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A Model-Based Assessment of the Potential Response of Snake River Spring–Summer Chinook Salmon to Habitat Improvements

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Abstract.—The current recovery strategy for threatened Snake River Chinook salmon *Oncorhynchus tshawytscha* relies heavily on improvements to the quality of freshwater spawning and rearing habitat; however, the potential survival benefit from these actions is unknown. To address this issue, we created a model for predicting the early freshwater survival rates (egg to smolt) of this species as a function of five easily measured physical habitat variables and used this model to evaluate survival rates under five alternative future habitat states. Model validation showed that the predictions were reasonably accurate for individual stocks as well as for the trend in predictions across stocks. The results for the future habitat scenarios suggest that the potential for improving survival rates through habitat restoration is high for a few populations and low to nonexistent for most others while the potential for reduction in survival rates due to reduced habitat quality is great for all populations. The effects of modeled egg-to-smolt survival rate changes should be evaluated across the entire Chinook salmon life cycle to assess recovery potential.

Snake River spring–summer Chinook salmon *Oncorhynchus tshawytscha* were listed as a threatened evolutionarily significant unit of Pacific salmon under the Endangered Species Act in 1992 due to the decline in spawner numbers observed during the late 20th century (NMFS 1992). Habitat degradation, hydropower development, hatchery practices, and overharvest have all been implicated as causal factors in this decline (Fleming 1994; Lichatowich 1999), and efforts aimed at mitigating the effects of these factors have been numerous and costly (GAO 2002). In recent years, several model-based evaluations of restoration alternatives have been made by various combinations of state, tribal, and federal agency personnel (e.g., the Cumulative Risk Initiative [CRI; Kareiva et al. 2000] and the Plan for Analyzing and Testing Hypotheses [PATH; Peters and Marmorek 2001; Wilson 2003]), with the primary focus on the configuration of the Federal Columbia River Power System dams in the main-stem Snake and Columbia rivers.

While some modeling analyses predict that breaching four dams on the lower Snake River has a high probability of furthering the recovery of Chinook salmon, the potential for improving survival rates in other life stages in the absence of dam breaching remains less certain. The results of the PATH modeling analysis suggested that of the actions under consideration recovery options including dam breach have the highest probability of achieving recovery standards (Peters and Marmorek 2001). On the other hand, the CRI modeling forum concluded that recovery could be achieved without breaching Snake River dams but instead directing efforts at increasing survival rates through the early life stages via restoration of tributary habitats, where the spring–summer Chinook salmon (hereafter referred to as salmon unless indicated otherwise) spend more than a year of their life before going to sea (Kareiva et al. 2000; but see Wilson 2003). While the relative benefits to overall life cycle survival from main-stem and tributary actions remain unknown, the current recovery strategy relies heavily on improvements to tributary and estuary habitats in lieu of dam breach (Federal Caucus on Salmon Recovery 2000; NMFS 2000).

The future of salmon populations in the Snake River basin rests heavily on the efficacy of this recovery strategy, as all existing broodlines of spring–summer Chinook salmon have been fore-

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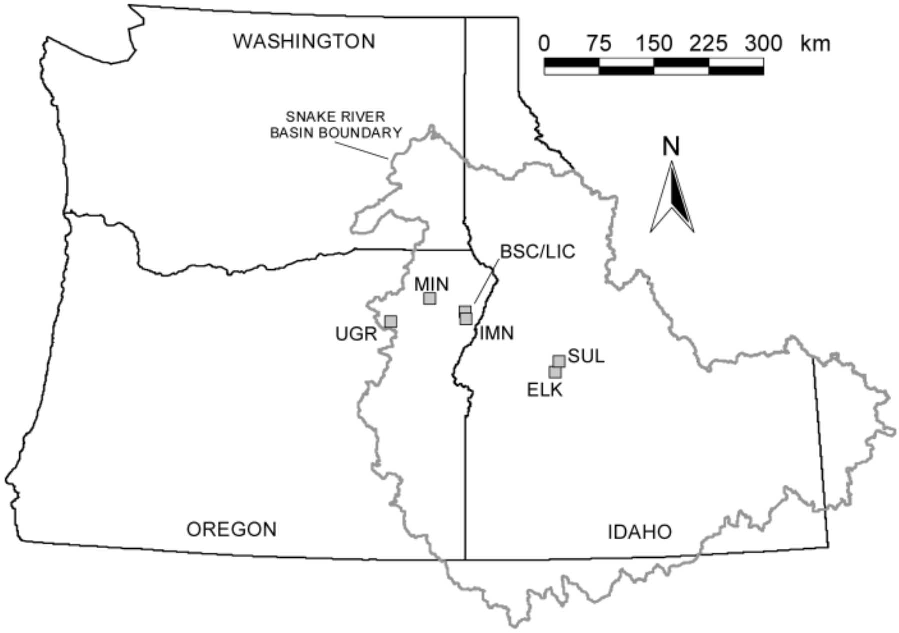

FIGURE 1.—Map of the Snake River basin showing the general locations of the index stock spawning and rearing streams used in this analysis. Abbreviations are as follows: ELK = Elk Creek, SUL = Sulphur Creek, MIN = Minam River, UGR = upper Grande Ronde River, BSC/LIC = Big Sheep and Lick creeks, and IMN = Imnaha River.

casted to be extinct as early as 2012 (Mundy 1999). This, coupled with the considerable amount of time required to realize the benefits of some habitat restoration efforts (e.g., channel changes resulting from the removal of livestock were not observed for 24 years in one stream; Kondolf 1993), demonstrate the importance of completing a field-based, quantitative assessment of the potential for improving early life stage survival rates based on the proposed habitat improvements. Such an evaluation could address the feasibility of achieving recovery under the current strategy and may provide a template for use in the prioritization of habitat restoration efforts. Our primary objective was to create a model that could be used in such an evaluation. To do this, we developed a simulation model that predicts egg-to-smolt survival rates as a function of simple physical habitat variables that (1) have strong survival rate linkages (i.e., are mechanistically explainable) and (2) are targeted for improvement under the Final Basinwide Salmon Recovery Strategy (Federal Caucus on Salmon Recovery 2000). Here we report on model development and validation as well as provide a relevant example of the use of our model to inform decisions on recovery plans for Snake River salmon.

Methods

Study site.—The Snake River Basin covers a large area characterized by a great diversity of geologic, climatic, habitat, and land management conditions. To best capture this diversity, we selected a subset of six indicator stocks for both field sampling and modeling efforts. These index stocks are associated with long-term data sets (nearly 50 years in most cases) on population trends and for this reason have been used in previous modeling assessments (e.g., Kareiva et al. 2000; Peters and Marmorek 2001). For our purposes, we selected a subset of index stocks based on general habitat quality (summarized in Beamesderfer et al. 1997) and the availability of survival rate data; thus, we included streams that were greatly impacted by past and present land management activities as well as those that are nearly ''pristine.'' Field habitat and survival rate data were collected for six index stocks, namely, those from the upper Grande Ronde River (UGR), Big Sheep Creek and Lick Creek combined (BSC–LIC), the Imnaha River (IMN), Elk Creek (ELK), Sulphur Creek (SUL), and the Minam River (MIN) (Figure 1).

Reported habitat quality varies considerably between and within the six streams selected for study.

