Watershed Controls on Stream Thermal Regimes: Effects on Salmon Spawn Timing and Species Interactions

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Abstract

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Global surface temperatures are warming at unprecedented rates and are expected to continue to warm for the rest of the century. Yet, we know very little about how freshwater ecosystems will respond to a warmer climate. Regardless of uncertainties in global climate projections and unknown thermal responses in freshwater ecosystems, recent responses of freshwater environments to climate variation can provide important insight to future conditions. In this dissertation, I describe the role of geomorphic variation within river basins as a driver of thermal heterogeneity among streams in southwest Alaska. Further, I describe the importance of this thermal heterogeneity in supporting variation in salmon life histories and the consequences of this life-history diversity for species that directly and indirectly depend on salmon.

In Chapter 2, I explore how geomorphic variation produces intraspecific diversity in salmon spawn timing throughout a river system due to large thermal differences among tributaries within a river basin. Here, salmon spawn later in warmer tributaries draining flatter watersheds with lakes and earlier in cooler tributaries draining steeper, high elevation watersheds. Research in Chapter 3 further explores the mechanisms for heterogeneity in water temperature among streams across the geomorphic gradient. Here, I show how snowmelt buffers

streams from warmer air temperatures in steeper watersheds. In Chapter 4, I show how lakes, well-known geomorphic features in boreal river systems, affect the thermal regimes of outlet-rivers through wind driven upwelling events. Rivers draining lakes are traditionally thought to be thermally stable environments, but I show how wind action on large upstream lakes can create temperature excursions in the river by 10^{o}C in few hours. Chapter 5 explores how the variation in salmon spawn timing among streams, supported by differences in water temperature, is associated with the phenology in a riparian plant. Specifically, I test the hypothesis that a pollinator mutualism indirectly ties riparian plant flower timing to the seasonal influx of salmon resources to streams.

Taken together, this research highlights how geomorphic variation within river basins filters climate responses in freshwater streams and rivers. Thus, river drainages may express a range of reactions to environmental change due to their geomorphic complexity. Aquatic species that have adapted specific life-history strategies to features within river basins may experience and exploit local filtering of climate forcing rather than responding to regionally coordinated climate responses.

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DEDICATION

To my parents, Gerard and Margaret Lisi.

Chapter 1:

Watershed controls on stream thermal regimes: effects on salmon spawn timing and species interactions.

Introduction:

Rivers are some of the most dynamic ecosystems on earth, continuously changing through erosional processes across space and through time. The physical characteristics of watersheds control many fundamental ecological processes along the river continuum (Vannote et al. 1980, Fausch et al. 2002, Benda et al. 2004). Understanding how physical variation affects ecological function is important for a variety of issues ranging from predicting how rivers will respond to climate change to the ability of rivers to produce and support aquatic biodiversity. Still, there remains a weak understanding of the physical controls in riverine habitat and how this variation supports biodiversity and a variety of ecosystem services valuable to people.

Climate change is expected to alter the thermal regimes of streams and other freshwater ecosystems, yet we still have little understanding about how climate will manifest itself in streams and rivers from local to regional scales (Schindler 2001, Woodward et al. 2010, Isaak et al. 2010). Even through large efforts seek to downscale climate models in freshwater ecosystems, our understanding of local topographic controls of water temperature remains in its infancy (Ver Hoef and Peterson 2010, Mantua et al. 2010, Isaak et al. 2014). In addition to increases in air temperatures that may have direct effects on water temperature, this effort is complicated by indirect effects due to changes in precipitation patterns, groundwater characteristics, riparian controls on insolation, and flow regimes (Perkins et al. 2010). Given broad uncertainties of thermal responses in freshwater ecosystems, recent conditions of freshwater environments to climate variation can provide important insight for future scenarios. In this dissertation, I explore how geomorphic features and water source regulate stream thermal regimes within a river basin in southwest Alaska, and the importance of this thermal variation among streams to aquatic species that are sensitive to water temperature.

Temperature is among the most important ecological variables in nature, particularly in aquatic ecosystems dominated by ectothermic organisms (Magnuson et al. 1979, Brown et al. 2004). In fluvial environments, temperature drives many key biological traits of aquatic animals such as reproduction, metabolism, behavior and has important influences on ecosystem processes such as nutrient cycling and productivity (Allan and Castillo 2007). Furthermore, variation in stream thermal regimes has substantial implications for the biota that inhabit these systems (Poole and Berman 2001, Olden and Naiman 2010). Here, I explore how salmon (*Oncorhynchus* spp.) have evolved certain aspects of their life-history to cope with the thermal challenges in the stream environments where they spawn. In particular, I show how water temperature, as influenced by watershed geomorphology, creates substantial variation in the timing of salmon spawning among tributaries of rivers.

Pacific salmon are undoubtedly an important species for a variety of people and wildlife that depend on salmon for their subsistence and livelihood across the north Pacific. An impressive amount of work shows the role of salmon as a resource subsidy in freshwater and terrestrial environments (Gende et al. 2002, Schindler et al. 2003, Wipfli and Baxter 2010, Bentley et al. 2012). Semelparous, anadromous salmon accumulate the majority of their growth in the ocean before returning to their natal freshwater rearing habitat to spawn and die. Marine-derived nutrients from salmon carcasses, eggs, and flesh permeate into aquatic and terrestrial food-webs often through a variety of trophic pathways (Schindler et al. 2003, Wipfli and Baxter

2010). Pacific salmon are also characterized by extensive intraspecific life-history diversity that is expressed both among and within the watersheds they use for spawning and rearing (Quinn 2005). In particular, inter-population differences in spawn timing produce substantial spatial variation in the seasonal timing of when salmon-derived subsidies are available to predators and scavengers of salmon (Schindler et al. 2010). Given a diverse schedule of salmon spawning across a river landscape, scavengers and predators can move to other spawning grounds to potentially extend the duration of their seasonal foraging (Ruff et al. 2011, Schindler et al. 2013).

While the importance of these cross-ecosystem subsidies can directly benefit consumers, much less is known about the secondary effects of these subsidies in supporting biodiversity in recipient communities. In particular, diversity within a subsidizing species may facilitate intraspecific variation in the species with which it interacts but such transmission of intraspecific diversity is not well understood. This dissertation shows how variation in the biological attributes of one species can produce variation in other species if they are linked through ecological interactions (e.g., predator-prey, mutualisms). Here, I explore indirect pathways in which scavengers of salmon interact with the bloom timing of riparian plants. Through this interaction, I show that salmon transmit their spawn-timing phenology, as regulated by differences in water temperature, to the bloom timing of riparian flowers that depend on pollination by a carrion flies that are attracted to salmon carcasses during spawning events.

The majority of this work was conducted in the Togiak Wildlife Refuge and the Wood-Tikchik State Park in the Bristol Bay of southwestern Alaska. These watersheds are essentially pristine from the perspective of land-use and salmon populations remain strong even through there is substantial annual harvest by commercial fisheries. In addition, these watersheds express substantial thermal variation among streams, but the mechanisms that explain the variation are not well described and we are only beginning to understand the importance of this variation in boreal river networks. With this research, I hope to gain critical insight into how landscapes impact water temperature, the ecology of animals that live in these diverse ecosystems, and how they may respond to future conditions.

Descriptions of individual chapters

Chapter 2 Association between geomorphic attributes of watersheds, water temperature, and salmon spawn-timing in Alaskan streams

In chapter 2, I sought to understand the association between geomorphic attributes of streams and their watersheds with stream water temperature. I show how broad characteristics of watershed geomorphology such as slope, elevation, drainage area and presence of lakes, control average stream thermal conditions. I found that the watershed features explain about (76%) of the variation in average summer temperature among streams. I examined how these habitat features are associated with salmon spawn timing. I suggest that salmon spawn timing patterns emerge through the effects of temperature and physical disturbance on the development of embryos and disease incidence in adults. Sites supporting early spawning populations tend to drain steeper and smaller watersheds, while late spawning populations occur in streams draining large, lower gradient watersheds with lakes in the drainage network. In addition, I show that stream temperature and spawn timing among streams have little spatial correlation across the landscape, thereby producing a fine-scale mosaic of spawn timing across the river basin. These results demonstrate that geomorphology and hydrology interact to produce a heterogeneous thermal template for natural selection to influence salmon spawn timing across river basins.

Chapter 3 *Topography and water source control stream thermal sensitivity to air temperature*

As described in chapter 2, the influence of topography is implied as a filter of climate that sets a unique thermal template across the river basin. In the 3rd chapter, I build on this work to quantify how these streams respond to daily changes in air temperature and ask how this variation is organized spatially within river basins due to differences in topography and water source among sub-watersheds. I hypothesized that many of the streams in southwest Alaska, in particular those draining higher elevation basins, are cooled by snowmelt (or groundwater derived from spring snowmelt) during the summer months. Here, I use hydrogen and oxygen stable isotopes of water to estimate summer contribution of snowmelt and rainfall to 80 boreal streams. These data suggest that snow-melt can contribute majority of the summer hydrology to steeper, higher elevation watersheds while lower sloped watersheds derive their surface water from rain. To understand the sensitivity of these streams to air temperature, I simultaneously analyzed stream summer temperature time-series with multivariate autoregressive state-space models. Streams from low-elevation watersheds were 5-8 times more sensitive to changes in summer air temperature compared to streams draining steeper topography, whose flows were dominated by snowmelt. Further, the watershed response seemed to be more homogenous during summers following winters with less snow pack, and therefore, a higher ratio of rain:snow in summer stream discharge. This suggests that not all streams will respond the same way to climate, and effects of changing climate will be highly heterogenous within river basins.

Chapter 4 *Wind-driven upwelling in lakes destabilizes thermal regimes of downstream rivers*.

The previous two chapters characterize patterns and drivers of thermal variation on unconnected 1st to 4th order tributaries. Here, I describe variation further downstream in larger – main stem rivers that had very unique and undescribed thermal variation. In western Alaska, main stem rivers often drain large lakes and the mixing characteristic of the lake control the thermal regime of downstream rivers. Lakes are generally assumed to provide warm surface water to downstream rivers that stabilizes lotic temperature regimes. Here, I examined the thermal variation in streams and rivers from 24 watersheds without lakes and 15 draining lakes that varied in their surface area. I found that rivers draining large lakes had summer thermal regimes with 1.8X more variation than both rivers draining smaller lakes and watersheds lacking lakes. I show that this variation is not driven by daily oscillations in temperature as in smaller streams, but a result of stochastic variation by wind driven upwelling events. I speculate that wind driven upwelling may be a common source of thermal variation in rivers containing large stratified lakes, making them more thermally variable than previously appreciated. Due to the magnitude and frequency of upwelling, I suggest that this thermal variation may be ecological relevant, but remains unexplored.

Chapter 5: *Spatial variation in marine subsidies influences riparian phenology through plant-pollinator mutualisms.*

In previous chapters, I show how the landscape and hydrology produce substantial spatial variation in water temperature that influences salmon spawning and therefore directly available for consumption by scavengers and predators. Here, I explore how this association propagates into adjacent riparian areas (Lisi and Schindler 2011). We know from other studies that streams and their adjacent riparian areas are closely linked through food webs and material fluxes (Baxter et al. 2005). In chapter 5, I examined fly-pollinated plants in the carrot family (Apiaceae) that flower at the same time as salmon arrive to streams to spawn. I use nitrogen and carbon stable isotopes to show how blowflies (Calliphoridae) are an important consumer of salmon carcasses as larvae and pollinate Apiaceae as adults. I also monitored the flowering phenology of kneeling

Angelica (*Angelica genuflexa*) across salmon bearing streams (n=20) that differ in the timing of salmon spawning. I found that salmon spawning date explained a substantial amount of the observed seasonal variation in peak flowering dates among streams. Together, these results suggest that spatial variation in salmon spawning timing is transmitted via the phenology of salmon-dependent consumers that affect the bloom timing of a common riparian plant.

Looking forward:

Given the cultural, economic and ecological importance of aquatic resources in southwestern Alaska, there is pressing need to develop scenarios of the trajectories and magnitude of climate driven changes to aquatic ecosystems in this region. From the combination of these studies, we can derive some general conclusions about how watersheds are likely to respond to future climate change and the impact on commercially and ecologically important species like salmon. The responses to a changing climate are going to be quite complex within an individual watershed. The results of this work highlight that ongoing climate change will have much different impacts on stream thermal regimes within the same river basin due to the physical characteristics of stream catchments. These results hold substantial promise to further constrain stream temperature scenarios under warmer climates in topographically complex watersheds and assess the potential impact on wildlife

This research shows that the current thermal variation across a river basin is important to wild salmon and the species that directly or indirectly rely on salmon. However, some salmon populations may be more susceptible to changes in air temperature compared to watersheds that are buffered by topography and snowmelt. It may be possible that behavioral, adaptive, or even evolutionary mechanisms by salmon can alleviate the changes that are likely to occur in these watersheds (Reed et al. 2011). My hope is that this dissertation contributes to our understanding of how landscapes support biodiversity and function and how ecosystems may respond to pressures on theses landscapes. If societies can conserve the processes that maintain intraspecific variation in genes¸ organisms, and ecosystems, we may be better buffered to future conditions brought by climate change and anthropogenic pressures on the environment.

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Chapter 2:

Association between geomorphic attributes of watersheds, water temperature, and salmon spawn-timing in Alaskan*

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Introduction

Individual species often show phenotypic differences among populations in traits such as reproduction timing, diet, body size, age at maturity. This intraspecific trait diversity can stabilize and enhance a variety of ecosystem processes and services, buffer populations from extreme temporal fluctuations in population density, and increase population persistence amid changes in environmental conditions (Luck et al., 2003; Schindler et al., 2010; Bolnick et al., 2011). While population ecology increasingly recognizes the importance of intraspecific trait diversity, less attention has been given to understanding the mechanisms and habitat attributes that produce this variation. Landscapes characterized by heterogeneous habitat conditions may support intraspecific variation through the evolution of life-histories adapted to certain habitat conditions (Southwood, 1977; Poff and Ward, 1990; Quinn et al., 2001; Lytle and Poff, 2004; Jonsson and Jonsson, 2011), yet little information is available on the relative role of regional and local physical processes in generating intraspecific variation. Understanding the associations between physical variation in landscapes and intraspecific diversity is critical for setting conservation goals and protecting habitat that provides ecosystem services specific to species that express intraspecific diversity (Beechie et al., 2006; Bisson et al., 2009).

Pacific salmon (*Oncorhynchus sp.*) exhibit considerable intraspecific trait diversity among populations (Quinn, 2005). Specifically within a river basin, salmon display substantial variation in the seasonal timing of entry to streams and rivers during spawning (Webb and McLay, 1996; Boatright et al., 2004; Beechie et al., 2008; Doctor et al., 2010; Ruff et al., 2011). At larger spatial scales (western North America) spawn timing is progressively earlier for several species at higher latitudes associated with large-scale changes in dominant climate regimes (Beechie et al., 2008). Yet, considerable uncertainty remains about the physical features of watersheds that produce variation in spawn timing among the watersheds of individual river basins, a spatial scale that has important implications for producing population diversity in salmon that is significant to sustainable commercial fisheries, and mobile wildlife that depend on salmon resources (Schindler et al., 2010).

Prevailing theory proposes that adult salmon spawn at a date that allows their offspring to emerge during a time window that optimizes growth the following spring (Quinn, 2005). Variation in spawn timing is most often tied to the variation in water temperature among spawning sites (Beechie et al., 2008). Cold streams tend to support earlier spawning salmon populations, whereas warmer streams tend to have salmon populations that spawn weeks to months later because of accumulated thermal degree differences eggs require for successful development (Webb and McLay, 1996; Quinn, 2005). However, warm water temperatures are also associated with increased disease prevalence in adult sockeye salmon (Bradford et al., 2010), where successful adult salmon delay spawning until the risks of encountering warm temperatures has declined (Crossin et al., 2008). While there is a general understanding of controls on salmon spawning, there are few studies that relate watershed controls on stream temperature with the spatial and temporal patterns of salmon spawning.

The thermal and physical template from reach to basin scale is largely dictated by a hierarchical arrangement of geologic and topographic features, which are ultimately formed by forces such as glaciation and plate tectonics (Frissell et al., 1986; Montgomery, 1999; Beechie et al., 2010). Basic physical attributes of each watershed (such as slope, elevation, and watershed area) interact with local climate to produce the long-term conditions in stream temperature, sediment characteristics, and stream flow regimes, which likely have selective effects on life history traits of salmon (Beechie et al., 2008). Despite such system-specific observations at the redd, reach, or single stream scale, we lack a general understanding of the geomorphic conditions that are associated with seasonal spawn timing in Pacific salmon among streams at the basin scale.

Here, we examine the association between geomorphic attributes of streams and their watersheds, stream water temperature, and the seasonal spawn timing of sockeye salmon throughout a single river basin in southwest Alaska. We show that simple, broad characteristics of watershed geomorphology (watershed slope, elevation, drainage area) and the presence of lakes are correlated with-stream thermal conditions, and hypothesize that spatial patterns in salmon spawn timing emerge through the effects of temperature and physical disturbance on the development of embryos and disease incidence in adults.

Methods

Study site

Research took place in the Wood River basin (59^{o}20’ N., 158^{o}40’ W.) in the Bristol Bay region of southwest Alaska (Fig. 2.1). The majority of the Wood River basin is within the Wood-Tikchik State Park; a system comprised of five large, interconnected lakes fed by numerous small streams that drain southward through the Wood River into Bristol Bay. Water temperatures vary substantially among streams during summer months, ranging from the temperature of groundwater (~ 3.5°C) to as warm as 20°C (Armstrong et al., 2010). Salmon return annually to streams, rivers, and beaches throughout the entire system and spawn between mid-July through late October (Schindler et al., 2010). From 2009-2011, the date of sockeye salmon (*Oncorhynchus nerka*) entry to their spawning ground was recorded after repeat visitations to each stream until we confirmed that salmon were actively spawning. In these systems, sockeye salmon generally initiate spawning within two days of entering the stream; and salmon entry to the streams is typically predictable within 2-5 days each year (Moore and Schindler, 2010). Active spawning typically extends for about 3-4 weeks once fish have entered a spawning site. While the majority of sockeye salmon spawning in the Wood River system occurs on lake beaches and in large rivers connecting lakes, we have focused on stream-spawning populations here.

Environmental data set

We monitored summer water temperatures in individual tributaries throughout the Wood River basin in 33 streams that support sockeye salmon populations and 3 that do not. I-button temperature recorders (Maxim Integrated Products, Sunnyvale, CA) were placed in the mouths of these tributaries to record temperature at 90-min intervals with 0.125 to 0.5°C resolution from 30 June to 1 September in 2010. Temperature loggers were suspended 3-5 cm above the streambed. All loggers were cross-calibrated before the start and at the end of the study and were found to be within ±0.5°C of each other. We corrected the temperature loggers to a standard calibration and then reduced the data to a single average summer temperature for each stream (Table 2.1).

ArcGIS (v10.0, Environmental Systems Research Institute, Redlands, CA, USA) was used to identify the location of the center of each stream's watershed (centroid) by latitude and longitude, and to estimate total watershed area, average elevation, average watershed slope (degrees) from a digital elevation model, and total area of lakes in each watershed. Large lakes were identified with polygon areas > 80,900 m^2 and small lakes and ponds > 800 m^2 at 50 m^2 resolution. Last, we used stream particle size from Wolman pebble counts (Wolman, 1954) in the upper, middle, and lower segments of the main stem of each stream where salmon spawn. The particle size was summarized by a common metric for scaling pebble counts with the 84th percentile (D84) of the cumulative particle size distribution (Pess, 2009). We hypothesized that watershed area likely controls the heating capacity of the stream; average watershed slope effects the hydrologic residence time; and watershed elevation influences whether precipitation is captured as rain or snow (Caissie, 2006). We presume that watersheds with lakes in their headwaters provide warm surface water during the summer months through the effects of lakes have on residence time in watersheds (Jones, 2010). While particle size may not be directly associated with stream temperature, it is correlated with several stream characteristics including sediment transport and supply, stream power, and channel gradient (DeVries, 2002; Buffington et al., 2004). Furthermore, particle size can characterize suitable salmon spawning habitat where salmon usually require smaller gravel to dig and incubate their eggs (Kondolf and Wolman, 1993).

Data analyses

First, we explored the associations between stream temperature and broad-scale geomorphic characteristics of watersheds such as average watershed slope, average elevation, watershed area, total lake area, and particle size (D84) for each stream. Multivariate statistical analyses were then performed to determine controls on patterns of salmon spawn timing among streams of similar geomorphology. All habitat variables were log-transformed prior to analysis to control for differences in scale among descriptor variables. Streams were separated for comparison among four categories for analysis, with one category for non-salmon streams and three spawning periods: early, middle, and late spawning based on the 33rd and 66th percentile of a cumulative normal distribution of the average spawning date for 33 streams in the Wood River basin from 2009-2011 (Early: 13 July to 22 July; Mid: 23 July to 30 July; Late: 31 July to 18 August). A normal probability plot (qqplot) suggested that these data were normally distributed (Shapiro-Wilk test W = 0.98, $p = 0.42$).

Principal components analysis (PCA; Pearson, 1901) on the correlation matrix was used to summarize dominant gradients of environmental variability among streams. Stream scores on principal component axis 1 and 2 were regressed (using ordinary least-squares linear regression) against stream temperature and spawn timing date. We used Akaike's information criterion (AIC; Burnham and Anderson, 2002) to compare correlations with temperature and spawning date against three linear models according to the equation: $y = \beta_{0+} \beta_{1*}X1 + \beta_{2*}X2$, where β_0 = the intercept, β_1 and β_2= the slopes, and ε = the residual error.

$\beta_0 + \beta_1*PC1 + \beta_2*PC2 + \varepsilon$ (1)

$\beta_0 + \beta_1*PC1 + \varepsilon$ (2)

$\beta_0 + \beta_1*PC2 + \varepsilon$ (3)

Third, we tested the null hypothesis that no difference in environmental characteristics occurs between streams grouped by salmon spawn timing using permutational multivariate analysis of variance (perMANOVA) (Anderson, 2001), and tested for differences in multivariate homogeneity of group dispersion (Anderson, 2006). Last, we tested for spatial autocorrelation in stream temperatures and spawn timing using a Mantel test (Mantel, 1967) to compare pairwise temperature and spawning date differences among streams to geographic distances between stream mouths. All multivariate data analyses were conducted using the *vegan* (Oksanen et al.,

2010) and *biostats* (McGarigal, 2009) packages in the program R (R Development Core Team, 2011).

Results

How are spawn timing and stream temperature associated with geomorphology?

