*CJFAS Article*

**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 exhibit extraordinary life history diversity, shaped by complex and heterogeneous environments across their range (Brannon et al. 2004). This diversity has evolved in response to spatiotemporal variation in both biotic and abiotic conditions (Stearns 1976), and acts as a bet-hedging strategy that reduces the risk year-class failure and buffers populations against environmental and anthropogenic change (Hilborn et al. 2003, Schindler et al. 2010). Chinook salmon (*Oncorhynchus* tshawyscha) in particular display a broad array of phenotypes, including variation in age and timing of seaward migration, duration of freshwater and marine residence, ocean distribution, and timing of spawning (Healey 1991).

Among these traits, spawning phenology has important ecological and evolutionary consequences. The timing of adult migration and spawning can shape reproductive isolation among temporally segregated groups and lead to fine-scale local adaptation (Manhard et al. 2017). While run timing (entry into freshwater) is often used to define populations segments (Waples et al. 2004), we focus here on spawn timing—the date when adults deposit eggs in the grave—as a finer-scale expression of phenotypic variation. Spawn timing varies within and across salmon populations and has a well-documented genetic component (Ricker 1972; Quinn et al. 2002; Beulke et al. 2023). For example, when high site fidelity and limited straying leads to fine-scale genetic structuring because of spatial segregation of related individuals on spawning grounds (Neville et al. 2006). Spatial heterogeneity in habitat conditions can promote this diversity by selecting for locally adapted phenologies (Ruff et al. 2011). In some cases, differences in spawn timing may reflect active adaptation; in others, they may result from environmental constraints on habitat access or egg incubation.

Temperature is a key proximate driver of salmonid spawn timing (Hendenon 1963; Morrison and Smith 1986; Beechie et al. 2008). Because embryonic development rates are tightly linked to thermal accumulation, salmon tend to spawn at times that synchronize fry emergence with favorable rearing conditions (Quinn 2018; though see Sparks et al. 2019). Several studies have linked site-specific thermal regimes to observed variation in spawning phenology (Sheridan 1962; Burger et al. 1985; Lisi et al. 2013). However, while the influence of temperature is well established, the underlying landscape drivers of thermal variation—such as physiography, geomorphology, and hydrology—are less clearly understood (Montgomery 1999; O’Sullivan et al. 2019). Geomorphic attributes like slope, elevation, confinement, and groundwater connectivity can shape reach-scale thermal regimes, thereby constraining or enabling different spawning strategies. For example, Lisi et al. (2013) demonstrated that variation in watershed slope, elevation, and lake area explained a large proportion of summer stream temperature and sockeye spawn timing in Alaskan streams, highlighting geomorphology’s indirect but powerful role in structuring phenological diversity.

Here we examine how variation in stream temperature, geomorphic features, and climatic factors, influence Chinook salmon spawn timing across intact tributaries of the Middle Fork Salmon River, 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 reach-scale spawning phenology and and physical data for wild Chinook salmon from 2002 to 2005, 2) summarize variation in spawn timing across years and streams, and 3) fit a series of linear mixed-effects models to identify environmental predictors of spawn timing.

**2. Methods**

**2.1 Study Area**

The Middle Fork of the Salmon River is one of eight original National Wild and Scenic Rivers designated in 1968, drains ~7,330 km2 of remote, mountainous terrain of central Idaho, flowing through the Frank Church River of No Return Wilderness (NWSRS 2016). Established in 1980, the 906,000-hectare wilderness remains the largest contiguous roadless area in the lower 48 states and the largest in the National Forest system (USFS 1998). From its headwaters at the confluence of Bear Valley and Marsh Creeks, the Middle Fork flows 171 km through north-northwest through the Salmon River Mountains before joining the Salmon River ~92 km downstream from Salmon, Idaho, and 1,144 km from the Pacific Ocean (Figure 1). Additional study area details are provided by Minshall et al. (1981), Thurow (2000), Servheen et al. (2001), and Thurow et al. (2019).

