

Using model selection and model averaging to predict the response of Chinook salmon to dam removal

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Abstract

Removal of four dams from the mainstem Klamath River depends on a cost-benefit analysis that includes expected benefits to fisheries. We predict expected escapement of Chinook salmon to watersheds above Iron Gate Dam using a log-linear modeling approach. Data from 77 populations of Chinook salmon in Washington, Idaho, Oregon, and California are assembled, including average escapement and measures of habitat quantity and quality. Nonmetric multidimensional scaling is used to reveal that adult run timing is related to environmental characteristics of watersheds and show that watersheds above Iron Gate are more similar to spring-run Chinook salmon-bearing watersheds than they are to fall-run Chinook salmon-bearing watersheds. We use model selection and averaging and bootstrap resampling to predict escapement to watersheds above Iron Gate. Models based on spring-run Chinook salmon data only predict escapement of about 3090 spawners per year (90% confidence interval 1420–25,300) to the upper basin, while models based on the complete dataset predict 3660 (2420–5510) spawners per year.

1 Introduction

Impassable dams are a significant factor in the decline of Chinook salmon in the western USA (Nehlsen et al., 1991; Myers et al., 1998; Lichatowich, 1999). Such dams, developed for hydropower production, flood and debris control, and water supply for irrigation and municipalities can block access to large amounts of spawning habitat (Sheer and Steel, 2006; Lindley et al., 2007) and degrade downstream habitats by altering the timing, quantity and quality of flows and degrading channel habitats by disrupting sediment regimes (Baxter, 1977; Ligon et al., 1995; Poff and Hart, 2002). Most dams were constructed before 1970, and many are now reaching the end of their useful lifespan or will need to be relicensed for further operations. Water and fishery managers are increasingly considering fish passage projects or dam removals at these junctures as part of a strategy to recover threatened and endangered fish populations (Kareiva et al., 2000; Pejchar and Warner, 2001; Doyle et al., 2003).

The Klamath River provides an example of this situation. Major impacts to salmon habitats began during the gold rush in the 1800s, and continued into the dam building era, beginning with the construction of the impassable Copco Dam in 1917 (NRC, 2004). Copco prevented anadromous fish from accessing Upper Klamath Lake and its tributaries, including the Sprague, Williamson and Wood rivers. Three additional dams were built in the mainstem Klamath River, the lowest being Iron Gate Dam, followed by Copco 2, and J. C. Boyle dams. Compared to many dams in the Columbia and Sacramento river basins, the dams on the mainstem Klamath are relatively small producers of hydropower and their impoundments are not important water supply reservoirs. The Klamath basin is also relatively sparsely populated and undeveloped, making it a potentially attractive target for restoration. The removal of the four mainstem dams is a central component of an ambitious proposed restoration program for the Klamath (Gosnell and Kelly, 2010). The decision to remove the dams may be based in part on the estimated costs and benefits of removal (Whitelaw and MacMullan, 2002). One potentially important benefit of dam removal is the restoration of depressed salmon runs in the Klamath basin. This raises the question of how many salmon should be expected to return to presently-blocked areas if they were to be made accessible.

Answering this question requires a model relating salmon abundance to the quantity and quality of habitat that would be made available by dam removal. Fausch et al. (1988), in a review of models relating salmon abundance to habitat measures, suggested that for basin-scale planning and fishery management, models based on measures made at the basin scale from analysis of maps are appropriate. Alternative approaches require data at finer scales that must be collected in the field (perhaps by remote sensing) and are typically not comprehensively available at large spatial scales. Although the distribution and abundance of fish are strongly influenced by fine-scale factors such as substrate composition and channel depth, these factors are controlled by and statistically related to basin-scale geomorphology (Frissell et al., 1986), which makes basin-scale metrics useful predictors of salmonid abundance (Lanka et al., 1987; Feist et al., 2010).

One challenge in developing models to predict abundance of salmon from geographic information arises from the abundance of potentially useful predictor variables that can be derived from maps. With n variables, the number of possible main-effects models is 2^n , so the number of models can quickly become large compared to the number of observations. One approach to this problem is to use stepwise regression with forward or backward selection of variables to arrive at a single “best” model with which to make inference and predictions. There is no guarantee, however, that the best model will be found by the stepwise regression procedure, and it is likely that this approach will identify spurious correlations and generate biased parameter estimates when many explanatory variables are considered (Lukacs et al., 2010). These problems can be ameliorated by using information theory as a basis for model selection and multi-model averaging (Burnham and Anderson, 1998), an approach that also better characterizes the real uncertainty in predictions and parameter estimates compared to inferences and predictions based on a single model (Buckland et al., 1997).

