A TWO-STAGE INFORMATION-THEORETIC APPROACH TO MODELING LANDSCAPE-LEVEL ATTRIBUTES AND MAXIMUM RECRUITMENT OF CHINOOK SALMON IN THE COLUMBIA RIVER BASIN

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ABSTRACT. Many anadromous salmonid stocks in the Pacific Northwest are at their lowest recorded levels, which has raised questions regarding their long-term persistence under current conditions. There are a number of factors, such as freshwater spawning and rearing habitat, that could potentially influence their numbers. Therefore, we used the latest advances in information-theoretic methods in a two-stage modeling process to investigate relationships between landscape-level habitat attributes and maximum recruitment of 25 index stocks of chinook salmon (*Onocorhynchus tshawytscha*) in the Columbia River basin. Our first-stage model selection results indicated that the Ricker-type, stock recruitment model with a constant Ricker a, i.e., recruits-per-spawner at low numbers of fish) across stocks was the only plausible one given these data, which contrasted with previous unpublished findings. Our second-stage results revealed that maximum recruitment of chinook salmon had a strongly negative relationship with percentage of surrounding subwatersheds categorized as predominantly containing U.S.

Forest Service and private moderate-high impact managed forest. That is, our model predicted that average maximum recruitment of chinook salmon would decrease by at least 247 fish for every increase of 33% in surrounding subwatersheds categorized as predominantly containing U.S. Forest Service and privately managed forest. Conversely, mean annual air temperature had a positive relationship with salmon maximum recruitment, with an average increase of at least 179 fish for every increase in 2°C mean annual air temperature.

KEY WORDS: Akaike's Information Criterion, Chinook salmon, model averaging, *Oncorhynchus tshawytscha*, Ricker model, stock-recruitment.

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 fisheries (Nehlsen et al. [1991]). 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]). 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.
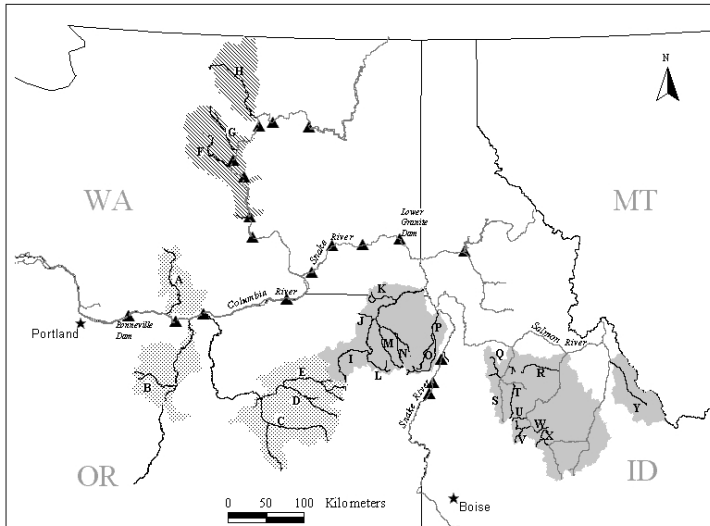
Quality and condition of freshwater habitats may affect productivity in salmonids (Hunt [1969], Scarnecchia and Bergersen [1987], Heggenes and Borgstrom [1991]), which in turn would affect their long-term persistence. However, to our knowledge, relationships between large-scale habitat/land management attributes and productivity in anadromous salmon stocks have never been rigorously quantified in the published

literature, particularly at the spatial scale of the Columbia River basin. Previous broadscale assessments of salmonid stocks in this region have been mostly 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 empirical data and status calls from experts) and landscape-level habitat variables. Schaller et al. [1999] modeled productivity and survival rates of spring-summer chinook salmon within the Columbia River basin.

Here, we applied the latest advances in information-theoretic modeling (Burnham and Anderson [1998]) to existing data sets to investigate potential relationships between various landscape-level attributes and estimates of maximum recruitment of 25 index stocks of spring/summer chinook salmon within the Columbia River Basin. Because this information-theoretic approach is probably unfamiliar to most ecologists and other natural resource professionals, an important objective of this paper is to describe and illustrate this modeling procedure. Note that the information-theoretic approach has general relevance to statistical modeling situations well beyond the application described herein.

2. Modeling approach. We employed a two-step modeling process to evaluate relationships between landscape-level attributes and fish productivity in 25 index stocks of spring-summer chinook salmon within the Columbia River basin (Figure 1). The first set of models were Ricker-type, stock-recruitment models (Ricker [1975]). Parameter estimates from these models were used in a response variable for a second set of second-stage models, which contained landscape-level predictor variables (Table 1). In the following, we describe our methodological approaches for each modeling step, including the latest information-theoretic (Akaike [1973], Burnham and Anderson [1998]) model selection and model-averaging techniques that we adapted for our needs.

2.1 Developing a set of candidate models. A crucial step in the modeling process is the construction of a set of candidate models

FIGURE 1. Location of 25 index stocks of spring/summer chinook salmon in the Columbia River basin that provided stock-recruitment data used in our analyses. Stocks are categorized by region, where the stippled area contains lower Columbia stocks (A–E), the cross-hatched area contains mid-Columbia stocks (F–H) and the gray area contains snake stocks (I–Y). Main stem dams are shown as triangles, with Bonneville Dam and Lower Granite Dam labeled to illustrate water transit time (WTT).

A	Klickitat River	I	Grande Ronde River	Q	Secesh River/Lake Creek
B	Warm Springs River	J	Lookingglass Creek	R	Upper Big Creek
C	John Day Mainstem	K	Wenaha River	S	Poverty Flat
D	John Day Middle Fork	L	Catherine Creek	T	Johnson Creek
E	John Day North Fork/Granite	M	Minam River	U	Sulphur Creek
F	Wenatchee River	N	Lostine River	V	Bear Valley/Elk Creek
G	Entiat River	O	Big Sheep/Lick Creek	W	Marsh Creek
H	Methow River	P	Imnaha River	X	Upper Valley Creek
				Y	Lemhi River

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 Section 2.4 Stock-recruitment models). For the landscape-level 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-level variables (Table 1) that may have

TABLE 1. Category, name and description of landscape-level variables initially included in a set of linear regression models attempting to predict maximum recruitment of 25 index stocks of spring/summer chinook salmon in their spawning/rearing area within the Columbia River basin.

