Characterization of Stream Thermal Regimes in the Matanuska-Susitna Basin, Alaska

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Introduction

Complexity is an important attribute of salmon habitats. It creates options for salmon to balance the costs and benefits associated with variation in conditions, such as food abundance, predation risk, flow, and temperature and allows them to meet their changing needs during incubation, rearing, and spawning. Additionally, habitat complexity at regional scales drives life history and phenotypic diversity among salmon populations (Blair et al. 1993, Kovach et al. 2013b, Lisi et al. 2013). This diversity, coupled with variation in the ways that different habitats filter regional environmental conditions, results in asynchronous population dynamics that stabilize fisheries by dampening year-to-year variation in regional salmon returns (Schindler et al. 2010).

Variation in water temperature is a key feature of habitat complexity that supports the productivity and persistence of salmon and other cold-water fishes. Salmon utilize thermal heterogeneity through a variety of behavioral responses to optimize metabolic and growth rates. For instance, salmon move among habitats of different temperatures to track shifts in seasonally abundant food resources (Ruff et al. 2011) or to maximize growth rates during periods of high food abundance (Armstrong and Schindler 2013). To avoid stressful periods of warm water temperatures, salmon seek out thermal refugia - areas within a stream that are persistently colder than adjacent areas - thus allowing them to remain in streams that would otherwise be unsuitable (Torgersen et al. 1999, Ebersole et al. 2003, Sutton and Soto 2012).

Recent monitoring efforts have improved our understanding of weekly average and maximum summer temperatures in salmon streams across the Matanuska-Susitna (Mat-Su) basin. Some streams remain cool all summer, while other attain daily maximum temperatures that routinely exceed thresholds regarded as deleterious for spawning, egg incubation, and fry emergence (13°C); and for rearing juveniles (18°C). During warm summers, some streams reach temperatures that may be harmful to migrating adults (>20°C) (U.S. Environmental Protection Agency 2003, Mauger et al. 2017). Streams draining low-elevation landscapes are likely to have the warmest summer temperatures and are also projected to warm the most as climate continues to change (Mauger et al. 2017).

While simple descriptors like averages and maximums are helpful to understand the range of temperatures experienced by salmon, these metrics do not capture the frequency, duration or timing of temperatures driving thermal heterogeneity. For example, streams with similar maximum temperatures may be ecologically quite different due to differences in the daily range of temperatures or the timing at which maximum temperatures occur. For salmon and other aquatic organisms, stream thermal “regimes” that characterize magnitude, frequency, duration, timing, and variability are likely to be more biologically relevant than simple temperature thresholds (Arismendi et al. 2013, Steel et al. 2017).

The physical processes controlling stream temperature occur over a hierarchy of spatial and temporal scales (Kelleher et al. 2012). Stream temperature models often rely on interactions between climate, topography, and landcover to describe patterns of temperature variation and act as proxies for the thermal heat budget (Caissie 2006). At the highest level, atmospheric energy fluxes such as air temperature and precipitation are used to describe climatological and hydrological controls on stream temperature. Air temperature has strong direct (e.g., sensible heat transfer and long-wave atmospheric radiation) and indirect relationships (e.g., snowmelt and glacier inputs) with stream temperature and is commonly used as a proxy for net radiation effects (Webb et al. 2008). Hydrologic controls can be described by seasonal contributions from rain, snowmelt, lakes, wetlands, and groundwater in addition to discharge and its effect on heat capacity. In regions where snowpack is an important hydrologic control, April 1st snow water equivalent and spring air temperature are used to relate winter snowpack accumulation to the magnitude and timing of spring freshet (Pederson et al. 2011). Inflows and outflows from lakes, glaciers, and wetlands can strongly influence stream temperatures and are best represented by their proximity and cumulated effects within a given catchment (Poole and Berman 2001). At the catchment scale, topography plays a key role in defining discharge patterns and stream reach geomorphology (Frissell et al. 1986). Stream reach characteristics (i.e., gradient, width, aspect, groundwater, and riparian vegetation) affect thermal variation at the finest scale and have the potential to mediate thermal warming effects of the upper hierarchies.

The goals for this project were to: 1) characterize the diversity of thermal regimes among streams in the Mat-Su basin using existing empirical temperature data; 2) investigate the drivers of these thermal regimes using variables that represent stream geomorphology, watershed landcover and climate; 3) evaluate potential future changes in thermal regimes and implications to habitat conservation strategies and priorities for Mat-Su basin salmon populations; and 4) compare thermal regime diversity within one watershed to diversity across the Mat-Su basin.

Methods

Study Area

The study area consists of the Matanuska and Susitna watersheds and adjacent smaller drainages, all of which flow into northern Cook Inlet (Figure 1). Collectively known as the Matanuska-Susitna (Mat-Su) basin, its perimeter is defined by the rugged arc of the Alaska Range to the west and north (including Denali, North America’s highest peak) and the Talkeetna and Chugach ranges to the east. The basin’s climate ranges from continental to transitional, with mean annual temperatures between - 6 and - 3°C and annual precipitation between 51 and 76 cm (Brabets et al. 1999). Precipitation is greatest in the mountains, much of which falls as snow during winter. The basin’s extensive lowland areas are covered by a mosaic of ponds, wetlands, and black spruce (*Picea mariana*) forest and the uplands support mixed forests dominated by white spruce (*P. glauca*) and paper birch (*Betula papyrifera*, Nowacki et al. 2001). Mountain slopes are covered with dense shrub communities, giving way to ericaceous communities, rock, snow fields, and extensive glaciers at higher elevations. The basin supports substantial wild runs of all five North American Pacific salmon (*Oncorhynchus* spp., Johnson and Coleman 2014) that are harvested in commercial, personal use, subsistence, and sport fisheries. The basin’s major rivers drain alpine glaciers that contribute high sediment loads and turbidity while many of the tributaries and smaller watersheds have little or no glacial influence and are therefore clear (Dorava and Milner 2000). Extensive unconsolidated deposits from past glaciation underlay much of the basin (Miller and Whitehead 1999) and enhance fish habitats by contributing spawning gravel and groundwater. Most of the basin is free from anthropogenic watershed disturbances, although human population and associated urban and suburban development is rapidly expanding around Wasilla, Palmer, and several smaller communities. The Mat-Su Borough is the fastest growing (3.4% annual growth for last 25 years) and second largest borough in Alaska with over 100,000 residents (Sandberg 2016).

Monitoring Sites

Stream temperature data were collected at monitoring sites located in the Mat-Su basin (Figure 1). We used data from monitoring efforts conducted by the U.S. Geological Survey (USGS), Cook Inletkeeper (CIK), and Aquatic Research and Restoration Institute (ARRI). Data were provided as quality-controlled daily maximums, minimums, and means (Appendix A). Duplicate sensors were identified for five site locations. For these monitoring sites, we compared data collected from the same year and removed one year to avoid duplicate site-years. We screened data to ensure that each site-year included 90% of days in the June, July, and August period.

The final dataset included 248 summers of stream temperature data from 68 sites. Data were collected from 1975 to 2015 with the majority of the data (84%) collected after 2000. Each site represents a point location on a stream reach, where the stability of stream thermal regimes upstream or downstream along the reach were not known. Sites were nested within seven independent watersheds: Susitna River (45 sites), Matanuska River (2), Knik River (2), Wasilla Creek (3), Cottonwood Creek (3), Fish Creek (5), and Little Susitna River (8).

The dispersion of 68 sites across such a large area limits our ability to represent the full range of thermal regimes present in the Mat-Su basin. To examine the representativeness of our dataset, we extracted contributing watershed area, elevation, and stream reach slope from the Netmap stream network for sampling sites within each of the seven subbasins (8th level hydrologic unit) and compared them to the same attributes for all stream reaches within each subbasin (Table 1). All of the monitoring sites were in low gradient (< 1%) reaches and below 1,000 meters elevation, except for one high elevation site in the Matanuska subbasin. The dataset developed for this study represents lowland streams in the Lower Susitna River subbasin and the lower portion of the Anchorage subbasin that drains into Knik Arm. Other subbasins within the Mat-Su basin are extremely remote and consequently, we found very little data that could be used to capture their thermal regime diversity.

