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**RELATIONSHIPS BETWEEN LANDSCAPE HABITAT
VARIABLES AND CHINOOK SALMON PRODUCTION
IN THE COLUMBIA RIVER BASIN**

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Relationships Between Landscape Habitat Variables and Chinook Salmon Production in the Columbia River Basin

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Introduction

Many anadromous salmonid populations in the Pacific Northwest have dramatically declined from previously recorded levels, presumably because of degradation or loss of freshwater spawning and rearing habitats, restricted upstream access and increased downstream passage mortality due to hydroelectric dams, commercial overfishing, and negative impacts from non-native and hatchery fishes (Nehlsen et al. 1991, National Research Council 1996, Lee et al. 1997). Therefore, long-term persistence for a number of these stocks is doubtful under present conditions (e.g., see Emlen 1995, Ratner et al. 1997). Although the need for remedial measures is clear, it is unclear which factors to focus these measures on. That is, complexity of the life history pattern of these anadromous fishes, as well as variability in this pattern among different stocks (Nehlsen et al. 1991), adds to the uncertainty associated with attempting to identify limiting factors that most influence stock size and persistence. For instance, there are a wide range of potential environmental conditions that anadromous fishes experience during their freshwater occupancy period; attempting to tease out the more influential of these factors is complex and difficult (Bisson et al. 1992). In addition, efforts to properly restore anadromous salmonid stocks to previously high levels will require a broadscale approach that incorporates landscape patterns and processes (Schlosser 1991), which adds further sources of uncertainty.

A huge effort has been undertaken by various federal, state, and tribal agencies to restore populations of anadromous salmonids within the Columbia River Basin in the northwestern United States - a complex area that accommodates a variety of uses and pressures on its natural resources, including those that are incompatible with the needs of anadromous salmonids (Lee and Grant 1995). In fact, exploitation of fish and degradation of their freshwater habitats within the Columbia River Basin over the past century has reduced numbers of salmon and steelhead from an estimated 10-16 million adults to 1.5-4 million adults (Northwest Power Planning Council 1986, Lee and Grant 1995). The entire basin covers approximately 670,000 km² in portions of seven states (mainly Idaho, western Montana, most of eastern Washington and Oregon with smaller portions in Wyoming, Utah, and Nevada) in the northwestern United States, as well as the southeastern part of British Columbia, Canada (Krutilla 1967). The sheer expanse of this basin requires salmonid recovery plans to have a broadscale approach that accounts for a complex interaction of sociopolitical, socioeconomic, and ecological issues related to salmon and salmon habitat.

An effort is currently underway by an interagency group of scientists to develop a formal decision analysis for evaluating alternative hypotheses and management options for restoration of threatened and endangered spring/summer chinook salmon (*Oncorhynchus tshawytscha*), fall chinook salmon, and steelhead trout (*Oncorhynchus mykiss*) stocks in the Columbia River Basin, a process referred to as PATH (Plan for Analyzing and Testing Hypotheses) (Marmorek and Peters 1998). A key element in this process is identifying and (when possible) resolving sources of uncertainty associated with biology and life history of anadromous salmonids as related to recovery efforts; these sources of uncertainty have been categorized as hydrosystem, habitat, hatcheries, harvest, and climate (Marmorek and Peters 1998). Although an emphasis has been placed on evaluating effects of different hydrosystem options on long-term persistence of salmonids, quality and condition of freshwater habitats may affect production in salmonids (Hunt 1969, Scarnecchia and Bergersen 1987, Heggenes and Borgstrom 1991), which in turn would

affect their long-term persistence. However, to our knowledge, relationships between large-scale habitat factors and production in anadromous salmon stocks have never been investigated, particularly at the scale of the Columbia River Basin. Indeed, previous broadscale assessments of salmonid stocks in this area have been mainly limited to compiling available status/risk information (e.g., Nehlsen et al. 1991, Frissell 1993, Huntington et al. 1996) or using GIS data to evaluate and map potential salmon freshwater habitat (Lunetta et al. 1997; western Washington State only). Conversely, Lee et al. (1997) attempted to rigorously quantify linkages between population status of fish species (based on current population data and expert judgement) and landscape habitat variables. Nevertheless, there are no published studies that have rigorously evaluated possible linkages between broadscale habitat metrics and salmonid stock production.

Here, we investigate potential relationships between various landscape habitat variables and estimates of fish production from 25 index stocks of spring/summer chinook salmon within the Columbia River Basin. Because we use recently-described techniques for model selection and inference (Buckland et al. 1997, Burnham and Anderson 1998) that are probably unfamiliar to most ecologists, we discuss our methodological approach in some detail. Note, however, that this approach may be applied more broadly to other modeling situations, and hence should be of general interest to ecologists.

Methods

We employed a two-step modeling process to evaluate relationships between landscape variables and fish production in 25 index stocks of spring/summer chinook salmon within the Columbia River Basin (Fig. 1). The first set of models were Ricker-type stock-recruitment models (Ricker 1954). Parameter estimates from these models were used to generate a response variable in the second set of models, which contained landscape habitat predictor variables. In the following, we describe our methodological approaches for each modeling step, including state-of-the-art model selection and inference techniques adapted for our needs.

