

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

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ABSTRACT

Intraspecific variation in the seasonal reproductive timing of Pacific salmon (*Oncorhynchus* sp.) has important implications for the resilience of salmon and for organisms in freshwater and terrestrial communities that depend on salmon resources. Stream temperature has well known associations with salmon spawn timing but how stream and watershed geomorphology relates to the variation in salmon spawn timing is less understood. We used multivariate statistics applied to five environmental variables to compare conditions across 36 watersheds in the Wood River basin in southwest Alaska. We found that the environmental conditions in the first two axes of a principal components analysis (PCA) explained 76% of the variation in summer temperature among streams and 45% of the variation in spawn timing of sockeye salmon. The average habitat characteristics of streams that characterized three spawn timing groups of sockeye salmon were significantly distinct from one another. Sites supporting early spawning populations tend to have steeper and smaller watersheds, while late spawning populations occur in streams draining large, lower gradient watersheds with lakes in the drainage network. Finally, we 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.

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1. Introduction

Individual species often show phenotypic differences among populations in traits such as reproduction timing, diet, body size, and 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 wild-life 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

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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 risk 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 reach, or single stream scale, we lack a general understanding of the geomorphic conditions that are associated with variation in 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, and 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.

2. Methods

2.1. Study site

Research took place in the Wood River basin (59°20' N, 158°40' W) in the Bristol Bay region of southwest Alaska (Fig. 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 to 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.

2.2. 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 June 30 to September 1 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 (Supplemental Table 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 of $>80,900$ m² and small lakes and ponds of >800 m² at 50 m² 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 controls the heating capacity of the stream; average watershed slope affects 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 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).

2.3. 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 to 2011 (early: July 13 to 22; mid: July 23 to 30; late: July 31 to August 18). 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 axes 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.