Sockeye salmon spawning date was positively correlated with summer stream temperature ($r^2 = 0.42$, $p < 0.0001$; Fig. 2.2). Later spawning salmon populations were found in warmer streams, while earlier spawning populations were found in cooler streams. Several watershed characteristics were significantly correlated with average summer temperature. Streams with larger watershed areas had warmer temperatures ($r^2 = 0.34$, $p < 0.01$; Fig. 2.3A). Streams were cooler in steeper gradient watersheds ($r^2 = 0.22$, $p < 0.01$; Fig. 2.3B). Higher average watershed elevation was also correlated with cooler stream temperatures ($r^2 = 0.16$, $p < 0.05$; Fig. 2.3C). The total lake area within watersheds had a strong positive effect on stream temperature where larger lakes contribute warmer outlet water, averaging 12^{o}C, while smaller lakes had less influence on stream temperature (Figure 2.3D). Watersheds with total lake areas >1 km^2 were on average 3.9°C warmer than streams with smaller lakes or no lakes (unpaired student's *t*-test, $df = 18$, $t = 7.1$, $p < 0.0001$). Stream temperature had no association with stream particle size, ($r^2 = 0.001$, $p = 0.85$) or with proximity to the ocean by latitude of the watershed centroid ($r^2 = 0.0004$, $p = 0.9$).

Which environmental characteristics are associated with salmon spawn timing ecotypes?

Principal components analysis summarized a large proportion (84%) of the variance in environmental stream characteristics (PC1 = 49%, PC2 = 35%). Average watershed elevation, gradient, and particle size distribution all had significant loadings on PC1 (Fig. 2.4; Table 2.2). Streams with late spawning populations were found in low elevation and low gradient watersheds (Fig. 2.4A). Streams that did not support salmon or had early spawning populations were grouped together in habitats with higher average elevations, steeper gradient watersheds, and larger streambed particle size (Fig. 2.4A). The second PCA axis was explained by a gradient of watershed area and total lake area (Fig. 2.4A). Mid-spawn timing groups were found in small watersheds, lacking lakes and having small particle sizes (Fig. 2.4A). Late spawning streams had large watershed areas, with streams interrupted by lakes (Fig. 2.4A). Non-salmon streams were best described in steep, high elevation streams and with large substrate (K3, Cottonwood Cr., and Rainbow Cr., Table 2.1). Visually, spawn timing groups were separated in ordination space by their environmental characteristics.

The environmental characteristics match predicted associations with variation in stream temperature (Fig. 2.4B) where 76% of the variation observed among streams in average summer temperature was explained from linear associations with PC1 ($r^2 = 0.21$, $p < 0.01$) and PC2 ($r^2 = 0.53$, $p < 0.001$; Fig. 2.5A). This suggests that the longer water residence time associated with larger lake and watershed areas explain most of the variation in summer temperatures among streams, but additional variation in temperature is captured by differences in elevation and watershed slope. We tested whether or not this additional variation captured by PC1 was significant. A multiple regression model including both PC1 and PC2 (model 1) explained substantially more of the variation among average stream temperatures than the models that only included only PC1 or PC2 (model 3 ΔAIC = 20, model 2 ΔAIC = 41). Salmon spawning date was also best reflected in the multiple regression of PC1 and PC2 ($p < 0.001$, $r^2 = 0.45$; Fig. 2.5B), which provided the lowest AIC score (AIC = 215). Model 3 has some support as the next best candidate model (ΔAIC = 5), but essentially no support for model 2 (ΔAIC = 13). These results show that watershed geomorphology used in our PCA captured a substantial amount of the variation in stream temperature and spawn timing.

Do spawn timing groups differ in their mean environmental characteristics?

We detected a significant difference between non-salmon, early, middle, and late spawning group means; that is streams within spawn timing groups are more similar to one another than among other groups ($p < 0.001$, $F = 6.8_{3,32}$; Fig. 2.4A). Pairwise comparisons between groups detected significant differences among all pairwise comparisons of group means (Table 2.3, lower diagonal). Non-salmon streams were substantially different in their environmental characteristics than streams with salmon. In particular, late versus early spawning streams were more different than mid versus late or mid versus early (Table 2.2; Fig. 2.5).

Are there differences in variation in the habitat characteristics expressed among spawn timing ecotypes?

We found some significant differences in dispersion of watershed characteristics among run-timing groups (Table 2.3 upper diagonal; Fig. 2.5). Late spawning populations occupied a larger range of habitats than non-salmon streams, showing the largest difference in dispersion and mean (Table 2.3). The late spawning period dispersion was significantly different than the dispersion between early-, mid-, or non-salmon sites. The late spawning group expressed the largest average distance to the centroid of their group, suggesting a larger array of habitat characteristics that support late spawning ecotypes. Non-salmon streams had the lowest differences among groups with shorter distance to the group centroid among the three streams sampled.

3.5 How are streams of similar characteristics and spawn timing distributed across the Wood River basin?

Spawn timing groups were distributed broadly throughout the Wood River basin (Fig. 2.1). We used a Mantel test to compare pairwise temperature and spawning date differences among streams to the geographic distances between stream mouths to evaluate the degree of spatial autocorrelation in water temperatures and spawn timing among streams. We found a very weak correlation between stream distance and temperature differences ($r = 0.12$, $p = 0.051$). Large differences in temperature (> 8^{o}C) were seen among pairs of streams that are near (< 1.5 km) and far (> 50 km) from each other (Fig. 2.6A). Our results suggest no correlation between stream distance and spawn timing differences ($r = 0.057$, $p = 0.16$). Large differences in spawn timing (> 25 days) are found among pairs of streams located both near and far from each other (Fig. 2.6B).

Discussion

Our results suggest that differences in topography and geomorphic features among the watersheds of individual streams in the Wood River basin are associated with variation in water temperature and, subsequently, the spawn timing of sockeye salmon. Our results highlight differences in the mean and distribution of environmental attributes found among habitats for three spawn timing periods and streams that do not support salmon. Together, these results provide evidence that topography and geomorphic features of watersheds support intraspecific diversity in salmon spawning life histories at the basin scale (Beechie et al., 2006, 2008; Jonsson and Jonsson, 2011). Finally, this heterogeneous environment is spread throughout the Wood River basin, generating a mosaic of spawn timing (Fig. 2.6) that may have important implications for animals that depend on salmon. While our results provide correlative associations, they do not provide a mechanistic evidence of watershed controls on stream temperature or salmon spawning. Nevertheless, such associations between geomorphic features and thermal regimes in streams provide a powerful basis to evaluate how intraspecific diversity may be expressed differently among watersheds at the basin scale depending on how landscape correlates to the thermal regimes of individual streams.

Geomorphic features likely affect the temperature regimes among streams through several mechanisms in the Wood River basin. Topography influences the heating capacity of streams through shading (aspect, riparian vegetation) and hydrologic controls on residence time, water source (rain/snow), and groundwater exchange (Isaak and Hubert, 2001; Pool and Berman, 2001; Caissie, 2006). Watershed area is an important variable related to temperature in our analysis because it controls the volume of water retained in each watershed, stream width, and heating capacity of the stream; where larger watersheds were warmer presumably because of longer surface water residence time (Caissie, 2006). Steeper gradient watersheds were cooler likely because they had snowmelt-dominated discharge (Lisi et al unpublished– see chapter 3), constrained valley width, shaded by topography and dense riparian vegetation, and had shorter surface residence times (Subehi et al., 2009; Isaak and Hubert, 2001). Lower gradient, meandering streams likely were warmer because of greater exchange with atmospheric temperature, longer surface water residence, or differences in vegetation that affect shading (Isaak and Hubert, 2001). Lakes, with surface areas > 1 km^2, had a significant effect on the thermal regimes of streams in Wood River basin in both steep and low gradient catchments, providing warm surface water to outlet streams during the late summer and fall (Jones, 2010). Smaller watersheds were likely cooler as their discharge predominately emerged from groundwater springs in deep alluvial channels (e.g., Baxter and Hauer, 2000; Isaak and Hubert, 2001; Pool and Berman, 2001). Many of the watersheds in the Wood River basin show combinations of these features and contain heterogeneity at the stream segment scale, yet the average thermal conditions recorded at the stream mouth seem to have a strong association with average watershed-scale attributes, which over longer timescales exert selective forces on salmon populations.

Our results show clear associations between watershed features of streams and salmon spawn timing, relationships likely mediated by physical controls on stream temperatures. Warmer streams in the Wood River basin were highly correlated with later spawning ecotypes, while cool streams were associated with earlier spawning ecotypes. These results are consistent with the hypothesis that fish have adapted later spawning schedules in warmer water where the rate of embryonic development requires less incubation time to the date of hatching or emergence (Quinn, 2005; Beechie et al., 2008) or where prevalence of disease in spawning adults has delayed spawn timing in warm sites (Crossin et al., 2008).

Our results also demonstrate that geomorphology and hydrology interact to affect the thermal regime of streams and, therefore, the evolution of salmon spawn timing within river basins (Montgomery, 1999). For example, the results of this study also show more variation in the types of streams that support late spawning compared to types of habitats that support early running populations. Streams such as Elva, Little Togiak River (LTR), and Grant all support late runs of sockeye, yet they have some physical characteristics of early running streams (large particle size, high gradient watersheds, and high elevation watersheds). However, these watersheds contain lakes that interrupt stream flow. Spawning populations in these streams have likely adapted to the warmer thermal conditions occurring in outlet tributaries. Habitat features such as lakes can create thermal diversity within stream networks (Jones, 2010) that would usually support earlier spawning sockeye populations. The presence of lakes explains why we found a larger number of habitat conditions that generate later spawning ecotypes than habitats associated with earlier spawning populations. In fact, many outlet populations show phenotypic differences in body size, where the largest fish use outlet habitats compared with smaller bodied fish that adapted in nearby streams without lakes (Roni and Quinn, 1995). Additionally, outlet emergent fry commonly show rheotaxis by swimming upstream to nursery lakes compared to the downstream migration of inlet-tributary populations (McCart, 1967).

Streams that currently do not support salmon have high gradient watersheds and cold stream temperatures in the Wood River basin. Cottonwood Creek typically runs dry at the lake outlet during drier periods of the summer and flooding occurs during major rain events, which is a likely reason why salmon are not able to enter this stream to spawn. K3 has similar habitat characteristics (elevation, watershed slope, particle size, watershed size and lacks a lake) as Joe, Allah, and Cabin Creeks, but currently does not support self-sustaining sockeye salmon populations (see Table 2.1). However, salmon that occupy these high gradient streams actually spawn in lower gradient reaches near the outlets of the streams and on beaches adjacent to where the streams discharge into lakes. Our analyses only consider average watershed slopes while reach-specific habitats may allow some low levels of salmon spawning at finer spatial scales (Baxter and Hauer, 2000; Beechie et al., 2008).

Landforms and alluvial deposits along stream segments can also create heterogeneity in salmon spawn timing where hyporheic groundwater exchange allows favorable spawning conditions of temperature and oxygen for egg incubation and emergence success (Baxter and Hauer, 2000). We identified several secondary topographic features that contributed to variation found among spawn timing groups that were likely influenced by groundwater. For example, mid-spawning populations from A, C, and Mission creeks have small watersheds (1.1 to 3.5 km^2), cool summer temperature and small particle sizes with obvious groundwater inputs in their headwaters (see Table 2.1). Even though these spring-fed streams are extremely cold during the summer (consistently ~ 4.6^{o} C), they have later salmon spawn timing than expected from average summer temperatures. Stream thermal regimes in this study were compared during the summer months when seasonal differences between streams during were more distinct. However, these spring fed streams have relatively warmer conditions during winter months at 2-3^{o}C compared to other early spawning streams with colder temperatures during the winter (1-0^{o}C). Salmon adults delay entry into these streams likely because their embryos accumulate the majority of their developmental degree days in relatively warmer winter habitats.

Last, our results suggest that spatial heterogeneity in watershed attributes translates into temporal heterogeneity in salmon residence among streams. Adjacent streams can be characterized by substantial temperature differences (> 8°C) rather than large-scale or lake-specific patchworks of similar temperature streams. This produces a fine-grained mosaic of available resources for mobile consumers such as bear, gulls, and resident fishes that are able to move among spawning sites to extend the duration of time that spawning salmon are available for consumption (Ruff et al., 2011; Schindler et al. 2013). Spatial variation in spawn timing is also reflected in the bloom timing of riparian plants that are pollinated by insects that rely on salmon carcasses (Lisi and Schindler, 2011). Growing evidence from other ecosystems suggests that mobile animals (mainly herbivores) respond to landscape-level asynchrony in resources by altering their distributions to match with the distribution of their food (Fryxell et al., 2005). The landscape features and hydrology that produce substantial spatial variation in salmon availability has created a dependable schedule of salmon resources available to mobile consumers across the Wood River basin. For example, resident fishes that rely on salmon eggs, can move among tributaries of streams to extend the seasonal duration of salmon resources (Ruff et al., 2011) because salmon are functionally only available to stream consumers once they have entered streams to spawn. Within an individual salmon population unique to each stream (McGlauflin et al., 2011; Ruff et al., 2011), salmon are available to scavengers and predators for 3-4 weeks. If we consider the range in salmon availability among streams in the Wood River basin, salmon are available to consumers for 2 to 3 months (Schindler et al., 2010). Thus, timing of salmon spawning can have a major impact on the duration, abundance, and growth of terrestrial and aquatic animals that rely on salmon.

Conclusions

This study demonstrates significant variation in spawning among sockeye salmon within a single river basin. Our results suggest that the temperature salmon encounter on their spawning grounds depends on geomorphic conditions (slope, elevation, area, presence of lakes) specific to each stream watershed. Such associations between geomorphic features and thermal regimes in streams provide a basis to evaluate how ongoing climate change may be expressed differently among watersheds at the basin scale depending on how landscape affects the thermal regimes of individual streams and, therefore, the susceptibility of salmon populations to changing climate conditions. Conservation strategies for salmon should consider maintaining the networks of habitat used by salmon not only to maintain evolutionary potential in salmon stocks but also to provide options in foraging locations for wide ranging consumers that rely on the seasonal pulses of salmon resources for maintaining their fitness (Schindler et al., 2010). By conserving the geomorphic conditions and hydrologic processes that produce intraspecific variation in salmon and heterogeneity in habitat conditions, species and ecosystems may be more resilient to future conditions.

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Table 2.1:
Environmental characteristics for each stream characteristic: location by watershed centroid by latitude and longitude, average summer temperature, watershed areas (WS area), watershed slope (WS Slope), watershed elevation (WS elev.) particle size (D84), total Lake area, salmon spawning day of year (Salmon DOY) and the principal component scores for the first two axes (PC1 and PC2). Streams marked with an asterisk do not support salmon.

Stream	Lat (°N)	Long (°W)	Salmon DOY	Ave. temp. (°C)	WS area (km)	WS elev. (m)	WS slope (°)	D84 (mm)	Lake area km^2	PC1	PC2
6th	59.58	-158.94	206	7.1	1.3	160	6.1	37	0.00	0.84	1.82
7th	59.59	-158.93	204	6.9	2.0	116	8.0	35	0.00	0.95	1.66
A	59.58	-159.12	210	3.6	1.1	247	22.9	35	0.00	-0.59	2.14
Allah	59.41	-158.68	201	5.7	9.5	278	19.3	134	0.00	-1.79	0.20
Bear	59.28	-158.83	200	8.1	13.8	199	12.7	32	0.04	0.14	0.69
Berm	59.60	-158.81	203	5.6	2.2	185	17.6	44	0.00	-0.33	1.60
C	59.58	-159.15	211	4.7	1.9	139	13.5	19	0.00	0.90	2.11
Cabin	59.62	-158.89	203	5.7	4.9	354	22.4	99	0.00	-1.85	0.74
Cold	59.51	-158.91	203	5.6	18.3	258	17.0	77	0.00	-1.13	0.13
Cottonwood*	59.64	-159.05		6.4	9.9	502	28.6	157	0.00	-2.80	0.14
Eagle	59.32	-158.66	211	7.5	4.1	80	7.3	46	0.01	1.12	1.10
Elva	59.62	-159.15	214	9.3	31.0	358	25.6	168	1.16	-2.29	-1.38
Fenno	59.39	-158.77	204	8.3	38.4	192	13.2	72	0.00	-0.61	-0.28
Grant	59.82	-158.56	221	11.1	123.5	240	7.0	71	8.40	0.24	-3.49
Hansen	59.33	-158.68	200	7.1	2.6	88	7.7	42	0.02	1.08	1.41
Happy	59.36	-158.68	194	6.5	18.0	245	12.5	66	0.00	-0.70	0.17
Hidden	59.52	-158.76	212	10.4	8.3	171	14.1	98	0.30	-0.74	0.11
Ice	59.34	-158.96	194	8.6	93.1	185	11.2	57	0.25	-0.20	-0.90
Joe	59.61	-158.91	202	7.1	10.8	414	24.5	115	0.00	-2.22	0.25
K3*	59.49	-159.01		5.7	19.0	382	24.3	110	0.01	-2.12	-0.06
Kema	59.51	-158.70	210	9.7	20.4	115	6.0	41	0.76	1.15	-0.36
LTR	59.61	-159.22	226	11.5	80.7	244	23.9	112	8.10	-1.18	-3.27
Lynx	59.50	-158.87	214	10.9	25.6	199	14.8	97	1.67	-0.75	-1.29
Mission	59.29	-158.58	208	4.6	3.5	127	9.2	36	0.00	0.73	1.37
Moose	59.71	-158.51	218	11.6	94.3	114	4.3	35	3.61	1.80	-2.23
Nerka Bear	59.49	-158.65	215	12.6	10.6	43	2.3	80	1.50	2.35	-0.90
Pick	59.53	-159.09	201	5.9	20.1	101	7.9	29	0.08	1.24	0.43
Pike	59.45	-158.52	215	10.3	51.6	53	2.1	43	1.30	2.74	-1.35
Rainbow*	59.72	-159.20		5.9	65.6	493	25.9	80	0.01	-2.13	-0.54
Sam	59.61	-158.95	202	7.4	10.0	358	20.2	84	0.12	-1.62	0.31
S. Salmon	59.23	-158.64	218	10.1	31.8	74	4.3	30	0.55	2.09	-0.34
Stovall	59.49	-158.56	214	12.3	30.8	58	2.6	45	0.87	2.40	-0.84
Teal	59.49	-158.76	209	8.6	10.6	100	7.0	48	0.14	0.92	0.41
Uno	59.71	-158.74	203	6.2	17.5	219	12.6	39	0.00	-0.13	0.49
Whitefish	59.25	-158.65	218	11.0	10.1	45	2.9	31	0.99	2.91	-0.06
Yako	59.26	-158.74	204	6.7	13.3	175	9.3	88	0.10	-0.37	0.02

Table 2.2

Linear correlations between original variables and the principal component scores (vector loadings)

	PC1	PC2
Watershed Area	-0.02	-0.68
Elevation	-0.61	-0.01
Watershed Slope	-0.60	0.12
Lake Area	0.14	-0.66
Particle Size D84	-0.48	-0.31

Table 2.3

The *F* statistics for pairwise comparisons of permutational multivariate analysis of variance (below the diagonal), which tests the centroid differences between spawning groups (above the diagonal are the *F* statistics for the test of homogeneity of multivariate dispersion, which compares the spread about the centroid for each spawn timing group; significant codes for each pairwise comparison given as $p < 0.01$ '**' $p < 0.05$ '*')

	Early	Late	Mid	No Salmon
Early	---	6.8*	0.1	3.0
Late	7.5**	---	9.0*	6.4*
Mid	3.8**	6.0**	---	1.8
No Salmon	3.5*	4.4**	8.7**	---

Figures

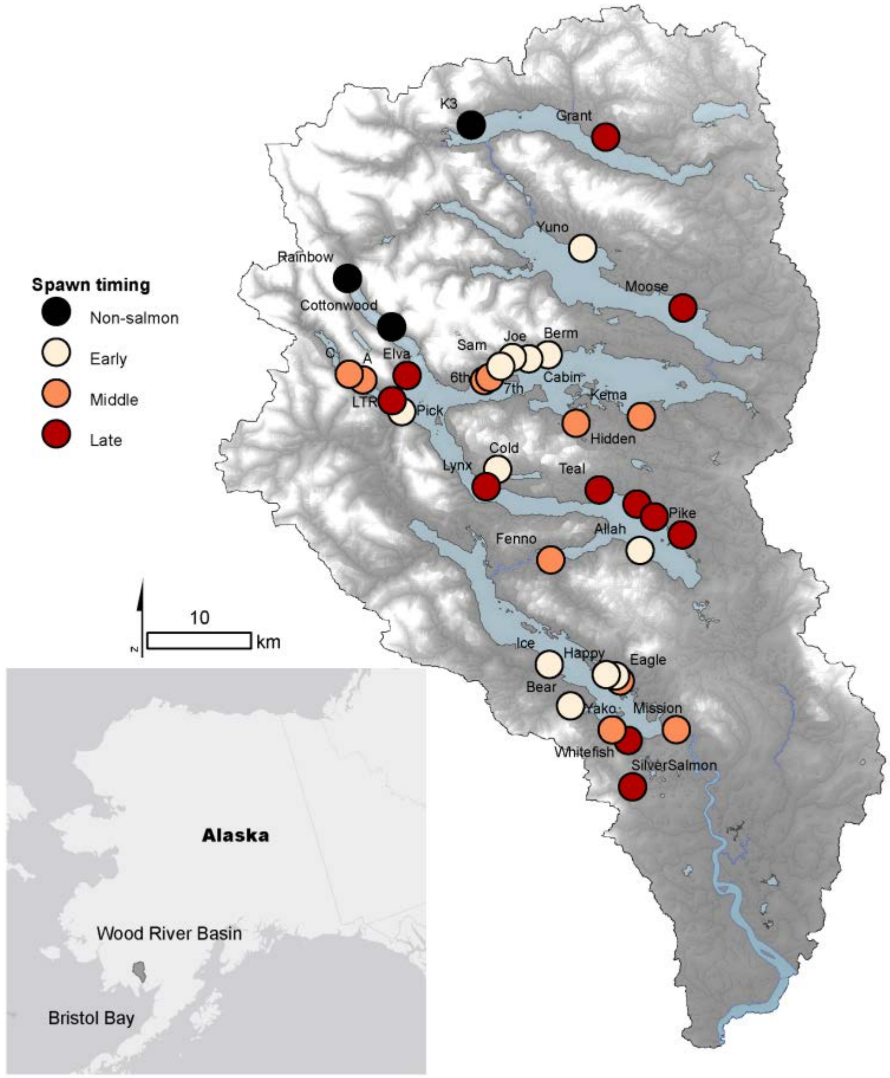

Fig. 2.1. The Wood River basin in southwest Alaska and locations of individual populations of sockeye salmon with different spawn timing (Early: 13 July to 22 July; Mid: 23 July to 30 July; Late: 31 July to 18 August).