Category	Variable Name	Description
Class		
	REGION	Variable subdividing the Columbia River basin into three sections: lower Columbia (LC), mid-Columbia (MC) and Snake (SN). Each index stock, as denoted by stream name or section, was categorized based on these subdivisions (Figure 1).
Physiographic & Geophysical		
	WPPRECIP	*Weighted mean annual precipitation (mm) (PRISM model; Daly et al. [1994])
	WMTEMP	Weighted mean annual air temperature (°C)
	WELEV	Weighted mean elevation (m)
	WERO	Weighted surface erosion index
Anthropogenic		
	WGEODENS	Weighted geometric mean road density (km/km^2)
	MNG_FOR	Weighted percent of subwatersheds containing a spawning/rearing area that were predominantly categorized as U.S. Forest Service and private forests with moderate to high impact practices (i.e., logging and grazing; see text for details)
	MNG_FW	Weighted percent of subwatersheds containing a spawning/rearing area that were predominantly categorized as U.S. Forest Service managed wilderness areas (see text for details)
Area		
	ST_LNGTH	Kilometers (km) of perennial and intermittent streams within the spawning/rearing area of each index stock of spring/summer chinook salmon

Note: The term "weighted" indicates that the variable was weighted by spatial areas of the subwatersheds where the spawning/rearing area of a particular stock occurred, i.e., if the spawning/rearing area (ST_LNGTH) stretched over more than one subwatershed.

had important influences on maximum recruitment of spring/summer chinook salmon in their spawning/rearing areas. Because of the paucity of data ($n = 25$ observations) and hence the danger of over-fitting the model, we only used a relatively small number of predictor variables to construct the global model. From this set of predictors we generated a subset of models that contained various combinations of variables we deemed ecologically relevant based on results from Lee et al. [1997], our knowledge of the species and system, and consultations with subject experts familiar with the study area.

2.2 Model selection. We used the small sample adjustment of 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

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

where n is the number of observations, 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. Equivalently, AIC $= -2\ln(L(\hat{\theta}|\text{data})) + 2k$, where $\ln(L(\hat{\theta}|\text{data}))$ is the maximized log-likelihood over the unknown model parameters (θ) given the data (Buckland et al. [1997], Burnham and Anderson [1998]). When $n/k < 40$, Burnham and Anderson [1998] recommended Hurvich and Tsai's [1989] small sample adjustment to AIC,

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

Note that AICc converges to AIC as the number of observations increases relative to the number of estimable parameters in the model. In other words, as n increases relative to k in the second term in equation (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 ranking 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 (equation (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) (Burnham and Anderson [1998]). 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 recording these 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 Akaike 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 Akaike weight, w_i (Burnham and Anderson [1998]). This weight is calculated as

$$(3) \qquad w_i = \frac{e^{(-\Delta \mathrm{AICc}_i/2)}}{\sum_{j=1}^{R} e^{(-\Delta \mathrm{AICc}_j/2)}},$$

where $\Delta \mathrm{AICc}_i$ is the $\Delta \mathrm{AICc}$ value for the ith model in a set of R 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.

2.3 Model-based inference. We incorporated model selection uncertainty into model inference as generally described by Burnham and Anderson [1998]. We did not select a single model from a candidate set and treat it as the "true" model unless its Akaike weight was at least eight times larger than the next highest weight (our modification). That is, we viewed the predictor variables contained in models whose Akaike weights were more than one-eighth of the largest Akaike weight as forming a composite model whose parameter estimates were computed based on the ΔAICc-weighted average of estimates from relevant models. Following from likelihood-based inference (Edwards [1992], Royall [1997]), Akaike weights correspond to strength of evidence of one model versus another, i.e., $L(M_i \mid \text{data})/L(M_B \mid \text{data})$, where M_i refers to the ith model and M_B refers to the "best" model (Burnham and Anderson [1998, pp. 128–129]). Our strength of evidence metric, $1/8$, was recommended by Royall [1997] as a general cutoff point.

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

$$(4) \qquad \hat{\bar{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i,$$

where $\hat{\beta}_i$ is the estimator of a regression coefficient for a specific predictor variable in model i and w_i is the Akaike weight that is calculated from the ΔAICc values for the R 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-eighth 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., $\hat{\bar{\beta}}$) for X_1 would only be based on ΔAICc values calculated from the $R = 3$ 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, vâr $(\hat{\beta})$; Buckland et al. [1997]) is calculated as

$$
(5) \qquad \text{vâr}\,(\hat{\beta}) = \left[\sum_{i=1}^{R} w_i \sqrt{\text{vâr}\,(\hat{\beta}_i \mid M_i) + (\hat{\beta}_i - \hat{\bar{\beta}})^2} \; \right]^2,
$$

where vâr $(\hat{\beta}_i \mid M_i)$ is the conditional variance (i.e., the square of the standard error for the regression coefficient in regression output) of model i and $(\hat{\beta}_i - \hat{\bar{\beta}})^2$ is the variance component due to model selection uncertainty. The w_i were computed based on the R models as described above. Technically, estimators should have been perfectly correlated for equation (5) to be used so that there would be no covariance term (Buckland et al. [1997]); however, based on extensive simulations, reasonable results can be obtained for a correlation between 0.5 and 1 (K.P. Burnham, CO Cooperative Fish and Wildlife Research Unit, Fort Collins, CO, [pers. comm.]).