Developing a Set of Candidate Models

A crucial step in the modeling process is the construction of a set of candidate models that are ecologically meaningful (Lebreton et al. 1992, Burnham and Anderson 1998). Based on results from Deriso et al. (1996), we used a stock-recruitment, regression model with stock-specific Ricker a values as a base model from which we derived other candidate models (see *Stock-Recruitment Models*). For the landscape habitat models, we adopted the more general approach recommended by Burnham and Anderson (1998), i.e., we developed a global linear regression model containing various class, physiographic and geophysical, and anthropogenic landscape variables (Table 1) that may have had important influences on fish production. Because of the paucity of data ($n = 25$ observations) and hence the danger of over-fitting the model, we only used a small number of predictor variables to construct the global model. From this we generated a subset of models that contained various combinations of variables we deemed biologically relevant.

Model Selection

We used the small sample adjustment of Akaike's Information Criterion (AIC; Akaike 1973) to rank models and assess their relative plausibility given the data. AIC is an extension of likelihood theory and is derived from the Kullback-Leibler distance of information theory (Kullback and Leibler 1951, Kullback 1997), which is a measure of how much information is lost when a model is used to approximate reality (Cover and Thomas 1991, Burnham and Anderson 1998). AIC is defined as

$$\text{AIC} = n \log \left(\frac{\text{RSS}}{n} \right) + 2k, \quad (1)$$

where n is the number of observations, \log is the natural logarithm, RSS is the residual sum of squares (also called error sum of squares, SSE), and k is the number of estimable parameters in the model (Buckland and Anderson 1998). Equivalently, $\text{AIC} = -2 \log(L) + 2k$, where L is the likelihood function and is calculated from the maximum likelihood estimates of the model parameters (Buckland et al. 1997). When $n/k < 40$, Burnham and Anderson (1998) recommended Hurvich and Tsai's (1989) small sample adjustment to AIC,

$$\text{AICc} = \text{AIC} + \frac{2k(k+1)}{n-k-1}. \quad (2)$$

Note that AICc converges to AIC as the number of observations increases relative to the number of estimable parameters in a model. In other words, as n increases relative to k in the second term in Eq. 2, the denominator increases relative to the numerator and the whole term approaches zero. For large n/k ratios, the second term essentially drops out, leaving only the AIC term. Hence, AICc can be routinely used in place of AIC because its adjustment to AIC is necessary for smaller n/k ratios, whereas it is essentially equivalent to AIC for larger n/k ratios.

AIC and its derivatives operate on the principle of parsimony (Box and Jenkins 1970), i.e., the highest ranked models are those that best fit the data with the fewest parameters. The principle of parsimony states that there is an ideal point in the balance between increasing the number of parameters to decrease bias and decreasing the number of parameters to increase precision. This bias/precision trade-off can be seen in the AIC formula (Eq. 1), where the first term rewards a better-fitting model (i.e., leading to lower bias) and the second term penalizes an over-parameterized model (i.e., leading to higher precision). The smaller the sum of these two terms (or the smaller the AIC), the better fitting the model. However, AIC (or AICc) is a relative ranking statistic. Therefore, AIC values should be interpreted in terms of the magnitude of their differences among candidate models rather than the magnitude of any particular value. A simple method of model ranking is to order the relative differences among AIC values by subtracting the lowest value from all other values (these differences are called ΔAIC values), and then reordering ΔAIC values and their associated models from low (i.e., 0) to high (Burnham and Anderson 1998). One can interpret the relative plausibility of each model for a particular data set by calculating the ΔAIC model weights (see below). Note that AIC values are specific to the

data set that was used to compute them, and hence those computed from different data sets are not comparable.

We interpreted the relative plausibility of each candidate model for a specific data set by its ΔAICc weight, w_i . These weights are calculated as

$$w_i = \frac{e^{(-\Delta\text{AICc}_i/2)}}{\sum_{i=1}^I e^{(-\Delta\text{AICc}_i/2)}} , \quad (3)$$

where ΔAICc_i is the ΔAICc value for the i th model in a set of I candidate models (Buckland et al. 1997). Thus, the w_i sum to 1. Note that there may be more than one model that is reasonably plausible for a particular set of data, especially if the data set is small. We decided *a priori* to exclude predictor variables from further consideration that occurred *only* in models whose ΔAICc weights were less than one-tenth that of the model with the largest weight (see below). We used PROC GENMOD in SAS (SAS Institute, Inc. 1996), in conjunction with SAS programming code, to produce ΔAICc values and ΔAICc weights for all sets of candidate models.