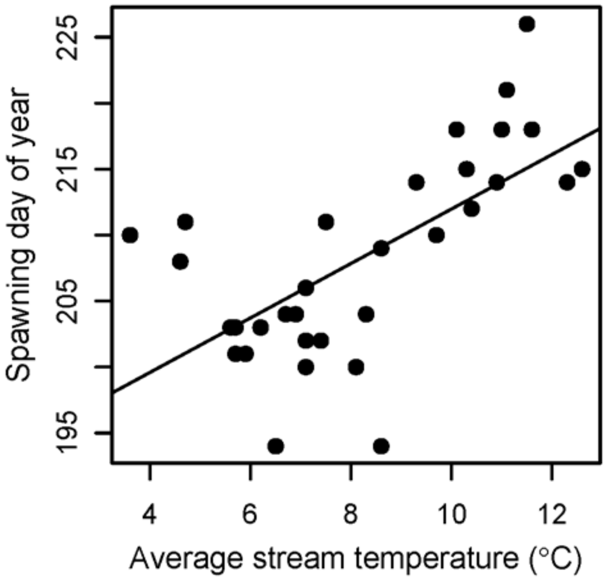

Fig. 2.2. Salmon spawn timing as a function of average summer stream temperature ($r^2 = 0.42$, $p < 0.001$, $n = 33$).

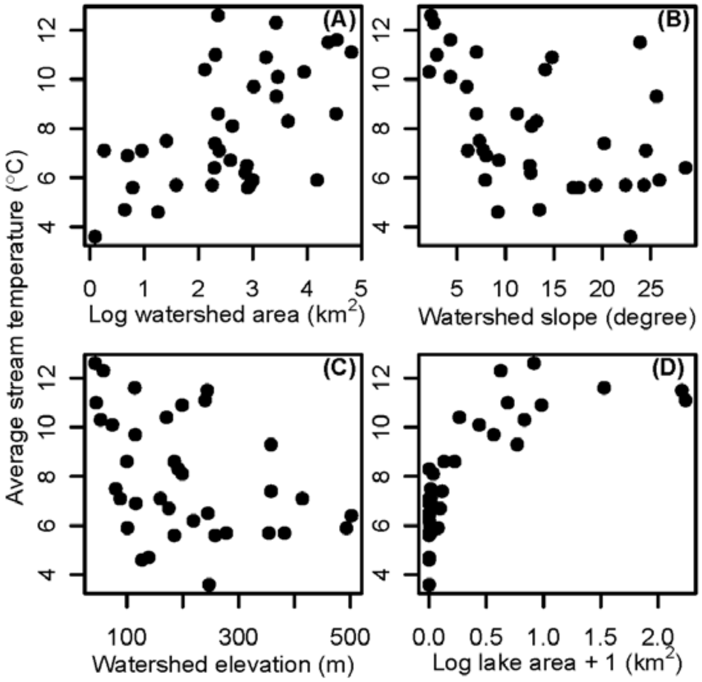

Fig. 2.3. Average summer stream temperature as a function of (A) watershed area, (B) watershed slope, (C) elevation, and (D) total lake area.

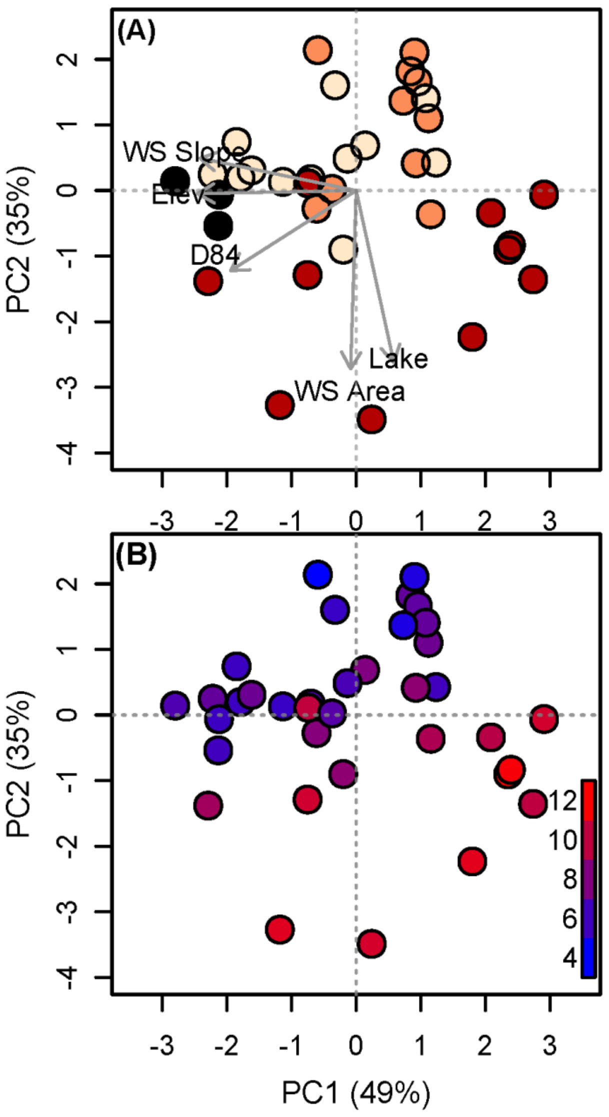

Fig. 2.4. Ordination plot from the principal components analysis of 36 streams on the basis of five habitat characteristics: watershed slope, elevation, D84, watershed area, and lake area. (A) Spawn timing: non-salmon (black), white (early), orange (mid), and late (red); (B) stream temperature from cool (4^{o}C) to warm (12^{o}C). Vector loadings added to aid with interpretation.

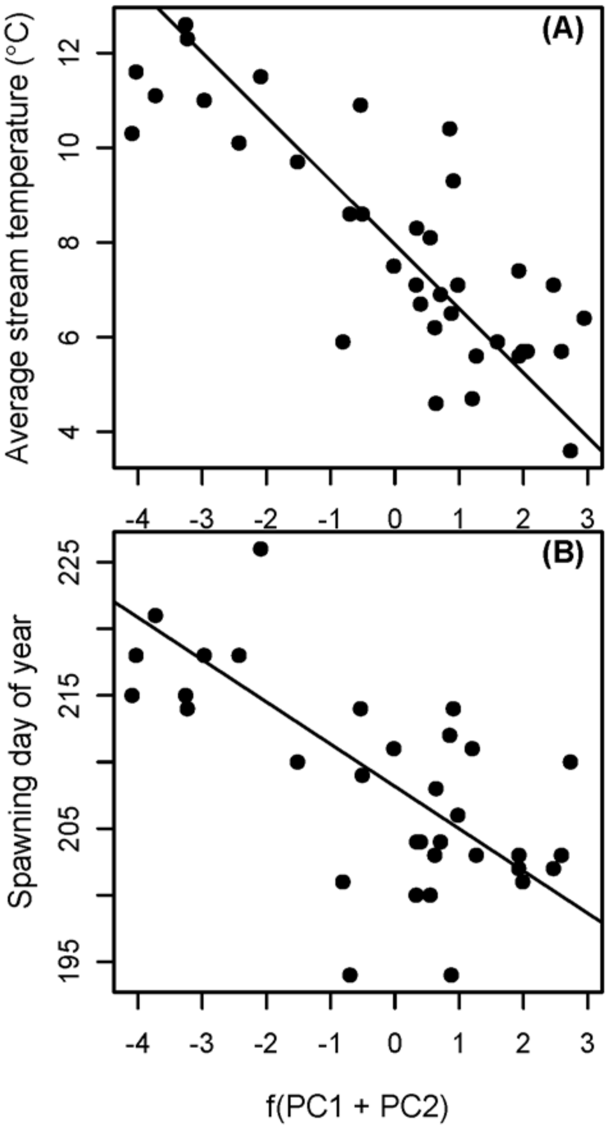

Fig. 2.5. (A) Average stream temperature as a function of the multiple regression of principal component axis 1 and 2 (y = -0.70*PC1 - 1.37*PC2 + 7.94, $r^2 = 0.76$). (B) Salmon spawn timing as a function of principal component axis 1 and 2 (y = 1.91*PC1 - 3.14*PC2 + 207.76, $r^2 = 0.45$).

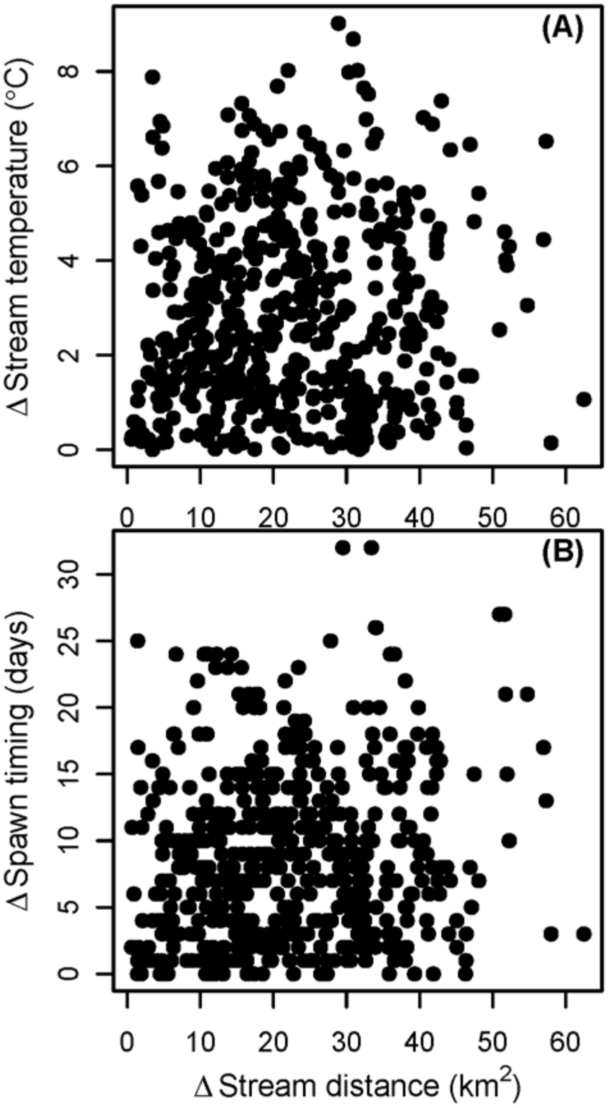

Fig. 2.6. (A) Temperature and (B) spawn timing difference among streams as a function of pairwise comparisons of geographic Euclidian distance between stream mouths.

Chapter 3

Topography and water source control stream thermal sensitivity to air temperature*

*This Chapter is formatted for submission to *Nature Geosciences.*
Contributing authors: Lisi P.J., D.E. Schindler, T.J. Cline and M.D. Scheuerell

Introduction

Response of river thermal regimes to changing climate is often controlled by local geomorphic and hydrologic filters, though a quantitative understanding of these processes is incomplete (Isaak et al. 2010, 2012). In particular, we lack critical information on the degree to which the local topography of watersheds modifies the sensitivity of streams to variation in air temperature, among the tributaries of river basins, a spatial scale that is relevant to wildlife and to management. Here, we present data on the hydrogen and oxygen stable isotopes of water to estimate summer contribution of snowmelt and rainfall to 80 boreal streams in southwest Alaska. Our data show differences in snow-melt contribution to summer hydrology that is associated with watershed topography and linked to the sensitivity of stream thermal regimes to changes in air temperature. Multivariate time-series analysis of stream temperature regimes suggests that streams in rain dominated, low-elevation watersheds had thermal regimes were 5-8 times more sensitive to variation in summer air temperature compared to streams draining steeper topography whose flows were dominated by snowmelt. Thus, the impact of climate warming on freshwater thermal regimes will be spatially heterogeneous across river basins and complicated by changes to precipitation which modify the relationship to air temperature and degree of thermal heterogeneity expressed within river basins.

In many regions, snowmelt is a critical source of water that sustains summer stream flows and supplying water for people and ecosystems during drier months (Barnett et al. 2005). Loss of summer water supply due to earlier onset of snowmelt and transition to rainfall during winter months is a major potential impact of warming climate (Barnett et al. 2005, Stewart 2009, Mantua et al. 2010). Indirect links between snowmelt and stream temperature have also been proposed, but a quantitative understanding of how snowmelt mediates stream temperature sensitivity to air temperatures is distinctly lacking (Isaak et al. 2010, 2012, Fellman et al. 2014), and is critical for forecasting suitability of freshwater ecosystems under shifting climate regimes. Here, we evaluate time-series of daily water temperature for boreal streams in southwest Alaska to quantify how individual streams track air temperatures in seasonally, snowmelt dominated watersheds. This region represents one of the fastest changing climates on the globe, with large expected changes in air temperature, freezing conditions, and therefore hydrological alterations for critical fluvial habitat that support riparian and aquatic biota (Maurer et al. 2007). Here we quantify water temperature sensitivity to changes in air temperature, and quantify how this variation is spatially structured across river basins varying in topography and water source.

To assess the different contribution of hydrologic sources to streams, we examined the δ^{18}O and δ^{2}H of rainfall, snowmelt, and stream flow from 52-80 streams over 3 summers in the Wood River, the Togiak River and Upper Nushagak River basins of in southwest Alaska (Fig. 3.1A). We hypothesize that the δ^{18}O and δ^{2}H of streams would be more isotopically similar to snowfall in streams draining steeper, high elevation basins that retain snowmelt-derived water later into the summer compared to flatter low elevation watersheds that collect less winter snow and whose flows are dominated by summer rainfall.

Hydrogen and oxygen stable isotope ratios from stream water and precipitation plotted closely to the global meteoric water line (GMWL); values of δ^{18}O and δ^{2}H (‰) in streams were bound between the two relationships defined for snow and rain, but were typically closer to that of the snow MWL (Figure 3.1) (Clark and Fritz 1997, Henderson and Shuman 2010). Reduced major axis regression indicated that precipitation and stream water were not measurably altered by evaporation, as the slope of the relationship between $\delta^{18}O$ and $\delta^{2}H$ was not significantly different than that expected for the GMWL (Craig 1961); $\delta^{2}H = 10+8.0*\delta^{18}O$ (rain 8.16±0.2, snow 8.0±0.2, mean±SD, Figure 3.1). However, rain orthogonally separated more than snow from the GMWL and we infer this difference reflects temperature dependent fractionation rates during the seasons in which the precipitation was formed (Gat 1996, Clark and Fritz 1997). Oxygen and hydrogen isotopes in rain showed deuterium in excess (*d*-excess) from the GMWL (3.6±2.5 pe rmil; mean± SD), while snow isotopes (8.8±1.5) had values much closer to 10 per mil, that of the GMWL (Craig 1961, Dansgaard 1964).

Results from a two source mixing model (Moore and Semmens 2008) on *d*-excess revealed wide variation in the relative contribution of rain and snow to each stream. Streams draining mountainous terrain derived the majority of their summer source water from snowmelt (Figure 3.2a). In comparison, stream water on the eastern boundary of the study region was composed mostly of rain. We summarized broad scale watershed characteristics of each stream (watershed slope, lake area, watershed area, elevation) using principal component analysis, and evaluated the relationship between these watershed features and the rain and snow-melt contribution to summer stream flow (Lisi et al. 2013). Watershed slope and elevation had high correlation loadings (-0.94, -0.87 respectively) on PC1 (Figure 3.2b). PC2 was primarily explained by strong loadings of watershed area (0.92) and lake area (0.52). However, only PC1 had strong associations with variation in water source, explaining 69% of the variation among streams (OLS, $p < 0.01$, Figure 3.2c). Warmer streams were also strongly associated with rain dominated watersheds, while cooler streams were associated with snow dominated watersheds (Figure 3.2c).

We deployed temperature data loggers to monitor high frequency changes in water temperature and quantify its sensitivity to changes in air temperature. Further, we wanted to quantify the extent to which watershed topography and water source (rain vs. snow) mediated stream temperature sensitivity to air temperature. Our expectation was that temperature variation in the study streams would have a common response to regional changes in air temperature, which would be modified at the individual stream level by local watershed features.

We used multivariate autoregressive state-space models (MARSS) to characterize common trends and local climate filtering within temperature time-series for 27 to 42 streams distributed across three river basins during the summers of 2011, 2012, and 2013. This class of models have a rich history in econometrics but only recently developed for analyzing multivariate ecological time-series data (Holmes et al. 2012). With MARSS, we reduced the dimensionality of many time-series to assess the strength of shared thermal patterns and air temperature that together describe the data. Further, we determined if geomorphic and water source conditions explain stream specific associations to air-temperature and shared thermal regimes.

Model results suggest that rain dominated streams draining flatter watersheds had thermal regimes that were much more sensitive to air temperature compared to snowmelt dominated streams draining steeper topography. For each stream and year of the study, we assessed the strength of effect sizes on the air temperature time series (Figure 3.3a,c) and coefficient loadings on the shared trend (Figure 3.3b, Figure 3.4).The effect sizes of air temperature indicate the Δ°C increase in stream temperature for every Δ°C increase in air temperature for each stream (Figure

3.3c). Stream specific temperature sensitivities ranged by ~5-8 fold across the river basins, showing both cooling and warming relationships with increased air temperatures (Figure 3.3c; 2013). Temperature sensitivities were strongly associated with geomorphic characteristics of the watershed (PC1 loadings) during each summer (r^2= 0.45, 0.70, 0.64; $P < 0.01$ all years; 2011, 2012, 2013 respectively; Figure 3.3c). Compared to flatter, rain dominated watersheds that were more sensitive to air temperature; steep watershed thermal regimes were best described by the shared trend, reflecting their low level of thermal variation, cooler overall June and July temperatures, and snowmelt hydrology (Figure 3.4).

Remarkably, we found a more homogenous response to air temperature among streams (e.g., larger intercept and lower regression slope) during the summer of 2011 (Figure 3.3c) that corresponded to a higher proportion of rain relative to snow in all streams during 2011. We found more model support for a linear model (air temperature effect size vs PC1) that included year specific intercepts and slopes compared to simpler models with shared intercepts or slopes (ΔAIC >4, ANCOVA). This was supported by local observations and snow monitoring stations (Snotel) that recorded below normal snow depths for 2011 compared to above normal snow depths in 2012 and 2013. We suspect that when snow pack is lower, streams draining steeper topography may be less buffered to summer air temperatures, creating a more homogenous response to air temperature across streams.

We found further evidence for geomorphic controls on stream thermal variation in the error of the variance/covariance matrix of the MARSS model, where streams with similar geomorphic features (e.g. slope and elevation) features had higher levels of covariance. An important feature of these models is their ability to describe the covariance between stream temperature responses and potentially discount associations using alternative error structures. We tested several contending hypotheses about the stream network's relationship with climate (see supplemental). We found substantial support (ΔAIC>>10) for streams having distinct scales of variance, and each pair of streams having a unique covariance between their temperature responses ("unconstrained" error matrix, Table 3.1). This result suggests that thermal responses described by the error are not equivalent across streams but also not entirely independent. Between-stream covariance may be the result of spatial autocorrelation, or alternatively, shared geomorphic conditions between streams. We used a Mantel test to compare pairwise differences in covariance in thermal response to the Euclidian distance between the geomorphic dissimilarity and geographic distance between each stream. Stream pairs that shared a positive covariance, were often closely related by their watershed geomorphic characteristics (PC1: Slope, elevation, lake area) while negative covariance was often found between streams with larger differences in their geomorphic conditions (Mantel test, pearson's r = -0.39 (2013),-0.47 (2012),-0.35 (2011); *P* < 0.01 all years). These relationships held even after controlling for spatial autocorrelation by geographic distance between streams (partial Mantel r = -0.36 (2011), -0.46 (2012), -0.33 (2013), *P* < 0.01 all years, Figure 3.5).

Our results indicate that for many streams in southwestern Alaska, stream thermal response to summer air temperature is controlled by a continuum of slope and elevation differences of watersheds, where snowmelt buffers the thermal regimes of streams draining steep watersheds. More precipitation falls as snow than as rain in watersheds with higher elevation and steeper topography (Stewart 2009). We conceptualize that snow and snow-melt are retained in surface snowpack or deep within the alluvial aquifer longer into the summer than that of lower sloped, lower elevation watersheds (Stewart 2009). Steeper, higher elevation topography can also modify the heating capacity of these streams through shading (aspect and riparian canopy), upwelling of snowmelt in groundwater, and short surface residence times in the stream channels (Caissie 2006). Lower gradient watersheds have streams with longer surface water residence due to higher levels of channel sinuosity and lake area, and thus more susceptible to changes in air temperature and solar radiation inputs during summer months (Caissie 2006).

An impressive array of stream monitoring networks has developed in recent years but, the methods to analyze multi-site datasets have lagged behind. Simple linear regression between summer air and stream temperature reveal a proxy for water sensitivity to air temperature, but often do not account for temporal autocorrelation, spatial relationships between monitoring stations, and seasonal changes in these relationships (Mohseni and Stefan 1999, Caissie 2006, Kelleher et al. 2012). Emerging statistical techniques such as those used here, account for these challenges with multiple high resolution temperature time-series in branched river networks (Ver Hoef and Peterson 2010, Isaak et al. 2014). Our results provide a unique case study of how these multivariate autoregressive state-space approaches can be used to more accurately determine drivers of hydrologic patterns and process with short duration and high frequency data

The results presented here highlight that ongoing climate change will have much different impacts on stream thermal regimes within the same river basin due to the physical characteristics of stream catchments. These results hold substantial promise to further constrain stream temperature scenarios under warmer climates and assess the potential impacts on wildlife. In this region, it is clear that the current thermal variation across a river basin is important to wild salmon spawning habitat and the terrestrial species that rely upon them. Here, variation in the phenology of salmon spawn-timing, determined by variation in water temperature (Lisi et al. 2013), extends the foraging season for predators and scavengers (Ruff et al. 2011, Schindler et al. 2013). Ongoing climate change may affect the extent of this phenological variation because of substantial changes to snowpack accumulation as well as increased air temperatures (Maurer et al. 2007, SNAP 2014). Further, human development of watersheds may reduce the spatial variation in water temperatures and the specific life-history phenology of aquatic organisms and the animals that depend on them.

Methods:

This study was conducted in southwestern Alaska in the Wood, upper Nushugak, and Togiak river basins (Figure 3.2.). These river basins consist of several large lakes which are fed by numerous tributaries and connected by short rivers. Streams in this region are characterized by a snowmelt hydrology, with peak discharge occurring in mid-May to June. We monitored 1st to 4th order stream thermal regimes with i-button recorders (Maxim Integrated Products, Sunnyvale, CA) and Hobo Level Loggers (Onset Computer Corp., Bourne, MA) summarized to daily averages from June 1st to September 9th. All loggers were cross-calibrated and crossed checked with ambient reading in the field. Air temperature was monitored on Lake Aleknagik Hobo micro weather station and Dillingham, Alaska airport (PADL).

Oxygen and hydrogen stable isotopes (δ^{18}O and δ^{2}H‰) in water were used to trace the relative contributions of rain and snow to surface discharge (Clark and Fritz 1997, Brooks et al. 2012, Fellman et al. 2014). Streams were sampled monthly, from June to September to characterize the spatial variation of δ^{18}O and δ^{2}H in streams during the open water season. Depth-integrated samples of the snow pack were collected in late March 2012 and 2013 using snow cores across the spatial extent of the study area. Rainfall was collected with rain gages at Lake Nerka, Beverley, Aleknagik and on the Togiak River. Samples were collected in duplicate using gastight 8ml Nalgene bottles and frozen for later analysis at the University of Washington's Isolab facilities. A Micromass Isoprime dual inlet based instrument was used to determine the δ^{18}O and δ^{2}H of water. Ratios of ^{18}O/^{16}O and ^{2}H/^{1}H are expressed in delta units, per mil (‰), defined in relation to V-SMOW (Vienna standard mean ocean water).