2.4 Stock-recruitment models. A commonly used approach to modeling the relationship between fishery stock size (spawners) and number of recruits is the Ricker model (Ricker [1975]). One form of this model (Ricker [1975, p.283]) is

$$
(6) \qquad R = Se^{a-bS},
$$

where R is number of recruits, S is number of spawners, e^a (where a is Ricker a) is the slope of the Ricker curve near 0, (Figure 2a) and the inverse of b (i.e., Ricker b) is the maximum level of recruitment (Figure 2b). A natural logarithm transformation often is applied to equation (6) for ease of use, which yields $\ln R = \ln S + a - bS$.

Deriso et al. [1996] evaluated a set of Ricker-type models modified from equation (6) to develop a simple stock-recruitment model for estimating factors affecting survival of 13 index stocks of spring/summer chinook salmon in the Columbia River basin. They modified the basic Ricker model by adding various combinations of covariates representing in-river passage mortality of salmon traveling to the ocean and individual stream random effects. Estimates of spawners and recruits were generated by Beamesderfer et al. [1998] using run reconstruction methods (Starr and Hilborn [1988]). Numbers of spawners were estimated from redd counts, counts of live fish, and carcass counts, whereas
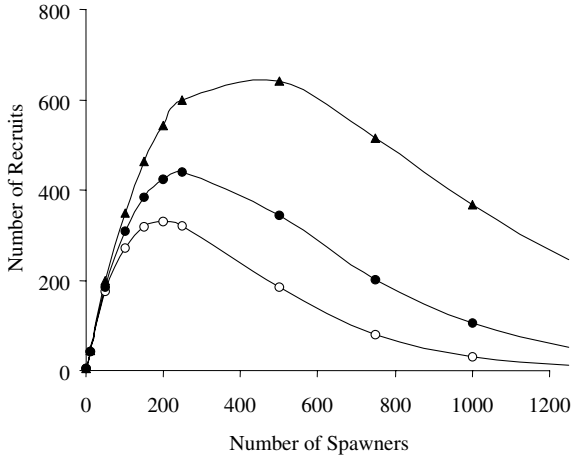
(a)
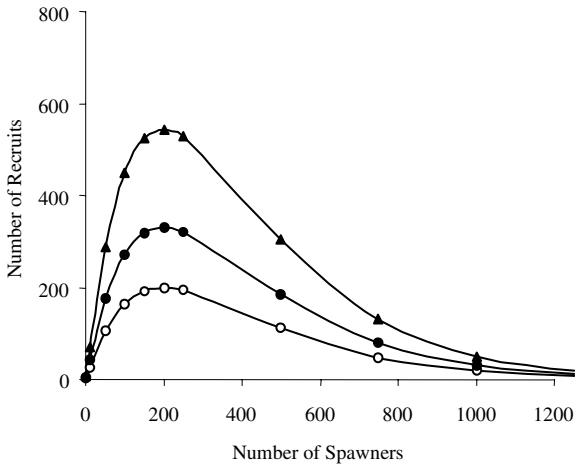
(b)

FIGURE 2 Effects of different Ricker a (slope near 0) and Ricker b (peak of curve) values on the Ricker stock-recruitment curve. (a) illustrates the effect of a constant Ricker b ($b=-.005$) and different values of Ricker a (open circle: $a = 1$; filled circle: $a = 1.5$; and triangle: $a = 2$) on the Ricker curve. (b) displays a constant Ricker a ($a=1.5$, which translates into 200 spawners) and different values of Ricker b (open circle: $b=0.005$; filled circle: $b=0.00375$; and triangle: $b=0.0025$).

numbers of recruits were returning fish measured to the mouth of the
Columbia River (Beamesderfer et al. [1998], Schaller et al. [1999]). Most
of the influences of hatchery fish on these spawner-recruit estimates for
each stock were assumed to be removed (Beamesderfer et al. [1998]).

Based on an AIC selection criterion, the best approximating model
chosen by Deriso et al. [1996] was the one with no spawner measurement
error and stock-specific Ricker a values,

$$(7) \qquad \ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t - b_i S_{t,i} - m_t + \varepsilon_{t,i},$$

where $R_{t,i}$ was the Columbia River observed spawning returns (recruit-
ment) for stock i during year t, $S_{t,i}$ was the observed spawners for stock
i during year t, a_i was the Ricker a parameter for stock i, b_i was the
Ricker b parameter for stock i, δ_t was the year-effect parameter for year
t, m_t was the in-river passage mortality during year t and $\varepsilon_{t,i}$ was the
multiplicative residual error (assumed to be distributed as $\mathbf{N}(0, \sigma_\varepsilon^2)$;
Deriso et al. [1996]). In this model, Ricker a contains the density-
independent sources of mortality for the various salmon life stages (fry
through adult), whereas the inverse of Ricker b reflects the maximum re-
cruitment of different spawning and rearing areas (Deriso et al. [1996]).
Note that equation (7) is the $\log_e$-transformed version of equation (6)
with additional subscripts for year t and stock i as well as δ_t, m_t and
$\varepsilon_{t,i}$ terms.

The year-effect parameter in equation (7) accounted for mortality fac-
tors affecting all stocks such as regional changes in terrestrial climate
and large changes in survival rates of chinook salmon in the marine en-
vironment; ocean conditions were assumed to be constant across stocks.
Although chinook salmon may spawn at ages 3, 4 or 5 years, Deriso et
al. [1996] assumed that inter-annual variation in ocean mortality was
limited to their first 2 years of life in the ocean (i.e., ocean survival
after age 4 is assumed constant).

As defined by Deriso et al. [1996], in-river passage mortality was
the sum of two components, $d \cdot X$ and μ_t. The first component
was a combination of the number of dams encountered by chinook
salmon during downstream migration (d), which differed depending
on year, and the dam passage mortality for each of these dams (X).
During recording years 1952–1969, d was the actual number of dams
encountered between the spawning/rearing area and the lowest dam in

the system (Bonneville Dam, Figure 1) inclusive (range = 1–9 dams), whereas during 1970–1990 it was the number of dams between John Day Dam and Bonneville Dam, i.e., 3. Splitting time intervals in this way was done because Deriso et al.'s [1996] original emphasis was on estimation of passage mortality of the Snake River stocks (Figure 1) since 1970.