TABLE 1.—Summary of spawning and rearing index watershed characteristics for Snake River spring–summer Chinook salmon stocks used in modeling efforts.

Index population	Ecoregion[a]	Dominant geology[b]	Management status[c]	Management activities[d]	Ownership[e]	Habitat limitations[f]
Elk Creek	Northern Rockies	Intrusive igneous	Managed/wilderness	T*, M*, R, G*	Public	Sedimentation: roads and historic grazing (minor)
Sulphur Creek	Northern Rockies	Intrusive igneous	Wilderness	None	Public	None
Minam River	Blue Mountain	Intrusive igneous	Wilderness	T*, G	Public	None
Upper Grande Ronde River	Blue Mountain	Mixed	Managed	T, M*, R, I, G	Mixed	Sedimentation: mining and livestock grazing related (major); high summer temperatures: loss of riparian areas due to grazing
Big Sheep and Lick creeks	Blue Mountain	Mixed	Managed	T*, M*, R, I, G	Public	Sedimentation associated with roads (minor)
Imnaha River	Blue Mountain	Mixed	Managed/wilderness	T*, M*, R, I, G	Public	None: limited road impacts

[a] Omernik (1987).
[b] Categories assigned on the basis of data from Johnson and Raines' (1995) 1:500,000-scale geologic map of the interior Columbia River basin. Index watersheds classified as intrusive igneous were characterized by >50% granodiorite bedrock. All other streams were characterized by mixed proportions of extrusive igneous (primarily basalts of the Columbia River group), metamorphic, and sedimentary rocks. These categories were chosen largely because of differences in weathering and erosion patterns (i.e., granodiorite produces coarse-grained, highly erodible soils, while basaltic bedrock does not weather as readily and produces finer-grained soils).
[c] Management status refers to the current designation. A minimum presence of roads in the index portion of the watershed is required for a stream to be classified as managed; index watersheds with areas of designated wilderness and managed areas are classified as managed/wilderness.
[d] Activities are as follows: T = timber harvest, M = mining, R = road construction/presence, I = irrigation, and G = cattle grazing. An asterisk denotes that the activity has occurred in the past but not currently.
[e] Public ownership is largely by the U.S. Forest Service.
[f] Based on information reviewed in Beamesderfer et al. (1997).

Index areas that occur within designated wilderness areas, like SUL and MIN, are characterized by good habitat conditions, while those that have experienced greater anthropogenic disturbance, like ELK and UGR, are considered to have fair to poor quality habitat (Beamesderfer et al. 1997). Habitat problems reported for degraded index areas include, but are not limited to, excessive sedimentation (BNF 2000), elevated summer stream temperatures (ODEQ 1999), and the loss of pool habitats (McIntosh et al. 1994; McIntosh et al. 2000). For a more detailed summary of relevant watershed characteristics and land management activities for all index areas, see Tables 1 and 2.

Chinook salmon life cycle.—Snake River spring–summer Chinook salmon enter spawning and rearing index areas during the early summer and remain in those areas until spawning during

TABLE 2.—Gross geomorphic and climatic setting of index streams. The data source is a direct field measurement unless otherwise noted.

Index site	Drainage area (km^2)[a]	Elevation (m)[b]	Base flow discharge (m^3/s)	Mean precipitation (cm)[a]	Wetted width (m)	Pools/km	% Igneous[a]	Valley width (m)[c]	Valley slope (m/m)[c]
Elk Creek	205	1,980	0.78	112	9.7	1.5	68	519	0.0023
Sulphur Creek	132	1,740	0.61	115	8.5	1.5	96	836	0.0111
Minam River	499	1,250	5.65	136	24.9	0.8	55	273	0.0134
Upper Grande Ronde River	371	1,220	0.75	74	7.5	0.8	19	242	0.0169
Big Sheep and Lick creeks	122	1,170	0.43	89	6.0	1.9	0	263	0.0273
Imnaha River	209	1,270	5.56	131	11.9	0.5	12	518	0.0130

[a] From Interior Columbia Basin Ecosystem Management Project geographical information systems data (Quigley et al. 2001); assumes values for index reach watershed from lower boundary to headwaters (inclusive of tributaries).
[b] Average of upstream and downstream of index reach boundaries.
[c] Measured using 7.5′ U.S. Geological Survey topographical maps.

August and September. Fertilized eggs incubate within redds until hatching as alevins in midwinter; they remain in the redds through early spring, at which time they emerge as fry. These salmon exhibit a stream-type life history, meaning that upon emergence they typically rear in their natal streams through the parr stage and migrate to the ocean as age-1 and older smolts on the spring freshet of the following year; thus, their life history requires that they remain in tributary streams until migration is initiated, and as a result they are exposed to existing habitat conditions for a part of their life cycle. Juveniles then remain in the ocean until reaching sexual maturity (after 1 to 4 years), at which time they enter the Columbia River and begin their upstream migration to complete the life cycle. We have focused our modeling assessment on the egg-to-smolt portion of the Chinook salmon life cycle, as the survival rate through these stages is a key performance measure under the current recovery strategy (NMFS 2000).

Model description.—We used published experimental data and habitat–survival rate functions to create a model that predicts egg-to-smolt survival rates for a given stock as a direct function of field habitat measurements. For this purpose, we were only interested in using variables that are both targeted for improvement and affect the survival rate or productive capacity of a stock in a mechanistically explainable way. One example would be high levels of fine sediments in spawning gravels, which can increase mortality by restricting water flow—and thus the delivery of oxygen and removal of metabolic wastes in salmon redds—as well as by obstructing the emergence of fry (Chapman 1988). Another example would be summer water temperatures, which can increase mortality when they exceed the species' inherent physiological limits to survival (e.g., its upper incipient lethal temperature threshold) and reduce growth when too low (Brett 1952; McCullough 1999). Based on similar considerations, five habitat variables were included in this model, including three sediment-related variables (percent fines in spawning gravels and riffle and pool cobble embeddedness) and two temperature-related variables (mean temperature from egg deposition to fry emergence and daily temperature during the summer parr rearing period).

Using stock-specific field habitat data, our model computes the survival component related to each of the five habitat variables independently; these survival rates are subsequently pooled (we do not consider potentially important sublethal effects). For example, our model computes the component of the egg-to-smolt survival rate due to the effects of fine sediments in spawning gravels (S_{Fines}) from the following function (calibrated from Stowell et al. 1983):

$$S_{\mathrm{Fines}} = [92.65/(1 + e^{-3.994+0.1067 \cdot \mathrm{Fines}})]/100. \quad (1)$$

Four other functions are used in conjunction with the previous one to compute the overall egg-to-smolt survival rate (S_{smolt}) as follows:

$$S_{\mathrm{smolt}} = (S_{\mathrm{Fines}})(S_{\mathrm{incT}})(S_{\mathrm{EMBr}})(S_{\mathrm{sumT}})(S_{\mathrm{EMBp}}), \quad (2)$$

where S_{incT} is the survival rate from egg deposition to fry emergence as determined by the average water temperature during this period, S_{EMBr} is the summer productive capacity (a surrogate for survival rate) due to the level of cobble embeddedness in riffle–run habitats, S_{sumT} is the survival rate due to the mean daily water temperature for the summer parr rearing period, and S_{EMBp} is the overwintering capacity (a surrogate for survival rate) due to the level of cobble embeddedness in pool habitats. We did not include other variables such as discharge, which may affect survival indirectly through its effects on temperature and sediment transport (e.g., Angelaski and Harbor 1995). Computational details for all functions appear in Appendix 1.