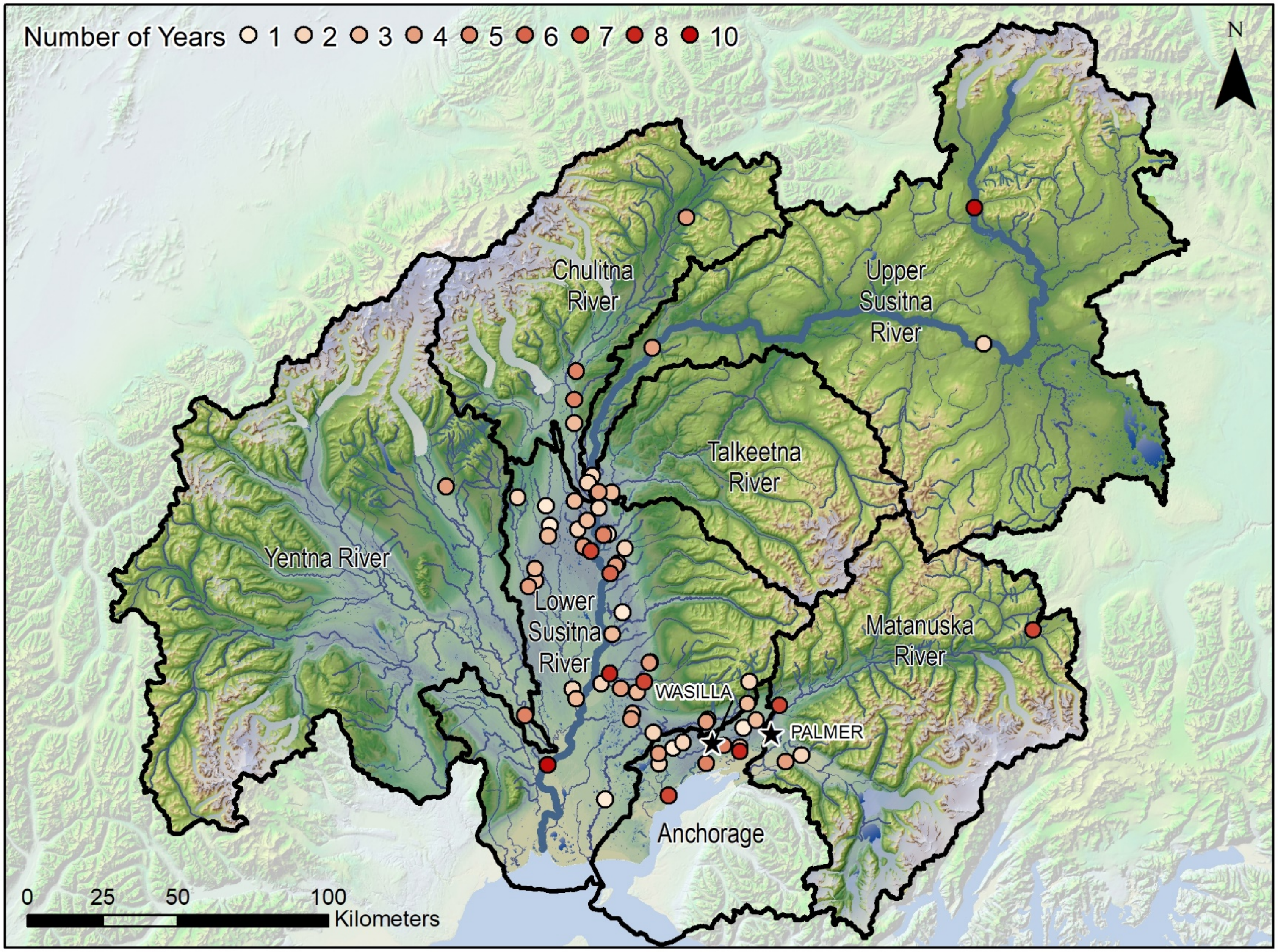


Figure 1. Location of 68 stream temperature monitoring sites across the Mat-Su basin.

Table 1. Range of geomorphic attributes at sample sites and for all stream reaches within seven subbasins of the Mat-Su basin.

Subbasin	Watershed Area (km^2)	Elevation (m)	Gradient (%)
Anchorage (1,054 km)	0 - 391	0 - 1,400	0.0 - 0.9
Sites (n = 11)	19 - 379	4 - 146	0.0 - 0.0
Matanuska (33,422 km)	0 - 8,636	3 - 3,511	0.0 - 3.5
Sites (n = 4)	2 - 134	16 - 1,006	0.0 - 0.1
Lower Susitna River (14,215 km)	0 - 51,088	0 - 2,215	0.0 - 2.6
Sites (n = 40)	2 - 50,050	10 - 463	0.0 - 0.0
Upper Susitna River (23,035 km)	0 - 16,294	105 - 3,735	0.0 - 5.7
Sites (n = 5)	47 - 16,221	114 - 743	0.0 - 0.0
Chulitna River (22,657 km)	0 - 6,684	104 - 5,460	0.0 - 11.6
Sites (n = 4)	100 - 6,541	150 - 537	0.0 - 0.0
Talkeetna River (13,314 km)	0 - 5,272	102 - 2,492	0.0 - 2.3
Sites (n = 2)	37 - 5,203	110 - 117	0.0 - 0.0
Yentna River (37,564 km)	0 - 15,810	13 - 6,015	0.0 - 12.3
Sites (n = 2)	169 - 15,737	17 - 235	0.0 - 0.0

Temperature Metrics and Stream Thermal Regimes

For each site-year, we calculated 44 temperature metrics that represent five aspects of the thermal regime: magnitude, variability, frequency, duration, and timing (see Appendix B for a list of all 43 descriptors with definitions, Poff et al. 1997). We chose temperature thresholds of 13, 18, and 20˚C to describe the duration and frequency of thermal events related to salmon spawning, rearing, and migration, respectively (U.S. Environmental Protection Agency 2003). We reduced the list to ten non-redundant descriptors that capture different aspects of the thermal regime by removing linearly correlated predictors (*r* > 0.8) within the five categories of metrics (Table 2).

Table 2. Ten temperature metrics used to classify thermal regimes.

Category	Abbreviation	Description
Magnitude	MA7d_DMT	Maximum 7-day moving average of maximum daily temperatures
Variability	SIGMA_MAX	Variance of daily maximum temperatures
Variability	CV_MAX	Coefficient of variation of daily maximum temperatures
Variability	DELTA_MAX	Maximum daily range
Frequency	SUM_13	Number of days greater than 13˚C
Frequency	SUM_18	Number of days greater than 18˚C
Duration	DUR_mx13	Duration of longest warm event above 13˚C
Duration	DUR_mx18	Duration of longest warm event above 18˚C
Timing	MxDMT_jd	Timing of maximum daily maximum temperature
Timing	MA7d_DMT_jd	Timing of maximum 7-day moving average of daily maximum temperature

We used the reduced list of temperature descriptors in a hierarchical cluster analysis to identify the types of thermal regimes present in the Mat-Su basin. Prior to clustering, the ten temperature metrics were standardized and converted to a distance matrix using Euclidean distances. We agglomerated site-years in the cluster analysis using Ward's minimum variance method (Ward 1963). The optimal number of thermal regimes was chosen using a weight of evidence approach by calculating 30 distinct indices on cluster analysis solutions from two to 15 groups. Cluster stability was assessed separately across 500 bootstrapped samples of the data (Hennig 2007). Jaccard similarities were calculated between each group in the observed data with the closest group in the bootstrap sample and averaged over all samples. Clusters with similarities > 0.75 are considered stable, while those between 0.6 and 0.75 are considered as indicative of patterns in the data. We summarized differences between thermal regimes using boxplots and mean differences in the ten temperature metrics.

Drivers of Stream Thermal Regimes

We investigated drivers of the thermal regimes identified in the cluster analysis using predictor variables representing climate, watershed landcover, and stream geomorphology (Table 3). Air temperature, precipitation, and snow water equivalent were used to investigate spatial and temporal variation in seasonal temperature and hydrology. For all climate datasets, rasters were averaged (except where noted below) over the drainage area contributing to each site and were specific to the year of data collection. Mean monthly raster surfaces of air temperature and precipitation from the Scenarios Network for Alaska and Arctic Planning (SNAP) were averaged over spring (March, April, and May) and summer seasons (June, July, August) (Scenarios Network for Alaska and Arctic Planning 2017a, 2017b). Precipitation was also summed over the summer season as a proxy for differences in stream discharge between years. Additionally, raster surfaces of April 1st snow water equivalent (SWE, Beamer et al. 2016) were processed and used to estimate spring snowpack.

To investigate downstream thermal influences of lakes, glaciers, and wetlands on sites in our study area, we used an inverse-distance weighting scheme to calculate spatially explicit effects of landcover on our sampling sites (Peterson and Pearse 2017). Each cell in the watershed where the landcover is present is multiplied by a weight that incorporates the distance from that cell to the watershed outlet (i.e. sampling site). The formula for the distance weighted landcover metric is

$$Landcover\ \% = \frac{\sum_{i=1}^{n} I(k_i)\, w_i}{\sum_{i=1}^{n} w_i} \times 100$$

$$w_i = (d_i + 1)^p$$

where $I(k_i)$ = 1 when the landcover is present in the ith raster cell and 0 otherwise, n is the total number of cells in the drainage area upstream of the sampling site, w_i is the weight, d_i is the distance from the cell to the sampling site, and p is the weighting power. We used flow distances and a weighting power of -1, which corresponds to inverse distances (cells that are closer have more weight than cells that are farther from the sampling site).

Reach geomorphology variables were selected from the Netmap stream network generated for the Mat-Su basin (Woll 2015), which included aspect, gradient, sinuosity, valley width, and local road density within each subbasin contributing area. Aspect was folded to better approximate heat load using the equation 180 – | *aspect* – 180|, which shifts the maximum to southwest slopes and the minimum to northeast slopes (McCune and Keon 2002).

Table 3. Predictor variables used to assess drivers of thermal regimes.

Group	Variable	Definition	Data Source
Reach geomorphology	Aspect	Average downstream flow direction for reach (degrees)	Netmap
Reach geomorphology	Gradient	Slope of stream reach (%)	Netmap
Reach geomorphology	Sinuosity	Length of the channel divided by the length of the valley measured over 40 channel widths (unitless)	Netmap
Reach geomorphology	Valley width	Valley width calculated at five multiples of bankfull depth above the channel elevation (m)	Netmap
Landcover	Local road density	Local road density over the adjacent contributing area to each reach (km/km^2)	Netmap
Landcover	Glaciers	Inverse flow weighted distance from site to glaciers (%)	GLIMS glacier inventory 4.0
Landcover	Lakes	Inverse flow weighted distance from site to lakes (%)	National Hydrography Dataset
Landcover	Wetlands	Inverse flow weighted distance from site to wetlands (%)	2011 National Land Cover Dataset
Climate	Spring air temperature	Mean spring air temperature in watershed (March, April, and May) for each year (℃)	SNAP
Climate	Summer air temperature	Mean summer air temperature in watershed (June, July, and August) for each year (℃)	SNAP
Climate	Spring Precipitation	Mean spring precipitation in watershed (March, April, and May) for each year (mm)	SNAP
Climate	Summer precipitation	Mean summer precipitation in watershed (June, July, and August) for each year (mm)	SNAP
Climate	Total summer precipitation	Total summer precipitation in watershed (June, July, and August) for each year (mm)	SNAP
Climate	April 1st snowpack	Mean April 1st SWE across the watershed for each year (inches)	SnowModel

We modeled the relationship between these drivers and stream thermal regimes using random forests, which is a machine learning algorithm that combines predictions from a user-selected number of classification trees (Cutler et al. 2007). A bootstrap sample of the data (~ 63% of the observations occur at least once in a bootstrap sample) is used for each tree and a random sample of the predictor variables (square root of the number of predictor variables) is used for each node in the tree to maintain independence among trees in the forest. Predictions are made for the out-of-bag data not included in each tree and predictions are combined across all trees. Ten random forest models of 1,000 trees each were created using one year from each site to avoid pseudo-replication of the spatial predictors which did not vary in time. The longest dataset across all sites was ten years. For each site, we randomly selected one year of data, while ensuring that all years were included in one of the models. The ten random forest models were combined and predictions were obtained by passing each site-year through the full forest of 10,000 trees and calculating the fraction of votes for each thermal regime. The random forest model accuracy was assessed using a table of observed versus predicted thermal regimes (i.e. misclassification rate).