The second component of in-river passage mortality was the net dam passage mortality, μ_t, from both the mid-Columbia and Snake River stocks to the John Day Dam during 1970–1990 (Deriso et al. [1996]). This net mortality included effects of dam passage across all life stages of chinook salmon. For example, in-river passage mortality through 1969 was based on the actual number of dams encountered by chinook salmon from each stock during downstream migration (i.e., 1–9 dams), whereas after 1969 it was based on the number of dams encountered between John Day Dam and Bonneville Dam (i.e., 3) *plus* the net dam passage mortality from the mid-Columbia and Snake River stocks to the John Day Dam. Note that the first component of in-river passage mortality, $d \cdot X$, assumed passage mortality was proportional to the number of dams encountered during downstream migration (Deriso et al. [1996]). Other models containing passage mortalities differing by year and dam were considered in other candidate models by Deriso et al. [1996], but results indicated that they were implausible relative to the model form of equation (7) containing the $(d \cdot X) + \mu$ representation of in-river passage mortality.

Two factors led us to revisit modeling results of Deriso et al. [1996]. First, spawner-recruit data from the John Day Middle Fork during 1959–1973 had an unusually large influence upon parameter estimates, including a_i, generated by the model in equation (7) (R. Hinrichsen, University of Washington, Seattle, WA [pers. comm]). 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 equation (7) still would be chosen as the best approximating model. Second, Beamesderfer et al. [1998] and R. Beamesderfer (Oregon Dept. of Fish and Wildlife, Portland, OR [pers. comm.]) provided spawner-recruit data for an additional 12 stocks (compared to 13 stocks available to Deriso et al. [1996]), which afforded us the opportunity to more rigorously evaluate the relative importance of the Ricker-type models. Consequently, we considered a set of 8

candidate Ricker-type models, including equation (7), and 7 others
that differed from equation (7) by the Ricker a term and the in-river
passage mortality term (Table 2; R. Deriso, Inter-American Tropical
Tuna Commission, San Diego, CA [pers. comm.]). We considered two
separate parameterizations of in-river passage mortality: 1) $(d \cdot X) + \mu_t$
described above and 2) number of days, on average, required for water
to pass from the head of lower Granite Dam reservoir to Bonneville
Dam (Figure 1) during salmon spring migration (water transit time;
Deriso et al. [1996]).

2.5 Landscape-level habitat models. Landscape-level data for
physiographic, geophysical and anthropogenic variables (Table 1) were
developed from variables at the subwatershed level of spatial scale,
which averaged about 7,800 ha within the Columbia River basin,
obtained from the Interior Columbia Basic Ecosystem Management
Project (Lee et al. [1997]). Because spawning/rearing areas typically
occurred in more than 1 subwatershed, landscape-level variables were a
weighted average based on spatial area of relevant subwatersheds. We
did not have data on amount of spawning/rearing habitat within each
subwatershed so we had to assume they shared equal amounts of this
habitat.

The two variables used to index land management practices (i.e.,
MNG_FOR and MNG_FW; Table 1) were generated from management
cluster variables from Lee et al. [1997, pp. 1130, 1132], in which they
assigned each subwatershed a predominant category from results of a
cluster analysis of variables representing land-type classification, man-
agement classification, ownership, percent grazed and percent wilder-
ness. We further pooled Lee et al.'s [1997] forest management categories
into a single category, U.S. Forest Service and private forests with mod-
erate to high impact management practices (i.e., logging and grazing;
referred to as managed forests). We then calculated a percentage of
each category (i.e., managed forests and wilderness areas), contained
in a spawning/rearing area as defined by the spatial areas of the rel-
evant subwatersheds. For instance, say the spawning/rearing area for
a stock was contained in 2 subwatersheds, one of which was twice as
large as the other, with the larger one categorized as managed forest
and the other as wilderness. In this case, the managed forest vari-
able, MNG_FOR, would be assigned 67% and the wilderness variable,

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.

Model Formula	Model Number and Name	Description
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t$ $- b_i S_{t,i} - m_t + \varepsilon_{t,i}$	(1) Stock-specific Ricker a	Same as equation (7); in-river passage mortality (m_t) is the sum of two terms: 1) actual number of dams encountered (d) times the passage mortality for each dam (X) and 2) net dam passage mortality from both mid-Columbia and Snake River stocks (μ_t).
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t$ $- b_i S_{t,i} - m_t + \varepsilon_{t,i}$	(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.
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t$ $- b_i S_{t,i} - m_t^* + \varepsilon_{t,i}$	(3) Stock-specific Ricker a, common μ_t	Same as Model (1) except the net dam passage mortality (μ_t^*) within the in-river passage mortality term (m_t^*) is assumed to be the same for the mid-Columbia and Snake regions
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t$ $- b_i S_{t,i} - m_t^* + \varepsilon_{t,i}$	(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.
$\ln R_{t,i} = \ln S_{t,i} + a_i$ $+ \delta_t - b_i S_{t,i}$ $- \text{REGION}^*\text{WTT} + \varepsilon_{t,i}$	(5) Stock-specific Ricker a, REGION*WTT	Same as Model (1) except the in-river passage mortality term (m_t) is replaced by the interaction between REGION and water transit time (WTT)

TABLE 2.   (Continued)

Model Formula	Model Number and Name	Description
$\ln R_{t,i} = \beta_0 + \ln S_{t,i}$ $+ \delta_t - b_i S_{t,i}$ $- \text{REGION*WTT} + \varepsilon_{t,i}$	(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
$\ln R_{t,i} = \ln S_{t,i} + a_i + \delta_t$ $- b_i S_{t,i} - \text{WTT} + \varepsilon_{t,i}$	(7) Stock-specific Ricker a, common WTT	Same as Model (1) except the in-river passage mortality term (m_t) is replaced by water transit time (WTT)
$\ln R_{t,i} = \beta_0 + \ln S_{t,i} + \delta_t$ $- b_i S_{t,i} - \text{WTT} + \varepsilon_{t,i}$	(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.