Modeling survival rates in this way implicitly assumes that each habitat variable affects survival independently of the others and that there are no interactions between variables; that is, each habitat variable is weighted equally in the overall survival computation. We chose this approach because S_{smolt} is computed using functions derived largely from controlled laboratory experiments in which all variables were held constant except for the one of interest. In addition, the selected habitat variables generally affect different parts of the egg-to-smolt portion of the Chinook salmon life cycle and are thus independent (i.e., percent fines in spawning gravels affects a different life stage than does summer parr rearing temperature).

Field habitat and survival rate data collection.—To complete our modeling analysis, field habitat and survival rate data were collected for each index stock. We measured habitat variables within the primary spawning and rearing index areas detailed in Beamesderfer et al. (1997) during the summers of 2001 and 2002. The six surveyed reaches ranged from 7.4 to 29.5 km in length, and sample sites were selected systematically (based on channel units), with an approximate sample rate of 10% for each stream. At each sample site within the index reach, we measured pool and riffle–run cobble embeddedness using the hoop method (J. Skille and J. King, Idaho Department of Environmental Quality, unpublished). The percentage of fine (<10 mm) sediments (the size identified as affecting emergence success; Kondolf 2000) in spawning gravels was assessed from particle size distribution data collected by means of the Wolman pebble count method (Wolman 1954; Kondolf 1997) at potential spawning sites (pool tails). Continuous temperature data were collected by means of Onset Optic Stowaway temperature loggers deployed at two to four sites systematically spaced along the length of each index reach. In addition to collecting temperature data directly, we generated multiple years of continuous temperature data for our index stocks using the relationships between the temperatures measured at our sites and those measured at a National Marine Fisheries Service (NMFS) Baseline Environmental Monitoring Program long-term monitoring site (E. Hockersmith, NMFS, unpublished). This approach enabled us to use up to 8 years of temperature data in our model runs and thus to account for interannual variability in climatic patterns. All temperature data were summarized as the average of 18 measurements made throughout a given day.

Stock-specific estimates of egg-to-smolt survival rates were required for the model calibration and validation phases. These estimates were obtained from the most recent data available and were meant to reflect current conditions. Necessary data were collected directly by us, obtained from state and tribal agencies working in the index areas, or taken from published reports. For details on survival rate estimates used in this analysis, see Appendix 2.

Simulation approach.—Survival rates were predicted by sampling the empirical distribution for each of the measured habitat variables (i.e., the sediment-related variables) and randomly selecting one continuous year of temperature data (out of 8 possible years [except for IMN and MIN, for which only 1 year was used]) for each of 1,000 simulation trials. We chose 1,000 trials because this was the minimum number required for the variance to stabilize in our model development phase (see McHugh and Budy 2002 for details). Thus, our model produces a distribution of predicted survival rates instead of a single value and enables us to consider the entire range of conditions observed in an index area in our predictions. For additional details regarding model simulations, see Appendix 1.

Model calibration and validation.—Preliminary modeling results for two streams surveyed in 2001 (UGR and MIN) suggested that our model did reasonably well at predicting the trend in survival rates between streams of differing habitat quality (McHugh and Budy 2002); however, there was consistent negative bias in these predictions. Therefore, the model was calibrated with predicted and observed survival rates for the UGR and MIN stocks using a maximum likelihood optimization routine. Under this approach, model parameters were iteratively adjusted (10,000 iterations) within biologically realistic constraints until the bias was minimized. This calibration process caused minor adjustments to parameters in two of the five functions in our model (S_{Fines} and S_{EMBp}) while preserving the general nature of each habitat–survival relationship (Appendix 1). All calibrations occurred prior to model validation.

We validated our model through a comparison of the median predicted egg-to-smolt survival rate with the observed estimate for three index stocks that were not used in the model calibration phase (ELK, SUL, and IMN) within a regression framework. We simultaneously tested the hypotheses (using $\alpha = 0.10$ because of the small sample size) that the regression of the observations on the predictions had a slope of unity and an intercept of zero (Haefner 1996). If these simultaneous hypotheses were rejected, we could conclude that the model predictions were significantly different from the observed survival rates. Finally, these simultaneous hypotheses were also tested separately ($\alpha = 0.10$).

An example of model application: future habitat scenarios.—Following model calibration, we used our model to predict egg-to-smolt survival rates assuming three general future habitat states: the status quo, restoration, and degradation. Our status quo scenario assumed that habitat conditions remain unchanged in the future, while the various restoration and degradation (e.g., loss of habitat protection measures) scenarios assumed increased and diminished future habitat quality, respectively. The potential changes in survival rates under these scenarios were evaluated by manipulating the habitat and temperature model input files to produce the specific future condition (Table 3). While this approach neglects many physical processes that would lead to changes in the modeled habitat variables of interest, it does allow us to evaluate the survival rate that could be attained in a degraded

TABLE 3.—Description of input files and data manipulations used for future habitat scenarios.

	Scenario				
		Restoration		Degradation	
Variable	Status quo	Fix All	Fix Feasible	Worse1	Worse2
Percent fines in spawning gravel	Existing data set	Lowest in geology class	Intermediate in geology class	50% increase in each observed value	100% increase in each observed value
Incubation temperature[a]	Existing data set	Increase by 1.0°C	Increase by 0.5°C	Decrease by 0.5°C	Decrease by 1.0°C
Riffle–run embeddedness	Existing data set	Lowest in geology class	Intermediate in geology class	50% increase in each observed value	100% increase in each observed value
Summer parr rearing temperature	Existing data set	Best of all stocks	Intermediate of all stocks	Warmest observed for all stocks	Warmest observed for all stocks
Pool embeddedness	Existing data set	Lowest in geology class	Intermediate in geology class	50% increase in each observed value	100% increase in each observed value

[a] As current temperature conditions were at the low end of the optimum incubation temperature range for all streams, an improved state was assumed to be a higher temperature (attainable through riparian vegetation restoration) and a degraded state was assumed to be a lower temperature.

stream assuming a maximum restoration scenario (i.e., a managed degraded stream that attains the quality of a nearly pristine wilderness stream); thus, we were able to bracket the minimum and maximum potentials for a given index stream. Because of the strong influence of bedrock lithology on restoration potential (especially with respect to sediment variables), we constrained restoration potential by the range of habitat qualities observed in gross geologic groupings (see Tables 1 and 2). Embedded in this approach is the assumption that other controls on potential operate similarly across streams within a particular geology.

Status quo and degradation scenarios were modeled for all stocks, while restoration scenarios were evaluated for only the UGR and ELK stocks. An assessment of current habitat and survival rate conditions, watershed scale land management attributes, and field observations suggested that restoration opportunities were limited for all but these streams. Finally, we did not use a formal statistical test to evaluate the differences in predicted egg-to-smolt survival rates between streams within scenarios or between scenarios within streams, as even subtle differences are guaranteed to be statistically significant based on the Monte Carlo sample size (1,000); therefore, we assessed changes based on the differences in the median survival rates of different scenarios.