Variable importance was assessed by randomly permuting each variable in the out-of-bag data and passing it through the forest to get new predictions. The mean decrease in accuracy (MDA) is calculated by taking the difference between the misclassification rates using the observed versus permuted data and dividing by the standard error (Cutler et al. 2007). MDA scores range from 0 to 100%, where lower scores represent variables having the smallest impact on model performance and high scores indicate the most important variables.

All analyses were run using R statistical software and the tidyverse, fpc, NbClust, rgdal, raster, randomForest, and vegan libraries (Liaw and Wiener 2002, Charrad et al. 2014, Hijmans 2014, Hennig 2015, Bivand et al. 2017, Oksanen et al. 2017, R Core Team 2017, Wickham 2017).

Future Changes in Stream Thermal Regimes

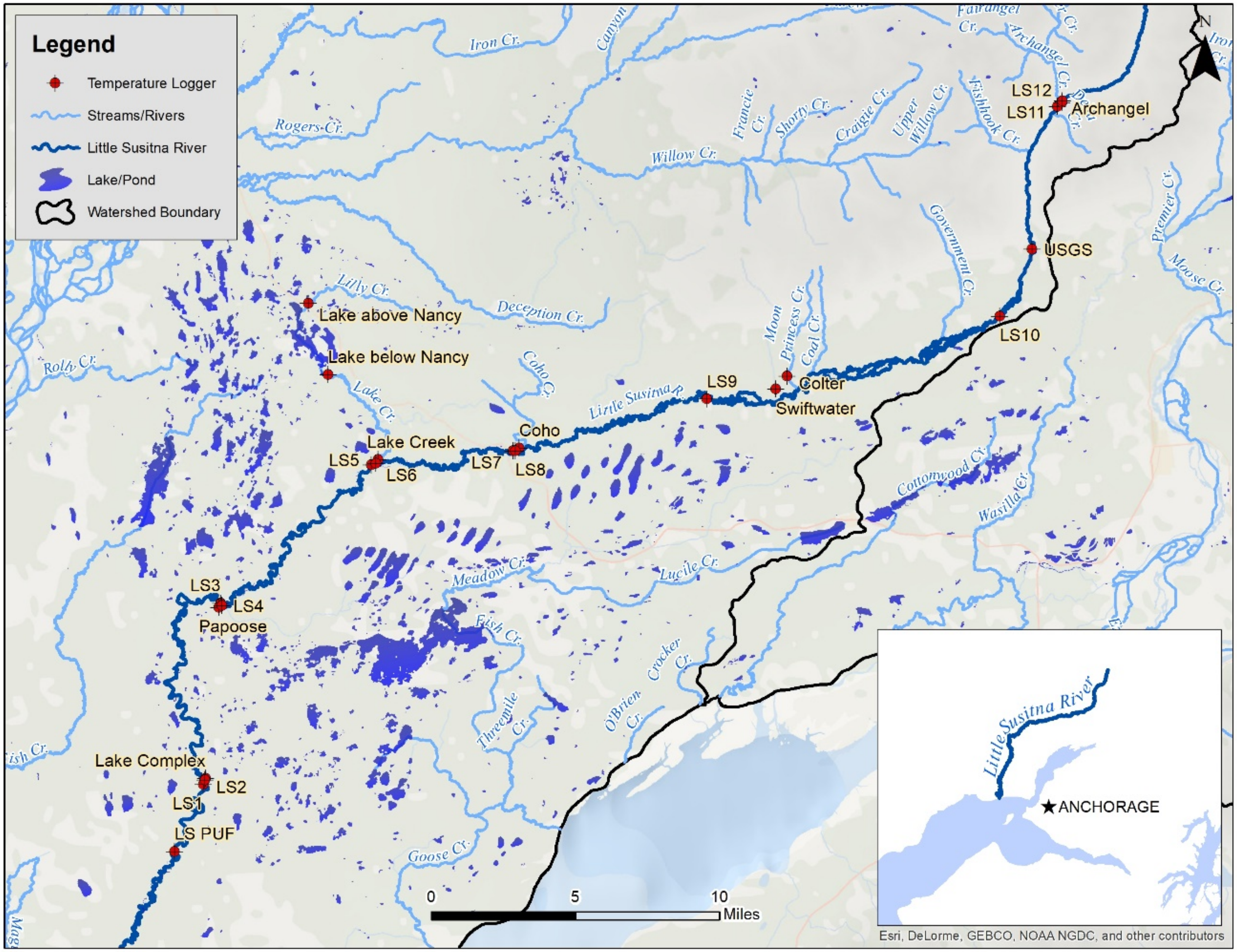
We investigated potential regime shifts for our 68 sites using PRISM climate normals for 1971 – 2000 (baseline, Gibson 2009a, 2009b) and a future scenario for 2050 – 2069 (future, Scenarios Network for Alaska and Arctic Planning 2017c, 2017d) using the random forest model described above. Air temperature and precipitation projections were obtained from SNAP using a five model average and Representative Concentration Pathway (RCP) 6.0, which is a middle range emissions scenario. We predicted thermal regimes for our 68 sites using watershed landcover and stream geomorphology variables, combined with climate predictors corresponding to the baseline or future time periods.

Changes in future thermal regimes can be described two ways: 1) a change in the thermal regime, or 2) a change in the distribution of votes across the thermal regimes (expressed as a percentage). Sites are classified into a thermal regime by majority vote, which doesn’t capture uncertainty in the model predictions. For this reason, we focused on the thermal regime percentages and plotted them for the baseline and future time periods. We plotted the percentage of votes for each thermal regime separately with the future time period on the y-axis and the baseline time period on the x-axis. Lines with intercept of zero and slope of one were overlaid on the scatterplots to identify sites where percentages increased (above the line) or decreased (below the line). We investigated drivers associated with regime shifts by sizing points according to landcover types.

We used non-metric multidimensional scaling (NMS) ordination as a secondary plotting technique to visualize differences between sites based on their vote percentages for all four thermal regimes. Ordination is a tool for finding patterns in multivariate data. Sites closer together in ordination space are more similar in terms of their vote percentages for the four thermal regimes than sites further apart. We calculated Euclidean distances between all 136 sites (68 current and 68 future) prior to running NMS. Arrows were used to represent regime shifts between the baseline and future time periods for each site in the ordination figure.

Thermal regimes in the Little Susitna Watershed

The dispersion of temperature sites across subbasins limited our ability to examine thermal heterogeneity within and along longitudinally connected habitats, which is important for salmon populations. To address this data gap, we used stream temperature data collected in 2016 at 23 sites within the Little Susitna watershed to evaluate thermal regime diversity within one watershed, while controlling for interannual variability (Figure 2). The Little Susitna watershed drains the Talkeetna mountains to Cook Inlet and contains four small glaciers in the uppermost portion of the watershed and extensive small lakes in the lower portion of the watershed. Fourteen sites were located on the mainstem Little Susitna River and nine sites were located on tributaries. We calculated stream temperature metrics for all sites and mapped and summarized their variability along the network. (Note: these data could not be used for the thermal regime classification because the climate variables used for modeling end in 2015.)



Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

Figure 2. Mainstem and tributary sites in the Little Susitna watershed with stream temperature data from 2016.

Results

Diversity of Stream Thermal Regimes

The four-group solution from our cluster analysis was selected by the most indices as the optimal solution (6 indices). The Jaccard similarities for the four groups indicated three stable groups (mean similarities all greater than 0.75) and one less stable group (mean similarity of 0.59).

The largest group of site-years (39%) were cold streams with relatively stable temperatures (cold-stable). The average maximum temperatures (MA7d_DMT) for these site-years was 12.4˚C and the variance of daily maximum temperatures (SIGMA_MAX) was 2.2˚C (Figure 3, Table 4). The second group (cold-variable, 22% of site-years) included cold streams (mean MA7d_DMT = 13.7˚C) with higher variability in daily maximum stream temperatures compared to cold-stable streams (mean SIGMA_MAX = 4.3˚C). Additionally, cold-variable sites had the latest timing of maximum stream temperatures (MA7d_DMT_jd), which averaged July 20th for cold-variable streams as opposed to early July (2nd through 4th) for the other thermal regimes. The third group (warm-variable, 30% of site-years) was characterized by warm temperatures that remained above 13°C for almost two months (mean DUR_mx13 = 57 days) but rarely exceeded 18˚C. Variation in maximum temperatures (SIGMA_MAX) for the warm-variable group was similar to cold-variable streams. The final group (warm-long, 9% of site-years) had the warmest and most variable maximum temperatures that remained above 13˚C for most of the summer and exceeded 18˚C for almost one month (mean DUR_mx18 = 29 days).

For sites with high fidelity to a specific thermal regime, comparison of their daily stream temperatures for each site-year helped to visualize differences among thermal regimes. Variation in stream temperatures over the summer is evident by the increasing and decreasing patterns in stream temperature in all but the cold-stable thermal regime (Figure 4). The warm-long thermal regime was the only group that regularly had temperatures above 18˚C.

Table 4. Mean values of ten temperature metrics used to characterize thermal regimes.

	Thermal Regimes			
Temperature Metrics[1]	cold-stable	cold-variable	warm-variable	warm-long
MA7d_DMT (˚C)	12.4	13.7	18.5	22.3
DELTA_MAX (˚C)	5.1	4.9	6.0	5.6
SIGMA_MAX	2.2	4.3	3.6	6.7
CV_MAX (˚C)	0.14	0.19	0.12	0.14
SUM_13 (days)	12	19	79	88
SUM_18 (days)	0	1	14	47
DUR_mx13 (days)	4	10	57	84
DUR_mx18 (days)	0	1	5	29
MxDMT_jd (julian date)	184	201	185	183
MA7d_DMT_jd (julian date)	183	208	184	191

[1] See Table 1 for definitions of temperature metrics.