In this paper, we use model selection and model averaging to identify the relationship of salmon escapement to map-derived metrics of habitat quantity and quality and to predict escapement for the presently inaccessible areas above Iron Gate Dam. We use an ordination technique, nonmetric multidimensional scaling (NMDS), to characterize the similarity of watershed physical characteristics and show the difference between watersheds that support

spring- and fall-run Chinook salmon. Our predicted escapements are compared to historical data, an analysis of spawning habitat in the upper Klamath basin, and the predictions of a simpler model of salmon abundance based solely on watershed area and based partly on more northerly populations of Chinook salmon.

2 Methods

2.1 Escapement data

We compiled a dataset of 77 Chinook salmon populations from California, Oregon, Washington and Idaho, selecting populations based on availability of escapement data and information about the geographic location of their spawning habitat, at the approximate scale of fifth-field hydrologic units (Seaber et al., 1987). We obtained escapement data from databases held by the Northwest Fisheries Science Center (for Pacific Northwest watersheds) and California Department of Fish and Game (for lower Klamath and Central Valley watersheds). We computed average abundances over the period of record for each watershed. Life histories of populations were characterized by the season that adults enter freshwater in the original databases, which included spring, spring/summer, summer, fall and late-fall run timing. In our analysis, we grouped spring, spring/summer and summer runs as “spring run”, and grouped fall and late-fall runs as “fall” run.

2.2 Watersheds and their attributes

Figure 1 shows the watersheds for which we compiled escapement estimates and geographic information. Klamath basin watersheds that are expected to support Chinook salmon after dam removal include the mainstem Klamath River between Iron Gate and the outlet of Upper Klamath Lake (Iron Gate-Keno), the Upper Klamath Lake basin (mainly the Wood River), the Sprague River basin, and the Williamson River basin; the Butte and Lost River basins apparently never supported Chinook salmon (Hamilton et al., 2005) and are not targeted for restoration.

We have strong *a priori* expectation that some measure of habitat size will be important, such as watershed area (Parken et al., 2006; Liermann et al., 2010; Kim and Lapointe, 2010), stream length (Bradford et al., 1997), or discharge (Healey, 1991). We characterized the quantity of habitat as the product of watershed area and precipitation, which captures both a spatial and flow-related component.

Natural factors affecting habitat quality were mean and maximum elevation, mean January and August air temperature, and average ratio of base flow to mean annual flow. The temperature regime of rivers and streams, which is related to mean air temperature (Mohseni et al., 1998), is considered to be a dominant structuring aspect of the environment that determines the population structure and life history tactics expressed by Chinook salmon (Brannon et al., 2004). Elevation, while correlated with temperature, also is a measure of the cost of migration for anadromous salmonids. Long migrations require energy that could otherwise be used for reproduction and take time (for adults) that could otherwise be used for feeding in the ocean. Thus populations spawning at high elevations might be expected to have lower productivity than low elevation stocks, all else equal. Streams with higher base flow in the summer might be expected to have relatively more habitat to support spring-running adults (which spend the summer holding in the river prior to spawning in the fall) and yearling juvenile migrants, which must spend a summer in freshwater.

We expect that in many cases, habitat degradation will reduce realized escapement to levels less than what one would expect given the amount of habitat. Measures of human impact on the landscape included road density, human population density, and the percentages of the watersheds subject to urban development, pasture and cultivated crops, most of which have been implicated as threats to river ecosystems generally (Vorosmarty et al., 2010) and to salmonids specifically (Pess et al., 2002; Steel et al., 2004).