Model Inference

We incorporated model selection uncertainty into model inference as generally described by Buckland et al. (1997) and Burnham and Anderson (1998). That is, we did not select a single model from a candidate set and treat it as the “true” model *unless* the ΔAICc weight was more than ten times the next highest weight (our modification). Rather, we viewed the predictor variables contained in models whose ΔAICc weights were more than one-tenth of the largest ΔAICc weight as forming a composite conceptual model whose parameter estimates were computed based on the ΔAICc -weighted average of estimates from relevant models. This arbitrary rule based on proportion of the maximum ΔAICc weight was used to limit the number of predictors in our composite conceptual model to those that seemed reasonably plausible for the data.

We computed model-averaged estimates of regression coefficients for relevant predictor variables via

$$\hat{\theta} = \sum_{i=1}^J w_i \hat{\theta}_i , \quad (4)$$

where $\hat{\theta}_i$ is the estimator of a regression coefficient for a specific predictor variable in model i and w_i is the ΔAICc weight that is calculated from the AICc values for the J candidate models containing a specific predictor variable (Buckland et al. 1997). For example, say 3 of the 8 candidate models contained predictor X_1 , which appeared in at least one model with w_i greater

than one-tenth of the maximum w_i . The w_i used in the model selection process for assessing the plausibility of each model would be based on ΔAICc values from all 8 models, whereas the w_i used in model inference for estimating the overall regression coefficient (i.e., $\hat{\theta}$) for X_1 would only be based on ΔAICc values calculated from the $J = 3$ models containing X_1 . Thus, the w_i always were scaled so that they summed to 1.

Variance estimators for regression coefficients also were calculated based on model averaging. There were two sources of uncertainty associated with each model parameter estimate: the variance based on a particular model (called conditional variance) and the variance due to uncertainty in the selection from a set of models (Buckland et al. 1997). The overall variance (called unconditional variance, $\text{v}\hat{\text{a}}\text{r}(\hat{\theta})$) is calculated as

$$\text{v}\hat{\text{a}}\text{r}(\hat{\theta}) = \left[\sum_{i=1}^J w_i \sqrt{\text{v}\hat{\text{a}}\text{r}(\hat{\theta}_i | \theta) + \left(\hat{\theta}_i - \hat{\theta} \right)^2} \right]^2, \quad (5)$$

where $\text{v}\hat{\text{a}}\text{r}(\hat{\theta}_i | \theta)$ is the conditional variance (i.e., the square of the standard error for regression coefficients in regression output) and $\left(\hat{\theta}_i - \hat{\theta} \right)^2$ is the variance component due to model selection uncertainty. The w_i were computed based on the J models as described above.

Technically, estimators should have been perfectly correlated for Eq. 5 to be used so that there would be no covariance term (Buckland et al. 1997); however, reasonable results can be obtained for a correlation between 0.5 and 1 (K. P. Burnham, pers. commun.).

Stock-Recruitment Models

Deriso et al. (1996) conducted preliminary analyses of spawner-recruit data from 13 index stocks of spring/summer chinook salmon in part to evaluate which Ricker-type model best fit the data, and to use the selected model to generate Ricker a estimates for further analyses (see below). Based on an AIC selection criterion, the best approximating model chosen was the one with no spawner measurement error and stock-specific Ricker a values,

$$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - m_{t,i} + \varepsilon_{t,i}, \quad (6)$$

where $R_{t,i}$ is the Columbia River observed spawning returns (recruitment) for stock i during year t , $S_{t,i}$ is the observed spawners for stock i during year t , a_i is the Ricker a parameter for stock i , b_i is the Ricker b parameter for stock i , δ_t is the year-effect parameter for year t , $m_{t,i}$ is the in-river passage mortality for stock i during year t , and $\varepsilon_{t,i}$ is the multiplicative residual error

(assumed to be distributed as $N(0, \sigma_\varepsilon^2)$; Deriso et al. 1996). Ricker a is a measure of productivity (recruits-per-spawner) at low numbers of fish, whereas Ricker b is a measure of the rate of decrease in productivity as fish numbers increase (Hilborn and Walters 1992). Hereafter we simply refer to these parameters as a and b , subscripted by stock i when appropriate. The year-effect parameter accounts for other factors affecting all stocks such as regional changes in terrestrial climate and large changes in survival rates of chinook salmon in the marine environment (i.e., this model assumes that large annual variation in ocean mortality is limited to the first 2 years of life; Deriso et al. 1996).

The in-river passage mortality is the sum of two components, X and μ_i . The first component is the number of dams encountered by chinook salmon during downstream migration, X , which is defined differently depending on year. During recording years 1952-1969, this component is the actual number of dams encountered between the spawning/rearing area and the lowest dam in the system (Bonneville Dam; Fig. 1) inclusive (range = 1-9 dams), whereas during 1970-1990 it is the number of dams between John Day Dam and Bonneville Dam (i.e., 3). The second component of in-river passage mortality is the net dam passage mortality, μ_i , from the Snake River stocks to the John Day Dam during 1970-1990 (Deriso et al. 1996). Thus, through 1969, the in-river passage mortality is the actual number of dams encountered by chinook salmon from each stock during downstream migration (i.e., from 1 to 9 dams), whereas after 1969 it is the number of dams encountered between John Day Dam and Bonneville Dam (the number was fixed at 3) *plus* the net dam passage mortality from the Snake River stocks to the John Day Dam.

