
Coho Egg Incubation	0.98	0.88	0.94	0.94	1.01	1.06	1.03
Coho Spawning	0.96	0.97	0.96	0.99	0.90	0.97	0.96
Steelhead Egg Incubation	0.85	0.79	0.91	0.92	1.01	1.02	1.03
Steelhead Spawning	0.96	0.89	0.96	0.96	1.02	1.05	1.04

commercial land use for models of the 13 metrics across seven time windows. For most metrics (AWAT, MWAT, MWMT, mWAT, VAR, Wv1.5 h, Wv6 h, Wv1 day, and Wv2 day), the confidence intervals of estimates for at least one of the parameters did not overlap when we compared parameters for multiple time windows. For traditional metrics, the elevation parameter estimates showed the most dramatic changes across time windows, while mean annual discharge and commercial land use parameters were relatively consistent (Table 4a). Models of the wavelet metrics exhibited a somewhat reversed pattern (Table 4b). For the wavelet metrics, elevation (Table 4b) and commercial parameter estimates (results not shown) rarely differed across time windows while confidence intervals for mean annual discharge parameters estimated for data from different time windows did not overlap in 9 of 21 possible comparisons for Wv1 day and 4 of the possible 21 comparisons for Wv2 day (results not shown).

We note that the model intercept exhibited the greatest number of differences across time windows; however, this parameter explains the thermal regime as summarized over the river network and does not describe the spatial trends in the thermal regime on the river network. We would, of course, expect the thermal regime over the whole river network to vary with time as water temperatures are warmer overall in summer than in winter. Instead, it is differences in the coefficients of the spatial predictors between time windows that describe shifts in the spatial distribution of the thermal regimes. For example,

seasonal differences in the elevation parameter estimates describe a steeper temperature gradient from the high-elevation headwaters to the lower-elevation mouth of the river in summer than in winter. An increase in 1,000 m of elevation was associated with a decrease of -6.2° in the winter and -9.8° in the summer (Table 4a).

The empirical variance (VAR) was the only metric to exhibit differences across time windows in all three parameters and this produced distinct spatial patterns on the network. In the summer and the steelhead egg incubation windows, VAR was positively associated with mean annual discharge and with elevation. In contrast, VAR was negatively associated with these same predictors during winter, coho egg incubation, coho spawning and steelhead spawning windows. These differences produced clear shifts in the spatial distribution of VAR at different time windows (Figure 3). Empirical variance was high in the large, mainstem and high elevation, headwater streams in the summer (Figure 3a) and steelhead egg incubation (Figure 3f) window. The opposite spatial pattern was observed in the other time windows, where VAR tended to be the highest in mid-size, mid-elevation streams. Because predictions for the VAR across the entire year smooth away these seasonal differences, variability appears highest in low elevation streams (Figure 3c).

We also observed differences in spatial patterns between predictions of different temperature metrics over the network, but within the same time window. To highlight these differences, we focus on one

TABLE 4. The First Rows Describe the Number of Pair wise Instances in which the 95% Confidence Intervals for the Intercept, Elevation, Percent Commercial Area, and Mean Annual Discharge Parameters Differed from One Another for a Given Metric (out of 21 possible differences) across the Seven Time Windows for the (a) Traditional Temperature Metrics and (b) Wavelet Variances. To explore observed differences in the elevation parameter, the following rows provide the estimated elevation parameter and standard error estimates for each combination of time period and metric. Estimates are given in °C/km for AWAT, MWAT, MWMT, mWAT, and AvgDelT and °C²/km for VAR and all wavelet variance metrics.

(a)						
Covariate/Season	AWAT	MWAT	MWMT	mWAT	VAR	AvgDelT
Intercept	17	16	16	14	14	14
Elevation	5	8	5	12	13	0
Commercial	0	0	0	0	2	0
Discharge	0	0	0	0	12	0
Summer	-9.81 (1.44)	-4.23 (2.04)	-6.35 (2.54)	-10.27 (1.28)	17.84 (4.37)	-1.09 (0.81)
Winter	-6.16 (0.59)	-5.04 (0.67)	-5.55 (0.69)	-4.3 (0.63)	-0.9 (0.46)	-0.49 (0.18)
Full	-7.55 (0.79)	-4.45 (2.07)	-6.39 (2.63)	-4.21 (0.67)	-1.91 (5.28)	-0.86 (0.45)
Coho eggs	-8.33 (0.88)	-11.57 (1.63)	-12.69 (1.84)	-4.15 (0.6)	-14.5 (3.36)	-0.76 (0.34)
Coho spawn	-5.54 (0.63)	-4.7 (0.68)	-5.12 (0.71)	-4.4 (0.63)	-0.85 (0.54)	-0.46 (0.17)
Steelhead eggs	-10.74 (1.43)	-5.17 (1.8)	-6.53 (2.15)	-10.17 (1.3)	11.3 (4.08)	-1.04 (0.73)
Steelhead spawn	-10.08 (1.13)	-13.68 (2.06)	-14.94 (2.12)	-7.43 (0.62)	-9.66 (2.55)	-1.14 (0.48)

