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**Habitat Heterogeneity and Phenotypic Diversity: The Influence of**

**Stream Attributes on Timing of Chinook Salmon Spawning**

(Author order to be determined).

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**Abstract**

**1. Introduction**

Pacific Salmon populations are an assimilation of life history forms that evolved in synchrony with diverse and complex environments across their range (Brannon et al. 2004). As a reflection of this diversity, Waples et al. (2004) described salmon as exhibiting *enormous* complexity in life-history traits. The evolution of life-history tactics is strongly influenced by patterns of biotic and abiotic variation over space and time (Stearns 1976). Having a variety of life history phenotypes serves to spread the mortality risk across habitats and thus reduces the probability of complete year class failure (Healey 1991) and buffers against stochastic change and exploitation (Hilborn et al. 2003, Schindler et al. 2010). Chinook salmon display an especially broad array of phenotypes including variations in age at seaward migration; length of freshwater, estuarine, and oceanic residence; ocean distribution and ocean migratory patterns; age and season of migration; and age and timing of spawning (Healey 1991).

Directed spawning migrations have consequences for both individuals and populations (Dingle and Drake 2007). The precision with which adult salmonids time their migration can constrain gene flow between seasonally distinct spawning segments, thereby enabling local, phenological adaptation (Manhard et al. 2017). Although adult run timing (time of entry into fresh water of the adult spawning migration) is the life history trait commonly used to discriminate among and define salmon populations (Waples et al. 2004), here we focus on spawn timing as a metric to examine phenotypic diversity across populations. Like migration timing, spawn timing can vary widely within and across Pacific salmon populations and has a significant genetic component (Ricker 1972). Thus, early and late spawning stocks within the same river can be genetically different (Beacham and Murray 1986). High site fidelity and limited straying leads to fine-scale genetic structuring because of the spatial segregation of related individuals on spawning grounds (Neville et al. 2006) and significant spawn timing heritability has been repeatedly demonstrated (Quinn et al. 2002; Carlson and Seamons 2008; Beulke et al. 2023)). Spatial heterogeneity in habitat conditions can generate intraspecific diversity through evolution of local adaptations in populations (Ruff et al. 2011). Biological characteristics of salmon stocks spawning at different times might reflect adaptations to their environment or be a consequence of environmental differences during spawning and egg incubation (Beacham and Murray 1986). Consequently, a variety of locally adapted population characteristics, habitat features, environmental conditions, and climatic factors may interact with populations to influence the specific timing of salmon spawning.

Important physical factors influencing spawn timing may include fine-scale environmental characteristics (i.e., water temperature and habitat conditions) and broad-scale geomorphic features. Water temperature is an important environmental characteristic that plays a role in determining the time of spawning of salmonids (Hendenon 1963; Morrison and Smith 1986) and variation in water temperature is often associated with variation in salmon spawn timing (Beechie et al. 2008). Several studies have demonstrated a causal relation between site-specific thermal regime and time of spawning (Sheridan 1962; Burger et al. 1985; Heggberget 1988; Lisi et al. 2013) and because embryonic development rates have a near mechanistic relationship with temperature, spawn timing is the master variable controlling developmental phenology (Heggberget 1988, Quinn 2018). Consequently, adult salmon spawn timing may be synchronized with fry emergence. That is, adults spawn at a time that enables subsequently emerging offspring to benefit from optimized growth and survival (Quinn 2018; though see Sparks et al. 2019). Despite the strong association between temperature and spawn timing, considerable uncertainty exists about how physical features of watersheds and climatic factors may influence variation in the salmon spawn timing (Montgomery 1999). Physiography and geomorphology are known to influence thermal processes in flowing waters at both landscape and local scales (O’Sullivan et al. 2019). Beechie (et al. 2006, 2008) and Jonsson and Jonsson (2011) reported that geomorphology and hydrology interact to affect the thermal regime of streams and, therefore, the evolution of salmon spawn timing within river basins. Accordingly, Lisi et al. (2013) found that geomorphology and hydrology interacted to produce a heterogeneous thermal template for natural selection that influences sockeye salmon spawn timing.