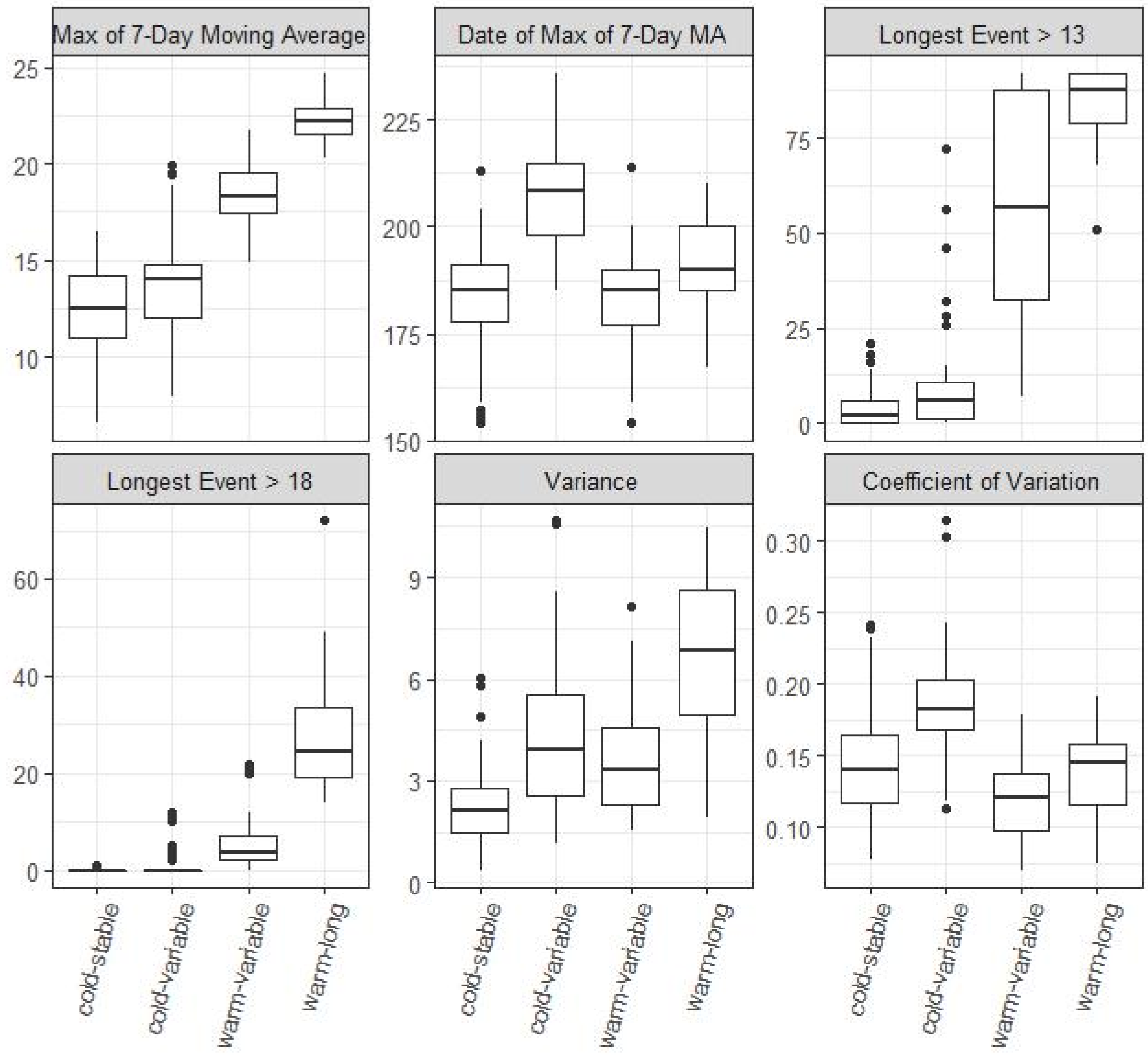


Figure 3. Comparison of six temperature metrics across thermal regimes.

Figure 4. Summer stream temperatures for four sites with high fidelity to each of the thermal regimes. Colors indicate different years for each site.

Drivers of Stream Thermal Regimes

The overall misclassification rate for the random forest model was 17%. The cold-stable and warm-variable thermal regimes had the lowest misclassification rates: 4 and 7%, respectively. Cold-variable thermal regimes proved difficult to predict (48% misclassification) with almost half of the observed site-years misclassified as cold-stable thermal regimes. One-third of the observed site-years for warm-long thermal regimes were misclassified as warm variable thermal regimes (33% misclassification).

Climate and landcover drivers had the highest variable importance in the random forest model (Figure 5). Spring and summer air temperatures, snow water equivalent, and total summer precipitation were the most important climate drivers differentiating thermal regimes, while thermal contributions from wetland and lakes were the most important landcover drivers. Of lesser importance were stream reach morphology characteristics, glacier effects, and seasonal precipitation. The relative importance of climate and landcover drivers, however, varied across thermal regimes (Figure 6). Cold-stable regimes were best described as systems with low lake and wetland covers and cold summer air temperatures. Cold-variable regimes occurred when both spring and summer air temperatures were cold and there was a high snowpack from the previous winter. Warm-variable regimes were associated with non-glacial systems with high wetland cover, low snow inputs, and warm spring and summer air temperatures. Lastly, warm-long thermal regimes had high lake cover and warm summer air temperatures.

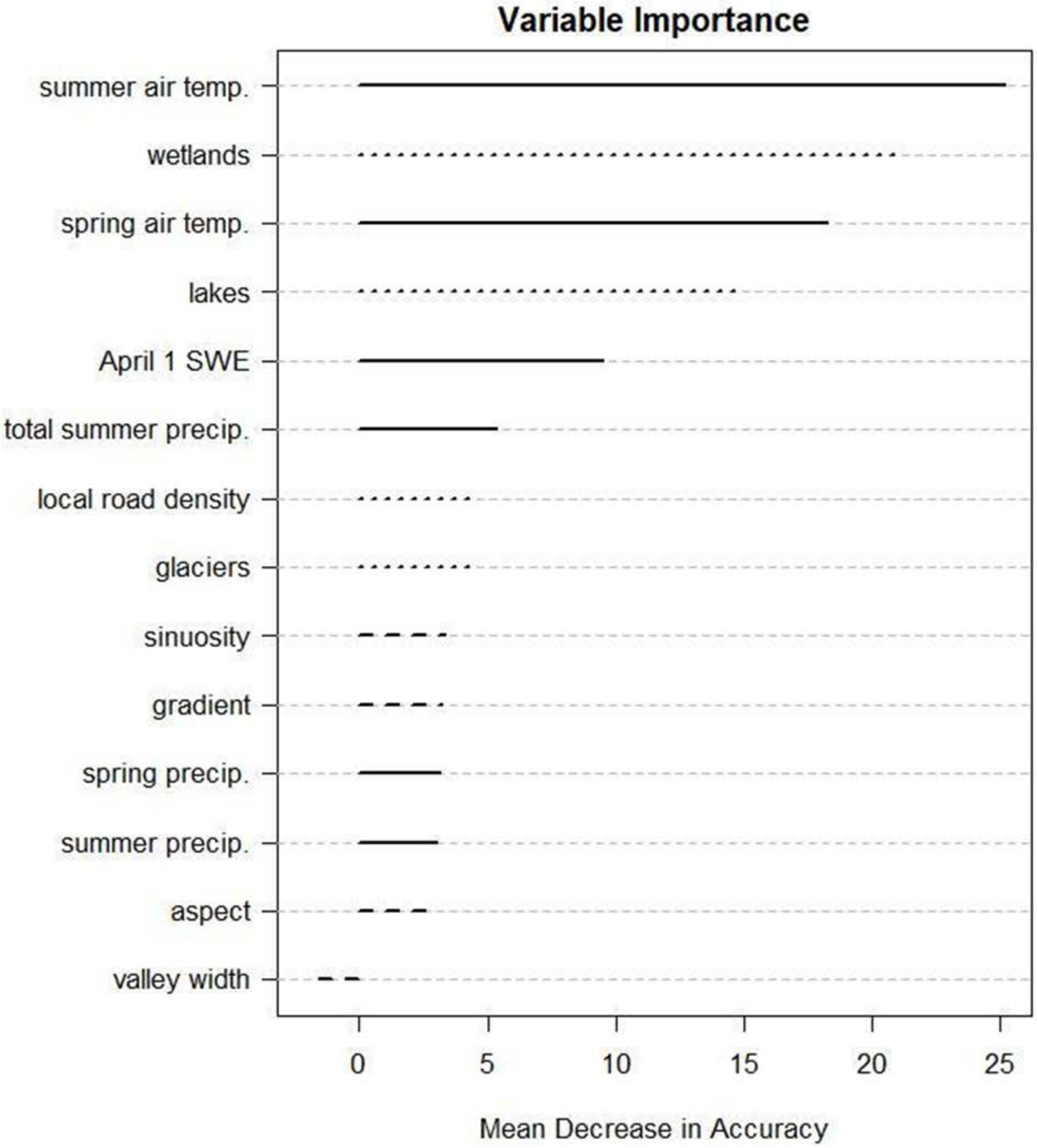


Figure 5. Variable importance results from random forest model. Dashed line represents reach geomorphology variables, dotted line represents landcover variables, and solid line represents climate variables.