(b)							
Covariate/Season	Wv1.5 h	Wv3 h	Wv6 h	Wv12 h	Wv1 day	Wv2 day	Wv4 day
Intercept	9	11	11	10	0	0	0
Elevation	4	0	0	0	0	0	0
Commercial	0	0	0	0	0	1	0
Discharge	0	0	1	0	9	4	0
Summer	-0.005 (0.002)	-0.039 (0.027)	-0.29 (0.26)	-0.3 (0.27)	-0.07 (0.03)	-0.2 (0.07)	-0.22 (0.08)
Winter	0.001 (0.001)	-0.002 (0.003)	-0.03 (0.02)	-0.04 (0.02)	-0.05 (0.02)	-0.21 (0.06)	-0.2 (0.08)
Full	-0.002 (0.001)	-0.021 (0.015)	-0.17 (0.13)	-0.18 (0.12)	-0.07 (0.02)	-0.25 (0.05)	-0.3 (0.08)
Coho eggs	-0.001 (0.001)	-0.011 (0.009)	-0.13 (0.08)	-0.15 (0.09)	-0.06 (0.02)	-0.34 (0.08)	-0.32 (0.09)
Coho spawn	0.001 (0.001)	-0.001 (0.002)	-0.02 (0.01)	-0.03 (0.02)	-0.08 (0.03)	-0.21 (0.06)	-0.2 (0.09)
Steelhead eggs	-0.004 (0.002)	-0.024 (0.022)	-0.22 (0.22)	-0.24 (0.23)	-0.09 (0.03)	-0.27 (0.08)	-0.38 (0.13)
Steelhead spawn	-0.002 (0.001)	-0.02 (0.014)	-0.24 (0.13)	-0.28 (0.14)	-0.07 (0.02)	-0.45 (0.11)	-0.42 (0.1)

biologically relevant time window, the steelhead egg incubation window. Notice that each metric has a slightly different spatial pattern (Figure 4). For example, models of maximum and mean temperatures, as well as of metrics representing variability at a day or longer time step, did not produce distinct differences in predictions on the mainstem *vs.* the tributaries (Figures 4a-4d). In contrast, predictions of temperature metrics describing variance within a day (Figures 4f-4j) on the high-flow mainstem exhibited lower variability than surrounding tributaries. Interestingly, the empirical variance (VAR, Figure 4) and average daily range (AvgDelT, Figure 4f), which represent across- and within-day variance showed a nearly inverse pattern to one another on the mainstem.

Relative Influence of Predictors vs. Neighboring Sites across Metrics and Temporal Windows

Decomposing the variation in each model into the proportion explained by the predictors, the network

correlation structure, and the residual variation allowed us to examine how each component contributed to model fit and look for trends across metrics and seasons (Figure 5). The covariate model (i.e., predictor variables) captured a majority of the variability in AWAT and mWAT in all seasons (Figures 5a-5c). For AWAT, these percentages ranged from 82% in the full-year to 69% in the summer. For mWAT, these percentages ranged from 74% in summer to 67% over the full-year. However, the contribution of the predictors was inconsistent across seasons for other traditional temperature metrics (MWAT and MWMT). For example, the predictors explained a greater percentage of variability in both MWAT and MWMT during winter months (Figure 5c) than in summer months (Figure 5b). Interestingly, we also noticed within-season differences when we compared wavelet models; the predictors explained a greater proportion of variability in the across-day wavelet variance than they did in the within-day wavelet variances or the daily range, with the exception of the winter Wv4 day model (Figures 5a-5c).