Deriso et al.'s (1996) choice of the stock-specific Ricker a model in Eq. 6 was consistent with the rationale that, because of the depressed levels of many spring/summer chinook stocks, a_i would be better than b_i for evaluating effects of habitat on fish production. Thus, Eq. 6 was used in preliminary analyses by the PATH group to generate estimates of a for each of the 25 index stocks (which included 12 additional stocks - see below), which then were to be used as the response variable in a set of linear regression models containing various combinations of class, physiographic and geophysical, and anthropogenic landscape variables (Table 1). However, spawner-recruit data from the John Day Middle Fork during 1959-1973 had an unusually large influence on parameter estimates, including a_i , generated by the model in Eq. 6 (R. Hinrichsen, pers. commun.). Therefore, we needed to remove the pre-1974 data from John Day Middle Fork and refit at least some of the Ricker-type models considered by Deriso et al. (1996) to see if Eq. 6 still would be chosen as the best approximating model. Further, Beamesderfer et al. (1997) and R. Beamesderfer (Oregon Dept. of Fish and Wildlife) provided spawner-recruit data for an additional 12 stocks, which afforded us the opportunity to more rigorously evaluate the relative importance of the Ricker-type models. Consequently, as per a general suggestion by R. Deriso (Inter-American Tropical Tuna Commission), we considered a set of 8 candidate Ricker-type models, including Eq. 6, and 7 others that differed from Eq. 6 by the Ricker a term and/or the in-river passage mortality term (Table 2).

Landscape Habitat Models

Habitat data for physiographic, geophysical, and anthropogenic landscape variables (Table 1) were obtained from the Interior Columbia Basin Ecosystem Management Project (Lee et al. 1997). These landscape variables are at the HUC6 or subwatershed level of spatial scale, which is about 7,800 ha on average within the Columbia Basin (Lee et al. 1997). Because the model containing common a values was the only plausible model given the data (see Results), we used $\hat{d}_i = \hat{a} - \ln(\hat{b}_i)$ (R. Deriso, pers. commun.) instead of \hat{a}_i as the response variable in the landscape habitat models. Note that $e^{\hat{d}_i}$ is the estimator of maximum recruitment for the i th stock. To incorporate the uncertainty associated with \hat{d}_i into the model parameter estimates, we generated 1000 random \hat{d}_i values from a normal distribution with $\text{mean}(d_i)$ and $\text{var}(d_i)$, fit each of the candidate models 1000 times, and averaged over the 1000 parameter estimates and AICc values to obtain single values for each candidate model. Given $\text{mean}(d_i) = \text{mean}(a) - \text{mean}(\ln[b_i])$, we obtained an estimate of $\text{mean}(a)$ from the regression output. The method of moments (Wackerly et al. 1996) was used to define $\text{mean}(\ln[b_i])$, which was lognormally distributed with mean $e^{\mu_i + \frac{1}{2}\sigma_i^2}$, in terms of the sample mean (m_i) and variance (s_i^2) of b_i . Thus,

$$\text{mean}(\ln[b_i]) = 2\ln(m_i) - \frac{1}{2}\ln(s_i^2 + m_i^2),$$

where m_i and s_i^2 were obtained from regression output. The general formula for the variance of d_i is

$$\text{var}(d_i) = \text{var}(a) + \text{var}(\ln[b_i]) - \text{cov}(a, \ln[b_i]).$$

Because estimates of the second and third terms were not available, we used the delta method (Rao 1965, Oehlert 1992, White 1998) to define the variance of d_i in terms of the variance and covariance estimators of a and b_i . In general, the variance for the function of 2 random variables, such as $d_i = a - \ln(b_i)$, may be derived via

$$\text{var}(d_i) = \left(\frac{\partial d_i}{\partial \theta_j} \right) \cdot \Sigma \cdot \left(\frac{\partial d_i}{\partial \theta_j} \right)',$$

where θ_j is the j th random variable, $\left(\frac{\partial d}{\partial \theta_j}\right)$ is the row vector of partial derivatives with respect to θ_j , $\left(\frac{\partial d}{\partial \theta_j}\right)'$ is the column vector of partial derivatives with respect to θ_j , and Σ is the variance-covariance matrix of the θ_j (White 1998). In this case, $\theta_1 = a$ and $\theta_2 = b_i$. Thus, the variance of d_i is derived using

$$\text{var}(d_i) = \begin{bmatrix} \frac{\partial d_i}{\partial a} & \frac{\partial d_i}{\partial b_i} \end{bmatrix} \bullet \begin{bmatrix} \text{var}(a) & \text{cov}(a, b_i) \\ \text{cov}(a, b_i) & \text{var}(b_i) \end{bmatrix} \bullet \begin{bmatrix} \frac{\partial d_i}{\partial a} \\ \frac{\partial d_i}{\partial b_i} \end{bmatrix},$$

which reduces to

$$\text{var}(d_i) = \left(\frac{\partial d_i}{\partial a}\right)^2 \text{var}(a) + \left(\frac{\partial d_i}{\partial b_i}\right)^2 \text{var}(b_i) + 2\left(\frac{\partial d_i}{\partial a}\right)\left(\frac{\partial d_i}{\partial b_i}\right)\text{cov}(a, b_i).$$