Note: 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], Figure 1). REGION is described in Table 1; all other terms in the equations are defined in the text.

MNG_FW, would be assigned 33%. Thus, these two variables represented a weighted percentage of categorical variables, which themselves were based on a predominant category for each subwatershed generated from a mixture of land-type classification, management classification, ownership, percent grazed and percent wilderness. Further, a third variable, not included in our analyses because of its linear dependence with MNG_FOR and MNG_FW (i.e., all 3 summed to 1) contained private and Bureau of Land Management rangeland and U.S. Forest Service moderate impact (grazed) forest and rangeland.

Because the stock-recruitment model containing common $\hat{a}$ values was the only plausible model given the data (see Section 3) we used the inverse of $\hat{b}_i$ (which is maximum recruitment) instead of $\hat{a}_i$ as a response variable in the second-stage, landscape-level habitat models. We also attempted to use the coefficient of variation of $\hat{b}_i$ as the response variable in a second set of second-stage models to account for the variability in $\hat{b}_i$ among index stocks; however, model diagnostics (see below) revealed a poorly fitting model and typical transformations

would have changed the model form so as to make results biologically uninterpretable. Therefore, we limited our second-stage models to those with point estimates of maximum recruitment as the response variable.

For the second stage of modeling, 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 of chinook salmon in their spawning/rearing areas. Choice of predictors was guided by results reported in Lee et al. [1997], our knowledge of the species and system, and consultations with experts familiar with the study area. We also included a class variable, REGION (Table 1, Figure 1), as a predictor based upon preliminary modeling results of the 25 index stocks by I. Parnell (ESSA Technologies, Ltd., Vancouver, BC [pers. comm.]) in which $\hat{a}_i$ was the response variable. Further, we included a covariate containing kilometers of perennial and intermittent streams (ST_LNGTH; Table 1) within the spawning/rearing area for each index stock to account for areal differences among stocks. Scaling $\hat{b}_i$ directly (i.e., dividing by ST_LNGTH) yielded a global model with severe heteroscedasticity as well as severe non-normality.

Variance inflation factors, studentized residual plots, and normal probability plots were generated by SAS PROC REG (SAS Institute, Inc. [1990]) to check for any serious departures from the model assumptions of linear regression. Predictor variables with variance inflation factors of 10 or more (Neter et al. [1985]) were dropped from the models. If there were no serious departures from underlying model assumptions, SAS PROC GENMOD and SAS programming code (SAS Institute, Inc. [1996]) were used to fit each habitat model and to generate ΔAICc values, Akaike weights, estimated regression coefficients and estimated standard errors.

We assessed statistical significance of a given predictor variable by whether the 95% confidence interval for its regression coefficient contained 0. When computing the 95% confidence intervals, we multiplied the estimated regression coefficients and standard errors of continuous variables by a scalar (c), which was based upon the sample standard deviation of each predictor and rounded to the nearest unit (i.e., $c \cdot \hat{\beta}_i \pm c \cdot t_{n-1,1-\alpha/2} \cdot \hat{S}E(\hat{\beta}_i)$); modified from Hosmer and Lemeshow [1989]. This made the magnitude of change in average maximum

recruitment more biologically meaningful and interpretable, i.e., rather than based on a single unit change. For instance, a change of 225 mm in mean annual precipitation is more biologically meaningful than a change of 1 mm. Because the true parameter can occur anywhere within the 95% confidence interval, given it is within the interval, we used the value at either the lower bound (positive coefficient) or the upper bound (negative coefficient) to judge biological importance of statistically significant predictors.

3. Results. In the first stage of modeling, 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 $\hat{b}_i$ from this model as the best estimate, i.e., no model-averaging was necessary. Ricker a estimates were similar between common Ricker a models both with ($\hat{a}[\hat{S}E] = 1.74[0.39]$) and without ($\hat{a}[\hat{S}E] = 1.85[0.39]$) pre-1974 John Day Middle Fork data. Further, a scatter plot of $\hat{b}_i$ 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 included for generating the response variable for the second-stage landscape models. Interestingly, the stock-recruitment model containing stock-specific a_i (equation (7)) was highly implausible in both cases. Also notable was inclusion of a dam effect in lieu of water transit time to estimate in-river passage mortality. Note that inclusion of a dam effect in this model indicated that this effect was removed from the $\hat{b}_i$ used as the response variable in the second stage of models.

In the second stage of modeling, mean elevation exhibited high multicollinearity (variance inflation factor = 13) and hence was dropped from all models. Residual and normal probability plots generated for the global model with mean elevation removed 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 (Burnham and Anderson [1998]).

TABLE 3. Model description, AICc values, ΔAICc values, and Akaike weights (w_i) 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. Akaike weights represent relative plausibility of each model given the data.

Model	With pre-1974 John Day Middle Fork Data			Without pre-1974 John Day Middle Fork Data		
	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
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

In the candidate set of landscape attribute models, the one composed of the weighted percent of subwatersheds containing a spawning/rearing area that were predominantly categorized as either U.S. Forest Service (USFS) and private forests with moderate to high impact management practices percent or USFS managed wilderness was the most plausible model, given the data (Akaike weight = 0.58; Table 4). However, 3 other models had Akaike weights that were at least one-eighth of 0.58. Therefore, we applied model averaging to produce a composite model, which displayed a reasonably strong correlation between observed and predicted maximum recruitment of spring/summer chinook salmon (Figure 3). Note, however, that the composite model's predictive ability was much more variable and hence less strong at lower observed maximum recruitment of salmon stocks, especially those below 500 fish. Two of the 9 stocks with observed maximum recruitment below 500 fish were in the lower Columbia region; both of these stocks were predicted to have about a 4 times larger maximum recruitment than