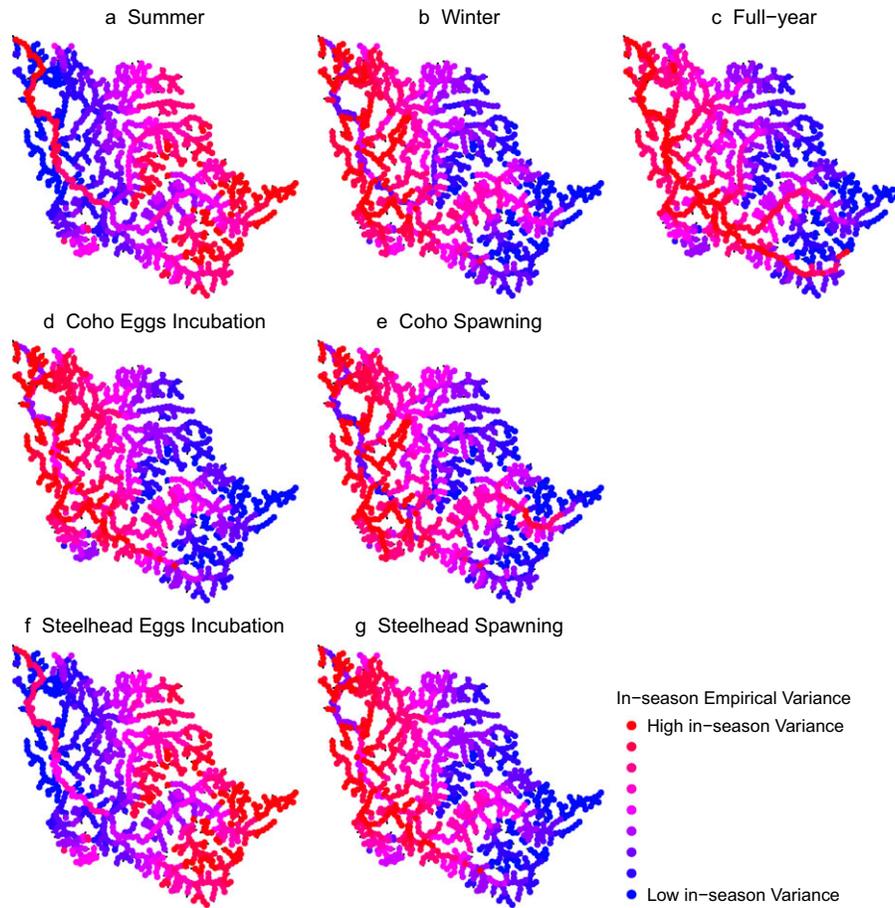


FIGURE 3. Relative Empirical Variance Predictions in the Snoqualmie River for Temporal Windows (a) Summer (May 1-August 31, 2012), (b) Winter (November 1, 2011-March 31, 2012), (c) Full-Year (August 20, 2011-August 19, 2012), (d) Coho Eggs Incubation (December 15, 2011-July 1, 2012), (e) Coho Spawning (November 1, 2011-January 31, 2012), (f) Steelhead Eggs Incubation (April 15-August 15, 2012), and (g) Steelhead Spawning (March 1-June 1, 2012).

After accounting for the variability explained by the predictors, the percentage of remaining variability explained by the network correlation structure also differed between metric and season. The network correlation structure is, essentially, the spatially structured component of the residual error, which can be described by the tail-up model after the predictors have been accounted for, e.g., the importance of information at neighboring sites. Not surprisingly, the network correlation structure accounted for little of the variability in traditional temperature metrics (AWAT, mWAT), which tended to have strong relationships with the predictors across all seasons. However, this was also true in the case of MWAT and MWMT in the full-year and summer, which had weaker relationships with the predictors (Figure 6). In each of these cases, most of the remaining variability was apportioned to the residual variance, indicating this variability could not be accounted for by the predictors or by information from nearby, flow-connected sites. The one exception in the traditional

metrics was VAR, where, after accounting for information in the predictors, the network correlation structure accounted for almost none of the variability over the full-year and summer, but nearly 52% of the remaining variability in winter (Figure 6).

The averages, maximums, and across-day wavelet variances, all followed a consistent pattern with a greater proportion of variability explained by the network structure in the winter than in the full-year or summer time windows. The network correlation structure rarely explained much, if any, of the across-day wavelet variances or the empirical variance (Figure 6). Again, the within-day variance metrics, including wavelet variances and daily range, followed a different trend. These metrics had a relatively large proportion of this variability explained by the network correlation structure in the full-year and summer time windows, with a smaller proportion in the winter time window. We note there are cases in which proportion of excess variability explained by the network spatial correlation model for the full-year of data or for