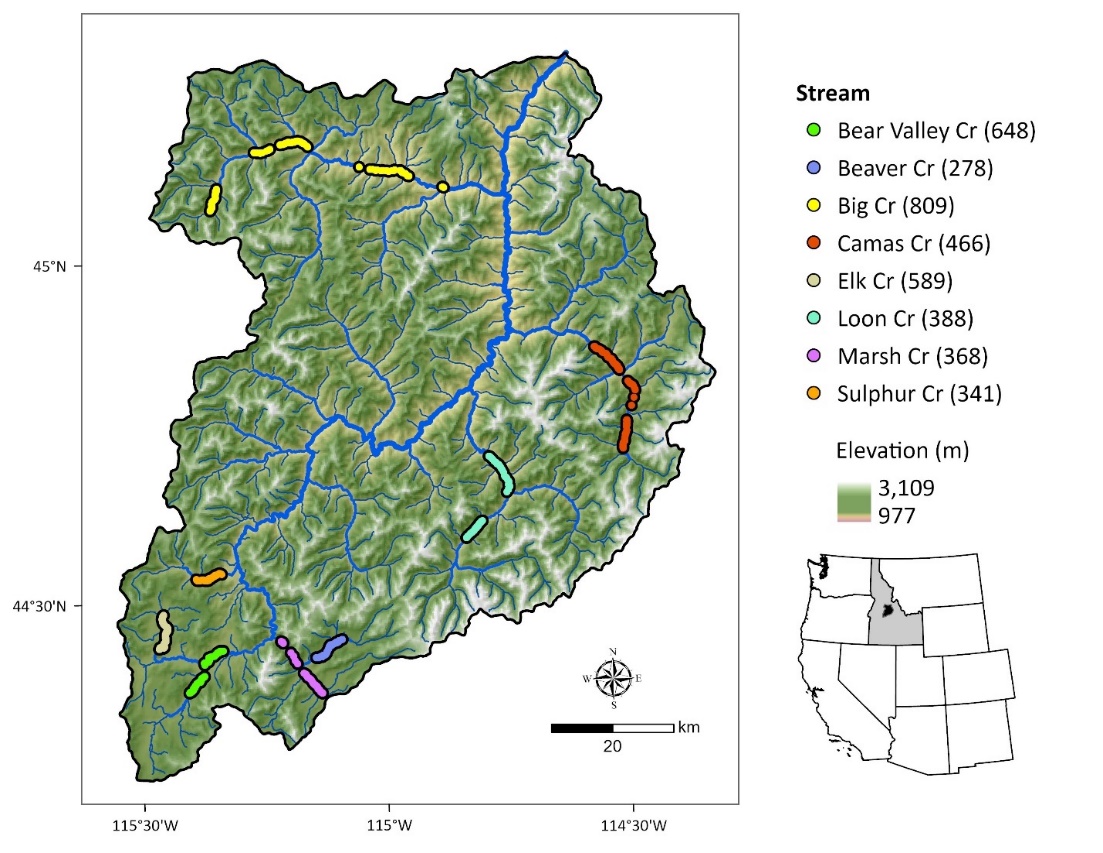


Figure 1. Map of the Middle Fork Salmon River watershed showing major tributaries and surveyed Chinook Salmon redd locations from 2002 to 2005.

The Middle Fork watershed spans deep, high relief terrain underlain by diverse geology. Field surveys by Lewis et al. (2012) delineated four dominant lithologies—granitic, metamorphic, sedimentary, and volcanic—that shape channel form and Chinook salmon spawning substrates. Lithologic and hydrologic variation also contributes to differences in the size, shape, and, and composition of spawning gravel and may also influence stream physiography and geomorphology, which in turn affect local thermal regimes (O’Sullivan et al. 2019).

Native fishes in the watershed 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). Historically, adult Chinook salmon migrated up the Columbia River from March to October, with run timing forming a continuum rather than discrete groups (Thompson 1951; Brannon et al. 2004). For management purposes, Chinook in the Columbia Basin are commonly classified into spring, summer, and fall runs based on their time of passage at Bonneville Dam (Matthews and Waples 1991).. In the Middle Fork, Chinook salmon exhibit a stream-type life history, with juveniles rearing in freshwater for one year before outmigration (Healy 1991). Observations suggest early-arriving fish spawn at higher elevations and latter arriving fish spawn lower in the watershed (Fulton 1968; Gebhards 1959; IDFG 1992; Parkhurst 1950), though genetic data confirming this phenotypic variation are lacking (Helen Neville, pers. comm.).

The Middle Fork basin offers a unique setting for studying natural phenotypic variation in Chinook salmon (Thurow et al. 2019). Chinook salmon stocks are wild, indigenous, and unaltered by hatchery supplementation; the river is designated as a wild anadromous fish sanctuary to protect the genetic integrity of native salmonids (IDFG 2019). Natural processes operate largely unimpeded by humans activities, maintaining high quality, connected habitats throughout the watershed (Thurow 2000; Isaak and Thurow 2006; Thurow 2015). Anthropogenic disturbance is minimal, exotic species fishes are rare, and the basin’s large size supports the persistence of natural processes such as wildfire, floods, debris flows, and avalanches (Isaak et al. 2003; Thurow 2015). As a result, stream habitats are continually created and reshaped. Approximately 800 km mainstem and tributary habitat are accessible to Chinook salmon (Mallet 1974; Thurow 1985) and population connectivity across the basin is high (Fullerton et al. 2016).