TABLE 4. Predictor variables, AICc values, ΔAICc values, Akaike weights (w_i) and proportions of largest weight for the set of candidate models linking maximum recruitment of spring/summer chinook salmon with landscape variables. Akaike weights represent degree of plausibility of each model given the data. Predictors contained in models whose proportions of the largest Akaike weight were at least 0.125 (1/8) were included in the composite model, Table 5.

| Predictor Variables	AICc	ΔAICc	w_i	Proportion of Largest w_i
MNG_FOR, MNG_FW, ST_LNGTH	390.06	0	0.58	1.00
WMTEMP, WGEODENS, ST_LNGTH	392.21	2.15	0.20	0.34
WPPRECIP, MNG_FOR, MNG_FW, ST_LNGTH	393.75	3.69	0.09	0.16
WGEODENS, MNG_FOR, MNG_FW, ST_LNGTH	393.75	3.69	0.09	0.16
WPPRECIP, WMTEMP, WERO, WGEODENS, ST_LNGTH	398.28	8.22	0.01	0.02
WPPRECIP, WERO, MNG_FOR, ST_LNGTH	398.88	8.82	0.01	0.02
ST_LNGTH	399.13	9.07	0.01	0.02
WGEODENS, ST_LNGTH	399.72	9.66	< 0.01	< 0.01
WPPRECIP, WMTEMP, ST_LNGTH	401.68	11.62	< 0.01	< 0.01
WPPRECIP, ST_LNGTH	401.74	11.68	< 0.01	< 0.01
WPPRECIP, WERO, WGEODENS, MNG_FOR, ST_LNGTH	403.07	13.01	< 0.01	< 0.01
WPPRECIP, WERO, ST_LNGTH	404.27	14.21	< 0.01	< 0.01
REGION, ST_LNGTH	404.80	14.74	< 0.01	< 0.01
REGION, WPPRECIP, WMTEMP, WERO, WGEODENS, MNG_FOR, MNG_FW, ST_LNGTH (Global Model)	405.36	15.30	< 0.01	< 0.01
WPPRECIP, WERO, WGEODENS, ST_LNGTH	405.38	15.32	< 0.01	< 0.01
REGION, WGEODENS, ST_LNGTH	406.51	16.45	< 0.01	< 0.01
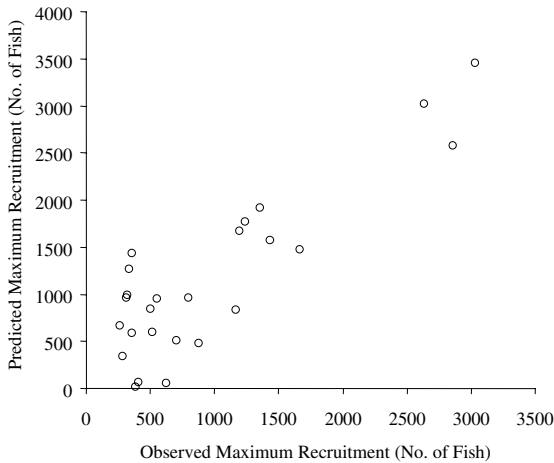
FIGURE 3. Plot of observed versus predicted values of maximum recruitment of 25 index stocks of spring/summer chinook in their spawning/rearing areas within the Columbia River basin.

was observed. The remaining 7 stocks were from the Snake River region and 5 of these were predicted to be about 1.2 to 3 times larger maximum recruitment than was observed.

Model-averaged results indicated statistically significant relationships between estimated maximum recruitment of spring/summer chinook salmon and mean annual air temperature, weighted percent of sub-watersheds predominantly categorized as either USFS and privately managed forests or USFS managed wilderness lands, and length of streams within the spawning/rearing area (Table 5). However, only mean annual air temperature, weighted percent of subwatersheds predominantly categorized as USFS and privately managed forests, and length of streams within the spawning/rearing area had lower or upper bounds of a magnitude that could be considered biologically important. We deemed the average change in maximum recruitment predicted for weighted percent of USFS managed wilderness lands (i.e., at least 61 fish) to be of marginal importance relative to these other three predictors.

Both mean annual air temperature and length of streams within the spawning/rearing area were positively related to predicted maximum recruitment of spring/summer chinook salmon in their spawning/rearing areas (Figures 4 and 5). Index stocks in areas with mean
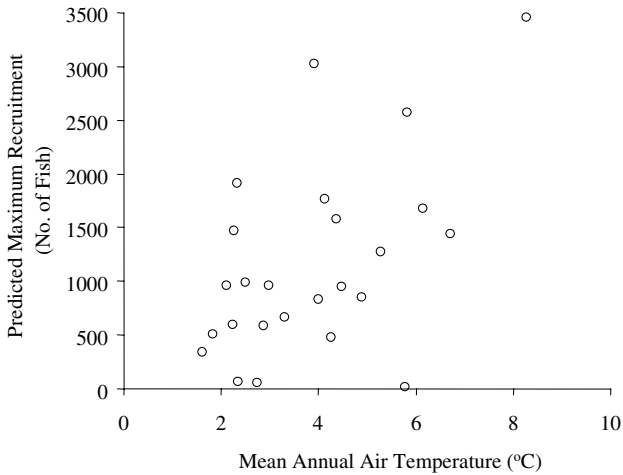
FIGURE 4. Mean annual air temperature ($^{\circ}$C) and predicted values of maximum recruitment of 25 index stocks of spring/summer chinook in their spawning/rearing areas within the Columbia River basin.
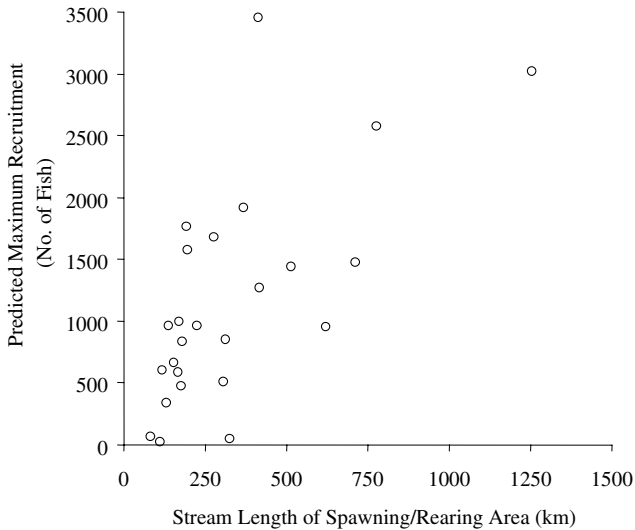

FIGURE 5. Kilometers of perennial and intermittent streams within spawning/rearing areas and predicted values of maximum recruitment of 25 index stocks of spring/summer chinook within the Columbia River basin.