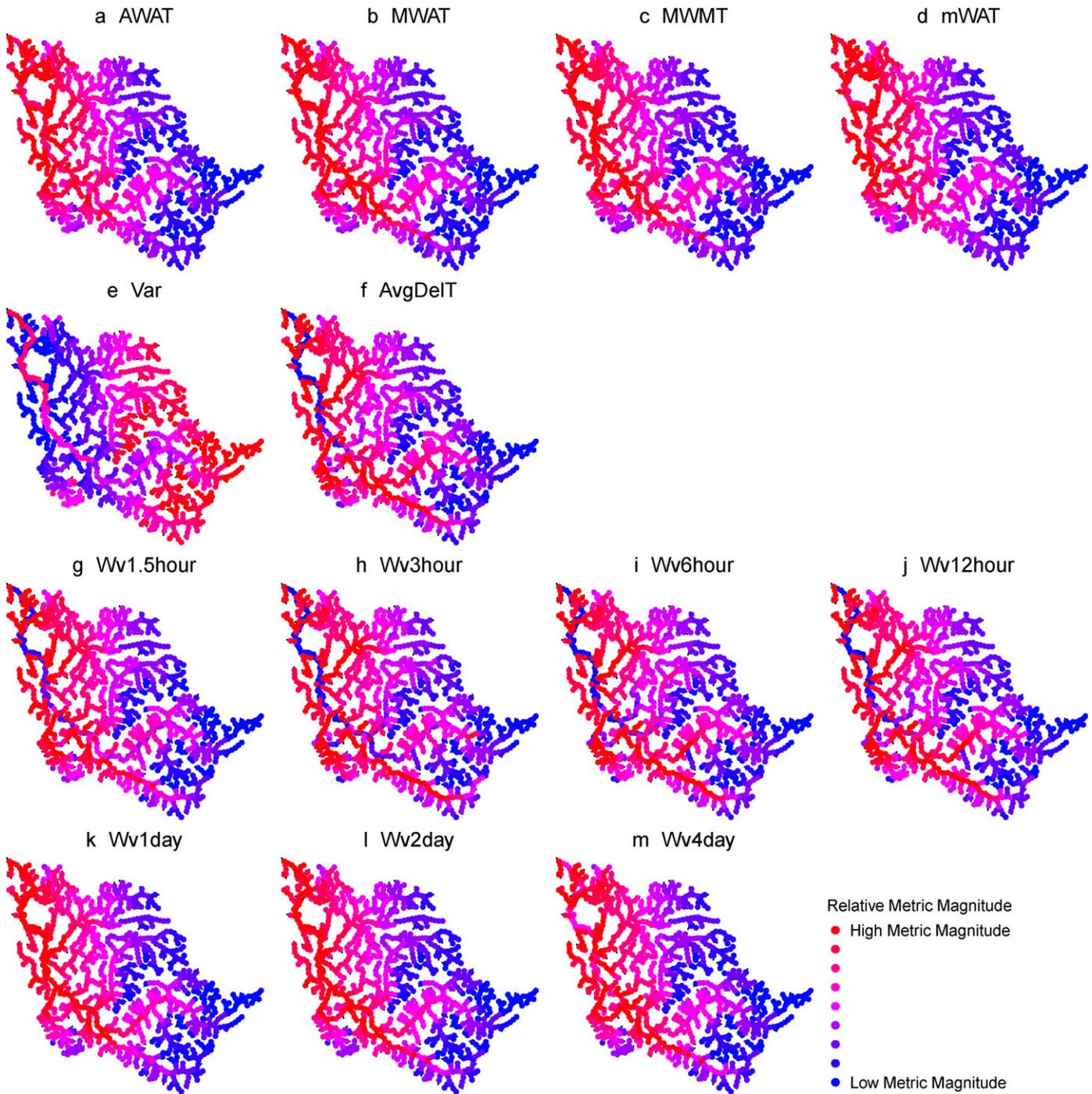


FIGURE 4. Stream Temperature Metric Predictions during the Steelhead Eggs Incubation Window (April 15-August 15, 2012): (a) AWAT, (b) MWAT, (c) MWMT, (d) mWAT, (e) VAR, (f) AvgDelT, (g) Wv1.5 h, (h) Wv3 h, (i) Wv6 h, (j) Wv12 h, (k) Wv1 day, (l) Wv2 day, and (m) Wv4 day.

summertime temperatures was fairly small, as was the case for MWAT and Wv1 day; yet, in the biologically relevant time windows such information about upstream and downstream temperatures was extremely useful for these same metrics. The importance of network spatial correlation also varied within a

particular type of biologically relevant time window (e.g., egg spawning periods) for the two different species. The network correlation structure explained 81% of the variance in mWAT during winter steelhead spawning, but only 28% when coho salmon are likely to be spawning (28%) (Figure 6).