Given $\frac{\partial d_i}{\partial a} = 1$ and $\frac{\partial d_i}{\partial b_i} = -\frac{1}{b_i}$, the variance of d_i is defined as

$$\text{var}(d_i) = \text{var}(a) + \frac{1}{b_i^2} \text{var}(b_i) - \frac{2}{b_i} \text{cov}(a, b_i),$$

where estimates for b_i , $\text{var}(a)$, $\text{var}(b_i)$, and $\text{cov}(a, b_i)$ are obtained from regression output.

After deriving estimators for d_i needed to parameterize its distribution for generating 1000 random values, we constructed a global linear regression model containing various physiographic, geophysical, and anthropogenic landscape variables (Table 1) that may have had important influences on maximum recruitment. Habitat data were standardized based on mean 0 and standard deviation 1 so that magnitude of regression coefficients could be interpretable across predictor variables. We also included a class variable, REGION (Table 1, Fig. 1), as a predictor based on preliminary modeling results where \hat{a}_i was the response variable.

Residual and normal probability plots were generated for the global model to check for any serious departures from the model assumptions for linear regression. If no serious departures were detected, we fit the set of class and habitat variables in regression models with \hat{d}_i as the response variable. SAS (SAS Institute, Inc. 1996) was used to generate 1000 \hat{d}_i values, fit these to each habitat model, and generate ΔAICc values, ΔAICc weights, estimated regression coefficients, and estimated standard errors.

We assessed statistical significance of predictor variables by whether the confidence intervals for their estimated regression coefficients contained 0, and biological importance by whether these intervals contained a range of values of a magnitude that could be considered ecologically meaningful (Yoccoz 1991, Gerard et al 1998). Because choice of confidence level is arbitrary, we computed 90%, 95%, and 99% confidence intervals (based on a t-statistic with $n - 1$ degrees of freedom) to display a range of confidence levels.

Results

The stock-recruitment model containing a common Ricker a was the only plausible model in our set of candidate models for our data. This was true regardless of inclusion or exclusion of pre-1974 spawner-recruitment data from John Day Middle Fork (Table 3). Therefore, we treated a and b_i estimates from this model as “true” estimates (i.e., no model-averaging was necessary). Interestingly, the model containing a_i (Eq. 6) was highly implausible in both cases.

Ricker a estimates were similar between common Ricker a models both with ($\hat{a}[\hat{SE}] = 1.74[0.39]$) and without ($\hat{a}[\hat{SE}] = 1.85[0.39]$) pre-1974 John Day Middle Fork data. Further, an x - y plot of b_i from both models closely followed a straight-line relationship, which indicated estimates were similar in size and ordering. Thus, we used estimates from the common Ricker a model with pre-1974 John Day Middle Fork data for generating the response variable (\hat{d}_i) for the habitat models (Table 4).

Residual and normal probability plots generated from the global landscape habitat model did not reveal any serious violations of assumptions underlying the linear regression model; hence, we assumed a linear regression model was appropriate for all subsets of the global model. The landscape model containing mean elevation, percent managed forests, and percent USFS low impact and wilderness areas, was the most plausible ($\Delta AICc = 0.37$) model, given the data, in the set of models (Table 5). However, 5 other models had $\Delta AICc$ values that were at least one-tenth of $\Delta AICc = 0.37$, including those containing mean annual precipitation, mean annual temperature, and geometric mean road density. Model-averaged parameter estimates for these 6 predictor variables showed statistically significant negative relationships between estimated maximum recruitment of spring/summer chinook salmon and both percent managed forest (95% level) and mean elevation (90% level) (Table 6). However, we felt only the 90% confidence interval associated with percent managed forests contained a range of values with magnitudes of biological importance. Thus, as percent managed forest increased, maximum recruitment (i.e., carrying capacity) of salmon decreased.

Discussion

There are several obvious shortcomings in our analyses. First, stocks used in our analyses were not a random sample from all possible stocks within the Interior Columbia River Basin, but rather included those stocks that had adequate numbers of fish and data to generate spawner-recruit data. Thus, inferences beyond our index streams are problematic. However,

analysis of boxplots generated by physiographic and geophysical variables from index areas revealed that they were mostly within the range of values for the lower Columbia, mid-Columbia, Snake regions (Fig. 1) as a whole. Therefore, based on landscape habitat variables, we assumed that index streams were representative of chinook spawning/rearing streams in the entire Interior Columbia River Basin.