TABLE 5. Model-average results for the composite model linking
maximum recruitment of spring/summer chinook salmon
spawning/rearing areas with various landscape-level variables.

Model Parameter	Model-Averaged Regression Coefficient ($\hat{SE}$)	Scalar (c)	Scaled Regression Coefficient	95% Confidence Interval Lower Bound	Upper Bound
Intercept	1104.63 (703.27)	–	–	–	–
WPPRECIP	-0.15 (0.55)	225	-33.75	-290.10	222.60
WMTEMP	238.32 (71.88)	2	476.64	179.92	773.36
WGEODENS	-195.39 (145.05)	1	-195.39	-494.78	104.00
MNG_FOR	-15.28 (3.77)	33	-504.24	-760.95	-247.53
MNG_FW	-10.81 (4.33)	33	-356.73	-651.66	- 61.80
ST_LNGTH	1.92 (0.39)	250	480.00	278.24	681.76

Note: The scalar (c) was based on the sample standard deviation of the predictor
variable (rounded to the nearest unit) and was applied to make the magnitude of
change in average maximum recruitment more biologically meaningful; the formula
for the 95% confidence interval was $c \cdot \hat{\beta}_i \pm c \cdot t_{24,0.975} \cdot \hat{SE}(\hat{\beta}_i)$ (modified from
Hosmer and Lemeshow [1989]). Scalars for MNG_FOR and MNG_FW were set to
the same value to facilitate comparison between them.

annual air temperatures less than 3°C tended to have predicted maxi-
mum recruitment of 1000 fish or less, whereas those in areas with tem-
peratures above 5°C tended to have predicted maximum recruitment
of more than 1000 fish (Figure 4). Our composite model predicted that
average maximum recruitment would increase by at least 179 fish for
every increase in 2°C mean annual air temperature, whereas it would
increase by at least 278 fish for every increase in 250 km of streams
within the spawning/rearing area (Table 5).

Weighted percent of subwatersheds predominantly categorized as
USFS and privately managed forests was negative related to predicted
maximum recruitment. Predicted maximum recruitment was more
variable at low percentages and less variable at higher percentages
(Figure 6). Further, there was not a strong regional effect, whereas
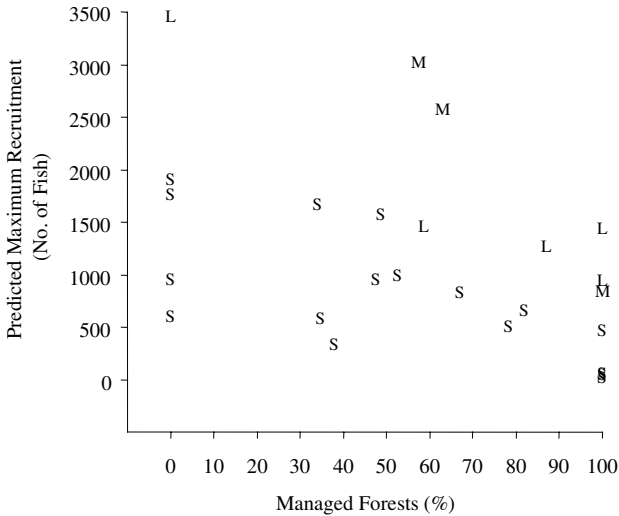
FIGURE 6. Weighted percent of surrounding subwatersheds categorized as predominantly containing U.S. Forest Service and private forests with moderate to high impact management practices and predicted values of maximum recruitment of 25 index stocks of spring/summer chinook in their spawning/rearing areas with the Columbia River basin. Letters refer to the lower Columbia (L), mid-Columbia (M), and Snake (S) regions.

there was one evident in the plot of predictive values for weighted percent of USFS managed wilderness lands (Figure 7). Our composite model predicted that average maximum recruitment of spring/summer chinook in their spawning/rearing areas would decrease by at least 247 fish for every increase in 33% in surrounding subwatersheds categorized as predominantly containing USFS and privately managed forest.

4. Discussion. In contrast to traditional model selection methods based on null hypothesis testing (e.g., backward, forward, and stepwise selection procedures), the information-theoretic approach employed in this paper has a firm statistical foundation in both likelihood and information theory (Burnham and Anderson [1998]). Moreover, recent advances in model averaging allow incorporation of model selection uncertainty into parameter estimates as well as multi-model inference, which is useful when no single model is clearly better than all other candidate models. Our modeling situation presented additional obstacles because of its two-stage nature, i.e., output from the stock-recruitment
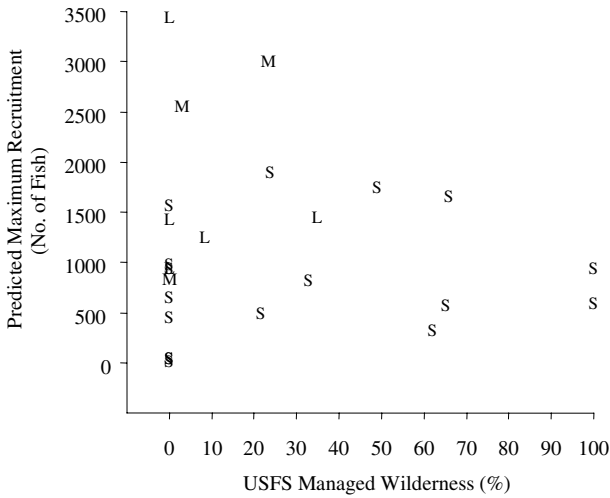
FIGURE 7. Weighted percent of surrounding subwatersheds categorized as predominantly containing U.S. Forest Service managed wilderness areas and predicted values of maximum recruitment of 25 index stocks of spring/summer chinook in their spawning/rearing areas with the Columbia River basin. Letters refer to the lower Columbia (L), mid-Columbia (M), and Snake (S) regions.