2.3 Data analysis

2.3.1 Ordination of habitat data

We used non-metric multidimensional scaling (NMDS) to examine whether the environmental characteristics of watersheds, as characterized by the habitat quality measures, differed between spring and fall chinook bearing watersheds. NMDS represents multivariate data in a lower dimensional space (we used two dimensions) by mapping the watershed position in ordination space such that the distances in this space among them are monotonically related to the Euclidean distances among them computed from scaled (transformed to have zero mean and unit variance) environmental characteristics. If spring and fall Chinook salmon use habitats with consistently different physical conditions then there will be a separation of the watersheds on the NMDS plot and we can infer which upper Klamath basins will support spring or fall chinook based on where they are located on the NMDS plot.

2.3.2 Modeling escapement

To identify which variables best explain variations in the escapement of chinook salmon, we used an information theoretic approach [Akaike's information criterion (AIC), Burnham and Anderson (1998)] to select among log-linear models relating log(escapement) to the various predictor variables.

The log-linear models are of the general form

$$\log(E_i) = a + b \log(H_i) + cY_i + \varepsilon_i, \quad (1)$$

where E_i is the average escapement in watershed i , H_i is a measure of habitat quantity in watershed i , Y_i is a vector of habitat quality measures, a , b , and c are parameters or vectors of parameters, and ε_i is a random variable with mean = 0 that accounts for other sources of variation. We log or arcsine-square root (proportional data) transformed, centered and scaled all variables to improve normality and stability of the statistical analysis.

To reduce the number of variables slightly from that considered in the NMDS ordination, we dropped mean January temperature and maximum elevation, as these were strongly

correlated with August air temperature and mean elevation, respectively. While we have strong *a priori* reasons for thinking that our proposed explanatory variables might be related to variations in escapement, we do not have strong reasons to favor any particular combination of explanatory variables. We therefore fit all 256 possible main effects models that could be constructed with the eight explanatory variables and compared their ability to explain variation in escapement on the basis of Akaike’s information criterion, corrected for small sample sizes [AICc; (Burnham and Anderson, 1998)].

When there is more than one model that is a plausible explanation for the data, model averaging is better than basing inference and prediction on the best model alone. Differences between the AICc scores of models and the “best” model (the one with the lowest AICc) form the basis of model averaging. The weight w_i of the i th model is

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{j=1}^J \exp(-\frac{1}{2}\Delta_j)} \quad (2)$$

where Δ_i is the AICc of model i minus the AICc of the best model (Burnham and Anderson, 1998). The w_i values can be interpreted as relative weights of evidence for the corresponding models based on the data. The full suite of J models can be used together to make predictions by weighting the prediction of each model by its w_i . We computed 95% confidence intervals for these predictions using bootstrap methods (Efron and Tibshirani, 1993) by resampling the original data 1000 times with replacement, calculating weights for all of the models, and making model-averaged predictions of escapement for each bootstrap resample (Buckland et al., 1997).

3 Results

Upper Klamath basins have habitat conditions most similar to watersheds that bear spring-run Chinook salmon (Figure 2). All four upper Klamath basins have negative x-axis scores, and only two fall-run Chinook salmon populations have negative x-axis scores (Shasta River fall-run Chinook salmon (near $\{-1, 2\}$) and Upper Skagit fall-run Chinook salmon, (near $\{0, -5\}$)); most fall-run Chinook salmon populations have x-axis scores > 1.0 . The x-axis

score is positively correlated with temperature and negatively correlated with elevation and the index of base flow. The y-axis, which does not show a separation of spring-run and fall-run, is positively correlated with flow.

While NMDS does generally show a separation of spring- and fall-run basins, and upper Klamath basins plot with spring-run Chinook salmon basins, there is some overlap between spring-run Chinook salmon and fall-run Chinook salmon basins. We therefore present results of models based on spring-run Chinook salmon data only, and on the combined spring- and fall run dataset.

3.1 Models based on spring-run Chinook salmon data only

The model selection strategy identified precipitation \times area and mean August air temperature as the best explanation for variation in log(escapement) for spring-run Chinook salmon, although the next 9 best models were within 2.5 AICc units of the best model and can also be considered good explanations for the data (Table 1). Precipitation \times area was included in 91 of the top 100 models, had the largest effect size at 0.371, and was the only covariate whose 95% confidence interval did not include 0 (Table 2). Other covariates appeared in less than half of the top 100 models and 95% confidence intervals on their estimates included 0.

Table 3 shows model-averaged predictions for the upper basin watersheds. Model averaging predicts a total escapement of 3093 Chinook salmon, and the total of the basin bootstrap medians is 3921 (90% CI = 1424–25,283).