We calculated the deuterium excess of source and stream isotope measurements, which is the orthogonal distance from the global meteoric water line (d‰ = δ^{2}H - 8*δ^{18}O) (Craig 1961, Dansgaard 1964). ^{2}H on water diffuses at slightly higher rates compared to ^{18}O on water, resulting in excess deuterium in various phases of the water cycle (Clark and Fritz 1997). Winter precipitation tends to keep a higher excess values relative to summer precipitation reflecting temperature dependent rates of fractionation during water vapor formation(Merlivat and Jouzel 1979). We used a mixing model to estimate the contribution of snow and rain to streams with MixSIR v1.04(Moore and Semmens 2008). This allowed us to incorporate error in our sources and generate posterior probability distributions about the median contribution of snow and rain to summer discharge.

Multivariate statistical analyses were performed to determine controls on patterns of rain and snow contribution to stream discharge. ArcGIS (v10.0, Environmental Systems Research Institute, Redlands, CA, USA) was used to estimate each stream’s total watershed area, average elevation, average watershed slope (degrees) from a digital elevation model, and total area of lakes in each watershed. All habitat variables were log-transformed prior to analysis to control for differences in scale between descriptor variables. Principal component analysis (Pearson 1901) (PCA) on the correlation matrix was used to summarize dominant gradients of environmental variability among streams using the *vegan* (Oksanen et al. 2010) and *biostats* (McGarigal 2009) package in R (version 3.0.2) (R Development Core Team 2011). Stream scores on principal component axis 1 and 2 were regressed (using ordinary least-squares linear regression) against rain-snow contribution to streams and compared using Akaike information criterion (AIC).

Last, we used dynamic factor analysis (DFA) (Zuur et al. 2003), a multivariate autoregressive state-space model, on daily stream temperature regimes using the MARSS (Holmes et al. 2012) package in R. With DFA, we are trying to explain temporal variation in a set of n observed time series using linear combinations of a hidden random walk and covariate time series of temperature. We used the following model structure:(Zuur et al. 2003)

The state equation of a single common trend over time:

$$x_t = x_{t-1} + w_t \text{ where } w_t \sim \mathrm{N}\ (0,q)$$

Observation equation relates trend (x) and covariate (d) to observations ($\boldsymbol{y}$).

$$\boldsymbol{y}_t = \boldsymbol{Z}x_t + \boldsymbol{D}d_t + \boldsymbol{v}_t \text{ where } \boldsymbol{v}_t \sim \mathrm{MVN}\ (0,\mathbf{R})$$

Here, the vector of observations for each stream at time t ($\boldsymbol{y}_t$) are modeled as linear combinations of hidden trend (x_t) and factor loadings on the hidden trend for each streams ($\boldsymbol{Z}$), and the effect sizes ($\boldsymbol{D}$) of the air temperature covariate time series (d) on the observations. $\boldsymbol{v}_t$ and w_t represent the observation and process error structures respectively. To make the model estimable (Zuur et al. 2003), process error (q) was set to 1. Observation errors (**R**) are from a multivariate normal distribution. Candidate models were compared using AIC based on the maximum likelihood of the model fit. All data were z-scored to account for differences in means and intrinsic variance dynamics. We assessed the effect of air temperature as a covariate in the model as an indication of stream sensitivity to air temperature after re-transforming the stream specific effect sizes to indicate the °C increase in stream temperature for every °C increase in air temperature. Stream geomorphic conditions (PC1 and PC2) were then regressed (ordinary least-squares regression) against factor loadings for the dominate trend(s) and effect sizes of air temperature.

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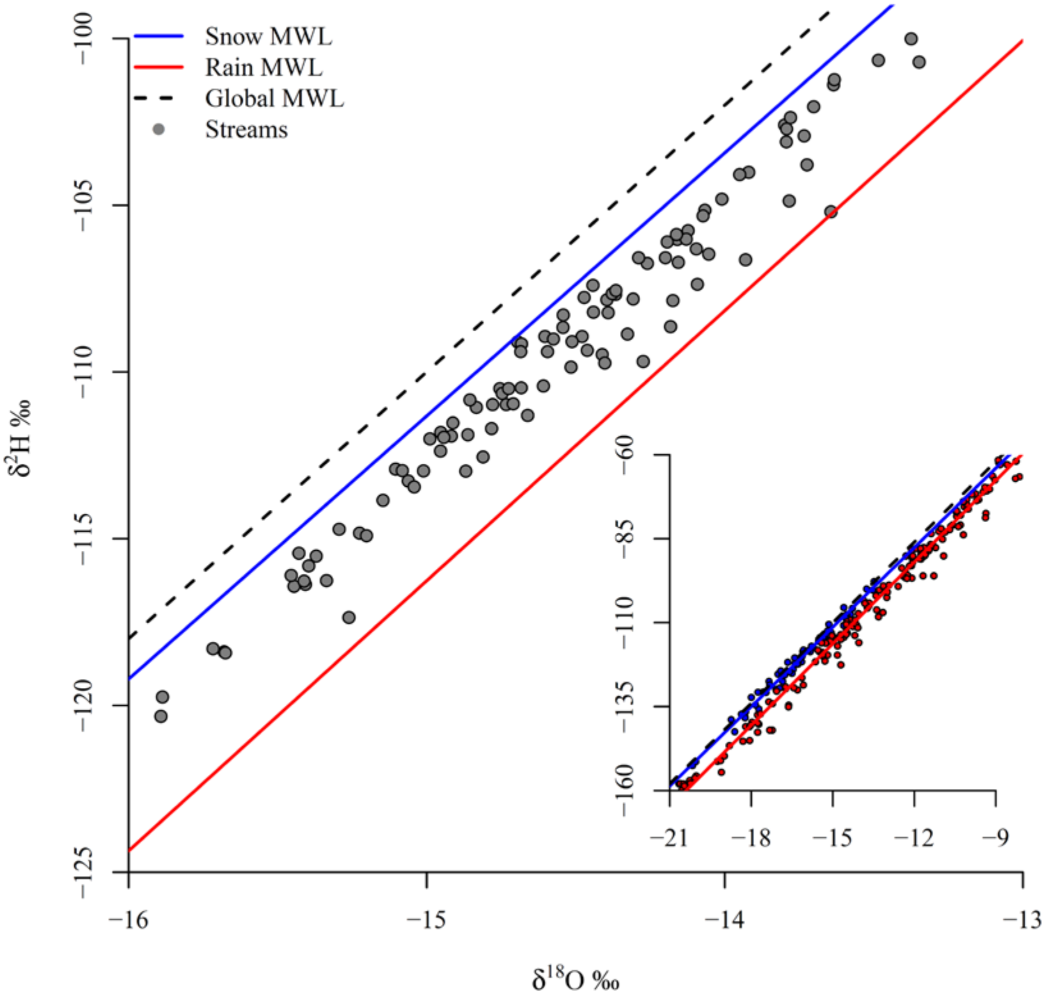

Figure 3.1. Water isotopes (δ^{18}O and δ^{2}H per mil) of rain, snow, and stream water. The MWL represents the local meteoric water line for snow and rain, dashed line indicates the global MWL ($\delta^{2}H = 10 + 8*\delta^{18}O$)(Craig 1961). The inset plot shows water isotope values detected for snow and rain for this system.

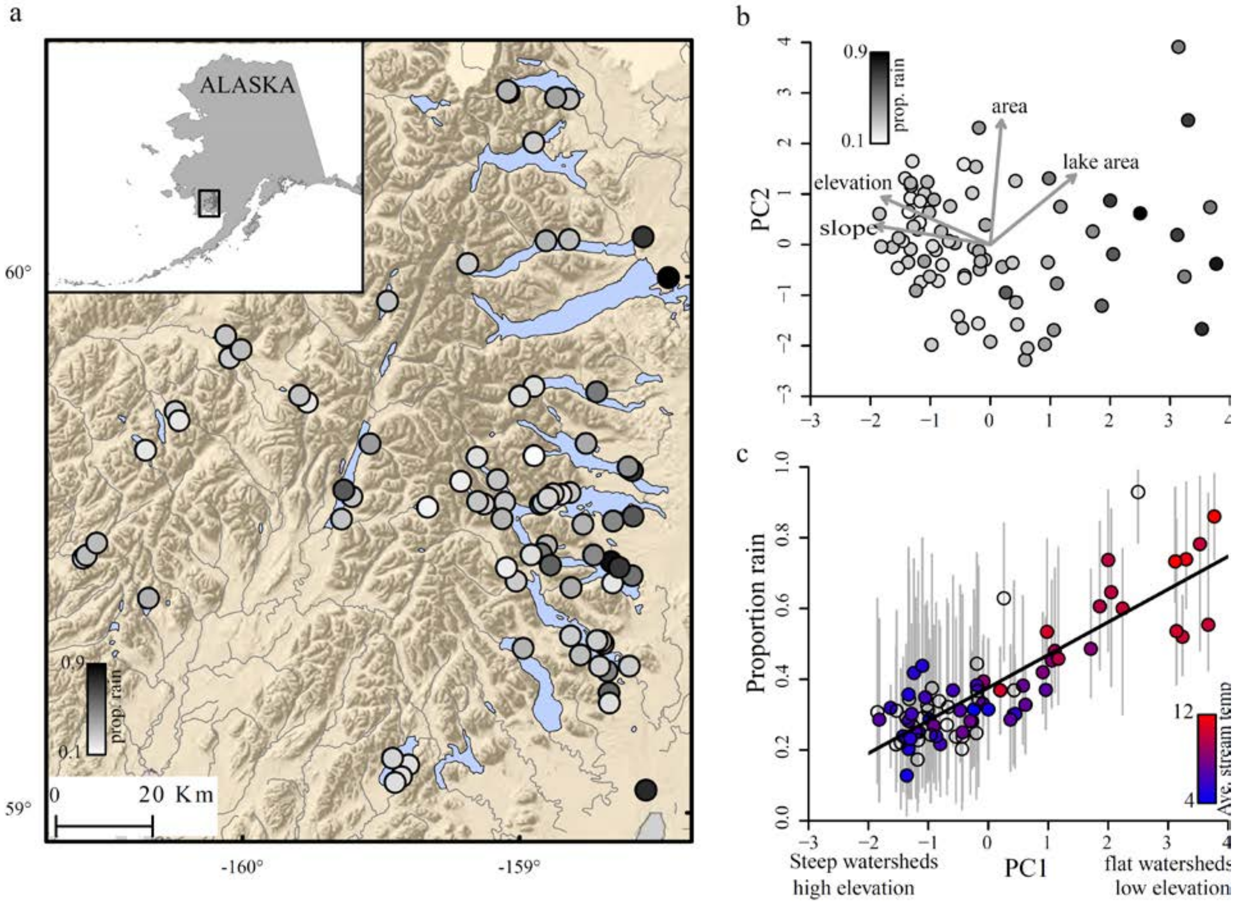

Figure 3.2: A) Locations of study streams in SW Alaska and B) ordination plot from principal component results of stream watershed characteristics, points colored by the median proportion rain from mixing model results. Length and direction of arrows on ordination are proportional to vector loading of watershed predictors into each principal component. C) Median proportion of rain in stream discharge as a function of first principal component. Vertical grey lines indicate the 90% credible intervals from the posterior distribution of the isotope mixing model. If filled, points are colored by their average stream summer temperature (°C).

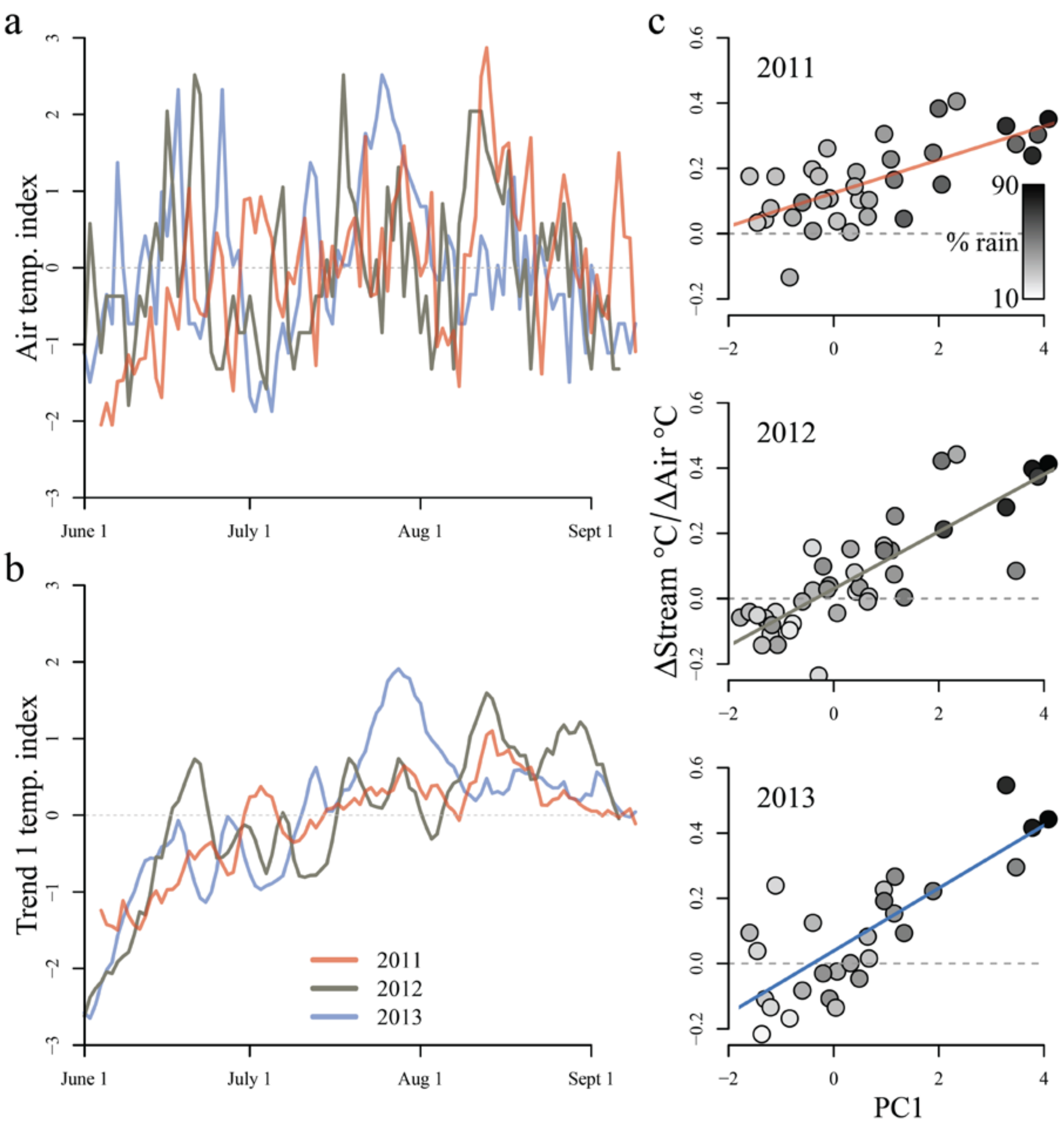

Figure 3.3: Results from MARSS analysis; A) Z-scored air temperature time series for three years (2011, 2012, and 2013); B) the most parsimonious temperature trend not explained by air temperature for 2011, 2012, and 2013 and C) the effect sizes of air temperature, as a function of watershed topography as PC1. Points are shaded by their median % rain. 2011 had a higher ratio of snow in all streams compared to recent years, 6% higher ratio than 2013, 4% higher than 2012, pairwise t-test, *P* < 0.01.

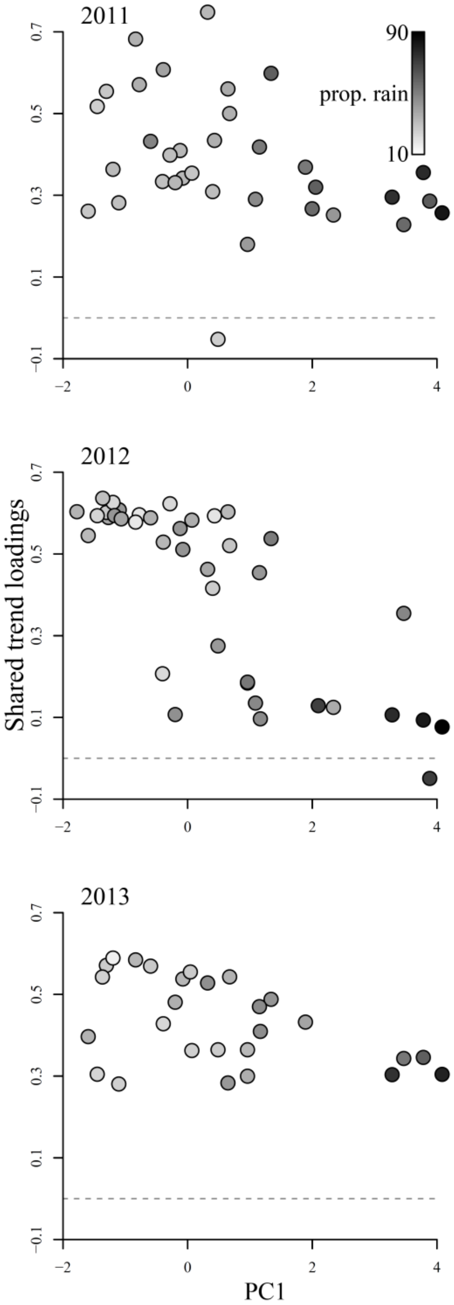

Figure 3.4: Stream specific trend loadings into PC1, as a function of watershed topography as PC1. Points shaded by their median rain:snow.

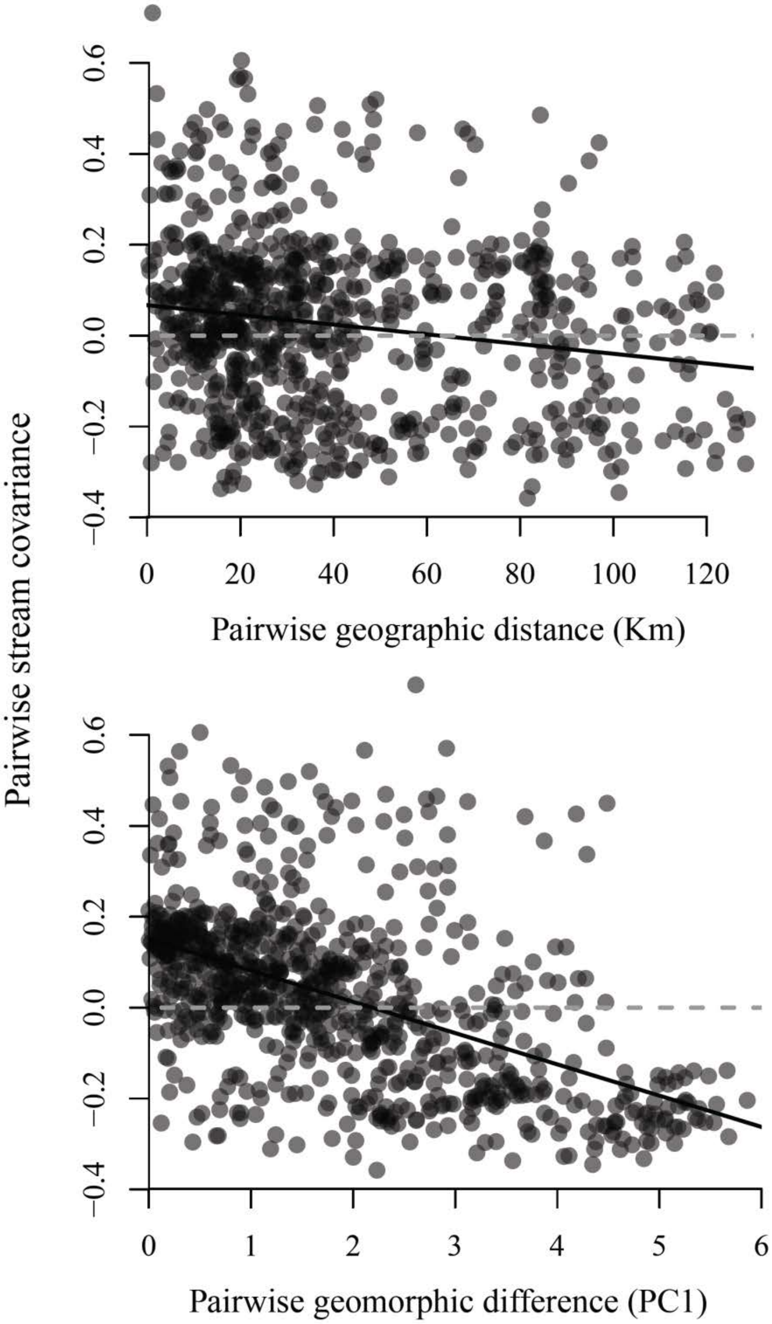

Figure 3.5 pairwise stream covariance vs A) pairwise stream geographic difference and B) geomorphic dissimilarity from the 2012 data set. Streams that shared a positive covariance, were often closely related by their watershed geomorphic characteristics while negative covariance was often found between streams with larger differences in their geomorphic conditions (Mantel test, pearson's r = -0.47, 2012). This was true even after controlling spatial autocorrelation by geographic distance between streams (partial Mantel r = -0.46, *P* < 0.01).

Table 3.1: MARSS AIC table

Model	Various form of R	2013 AICc	2012 AICc	2011 AICc
1	“unconstrained”	-836	-30	532
2	“equalvarcov”	2507	4681	3375
3	“diagonal and unequal”	2877	4475	4129
4	“diagonal and equal”	3484	6788	4632

An important feature of the MARSS models is their ability to describe the covariance between stream temperature responses and potentially discount associations using alternative error structures. Here, we compared different forms of R matrix on observation errors in the MARS model. In this case, the model incorporates the deviations from the state and the true measurement error. We assume that measurement error is equal among sites and ultimately negligible. Each error configuration tests a separate contending hypothesis about the stream network’s relationship with climate and covariance with one another. Contending model configuration was evaluated by Akiake’s Information Criterion (AICc) where models >2 ΔAICc apart are considered significantly different. We found substantial support (100 > ΔAICc) for streams having distinct scales of variability, and each pair of streams having a unique covariance between their temperature responses (“unconstrained” error matrix). This result suggests that thermal responses are not equal across all streams but not entirely independent. Several streams have common associations with respect to their variation to climate across the river basin. Below describe the covariance model structure as provided by Holmes et al 2013.

1) “Unconstrained”. Each stream temperature series has a unique level of observation-error variance and each pair of streams has a different level of covariance.

2) “Equal varcov” A covariance matrix with equal variances and covariances. Each stream has the same level of variance and the same level of covariance between streams.

3) “Diagonal and unequal”. A diagonal covariance matrix with unequal diagonal entries. Each stream has a unique level of variance and there is no relationship of covariance between streams.