Results

Field Habitat Data

Noticeable differences in habitat quality were observed across the reaches surveyed for the six index stocks. With respect to the sediment-related variables, ELK and UGR were the most impaired streams within their respective geologic classes while MIN and IMN were generally the best (Figure 2). Field-measured and extrapolated incubation temperatures were coldest in ELK and SUL (2–3°C), and warmest in IMN (4.5°C; Table 4). Summer parr rearing temperatures were on average the warmest and most limiting in UGR (Table 4).

Model Validation

Using the previously described habitat data set, we calibrated our model and predicted egg-to-smolt survival rates for three independent sites where survival rates were known (ELK, SUL, and IMN; note that an observed survival rate estimate was not obtained for BSC–LIC). Predicted egg-to-smolt survival rates were nearly perfectly correlated with observed values for these three stocks ($r = 0.999$, $P = 0.03$). Based on a simple linear regression of the observations on the predictions, the simultaneous hypotheses of a slope of unity and an intercept of zero were rejected ($F = 478.02$, df = 2, $P = 0.032$; Figure 3), indicating that model predictions deviated significantly from the observations. Testing the same hypotheses separately, however, indicated that the slope ($\hat{\beta}_1 = 1.03$, SE $= 0.05$) did not differ significantly from one ($F = 0.42$, df $= 1$, $P = 0.63$) but that the intercept ($\hat{\beta}_0 = -0.036$, SE $= 0.005$) did differ from zero ($F = 48.25$, df $= 1$, $P = 0.09$). In sum, there was a consistent but minor systematic bias in our calibrated model predictions, predicted survival rates being approximately 0.036 higher than those ob-

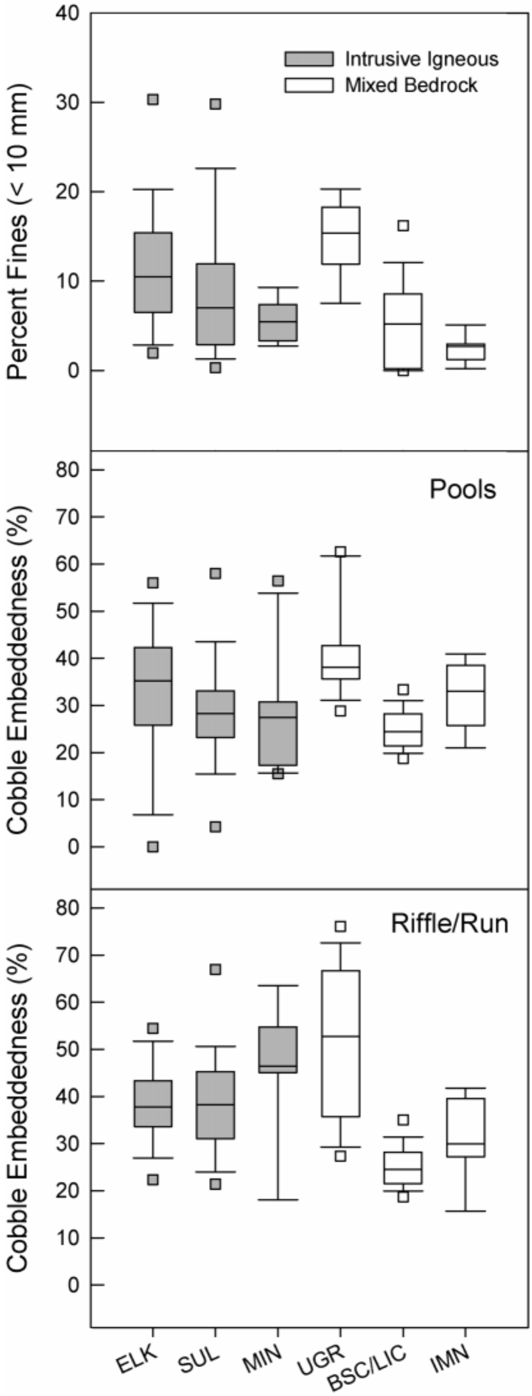

FIGURE 2.—Box-and-whisker plots of percent fines (<10 mm) and percent cobble embeddedness in pool and riffle habitats in modeled index streams, by gross lithology. For each box, the midline is the median, the lower and upper bounds are the 25th and 75th percentiles, the lower and upper whiskers are the 10th and 90th percentiles, and points beyond whiskers represent outliers. Sample sizes are as follows: Elk Creek, 43; Sulphur Creek, 17; Minam River, 6; upper Grande Ronde River, 9, Big Sheep and Lick creeks, 94; and Imnaha River, 7. See the caption to Figure 1 for abbreviations.

served in the field. Also, as one might expect, the survival rates for stocks used in the model calibration phase (UGR and MIN) were predicted accurately. The observed bias in model predictions probably arises for two reasons: (1) the simple nature of our model (i.e., we did not account for all of the factors affecting survival) and (2) the potential for a negative bias in field-estimated survival rates (e.g., snorkel census techniques often underestimate true abundance, thereby underestimating ''observed'' survival; Hankin and Reeves 1988). While additional validation could be informative, these observations indicate that our model does a reasonable job of predicting survival for individual stocks. More importantly, however, it accurately predicts the trend in survival rates observed across stocks as an explicit function of habitat quality.

Future Habitat Scenarios

Status quo.—Under the assumption that current habitat conditions remain unchanged, the median predicted egg-to-smolt survival rates from 1,000 Monte Carlo trials ranged from a low of 0.07 (UGR and ELK) to a high of 0.19 (BSC–LIC; Figure 4; Table 5). Under this scenario, the variability in the range of predictions was similar across all streams, coefficients of variation (CVs [100 × SD/mean]) ranging from 22% to 45%. As suggested in the previous section, these predictions closely matched current field estimates of survival rates.

Restoration.—The potential change in survival rates assuming a future increase in habitat quality was large for the UGR index stock and minor for the ELK index stock. Due to the limited opportunities for habitat improvements in SUL, MIN, IMN, and BSC–LIC, restoration was not modeled for these stocks. For the Fix All scenario (which assumed, for example, that UGR can achieve the quality of BSC–LIC), the egg-to-smolt survival rate was predicted to be 179% higher than it currently is (based on status quo runs) for the UGR index stock (0.07 versus 0.19) and 27% higher for the ELK stock (Figure 5; Table 5). The survival rate was nearly double that of status quo for the Fix Feasible scenario (which assumed the achieve-

TABLE 4.—Selected temperature metrics for the summer 2002 juvenile Chinook salmon rearing and incubation periods; T_{OPT} is the optimum temperature for growth by juvenile Chinook salmon (14.8 ± 1.0°C), and T_{ZNG} is the temperature above which zero net growth is observed (reviewed in Armour 1991).

Index area	No. of data loggers	Summer rearing temperature (°C)[a] Mean ± SD (range)	Days at T_{OPT}	Days above T_{ZNG}	Incubation temperature (°C; mean ± SD [range])[b]
Elk Creek	3	12.0 ± 3.6 (2.8–17.4)	43	0	2.5 ± 0.1 (2.3–2.7)
Sulphur Creek	2	10.3 ± 3.4 (2.5–14.7)	7	0	2.6 ± 0.1 (2.4–2.7)
Minam River	3	12.4 ± 4.9 (3.9–19.0)	21	0	4.3[c]
Upper Grande Ronde River	3	14.5 ± 4.4 (4.3–22.9)	30	20	3.7 ± 0.2 (3.4–3.9)
Big Sheep and Lick creeks	7	9.8 ± 3.1 (3.7–15.2)	13	0	4.2 ± 0.1 (4.1–4.3)
Imnaha River	4	9.7 ± 2.7 (4.4–14.3)	7	0	4.5[c]

[a] Mean daily average temperature for all days when temperature loggers were operating during the period 1 May to 30 September 2002 (the approximate time period the model uses).