3.2 Models based on the combined spring- and fall-run dataset

Model selection identified a similar suite of models as the best explanation for the entire dataset, with precipitation \times area and August air temperature as the most important variables (Tables 4 and 5). For these two variables, the direction of effect was the same as in the models based only on spring-run Chinook salmon data (positive), although the estimated effect sizes are larger when the combined data set is used. All of the top 10 models included these terms, while the other effects, whose 95% confidence intervals included 0, appeared in some but not

all of the top 10 models. The directions of the human population density, baseflow index, development and elevation effects were not consistent between the analysis based on the full data set and the analysis based on just spring-run Chinook salmon data.

Model-averaged predictions based on the complete dataset are shown in Table 6. Mean and median bootstrap predictions were slightly larger than that of the models based only on spring-run Chinook salmon data (3668 and 3633, respectively) , but the bootstrap 90% confidence interval was much narrower (2415–5509).

4 Discussion

Before we can relate our findings to relevant information in the literature, it is first necessary to discuss the relationship between life history type and the timing of adult return to freshwater (spring and fall run time). Healey (1991), following Gilbert (1913), identifies two main types of life histories within Chinook salmon: stream-type and ocean-type. These types differ by their age at ocean entry, degree of offshore migration, and timing of adult return. Stream-type Chinook salmon spend at least a year in freshwater as juveniles, undertake extensive offshore migrations in the open ocean, and return to freshwater in the spring. Ocean type Chinook salmon migrate to the sea after just a few months of freshwater rearing, remain in coastal marine waters, and return to freshwater in the fall for spawning. Because ocean-type Chinook salmon spend more of their life in the ocean, they should be more productive, but because they are coastally oriented, they suffer higher harvest rates in ocean fisheries. It is tempting to equate stream-type with spring-run and ocean-type with fall-run Chinook salmon, but Waples et al. (2004) shows that life history tactics vary widely among Chinook salmon populations. For instance, in California, many spring-run Chinook salmon populations produce sub-yearling migrants and do not undertake oceanic migrations. So, while Klamath spring-run Chinook salmon might be expected to have lower productivity than fall-run Chinook salmon due to their longer freshwater migration and perhaps reduced ocean residency, they aren't expected to have harvest rates as low as those stocks with oceanic rather than coastal migrations.

Our analysis of the environmental characteristics of the upper Klamath basin in relation to Chinook salmon habitat in the Pacific Northwest and California suggests that the upper Klamath is best suited for spring-run Chinook salmon. Thurow et al. (1997) used a modeling approach based on classification trees to conclude that the upper Klamath basin has habitat conditions that could have supported stream-type Chinook salmon, but not ocean-type Chinook salmon. This is consistent with our findings based on ordination of habitat variables, but in contrast with information presented by Fortune et al. (1966) and Hamilton et al. (2005), who review historical accounts indicating that distinct runs of Chinook salmon entered the upper Klamath in the early summer (i.e., spring-time entry into freshwater) and in the autumn. Fortune et al. (1966) indicates that spring-run Chinook salmon were largely gone from the upper basin before that area was settled by Europeans, so perhaps fall-run Chinook salmon were a small portion of total returns prior to the 1850s.

Our model is most directly comparable to that of Liermann et al. (2010), but such a comparison is complicated by the influence of harvest. Our model predicts escapement (the spawning run after harvest in the ocean and river), while Liermann et al. (2010) predict the equilibrium population size in the absence of fishing. Applying their stream-type equation to the individual upper Klamath basins separately and summing over basins predicts a non-fished equilibrium run size $\approx 41,000$.