Here we examine how water temperature profiles, habitat features, and climatic factors, influence wild Chinook salmon spawn timing. We compare detailed salmon spawn timing data across years in multiple, intact stream reaches in central Idaho. Characterizing variation in natural processes within stream networks and understanding how spatial and temporal variability in physical processes and Pacific salmon interact, is critical for establishing recovery targets (Bisson et al. 2009) and for evaluating population persistence under changing environmental conditions (Isaak et al. 2018).

Our objectives were to: 1.)compile Chinook salmon spawn timing and spawning reach-specific physical data for the Middle Fork Salmon River (Middle Fork) from 2002 to 2005; 2.) compute summary statistics and data visualizations to examine phenotypic variation in Chinook salmon spawn timing; and 3.) fit a series of linear mixed models to test for relationships between spawn timing (day of year) and environmental covariates.

**2. Methods**

**2.1 Study Area**

The Middle Fork is one of eight original National Wild and Scenic Rivers designated in 1968 (NWSRS 2016) and drains about 7,330 km2 of a remote area of central Idaho while flowing through the Frank Church River of No Return Wilderness. In 1980, the Central Idaho Wilderness Act established the 906,136 hectare wilderness that remains the largest contiguous wilderness in the lower 48 states and the largest in the National Forest system (US Forest Service 1998). From its origin at the confluence of Bear Valley and Marsh Creeks, the Middle Fork flows north-northwest for 171 km through the Salmon River Mountains and joins the Salmon River 92 km downstream from Salmon, Idaho (Figure 1), and 1,144 km from the Pacific Ocean. Minshall et al. (1981), Thurow (2000), Servheen et al. (2001), and Thurow et al. (2019) provide more detailed study area descriptions.

The Middle Fork exhibits diverse geology and topography with high relief. Lewis et al. (2012) used field surveys to develop a detailed geologic map that illustrates the distribution of four major lithologies: Granitic, Metamorphic, Sedimentary, and Volcanic (Figure 2). These diverse geologies influence the size, shape, and color of Chinook salmon spawning gravels which vary widely across the Middle Fork basin. Lithology may also affect stream physiography and geomorphology, which are known to influence thermal processes in streams (O’Sullivan et al. 2019).

Native fishes include seven salmonid taxa: bull trout (*Salvelinus confluentus)*, westslope cutthroat trout (*Oncorhynchus clarki lewisi*), anadromous and resident redband trout (*O. mykiss* *gairdneri)*), mountain whitefish (*Prosopium williamsoni*), and spring/summer Chinook salmon (Thurow 1985). Prior to overfishing and habitat alterations, adult Chinook salmon migrating up the Columbia River formed a continuum from March to October with the largest part of the run likely consisting of summer Chinook salmon (Thompson 1951). In recent decades, for management convenience Columbia River Basin Chinook salmon have been described as spring, summer, and fall ecotypes; separated primarily by their time of passage over Bonneville Dam (Matthews and Waples 1991). Chinook salmon are more correctly described as a continuum of forms falling along a temporal cline related to incubation and rearing temperatures (Brannon et al. 2004). Chinook salmon population structure in the Columbia River Basin reflects the genetic composition of the founding sources within the region, shaped by the environment (principally temperature), resulting in a life history evolutionary strategy to maximize fitness under the conditions delineated (Brannon et al. 2004). Healey (1991) categorized juvenile Chinook salmon that migrate seaward after one or more years as stream-type and those that migrate as subyearlings as ocean-type. Within the Middle Fork, only stream-type Chinook salmon are present and spring-run fish predominate. Summer-run fish occur sympatrically with spring-run fish in several drainages, including Big, Camas, and Loon creeks (Fulton 1968; Gebhards 1959; IDFG 1992; Parkhurst 1950), Rapid River, and the lower mainstem Middle Fork. Our observations of Middle Fork fish are consistent with those reported by Mathews and Waples (1991); spring-runs spawn earliest in higher elevation headwater stream reaches compared to summer-runs that spawn later at lower elevations.