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

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

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

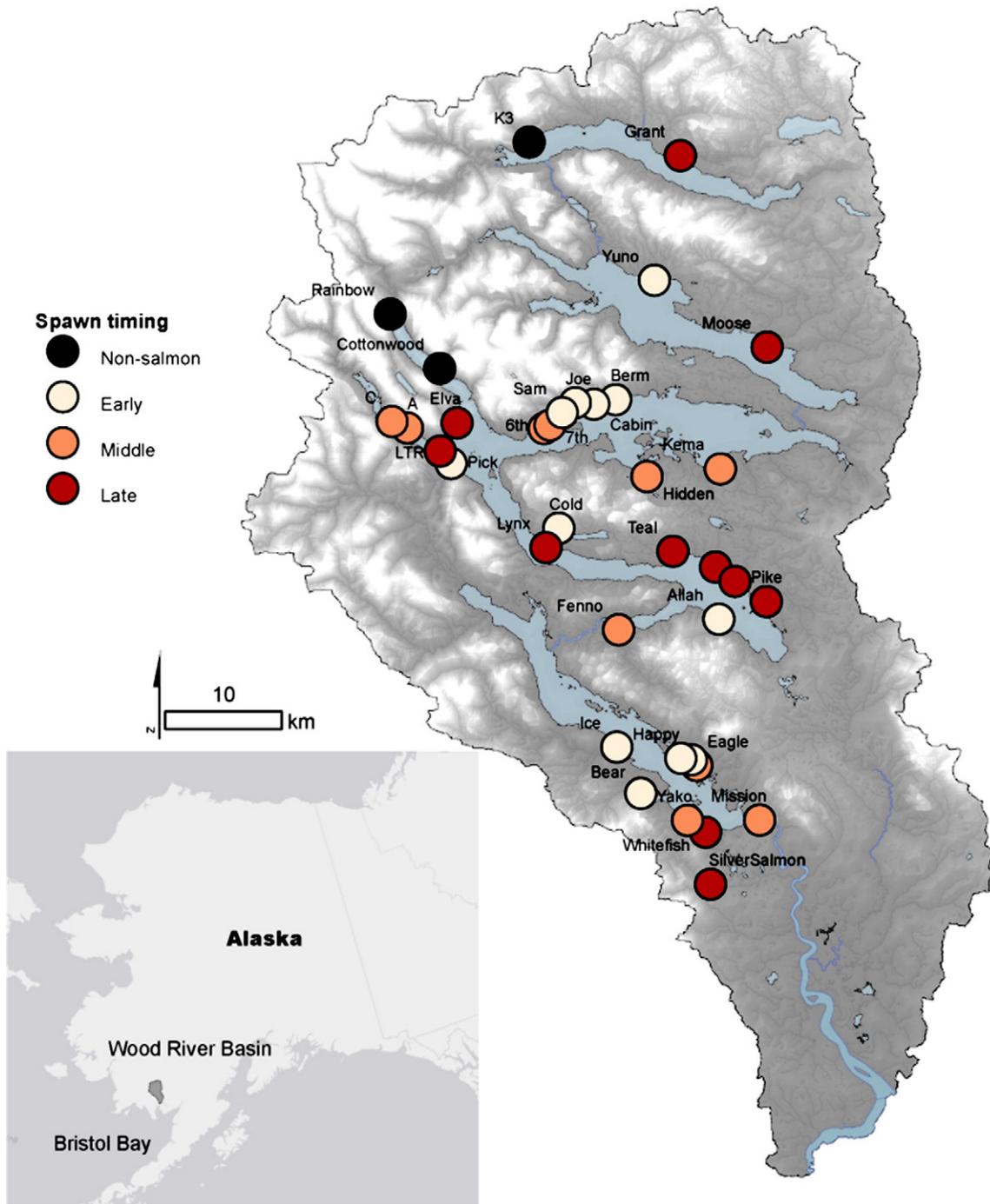


Fig. 1. The Wood River basin in southwest Alaska and locations of individual populations of sockeye salmon with different spawn timing (Early: July 13 to 22; Mid: July 23 to 30; Late: July 31 to August 18).

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).

3. Results

3.1. 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). 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. 3A). Streams were cooler in steeper

gradient watersheds ($r^2 = 0.22$, $p < 0.01$; Fig. 3B). Higher average watershed elevation was also correlated with cooler stream temperatures ($r^2 = 0.16$, $p < 0.05$; Fig. 3C). The total lake area within watersheds had a strong positive effect on stream temperature where larger lakes contribute warmer outlet water, averaging 12 °C, while smaller lakes had less influence on stream temperature (Fig. 3D). Watersheds with total lake areas of $> 1 \text{ km}^2$ 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 ($r^2 = 0.0004$, $p = 0.9$).

3.2. 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. 4; Table 1). Streams with late spawning populations were found in low elevation and low gradient watersheds (Fig. 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. 4A). The second PCA axis was explained by a gradient of watershed area and total lake area (Fig. 4A). Mid-spawn timing groups were found in small watersheds, lacking lakes and having small particle sizes (Fig. 4A). Late spawning streams had large watershed areas, with streams interrupted by lakes (Fig. 4A). Non-salmon streams were best described in steep, high elevation streams and with large substrate (K3, Cottonwood Cr., and Rainbow Cr., see Supplemental Table). 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. 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. 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

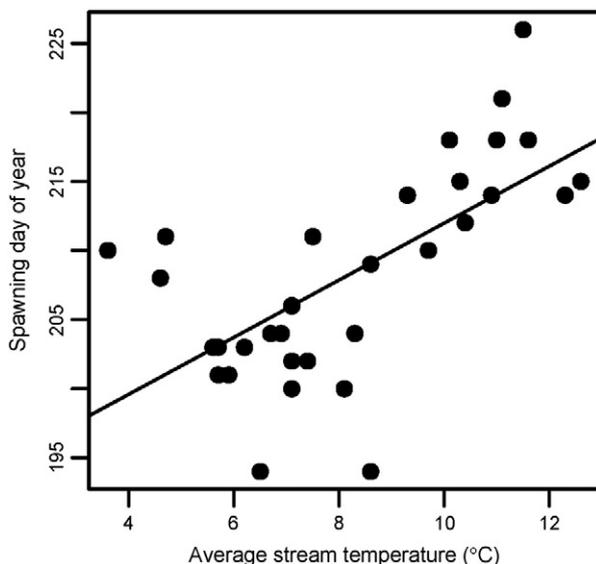


Fig. 2. Salmon spawn timing as a function of average summer stream temperature ($r^2 = 0.42$, $p < 0.001$, $n = 33$).

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 $\Delta\text{AIC} = 20$, model 2 $\Delta\text{AIC} = 41$). Salmon spawning date was also best reflected in the multiple regression of PC1 and PC2 ($p < 0.001$, $r^2 = 0.45$; Fig. 5B), which provided the lowest AIC score (AIC = 215). Model 3 has some support as the next best candidate model ($\Delta\text{AIC} = 5$), but essentially no support for model 2 ($\Delta\text{AIC} = 13$). These results show that watershed geomorphology used in our PCA captured a substantial amount of the variation in stream temperature and spawn timing.