Second, inferences based on landscape variables are obviously scale dependent. That is, inferences are limited to the scale of our predictor variables; localized physiographic, geophysical and anthropogenic variables that may be affecting maximum recruitment of chinook salmon may not be discernible at the landscape scale. Thus, a negative relationship between percent managed forests and maximum recruitment of chinook salmon should be interpreted relative to index stocks at the subwatershed level and across the Interior Columbia River Basin rather than applying it on a finer scale, such as attempting to draw conclusions based on percent managed forests along a particular stream reach.

Third, our estimates of maximum recruitment were not scaled by size of area containing a particular stock because there was not a strong correlation (Pearson correlation coefficient = 0.30) between maximum recruitment and length of perennial streams for each stock area. Unfortunately, we did not have estimates of the amount or percentage of spawning/rearing habitat (or quality therein) within areas containing each stock, and therefore we assumed that length of perennial streams was an adequate surrogate for this metric. Note that variables based on percent composition, like percentage managed forests, would be unaffected by scaling.

Despite their shortcomings, our analyses produced some interesting results. Given the level of uncertainty and noise inherent in our data, detecting any signal at all is in itself noteworthy. This lends support to the idea that, despite the uncertainty involved, broadscale analyses can be worthwhile. Beyond this, one of the more interesting of our results was that the stock-recruitment model containing a common Ricker a was the only plausible model for our data. This is surprising because of the apparent soundness of the biological rationale for using stock-specific Ricker a values, being a measure of fish production at low stock sizes, to help discern differences in spawning/rearing habitats across stocks of chinook salmon that are at historically low levels. However, previous analyses in which a values were used in the response variable in landscape habitat models indicated REGION (Table 1; Fig. 1) was the only variable that was statistically significant. This result implies that any differences in a values among stocks were overwhelmed by the uncertainty in the region effect. Conversely, REGION was not even contained in a plausible habitat model when maximum recruitment was the response variable. This contrast in results reinforces the importance of model selection to the overall modeling process. Given the implausibility of the stock-specific Ricker a model for these spawner-recruit data, we recommend maximum recruitment be used instead of a values in any PATH retrospective or prospective analysis of potential effects of broadscale habitat changes on productivity of spring/summer chinook in the 25 index stocks.

The negative relationship between maximum recruitment and percentage of forests with moderate to high intensity management status warrants consideration of forest management practices as a factor to be included in the PATH prospective analyses. However, a more rigorous, experimental management approach (Walters 1986, Walters 1997) is needed to better

understand broadscale effects of land management actions on spawning/rearing habitat of spring/summer chinook stocks. There is too much uncertainty associated with the life history patterns of anadromous salmon for us to expect a clear answer from correlative data, which is why an experimental management approach has been incorporated into the objectives of PATH (Marmorek and Peters 1998). Although this paper does not resolve uncertainties related to broadscale habitat features and production of spring/summer chinook, it does provide direction for future research that we hope will ultimately answer fundamental questions related to conservation of anadromous salmon in the Columbia River Basin.

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Table 1. Category, name, and description of landscape variables included in a set of linear regression models attempting to predict fish production for 25 index stocks of spring/summer chinook salmon within the Columbia River Basin. Physiographic, geophysical, and anthropogenic variables are at the HUC6 code (subwatershed) level (Lee et al. 1997). The term weighted indicates that the variable was weighted by spatial areas of the subwatersheds where a particular stock occurred, i.e., if the stream section stretched over more than one subwatershed.

Category	Variable Name	Description
Class	REGION ¹	<u>Name</u> Lower Columbia (LC)
		<u>Fourth Hydrologic Field (HUC4)</u> 17070101-17070106, 17070201-17070204, 17070301-17070307
		Mid-Columbia (MC) Snake (SN)
		17020001-17020016 17060101-17060107, 17060110, 17060201-17060210
Physiographic and Geophysical	WPPRECIP	Weighted mean annual precipitation (mm) (PRISM model; Daly et al. 1994)
	WMTEMP	Weighted mean annual temperature (°C)
	WELEV	Weighted mean elevation (m)
	WERO	Weighted surface erosion index
Anthropogenic	WGEODENS	Weighted geometric mean road density (mi/mi ²)
	MNG_FOR	Percent USFS and private forests with moderate to high impact management practices
	MNG_FW	Percent USFS low impact and wilderness areas

¹ See Fig. 1 for a graphical display of the three regions.

Table 2. Formula, number and name, and description of Ricker-type models composing the candidate set that were fitted with spawner-recruit data from 25 index stocks of spring/summer chinook salmon in the Columbia River Basin. Water transit time (WTT) is the number of days, on average, required for water to pass from the head of lower Granite Dam reservoir to Bonneville Dam during salmon spring migration (Deriso et al. 1996; Fig. 1). REGION is described in Table 1; all other terms in the equations are defined in the text.