[b] Mean incubation temperature from 15 August to 30 April across all years for which it was possible to recreate winter temperatures (n = 8 for all areas except Minam and Imnaha rivers, where n = 1); see Appendix 1 for details on extending the existing temperature data set into previous years.

[c] Only one year of winter temperature data was available for these rivers.

ment of intermediate habitat quality) for the UGR stock, while it increased by only 20% for the ELK stock. The CVs for Fix All and Fix Feasible scenarios were minimal, ranging from 19% to 35%. In sum, these results suggest that there is great potential for improving the survival rate for UGR via habitat restoration, but only limited potential for ELK.

Degradation.—Across the six stocks, survival rates were predicted to be considerably lower under the two increased-degradation scenarios. For the Worse1 scenario (in which conditions get approximately 50% worse), survival rates were predicted to be as low as 0.02 (UGR) and as high as 0.11 (BSC–LIC); these changes represent approximately 69% and 41% decreases from the status quo predictions, respectively (Figure 5; Table 5). Under the Worse2 scenario (in which conditions get approximately 100% worse), the predicted egg-to-smolt survival rates ranged from a low of 0.01 (UGR and ELK) to a high of 0.06 (BSC–LIC). Under both degradation scenarios, there was considerable variability in the distributions of predicted survival rates for the 1,000 Monte Carlo trials across the six stocks, CVs averaging 58% and 82% for the Worse1 and Worse2 scenarios, respectively.

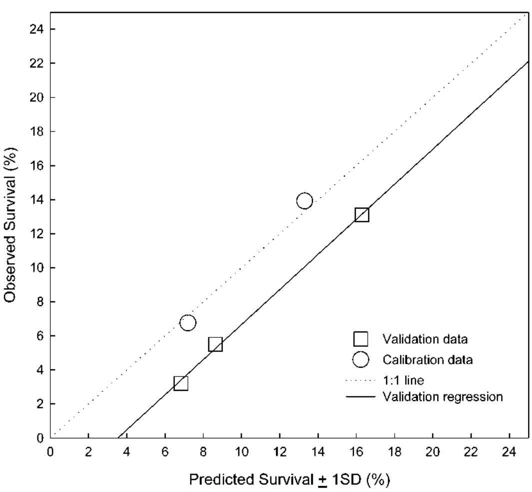

FIGURE 3.—Scatter plot of observed versus median predicted egg-to-smolt survival rates for modeled index stocks. The 1:1 line and the best-fit linear regression line for the test data set (Elk Creek, Sulphur Creek, and the Imnaha River) are also displayed for reference.

Discussion

Predicting the response of threatened salmon populations to restoration efforts is a critical step

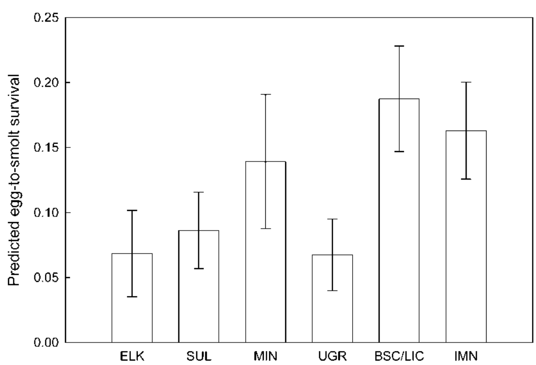

FIGURE 4.—Median predicted egg-to-smolt survival (±SD) under present habitat conditions (status quo scenario) based on 1,000 iterations of a Monte Carlo sampling of empirical habitat distributions. See the caption to Figure 1 for abbreviations.

TABLE 5.—Predicted egg-to-smolt survival rates for modeled scenarios, by index stream. Note that improvement scenarios (Fix All and Fix Feasible) were not modeled for Big Sheep–Lick, Imnaha, Minam, and Sulphur index stocks, as restoration opportunities are limited in these streams. The change from the status quo is the percent change in median survival from the status quo scenario. All results are for 1,000 Monte Carlo trials. See the caption to Table 3 for scenario descriptions.

Index stock	Scenario	Median	Change from status quo	Range	CV[a]
Elk Creek	Status quo	0.07		0.02–0.20	45
	Fix All	0.09	27	0.02–0.16	34
	Fix Feasible	0.08	20	0.01–0.19	35
	Worse1	0.03	−63	0.00–0.17	89
	Worse2	0.01	−90	0.00–0.14	142
Sulphur Creek	Status quo	0.09		0.02–0.20	34
	Fix All				
	Fix Feasible				
	Worse1	0.05	−47	0.00–0.17	61
	Worse2	0.02	−80	0.00–0.16	87
Minam River	Status quo	0.14		0.05–0.28	36
	Fix All				
	Fix Feasible				
	Worse1	0.06	−56	0.01–0.18	59
	Worse2	0.03	−78	0.00–0.12	75
Upper Grande Ronde River	Status quo	0.07		0.01–0.14	40
	Fix All	0.19	179	0.04–0.32	19
	Fix Feasible	0.13	86	0.07–0.24	23
	Worse1	0.02	−69	0.00–0.07	62
	Worse2	0.01	−92	0.00–0.03	79
Big Sheep and Lick creeks	Status quo	0.19		0.05–0.31	22
	Fix All				
	Fix Feasible				
	Worse1	0.11	−41	0.01–0.25	34
	Worse2	0.06	−69	0.00–0.16	44
Imnaha River	Status quo	0.16		0.11–0.28	22
	Fix All				
	Fix Feasible				
	Worse1	0.08	−51	0.04–0.19	40
	Worse2	0.03	−80	0.01–0.13	64

[a] 100 × SD/mean.

in identifying actions that will provide the greatest overall benefit for stock recovery. To aid in evaluating habitat-restoration-based recovery efforts, we used published salmon–habitat relationships to create a simple model capable of predicting egg-to-smolt survival rates for individual stocks as a direct function of five easily measured physical habitat variables; based on a modest validation data set, our model predictions were relatively accurate across a wide range of habitat quality (from degraded to pristine). In addition, our analysis demonstrates that while there is great potential for improving tributary survival for a few isolated stocks, most streams have little to no room for improvement.