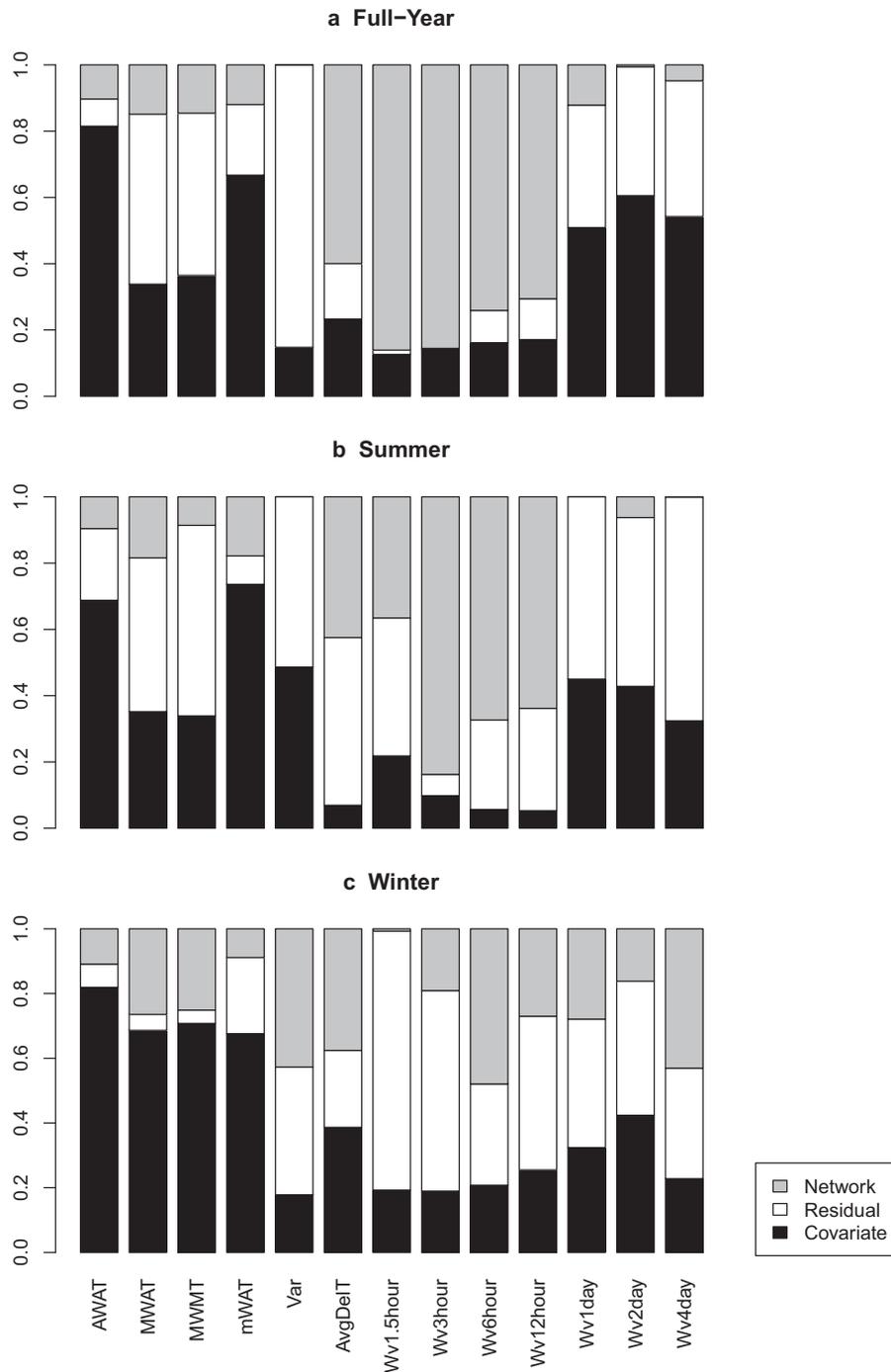


FIGURE 5. Variance Decomposition into Proportion of Variation Explained by the Predictors, Network Spatial Correlation Structure, and Residual Variation by Stream Temperature Metric for (a) Full-Year, (b) Summer, and (c) Winter Time Windows.

DISCUSSION

There is a great deal of research on the distribution and drivers of mean stream temperature on stream networks, often in summertime. However, fishes and other aquatic organisms do not experience mean temperatures. Instead, they live in microclimates that are

highly variable and may be dramatically different from those that are nearby in space or those that they might experience with even a small phenological shift in time (*sensu* Potter *et al.*, 2013). We demonstrate here that conclusions about the spatial distribution and drivers of other facets of the thermal regime, such as minimums or variability, cannot be extrapolated from the spatial distribution and drivers of mean