To explore whether fishing could plausibly account for the difference between our escapement (P_e) prediction and Liermann et al.'s equilibrium unfished population size (P_r) prediction, we calculated P_e/P_r for all of the populations in our data set, which averages 0.130. From this ratio we can infer an implied harvest rate u_e (Ricker (1975), Appendix 3):

$$u_e = 1 - \exp \left[r \left(\frac{P_e}{P_r} - 1 \right) \right] \quad (3)$$

where r is the productivity parameter estimated by (Liermann et al., 2010) (1.455 for stream-type Chinook salmon). Using the stream-type r , our analysis implies an average brood exploitation rate of 0.712 (SD=0.071), high by recent standards but not out of line with harvest rates of coastal-migrating Chinook salmon in the 1980s. This implies that unfished

equilibrium population sizes might be about 7.70 times the size of our predicted escapements on average. Thus, the effects of fishing are probably not large enough to explain the difference between predictions of our model and that of Liermann et al. (2010). The other major difference between the two modeling approaches is the underlying data sets: Liermann et al. (2010) used data from British Columbia, and for which detailed harvest information is available (which might tend to be the more important stocks for fisheries, which would be the large and productive ones). We restricted our analysis to populations closer to the Klamath basin, and included populations that aren't the focus of fisheries management.

Fortune et al. (1966) provides two more points of reference. They report counts of Chinook salmon at the Klamathon fish racks (near the present site of Iron Gate Dam), which averaged 10,456 per year over the 1925-1961 period. Chinook salmon were intercepted at the fish rack to collect eggs for the Fall Creek fish hatchery, located on a tributary to the Klamath River below Copco Dam and upstream of Iron Gate, and later to Iron Gate Hatchery (Leitritz, 1970). Counts at the Klamathon racks therefore presumably reflect some contribution from hatchery production. Fortune et al. (1966) also surveyed the river and its tributaries above Iron Gate and quantified the area of spawning gravel. They concluded that there was enough gravel above Iron Gate to support 4590 Chinook salmon without crowding of redds.

Other efforts to predict the response of salmon to dam removal appear to be rare in the literature. Pess et al. (2008) conducted a detailed assessment of the distribution of habitat and salmonids in the Elwha River in Washington, but made only qualitative predictions about the relative likelihood of various species recolonizing areas above two dams proposed for removal. They found that the primary effect of the dams was that they were blocking the migration of anadromous salmonids to areas above the dam, but that downstream effects of the dam were also important. Kareiva et al. (2000) used a matrix population model to predict whether removing a series of large but passable dams in the Columbia basin would be sufficient to recover Chinook salmon in the Snake River. They found that removing the dams would not necessarily prevent extinction of Snake River spring/summer Chinook salmon, although that conclusion is contested (Dambacher et al., 2001).

Our modeling approach provides an estimate of expected escapement of Chinook salmon

to areas above Iron Gate dam, based on the simple assumption that we can extrapolate the relationship between levels of escapement in other watersheds in the region and the characteristics of those watersheds, especially their size. The models, of course say nothing about important dynamics that are likely to result from the removal of the dams, which will essentially be a large disturbance to the ecosystem. Simulation modeling can attempt to capture some of the transition, such the recolonization process, disease dynamics, sediment movements and effects on fish, and water quality impacts on migration timing and success, and thereby provide useful insights into the roles that various ecological and physical processes might play (Hart et al., 2002). However, increased realism and detail comes with the price of greatly increased data requirements and modeling effort. As model complexity rises, it becomes increasingly difficult to rigorously quantify the uncertainties that arise from the underlying data and the assumptions underpinning the model structure. While such efforts are worthwhile, simpler empirically-based approaches such as we have illustrated here provide a transparent, data-based, and easily understood point of reference with which to compare the results of more detailed analyses.

Our model predicts a fairly modest increase in escapement of Chinook salmon to the Klamath basin if the dams are removed. The addition of several populations of spring-run Chinook salmon with greater than 800 spawners per year to the upper Klamath would significantly benefit Klamath Chinook salmon from a conservation perspective, in addition to the fishery benefits. Stable spawning populations of that size are potentially viable independent populations that would contribute to the viability of the Upper Klamath and Trinity Rivers (UKTR) Chinook salmon Evolutionarily Significant Unit (ESU), according to the viability assessment framework of Lindley et al. (2007). The last status review of the UKTR ESU expressed significant concern about the very poor status of the spring-run component of the ESU (Myers et al., 1998). Viable populations of spring-run Chinook salmon in the upper Klamath would increase the diversity and improve the spatial structure of the ESU, enhancing its viability (McElhany et al., 2000) and improving the sustainability of this ESU into an uncertain future.

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Table 1: Comparison of the 10 best linear models explaining variation in spring-run Chinook salmon escapement.