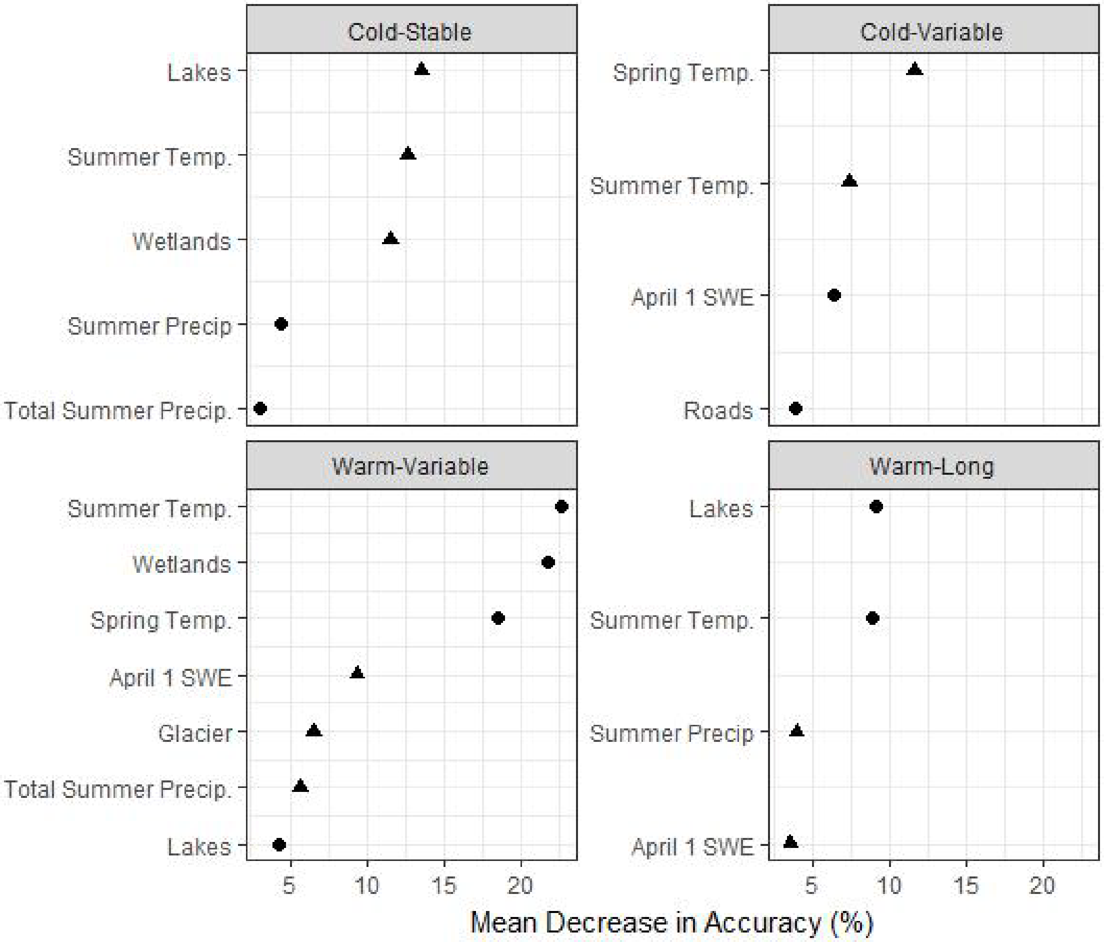


Figure 6. Variable importance results for each thermal regime. Positive effects are shown by circles and negative effects are shown by triangles.

Future Changes in Stream Thermal Regimes

Changes in thermal regimes between the baseline and future time periods included decreases in the number of sites classified as cold-stable (31 to 28) and cold-variable (6 to 1) and increases in the number of sites classified as warm-variable (31 to 36) and warm-long (0 to 3). Because the baseline period did not match the time period represented by the majority of the empirical data (1971-2000 versus 2000-2015, respectively), warm-long thermal regimes were not represented in the baseline period, although they were identified in the characterization. Generally, the results indicated substantial shifts towards warm-variable and warm-long thermal regimes (Figure 7, arrows pointing to the right and down, respectively). For over half of the sites (51%), there was an increase in the percentage of votes for warm-variable thermal regimes (Figure 8). All sites but two had an increase in the percentage of votes for warm-long thermal regimes. Glacial systems remained predominantly cold-stable under future conditions, but had a notable increase in the percentage of votes for warm-variable thermal regimes.

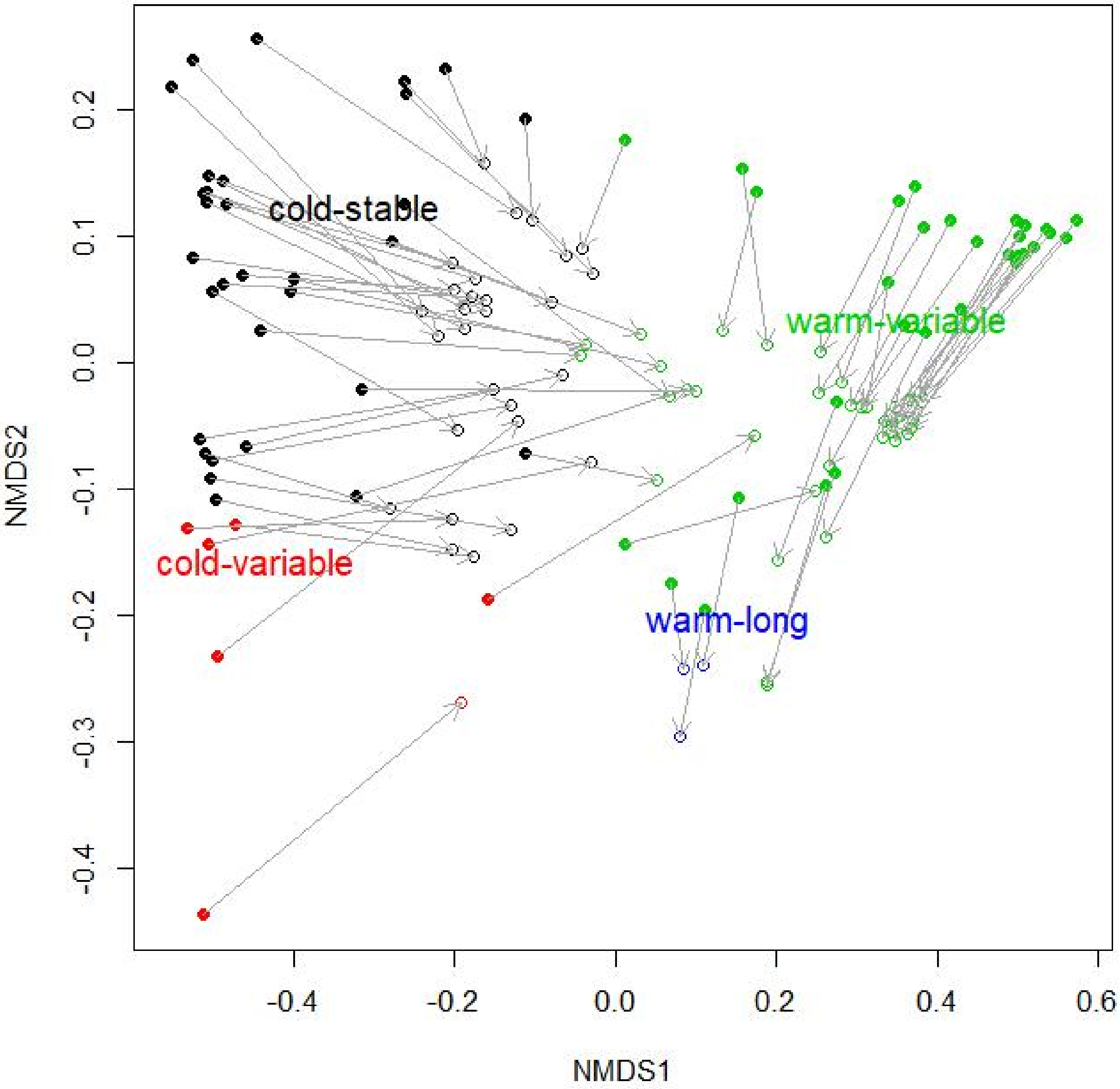


Figure 7. Non-metric multidimensional scaling ordination of baseline and future thermal regimes. Baseline thermal regimes are shown by filled circles and arrows point to future thermal regimes (open circles).