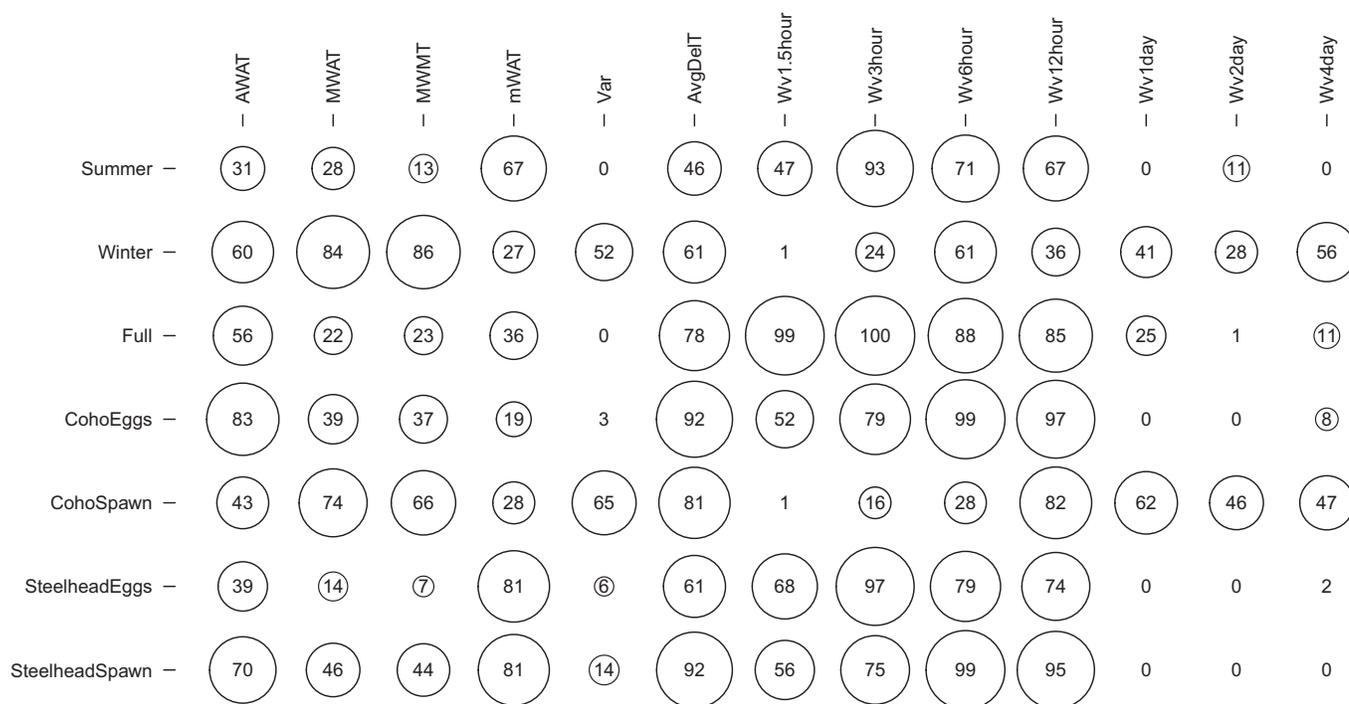


FIGURE 6. The Percentage of Excess Variability Explained by the Network Spatial Correlation Structure after Accounting for Variability Explained by the Predictors for Each Time Window and Metric Pair. Numbers represent the percentage, and the area of each circle is proportional to that percentage.

temperature. Additionally, the spatial distribution of any facet of the thermal regime during one time period may be quite different from the spatial distribution of that same facet during another time period. Thermal patterns across the network, correlations among temperature metrics, and relationships between temperature metrics and common predictors of water temperature cannot be extrapolated from, for example, summertime data to other time windows such as spawning seasons, migration windows, or egg incubation periods. Essentially, the thermal regime on the Snoqualmie River is not simply warmer at low elevations or warmer in summer. Much complexity of thermal networks can then be understood as arrangements of facets, each of which can be modeled independently on the network and for time windows of interest within the annual cycle.

Spatial Patterns of Thermal Regime across Time Windows and Metrics

There were clear spatial patterns in all temperature metrics (e.g., Figure 4) and, for most metrics, these patterns were inconsistent across time windows (e.g., Figure 3). Thus, information about one facet of the thermal regime (e.g., average temperature or across-day variability) in one part of the network may not be transferable to other parts of the network or other

time periods. Our findings are consistent with other research indicating high variability in river and even air temperature regimes over space and variation in the pattern of that variability across seasons. In western Oregon, for example, headwater streams displayed high spatial variability with greater spatial variability during summer and during cold, dry winter periods than in spring, fall, or warm, wet winter periods (Jason Leach, Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden). Within these same sites, researchers observed considerable spatial heterogeneity at scales smaller than those provided by regional stream temperature models; recognizing this variability will be important when predicting future distributions of aquatic species. Minder *et al.* (2010) explored the spatial variability in air temperature regimes, often highly correlated with stream and river temperatures. They found surprisingly large local differences in air temperature patterns across the Cascade Mountain range. For example, air temperatures on leeward sites had a stronger winter daily variability than those on windward sites. They also found that particular facets of the air temperature regime, maximums and minimums, had different relationships to elevation (lapse rates) from each other and across seasons so that many details of air temperature patterns could not simply be extrapolated from one location to another.

Spatial heterogeneity in thermal regimes across river networks has important implications for aquatic habitats and species. Winter steelhead, for example, tend to spawn in the lower gradient reaches of the watershed and may rear for up to two years in nearby tributaries, upstream tributaries, or mainstem habitats. Management of winter steelhead therefore requires a clear understanding of the juxtaposition of thermal habitats. In the Snoqualmie River, both maximum temperatures and minimum temperatures are distributed quite differently when winter steelhead are spawning *vs.* when winter steelhead eggs are incubating (Figure 6). Considering just the steelhead egg incubation window, there are also fairly dramatic differences between the spatial distribution of average (AWAT) temperatures *vs.* daily range (AvgDelT)(Figure 4). A complete understanding of winter steelhead thermal habitat, from holding to egg incubation to juvenile rearing, cannot be gained from temperature data summarized as just one metric, collected only in the more accessible tributaries or only in the downstream portions of the river network, or from data collected within a single season. In this case, for example, managing for multiple facets of the thermal regime during each phase of winter steelhead freshwater residence could lead to alternative spatially explicit management recommendations as compared to managing for any one facet or any one life-history stage.

Relative Influence of the Predictors and the Spatial Correlation Structure across Metrics and Temporal Windows

Much research has focused on the complex and diverse set of forces that drive stream temperature throughout a watershed. Many of these relationships are well understood (Caissie, 2006; Webb *et al.*, 2008). For example, streamflow, either mean annual discharge or estimates of baseflow, is an indicator of the amount of thermal storage capacity a reach has, as well as the speed with which thermal energy is transmitted downstream (Poole *et al.*, 2004; Caissie, 2006). Percent commercial land use, related to the amount of impervious area and human development, affects the interaction between the reach and alluvial aquifer (Brown and Vivas, 2005; Caissie, 2006; Somers *et al.*, 2013). Elevation is often used as a proxy for both air temperature and the amount of precipitation in mountainous regions (Eder *et al.*, 2005; Hong *et al.*, 2005), both of which have been shown to be strongly related to stream temperature metrics (Mayer, 2012). We found that these same drivers, while highly correlated with mean temperatures in the Snoqualmie River are not particularly useful for

predicting or understanding some other facets of the thermal regime. These findings open up the possibility that other mechanisms may be controlling other facets and initiates a better understanding of the processes creating complexity in thermal regimes. Identification of which land management activities are associated with shifts in particular facets of the thermal regime builds a foundation for a more nuanced understanding of how development and climate change may affect particular species across life stages.