3.3. 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. 4A). Pairwise comparisons between groups detected significant differences among all pairwise comparisons of group means (Table 2, lower diagonal). Non-salmon streams were substantially different in their environmental characteristics from streams with salmon. In particular, late versus early spawning streams were more different from mid versus late or mid versus early (Table 2; Fig. 5).

3.4. 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 upper diagonal; Fig. 5). Late spawning populations occupied a larger range of habitats than non-salmon streams, showing the largest difference in dispersion and mean (Table 2). The late spawning period dispersion was significantly different from 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. 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 ($> 8 \text{ }^\circ\text{C}$) were seen among pairs of streams that are near ($< 1.5 \text{ km}$) and far ($> 50 \text{ km}$) from each other (Fig. 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. 6B).

4. 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

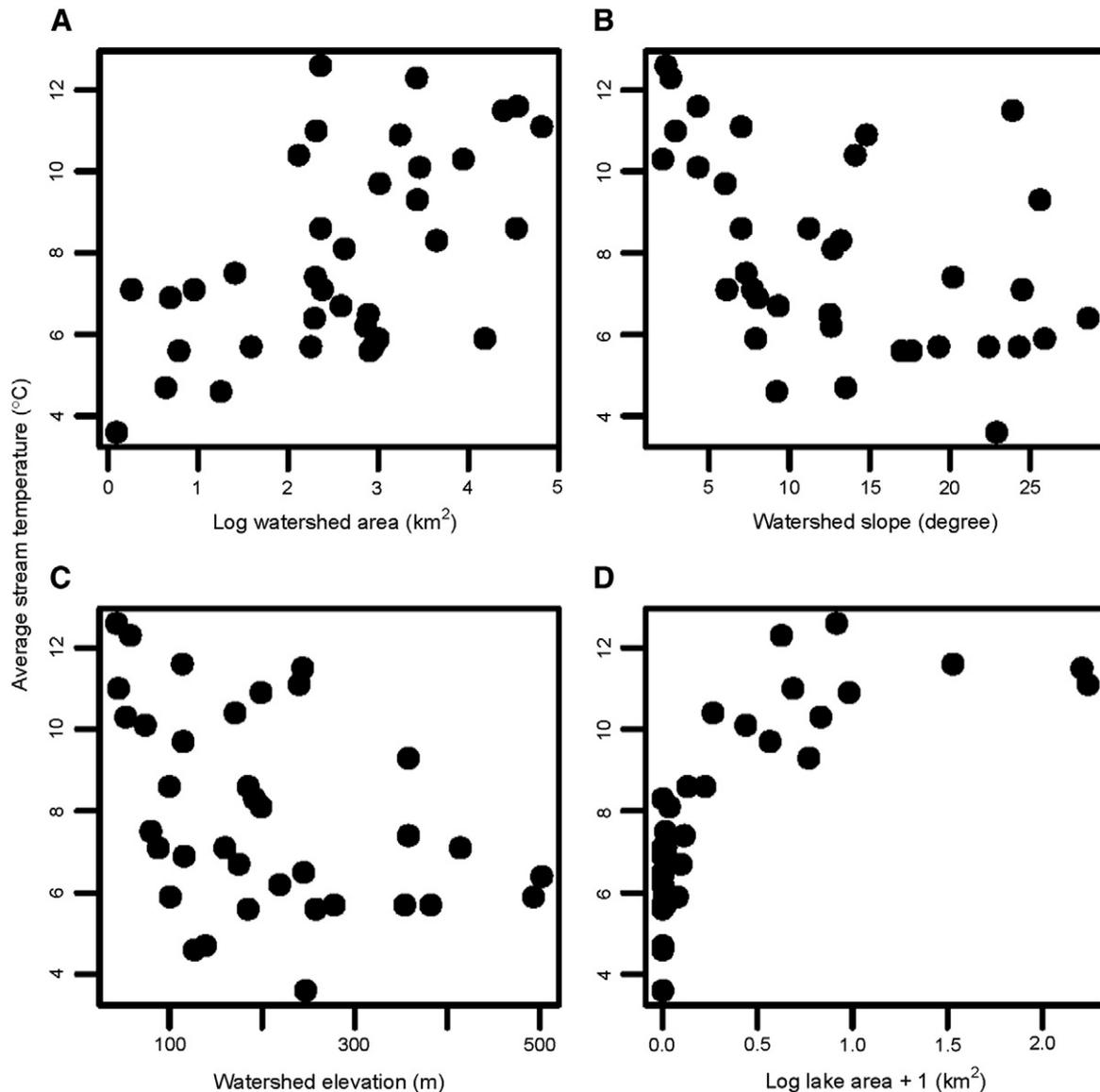


Fig. 3. Average summer stream temperature as a function of (A) watershed area, (B) watershed slope, (C) elevation, and (D) total lake area.