**2.2 Reach selection, redd observations, and Chinook spawn timing**

We selected study reaches in known Chinook salmon spawning areas to encompass a range of variation in parent geology, channel morphology, elevation, stream siz, riparian canopy, instream cover type, and redd density. The Middle Fork is fed by twelve major tributaries and hundreds of smaller streams (Figure 1). Chinook salmon spawn throughout the basin, 98% of redds are concentrated in ten major tributaries, with the remainder in the mainstem (Thurow et al. 2019). Spawning occurs across a broad elevation range—from below 920 m in the lower mainstem to above 2000 m in the headwaters of Bear Valley, Camas, Loon, and Marsh creeks.

From 2001-2005, we established study reaches in six primary spawning tributaries: Big, Bear Valley, Camas, Loon, Marsh, and Sulphur creeks. To support interagency collaboration and field efficiency, some study reaches overlapped with existing index reaches monitored annually by the Idaho Department of Fish and Game, the Nez Perce or Shoshone-Bannock tribes, and the U.S. Forest Service (see Thurow et al. 2019 for index reach methods and locations).

We intensively monitored Chinook salmon spawning activity from the onset of redd construction through the completion of spawning. From late July through mid-September, trained observers walked stream banks adjacent to each study reach every 3-4 days to search for newly constructed redds. Observers began surveys before the onset of spawning and recorded redd locations handheld GPS units.. Based on our prior observations in the Salmon River basin, female Chinook salmon typically remained on newly constructed redds for 3 to 5 days. Thus, we assumed that a 3 to 5 day survey interval would maximize the likelihood of detecting all redds soon after construction while minimizing double-counting.

We excluded data from 2001, and from Knapp and Cape Horn creeks, due to inconsistent sampling. Because surveys were done every 3-4 days, we inferred spawn timing from the date a redd was first recorded as fully constructed. Redd locations were spatially joined to stream reaches in the NHDPlus dataset (Moore et al. 2019) and assigned a common identifier (COMID). This identifier was used to link each redd with environmental covariates from the corresponding stream reach. The final dataset comprised 3,016 redd observations (i.e., inferred spawn date) across 108 stream reaches (COMIDs), nested within eight streams, and spanning four years.

**2.3 Covariates**

To identify environmental predictors of spawn timing, we linked each redd location to stream temperature, discharge, elevation, and slope at the stream reach scale (COMID). Covariates were selected based on ecological relevance, full coverage across the study area, and low collinearity. Elevation and slope were obtained from NHDPlus (Moore et al. 2019). Thermal conditions were indexed using modeled daily stream temperatures from Siegel et al. (2023), which showed strong agreement to logger data from sites in Idaho (R2 > 0.90; Appendix X). Stream discharge data were drawn from a single USGS gage (13309220) near the basin outlet. For each redd, we calculated time-windowed summaries of temperature and flow (e.g., 30-, 60-, and 90-day averages prior to, during, and following the inferred spawn date).

We used exploratory data analysis and visualizations to evaluate variation in spawn timing across years and streams, examine bivariate relationships between spawn date and continuous covariates, and assess pairwise correlations among predictors. Based on these results, we retained only 90-day antecedent temperature (`temp\_90`) as a focal thermal covariate; post-spawn and fixed-date summaries were more weakly associated with spawn timing and showed higher collinearity. A clear nonlinear relationship emerged between `temp\_90` and spawn date, with quadratic temperature terms consistently improving model fit over linear specifications. Adding stream and year as fixed effects further improved model performance, indicating spatial and interannual variation in phenology. Elevation showed a weak association with spawn timing and was retained for its ecological interpretability, while slope was uncorrelated but provisionally included. Although 90-day antecedent streamflow was initially considered, we excluded it due to poor spatial resolution, strong collinearity with year, and limited ecological relevance at the reach scale. Full covariate descriptions and exploratory results are provided in Appendix A.

**2.4 Data analysis**

We used linear mixed-effects models to evaluate environmental predictors of Chinook salmon spawn timing, with redd observation day-of-year (yday) as the response variable. Continuous covariates were scaled (mean = 0, SD = 1) to aid convergence and interpretation. We fit 31 additive models representing all combinations of fixed effects (temp\_90, stream, year, slope, and mean\_elevation). All models included a random intercept for COMID to account for repeated measures across stream reaches. Based on exploratory analysis and biological expectations of nonlinear thermal responses, temperature effects were modeled using both linear and quadratic terms for the 90-day average stream temperature prior to spawning (temp\_90 and I(temp\_90^2)).

Model selection was based on AIC, and model performance was evaluated using marginal and conditional R², RMSE, and intraclass correlation coefficients (ICC). Candidate models were fit using maximum likelihood to allow direct comparison across differing fixed-effect structures. We also tested whether model performance improved by allowing the effect of temperature to vary across stream reaches by adding a random slope for temp\_90 to the COMID grouping factor. This random slope model was fit with restricted maximum likelihood (REML) and compared to the simpler random intercept model. To determine whether the quadratic temperature term remained necessary with random slopes, we re-fit the model with and without I(temp\_90^2) using maximum likelihood. Finally, we evaluated whether additional fixed-effect interactions improved model performance by adding interaction terms between temp\_90 and either stream or year.