4) “Diagonal and equal”. A diagonal covariance matrix with equal diagonal entries. Each steam has the same level of variance, but errors between streams are independent.

Chapter 4

Wind-driven upwelling in lakes destabilizes thermal regimes of downstream rivers.*

*This chapter has been formatted for submission to *Limnology and Oceanography*. Lisi, P. J. and D.E. Schindler.

Introduction

A central challenge for river ecologists is to understand how the thermal regimes of river systems are influenced by atmospheric, hydrologic, and geomorphic processes at multiple spatial scales (Caissie 2006). Temperature is fundamental for organizing ecological processes in ecosystems (Brown et al. 2004), directly modifying a variety of biological processes such as reproduction, metabolism, and behavior in ectothermic aquatic animals (Poole and Berman 2001), and ecosystem processes such as nutrient cycling and primary production (Allan and Castillo 2007). Thermal variation, like many physical attributes of rivers, is often hierarchically controlled by the geomorphic template that filters climate signals through various physical features along the river continuum (Vannote et al. 1980, Frissell et al. 1986; Benda et al. 2004). Caissie (2006) provided a conceptual model to describe how thermal variation in rivers was regulated by their watershed size (Fig. 4.1 – solid line). Short, narrow and often shaded headwater streams draining small watersheds should display less thermal variation relative to larger downstream rivers. As rivers grow in size, they are generally shallow and wide, exchanging rapidly with ambient air-fluctuations and solar irradiation. Large higher order rivers are expected to show less diel variation as they are buffered by more thermal mass. Still, empirical data are lacking that describe the various physical mechanisms producing thermal variation through discontinuous river features, such as in river systems inundated with natural lakes (Jones 2010). This knowledge gap is likely widened because rivers and lake systems are often studied separately despite their physical connections.

Lakes are common features of river networks, having substantial influence on the structure and function of rivers that drain them (Malmqvist and Rundle 2002, Jones 2010). Lakes can influence downstream morphology (Arp et al. 2007), water chemistry (Kling et al. 2000), primary productivity (Stockner et al. 2000), invertebrate communities (Robinson and Minshall 1990), and fish communities (Degerman and Sers 1994) of rivers that drain them. Many of these ecological dynamics at lake outlets are determined by seasonal variation in water temperature that are governed by lake circulation, stratification, and mixing (Wetzel 2001, Jones 2010). Conventional wisdom suggests that longer water residence times in lakes relative to free-flowing rivers allows source water from lake inflows to warm at the surface during summer months in lakes that thermally stratify (Wetzel 2001, Marcarelli and Wurtsbaugh 2007). The longer residence time of water, and greater thermal mass in lakes buffers outlet temperatures against rapid changes in air temperatures and irradiance thereby reducing the annual amplitude and daily fluctuations in river temperatures downstream because lakes typically warm and cool more gradually than shallower rivers (Wetzel 2001, Jones 2010,). However, there are only a few empirical examples that show how river thermal regimes are influenced by upstream lakes (Mellina et al. 2003, Laval et al. 2008, Jones 2010). Further, how the size of a lake influences the thermal variability of lake outlets remains virtually unexplored.

Most lakes vertically stratify during summer months causing isolation of cooler hypolimnetic water from entering surface discharge at lake outlets (Wetzel 2001). However, high velocity winds along the fetch of a lake can push warm surface waters in the direction of the wind and produce a pronounced tilt in the thermocline along the fetch axis of the lake (Wedderburn 1912, Wetzel 2001). At the point the wind subsides, the thermocline will move back towards equilibrium, forming an internal seiche – an oscillation of the thermocline lasting for hours to several days depending on the length of the lake basin and the density difference between surface water and the hypolimnion (Monismith 1986, Wetzel 2001). After particularly large winds, the initial oscillation of the thermocline may even allow deep cool water to reach the surface of lake via 'upwelling'. If such upwelling occurs at river outlets, cold water would be transported to downstream rivers. Upwelling is known to generate abrupt temperature declines by as much as 10°C at lake outlets in as little as an hour (Stevens and Lawrence 1997, Laval et al. 2008). Although the mechanisms behind upwelling and internal seiches in lakes are well understood, their effects on water temperature at lake outlets are not incorporated into models of thermal regimes of river networks (Caissie 2006).

Here, we studied the thermal regimes of streams and rivers in southwest Alaska to evaluate whether lakes stabilize or destabilize thermal regimes of their outlets. We hypothesized that large lakes are particularly susceptible to wind-driven upwelling of the hypolimnetic water thereby destabilizing the thermal regimes of downstream rivers. We expect that rivers draining large lakes express more thermal variation than large rivers without lakes (Fig. 4.1, dashed line). To test this conceptual model, we examined the variation of thermal regimes among a series of streams and rivers with and without lakes. We used water temperature data, meteorological stations and vertical thermal arrays in several lakes to test whether temperature changes in streams are linked with wind driven events that cause the surface and thermocline of the lakes to upwell across the region.

Methods

Study site— This study was conducted in southwestern Alaska in three neighboring basins of the Wood, upper Nushugak, and Togiak rivers, which all drain south into Bristol Bay (Fig. 4.2). These river basins and the surrounding region consist of several large, deep, oligotrophic lakes which are fed by numerous tributaries and connected by short rivers. Each of these rivers has distinct geomorphic features and drains lakes among which there is also substantial variation in their bathymetry, orientation, and surface area. Lakes within these drainages annually stratify within weeks after the lake surface is free of ice in the spring, typically the last week of May to the first week in June (Schindler et al. 2005). We monitored summer water temperatures in the mouth of tributary streams and larger main stem rivers of 24 watersheds lacking lakes and 15 watersheds draining lakes with lake surface areas that ranged from 0.3 to 202 km^2 (Fig. 4.2). For the largest lake we examined (Lake Nerka) we only considered half of the total lake area (101 km^2), because of the distinct articulation between the upper and lower basins and the outflowing river leaves the lake near the end of the south arm.

The majority of stream thermal regimes were monitored with i-button temperature recorders (Maxim Integrated Products, Sunnyvale, CA) programmed to log at hourly intervals (0.125 to 0.5^{o}C resolution) between early June and early September. Temperature loggers were placed above the streambed by attaching them to steel rebar and tied to features along the river bank or fixed to the river bottom. In the Nushugak drainage, we used publicly available river temperature data from USGS stage gage located on the Allen River below Lake Chikuminuk (http://waterdata.usgs.gov, station 15301500). In the Togiak drainage, we used hourly stage gage loggers maintained by the US Fish and Wildlife Service in the Togiak National Wildlife Refuge. Vertical temperature profiles of the lakes were monitored continuously with i-button temperature recorders and Hobo ProV2 (Onset Computer Corp., Bourne, MA) suspended from the lake surface at 1, 3, 10, 15, and 30 meters on Lake Beverley, Lake Nerka, Lake Aleknagik and Little Togiak Lake in 50 meters of water near the lake end (Fig. 4.2). All loggers were cross-calibrated before the start and at the end of the study and crossed checked with ambient readings in the field. Vertical temperature profiles with a YSI sonde were taken every 10 days from June to September 10th on Lake Aleknagik, Lake Nerka, and at three limnological stations and one station on Little Togiak Lake and Lake Beverley. Local weather was monitored by measuring wind speed, direction, rain with from a weather station on a small island on Lake Nerka with a Hobo micro weather station (Onset Computer Corp., Bourne, MA) and compared with a nearby coastal airport weather station in Dillingham Alaska (NOAA weather station PADL) at the base of the Wood River.

Data Analyses—We used the coefficient of variation to compare how stream thermal variation corresponded with its watershed area in watersheds with and without lakes at both hourly and daily averaged time steps from June 30 to Sept 9, 2012. Using least squares regression, we tested the hypothesis that variation (CV) in summer water temperature is associated with watershed area, but that the strength and sign of this relationship is different in watersheds with and without lakes. The conventional expectation would be that larger lakes buffer diel thermal variation (Wetzel 2001, Jones 2010). However, we propose that thermal variation is more variable in rivers draining large, deep lakes reflecting the episodic disturbances of wind events on thermal structure in lakes.

We used time-series decomposition to understand how diel variability contributes to the total variation in the thermal regime compared to longer modes of variation. We separated high frequency diel signals from the complete temperature time-series using seasonal and trend decomposition (STL) based on the Loess procedure (Cleveland et al. 1990). STL is an iterative non-parametric filtering procedure that decomposes time-series into three main components: a low frequency trend, diel cyclic variation (often called seasonal), and a remainder component. We then calculated the proportion of variance of the original time series (r^2) explained by the trend, diel, and remainder components. The compiled component variances from all 24 streams were then regressed against watershed area and lake area to test the hypothesis that less diel variation is observed in streams draining larger watersheds, and that the variance in rivers draining large lakes is dominated by low-frequency 'trend' variation over finer-scale diel variation that dominates in small streams or rivers without upstream lakes. Time series decomposition was conducted with the STL function in R (R Development Core Team 2011).

As a final analysis, we examined three river thermal regimes below lakes to understand if their unique regimes are linked to wind driven, upwelling events and thus, providing a mechanism to explain the unique variation observed in thermal regimes below large lakes. Potential upwelling events during stratification are traditionally described using the parameter W, the Wedderburn number (Monismith 1986; Stevens and Lawrence 1997; Laval et al. 2008). W is a dimensionless number defined as:

$$W = \frac{g' h_1^2}{u_*^2 L} < 1$$

Here, h_1 is the surface layer depth, u_* is the shear velocity induced by wind, L is the length of the basin or lake fetch, the reduced gravity is $g' = g(\rho_1 - \rho_2)/\rho_2$ due to difference in water density of warmer surface and cooler lower layers (Thompson and Imberger 1980). Wind speed (m/s) was filtered with a simple moving average with a temporal window spanning one quarter of the internal seiche period; equations for the seiche period (T_1) and shear wind velocity (u_*) are described by Stevens and Lawrence (1997). *W* does not take into account the geometry or bathymetry of the lake, or wind direction. For values of $W < 1$, there is a high probability that the thermocline will tilt at a sufficient angle to allow upwelling of hypolimnetic or metalimnetic water. The Wedderburn number provides a scale for the magnitude of seiching expected from surface winds rather than an exact estimate of thermocline displacement (Shintani et al. 2010). We calculated *W* for Little Togiak Lake, Lake Aleknagik and Lake Beverley during periods when we expected upwelling to occur given our continuous record of the lakes' surface and hypolimnetic temperatures.

Results:

Stream and river temperatures varied substantially among sites and through time, ranging between 2.8 to 18.1°C from June 30 to September 9, 2012 (Fig. 4.3). Visually, temperature regimes of larger outlet rivers displayed 5 to 7 distinct temperature excursions that dropped 5 to 10°C within 8 to 20 hours. Often these thermal divergences occurred synchronously among the larger rivers draining larger lakes (Fig. 4.3A), but were not observed in streams draining smaller lakes or streams without lakes (Fig. 4.3B-D). Streams from lake-less watersheds were coolest among small headwater streams, with warmer average conditions found in larger watersheds (least squares on log-watershed area, $r^2 = 0.52$, $p < 0.01$, Fig. 4.4). In comparison, watersheds containing lakes showed the opposite pattern. Streams from small watersheds with lakes displayed some of the warmest streams overall, even warmer compared to average water temperatures in larger watersheds with lakes ($r^2 = 0.46$, $p < 0.01$, Fig. 4.4).

Do lakes destabilize thermal regimes of streams and rivers?

Stream thermal variation at the hourly scale (calculated as the CV, standard deviation/mean) varied by 3X (0.09 to 0.27) among streams ranging from the least variable below the outlet of Lynx lake (lake area = 1.6 km^2) and most variable below a larger lake outlet at the Agulukpak River (Lake Beverley area = 90.1km^2). Rivers draining large lakes (>10km^2 surface area) had summer thermal regimes with 1.8X more variation than both rivers draining smaller lakes and watersheds lacking lakes. Among lake-less watersheds, we found no linear association between watershed area and water temperature CV ($r^2 = 0.01$, $p > 0.2$; Fig. 4.5A). In comparison, CV was positively associated with increasing (log) watershed area in watersheds containing lakes, against conventional wisdom that large lakes provide stable stream temperatures (least squares, $r^2 = 0.59$, $p < 0.01$, Fig. 4.5A).

We also compared summer CV at daily average time intervals. If diel-scale variation is important, the CV calculated at the daily time scale should be less than the CV calculated at the hourly scale. For lake-less watersheds, the seasonal CV calculated at the daily scale was on average ~30% lower compared to the seasonal CV at the hourly scale (Fig. 4.5B). We found some support for a linear positive association between log watershed area and CV for lake-less watersheds at the daily scale ($r^2 = 0.17$, $p < 0.05$). Smaller streams draining lakes had ~17% less variation at the daily scale, indicating that some diel variation contributed to the overall summer thermal variability. In comparison, watersheds draining large lakes only had a 3% reduction in their CV at the daily scale, suggesting that diel fluctuations were not important in large lake and likely buffered by upstream thermal mass (Fig. 4.5A vs 4.5B). Again, we found a positive linear relationship between log watershed area and summer CV at the daily scale (least squares: $r^2 = 0.63$, $p < 0.001$ Fig. 4.5B).

Decomposition of thermal regimes with STL was effective at separating diel cycles from the original temperature time series (e.g., Fig. 4.6A). This analysis revealed that diel variation explained only 3% (0.01 to 5%) of the total variation in rivers below large lakes, confirming that large lakes buffered diel temperature variation (Fig. 4.6B). Instead, non-stationary trends, that include episodic but large temperature excursions, explained ~94% (90 to 96%) of total thermal variation in rivers below large lakes (Fig. 4.6B). By comparison, diel scale variation contributed on average 35% (57% to 14%) of the total thermal variability in streams without lakes (Fig. 4.6B) and 16% (2 to 33%) to those draining smaller lakes with surface areas less than 10km^2. The trend component explained ~54% (35 to 80%) of the variation for lake-less watersheds (Fig. 4.6C). Only 8% (2 to 16) of the variation was explained by the remainder component for all streams and rivers, with more residual variation associated with headwater tributaries.

Does lake upwelling destabilize temperatures in rivers below large lakes?

We explored the mechanisms that might explain why rivers below large lakes appeared to be the most thermally variable environments compared to other drainages even though diel variation appeared to be ameliorated by upstream lakes. Here, we examined thermal variation in the Agulukpak, Little Togiak, and the Wood River, where lake thermal arrays could be used to detect periods of lake upwelling and therefore cooling pulses to downstream rivers that appeared to characterize the regimes below larger lakes. We observed several wind events over the course of the summer (Fig. 4.7A) that were followed by large temperature swings throughout the water column of each lake (Fig. 4.7B-D). For example, on 18 August, heavy winds resulted in an internal seiche with a period of 3.6 days on Lake Beverley, with temperatures at 30m of water oscillating between 4 and 10^{o}C. Similarly, we observed Lake Aleknagik with a 3.4 day seiche period and Little Togiak 1.2 day seiche period. On occasion, the Wedderburn number was < 1 for all three lakes, indicating that wind events created conditions where upwelling should occur (Fig. 4.7B-D *note figure's* $log_{10}W$ *scale*). All three lakes had upwelling conditions (W<1) in early

July when the epilimnion in each lake was relatively shallow (7 to 8m) and density differences were less distinct between the surface and hypolimnion.

Temperature conditions at the river outlets were often linked with surface conditions in the lake during upwelling. Abrupt drops in temperature occurred for the Agulukpak River on 29 July, 2 August, 18 August, and 3 September with these events associated with periods where $W < 1$ in Lake Beverley (Fig. 4.7B). The Wood River did not always indicate upwelling even on a few occasions when W was < 1 for upstream Lake Aleknagik (e.g. Aug 18th, Fig. 4.7C). In comparison, Little Togiak Lake (lake area = 8.9 km^2), a much smaller lake than Beverley or Aleknagik, showed stable river temperatures, supported by conditions where upwelling was unlikely to occur in August and September (Fig. 4.7D).

Discussion

We observed that rivers draining large lakes are much more thermally variable than is currently appreciated in the literature. Day to day thermal dynamics in rivers appeared to be associated with episodic upwelling of cool hypolimnetic water in large upstream lakes, which periodically destabilize river thermal regimes. We speculate that upwelling may be a common source of thermal variation during stratification in many temperate river drainages due to the high presence of large lakes in these regions. Given the magnitude and frequency of such thermal variation associated with upwelling events we postulate that this variation imposes novel but undescribed challenges to lotic organisms living downstream of large lakes.

Our results contribute to the evolving conceptual models describing how geomorphic characteristics of river basins translate into thermal variation across landscapes. This study confirms much of what is described by Caissie (2006) for watersheds lacking large lakes. Headwater streams draining small watersheds displayed less thermal variation than intermediate sized streams (watershed areas from 10 to 90 km^2). Large higher order rivers (200 to 1000 km^2 watersheds) did appear to show less diel variation relative to intermediate sized streams, likely as they are buffered by more thermal mass. However, our results provide an interesting contrast when considering the potential effects of lakes on stream temperature regimes. We found that larger watersheds are more likely to hold large lakes which are prone to instabilities in their thermal stratification which can cause upwelling of hypolimnetic water with profound effects on the thermal regimes of rivers that drain them (Fig. 4.1).

We were limited in the extent to which we were able to explore the association between watershed size and thermal variation in this landscape. The river drainages we sampled are many times smaller than the watersheds that river ecologist would consider “large” (e.g., Columbia, Amazon). Yet, watersheds that we considered large contained lakes that were 101 to 10km^2 which represent approximately the upper 0.01% of world lakes. Consequently, this also illustrates that upwelling events are probably an uncommon phenomenon in many river drainages that contain only small lakes that are much less than 1km^2 (Downing et al. 2006). Many of these temperature recorders were positioned within 2 km of the lake outlet, thus the lake effect of upwelling is likely dissipated further downstream (Jones 2010). Although the data are not shown here, we did detect upwelling events on the Togiak River >50km downstream of Togiak Lake (lake area = 38.8 km^2).

Here, we considered lake size as general descriptor of the sensitivity of lake thermal structure to wind action and, therefore, the tendency of a lake to upwell deep water to the river outlet. Other physical features that describe a lake’s morphology such as lake depth, articulation, bathymetry, watershed topography, orientation relative to prevailing wind direction, and outlet position may also provide useful information about the potential for a lake to upwell deep water to the outlet. Although our study lakes varied in terms of the orientation and outlet position, all the large lakes >10 km^2 appeared to be susceptible to wind and some degree of upwelling. We did not observe repeat upwelling when the lake thermocline seiched; rather, upwelling occurred only during the initial tilt of the thermocline during the maximum wind speeds. It is possible that upwelling may have occurred on the first deflection of the thermocline if the outlet was position in the direction of the wind or during the initial tilt of the thermocline in the opposite direction of the wind.

Wind is known as a potential factor controlling stream temperatures, but often the mechanisms are rather unclear. Stream surfaces are positioned low in river valleys and therefore protected from wind by riparian vegetation or high channel stream banks (Poole and Berman 2001, Caissie 2006). Therefore, wind is thought to contribute much less to the thermal variability in streams relative to other drivers such as air temperature, sunlight, and precipitation. Cooler weather associated with low pressure cold fronts and heavy rainfall likely cooled some of the streams in the Wood River basin, including the surface layers of lakes. Yet, a few of the wind events occurred during periods of light rainfall and heavy wind in early July, suggesting wind events cool rivers through upwelling rather than via radiative heat loss during cold weather.

We speculate that lake upwelling may have important ecological consequences for lotic communities. At present, we know of no research that has assessed the ecological effects of abrupt changes in river temperatures associated with wind-driven plunges in river temperatures. In addition to de-stabilizing river thermal regimes, lake upwelling could also provide rivers with a midsummer pulse of hypolimnetic water, rich in nutrients for primary producers. Stratified lakes often have large differences in nutrients and dissolved oxygen above and below the thermocline. Nutrient-rich hypolimnetic water has the potential to support benthic production during upwelling or mixing events (MacIntyre and Flynn 1999). Alternatively, larger eutrophic lakes may promote periods of stressful or lethal oxygen conditions for fish and other aquatic animals because anoxic conditions can occur in the hypolimnion of stratified eutrophic lakes. For example, an upwelling event on a culturally eutrophic lake (Onondada Lake, NY USA) produced surface oxygen concentrations < 1mg L^{-1} at the lake end, where typically they are 10 mg L^{-1}, creating "rotten egg" smell from upwelling of H_2S and juvenile fish kills (Effler et al. 2004). At this point, we have a limited understanding of how upwelling dynamics of lakes influence the community ecology of downstream rivers, but presume they may be more significant than previously appreciated.

Across southwest Alaska the majority of rivers drainages are inundated with lakes large enough to be susceptible to upwelling given their size, length, and outlet position near the end of the lake at the terminal moraine (e.g., Lake Illiamna, Becharof, Ugashik, Naknek, Nonvianuk, Kukaklek, Ualik in addition to those lakes studied here). These river drainages, in addition to the study rivers, also support high quality spawning habitat for the majority of the world's largest sockeye salmon (*Oncorhynchus nerka*) fishery and recreational fisheries for rainbow trout (*Oncorhynchus mykiss*) and other resident freshwater fishes. In this study, the Agulukpak River alone annually supports 100,000 to 400,000 spawning sockeye salmon in less than 1.3km of river length (University of Washington, Alaska Salmon Program, unpublished data). In addition, the Agulukpak River receives ~700 to 1500 angler days per year with each visitor paying several thousand dollars per week of fishing (Dye and Schwanke 2009). Local sport fishing guides acknowledge that large wind storms create un-favorable fishing conditions for rainbow trout for 1 to 3 days following a storm and they speculate that poor fishing conditions may be related to stressful conditions induced by rapid fluctuations in river temperatures from upwelling. The physiological and ecological basis for these observations remains unresolved.

Scientific and management plans often focus on describing changes to seasonal averages and lethal limits in river basins rather than the conditions that maintain natural thermal variability in streams and rivers. However, increasing evidence suggests that the temporal variation that is characteristic of natural thermal regimes is equally important to the health fluvial ecosystems and aquatic ectothermic species (Olden and Naiman 2010, Steel et al. 2012, Vasseur et al. 2014). Our data revealed how lakes as features within landscapes create natural thermal variation in rivers through wind action and upwelling, but the effect may only be characteristic of rivers with larger lakes. Such variation highlights the unique complexity of river systems inundated with natural lakes, with perhaps unappreciated ecological significance.