The study area is unique for several reasons (Thurow et al. 2019). Chinook salmon stocks in the Middle Fork basin are wild, indigenous, and unaltered by direct hatchery supplementation and the Middle Fork is managed as a designated wild anadromous fish sanctuary to preserve the genetic integrity of wild, native salmonids (IDFG 2019). Natural processes in the Middle Fork function relatively unimpeded by humans so natal habitats remain diverse, high quality, and connected (Thurow 2000; Isaak and Thurow 2006; Thurow 2015). Within most of the drainage, habitat quality has not been substantially altered by anthropogenic activities and exotic fishes are uncommon. Minimal anthropogenic effects and a geographic size that facilitates the existence of natural processes including wildfire, floods, debris flows, and snow avalanches ensure continual generation and maintenance of a diversity of stream habitats (Isaak et al. 2003; Thurow 2015). About 800 km of tributaries and the mainstem are accessible to Chinook salmon (Mallet 1974; Thurow 1985) and connectivity among its populations is high (Fullerton et al. 2016).

**2.2 Reach Selection**

We selected study reaches in known Chinook salmon spawning areas to encompass a range of parent geologies, channel morphologies, elevations, stream sizes, riparian canopies, instream cover types, and redd densities. Twelve major streams and hundreds of smaller ones are tributary to the mainstem Middle Fork (Figure 1). Chinook salmon spawn throughout the drainage with most redds (98%) constructed in ten major tributaries and the remainder in the mainstem (Thurow et al. 2019). Spawning occurs at elevations ranging from less than 920 m in the lower mainstem Middle Fork and more than 2000 m in the headwaters of Bear Valley, Camas, Loon, and Marsh creeks.

From 2001-2005, we selected study reaches in six major spawning tributaries (Big, Bear Valley, Camas, Loon, Marsh, and Sulphur creeks). To assist collaboration and increase efficiency, some study reaches were selected within index reaches monitored annually by the Idaho Department of Fish and Game (IDFG), the Nez Perce or Shoshone-Bannock tribes, and the US Forest Service (see explanation of index reaches in Thurow et al. 2019).

**2.3 Redd Counts**

We intensively monitoring the construction of redds from the onset of redd construction to the completion of spawning. Beginning in late July and extending to mid-September, trained redd monitors intensively and periodically (every 3-4 days) walked stream banks adjacent to each study reach, searched for newly constructed redds, and recorded redd locations with a GPS (Datum NAD27, lat.-long coordinates). Redd monitors began the surveys prior to the onset of spawning. Our prior observations in the Salmon River basin, Idaho suggested that female Chinook salmon typically remained on newly constructed redds for 3-5 days. We assumed that censusing redds on a 3-5 day frequency would increase the likelihood of detecting all newly constructed redds.

**2.4 Datasets**

*2.4.1 Spawn timing*

Chinook salmon spawn timing data were collected from 2001 to 2005. We rejected 2001 data, and data from Knapp and Cape Horn creeks, as these sites were not consistently sampled. Because redds were not surveyed daily, spawn date is a putative measure derived from the first date a redd was considered fully constructed in our dataset. We spatially joined each redd GPS location to the NHDPlus Version 2 (Horizon Systems 2018) and assigned stream reaches based on a common identifier (COMID). We used the COMID to link redd data with covariate data associated with the stream reach in which it is located (Table [1](file:///C:\Users\rthurow\AppData\Local\Microsoft\Windows\INetCache\Content.Outlook\Y25TJ4NF\b_workflow.html#tab:spawn-summary)).

*2.4.2 Covariates*

To test for environmental factors influencing variation in spawn timing, we quantified associations between metrics describing thermal and physical conditions in stream reaches. We selected and interrogated covariates based on the following criteria: (1) known to influence spawn timing, (2) available for all streams, and (3) not highly correlated with each other.

Our initial, focal independent variables included: stream temperature (°C), stream discharge (cms), elevation (m above sea level), stream gradient (slope).

2.4.2.1 Stream temperature

We used modeled daily average stream temperatures predicted at the stream segment (COMID) scale (Siegel et al. 2023). These data were downloaded and filtered to the Middle Fork from 2002-2005. Figure 3 illustrates modeled thermal regimes for Middle Fork tributaries. We calculated metrics relative to the COMID where a redd was constructed and with redd completion dates; before, after, and spanning that date. For example, temp\_30\_before represents the average temperature for a COMID where a redd was constructed, calculated over the previous 30 days. We calculated this for 30, 60, and 90 days. We also calculated a time invariant metric relative to a fixed date that was chosen to represent an initial spawning window across all years (e.g., August 1). The time invariant and after metrics were omitted from further consideration after preliminary data exploration revealed a weak, if any, relationship with spawn timing.