Rank	Model formula	AIC _c	Weight
1	log.spawners \sim 1 + log.preciparea + AugT	107.3	0.08329
2	log.spawners \sim 1 + log.preciparea + log.elev	108.3	0.05000
3	log.spawners \sim 1 + log.preciparea + baseflow	108.6	0.04369
4	log.spawners \sim 1 + log.preciparea + log.elev + development	109.1	0.03480
5	log.spawners \sim 1 + log.preciparea + log.elev + development + roads	109.2	0.03287
6	log.spawners \sim 1 + log.preciparea + log.elev + AugT	109.4	0.02926
7	log.spawners \sim 1 + log.preciparea + baseflow + AugT	109.5	0.02820
8	log.spawners \sim 1 + log.preciparea + AugT + crops	109.6	0.02633
9	log.spawners \sim 1 + log.preciparea + AugT + humans	109.6	0.02599
10	log.spawners \sim 1 + log.preciparea + AugT + roads	109.7	0.02483

Table 2: Model-average estimates of coefficients based on best 100 models using spring-run populations. No. models is the number of models (out of the top 100) including that parameter.

Variable	Estimate	Unconditional variance	No. models	Importance	+/- $\alpha = 0.05$
crops	-0.00656	0.00173	37	0.201	0.0843
humans	0.02551	0.00535	35	0.222	0.1483
roads	0.07679	0.02521	37	0.277	0.3221
baseflow	-0.05273	0.01459	39	0.289	0.2450
development	-0.14935	0.06510	46	0.365	0.5176
log.elev	-0.14613	0.05078	44	0.411	0.4571
AugT	0.15344	0.03916	49	0.505	0.4014
log.preciparea	0.37128	0.02407	91	0.959	0.3147
(Intercept)	0.02399	0.02016	100	1.000	0.2880

Table 3: Model-averaged predictions for escapement to Upper Klamath basin watersheds with bootstrap median and 90% interval, based on the spring-run Chinook salmon dataset.

Watershed	Model Average	0.50 Quantile	0.05 Quantile	0.95 Quantile
Williamson River	806	1,054	317	5,599
Sprague River	989	1,370	511	12,555
Upper Klamath Lake	578	522	163	1,158
Klamath Mainstem - Iron Gate to Keno	720	975	433	5,471
Total	3093	3921	1424	25,283

Table 4: Comparison of the 10 best linear models explaining variation in Chinook salmon escapement, based on both spring-run and fall-run Chinook salmon data.

Rank	Model formula	AIC_c	Weight
1	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT} + \text{crops}$	173.1	0.06492
2	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \text{AugT}$	173.6	0.05217
3	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT} + \text{development} + \text{crops}$	173.6	0.05162
4	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \text{AugT} + \text{crops}$	173.7	0.04922
5	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \text{baseflow} + \text{AugT} + \text{crops}$	173.8	0.04675
6	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT}$	173.8	0.04663
7	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT} + \text{crops} + \text{roads}$	173.9	0.04429
8	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT} + \text{development}$	174.0	0.04217
9	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \text{baseflow} + \text{AugT}$	174.3	0.03585
10	$\log.\text{spawners} \sim 1 + \log.\text{preciparea} + \log.\text{elev} + \text{AugT} + \text{roads}$	174.4	0.03373

Table 5: Model-average estimates of coefficients based on best 100 models using data from all populations. No. models is the number of models (out of the top 100) including that parameter.

Variable	Estimate	Variance	No. models	Importance	+/- $\alpha = 0.05$
humans	-0.01353	0.003522	46	0.2623	0.1185
development	0.00646	0.007289	44	0.2862	0.1704
roads	0.06910	0.019031	47	0.3318	0.2754
baseflow	0.04541	0.009327	43	0.3572	0.1928
log.elev	0.14817	0.035362	48	0.5334	0.3754
crops	-0.09559	0.013680	43	0.5456	0.2335
AugT	0.47028	0.019018	68	0.9974	0.2753
log.preciparea	0.43030	0.010020	96	0.9999	0.1998
(Intercept)	0.01374	0.008640	100	1.0000	0.1855

Table 6: Model-averaged predictions for escapement to Upper Klamath basin watersheds with bootstrap median and 90% interval.