In our modeling exercise, we considered only habitat variables that can be explicitly linked to fish survival rates and that are likely to change as a result of habitat restoration efforts. As our comparisons were made across streams, our concern was not with the accuracy and precision of habitat assessment methods; many have evaluated this issue (e.g., Wang et al. 1996; Sylte 2002), and we provide an evaluation specific to this data set elsewhere (McHugh 2003). Our ability to predict early life stage survival rates relatively accurately using such a simple combination of habitat variables is, therefore, noteworthy. First, our model uses only five variables to predict survival rates, when in reality a multitude of other factors are likely to be involved. For example, the abundance of large woody debris is not included in our analysis, though it has been linked to the productive capacity of the spawning and rearing streams of coho salmon *O. kisutch* in the Pacific Northwest (e.g., Solazzi et al. 2000; Roni and Quinn 2001). This variable and others like it were not included in our analysis because strong, generalized functional relationships with salmon survival rates or capacity are not available. Beyond certain physical habitat features, we purposefully omitted the biotic attributes of habitat that can affect survival rates, such

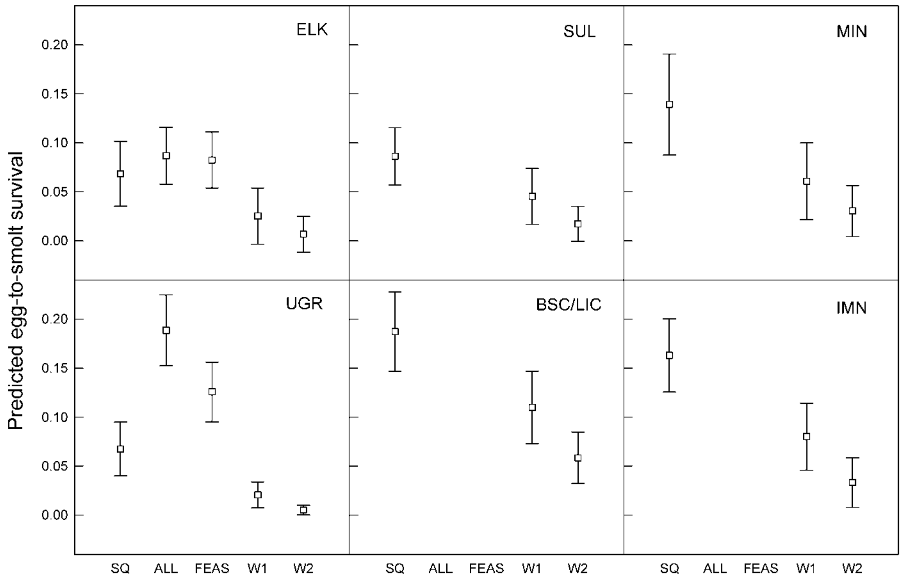

FIGURE 5.—Median model-predicted egg-to-smolt survival (±SD) under alternative future scenarios for selected index streams. Scenario abbreviations are as follows: SQ = Status Quo (baseline conditions persist); ALL = Fix All (a degraded stream attains the habitat quality of a wilderness stream); FEAS = Fix Feasible (a degraded stream attains intermediate habitat quality); W1 = Worse1 (habitat is degraded moderately); and W2 = Worse2 (habitat is degraded severely). See the caption to Figure 1 for abbreviations. Note that restoration scenarios are only presented for Elk Creek and the upper Grande Ronde River, as opportunities for restoration are limited in the other four streams.

as the productivity of the system and the presence of competitors and predators (Hayes et al. 1996). While the incorporation of these features would have added realism to our approach, their quantification is difficult, the mechanistic linkages to survival rates are poorly understood, and modeling this degree of biological complexity could have made our approach unwieldy. Despite the relative simplicity of our approach, we found a strong correspondence between our model predictions and the observed survival rates for the individual stocks in question and our model predictions accurately reflected the trend in survival rates observed across stocks with varying habitat conditions.

Our approach differs considerably from other model-based evaluations of salmonid production and survival potential that have been or are currently being used in the Snake River basin and elsewhere. To begin with, our approach to linking survival to habitat variables is founded entirely on existing knowledge obtained through controlled experiments; similar model-based fish habitat assessments rely on empirical relationships fitted to observations of fish standing stock or survival made across streams of different habitat quality (reviewed in Fausch et al. 1988). Compared with the data-intense Ecosystem Diagnosis and Treatment model (EDT; Mobrand et al. 1997), which is also used in the Snake and Columbia River basins, our approach has some similarities in objectives but distinct differences in approach. As in our model, the goal of EDT is to identify limiting factors in the environment and prioritize management activities. Thus, EDT attempts to portray the landscape of an environment ''as seen through the eyes of the species'' not only across their entire life history but also by life stage. Consequently, EDT summarizes many environmental variables that are potentially important and attempts to relate these to survival. While this approach is more inclusive than ours, a major limitation of EDT is that it requires inputs for 47 variables; such information is often unavailable for a given stock (and thus is based on expert opinion), and model behavior can be difficult to decipher (Ruckelshaus et al. 2002). Both our model and EDT have some similarity to the Salmonid Watershed Assessment model (SWAM; Steel et al. 2003); however, SWAM is used primarily for prioritizing restoration actions at a very large scale by means of spatially referenced biophysical data sets (e.g., GIS coverages of land use and cover and bedrock lithology). Our model may serve as a useful alterative or complement to both SWAM and EDT in that it provides a local-scale reference for one (SWAM) and a simpler, data-based validation for the other (EDT).

Model Strengths and Weaknesses

Due to our intentional selection of only a limited number of habitat variables, our model is very simple in its scope and structure. Furthermore, model inputs are based on easily measured variables collected using standard protocols and a simple survey design. In using an empirical-distribution-based Monte Carlo simulation approach, we have also included the entire range of conditions for the variables measured within an index area in our model predictions. Thus we have retained the inherent variability of the system while avoiding having to make assumptions about underlying variable distributions.

For any fisheries modeling approach to be truly useful, however, its limitations also need to be recognized (Schnute and Richards 2001). Several limitations are inherent in our approach. First, our model does not consider the temporal and spatial complexities of habitat quality as experienced by salmon. For example, while the water temperatures measured in the main-stem stream channel can be quite warm, there exists the potential for fish to actively avoid these areas by seeking local thermal refugia (Berman and Quinn 1991; Torgersen et al. 1999; Ebersole 2001). Also, by assuming equal weights for the habitat variables in our final survival computation, we neglect the potential for interaction among and compensation between habitat variables. Further, while it is justifiable to ignore a density-dependent survival rate response under the current low-spawner-escapement levels, it may be necessary to consider such factors under future scenarios or for some isolated cases (e.g., some stocks in the Snake River basin experienced relatively high escapement in 2001). However, our model was designed to evaluate the survival rate potential for threatened Chinook salmon stocks, which have generally been well below carrying capacity for approximately 25 years. Finally, our approach to evaluating future habitat scenarios does not directly consider watershed processes that may lead to improved habitat conditions (e.g., road-density-related changes in watershed level erosion rates and sediment routing patterns) or the subtle controls on potential that vary between watersheds. To more thoroughly evaluate the feasibility of increasing freshwater survival rates via habitat restoration, our model could easily be combined with process-based sediment loading models (e.g., HEC-6; USACE 1977) and temperature models (e.g., SNTEMP; Theurer et al. 1984). While parameterizing such models can be cumbersome and may be limited by data availability, the survival rate predictions produced with output from such models could provide a more complete reference for potential.

Application to Snake River Chinook Salmon Recovery Efforts

While the potential applications of our model are numerous, we offer two ways in which it can be useful to managers concerned with evaluating recovery options involving freshwater spawning and rearing habitat restoration. First, the overall survival rate benefit (across the entire life cycle) of alternative habitat restoration strategies can be evaluated by coupling the egg-to-smolt survival rate predictions of our model with a total life cycle model to compute relevant population growth parameters (e.g., λ, the population growth rate). For example, this could be done by substituting our egg-to-smolt survival rate predictions into the stage-structured Leslie matrix population model of Kareiva et al. (2000) and solving for λ. Knowledge of population growth rates under different management scenarios could assist managers in selecting the best recovery strategy. These assessments should be made for a number of populations inhabiting a wide range of habitat conditions so as to more thoroughly address the recovery potential of the evolutionarily significant unit at large.