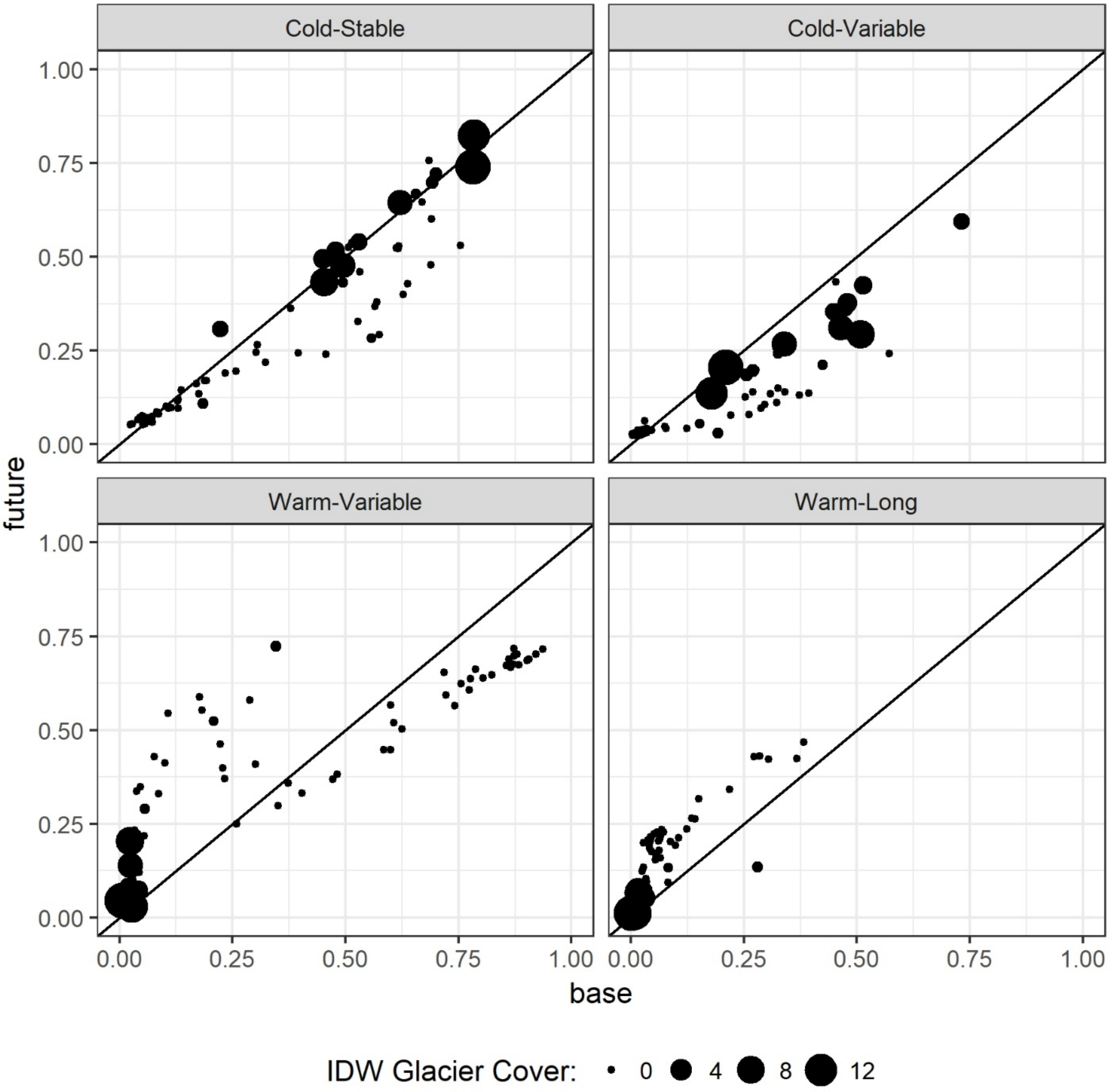


Figure 8. Change in percentage of votes for each thermal regime from baseline to future time periods. Sites (points) are sized by inverse-distance weighted glacier cover.

Thermal Regimes in the Little Susitna Watershed

Stream temperature metrics for the 23 sites in the Little Susitna watershed were highly variable across the watershed (Table 5). Maximum temperatures in the mainstem were highly buffered and only reached 18°C after several warm tributaries joined the system. The warmest temperatures were in the tributaries and the mainstem below Papoose Creek. The timing metrics were stable throughout the network as maximum stream temperatures occurred in a short window from July 14 to July 19 at all sites.

Although we could not use these data to predict thermal regimes in the Little Susitna watershed, the large ranges for all but the timing metrics indicate high thermal regime diversity in the watershed. The Little Susitna watershed has a large elevational gradient and includes glaciers at the top of the watershed and extensive small lakes and wetlands towards the bottom of the watershed, all of which were important drivers of stream thermal regimes.

Table 5. Minimum and maximum temperature metric values across 23 sites in the Little Susitna watershed.

Metric	Minimum	Maximum
MA7d_DMT	11.2	25.4
DELTA_MAX	2.9	7.0
SIGMA_MAX	1.6	5.1
CV_MAX	0.08	0.22
SUM_13	0	92
SUM_18	0	87
DUR_mx13	0	92
DUR_mx18	0	81
MxDMT_jd	195	200
MA7d_DMT_jd	196	198

Discussion

Comparison of Stream Thermal Regimes

Summer temperatures in Mat-Su basin streams tend to be warmer than other Alaska regions where temperature data are available. Mat-Su streams were seven of the ten warmest in a study of 48 salmon streams across the larger Cook Inlet watershed (Mauger et al. 2017). Average July and August temperatures from 33 Bristol Bay streams ranged from 3.6 to 12.6˚C (Lisi et al. 2013), whereas the streams in our dataset ranged from 4.5 to 19.3˚C. Additionally, the maximum MWAT (maximum weekly average temperature) for nine streams in Southeast Alaska was 18.6˚C (Fellman et al. 2014), compared to 22.9˚C for the sites and years in this study. Because our study included all available data across multiple years for many sites, we may have captured warm years not represented in other studies that were based on only one summer of data. Aspects of stream thermal regimes other than magnitude have yet to be explored for other parts of Alaska, which limits our ability to make additional comparisons within the State.

When considered in a larger context, stream thermal regimes in the Mat-Su basin differ from those in the contiguous United States by having earlier timing of maximum temperatures and colder maximum temperatures. Maximum stream temperatures occurred approximately two weeks earlier in the Mat-Su basin than for the six thermal regimes described for the contiguous U.S. (Maheu et al. 2016). In Southcentral Alaska, August has the highest average rainfall of any month and cools stream temperatures at the end of the summer, whereas August tends to be the hottest month for most streams in the contiguous U.S. Summer precipitation likely moderates the duration of maximum stream temperatures as well. In both classifications, there was one thermal regime distinguished by having later timing of maximum temperatures, which was tied to snowmelt contributions into midsummer. Although the duration of maximum stream temperatures in Alaska is likely much shorter than the durations in systems further south, many Chinook and sockeye salmon populations migrate in July through the hottest part of the summer (Burger et al. 1985, Quinn 2005), which may make them sensitive to increasing temperatures in the future.

Cold thermal regimes, with maximum temperatures below 20˚C, were predominant in our classification (3 of 4 thermal regimes) but less common in the contiguous U.S. (2 of 6 thermal regimes, Maheu et al. 2016). Cold thermal regimes are dominant in the Mat-Su basin because of its high latitude and the contributions of glacial meltwater and snowmelt during the summertime. We suspect that many watersheds in the Mat-Su basin are either dominated by cold thermal regimes or contain a mixture of cold and warm thermal regimes due to the large elevational ranges in all of the subbasins. This diversity will provide important thermal refugia for salmon populations into the future, whereas watersheds dominated by warm thermal regimes may become less suitable for salmon.

Future Changes in Thermal Regime Drivers

In our analysis, spring and summer air temperatures, spring snowpack, and summer precipitation rates were important drivers of thermal regimes, describing combined hydrologic and solar sensitivities. Over the past 60 years, Alaska has warmed at more than twice the rate of the lower

48 states (Chapin et al. 2014). Similarly, climate models project such trends to continue with significant increases in air temperature (2.4 - 6.3˚C) and annual precipitation (14 - 28%) expected by the end of the 21st century (Christensen et al. 2007). Hydroclimatic changes (i.e., changes in air temperature and precipitation) are likely to result in precipitation falling as rain rather than snow during the winter months, increases in winter flow events, decreases in annual snowpack, and earlier timing and decreased magnitude of spring runoff (Leppi et al. 2014). Models forecast that annual hydrographs will no longer be dominated by a single spring thaw and freshet event, but will instead be characterized by numerous high flow events throughout the winter (Wobus et al. 2015). Despite the fact that models predict increases in total annual and monthly precipitation, summers are expected to be warmer and water availability is expected to decrease due to longer growing seasons and increased rates of evapotranspiration (Chapin et al. 2014). How hydrologic regime shifts will impact stream temperature is uncertain, especially in Alaska where summer discharge patterns are complicated by glacial runoff and variable precipitation rates. Future research and model projections, therefore, should include coupled model response between discharge and temperature.

In the Mat-Su basin, streams and rivers will not respond uniformly to hydroclimatic changes, as landscape attributes filter these effects differently causing nonlinear responses between climate and stream temperature (Schindler et al. 2008, Arismendi et al. 2014). Glacial meltwater increases summer discharge and buffers summertime temperatures and, as climate warms, will be an important driver decreasing the sensitivity of some streams to warming air temperatures (Kyle and Brabets 2001). Glacially-influenced rivers in the Mat-Su basin, such as the Susitna River, will continue to experience colder thermal regimes relative to non-glacial systems (Brittain and Milner 2001, Hood and Berner 2009). Other landscape features may increase the sensitivity of stream temperatures to rising air temperatures, making streams more vulnerable to warming (Schoen et al. 2017). In this study, lakes and wetlands were important drivers of warm thermal regimes. Over the past 50 years, southern portions of Alaska have seen a significant decrease in lake and wetland area due to warmer drier summers, increased rates of evapotranspiration, and a longer growing season (Klein et al. 2005, Chapin et al. 2014). Similar to our results, other studies have also shown that landscape features such as low-elevation, rain-dominated watersheds with lower average slopes are likely to be more sensitive to low summer flows and temperature warming than streams fed by high-elevation snow or glaciers (Fellman et al. 2014, Lisi et al. 2015, Mauger et al. 2017, Winfree 2017). Additionally, the Mat-Su basin is the fastest growing area of Alaska and hydrologic impacts from development activities include loss of wetlands and alteration to groundwater flows, which could negatively impact key habitats and threaten thermal diversity. Due to combined effects from a rapidly changing climate and the landscapes themselves, more information is needed to better understand ecosystem response and how these changes will impact thermal regimes on intra- and inter-annual timescales.

Species Response to Thermal Regime Shifts

Our analysis predicted a general shift from colder and stable baseline conditions towards warmer and more variable thermal regimes for future Mat-Su streams. Ambient temperature conditions control salmon metabolic rates which have direct consequences for individual growth and survival and population dynamics. In general, elevated temperatures have been shown to result in increased rates of disease (Farrell et al. 2008, Lafferty 2009) and reduced growth and survival across numerous salmonid populations (Isaak et al. 2012). However, the effects of warmer and more variable stream temperatures will vary by species, life stage, and life history, and may be mediated in intact habitats and where anthropogenic pressures are less pronounced.