Watershed	Model Average	0.50 Quantile	0.05 Quantile	0.95 Quantile
Williamson River	926	913	587	1,373
Sprague River	1,090	1,100	777	1,739
Upper Klamath Lake	701	676	389	952
Klamath Mainstem - Iron Gate to Keno	941	944	662	1,445
Total	3658	3633	2415	5509

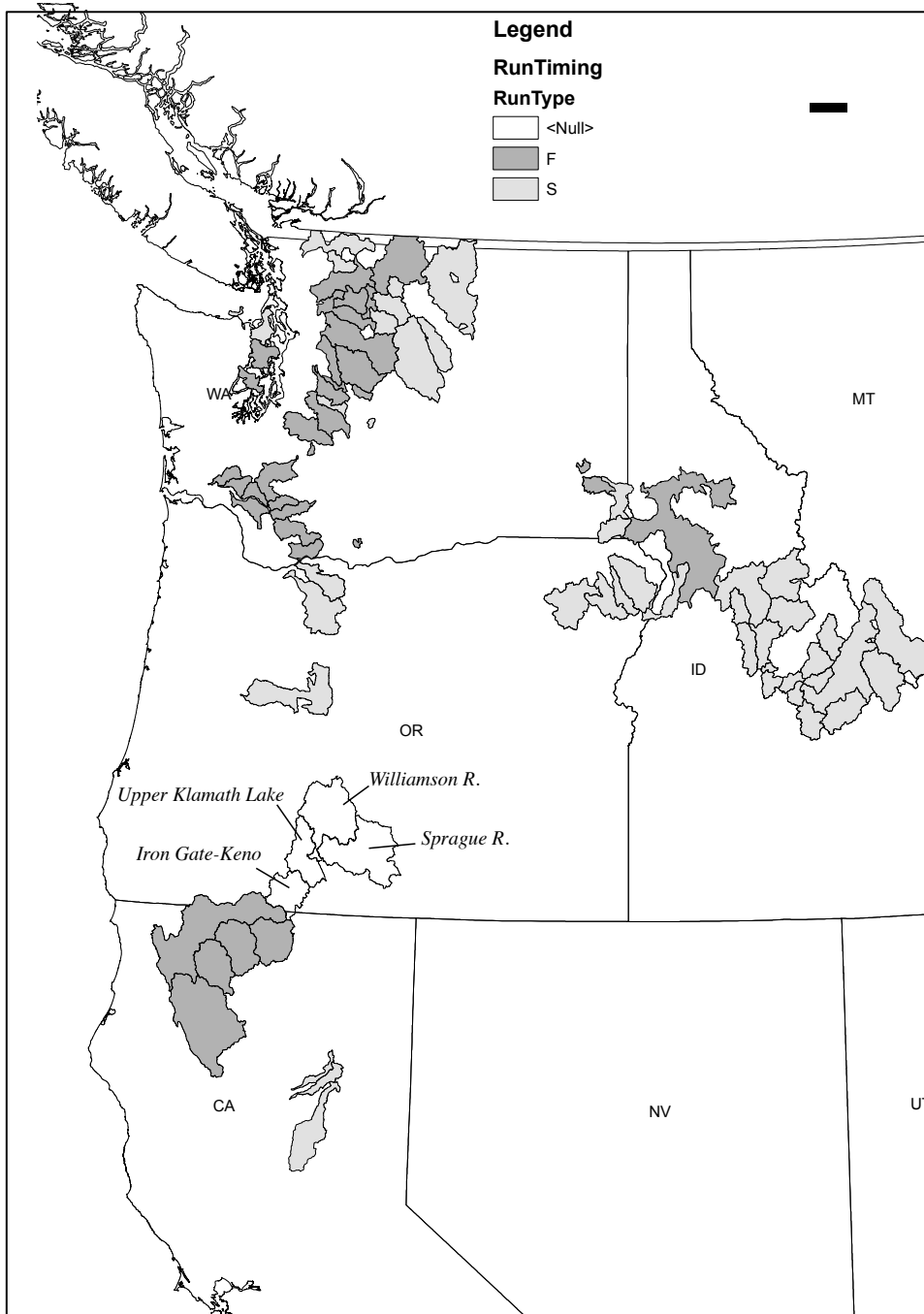


Figure 1: Map of study basins.