**3. Results**

**3.1 Spawn timing variation in space and time**

Across all streams and years, Chinook salmon spawning showed a broadly unimodal distribution, with most activity concentrated between mid-August and early September (Figure 2A). The global mean spawn date was day 240 (late August), but year-specific means varied by nearly three weeks (Figure 2A). Stream-level distributions revealed additional spatial structure (Figure 2B), with some streams (e.g., Bear Valley, Beaver) exhibiting tighter peaks, while others (e.g., Big, Camas) displayed broader or later distributions. Year effects were also evident (Figure 2C), with 2005 skewed later than preceding years.

Chart, diagram

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Figure 2: Histogram and density of Chinook salmon spawn timing for all streams and years (A), by stream (B), and by year (C). In panel (A), the histogram and kernel density illustrate the overall distribution of spawn dates; vertical colored lines show year-specific means, and the black line shows the global mean. Spawn timing was generally unimodal, peaking in late August to early September.

When examined jointly by stream and year, density curves showed that each stream expressed a characteristic timing “signature,” but the strength and consistency of this signature varied (Figure 3). Some streams (e.g., Beaver, Marsh) displayed sharp, highly synchronous peaks, whereas others (e.g., Big, Camas, Elk) exhibited broader, more heterogeneous distributions. These stream-level differences were nested within year effects, reinforcing the combined influence of space and time on spawning phenology.

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Figure 3: Stream-specific density plots of Chinook salmon spawn timing by year. In each panel, the black density curve shows the overall distribution for the stream, and colored curves represent individual years (2002–2005). Dashed vertical purple lines indicate the 5th and 95th percentiles of basin-wide spawn timing. Streams varied in both the central tendency and spread of spawn timing, with some exhibiting sharp peaks and others more diffuse, multi-modal patterns.

The cumulative proportion of redds (Figure 4) provided an intuitive view of the pace and duration of spawning. Streams such as Marsh and Sulphur exhibited rapid increases, suggesting short, concentrated spawning windows. In contrast, Big and Camas showed more gradual accumulations, indicative of extended spawning seasons. Interannual variability was also evident, with some streams shifting substantially across years. Together, these patterns highlight the pronounced spatial and temporal heterogeneity in Chinook salmon spawn timing across the Middle Fork Salmon River basin.

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Figure 4. Proportion of cumulative Chinook salmon redds over time (day of year) across years (2002–2005) and streams. Each line represents a different year, with color denoting the year. Stream-specific panels illustrate temporal variation in the progression of spawning activity, as measured by cumulative redd counts normalized to the maximum value in each stream-year combination.

**3.2 Model comparison**

Model comparison identified stream identity, interannual variation, and nonlinear temperature responses as the strongest predictors of Chinook salmon spawn timing, while topographic variables contributed less consistently (Table 1).

Table 1. AIC selection performance metrics for additive linear models; top 10 of 31 shown.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | df | AIC | delta\_AIC | R2\_marginal | R2\_conditional | RMSE | ICC |
| m26 | 16 | 13356.04 | 0 | 0.785 | 0.956 | 2.023 | 0.796 |
| m31 | 17 | 13358.04 | 1.998 | 0.785 | 0.956 | 2.023 | 0.795 |
| m27 | 16 | 13468.96 | 112.925 | 0.737 | 0.979 | 2.022 | 0.922 |
| m16 | 15 | 13473.12 | 117.079 | 0.729 | 0.98 | 2.022 | 0.926 |
| m29 | 10 | 13487.82 | 131.783 | 0.727 | 0.984 | 2.022 | 0.942 |
| m19 | 9 | 13488.73 | 132.69 | 0.726 | 0.984 | 2.022 | 0.943 |
| m7 | 8 | 13531.17 | 175.128 | 0.66 | 0.987 | 2.022 | 0.962 |
| m20 | 9 | 13532.9 | 176.858 | 0.66 | 0.987 | 2.022 | 0.962 |
| m17 | 13 | 15787.25 | 2431.21 | 0.783 | 0.88 | 3.112 | 0.446 |

Model m26 (temp\_90 + quadratic term + stream + year + mean\_elevation) had the lowest AIC among the candidate set, but predicted later spawning at higher elevations—counter to raw data patterns showing earlier spawning in cooler, high-elevation reaches. We therefore did not retain m26 despite its statistical support. Model m31 (adds slope to m26) performed nearly identically (ΔAIC = 2) and retained the same inconsistent elevation effect, leading us to exclude it as well. Model m27 (replaces mean\_elevation with slope) performed substantially worse (ΔAIC > 110, lower marginal R²), indicating that elevation, not slope, was the topographic driver of likelihood gains. Together, these results suggest that topographic terms improved model likelihood but introduced biologically implausible effects, likely due to collinearity with temperature and confounding with stream identity (Appendix A). We therefore selected model m16 (temp\_90 + quadratic term + stream + year) as the most interpretable and parsimonious model. Model m16 had nearly identical predictive accuracy (RMSE = 2.02) and conditional R² (0.980) compared to m26, despite a modest reduction in marginal R² (0.729 vs. 0.785). This model was used as the base structure for subsequent evaluation of random slopes and interaction terms.