Quantifying correlations between particular facets of the thermal regime and landscape conditions allows us to predict biologically relevant metrics at unobserved locations (Ruesch *et al.*, 2012; Isaak *et al.*, 2014) and to explore the degree to which aquatic communities are structured by complex thermal cues. Understanding amphibian distributions, for example, may require an understanding of maximum temperatures. Previous work indicates that the probability of both larval and adult tailed frog, *Ascaphus truei*, presence is strongly related to maximum temperatures (Dunham *et al.*, 2007) which have a much weaker relationship to elevation in summer than in the earlier parts of the year (Table 4a). Exploring the effects of wildfire might also require a consideration, in particular of maximums (Dunham *et al.*, 2007). Correlations between landscape condition and particular facets of the thermal regime allow us to make predictions of these facets of water temperature across large spatial extents and within particular time windows. Such predictions can help us refine estimates of how river thermal regimes are likely to respond to future climatic conditions. For example, Arismendi *et al.* (2013) observed that daily minimum temperatures in winter and spring were particularly responsive to regional climatic conditions.

We found that relationships with elevation, considered a very good predictor of air and water temperature, can vary substantially by metric and time window. Mean winter temperatures (AWAT) are not only colder in general, but vary less by elevation than mean summer temperatures (Table 4a). The seasonal influence of elevation or the potential effects of climate change across a range of elevations may be more involved than a simple uniform shift. A particularly important finding of our work is that the assumption of a uniform shift in stream temperatures with elevation, across facets of the thermal regime or seasons, is a poor one. Similar results have been found for air temperature regimes (Minder *et al.*, 2010).

Although our predictor model could explain spatial patterns of mean temperature across the river network, it could not explain spatial pattern in all facets

of the thermal regime (Figure 5). Our predictor model, for example, could not explain within-day variability, as captured by any of the four within-day wavelet variance metrics, in any of the time windows; however by using SSNMs we identified a strong spatial pattern in these same metrics. We conclude that there are spatially structured processes driving within-day variability which are not well represented by the predictors traditionally used to model mean temperature. Although we can identify spatial structure in residuals of the within-day variability models, we do not know what the specific process driving that spatial structure might be. The process could be related to direct solar radiation or riparian shading (Johnson, 2004; Jones *et al.*, 2006) but more work is needed to better explain and understand spatial patterns of within-day variance.

While the amount of spatial autocorrelation in the metrics varied by metric and time window, additional variability was accounted for by the SSNMs for every facet of the thermal regime in at least one time window (Figure 6). Our results are similar to other studies which have found that SSNMs substantially increase the accuracy of mean and maximum temperature predictions when compared to more traditional models that do not account for the spatial structure in the data (Peterson *et al.*, 2006; Ruesch *et al.*, 2012; Isaak *et al.*, 2014).

Building a Better Understanding of Riverine Thermal Regimes

Riverine thermal regimes, like many complex signals, can be classified by the frequency, variability, duration, magnitude, and timing of particular events. Maheu *et al.* (2015), for example, were able to classify 135 long-term records of stream temperature regimes across the conterminous USA into six distinct types based on only magnitude, amplitude, and timing characteristics using Fourier transformations. We have shown that, even within one basin, water temperature patterns at particular locations can differ from one another with respect to magnitude (averages, minimums, and maximums) and also with respect to variability (variance, daily range, wavelet variances at multiple time scales). Consideration of fluctuations and variability, though less common than studies of magnitude, also yields important ecological insights (Gaines and Denny, 1993). By combining results of all our models, each describing a facet of water temperature, we begin to build a picture of riverine thermal regimes over space and time.

In our study watershed, summer is generally more variable than winter, with spatial trends that are easier to detect and strong elevational gradients in

water temperature. Common predictors of water temperature (i.e., elevation, mean annual discharge, and land use) can be excellent predictors of mean temperatures and even medium-scale variability in stream temperature; however, they may not be strongly correlated with fine-scale, within-day thermal fluctuations. Interestingly, metrics representing fine-scale temporal fluctuations are spatially correlated with each other on the network and somewhat muted along the mainstem. Our best predictions of those fine-scale fluctuations are therefore based on nearby observations, found either up or downstream, rather than external predictors. Minimum temperatures exhibit much more spatial structure in summer than average temperatures, and much less spatial structure than average temperatures in winter. By enabling an understanding of, say, where in the watershed minimum temperatures might be increasing or decreasing with land management and climate change, we provide one of the necessary pieces of information for estimating future phenology of, say, aquatic insect emergence timing. Eventually, this type of understanding can enable predictions about, for example, which suites of areas might support particular emergence timing opportunities.