Model Formula	Model Number and Name	Description
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - X - \mu_t + \varepsilon_{t,i}$	(1) Stock-specific Ricker a	Same as Eq. 6; in-river passage mortality is the actual number of dams encountered (X) plus μ_t .
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t - b_i S_{t,i} - X - \mu_t + \varepsilon_{t,i}$	(2) Common Ricker a	Same as Model (1) except Ricker a is assumed to be the same across all stocks, and is contained in the intercept term, β_0 .
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - X - \mu_t^* + \varepsilon_{t,i}$	(3) Stock-specific Ricker a , common μ_t	Same as Model (1) except the net dam passage mortality is assumed to be the same across all regions, μ_t^* .
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t - b_i S_{t,i} - m_{t,i} + \varepsilon_{t,i}$	(4) Common Ricker a , common μ_t	Same as Model (3) except Ricker a is assumed to be the same across stocks, and is contained in the intercept term, β_0 .
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - REGION * WTT + \varepsilon_{t,i}$	(5) Stock-specific Ricker a , REGION*WTT	Same as Model (1) except the in-river passage mortality is set equal to the interaction between region and water transit time.
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t - b_i S_{t,i} - REGION * WTT + \varepsilon_{t,i}$	(6) Common Ricker a , REGION*WTT	Same as Model (5) except Ricker a is assumed to be the same across stocks, and is contained in the intercept term, β_0 .
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - WTT + \varepsilon_{t,i}$	(7) Stock-specific Ricker a , common WTT	Same as Model (1) except the in-river passage mortality is set equal to the water transit time.
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t - b_i S_{t,i} - WTT + \varepsilon_{t,i}$	(8) Common Ricker a , common WTT	Same as Model (7) except Ricker a is assumed to be the same across stocks, and is contained in the intercept term, β_0 .

Table 3. Model description, AICc values, Δ AICc values, and Δ AICc weights for two sets of Ricker-type models generated with and without spawner-recruitment data of spring/summer chinook salmon from pre-1974 John Day Middle Fork. Δ AICc weights represent relative degree of plausibility for each model given the data.

Model	With pre-1974 John Day Middle Fork Data			Without pre-1974 John Day Middle Fork Data		
	AICc	Δ AICc	Δ AICc Weight	AICc	Δ AICc	Δ AICc Weight
Common Ricker a	2011.78	0	0.96	1970.60	0	>0.99
Stock-specific Ricker a , common μ_t	2018.13	6.35	0.04	1984.57	13.97	<0.01
Common Ricker a , common μ_t	2028.79	17.01	<0.01	1985.76	15.16	<0.01
Stock-specific Ricker a	2031.50	19.72	<0.01	1995.81	25.21	<0.01
Common Ricker a , REGION*WTT	2201.90	190.12	<0.01	2162.65	192.05	<0.01
Stock-specific Ricker a , REGION*WTT	2222.94	211.16	<0.01	2187.12	216.52	<0.01
Common Ricker a , common WTT	2252.84	241.06	<0.01	2208.92	238.32	<0.01
Stock-specific Ricker a , common WTT	2257.81	246.03	<0.01	2213.34	242.74	<0.01

Table 4. Name, region, and point estimates (estimated standard errors) for d_i , Ricker a , Ricker b_i , and covariance of Ricker a and b_i , as generated from the stock-recruitment model containing a common Ricker a , for 25 index stocks of spring/summer chinook salmon in the Columbia River Basin. Note that $\hat{d}_i = \hat{a} - \ln(\hat{b}_i)$, where $e^{\hat{d}_i-1}$ is the estimator of maximum recruitment for the i th stock.

Stock Name	Region	\hat{d}_i (\hat{SE}_i)	\hat{a} (\hat{SE})	\hat{b}_i (\hat{SE}_i) ¹	Côv(\hat{a}, \hat{b}_i) ¹
Bear Valley/Elk Creek	SN	8.97 (0.43)	1.74 (0.39)	0.74 (0.13)	-0.001
Big Sheep/Lick Creek	SN	7.31 (0.42)	1.74 (0.39)	3.88 (0.58)	-0.003
Catherine Creek	SN	8.53 (0.42)	1.74 (0.39)	1.14 (0.18)	-0.001
Entiat River	MC	7.98 (0.47)	1.74 (0.39)	1.99 (0.41)	-0.025
Grande Ronde River	SN	8.20 (0.43)	1.74 (0.39)	1.60 (0.30)	-0.002
Imnaha River	SN	8.87 (0.41)	1.74 (0.39)	0.81 (0.10)	-0.001
John Day Main Stem	LC	7.56 (0.38)	1.74 (0.39)	3.02 (0.53)	0.053
John Day Middle Fork	LC	8.07 (0.39)	1.74 (0.39)	1.81 (0.33)	0.026
John Day North Fork/Granite	LC	9.17 (0.38)	1.74 (0.39)	0.60 (0.10)	0.010
Johnson Creek	SN	7.76 (0.42)	1.74 (0.39)	2.47 (0.36)	-0.002
Klickitat River	LC	7.64 (0.38)	1.74 (0.39)	2.82 (0.63)	0.079
Lemhi River	SN	9.02 (0.43)	1.74 (0.39)	0.70 (0.12)	-0.0005
Lookingglass Creek	SN	7.71 (0.42)	1.74 (0.39)	2.59 (0.43)	-0.002
Lostine River	SN	7.80 (0.44)	1.74 (0.39)	2.83 (0.47)	-0.003
Marsh Creek	SN	8.32 (0.43)	1.74 (0.39)	1.42 (0.26)	-0.001
Methow River	MC	9.66 (0.52)	1.74 (0.39)	0.38 (0.11)	-0.007
Minam River	SN	8.43 (0.42)	1.74 (0.39)	1.26 (0.20)	-0.001
Poverty Flat	SN	8.81 (0.42)	1.74 (0.39)	0.86 (0.13)	-0.0005
Secesh River/Lake Creek	SN	7.52 (0.42)	1.74 (0.39)	3.14 (0.48)	-0.002
Sulphur Creek	SN	8.00 (0.43)	1.74 (0.39)	1.96 (0.36)	-0.002
Upper Big Creek	SN	7.39 (0.42)	1.74 (0.39)	3.58 (0.61)	-0.002
Upper Valley Creek	SN	7.51 (0.43)	1.74 (0.39)	3.19 (0.58)	-0.003
Warm Springs River	LC	9.98 (0.74)	1.74 (0.39)	0.33 (0.25)	0.028
Wenaha River	SN	8.84 (0.44)	1.74 (0.39)	0.84 (0.18)	-0.001
Wenatchee River	MC	9.72 (0.45)	1.74 (0.39)	0.35 (0.06)	-0.003