To account for site-level variation in thermal sensitivity, we extended the additive base model by allowing COMID-specific random slopes for temperature. This substantially improved model fit (ΔAIC = 510), reduced prediction error (RMSE = 1.78 days), and slightly increased conditional R², indicating that temperature effects vary meaningfully among stream reaches and are better represented as random slopes (Appendix A).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | df | AIC | delta\_AIC | R2\_marginal | R2\_conditional | RMSE | ICC |
| m16\_rs | 17 | 12948.763 | 0 | 0.698 | 0.985 | 1.781 | 0.949 |
| m16 | 15 | 13459.046 | 510.283 | 0.714 | 0.981 | 2.022 | 0.932 |

We next evaluated whether the quadratic temperature term remained necessary in the presence of random slopes. A model including both random slopes and a quadratic temperature effect outperformed the linear version (ΔAIC = 20.4), suggesting that both components contributed complementary information (Appendix A).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | df | AIC | delta\_AIC | R2\_marginal | R2\_conditional | RMSE | ICC |
| m16\_rs | 17 | 12965.969 | 0 | 0.713 | 0.984 | 1.782 | 0.945 |
| m16\_rs\_noquad | 16 | 12986.41 | 20.441 | 0.714 | 0.984 | 1.788 | 0.943 |

Finally, we assessed whether interactions between temperature and either stream or year provided additional explanatory power. A model including temp\_90 × year showed a large AIC improvement, but predicted an implausible inverted quadratic response, suggesting overfitting or confounding. A model with temp\_90 × stream produced more reasonable predictions but offered minimal improvement, and most interaction terms were non-significant. These results indicate that the random slope structure already accounts for much of the variation captured by fixed-effect interactions (Appendix A).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | df | AIC | delta\_AIC | R2\_marginal | R2\_conditional | RMSE | ICC |
| m202 | 20 | 11568.629 | 0 | 0.62 | 0.994 | 1.359 | 0.985 |
| m201 | 24 | 12948.514 | 1379.886 | 0.736 | 0.985 | 1.786 | 0.944 |
| m16\_rs | 17 | 12965.969 | 1397.34 | 0.713 | 0.984 | 1.782 | 0.945 |

On this basis, we retained the random slope model without interactions as our final model (m16\_rs), which was refit with REML for interpretation. This model balances explanatory power, biological realism, and parsimony: it captures general patterns in spawn timing via fixed effects and accommodates local deviations in thermal sensitivity via random slopes. This structure forms the basis for subsequent diagnostics, predictions, and ecological interpretation.

**3.3 Final model fit and diagnostics**

Model fit for the final model (`m16\_rs`) was strong (Table 2): marginal R² (fixed effects only) was 0.698, while conditional R² (fixed + random effects) was 0.985, indicating that most explanatory power came from spatially varying temperature responses. Combined with high ICC (0.95), these diagnostics and confirm that the final model effectively captured both broad-scale structure and stream-level heterogeneity in spawn timing.

Table 2. Parameter estimates from final model.

|  |  |  |  |
| --- | --- | --- | --- |
|  | m16\_rs | | |
| *Predictors* | *Estimates* | *CI* | *p* |
| (Intercept) | 235.09 | 230.95 – 239.22 | **<0.001** |
| temp 90 | 13.9 | 13.06 – 14.74 | **<0.001** |
| temp 90^2 | -0.85 | -1.15 – -0.55 | **<0.001** |
| stream [Beaver] | 17.41 | 10.62 – 24.19 | **<0.001** |
| stream [Big] | -0.19 | -5.37 – 5.00 | 0.944 |
| stream [Camas] | 2.3 | -3.08 – 7.69 | 0.402 |
| stream [Elk] | 11.97 | 4.88 – 19.06 | **0.001** |
| stream [Loon] | 2.8 | -2.47 – 8.06 | 0.298 |
| stream [Marsh] | 7.93 | 2.30 – 13.56 | **0.006** |
| stream [Sulphur] | 14.69 | 8.69 – 20.69 | **<0.001** |
| year [2003] | -5 | -5.23 – -4.77 | **<0.001** |
| year [2004] | 2.77 | 2.53 – 3.01 | **<0.001** |
| year [2005] | 3.68 | 3.38 – 3.98 | **<0.001** |
| **Random Effects** | | | |
| σ2 | 3.36 | | |
| τ00 COMID | 49.73 | | |
| τ11 COMID.temp\_90 | 12.63 | | |
| ρ01 COMID | -0.23 | | |
| ICC | 0.95 | | |
| N COMID | 104 | | |
| Observations | 3016 | | |
| Marginal R2 / Conditional R2 | 0.698 / 0.985 | | |