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Figures

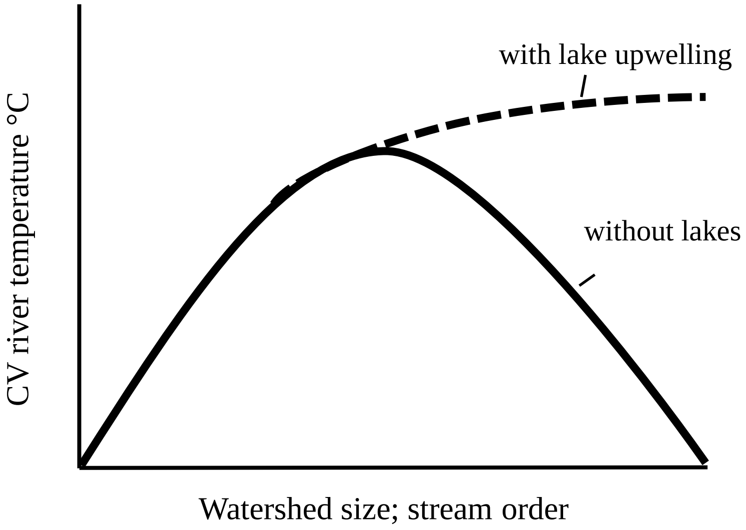

Figure: 4.1. Conceptual diagram showing the proposed relationship between stream temperature variability and watershed size or stream order. Solid line indicates the relationship proposed by Caissie (2006) which did not include the effects of upstream lakes. Dashed line is the proposed alternative relationship for watersheds containing large lakes that are the water source for downstream rivers. Increased variability at large watershed sizes would result from wind-driven upwelling in source lakes.

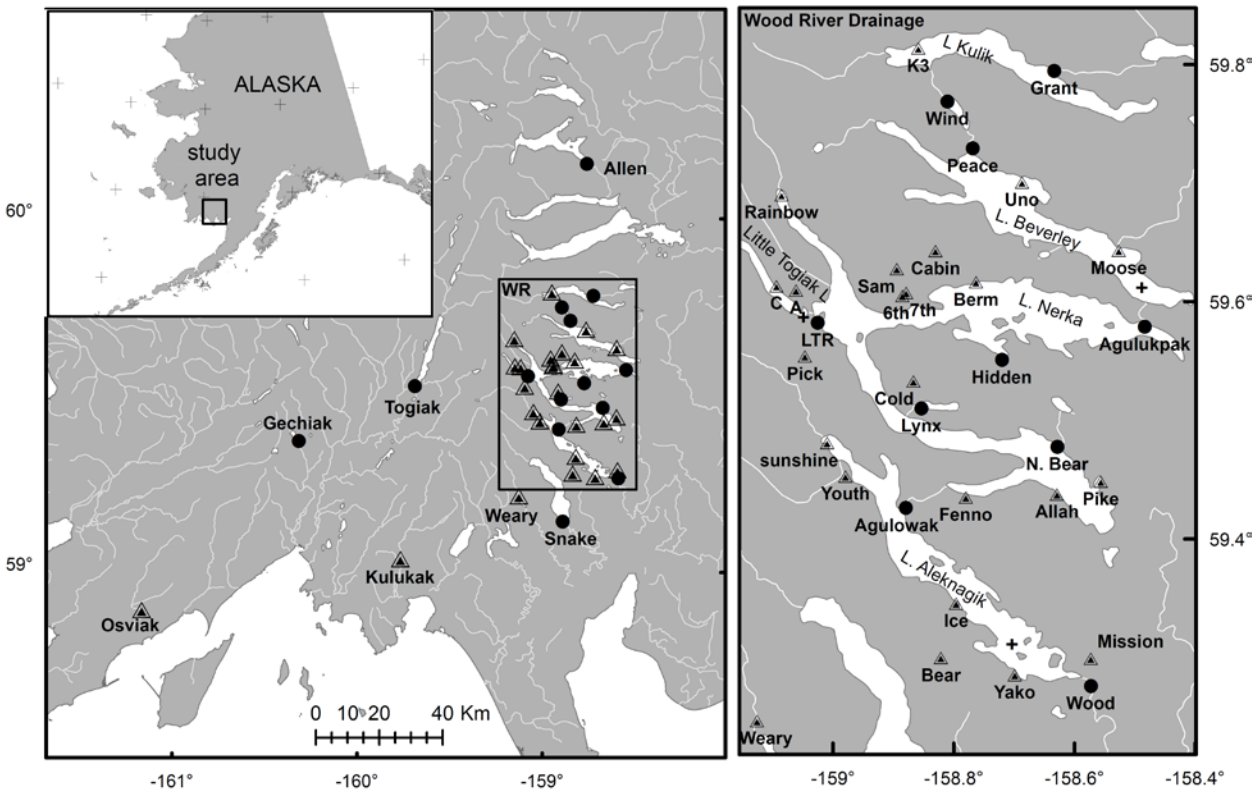

Figure: 4.2. (A) Map of study region in Alaska and (B) locations of data loggers in Togiak and Upper Nushugak drainage. (C) Enlarged version of the Wood River drainage. Position of stream loggers on streams draining lakes (circles), streams without lakes (triangles), and position of temperature arrays (plus sign) on Little Togiak Lake, Lake Beverley and Lake Aleknagik.

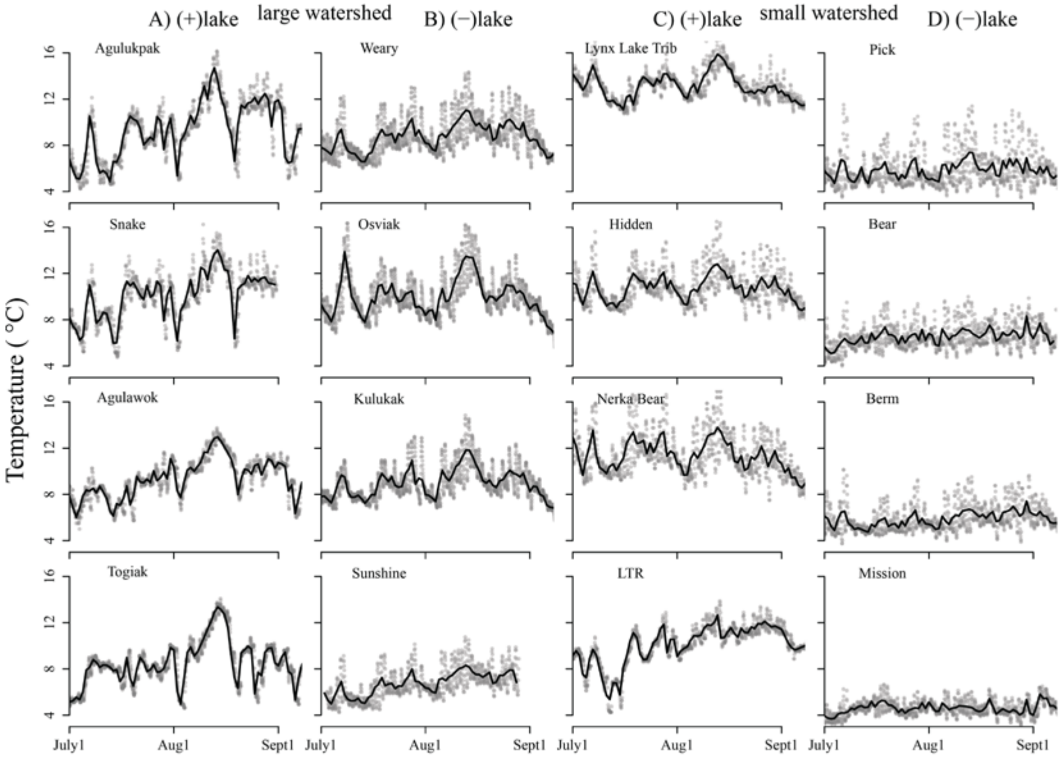

Figure: 4.3. Examples of the variation in temperature regimes from 20 of 39 study streams and rivers. Solid line indicates the average temperature, while grey points indicate sub daily (hourly or 90min) temperatures. (A) rivers draining large lakes (watershed area 1070-270 km^2); (B) rivers from large lake-less basins (1010 to 93 km^2); (C) streams draining medium and small lakes with watershed areas (85 to 8.5 km^2), and (D) streams and headwater tributaries lacking lakes (20 to 1.1 km^2)

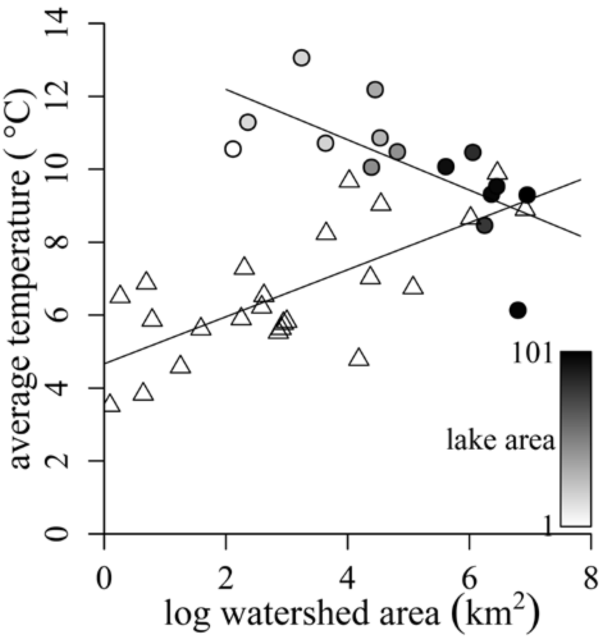

Figure: 4.4. Average summer temperature as a function of watershed size for streams and rivers draining lakes as open circles and shaded as a function of their lake area. Streams lacking lakes are the open triangles.

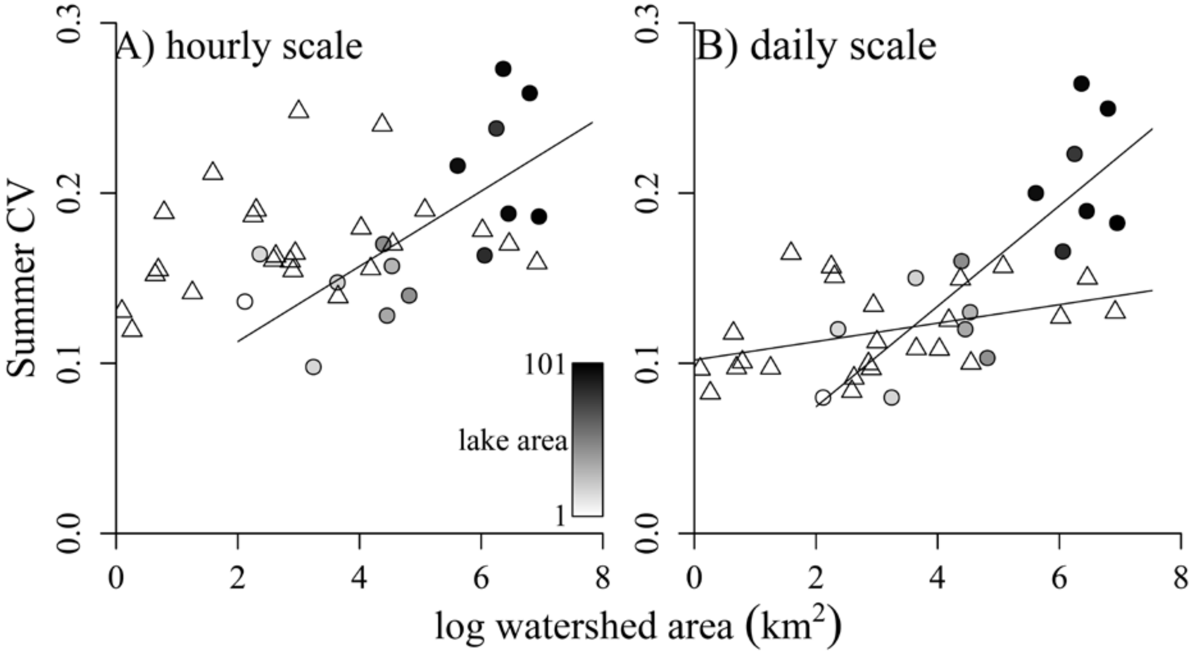

Figure: 4.5 Total summer thermal variation (CV) of 41 streams as a function of log watershed area (km^2) at hourly time intervals and (B) Summer CV at daily average time scales. Streams and rivers draining lakes as open circles and shaded as a function of their size. Streams lacking lakes are the open triangles.

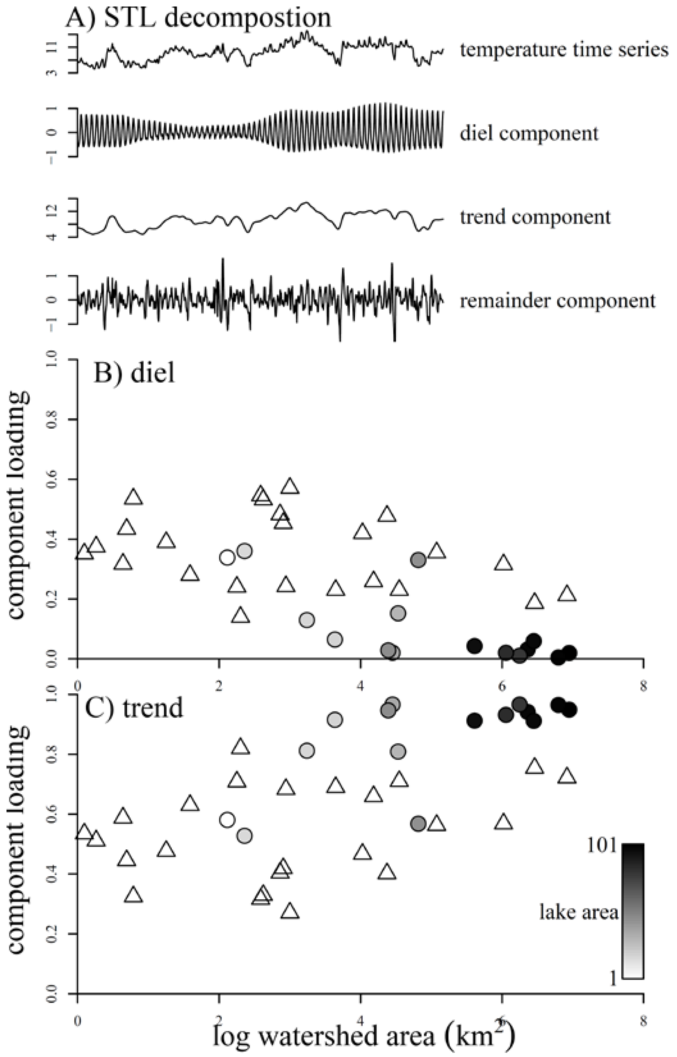

Figure: 4.6. (A) Example of seasonal trend decomposition of a temperature time series in to the diel, trend, and remainder components. (C) “diel”, and (D)“trend” component contribution to stream thermal regimes. Streams and rivers draining lakes as open circles and shaded as a function of their size. Streams lacking lakes are the open triangles.

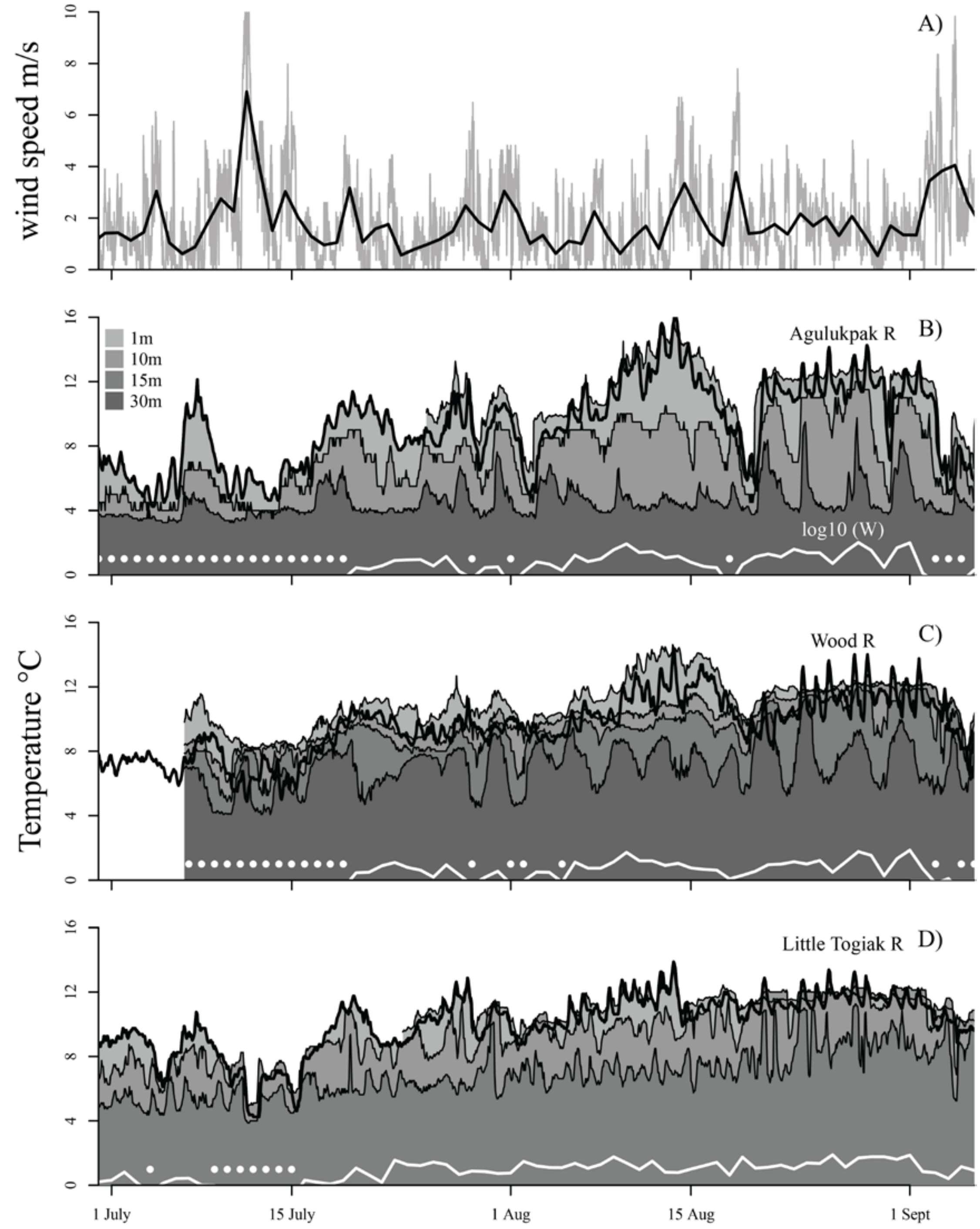

Figure:4.7 (A) Hourly wind speed m/s (grey line) and the daily average (black line). (B-D) River thermal regimes of the (B) Agulukpak River, (C) Wood River, and (D) Little Togiak River as the dark solid line and each of their upstream lake temperatures from vertical arrays in each lake. Polygon color corresponds to water temperatures at different depths. White line indicates $\log_{10}(W)$ for each upstream lake, where upwelling may be possible during wind events when $W<1$, as indicated with white dots above this line.

Chapter 5:

Spatial variation in marine subsidies influences riparian phenology through plant-pollinator mutualisms.*

**Published chapter*. Lisi, P. J., and D. E. Schindler. 2011. *Ecosphere* 9:1–13.

Introduction

The transport of materials among habitats by migratory animals can have profound consequences for the structure and composition of recipient communities (Polis et al. 2004). These subsidies produce trophic and nutrient cycling responses through direct consumer pathways (Anderson and Polis 1998, Polis et al. 2004). However, consumers that benefit from these subsidies may also have broader ecological impacts through non-trophic pathways such as pollination and disturbance (Hutchinson 1959, Olff et al. 2009), though these indirect effects of subsidies on communities are poorly understood. Seasonally pulsed resource subsidies can alter the abundance and phenology of consumers which, in turn, may affect other species through many pathways such as mutualisms. In such ecosystems, the phenology of mutualistic relationships may therefore be regulated by and dependent upon the seasonal availability of resource subsidies.

An emerging interest in population diversity has shown that intraspecific diversity can stabilize or enhance a variety of ecosystem processes and services (Luck et al. 2003, Bolnick et al. 2011). Variation in the biological attributes of one species can produce variation in other species if they are linked through ecological interactions (e.g., predator-prey, mutualisms). In particular, diversity within a subsidizing species may facilitate intraspecific variation in the species with which it interacts but such transmission of intraspecific diversity is not well understood.

Anadromous Pacific salmon (*Oncorhynchus* spp.) provide subsidies of marine-derived nutrients and energy to freshwater and riparian habitats where they spawn and die (Gende et al. 2002, Naiman et al. 2002). Nutrients and energy from salmon permeate aquatic and terrestrial systems via a wide variety of direct trophic pathways (Bilby et al. 1996, Helfield and Naiman 2001, Hilderbrand et al. 2004, Hocking and Reimchen 2006). However, little is known about the indirect consequences of salmon subsidies in terrestrial communities. Pacific salmon are also characterized by extensive intraspecific life history diversity that is expressed both among and within the watersheds they use for spawning and rearing (Quinn 2005). In particular, inter-population differences in spawn timing, a reflection of hydrologic characteristics in specific spawning sites, produce substantial spatial variation in the seasonal timing of when salmon-derived subsidies are available to salmon predators and scavengers (Schindler et al. 2010).

We assessed whether the variation in spawn timing among populations of sockeye salmon was associated with the flowering phenology of a common riparian plant along streams within the same river network. We hypothesized that this association was mediated by blowflies that rely heavily on salmon resources but which also serve as a key pollinator for many riparian plants. In particular, adult blowflies (Calliphoridae spp.) are common pollinators of kneeling Angelica (*Angelica genuflexa)*, their larvae are a major consumer of salmon carcasses (see Plate 5.1a) and their local densities appear to be synchronized in space and time to the seasonal arrival of spawning salmon.

Flowering time is a phenotypically plastic character in plants that adds to the diversity produced by genetic variation within species (Munguia-Rosas et al. 2011, Elzinga et al. 2007). Flowering phenology is broadly affected by bottom-up environmental conditions such as temperature, photoperiod, and resource availability, while pollinators, seed dispersers, pathogens and seed predators impose top down selective forces on flowering phenology (Elzinga et al. 2007). We hypothesize that blowfly pollinators mediate significant selective pressure on flowering phenology of Angelica associated with variation in salmon spawn timing among streams that alters the spatial variation in when salmon carcasses are available to insect scavengers which function as riparian pollinators as adults.

First, we used stable isotopes of carbon (C) and nitrogen (N) to estimate the degree of reliance on salmon resources versus riparian material in adult blowflies observed pollinating riparian plants including kneeling Angelica (see Plate 5.1b). Second, we investigated whether the variation in flowering phenology of kneeling Angelica in riparian habitats was associated with the seasonal spawn timing of salmon to their natal stream throughout a river system in southwest Alaska.

Methods

Site description: Research was conducted in the Wood River system in southwest Alaska (Figure 5.1). The system is comprised of five large interconnected lakes fed by numerous small streams that drain through the Wood River into Bristol Bay. The watershed contains a diversity of riparian vegetation including forest (*Picea glauca*, *Betula papyrfera*, and *Populus balsamifera*), scrub (*Alnus crispa*, and *Salix alaxensis*) and wet meadows (Bartz and Naiman 2005). Salmon return to streams, rivers, and beaches throughout the entire system and spawn between mid-July and mid-September (Schindler et al. 2010). Within individual streams, salmon spawn timing and entry to each stream is very consistent among years but differs substantially between streams (Moore and Schindler 2010). Over the last 50 years, sockeye salmon (*Oncorhynchus nerka*) escapement (fish that escape the commercial fishery to spawn) to the

Wood River system has averaged 1.1 million (Baker et al. 2006).