2.4.2.2 Discharge (streamflow)

Stream flow data were compiled from a single gage low in the watershed (USGS Gage 13309220, Middle Fork at Middle Fork Lodge; Figure 4). We calculated flow metrics relative to the COMID where a redd was constructed with a redd completion date; before, after, and spanning that date. For example, temp\_30\_after is the average flow for a COMID where a redd was constructed, calculated over the 30 days after redd completion. We calculated this for 30, 60, and 90 days. The spanning and after metrics were omitted from further consideration because preliminary data exploration again revealed a weak, if any, relationship with spawn timing.

2.4.2.3 Elevation and stream gradient (slope)

We obtained elevation and stream slope data at the COMID (stream reach) scale from the NHD.

**2.5 Exploratory Data Analysis**

We conducted exploratory data analysis on the compiled dataset to identify candidate covariates for inclusion in our model selection. Bivariate relationships were plotted between spawn date (yday) and continuous predictors and pairwise correlations between continuous covariates temp\_90, mean\_elevation, slope, and flow\_90 (see online Supplementary material1).

**2.6 Model fitting**

The final dataset included: 1.) yday: spawn date, continuous response variable; comid, stream, 2.) year: grouping variables; temp\_90: 90-day mean temperature pre-spawn, continuous predictor variable; 3.) and slope and mean\_elevation: provisionally retaining continuous predictor variable (see online Supplementary material1). We scaled the continuous covariates to have a mean of 0 and standard deviation of 1 to assist convergence and interpretation.

**2.7 Targeted model comparison**

We compared the best base additive model (m16, yday ~ temp\_90 + stream + year) to a series of models with increasing complexity and evaluated the contribution of each fixed effect and random effect structure.

m16\_re <- lmer(yday ~ temp\_90 + stream + year + (1 | COMID), data = df\_mod, REML = FALSE.

1Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0111>.

2.7.1 Random intercepts

We began with a random intercept model to account for the repeated measures on COMIDs. This is a baseline mixed model that we compared to the additive linear model (m16). We also compared it to model m26 (elevation included as a fixed effect) with COMID random intercepts to see if it improves performance.

m26\_re <- lmer(yday ~ temp\_90 + stream + year + mean\_elevation + (1 | COMID), data = df\_mod, REML = FALSE).

Adding a random intercept for COMID significantly improved model performance, reducing AIC by >2,700 points compared to the additive fixed-effect model (m16 vs. m16\_re; Table 2). This confirmed the necessity of accounting for repeated measures and reach-specific baseline differences in spawn timing. Adding mean elevation as a fixed effect (m26\_re) yielded a further AIC improvement of 126 points over m16\_re. However, this is substantially smaller than the apparent benefit observed in the fixed-effects-only comparison (296 AIC points; m26 vs. m16), suggesting that much of elevation’s explanatory power is absorbed by the random intercepts. Moreover, the parameter estimates for elevation remained positive (Table 3) and counter to biological expectations (i.e., higher elevation reaches spawning later), and the associated prediction plot (Figure 5C) suggest a weak and potentially misleading relationship.

This, combined with collinearity concerns and limited interpretability, led us to exclude mean elevation from further models. Subsequent model refinement focused on fixed effects of temperature, stream, and year, with COMID modeled as a random intercept or slope to capture spatial variation in thermal response.

2.7.2 Quadratic Term for Temperature

We next tested whether a nonlinear temperature response improved model fit by adding a quadratic term for temp\_90 to the random intercept model (m16\_re).

m16\_re\_quad <- lmer(yday ~ temp\_90 + I(temp\_90^2) + stream + year + (1 | COMID),

data = df\_mod, REML = FALSE)

This resulted in a lower AIC (ΔAIC = 91.7; Table 4), providing substantial support for the quadratic formulation (m16\_re\_quad). The fitted curve reflects biologically plausible curvature (a decelerating response at higher temperatures which is consistent with expectations for thermal constraints on salmonid spawning) (Figure 6C). We therefore retained the quadratic term for temperature in all subsequent models.