Warming water temperatures have implications across multiple salmon life stages. Spawning migration timing has been shown to shift earlier under warmer conditions (Crozier et al. 2011), with adult salmon entering freshwater (Kovach et al. 2015), arriving at the spawning grounds, and spawning sooner (Hayes et al. 2014) in given year. In-river thermal conditions during the spawning migration period may lead to increased pre-spawning mortality where dense congregations of spawning adults, warm water temperatures, and low stream flows contribute to low dissolved oxygen levels (Sergeant et al. 2017, Tillotson and Quinn 2017). Salmon eggs have the lowest heat tolerance of any life stage and are subject to direct mortality if exposed to warm water temperatures. Moreover, embryonic development rates are governed by ambient thermal conditions, thus under warmer conditions embryos develop faster and hatch earlier (Beacham and Murray 1990, Quinn 2005). Alevins hatching under such conditions have been shown to be smaller at emergence (Hendry et al. 1998, Burt et al. 2012). Earlier emergence and smaller body size could result in a mismatch with rearing habitat environmental conditions and food resources (Post and Forchhammer 2008), although in some cases such mismatches may not occur as predator and prey dynamics remain synchronized (Sergeant et al. 2015). Thermal conditions are highly important at juvenile life stages as temperature is a dominant factor controlling metabolic and consumption rates (Brett 1995). Increased growth during the juvenile life stage has been documented with warming water temperatures in Alaska (Schindler et al. 2005, Kovach et al. 2015), and growth performance during this period can have strong repercussions for adult fitness (Bond et al. 2008). Finally, smolt outmigration timing has been shown to be earlier as a function of warming stream temperatures (Otero et al. 2014) and resulted in a reduced period during which downstream migration occurs, although the magnitude varies by species and life history (Kovach et al. 2013a).

Less is known of the effects of increased thermal variability on salmon by life stage, although recent research highlights the importance of increased thermal regime variation, particularly during incubation and juvenile rearing. Variability can have large impacts on salmon because their thermal performance is non-linear (Vasseur et al. 2014). In other words, the response of an individual may be very different under a constant relative to a variable regime (Ruel and Ayres 1999). For example, under variable conditions (e.g., increased temperature fluctuations) embryos have been shown to accumulate significantly more thermal units (Sparks et al. 2017), emerge partially developed (Steel et al. 2012, Fuhrman et al. 2018), and have increased variation in developmental traits (Dammerman et al. 2016) relative to those reared under constant conditions. Juvenile salmon experienced up to 50% reduced growth when exposed to variable thermal conditions, even when mean temperatures under such conditions were similar to constant (Geist et al. 2010). Habitat use by juvenile salmon has also been shown to change under variable temperature conditions; smaller individuals sought out thermal refugia more often when exposed to increased diel variation (Brewitt and Danner 2014). Clearly, increased thermal variation can have major implications for salmon, especially during earlier life stages. However, little is known of the effects of thermal variation on salmon during their spawning migrations, on the spawning grounds, or during smolt outmigration.

Conservation and Management Strategies

Improving our understanding of thermal diversity related to ecological outcomes, such as growth, productivity, spawning, rearing, migrations, and survival (Steel et al. 2017) will allow for prioritization of on-the-ground management strategies. On-going and future management strategies include efforts to protect and restore critical cold water habitats supporting salmon life histories. Strategies to ameliorate stream temperature warming include restorative actions that promote physical and biological processes thereby increasing resiliency of habitats and populations to climate variability (Waples et al. 2009, Beechie et al. 2013). Local restoration efforts should focus on restoring lateral, longitudinal and vertical connectivity, such as reconnecting stream channels with active floodplains to facilitate groundwater contributions. Identifying and protecting areas of groundwater recharge and shallow groundwater flow paths will help to maintain cool subsurface flows. Additionally, protecting or re-establishing riparian vegetation buffers provides many benefits to fish habitat, including thermal shading (Pierce et al. 2014). Mitigation strategies to restore both thermal and hydrologic habitat connectivity is important to maintaining the availability of thermally diverse habitats which support salmon populations. Removal of barriers or installation of appropriate culverts will help to maintain habitat connectivity, including access to thermal refugia (Schmetterling 2003). Additionally, maintaining adequate streamflow within streams (i.e., instream flow reservations, flood mitigation) will buffer against temperature changes and help to maintain habitat connectivity. Strategies for protecting salmon populations include addressing any additional threats to current or future thermally suitable habitats. This may include natural and human-induced threats such as population growth, recreational activities, road construction, loss of wetlands, and non-native invasions.

Recommendations for Future Work

Our work here explains the variation of summer thermal regimes across 68 sites in the Mat-Su basin. To improve spatial and temporal representation in the Mat-Su basin, we should expand monitoring efforts to include: (1) sites which cover a range of environmental characteristics and thermal drivers of diversity (i.e., hydrologic, climatic, and geomorphic); (2) co-location of sensors with on-the-ground hydrologic and biologic data collection efforts; (3) continuous monitoring across all seasons; and (4) establishment of long-term sentinel sites. It would be beneficial to design an efficient monitoring system within the Mat-Su basin, which maximizes historic, existing, and future monitoring efforts across multi-disciplinary management objectives.

Every component of the thermal regime, such as magnitude, duration, or frequency, has potential ecological and biological consequences. Coupling thermal and biological information, therefore, will improve our ability to make effective management decisions. Future research should use in-situ or quantitative models of ecologically-significant thermal regime metrics to investigate spatial and temporal variability of species habitat distributions (i.e., Alaska's Anadromous Waters Catalog), population demographics (i.e., age, size, length, returns), movement (i.e., run timing), habitat use (i.e., spawning, rearing, migrations), and genetic diversity. Linking thermal diversity to life-history diversity will help us to assess future vulnerabilities, sensitivities, and overall population resilience of salmon in the face of changing freshwater conditions.

Literature Cited

Arismendi, I., S. L. Johnson, J. B. Dunham, and R. Haggerty. 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. Freshwater Biology 58:880–894.

Arismendi, I., M. Safeeq, and J. B. Dunham. 2014. Can air temperature be used to project influences of climate change on stream temperature ? Environmental Research Letters 9:1–12.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16:1429–1441.

Beacham, T., and C. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927–945.

Beamer, J. P., D. F. Hill, A. Arendt, and G. E. Liston. 2016. High-resolution modeling of coastal freshwater discharge and glacier mass balance in the Gulf of Alaska watershed. Water Resources Research 52:3888–3909.

Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, J. Kimball, J. Stanford, P. Kiffney, and N. Mantua. 2013. Restoring salmon habitat for a changing climate. River Research and Applications 29:939–960.

Bivand, R., T. Keitt, and B. Rowlingson. 2017. rgdal: Bindings for the Geospatial Gata Abstraction Library.

Blair, G. R., D. E. Rogers, and T. P. Quinn. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Transactions of the American Fisheries Society 122:550–559.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Brabets, T. P., G. L. Nelson, J. M. Dorava, and A. M. Milner. 1999. Water quality assessment of the Cook Inlet Basin, Alaska. Anchorage, AK.

Brett, J. R. 1995. Energetics. Pages 1–68*in* C. Groot, L. Margolis, and W. C. Clarke, editors.Physiological ecology of Pacific Salmon. University of British Columbia Press, Vancouver, BC.

Brewitt, K. S., and E. M. Danner. 2014. Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. Ecosphere 5:1–26.

Brittain, J. E., and A. M. Milner. 2001. Ecology of glacier-fed rivers: Current status and concepts. Freshwater Biology 46:1571–1578.

Burger, C. V, R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times for two runs of Chinook Salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693–700.

Burt, J. M., S. G. Hinch, and D. A. Patterson. 2012. Parental identity influences progeny responses to incubation thermal stress in sockeye salmon (*Onchorhynchus nerka*). Journal of Fish Biology 80:444–462.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Chapin, F. S. I., S. F. Trainor, P. Cochran, H. Huntington, C. Markon, M. McCammon, A. D. McGuire, and M. Serreze. 2014. Ch. 22: Alaska. Pages 514–536*in* J. M. Melillo, T. C. Richmond, and G. W. Yohe, editors.Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program.

Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. NbClust : An R Package for Determining the Relevant Number of Clusters in a Data Set. Journal of Statistical Software 61:1–36.

Christensen, J. H., B. Hewitson, and A. Busuioc. 2007. Regional climate projections. Pages 847–940Climate Change 2007: The Physical Science Basis. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Solomon S, Qin D, Manning M, et al.). Cambridge University Press, Cambridge, UK and New York, NY, USA.

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: A case study of a shift toward earlier migration date in sockeye salmon. The American Naturalist 178:755–773.

Cutler, D., T. J. Edwards, K. Beard, A. Cutler, K. Hess, J. Gibson, and J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Dammerman, K. J., J. P. Steibel, and K. T. Scribner. 2016. Increases in the mean and variability of thermal regimes result in differential phenotypic responses among genotypes during early ontogenetic stages of lake sturgeon (*Acipenser fulvescens*). Evolutionary Applications 9:1258–1270.

Dorava, J. M., and A. M. Milner. 2000. Role of lake regulation on glacier fed rivers in enhancing salmon productivity: The Cook Inlet watershed south central Alaska, USA. Hydrological Processes 14:3149–3159.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 60:1266–1280.

Farrell, A. P., S. G. Hinch, S. J. Cooke, D. A. Patterson, G. T. Crossin, M. Lapointe, and M. T. Mathes. 2008. Pacific salmon in hot water: Applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiological and Biochemical Zoology 81:697–709.

Fellman, J. B., S. Nagorski, S. Pyare, A. W. Vermilyea, D. Scott, and E. Hood. 2014. Stream temperature response to variable glacier coverage in coastal watersheds of Southeast Alaska. Hydrological Processes 28:2062–2073.

Frissell, C. a, W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershead context. Environmental Management 10:199–214.

Fuhrman, A. E., D. A. Larsen, E. A. Steel, G. Young, and B. R. Beckman. 2018. Chinook salmon emergence phenotypes: Describing the relationships between temperature, emergence timing and condition factor in a reaction norm framework. Ecology of Freshwater Fish 27:350–362.

Geist, D. R., Z. Deng, R. P. Mueller, S. R. Brink, and J. A. Chandler. 2010. Survival and growth of juvenile Snake River fall Chinook salmon exposed to constant and fluctuating temperatures. Transactions of the American Fisheries Society 139:92–107.

Gibson, W. 2009a. Mean average temperature for Alaska 1971-2000. National Park Service, Alaska Regional Office GIS Team.

Gibson, W. 2009b. Mean precipitation for Alaska 1971-2000. National Park Service, Alaska Regional Office GIS Team.

Hayes, D. B., B. J. Bellgraph, B. M. Roth, D. D. Dauble, and R. P. Mueller. 2014. Timing of redd construction by fall chinook salmon in the hanford reach of the Columbia river. River Research and Applications 30:1110–1119.