Management of any species requires spatial predictions of suitable habitat. For fishes and most aquatic organisms, such spatial predictions must be built on the particular facets of the stream thermal regime that limit the species of concern as well as its competitors and on a clear understanding of the local and landscape drivers of those facets of the thermal regime. Isaak *et al.* (2015), for example, developed a framework for identifying future refugia of native fish based on predictions of August mean temperature. In order to be able to use metrics that represent particular facets of biological interest, some understanding of their correlation with common drivers of thermal regime such as elevation, drainage area, and land development as well as an understanding of how they shift on river networks and between different time windows is necessary. Our results have demonstrated that we cannot assume that our models of the local and landscape drivers of, say, mean or of maximum temperatures, will be sufficient to understand and predict other facets of the thermal regime. Within-day fluctuations, for example, are a part of the microclimate experienced by individual organisms, potentially related to phenology of life-history timing or other sublethal effects. The models that worked well to predict mean temperature in this watershed did not work well to predict these within-day fluctuations. Conceptual frameworks that allow this more nuanced definition of thermal habitat will provide a better platform for understanding and managing thermally sensitive organisms.

Limitations

As in any study, our ability to generalize results and make inferences about other watersheds is limited by our sampling design, dataset, and the models considered. Because the predictive ability of SSNMs depends on spatial autocorrelation in the dataset, the sampling design is expected to have a strong impact on that predictive ability. River temperature tends to have strong patterns of spatial correlation (Ruesch *et al.*, 2012; Isaak *et al.*, 2014) and we believe that our survey design adequately captured the branching structure of our network. Som *et al.* (2014) found that a spatially balanced survey design, similar to the one used here, provides reasonably accurate parameter estimates for the predictors and the tail-up covariance structure. Our leave-one-out cross-validation analysis also indicates reasonable model fits and predictive abilities (Table 3). Nevertheless, we only focused on one river network over a period of one year. As we continue to collect temperature data, it will be possible to compare these results to those of subsequent years in the Snoqualmie as well as other watersheds.

Monitoring Implications

Managers need a way to measure, describe, and conceptualize the complexity in riverine thermal regimes that occurs across space and time. Managing or monitoring for one or two metrics is likely to be insufficient (Poole *et al.*, 2004). Looking at a variety of descriptors provides a window into the biologically relevant complexity of water temperature patterns (Arismendi *et al.*, 2013). By combining both traditional and nontraditional metrics, over particular time windows of interest, a manager can target the facets of a thermal regime that are of the most biological significance. For example, it may be important to understand the distribution of temperatures above a threshold during a particular insect life-stage or the distribution of thermal minima with warming air temperatures.

In fact, by using a suite of temperature metrics on the whole network over several time windows, our analyses provide an efficient and holistic view of thermal regimes; allowing managers to explore multiple facets of the thermal regime using scarce monitoring resources. Using SSNMs, we can also predict and visualize many facets of that complex, spatiotemporal thermal regime simultaneously (e.g., Figures 3 and 4). Such predictions and visualizations are useful for siting restoration actions, public access points, conservation areas, and monitoring stations.

In general, our results argue for full-year monitoring of riverine thermal regimes (Poole *et al.*, 2004;

Arismendi *et al.*, 2013). Often only one metric is used to evaluate the temperature regime of a river. For example, the Environmental Protection Agency Region 10, which includes Washington State and the Washington State Department of Ecology, set recommendations for upper limits on stream temperatures for salmonids based on MWMT (Washington State Department of Ecology, 2002; U.S. Environmental Protection Agency, 2003). While high MWMT corresponds to lethal and sub-lethal effects in salmonids (Richter and Kolmes, 2005), evidence also suggests that variance plays a role in determining lethal and sub-lethal events, stress, and the phenology of key life-history transitions (Steel *et al.*, 2012). We found that in the Snoqualmie River, there is little correlation between MWMT and the suite of temperature metrics used to describe variability (Figure 2). Instead of focusing on maximum temperatures, multiple metrics may be required to design water quality standards that maintain biologically and ecologically relevant facets of the thermal signal (Poole *et al.*, 2004) as well as monitoring programs for facets of the thermal regime that are likely to be most sensitive to changes in future climate (Arismendi *et al.*, 2013).

CONCLUSIONS

Water temperature regimes on a river network are an important ecological resource (Magnuson *et al.*, 1979), controlled by a variety of seasonally shifting factors across the entire watershed. By modeling multiple temperature metrics in both traditional time windows and during key periods in the life cycles of river biota, we provide a framework for describing and predicting some of the richness of river temperature regimes. Our results for the Snoqualmie River demonstrate that (1) we cannot assume a uniform shift in stream temperature with elevation or season; (2) spatial pattern in one facet of the thermal regime may differ substantially from spatial pattern in another facet of the thermal regime; (3) some facets of the thermal regime have more spatial structure than other facets of the thermal regime; and (4) the amount of spatial structure in any facet may shift over time. Using models, such as the ones presented here, that target particular facets of the thermal regime and that account for the spatial structure of river networks, restoration and mitigation efforts can more precisely focus management objectives on a species, on a facet of the thermal regime, or on the natural thermal complexity of river systems. As policy makers seek to mitigate the effects of natural and anthropogenic disturbances on stream temperatures

now and into the future, such tools will enable improved understanding of how unique facets of the thermal regime and species-specific microclimates may respond to mitigation efforts, restoration actions, and future climates.

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