In addition to this application, our model can be used to prioritize restoration activities within watersheds. In recent years, large-scale prioritization models have been developed to aid in selecting watersheds or stocks for conservation and restoration efforts (e.g., Allendorf et al. 1997; Pess et al. 2002). While such approaches provide an initial filter for directing efforts at the large scale, there is a need for an objective tool with which to identify the areas within high-priority stocks or watersheds where localized activities would provide the greatest benefit. As habitat inputs are easily and inexpensively collected, our model could satisfy this need. For example, one might use our model and reach-specific habitat data to predict egg-to-smolt survival rates for different reaches in the range of a high-priority stock. Given a similar land management and geomorphic setting for the different reaches, restoration activities might be directed at the reach with the lowest predicted egg-to-smolt survival rate.

Management Implications and Future Direction

The future status of Snake River salmon depends largely on the efficacy of freshwater habitat actions, such that there is a need to quantify the potential for actually increasing fish survival based on protection, restoration, or both. Based on our results, it appears that egg-to-smolt survival rates (as they explicitly relate to habitat quality) can be greatly improved for a few stocks and only minimally for others. Perhaps more importantly, the large reductions in survival associated with increased habitat degradation demonstrate the importance of maintaining existing stream protection measures. Our results also show that survival rates may be naturally low for some stocks, even in the absence of deleterious land management activities (e.g., Sulphur Creek). This, coupled with the fact that our restoration scenarios largely ignore both the temporal aspects of stream habitat change (which can be lengthy; e.g., Kondolf 1993) and the watershed processes that lead to improved instream habitat quality, suggests that the results of our model be interpreted with some caution. Further, our estimates are intended to bracket the potential results (i.e., to provide minimum and maximum values), not to provide a precise future value that can be expected under a restored or degraded state. Nevertheless, we suggest that the best recovery strategy for Snake River salmon is one that can directly consider the limitations of efforts aimed at increasing egg-to-smolt survival rates through habitat restoration.

Our model could have considerable utility in the Snake River salmon recovery planning process. Additional model predictions could be made through data collection or the assembly of existing habitat data for other index areas throughout the Snake River basin. In addition, these predictions could be further validated for stocks for which egg-to-smolt survival rates are known. Furthermore, steps could be taken to parameterize existing process-based sediment loading and temperature models for use in forecasting survival under future scenarios. These steps will increase the utility of our model as a tool for decision making.

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Appendix 1: Computational Details

Our model computes egg-to-smolt survival rates (S_{smolt}) as the product of independent habitat-related early life stage survival rates:

$$S_{\text{smolt}} = (S_{\text{Fines}})(S_{\text{incT}})(S_{\text{EMBr}})(S_{\text{sumT}})(S_{\text{EMBp}}), \quad \text{(A.1)}$$

where S_{Fines} and S_{incT} are the survival rates from egg deposition to fry emergence as a function of fine sediments and average water temperature, respectively, S_{EMBr} is the summer productive capacity (a surrogate for survival rate) as related to cobble embeddedness in riffle–run habitats, S_{sumT} is the survival rate related to the mean daily water temperature for the summer parr rearing period, and S_{EMBp} is the overwintering capacity (a surrogate for survival rate) due to the degree of cobble embeddedness in pool habitats.

Fine Sediment Survival Rate Function

Variable S_{Fines} is calculated using a calibrated version of a function published in Stowell et al. (1983), which was developed from laboratory experiments conducted by Tappel and Bjornn (1983). In those experiments, Chinook salmon embryos were incubated in experimental mixtures of gravel containing different levels of fine sediment, and the subsequent survival rate to fry emergence was noted for each mixture. From these data, the following function was produced:

$$S_{\mathrm{Fines}} = [92.95/(1 + e^{-4.559+0.1442\cdot \mathrm{Fines}})]/100, \quad (A.2)$$

where Fines is the percentage of fine sediments in spawning gravels less than 6.35 mm in diameter. This relationship was developed on the basis of the percentage of surface and subsurface fine sediments; however, our model input data consist of only surface fines (<10 mm). Using this function with our data set therefore assumes that surface and subsurface fines are strongly related. The calibrated form of this function (see the subsection in text titled Model Calibration and Validation for this and all following calibrated functions) used in our simulations is

$$S_{\mathrm{Fines}} = [92.65/(1 + e^{-3.994+0.1067\cdot \mathrm{Fines}})]/100. \quad (A.3)$$

Incubation Temperature Survival Rate Function

Variable S_{incT} is calculated using a polynomial function fitted to experimental data published in Murray and McPhail (1988); two additional data points needed for curve-fitting were estimated from information reviewed in Armour (1991) and McCullough (1999). Murray and McPhail (1988) performed laboratory experiments in which fertilized Chinook salmon eggs (among those of other species of Pacific salmon species) were incubated at five different constant temperatures (range, 2–14°C) and monitored to hatching. With these data and the data points taken from the other sources, the following quadratic polynomial equation was produced (F = 62.49, df = 6, P = 0.001):

$$S_{\mathrm{inc}T} = -0.26 + 0.27\cdot \mathrm{incT} - 0.02\cdot \mathrm{incT}^2, \quad (A.4)$$

where incT is the mean temperature during the period between egg deposition (assumed to be 15 August) and fry emergence (assumed to be 30 April the following year). Using this function in this way assumes that an average incubation temperature measured in the field approximates a temperature held constant in a laboratory setting. In addition, using this function in this way assumes that stream water temperature is a reasonable surrogate for intragravel water temperature (what the eggs experience).

Riffle–Run Embeddedness Survival Rate Function

Variable S_{EMBr} is calculated using a polynomial function reported in Stowell et al. (1983) based on the work of Bjornn et al. (1977). In their experiments, Bjornn et al. (1977) investigated the effects of cobble embeddedness (a measure of the loss of interstitial cover due to the effects of excessive fine sediment loading) on summer rearing capacity in experimental channels (with pool and riffle structure). They added the same number of Chinook salmon parr to channels with different levels of embeddedness and monitored how many fish emigrated from the channels over a 5-d period. The rearing capacity was estimated as the percentage of the initial number of fish remaining in the channels after the period. The summer capacity function reported in Stowell et al. (1983) relates percentage summer stream capacity to the degree (%) to which cobbles are embedded in run habitat (EMBr [our riffle/run category]):

$$S_{\mathrm{EMBr}} = [100.0 - 1.79\cdot \mathrm{EMBr} + 0.0081\cdot \mathrm{EMBr}^2]/100. \quad (A.5)$$

We assume that the survival rate is affected by cobble embeddedness in a manner parallel to the rearing capacity of Bjornn et al. (1977). However, if parr leave a natal stream because of impaired rearing habitat, they may still survive beyond that stage. If they are leaving natal streams because of impairment, however, it may be possible to increase the productive capacity in index streams by altering this variable.