Resource use by blowflies: Two dominant species of blowflies have been identified in this region, both of which are in the *Calliphoridae* family: *Calliphora terranovae and Lucillia illustris* (Meehan et al. 2005) and are also widespread in British Columbia, Canada, in other ecosystems that support Pacific salmon (Hocking et al. 2009). We captured blowfly adults from salmon carcasses and kneeling Angelica along salmon streams and rivers for analysis of their nitrogen and carbon stable isotopic ratios to determine the degree to which they depended on salmon resources versus riparian plants for sustenance. This process was replicated on three salmon spawning sites (Lynx Creek, the Agulukpak River and the Agulowak River) during the peak of salmon spawning in August of 2008 and 2009. Blowfly adults were also collected several kilometers up two non-salmon streams on the northwest arm of Lake Nerka in 2010 to evaluate their isotopic composition in the absence of local salmon resources. Adult blowflies were placed in coin envelopes and frozen or air-dried for later isotopic analysis. Because salmon tissues have a unique isotope composition relative to most terrestrial resources, including terrestrial carrion, stable isotopes of carbon and nitrogen can be used to assess the relative contributions of salmon resources versus terrestrial plant resources on salmon streams to the nutrition of blowflies over the course of their lives (Fry 2006, Hocking and Reimchen 2006). Adult blowflies have sponge-like mouthparts that physically limit ingested foods to liquids or fine solids dispersed in liquids, such as plant nectar or wet mucus. The majority of protein is consumed in the larval life-stage after carrion is dissolved, exogenously, with enzymes in larval saliva (Sandeman et al. 1987).

We followed visitation of blowflies to riparian plants to identify their potential carbon and nitrogen sources from terrestrial plants. Species included golden rod (*Solidago* spp.*)*, marsh cinquefoil (*Potentilla palustris*), cow parsnip (*Heracleum maximum*) and kneeling Angelica (*Angelica genuflexa).* We identified plants and dried their flowers in coin envelopes for stable isotope analysis. The remainder of this study focuses on kneeling Angelica because they are a common riparian plant that flowers during the spawning of salmon and blowflies tended to congregate on them more than any other riparian plants.

To evaluate the isotopic responses of developing blowflies feeding on salmon carcasses we incubated 5 salmon freshly killed by bears and 5 senescent salmon on a small island (to avoid scavenging by bears and small mammals) near a salmon stream on Lake Nerka in 2009. We observed blowflies ovipositing on carcasses within an hour of the start of the experiment and then collected egg and larval blowfly samples every 2 to 3 days until the larvae consumed the entire carcass or began to migrate underground to pupate (~9 days later). We excavated pupae from the soil the following spring and hatched a subset of these to adults. Samples were stored in 70% ethanol which was eventually evaporated from the samples prior to preparation for isotopic analysis.

All samples were oven-dried at 60°C for three days and then homogenized using a mortar and pestle. Samples were packed in tin capsules and standardized to contain 40 to 45 micrograms of nitrogen (N) according to 11.5% N by dry mass for blowflies and 3% N by dry mass for plant matter. All samples were analyzed with a Costech elemental analyzer (Analytical Technologies Inc, Valencia, CA) coupled to a Finnigan MAT253 isotope-ratio mass spectrometer (Thermal Electron Corporation, Bremen, Germany) at the University of Washington Isolab. Isotope ratios were expressed in standard notation of per mil differences from the universal standards of Vienna Pee Dee Belemnite and atmospheric nitrogen gas for carbon and nitrogen, respectively (Fry 2006).

Isotope mixing model: We used a mixing model to estimate the contributions of food sources to various life stages of blow flies using MixSIR v 1.04 (Moore and Semmens 2008). This model generates posterior probability distributions of the relative contributions of potential food sources to consumers based on the stable isotope characteristics of the consumer relative to those of its potential prey. The model allows the user to incorporate variation in the stable isotope ratio of consumers, their food resources, and fractionation rates. We assumed only riparian plants and salmon as the potential food sources for calliphorid blowflies. For salmon, we used isotope data from a meta-analysis of spawning sockeye salmon tissue from the Wood River system (Johnson and Schindler 2009). Plant sources of C and N were represented by the average and standard deviation of flowers for plants that we observed adult blowflies visiting ($n = 8$ from 4 plant species). Carbon isotope signatures of sources and consumers were corrected for lipids according to their C:N ratio (Post et al. 2007) prior to running the model. We assumed a trophic fractionation for terrestrial animals of 2.3 ± 1.52‰ (±SD) per trophic step for nitrogen and 0.5 ± 1.37‰ per trophic step for carbon (McCutchan et al. 2003). MixSIR can be informed with priors, such as gut content data; however, lacking such information we used non-informative priors in our analysis.

Salmon and kneeling Angelica phenology: Salmon entry date to spawning habitat was documented by repeated visits to each stream until we confirmed that salmon were actively spawning. In these systems, salmon generally initiate spawning within 2 days of entering streams and salmon entry to the streams is predictable to within 2-5 days each year (Moore and Schindler 2010).

The flowering phenology of kneeling Angelica was measured on 6 streams by visiting 75 to 100 individually tagged plants every 4 to 5 days near the stream edge within the alluvial floodplain until the plants had finished flowering and completely seeded. The compound inflorescence, or umbel, was classified as “flowered” if the majority of the flowers on an umbel presented their stamens. The number of individual umbels that had flowered or not was recorded to estimate the total proportion flowered on the stream on the day of the survey.

In order to characterize the peak flowering date on many streams without having to intensely monitor each stream due to logistical constraints, we first estimated the average blooming rate of kneeling Angelica by repeatedly monitoring several streams ($n = 6$ in 2008 and $n = 4$ in 2009) and then using these data to parameterize a normal distribution with a defined mean and variance that characterized the flowering phenology on each stream. Based on the observed proportion of plants that flowered on a given date on streams we visited once, we were then able to calculate the mean flowering date by assuming a cumulative normal distribution of flower development, with shape defined by a common variation determined from the intensively monitored streams. To calculate the common variation, we fit the observed flowering proportions on an individual stream to a cumulative normal distribution using least squares to estimate the mean date of flowering (m) and standard deviation (s). We took the average standard deviation of 10 flowering events on 6 streams over 2 years in the cumulative normal model to estimate the average duration of the bloom within all streams (s*). Using this constant distribution of blooming (s*) among streams, we calculated the mean day of year (m) on additional streams that we visited only once during the flowering season based on the proportion of flowers that had fully bloomed on the sampling date. This strategy allowed us to expand our dataset to a total of 20 streams in 2009 and 15 streams in 2010.

Physical parameters: We monitored stream temperatures to define thermal characteristics of individual tributaries associated with sites where Angelica bloom timing was measured.

Stream temperatures are highly correlated with riparian soil temperatures (Naiman and Decamps 1997) and soil temperature is often a strong predictor of plant development. I-button temperature recorders (Maxim Integrated Products, Sunnyvale, CA) were placed in the mouth of salmon-bearing tributaries to record temperature at 90 minute intervals from June 30th to September 1st in 2010 and 2009. Temperature loggers were suspended 3-5 cm above the streambed by attaching them to steel rebar set in the streambed. All loggers were cross-calibrated before the start and at the end of the study and found to be within ± 0.5°C of each other. We corrected temperature loggers deviating substantially from the average during calibration.

To determine riparian habitat characteristics in the portion of the stream that we surveyed plant bloom timing, we used ArcGIS (v10.0, Environmental Systems Research Institute, Redlands, California, USA) to classify the section of streams with a variety of physical metrics using a digital elevation model. We created a 30 meter buffer in ArcGIS on both sides of the stream to capture the habitat characteristics of the riparian zone in the portion of the watershed where we monitored Angelica flowering phenology. Kneeling Angelica was most abundant within 30 m the stream edge and largely absent further upslope. Using zonal statistics and the digital elevation model, we found the center location of the survey (latitude and longitude), the average elevation, average degree slope, and average aspect under buffered region for each stream. Higher elevation, greater distance from ocean, and steeper slopes in the riparian area may impact snow cover, local air temperature, water retention, and therefore, the effect the onset of plant development. The degree to which sunlight hits a hillside depends on its aspect, where north-facing hillsides receive less sunlight than south-facing slopes, which may control local temperature and light differences as another possible driver of local bloom timing (Jackson 1966).

We used the Akaike information criterion corrected for small sample sizes, AICc, (Burnham and Anderson 2002) to determine the most parsimonious regression model explaining variation in Angelica flowering day of year when considering salmon spawn timing, stream temperature, aspect, slope, elevation and location among the study streams. We used multiple linear regression to build and contrast competing candidate models. All models were fit using the minimum sum of the negative log-likelihood assuming normally distributed errors. We created a number of candidate models including reasonable linear combinations of the predictors listed above. The resulting candidate models were ranked by the difference between each model (i) and the best model according to $\Delta_i = AIC_{ci} - AIC_{cmin}$, where AIC_{cmin} is the AICc value of the best model, and AIC_{ci} is the AICc of another candidate model. In general, when $\Delta i > 10$ there is essentially no support for the candidate model and when Δi is between 0-2 there is substantial support for a candidate model being as good as the best model (Burnham and Anderson 2002).

Results

Isotopic analysis: Kneeling Angelica, cow parsnip, goldenrod, and marsh cinquefoil (grand mean ± SD: $\delta^{15}N$ 3.5 ± 1.1‰, $\delta^{13}C$ -26.9 ± 1.9‰) were distinctly depleted by 7.5‰ $\delta^{15}N$ and 5.6‰ $\delta^{13}C$ relative to salmon ($\delta^{15}N$ 11.1 ± 0.5‰, $\delta^{13}C$ -21.3 ± 0.5‰, Johnson and Schindler 2009). Blowflies captured on salmon streams or incubated with salmon had enriched stable isotope distributions indicating that salmon resources were present in all life stages (grand mean: $\delta^{15}N$ 12.9 ± 0.9‰, $\delta^{13}C$ -21.4 ± 0.9‰)**.** In the spring, blowfly pupae ($n = 10$) reared from salmon carcasses the previous summer had similar carbon and nitrogen signatures to salmon ($\delta^{15}N$ 12.1 ± 0.8‰, $\delta^{13}C$ -21.3 ± 0.1‰). Blowfly adults ($n = 10$) hatched from these pupae had slightly enriched $\delta^{15}N$ signatures relative to the pupae but virtually the same carbon signature ($\delta^{15}N$ 13.8 ± 0.3‰, $\delta^{13}C$ -21.3 ± 0.2‰, Figure 5.2).

In late summer, blowfly adults (*n* = 10 flies) captured on two non-salmon streams (Rainbow and Cottonwood) were distinctly depleted in δ^{15}N and δ^{13}C (δ^{15}N 8.6 ± 3.9‰, δ^{13}C -24.1 ± 1.5‰) compared to those caught on salmon bearing streams, indicating reliance on terrestrial resources. Blowflies from non-salmon streams also had wider variance among individual δ^{15}N signatures compared to adults captured on salmon streams (*n* = 28) that were slightly enriched relative to salmon in nitrogen (δ^{15}N 12.6 ± 2.7‰, δ^{13}C -22.4 ± 1.4‰), but depleted in carbon relative to salmon (Figure 5.2).

The 10 salmon carcasses incubated on land were completely consumed by blowfly larvae with only a dry layer of skin and bones remaining after about 9 days. Blowfly eggs, collected on these carcasses within hours of the start of the incubation, were similar to the maternal carbon and nitrogen signatures (δ^{15}N 11.8 ± 1.2‰, δ^{13}C -22.4 ± 0.4‰) of adult blowflies collected on salmon streams. Both adults and eggs had slightly depleted isotope signatures relative to larvae reared on salmon carcasses, which were the most-enriched life-stage (Figure 5.2).

Blowflies are generalist carrion feeders and some proportion of adults may have been raised as larvae on alternative carrion sources. We compared the isotope signatures of eggs, blowfly adults captured on salmon streams and on non-salmon streams to screen for individuals that may have been raised on terrestrial carrion. We plotted Gaussian bivariate ellipsoids (with SYSTAT v11) with a confidence level of 62.9%, which is equivalent of 1 standard deviation about the mean of the x and the y variables (Figure 5.3). Of the adults captured in the late summer on salmon streams, 3 of the 28 adults had C and N isotope values indicating a predominately terrestrial carrion source. On non-salmon streams, 4 of the 10 adults collected had isotope signatures suggesting they reared as larvae on salmon. These data suggest that there is some dispersal of adult flies between non-salmon and salmon streams, but that most adult flies remain on the stream where they were hatched. C and N isotope values of blowfly eggs on salmon streams were all highly enriched indicating that they were laid by adult flies that reared as larvae on salmon carcasses (Figure 5.3).

The means of the posterior distributions from the isotope mixing model indicated that spring blowfly pupae were composed of 84% salmon material (90% credible interval: 78-92%). Adults hatched from the pupae were 95% salmon (CI: 89-99%). Blowfly adults captured on salmon streams were composed of 91% salmon (CI: 86-96%), with the balance from riparian plants. For these analyses we excluded 3 individuals which likely reared as larvae from terrestrial carrion (Figure 5.3). Although blowfly adults on salmon streams are mostly comprised of salmon resources in late summer, they appeared to accumulate some of their carbon and nitrogen from terrestrial plants. A lower proportion (76%) of salmon material was found in freshly deposited blowfly eggs on salmon carcasses (CI: 70-83% salmon), indicating dilution with terrestrial material transferred from mothers to eggs. After 4 days of incubation on salmon carcasses, blowfly larvae were 97% (CI: 91-99.7%) salmon. By day 9, larvae were composed of 98% (CI: 98-99.8%) salmon material with only trace amounts of terrestrial material (Figure 5.4).

Angelica bloom phenology: The mean flowering date showed a range of 24 days among the 20 study streams. A cumulative normal distribution provided excellent fit to the observed bloom proportions on intensively monitored plants in 2008 and 2009 (Figure 5.5). The average standard deviation in bloom date from the focal streams was 6.8 days. We found no correlation between the standard deviation and the mean date of blooming across streams, so therefore assumed that late and early flowers bloom had the same local variation in bloom timing throughout the Wood River system. This parameter value was then used to expand our estimates of the proportion of flowering plants on a single date to an estimate of the mean flowering time. The day of flowering was generally consistent between streams in both 2010 and 2009 (Pearson's $r = 0.72$, figure 5.6).

Among the potential combinations of parameters (latitude, longitude, slope, elevation, aspect, average stream temperature, and salmon entry day of year), the model with the lowest AICc was one that included longitude and salmon entry day of year (Table 5.1, model 12, Figure 5.7, $r^2 = 0.88$). Bloom timing was positively associated with salmon spawn timing and negatively correlated with longitude as streams toward the west tending to bloom later. No other candidate model had substantial support (i.e., Δi between 0 and 2). Latitude was also correlated with the bloom timing of Angelica ($r^2 = 0.27$), as an increase in latitudes correspond with areas further from the ocean, although further north latitudes also had watersheds with higher average elevations and later running salmon. Surprisingly, stream temperature alone did not have a clear relationship with bloom timing (model 29, Table 5.1). Salmon entry date was present in all of the best candidate models with a ΔAICc between 0 and 10. Finally, it is noteworthy that the onset of flowering was offset by 19 days, on average, after the entry of salmon in each stream. This delay in flowering would allow spawning, transfer, and decomposition of salmon carcasses in the riparian area prior to the onset of flowering.

Discussion

The flowering phenology of kneeling Angelica was strongly and positively associated with the seasonal timing of salmon spawning among streams of the Wood River system. This pattern suggests that these flowers depend on blowfly visitation, which, in turn, depend both on the phenology of salmon spawning and kneeling Angelica blooming to overlap in time. Geomorphic features of watersheds within the Wood River System were only weakly associated with the bloom timing of these plants, and these relationships were much weaker than the association with salmon spawn timing. Our results suggest that population diversity in salmon run-timing

(Schindler et al. 2010) influences the diversity in riparian plant life-histories along salmon-bearing streams by supporting terrestrial mutualisms.

Our data indicate that blowflies use both salmon and terrestrial sources of nutrients and energy to complete their lifecycle. Adult blowflies captured on salmon streams had isotope signatures indicative of a heavy reliance on salmon whereas adults blowflies on non-salmon streams had fed almost exclusively on terrestrially derived resources, consistent with observations from other systems (Hocking et al. 2009). Adult blowflies require carbohydrates in the form of nectar from plants to fuel reproduction of eggs and a rich protein source (salmon) for their larvae to grow (Norris 1965). Our results show that terrestrial material from plants is passed maternally to the next generation in eggs that are deposited on salmon carcasses over course of the summer. The isotope mixing model indicated that blowfly pupae have an isotope signature that was 15% terrestrial. Given that pupae do not feed, we expected the isotope signature of pupae to be similar to their previous larval life-stage (99% salmon). The change in isotope signature suggests that metabolic processes or contamination by soils influence the isotopic composition of pupae rather than a terrestrial food source.

Indirect connections between salmon subsidies, blowfly pollinators and riparian flowers could explain why blooming in kneeling Angelica is coincident with the arrival of salmon to their respective spawning grounds. However, salmon and kneeling Angelica could also be responding to the same environmental cues that synchronize their phenology. The variation in stream spawn dates of sockeye salmon is largely driven by thermal regime differences in streams owing to the required number of degree days eggs need to incubate prior to hatching (Quinn 2005). Thus, warmer streams tend to have later spawning salmon populations, whereas cold streams support earlier spawning salmon populations. If water temperature co-varied with riparian soil temperature, we would predict that warmer streams should support earlier blooming plants while cold streams support later blooming plants. However, our results demonstrate the opposite relationship between temperatures and bloom timing. Streams towards the east of the Wood River watershed also had predominately later spawning fish with warmer than average stream temperatures, thus longitude was an important predictor among candidate models. We also considered latitude, aspect, elevation, and slope with plant phenology to investigate whether other physical factors were correlated with bloom timing. We found that these other predictors did not significantly add to our ability to estimate bloom timing. Other environmental characteristics (soil depth, soil saturation, frost depth, canopy cover) might influence flowering phenology (Munguia-Rosas et al. 2011) but were not monitored explicitly in this study. Taken together, our results suggest that flower phenology is not likely driven by local thermal conditions directly but, rather, indirectly through the effects on salmon spawning which ultimately affects the timing of when resources are available for rearing larval blowflies.

Finally, flowering phenology of Angelica could be responding to the fresh arrival of available marine derived nutrients (MDN), which drive flower timing with a nutrient boost irrespective of the availability of pollinators. In our study, Angelica peak bloom date is 2-3 weeks after salmon enter the streams to spawn. Angelica might be able to capitalize on pulsed nutrient resources of carcasses delivered to riparian areas by bears or other animals during the spawning period. Riparian plants in salmon areas have stable N isotope signatures that indicate that they are enriched in salmon-derived N compared to non-salmon streams, however, the temporal scale at which MDN accumulate in riparian environments is unknown but likely a slow process (Helfield and Naiman 2001). In our study area, nitrogen cycling in riparian soils changes little with the seasonal arrival of salmon, except in very localized areas associated with bear middens (Holtgrieve et al. 2009). Therefore, a direct seasonal pulse of a MDN subsidy to plants is an unlikely mechanism producing the variation in flowering phenology in Angelica that we observe associated with salmon spawn timing among streams. While correlational, our data suggest that Angelica flowering timing is cued to the seasonal activities of scavenging blowflies which are linked to the seasonal availability of resources from salmon that have moved substantial quantities of energy from marine ecosystems to freshwater streams where they spawn and die.

Summary

The annual return of sockeye salmon to their natal streams can have a substantial effect on the abundance of invertebrate communities in riparian areas. Hocking et al. (2009) recorded 60 species from 36 families and 17 orders that were present on salmon carcasses during spawning events. These insects arrive on salmon spawning streams to take advantage of the largest, most reliable, pulsed resource of carrion available in these ecosystems (Gende et al. 2002, Schindler et al. 2003). This pulse can have a substantial effect on the local abundance of scavenging flies. For example, Meehan et al. (2005) estimated that a single, second-order, salmon stream in our study region can support up to 10 million blowfly larvae in a typical year even after a substantial proportion (66%) of the returning adult salmon have been harvested in Bristol Bay commercial fisheries (Clark et al. 2007). Disturbance by salmon during redd digging is also thought to have potential evolutionary effects on the emergence timing of aquatic insects residing in salmon streams (Moore and Schindler 2010). Thus, salmon can have major impact on the timing and abundance of both terrestrial and aquatic insects in riparian areas. However, little attention has been given to possible ecological roles of invertebrates after being supported or impacted by salmon. Our study is the first to consider that insects supported by salmon resources visit riparian plants that flower along salmon streams. Other invertebrate species impacted by salmon may also serve pollination roles or attract seasonal insectivores. Migratory animals that provide resource subsidies or create disturbance also create a richer array of indirect ecological effects in the animals they support.

Streams and their adjacent riparian areas are closely linked through food webs and material fluxes (Baxter et al. 2005). Yet, there are few examples where fish directly or indirectly support riparian plants. Fish insectivores in Florida ponds have been shown to indirectly affect the reproductive success of riparian plants by consuming dragonfly predators that prey on riparian pollinators (Knight et al. 2005). Others have observed long distance, upstream seed dispersal by frugivorous fish in the Amazon floodplain (Anderson et al. 2011). Salmon are also known to shape riparian plant communities through nutrient enrichment in the riparian area (Hocking and Reynolds 2011). Our study, including the above literature, suggests that fishes act in a variety of pathways that support riparian plants and couple aquatic and terrestrial ecosystems.

Changing climate will likely affect temperatures of streams with warmer air temperatures or changes to regional hydrology, particularly in high latitude systems (Perkins et al. 2010). Changes to aquatic thermal regimes has altered the phenologies of many plant and animal species (Parmesan 2006) including the period of migration for spawning salmon (Quinn and Adams 1996, Hague et al. 2011). Communities with species that have evolved their life-history to overlap with seasonal abundance of salmon will need to adapt to a warmer climate and local shifts in the timing of their food source. Future research not only needs to consider the direct effect of nutrient subsidies, but also the secondary effects on the diversity of communities which are influenced indirectly by the inherent spatial and temporal variation in the subsidy of interest.

Our results suggest that indirect pathways from spatial subsidies are likely important to the biodiversity of communities and their effects should be integrated with the more conventional assessment of direct effects of subsidies on recipient communities.