¹ Estimates should be divided by 1000 to adjust for rescaling of \hat{b}_i .

Table 5. Predictor variables, AICc values, Δ AICc values, Δ AICc weights, and proportions of largest weight for the set of candidate models attempting to link maximum recruitment of spring/summer chinook salmon with landscape variables. AICc-related values were averaged over 1000 models from 1000 randomly-generated response variables (i.e., \hat{d}_i). Δ AICc weights represent degree of plausibility of each model given the data. Proportion of a given model Δ AICc weight to the largest one was used as a guideline for selecting which predictor variables (Table 1) to include in the composite model (Table 6).

Predictor Variables	AICc	Δ AICc	Δ AICc Weight (w_i)	Proportion of Largest w_i
WELEV, MNG_FOR, MNG_FW	65.27	0	0.37	1.00
WELEV, WGEODENS, MNG_FOR, MNG_FW	67.51	2.24	0.12	0.32
WPRECIP, WELEV, MNG_FOR, MNG_FW	67.54	2.27	0.12	0.32
MNG_FOR, MNG_FW	68.00	2.73	0.09	0.24
WMTEMP, WELEV, WGEODENS	68.53	3.26	0.07	0.19
WPPRECIP, WELEV	69.27	4.00	0.05	0.14
WPPRECIP, WMTEMP	69.96	4.69	0.03	0.08
REGION	69.97	4.70	0.03	0.08
WGEODENS	70.22	4.95	0.03	0.08
WPPRECIP, WERO, MNG_FOR	70.40	5.13	0.03	0.08
WPPRECIP, WERO	71.21	5.94	0.02	0.05
REGION, WGEODENS	71.41	6.14	0.02	0.05
WPPRECIP, WMTEMP WELEV, WERO	73.34	8.07	<0.01	<0.01
WPPRECIP, WERO, WGEODENS	73.52	8.25	<0.01	<0.01
WPPRECIP, WERO, WGEODENS, MNG_FOR	73.64	8.37	<0.01	<0.01
REGION, WPPRECIP, WMTEMP, WELEV, WERO, WGEODENS, MNG_FOR, MNG_FW (Global Model)	88.79	23.52	<0.01	<0.01

Table 6. Model-averaged estimate of standardized regression coefficient and standard error, and lower and upper limits of various confidence intervals for parameters contained in one or more candidate models (Table 5) with ΔAICc weights within more than 10% of the largest ΔAICc weight. Confidence intervals not containing 0 are statistically significant at the associated level of confidence.

Model Parameter	Stdzed. Regr. Coeff.	Std. Error	90% CI		95% CI		99% CI	
			Lower Limit	Upper Limit	Lower Limit	Upper Limit	Lower Limit	Upper Limit
INTERCEPT	8.34	0.16	8.07	8.61	8.01	8.67	7.89	8.79
WPPRECIP	-0.17	0.18	-0.48	0.14	-0.54	0.20	-0.67	0.33
WMTEMP	0.13	0.31	-0.40	0.66	-0.51	0.77	-0.74	1.00
WELEV	-0.38	0.19	-0.71	-0.05	-0.77	0.01	-0.91	0.15
WGEODENS	-0.25	0.23	-0.64	0.14	-0.72	0.22	-0.89	0.39
MNG_FOR	-0.51	0.22	-0.89	-0.13	-0.96	-0.06	-1.13	0.11
MNG_FW	-0.24	0.22	-0.62	0.14	-0.69	0.21	-0.86	0.38