Hendry, A. P., J. E. Hensleigh, and R. R. Reisenbichler. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. Canadian Journal of Fisheries and Aquatic Sciences 55:1387–1394.

Hennig, C. 2007. Cluster-wise assessment of cluster stability. Computational Statistics and Data Analysis 52:258–271.

Hennig, C. 2015. fpc: Flexible Procedures for Clustering.

Hijmans, R. J. 2014. Raster: Geographic data analysis and modeling.

Hood, E., and L. Berner. 2009. Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. Journal of Geophysical Research: Biogeosciences 114:1–10.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Johnson, J., and J. Coleman. 2014. Catalog of Waters Important for Spawning, Rearing, or Migration of Anadromous Fishes – Southcentral Region, Effective July 1, 2014. Anchorage, AK.

Kelleher, C., T. Wagener, M. Gooseff, B. McGlynn, K. McGuire, and L. Marshall. 2012. Investigating controls on the thermal sensitivity of Pennsylvania streams. Hydrological Processes 26:771–785.

Klein, E., E. E. Berg, and R. Dial. 2005. Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. Canadian Journal of Forest Research 35:1931–1941.

Kovach, R. P., S. C. Ellison, S. Pyare, and D. A. Tallmon. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. Global Change Biology 21:1821–1833.

Kovach, R. P., A. J. Gharrett, and D. A. Tallmon. 2013a. Temporal patterns of genetic variation in a salmon population undergoing rapid change in migration timing. Evolutionary Applications 6:795–807.

Kovach, R. P., J. E. Joyce, J. D. Echave, M. S. Lindberg, and D. A. Tallmon. 2013b. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. PloS one 8:e53807.

Kyle, R. E., and T. P. Brabets. 2001. Water Temperature of Streams in the Cook Inlet Basin, Alaska, and Implications for Climate Change. Anchorage, AK.

Lafferty, K. D. 2009. Calling for an ecological approach to studying climate change and infectious diseases. Ecology 90:932–933.

Leppi, J. C., D. J. Rinella, R. R. Wilson, and W. M. Loya. 2014. Linking climate change projections for an Alaskan watershed to future coho salmon production. Global Change Biology 20:1808–1820.

Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. R News 2:18–22.

Lisi, P. J., D. E. Schindler, K. T. Bentley, and G. R. Pess. 2013. Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. Geomorphology 185:78–86.

Lisi, P. J., D. E. Schindler, T. J. Cline, M. D. Scheuerell, and P. B. Walsh. 2015. Watershed geomorphology and snowmelt control stream thermal sensitivity to air temperature. Geophysical Research Letters 42:3380–3388.

Maheu, A., N. L. Poff, and A. St-Hilaire. 2016. A classification of stream water temperature regimes in the conterminous USA. River Research and Applications 32:896–906.

Mauger, S., R. Shaftel, J. C. Leppi, and D. J. Rinella. 2017. Summer temperature regimes in southcentral Alaska streams: watershed drivers of variation and potential implications for Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 74:702–715.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.

Miller, J. A., and R. L. Whitehead. 1999. Groundwater Atlas of the United States: Alaska. Reston, VA.

Nowacki, G., P. Spencer, M. Fleming, T. Brock, and T. Jorgenson. 2001. Ecoregions of Alaska. Anchorage, AK.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: Community Ecology Package.

Otero, J., J. H. L’Abée-Lund, T. Castro-Santos, K. Leonardsson, G. O. Storvik, B. Jonsson, B. Dempson, I. C. Russell, A. J. Jensen, J. L. Baglinière, M. Dionne, J. D. Armstrong, A. Romakkaniemi, B. H. Letcher, J. F. Kocik, J. Erkinaro, R. Poole, G. Rogan, H. Lundqvist, J. C. Maclean, E. Jokikokko, J. V. Arnekleiv, R. J. Kennedy, E. Niemelä, P. Caballero, P. A. Music, T. Antonsson, S. Gudjonsson, A. E. Veselov, A. Lamberg, S. Groom, B. H. Taylor, M. Taberner, M. Dillane, F. Arnason, G. Horton, N. A. Hvidsten, I. R. Jonsson, N. Jonsson, S. Mckelvey, T. F. Næsje, Ø. Skaala, G. W. Smith, H. Sægrov, N. C. Stenseth, and L. A. Vøllestad. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). Global Change Biology 20:61–75.

Pederson, G. T., S. T. Gray, T. Ault, W. Marsh, D. B. Fagre, A. G. Bunn, C. A. Woodhouse, and L. J. Graumlich. 2011. Climatic controls on the snowmelt hydrology of the northern Rocky Mountains. Journal of Climate 24:1666–1687.

Peterson, E. E., and A. R. Pearse. 2017. IDW-Plus: An ArcGIS toolset for calculating spatially explicit watershed attributes for survey sites. JAWRA Journal of the American Water Resources Association 4001:1–9.

Pierce, R., C. Podner, L. Marczak, and L. Jones. 2014. Instream habitat restoration and stream temperature reduction in a whirling disease-positive spring creek in the Blackfoot River basin, Montana. Transactions of the American Fisheries Society 143:1188–1198.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience 47:769–784.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27:787–802.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2367–2373.

Quinn, T. P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. UBC Press, Vancouver, BC.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ruel, J. J., and M. P. Ayres. 1999. Jensen’s inequality predicts effects of environmental variation. Trends in Ecology and Evolution 14:361–366.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92:2073–2084.

Sandberg, E. 2016. Settlement of the Mat-Su: How Alaska’s fastest-growing borough came to be. Alaska Department of Labor and Workforce Development, Juneau, AK.

Scenarios Network for Alaska and Arctic Planning. 2017a. Historical Monthly and Derived Precipitation Products Downscaled from CRU TS data via the delta method – 2 km. University of Alaska Fairbanks.

Scenarios Network for Alaska and Arctic Planning. 2017b. Historical Monthly and Derived Temperature Products Downscaled from CRU TS data via the delta method – 2 km. University of Alaska Fairbanks.

Scenarios Network for Alaska and Arctic Planning. 2017c. Projected Monthly and Derived Precipitation Products - 771m CMIP5/AR5. University of Alaska Fairbanks.

Scenarios Network for Alaska and Arctic Planning. 2017d. Project Monthly and Derived Temperature Products - 771m CMIP5/AR5. University of Alaska Fairbanks.

Schindler, D. E., X. Augerot, E. Fleishman, N. J. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and M. Webster. 2008. Climate Change, Ecosystem Impacts, and Management for Pacific Salmon. Fisheries 33:502–506.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. Ecology 86:198–209.

Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown dam, Montana. North American Journal of Fisheries Management 23:721–731.

Schoen, E. R., M. S. Wipfli, E. J. Trammell, D. J. Rinella, A. L. Floyd, J. Grunblatt, M. D. McCarthy, B. E. Meyer, J. M. Morton, J. E. Powell, A. Prakash, M. N. Reimer, S. L. Stuefer,

H. Toniolo, B. M. Wells, and F. D. W. Witmer. 2017. Future of pacific salmon in the face of environmental change: lessons from one of the world's remaining productive salmon regions. Fisheries 42:538.

Sergeant, C. J., J. B. Armstrong, and E. J. Ward. 2015. Predator-prey migration phenologies remain synchronised in a warming catchment. Freshwater Biology 60:724–732.

Sergeant, C. J., J. R. Bellmore, C. McConnell, and J. W. Moore. 2017. High salmon density and low discharge create periodic hypoxia in coastal rivers. Ecosphere 8:1–16.

Sparks, M. M., P. A. H. Westley, J. A. Falke, and T. P. Quinn. 2017. Thermal adaptation and phenotypic plasticity in a warming world: Insights from common garden experiments on Alaskan sockeye salmon. Global Change Biology 23:5203–5217.

Steel, E. A., T. J. Beechie, C. E. Torgersen, and A. H. Fullerton. 2017. Envisioning, quantifying, and managing thermal regimes on river networks. BioScience 67:506–522.

Steel, E. A., A. Tillotson, D. A. Larsen, A. H. Fullerton, K. P. Denton, and B. R. Beckman. 2012. Beyond the mean: The role of variability in predicting ecological effects of stream temperature on salmon. Ecosphere 3:104.

Sutton, R., and T. Soto. 2012. Juvenile coho salmon behavioural characteristics in Klamath river summer thermal refugia. River Research and Applications 28:338–346.

Tillotson, M. D., and T. P. Quinn. 2017. Climate and conspecific density trigger pre-spawning mortality in sockeye salmon (*Oncorhynchus nerka*). Fisheries Research 188:138–148.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications 9:301–319.

U.S. Environmental Protection Agency. 2003. EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards. Epa 910-B-03-002:Region 10 Office of Water, Seattle, WA.

Vasseur, D. A., J. P. Delong, B. Gilbert, H. S. Greig, C. D. G. Harley, K. S. Mccann, V. Savage, T. D. Tunney, M. I. O. Connor, J. P. Delong, B. Gilbert, H. S. Greig, C. D. G. Harley, K. S. Mccann, V. Savage, T. D. Tunney, and M. I. O. Connor. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proceeding of the Royal Society B 281:20132612.

Waples, R. S., T. Beechie, and G. R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? Ecology & Society 14:1–18.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58:236–244.

Webb, B. W., D. M. Hannah, R. D. Moore, L. E. Brown, and F. Nobilis. 2008. Recent advances in stream and river temperature research. Hydrological Processes 22:902–918.

Wickham, H. 2017. tidyverse: Easily Install and Load the "Tidyverse."

Winfree, M. 2017. The influence of geomorphic and landscape characteristics on stream temperature and streamwater sensitivity to air temperature in the coastal temperate rainforest of Southeast Alaska. University of Alaska Fairbanks.

Wobus, C., R. Prucha, D. Albert, C. Woll, M. Loinaz, and R. Jones. 2015. Hydrologic alterations from climate change inform assessment of ecological risk to pacific salmon in Bristol Bay, Alaska. PLoS ONE 10.

Woll, C. 2015. Landscape-scale mapping of Pacific salmon and their freshwater habitats in the Mat-Su Basin. Juneau, AK.