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. 6) that may have important implications for animals that depend on salmon. While our results provide correlative associations, they do not provide 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 data), constrained valley width, shaded by topography and dense riparian vegetation, and had shorter surface residence times (Isaak and Hubert, 2001; Subehi et al., 2009). 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 of $>1 \text{ km}^2$, 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.

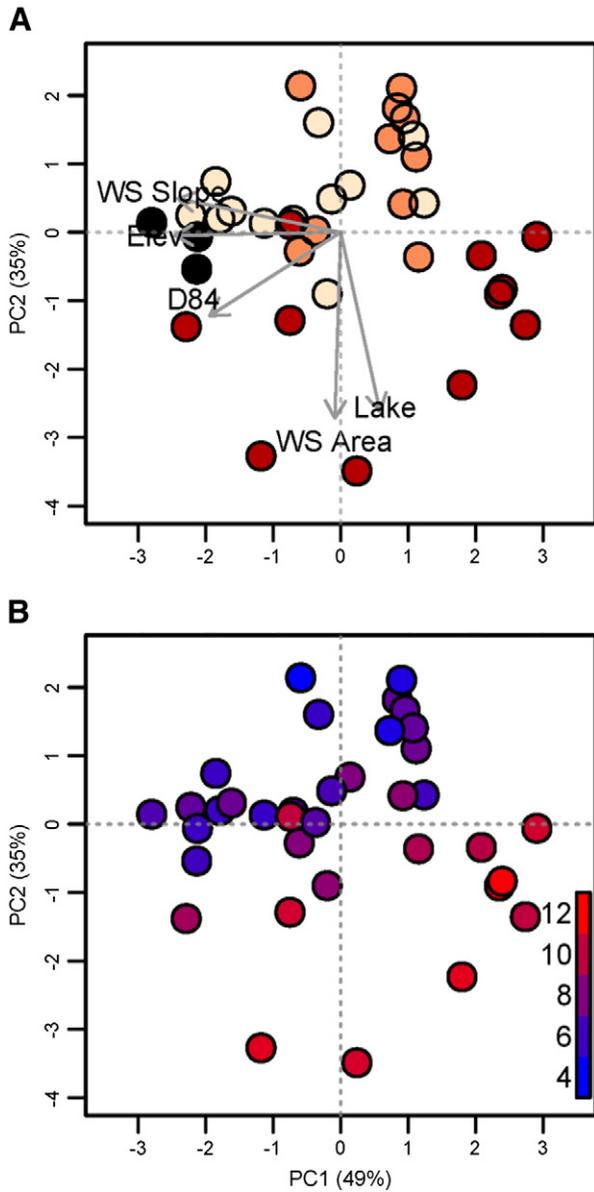


Fig. 4. Ordination plot from the principal components analysis of 36 streams on the basis of five habitat characteristics: watershed slope, elevation, D84, watershed area, and lake area. (A) Spawn timing: non-salmon (black), white (early), orange (mid), and late (red); (B) stream temperature from cool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