2.7.3 Random slopes for temp\_90

To account for variation in temperature sensitivity across sites, we extended our top random intercept model (m16\_re\_quad) by allowing COMID-specific random slopes for temperature (m16\_re\_quad\_rs). This model had the same fixed effect structure but included (1 + temp\_90 | COMID).

m16\_re\_quad <- lmer(yday ~ temp\_90 + I(temp\_90^2) + stream + year + (1 | COMID),data = df\_mod, REML = TRUE)

m16\_re\_quad\_rs <- lmer( yday ~ temp\_90 + I(temp\_90^2) + stream + year + (1 + temp\_90 | COMID), data = df\_mod, REML = TRUE)

The addition of random slopes substantially improved model fit (ΔAIC = 510; Table 5), and diagnostic plots confirmed adequate model behavior. Adding random slopes increased model flexibility, which redistributed explained variance from fixed to random effects. As a result, marginal R² (variance explained by fixed effects) decreased from 0.726 to 0.701, while conditional R² (total variance explained) remained high at 0.98 in both models (Table 6). This tradeoff reflects a more realistic partitioning of variance, acknowledging that some differences in thermal sensitivity are site-specific and better explained by random effects.

2.7.4 Partitioning Variation Between Nonlinearity and Heterogeneity

We compared the best random slope model with and without a quadratic effect. This tested whether random slope replaces the need for a quadratic term, or whether both were helpful.We refit with ML to compare models with different fixed effects.

m16\_re\_quad\_rs <- lmer(yday ~ temp\_90 + I(temp\_90^2) + stream + year + (1 + temp\_90 | COMID), data = df\_mod, REML = FALSE)

m16\_re\_linear\_rs <- lmer(yday ~ temp\_90 + stream + year + (1 + temp\_90 | COMID),

data = df\_mod, REML = FALSE)

The quadratic term improved fit modestly (ΔAIC = 20.4) while keeping the structure stable. Most of the model’s explanatory power was derived from the random slopes, not the curvature of temperature. However, the quadratic did meaningfully refine the relationship, especially at the tails of the temperature gradient (Figure 7), without overfitting or destabilizing the model. This model is supported; the structure offers a strong balance between flexibility and interpretability that we retained for subsequent analysis.

**2.8 Interactions**

We have built a strong foundation illustrating that COMID-level variation captures spatial structure in the data (m16\_re\_quad\_rs). This demonstrates support for a nonlinear (quadratic) thermal response and incorporated year and stream as fixed effects for interpretability across broad groups. Next, we checked interactions because, although random slopes already absorb much of the temperature-related heterogeneity, interactions might help us evaluate whether average responses differ systematically across stream or year, beyond what is explained by random effects. Logical interactions to test included: temp\_90 \* stream; does the average thermal slope vary among streams?, and temp\_90 \* year; does thermal sensitivity vary across years (e.g., wetter vs. drier)? We tested interactions and compared them to m16\_re\_quad\_rs.

m201 <- lmer(yday ~ temp\_90 \* stream + I(temp\_90^2) + year + (1 + temp\_90 | COMID), data = df\_mod, REML = FALSE)

m202 <- lmer(yday ~ temp\_90 \* year + I(temp\_90^2) + stream + (1 + temp\_90 | COMID), data = df\_mod, REML = FALSE)

We found that m201 lowered AIC by 18, while m202 lowered AIC by 1397, a massive improvement (Table 7). The interaction terms in m201 were mostly non-significant, and the model R² values were nearly identical to m16\_re\_quad\_rs (Table 8). For m202, while the interactions terms were significant, the Marginal R² values declined by ~10%. Figure 8 illustrates that the predicted effects of temperature are implausible, with a positive quadratic effect of temperature. This suggests that the model is overfitting or confounding the interaction structure.

In summary, to evaluate whether fixed-effect interactions improve model performance beyond what is captured by random slopes, we tested two candidate models: one with a temp\_90 × stream interaction (m201) and one with a temp\_90 × year interaction (m202), comparing them against our baseline random slope model with a quadratic temperature effect (m16\_re\_quad\_rs).