Summer Parr Rearing Temperature Survival Rate Function

The estimated survival rate due to the effects of summer rearing temperatures, S_{sumT}, is computed using a Weibull function that relates daily survival, S_i, to mean daily stream temperature, sumT, for any given day of the summer rearing period (taken as 1 May through 30 September). Using this function, the daily survival rate is decreased whenever the average daily temperature exceeds an upper temperature threshold (17.8°C):

$$S_i = \exp\left\{-\left[\left(\frac{\text{sumT}}{27.0271}\right)^{10.74}\right]\right\}. \quad \text{(A.6)}$$

This function was fitted to published data on the effects of high temperatures on salmon and trout using nonlinear regression (F = 6,907.71, df = 11, $P < 0.001$; data from Brett 1952; McCormick et al. 1972; and Coutant 1973). Variable S_{sumT}, the survival rate over the summer rearing period (as determined by temperature), is then computed as the product of all daily survival rates for that time period. Below the threshold temperature, the survival rate is not affected. Therefore, we modeled only the lethal effects of high temperature and did not include the sublethal effects (e.g., decreased growth). S_{sumT} is thus computed from the following product equation:

$$S_{\text{sumT}} = \prod_{i=1}^{152} S_i. \quad \text{(A.7)}$$

Pool Embeddedness Survival Rate Function

The computations of S_{smolt} include the effect of cobble embeddedness on overwinter survival rates using a calibrated form of a function published in Stowell et al. (1983). This function incorporates the effects of excess fine sediment on the overwintering capacity of a stream (taken as a surrogate for overwinter survival rate), S_{EMBp}. Based on work done by Bjornn et al. (1977; same design as described above, except during winter), this exponential function relates overwinter capacity for Chinook parr to pool embeddedness, EMBp, as follows:

$$S_{\text{EMBp}} = e^{-0.034\cdot\text{EMBp}}. \quad \text{(A.8)}$$

The same assumption applies regarding the use of capacity (winter here) as a surrogate for the survival rate. The calibrated form of this function used in the model computations is:

$$S_{\text{EMBp}} = 1.001e^{-0.013\cdot\text{EMBp}}. \quad \text{(A.9)}$$

Monte Carlo Simulation Details

Computing S_{smolt} by means of point estimates describing the central tendency of habitat variable distributions in a given index stream (e.g., the arithmetic mean or median value of Fines) implies that these distributions can be accurately characterized with such simple statistics. The distributions of the habitat variables used for modeling survival rates in our index streams tended to deviate from normality in most cases, however, suggesting that such a deterministic approach was not appropriate for our purposes (especially when using nonlinear habitat–survival rate functions). Therefore, we used a more robust Monte Carlo simulation approach whereby the entire distribution for each habitat variable was sampled and survival rates were computed for each trial (1,000 iterations).

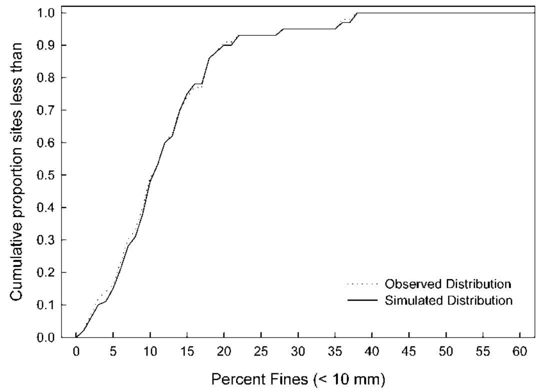

FIGURE A.1.—Example of the empirical distribution functions used in the Monte Carlo simulations. The data are percent fines at 43 potential spawning sites in Elk Creek; the simulated distribution was obtained from 1,000 samples drawn from the empirical distribution.

For each index stream, the range of conditions observed in sediment-related variables (Fines, EMBr, and EMBp) was incorporated into model predictions by sampling empirical distribution functions for these variables during each of the 1,000 trials (Figure A.1). In addition, the interannual variability in sumT and incT was incorporated by randomly selecting a temperature file from one of eight possible years during each step of the simulation. The end result of these simulations is a distribution of S_{smolt} predictions that explicitly incorporates the range of habitat conditions seen in a given index stream and that can be described by any number of statistics (e.g., median and SD). All Monte Carlo trials were conducted with a program coded in BASIC.

Sensitivity Analysis

We evaluated parameter and input sensitivity by proportionally changing (±0.10, 0.20, and 0.30) these values and computing the following standardized sensitivity index:

$$S_i = [(R_a - R_n)/R_n]/[(P_a - P_n)/P_n], \quad \text{(A.10)}$$

where R_a is the altered model response (S_{smolt} in our case), R_n is the nominal response, P_a is the altered parameter value, and P_n is the nominal pa-

Appendix 2: Survival Rate Estimate Details

TABLE A2.1.—Details of survival rate estimates used in model calibration and validation. Note that no estimate was available for the Big Sheep–Lick creeks index area.

Stream	Brood year	No. of redds	Fecundity (eggs/female)	Abundance by life stage			Survival rates			Comments
				Eggs[a]	Parr	Smolt	Egg-to-parr	Parr-to-smolt[b]	Egg-to-smolt	
Upper Grande Ronde River	1996	22[c]	4,384[c]	96,448		6,936[c]		0.209	0.072	Most recent year available in which all spawning reaches were surveyed
Minam River	1999	46[c]	4,384[c]	201,664		26,809[c]		0.205	0.133	Only year available
Imnaha River	1992	253[c]	4,630[d]	1,171,390		152,968[e]		0.266	0.131	Year with best trapping coverage of smolt out-migration
Elk Creek	2000	103[f]	5,900[g]	607,700	27,712[h]		0.046	0.214	0.026[i]	Egg-to-parr survival rate estimate similar to those estimated previously
Sulphur Creek	2000	5[f]	5,900[g]	29,500	5,864[h]		0.199	0.134	0.033[i]	Egg-to-parr survival rate estimate similar to those estimated previously

[a] Potential egg deposition assumes 1 female per redd.
[b] Mean for years reported in Paulsen and Fisher (2001); includes mortality that occurs between index area and Lower Granite Dam.
[c] Oregon Department of Fish and Wildlife, unpublished data.
[d] Messmer et al. (1991).
[e] Nez Perce Tribe, Lapwai, Idaho, unpublished data.
[f] Elms-Cockrum (2001).
[g] Petrosky and Holubetz (1988).
[h] McHugh and Budy (2002), adjusted for snorkel bias using a Hankin and Reeves (1988) type correction factor estimated from data collected in similar streams presented in Petrosky and Holubetz (1987) and Hillman et al. (1992).
[i] Product of egg-to-parr and parr-to-smolt survival rates adjusted for probable mortality occurring between the index area and Lower Granite Dam (>600 km downstream). The adjustment factor (0.02) was based on similar data (Walters et al. 1999) from an adjacent tributary to the Middle Fork Salmon River (Marsh Creek) for which egg-to-parr and egg-to-smolt survival rates in the index area and the parr-to-smolt survival rate to Lower Granite Dam were known for three separate years.

rameter value (Haefner 1996). Overall, our predictions were most sensitive to changes in the parameters of the S_{EMBr} function (absolute average sensitivity based on all parameters in the equation; $S_i = 1.4$) and least sensitive to changes in those of the S_{Fines} function ($S_i = 0.8$). The patterns in model input sensitivity were identical, overall S_{smolt} predictions being most sensitive to proportional alterations to EMBr ($S_i = 1.01$) and least sensitive to alterations to Fines ($S_i = 0.15$).