Model diagnostics indicated strong performance and no violations of key assumptions (Appendix A). The posterior predictive check showed excellent agreement between observed and predicted spawn timing, with overlapping distributions and no major deviations. Model predictions closely matched observed spawn timing, with predicted values aligning well along the 1:1 line. Residual plots revealed acceptable linearity and homoscedasticity: although the residuals vs. fitted values showed a slight trend and some funneling at lower fitted values, these patterns were minor and likely reflect skew in early spawn dates rather than model misspecification.

The normal Q-Q plot indicated slight right-skew and heavier-than-normal tails, but residuals were generally well-behaved. Random effect Q-Q plots for both intercepts and slopes were similarly close to normal. A small number of data points exceeded standard influence thresholds (|standardized residual| > 2, moderate leverage), but none were extreme enough to justify removal, and their influence was limited. Variance inflation factors (VIFs) for all fixed effects were below 2, suggesting low collinearity.

**3.4 Population-level effects**

We estimated marginal mean of `yday` at each factor level, averaging over the random effects, to provide an overall estimate of the effect in the population (Figure 5).

Chart

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Figure 5. Predicted mean spawn dates by stream (A), year (B) and stream and year (C), from the final mixed-effects model. Black points with black lines (A, B), and colored points with horizontal lines (C) represent estimated marginal means and 95% confidence intervals. Boxplots in panels A and B show the distribution of observed redd counts by group, with individual data points in grey. The modeled predictions represent marginal means accounting for fixed effects and averaged over random effects.

Significant differences in spawn timing were observed between many stream pairs (Table 3), particularly involving Loon (later spawning) and Sulphur (earlier spawning). For example, fish in Loon spawned significantly later than in Bear Valley, Camas, and Elk, while Sulphur exhibited significantly earlier timing than all other streams except Elk. These patterns reflect spatial heterogeneity in temperature and elevation across streams that are not fully captured by fixed effects alone.

Table 3. Pairwise contrasts among stream effects on predicted spawn timing. Contrasts represent estimated differences in predicted spawn day of year between streams from the final model. Positive values indicate later predicted spawn timing in the first stream compared to the second. P-values are uncorrected.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Level1 | Level2 | Difference | SE | CI\_low | CI\_high | t | df | p |
| Beaver | Bear Valley | -1.42785 | 3.469582 | -8.23085 | 5.375151 | -0.41153 | 2999 | 0.68071 |
| Big | Bear Valley | -2.65957 | 2.663021 | -7.8811 | 2.561964 | -0.9987 | 2999 | 0.318019 |
| Camas | Bear Valley | 0.62995 | 2.751802 | -4.76566 | 6.025561 | 0.228923 | 2999 | 0.818945 |
| Elk | Bear Valley | -6.60401 | 3.621972 | -13.7058 | 0.497791 | -1.82332 | 2999 | 0.068355 |
| Loon | Bear Valley | 8.897842 | 2.680929 | 3.641196 | 14.15449 | 3.31894 | 2999 | 9.14E-04 |
| Marsh | Bear Valley | 6.715956 | 2.872685 | 1.083323 | 12.34859 | 2.337867 | 2999 | 0.01946 |
| Sulphur | Bear Valley | -9.46985 | 3.1568 | -15.6596 | -3.28014 | -2.99983 | 2999 | 0.002724 |
| Big | Beaver | -1.23172 | 3.175517 | -7.45813 | 4.994694 | -0.38788 | 2999 | 0.698133 |
| Camas | Beaver | 2.057802 | 3.26672 | -4.34744 | 8.46304 | 0.629929 | 2999 | 0.528789 |
| Elk | Beaver | -5.17616 | 4.012614 | -13.0439 | 2.691597 | -1.28997 | 2999 | 0.19716 |
| Loon | Beaver | 10.32569 | 3.237654 | 3.977446 | 16.67394 | 3.189252 | 2999 | 0.001441 |
| Marsh | Beaver | 8.143808 | 3.406815 | 1.463877 | 14.82374 | 2.390446 | 2999 | 0.016889 |
| Sulphur | Beaver | -8.042 | 3.540372 | -14.9838 | -1.1002 | -2.27151 | 2999 | 0.023186 |
| Camas | Big | 3.289519 | 2.401202 | -1.41865 | 7.997688 | 1.369947 | 2999 | 0.170806 |
| Elk | Big | -3.94444 | 3.34929 | -10.5116 | 2.622697 | -1.17769 | 2999 | 0.239012 |
| Loon | Big | 11.55741 | 2.349649 | 6.950323 | 16.1645 | 4.918781 | 2999 | 9.18E-07 |
| Marsh | Big | 9.375525 | 2.573801 | 4.32893 | 14.42212 | 3.642676 | 2999 | 2.74E-04 |
| Sulphur | Big | -6.81029 | 2.780622 | -12.2624 | -1.35817 | -2.4492 | 2999 | 0.014374 |
| Elk | Camas | -7.23396 | 3.434652 | -13.9685 | -0.49945 | -2.10617 | 2999 | 0.035273 |
| Loon | Camas | 8.267891 | 2.446138 | 3.471613 | 13.06417 | 3.379977 | 2999 | 7.34E-04 |
| Marsh | Camas | 6.086006 | 2.658261 | 0.873807 | 11.2982 | 2.289469 | 2999 | 0.022121 |
| Sulphur | Camas | -10.0998 | 2.908947 | -15.8035 | -4.39607 | -3.47198 | 2999 | 5.24E-04 |
| Loon | Elk | 15.50185 | 3.398994 | 8.837257 | 22.16645 | 4.560718 | 2999 | 5.30E-06 |
| Marsh | Elk | 13.31997 | 3.557969 | 6.343658 | 20.29627 | 3.743699 | 2999 | 1.85E-04 |
| Sulphur | Elk | -2.86584 | 3.710867 | -10.1419 | 4.410259 | -0.77228 | 2999 | 0.440007 |
| Marsh | Loon | -2.18189 | 2.574604 | -7.23005 | 2.866283 | -0.84746 | 2999 | 0.396804 |
| Sulphur | Loon | -18.3677 | 2.908774 | -24.0711 | -12.6643 | -6.31458 | 2999 | 3.11E-10 |
| Sulphur | Marsh | -16.1858 | 3.101284 | -22.2667 | -10.105 | -5.21907 | 2999 | 1.92E-07 |