Although model m202 demonstrated a large AIC improvement (ΔAIC = -1397), inspection of its predicted effects revealed implausible curvature—specifically, a biologically unlikely inverted quadratic effect of temperature. This suggests overfitting or confounding in the interaction structure. In contrast, m201 demonstrated moderate AIC improvement over the baseline model (ΔAIC = 18), with predictions that remained biologically realistic. However, nearly all interaction terms in m201 were non-significant except one (list it?), and model R² values and parameter estimates remained essentially unchanged. These results confirm that most stream-specific variation in temperature responses is already accounted for by random slopes. Thus, when selecting our final model, the added complexity of fixed-effect interactions does not yield substantial inferential gains and is not justified.

**Redd- and Reach- Scale Habitat Variables**

**3. Results**

3.1 High spatial/biological population heterogeneity

3.2 Model interpretation

3.2.1 Final Model

3.2.2 Model summary and fit

3.3 Residual diagnostics

3.4 Population-level effects

3.4.1 Predictions against original data

3.4.2 Marginal means and contrasts of yday at each factor level

3.4.3 Estimating response vs. relation

3.5 Group-level effects (deviations from fixed effects)

3.6 Elevation effects embedded in random structure

**Discussion** (Potential topics below+ RT to re-read: Schindler et al papers, Crozier et al 2008, Fillatre et al. 2003, Gharrett et al. 2013, others?)

-Diverse spawn timing

-Effects of escapement

-Implications for persistence

-Limitations

My $0.02 :

1. Biggest takeaway is how dominant temperature is as an effect. We find a much larger effect than Lisi et al. 2013 (r^2 = 0.42).
   1. Temperature differences are largely going to be driven by physical factor, should highlight what drives that in these systems
   2. Also highlight how MFSR spawning systems are a mix of conventional Rocky Mountain, steep, rocky, cold habitats and meandering high mountain streams, sometimes even w/in the same tributary
   3. All of this creates a mosaic of spawning across the environment and translates to a portfolio of diversity within the population
2. Brannon et al. 2005 would say the reason spawn timing is structured the way it is because of developmental environment for progeny “The controlling mechanism in spawn timing, however, is the timing of fry emergence, which translates into fitness.” However, when we ran the different pre and post spawn metrics, this was not the case. This suggests to me that:
   1. There are some important selective forces in the pre-spawn and spawn phase that I imagine have to do with habitat availability and survival while spawning
   2. Temperature at a site is highly correlated throughout the year and it’s just a latent effect.
   3. We can further develop this point in the hatchR x MFSR paper if we get to write it

\*More Discussion topics listed in Bryans 5/30 doc

Although mean elevation was excluded as a fixed effect due to collinearity and inconsistent directionality, plots of random effects against elevation reveal underlying spatial structure that elevation helps to explain (Figure [29](file:///C:\Users\rthurow\AppData\Local\Microsoft\Windows\INetCache\Content.Outlook\Y25TJ4NF\b_workflow.html#fig:ranefs-elev)).

In panel A, there is a clear positive relationship between elevation and the random intercepts for some streams (e.g., Big), indicating that higher elevation sites within Big Creek tend to have later average spawn timing compared to the global (population) average.

In panel B, random slopes (i.e., thermal sensitivity) show more idiosyncratic patterns: for some streams (e.g., Camas, Marsh), thermal sensitivity appears to decrease with elevation, suggesting fish at higher elevations may respond less strongly to temperature variability.

However, these relationships are inconsistent across streams, supporting the decision to capture this spatial heterogeneity via COMID-level random effects rather than forcing a global fixed elevation term.

\*Text from Schindler et al. 2013: “*variation in spawn timing among populations probably enables mobile consumers to effectively locate particularly profitable foraging opportunities over the course of the salmon spawning season. If spawning were perfectly synchronous across the watershed, consumers would have about half as much time to locate and capitalize on locally profitable foraging opportunities. Further, because much of the stream temperature variation is expressed at relatively small spatial scales in this river basin [10], mobile consumers do not have to travel far to exploit the spatial and temporal variation in salmon.*”

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Description automatically generated**

**References**

**Figures**

**Tables**