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,

Table 1
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

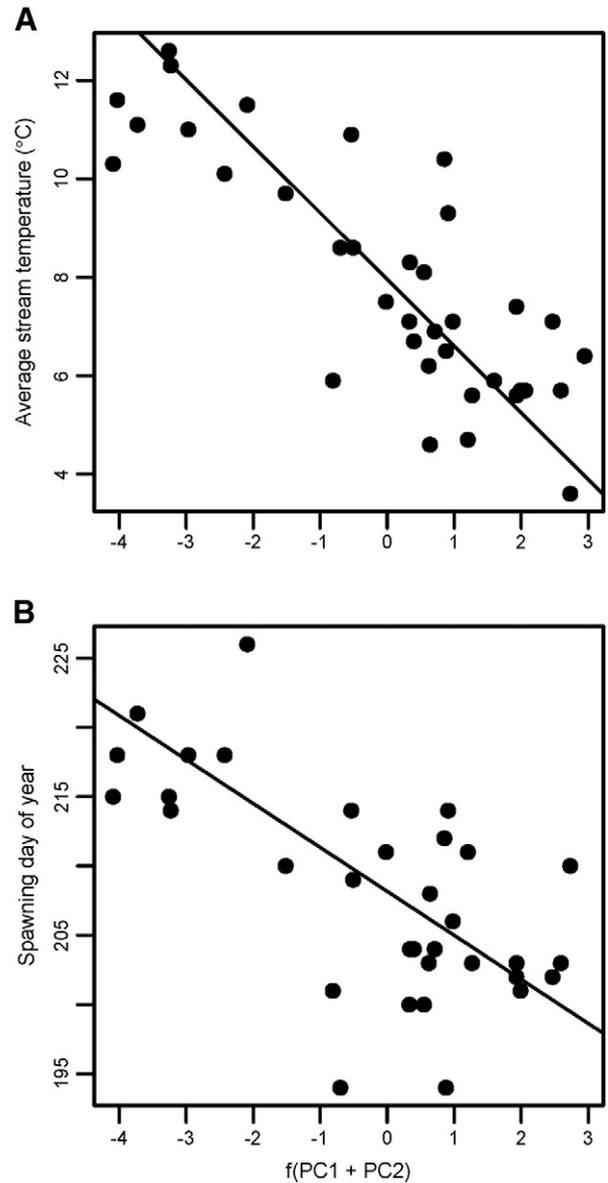


Fig. 5. (A) Average stream temperature as a function of the multiple regression of principal component axes 1 and 2 ($y = -0.70 \cdot PC1 - 1.37 \cdot PC2 + 7.94$, $r^2 = 0.76$). (B) Salmon spawn timing as a function of principal component axes 1 and 2 ($y = 1.91 \cdot PC1 - 3.14 \cdot PC2 + 207.76$, $r^2 = 0.45$).

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

Table 2
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**	–

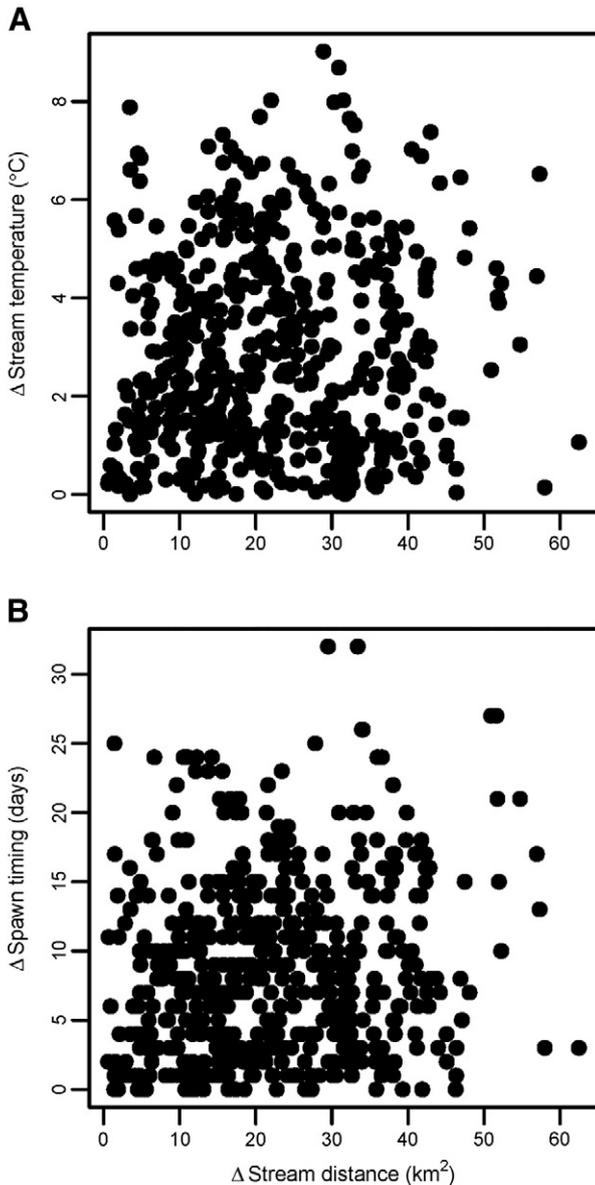


Fig. 6. (A) Temperature and (B) spawn timing difference among streams as a function of pairwise comparisons of geographic Euclidian distance between stream mouths.

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 Supplemental Table). 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 km²), cool summer temperature and small particle sizes with obvious groundwater inputs in their headwaters (see Supplemental data). Even though these spring-fed streams are extremely cold during the summer (consistently ~4.6 °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 °C compared to other early spawning streams with colder temperatures during the winter (1–0 °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., unpublished data). 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 (McGlaulin 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.

5. 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, and 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.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.geomorph.2012.12.013>.

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