There was a clear trend toward later spawning over the four-year period (Table 4). Spawning in 2005 occurred significantly later than in all previous years. Differences between 2002 and 2003 were not statistically significant, but later years (2004 and especially 2005) were associated with a progressive delay in mean spawn timing. This temporal shift likely reflects interannual variability in temperature and flow conditions.

Table 4. Pairwise contrasts among year effects on predicted spawn timing. Contrasts represent estimated differences in predicted spawn day of year between years from the final model. Positive values indicate later spawning in the first year compared to the second. P-values are uncorrected.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Level1 | Level2 | Difference | SE | CI\_low | CI\_high | t | df | p |
| 2003 | 2002 | 0.974458 | 0.573919 | -0.15086 | 2.099773 | 1.697901 | 2999 | 0.08963 |
| 2004 | 2002 | 2.348814 | 0.649888 | 1.074542 | 3.623086 | 3.614182 | 2999 | 3.06E-04 |
| 2005 | 2002 | 6.175689 | 0.607288 | 4.984947 | 7.366432 | 10.1693 | 2999 | 6.61E-24 |
| 2004 | 2003 | 1.374356 | 0.606842 | 0.184487 | 2.564226 | 2.264766 | 2999 | 0.023598 |
| 2005 | 2003 | 5.201232 | 0.714322 | 3.800622 | 6.601842 | 7.281358 | 2999 | 4.20E-13 |
| 2005 | 2004 | 3.826875 | 0.873084 | 2.114972 | 5.538779 | 4.383172 | 2999 | 1.21E-05 |

Stream-specific predictions show a consistent pattern: spawn timing increases nonlinearly with 90-day mean stream temperature, leveling off at high temperatures (Figure 5). This plateau is consistent with biological expectations, as spawning may be constrained by environmental or physiological thresholds. Stream-to-stream variation in predicted timing reflects both fixed stream effects and COMID-specific random intercepts and slopes. Year-specific predictions similarly show consistent thermal responses across years, with modest offsets in average spawn timing due to year effects.

Chart, scatter chart

AI-generated content may be incorrect.

Figure 5. Predicted relationship between spawn timing and 90-day pre-spawn mean temperature by stream and year. Lines represent model predictions from the final mixed-effects model. Colored points show observed redd timing, shaded ribbons represent 95% confidence intervals for predictions.

**3.5 Group-level effects (stream-reach / COMID deviations from fixed / population effects)**

Random intercepts and slopes varied considerably among COMIDs, reflecting spatial heterogeneity in both average spawn timing and thermal sensitivity (Figure 6A). We found considerable spread in intercepts, reflecting differences in average spawn timing between reaches. The random slopes for `temp\_90` likewise varied meaningfully across COMIDs, indicating that temperature–spawn timing relationships are not constant across space. Sites with earlier average spawn timing (lower intercepts) generally exhibited stronger positive responses to temperature (higher slopes), while later-spawning sites tended to show weaker temperature effects, a pattern also evident in the weak negative correlation between intercepts and slopes (r = -0.2; Figure 6B). This indicates that reaches with earlier average spawn timing (i.e., negative intercepts) tend to exhibit stronger temperature sensitivity (i.e., steeper positive slopes), whereas later-spawning reaches show weaker responses to temperature. Biologically, this suggests that early-spawning populations are more phenologically plastic and adjust their timing more closely to thermal cues, while late-spawning populations may be constrained by other factors—such as photoperiod, migration fatigue, or compressed spawning windows—resulting in diminished thermal responsiveness. These findings highlight spatial heterogeneity in phenological flexibility, with potential implications for how different populations may respond to climate change.