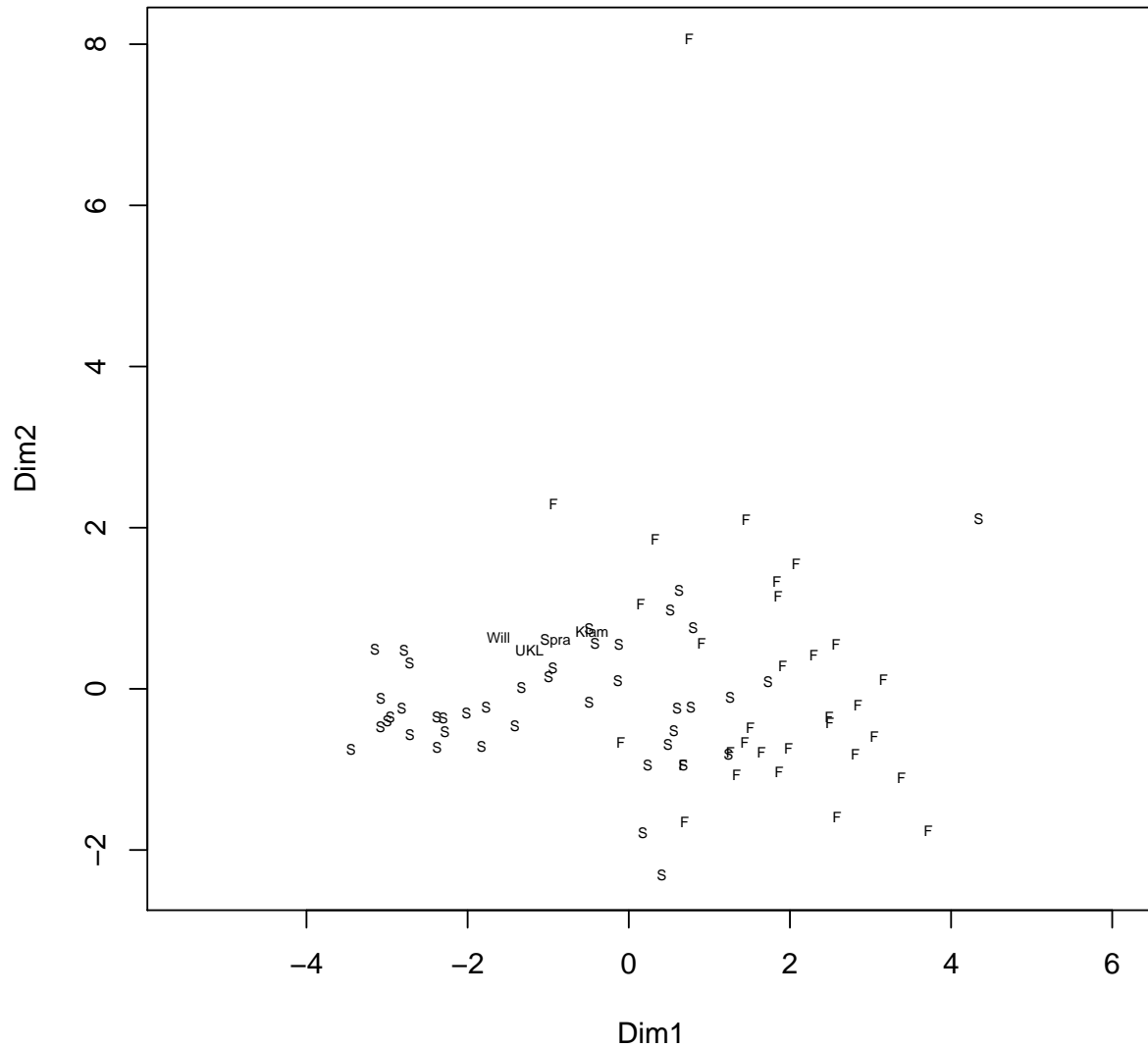


Figure 2: Ordination of environmental characteristics of chinook-bearing watersheds in California, Oregon and Washington. F indicates a basin bearing fall chinook, S indicates a spring chinook basin, and Will, Spra, UKL, and Klam indicates the Williamson River, Sprague River, Upper Klamath Lake basins, and the Klamath and its tributaries between Iron Gate dams and Link River.