Acknowledgements

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List of Figures

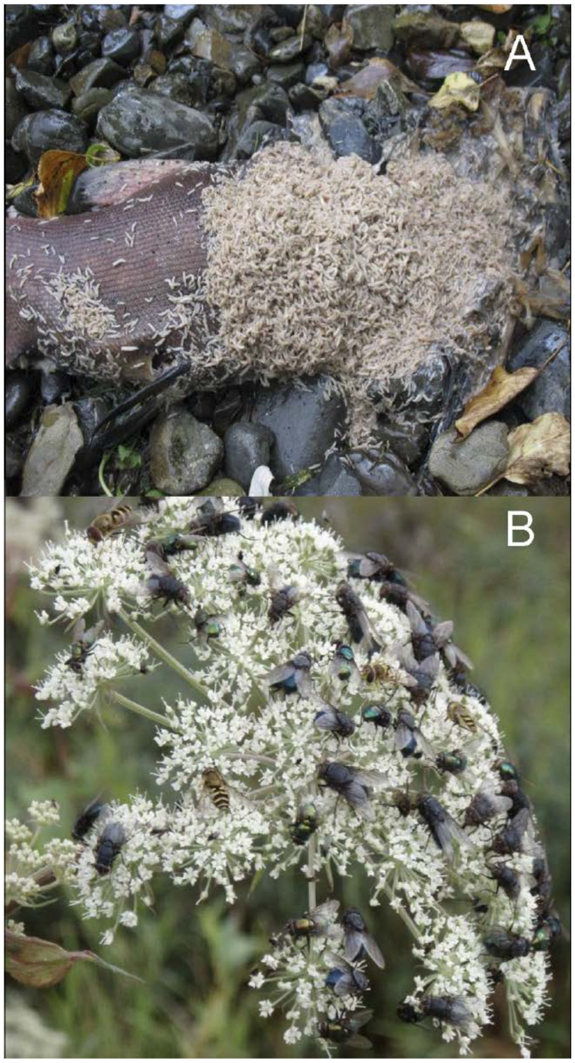

Plate 5.1: A) Blowfly larvae consuming a salmon carcass and B) blowfly adults visiting kneeling Angelica on a salmon stream

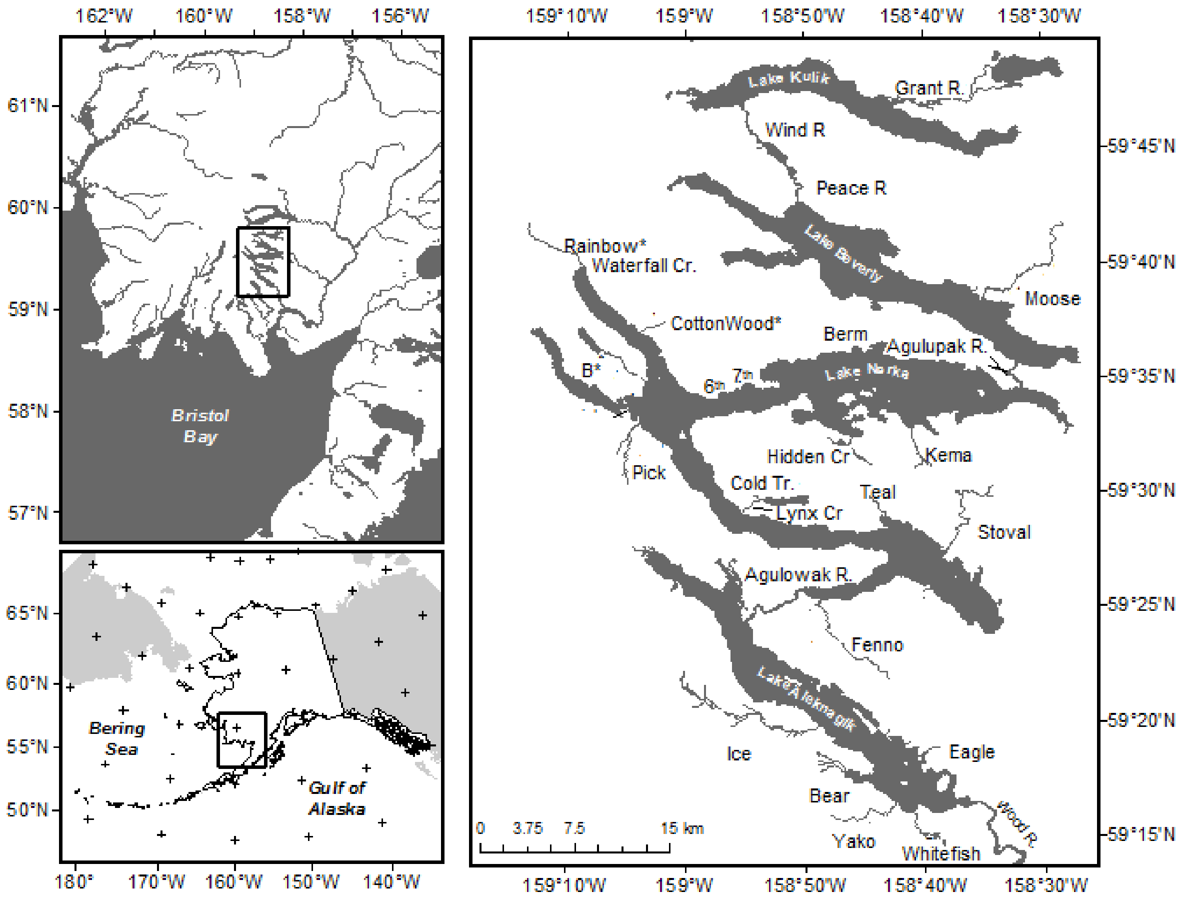

Figure 5.1: Lower left panel outlines the region in Alaska where research took place. Upper left panel shows the series of lakes that drain into Bristol Bay Alaska. Right panel gives the extent of the Wood River system and tributaries that feed into four lakes. Major salmon tributaries are highlighted with their respective names on the map. Tributaries in this study that do not have salmon spawning populations are marked with an asterisk after the name.

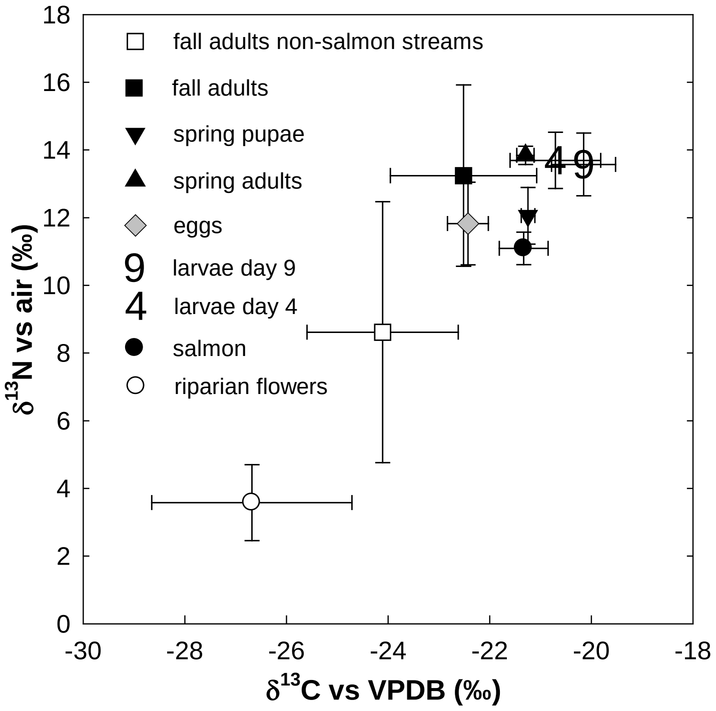

Figure 5.2: Mean values of δ^{15}N and δ^{13}C stable isotope signature (±SD) in calliphorid blowfly adults on salmon and non-salmon streams, eggs, pupae, and larvae and adults hatched from pupae after carcass were incubated on land. Salmon and riparian flowers are also shown as reference food sources. Data have been corrected for lipid fractionation of carbon according to their C:N ratios.

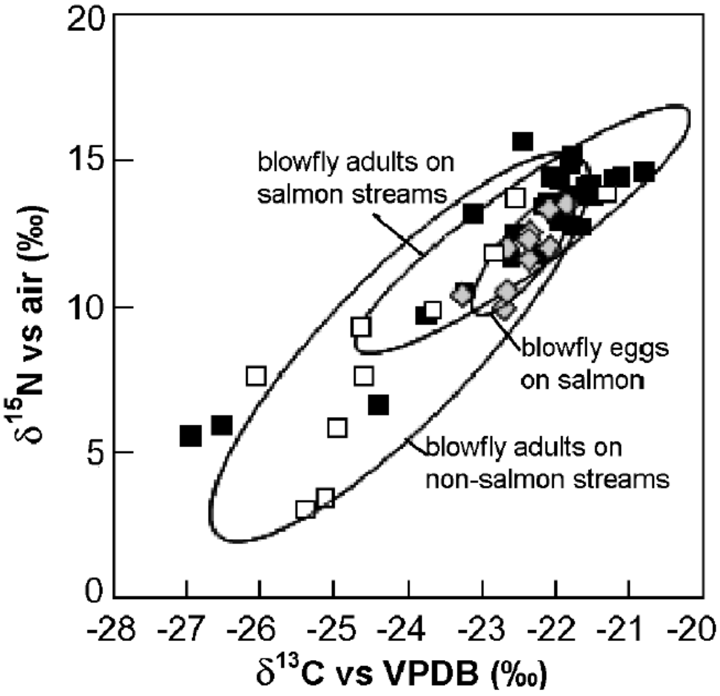

Figure 5.3: Life stage variation of δ^{15}N and δ^{13}C stable isotope signatures in calliphorid blowfly adults on salmon (filled squares) and non-salmon streams (open squares), and eggs (grey diamonds). Data have been corrected for lipid fractionation of carbon according to their C:N ratios. Each cluster has a Gaussian bivariate ellipsoid with a confidence level of 62.9%, which is equivalent of 1 standard deviation about the mean for each life-stage.

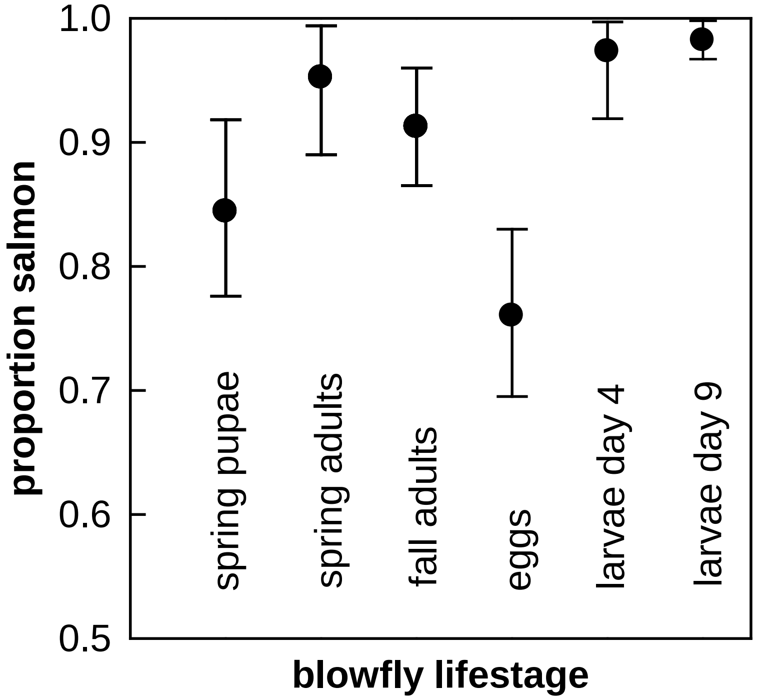

Figure 5.4: MixSIR results showing the mean proportion of salmon nitrogen and carbon to consumers to blowflies collected on or near salmon streams. Proportional values toward 0 indicate an increasing proportion of terrestrial nitrogen and carbon. Whiskers indicate the 90% credible interval (upper 95% and lower 5%) of the mixture distribution.

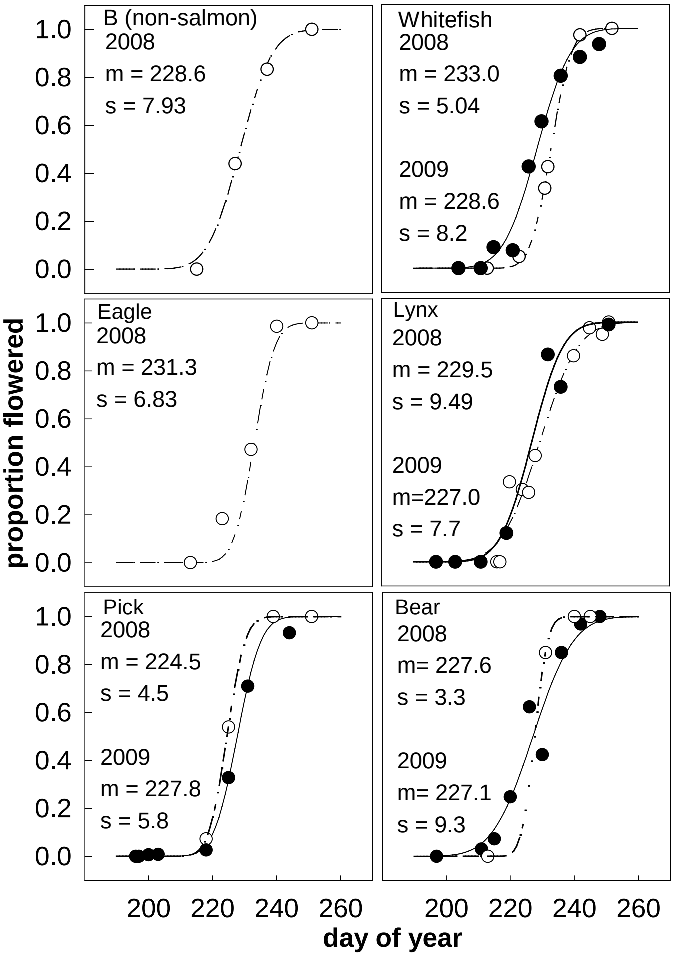

Figure 5.5: Observed flowering proportion of kneeling Angelica on salmon and non-salmon streams in 2008 (open circles, dotted line) and 2009 (closed circles, solid line). Each box is an individual stream with data representing proportion flowered from a single stream survey. A cumulative normal distribution was fit to the data by minimizing the sum of squares between the model and observed data by optimizing the standard deviation (s) and the mean day of year (m). Day 200 is July 19th.

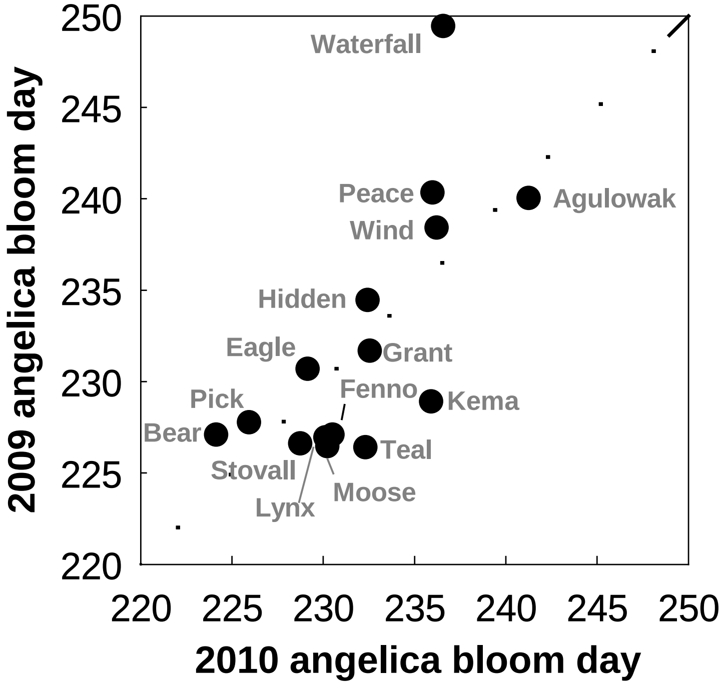

Figure 5.6: Mean Angelica flowering day in among 15 streams in 2010 versus 2009. The 1:1 relationship is shown by a dashed line.

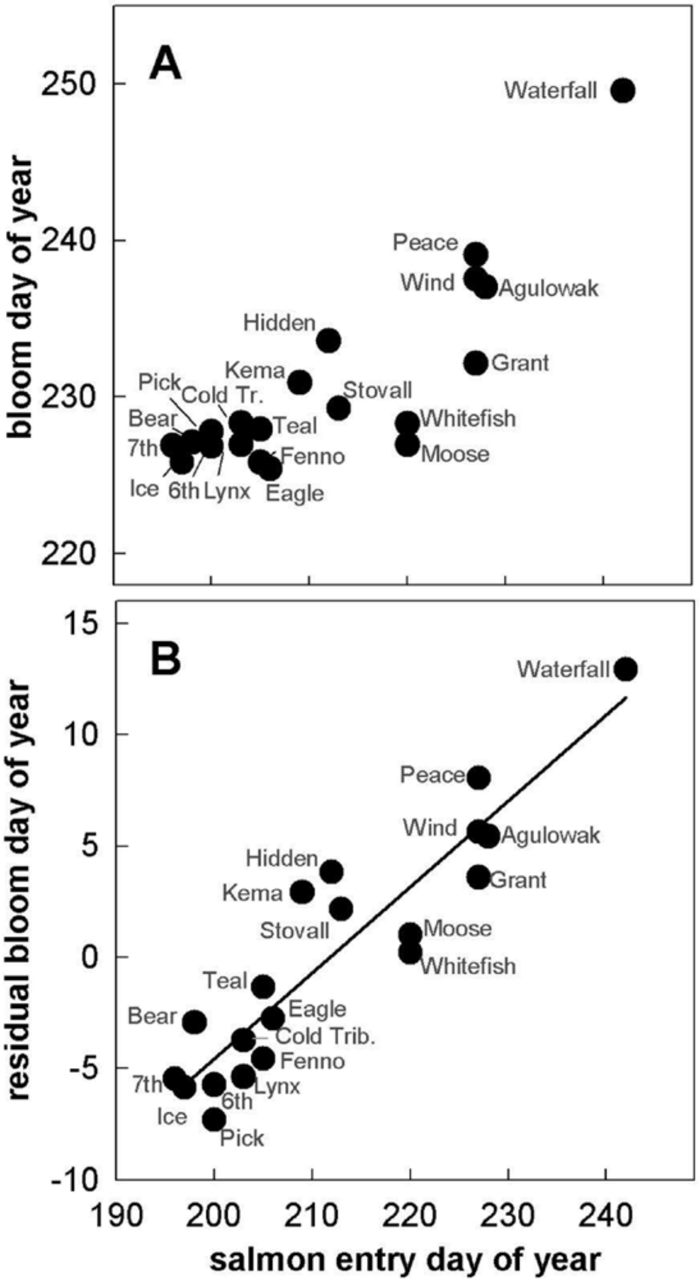

Figure 5.7: (A) Association between Angelica mean bloom date and the date of entry of salmon into 20 streams in the Wood River system. (B) Association between the residual flowering date after the effect of longitude is removed via linear regression (r^2=0.19), and the date of salmon entry to the 20 study streams (r^2=0.85).

Tables

Table 1: Candidate models using multiple linear regression to estimate the observed mean flowering date on 20 streams with the following predictors: center of the watershed latitude and longitude, mean watershed elevation, mean watershed slope, watershed area, salmon entry to stream day of year and average summer stream temperature. An intercept (β_0) and error (ε) were two additional parameters included in each model according to the equation $y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots \varepsilon$. Model 20 has the lowest AICc score (ΔAICc=0), indicating the best candidate model with the conventional r^2. This model was parameterized as y = -2552 – 17.0(long) + 0.387(salmon). The sign of the relationship for each predictor is given for the top 4 models. K represents the number of parameters used in each model, and W represents the AIC weights calculated from ΔAICc score.

Model	K	Likelihood	AICc	ΔAICc	r^2	W	Predictors
1	9	67.04	170.07	33.30	0.82	0.00	Lat., Long., Elev., Aspect, Slope, Temp., Salmon
2	8	79.87	188.81	52.04	0.41	0.00	Lat., Long., Elev., Slope, Aspect, Temp.
3	7	66.20	157.22	20.45	0.82	0.00	Lat., Long., Aspect, Temp., Salmon
4	6	67.19	152.85	16.08	0.82	0.02	Lat., Temp., Slope, Salmon
5	6	63.22	144.91	8.14	0.88	1.21	Long., Temp., Slope, Salmon
6	6	62.96	144.37	7.60	0.88	1.59	Long., Temp., Aspect, Salmon
7	6	62.95	144.37	7.60	0.88	1.59	Aspect, Temp., Slope, Salmon
8	6	63.08	144.62	7.85	0.88	1.40	Long., Temp., Elev., Salmon
9	5	67.33	148.90	12.13	0.82	0.17	Slope, Temp., Salmon
10	5	67.08	148.45	11.68	0.82	0.21	Aspect, Temp., Salmon
11	5	67.31	148.90	12.13	0.82	0.17	Lat., Temp., Salmon
12	5	63.02	140.50	3.73	0.88	11.01	Long. (-), Temp. (-), Salmon (+)
13	5	67.48	149.24	12.47	0.82	0.14	Elev., Temp., Salmon
14	5	63.81	141.90	5.13	0.88	5.47	Aspect (-), Long. (-), Salmon (+)
15	5	63.89	142.07	5.30	0.88	5.02	Lat. (+), Long. (-), Salmon (+)
16	4	71.71	154.08	17.31	0.72	0.01	Slope, Salmon
17	4	71.74	154.14	17.37	0.72	0.01	Elev., Salmon
18	4	67.49	145.65	8.88	0.82	0.84	Temp., Salmon
19	4	71.74	154.15	17.38	0.72	0.01	Aspect, Salmon
20	4	63.05	136.77	0	0.88	71.06	Long. (-), Salmon (+)
21	4	71.55	153.71	16.94	0.73	0.01	Lat., Salmon
22	4	80.88	172.42	35.65	0.37	0.00	Lat., Long
23	3	84.37	176.24	39.47	0.00	0.00	Slope
24	3	83.03	173.56	36.79	0.13	0.00	Aspect
25	3	84.34	176.16	39.39	0.00	0.00	Elevation
26	3	71.79	150.99	14.22	0.71	0.06	Salmon
27	3	81.21	169.92	33.15	0.27	0.00	Latitude
28	3	81.53	173.73	36.96	0.19	0.00	Longitude
29	3	84.32	176.16	39.39	0.005	0.00	Temperature

VITA

Peter Joseph Lisi was born and raised in northwest Wisconsin and graduated from Rice Lake High School in 2002. In 2006, he graduated with distinction with from the University of Wisconsin with a B.S in biology. During his undergraduate degree, Peter received the Research Experience for Undergraduates (REU) award from the National Science Foundation. As part of this experience, Peter worked with the UW Center for Limnology, Cascade research group on whole-lake ecosystem studies. Following graduation, Peter served as an aquatic field research technician in southwest Alaska for the University of Washington's Alaska Salmon Program and worked for three years at the School of Aquatic and Fishery Sciences before starting graduate studies at SAFS in 2009. His dissertation work was supported by empirically based field research in southwest Alaska. Peter received a National Science Foundation graduate student fellowship supporting 3 years of his research (2011-2014).