Chart, scatter chart

AI-generated content may be incorrect.

Figure 6: (A) COMID-specific random parameter estimates for intercepts (left) and slopes (right). Points represent best linear unbiased predictions (BLUPs) from the final model, with horizontal bars indicating ±1.96 standard errors. (B) Correlation between random intercepts and slopes for 90-day temperature across COMIDs. Each point represents a stream reach (COMID).

When grouped by stream, Bear Valley and Big Creek exhibited early average spawn timing and high thermal sensitivity, while Sulphur and Marsh Creeks had later average timing with flatter temperature responses (Figure 7).

Chart, box and whisker chart

AI-generated content may be incorrect.

Figure 7. Boxplots of random intercepts and slopes for 90-day pre-spawn temperature by stream. Each box represents the distribution of best linear unbiased predictions (BLUPs) for a COMID's random intercept (average spawn timing) or slope (thermal sensitivity).

However, when examining individual random effects for each COMID and stream, we observed considerable variation in both intercepts and slopes within streams (Figure 8 and 9). For example, Bear Valley and Big Creek had some of the earliest average spawn timings, but also exhibited a wide range of thermal sensitivities. In contrast, Sulphur Creek had later average spawn timing but also showed considerable variability in its response to temperature. While the overall relationship is positive and nonlinear, individual COMID slopes and intercepts vary considerably. Some reaches show steeper increases in spawn timing with temperature (i.e., stronger thermal sensitivity), while others are relatively flat, indicating a weaker or more buffered response. Grouping by stream shows that some streams (e.g., Bear Valley, Marsh) exhibit tightly clustered trajectories, while others (e.g., Camas, Big) show more divergence. This variation likely reflects fine-scale differences in local hydrology, geomorphology, or biological factors that influence how fish respond to thermal cues within stream systems. The consistency of the overall trend, despite local heterogeneity, supports the biological relevance of temperature in structuring spawn timing.

Chart, bar chart, funnel chart

AI-generated content may be incorrect.

Figure 8. Random intercepts and slopes for 90-day pre-spawn temperature by stream. Each bar represents the best linear unbiased prediction (BLUP) for a COMID's random intercept (average spawn timing) or slope (thermal sensitivity). Bars are colored by stream.

Chart

AI-generated content may be incorrect.

Figure 9. Predicted spawn timing by 90-day pre-spawn temperature and COMID. Each line represents the predicted spawn timing for a specific COMID, colored by stream. The black line and shaded ribbon represents the 95% confidence interval for the population-level predictions.

**3.6 Elevation effects embedded in random structure**

Although mean elevation was excluded as a fixed effect due to collinearity with temperature and inconsistent global directionality, examination of random effects against elevation reveals spatial structure that elevation helps explain (Figure 10). Random intercepts (average spawn timing) showed positive relationships with elevation in some streams (e.g., Big Creek), where higher-elevation sites tended to have later average spawning relative to the population mean. In contrast, other streams (e.g., Bear Valley, Beaver) showed little or no elevation pattern.

Random slopes (thermal sensitivity to temperature) exhibited similarly idiosyncratic patterns. In some cases (e.g., Camas, Marsh), thermal sensitivity declined with elevation, suggesting that fish at higher elevations may respond less strongly to interannual temperature variability. In others, relationships were weak or even opposite in direction.

Taken together, these patterns indicate that elevation influences both average spawn timing and thermal sensitivity, but in ways that differ across streams. This heterogeneity justifies our decision to capture elevation-linked variation through COMID-level random effects rather than imposing a single fixed elevation term.



Figure 10. Relationships between mean elevation and random effects from the final model (m16\_rs). Panels A and C show random intercepts (average spawn timing) plotted against elevation for tributaries above 1800 m elevation (A) and below 1800 m elevation (C). Panels B and D show random slopes (thermal sensitivity) plotted against elevation for the same sets of streams. Points represent COMID-level estimates, with fitted lines shown for each stream. Elevation was excluded as a fixed effect due to collinearity with temperature and inconsistent global directionality, but these plots illustrate that elevation is associated with both average spawn timing and thermal sensitivity in stream-specific ways. This supports modeling elevation-linked variation through COMID-level random effects rather than a single global fixed effect.

**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**