models were used as the response variable for the landscape attribute models. Thus, we applied information-theoretic methods separately to both sets of models but were unable to account for the uncertainty in estimates of maximum recruitment. Perhaps a better, but uninvestigated, alternative would have been to compute a single set of model selection criteria and Akaike weights based on both stages of models; this could be a topic for future research.

The importance of applying an information-theoretic, model selection approach to a set of candidate models was particularly evident in our stock-recruitment model results. That is, the stock-recruitment model containing a common Ricker a was the only plausible model for these data. This is somewhat surprising because of the apparent soundness of the biological rationale for using stock-specific Ricker a values, being a measure of fish productivity at low stock sizes, to help discern differences in spawning/rearing habitats across stocks of chinook salmon that are at their lowest recorded levels. However, there apparently was not a strong enough signal contained in these a_i to warrant inclusion of an additional 24 parameters into the model.

Another important result of our analyses was simply that we were able to detect a signal in the data, which is noteworthy given its inherent level of noise. This lends support to the idea that, despite the uncertainty involved, analyses of broadscale data can be worthwhile. It is not surprising that kilometers of perennial and intermittent streams in spawning/rearing areas would exhibit a strong positive relationship with maximum recruitment. One would expect that, on average, more stream habitat would result in more fish. More notable is the negative relationship between maximum recruitment of chinook salmon and weighted percent of surrounding subwatersheds categorized as predominantly containing USFS and private forests with moderate to high impact management practices (i.e., managed forests). Because these results are based on correlative data, our interpretations are necessarily speculative. Nonetheless, based on findings from previous studies, it seems reasonable that logging (and associated road building) and grazing practices could increase fine sediment inputs into nearby streams (Platts et al. [1989], Myers and Swanson [1995]) and hence increase stream turbidity and reduce extent and quality of spawning habitat by filling interstitial spaces in the spawning gravel (Chapman [1988]). Increased turbidity will decrease penetration of light and has been linked to decreased primary and secondary production as well as decreased fish production (Lloyd et al. [1987]).

Timber harvest also could reduce maximum recruitment of chinook salmon in their spawning/rearing habitats over time by adversely affecting quantity and quality of large woody debris (Ralph et al. [1994], Hauer et al. [1999]), which is an important component of salmonid stream habitat (Lisle [1986], Cederholm et al. [1997]). Although clear-cutting a forest stand may create an initial pulse of large woody debris into a nearby stream system (Murphy et al. [1986]), the lack of large trees for recruitment into the stream as woody debris in the near future would reduce the long-term habitat quality and hence maximum recruitment of salmonids (Andrus et al. [1988], Murphy and Koski [1989], Connolly and Hall [1999]).

In contrast to managed forests, mean annual air temperature was positively related to maximum recruitment. Increased temperatures may be associated with increased primary production in streams and thereby increased food available to young fish rearing in those areas and increased maximum recruitment.

Although we deemed it to be of marginal biological importance, the negative relationship between weighted percent of surrounding subwatersheds categorized as predominantly containing wilderness and maximum recruitment of chinook salmon may seem counterintuitive and therefore deserves comment. That is, one might expect spawning/rearing streams within wilderness areas to be essentially unaffected by human influence and therefore support higher numbers of fish than streams within managed forests. A possible reason why this may not be the case is that wilderness areas in the Columbia River basin are typically located at higher elevations and contain headwater streams with relatively low productivity. For instance, Scarnecchia and Bergersen [1987] reported an inverse relationship between elevation and stream production. Inspection of the plot of percent wilderness area versus predicted values (Figure 7) reveals an apparent regional effect; higher percentages of wilderness area are associated with index stocks in the Snake region. Subwatersheds containing index stocks within the Snake region have a higher mean elevation (1857m$\pm$77 [$\hat{S}E$]) than those in either the lower Columbia (1285m$\pm$176) or mid-Columbia (1176m$\pm$56) regions. Lower stream productivity is exacerbated further by much reduced inputs of nutrients from low numbers of spawning adults, which are considerably lower than previously recorded levels, particularly in the Snake region. Salmon carcasses likely played a key role in supporting and maintaining these stream systems historically (Bilby et al. [1998], Wipfli et al. [1998], Cederholm et al. [1999]). In addition, as mentioned previously, the correlative nature of the data prohibited us from drawing conclusions regarding cause and effect relationships between landscape-level attributes and maximum recruitment of chinook salmon. Such conclusions would have required field experimentation or an experimental management approach (Walters [1986]) at a broad scale. In the case of weighted percent of subwatersheds predominantly categorized as wilderness, we cannot be sure if the observed negative relationship is due to this variable or another single or set of variables correlated with it (e.g., mean elevation). Thus, there is potential for confounding that cannot be adjusted for due to the nature of the data.

The lower predictive ability of our composite model at lower observed maximum recruitment values probably indicated that variables other than those included in this model were important for predicting lower maximum recruitment of chinook salmon in their spawning/rearing

areas. Unfortunately, these are also the stocks of greatest interest because they are the ones whose continued persistence is particularly in doubt.

When considering our results, one should keep in mind that inferences based on landscape-level 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. For instance, a negative relationship between the managed forest variable and maximum recruitment of chinook salmon should be interpreted relative to index stocks at the subwatershed level and across the Columbia River basin rather than applying it on a finer scale, such as attempting to apply our results to a particular stream reach.

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