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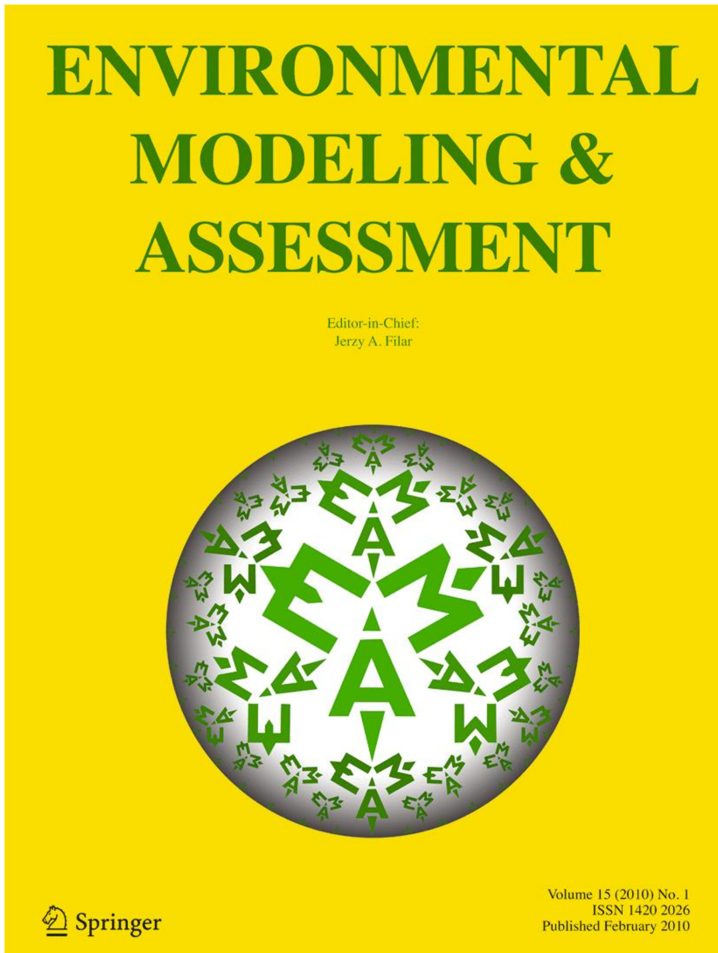

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How Certain Are Salmon Recovery Forecasts? A Watershed-scale Sensitivity Analysis

A. H. Fullerton · D. Jensen · E. A. Steel · D. Miller · P. McElhany

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Abstract Complex relationships between landscape and aquatic habitat conditions and salmon (*Oncorhynchus* spp.) populations make science-based management decisions both difficult and essential. Due to a paucity of empirical data, models characterizing these relationships are often used to forecast future conditions. We evaluated uncertainties in a suite of models that predict possible future habitat conditions and fish responses in the Lewis River Basin, Washington, USA. We evaluated sensitivities of predictions to uncertainty in model parameters. Results were sensitive to 60% of model parameters but substantially so (|partial regression coefficients| >0.5) to <10%. We also estimated accuracy of several predictions using field surveys. Observations mostly fell within predicted ranges for riparian shade and fine-sediment deposition, but large woody debris estimates matched only half the time. We provide suggestions to modelers for improving model accountability, and describe how managers can incorporate prediction uncertainty into decision-making, thereby improving the odds of successful salmon habitat recovery.

A. H. Fullerton (✉) · D. Jensen · E. A. Steel · P. McElhany
Northwest Fisheries Science Center, NOAA Fisheries,
2725 Montlake Blvd E.,
Seattle, WA 98112, USA
e-mail: Aimee.Fullerton@noaa.gov

D. Miller
Earth Systems Institute,
3040 NW 57th St,
Seattle, WA 98107, USA

Present address:
D. Jensen
710 W. 27th Ave.,
Eugene, OR 97405, USA

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1 Introduction

Wild Pacific salmonid (*Oncorhynchus* spp.) populations in the Pacific Northwest USA are considerably less abundant than they were in pre-colonial times [17, 25], and numerous populations are listed as endangered or threatened under the Endangered Species Act [22]. Because all salmon rely on cool and clean water and adequate habitat, destruction of habitat by human activities has been implicated as a partial cause for this decline [19]. After years of scientific research, policy debate, and dubious effectiveness of implemented restoration actions, we are at the stage of salmon recovery planning in which critical decisions on habitat management and restoration must be made in order to avoid accelerated extinction risk (e.g., [15]). Choosing among competing conservation objectives and implementation strategies can be difficult given the uncertainty that each course of action will provide the benefit intended, and the cost-benefit tradeoffs among differing potential habitat restoration sites and types of restoration actions (e.g., removing fish passage barriers, reducing sediment delivery to streams by decommissioning roads or restoring riparian vegetation). To date, existing management plans have failed to prevent population declines in part because of the failure to include a means of incorporating these inevitable uncertainties into decisions [5].

Computer simulation models are a useful and necessary tool for both predicting and comparing habitat and fish responses to potential restoration or conservation actions. However, models rely on parameters that are either statistically fitted or theoretically derived and on input data for which there is limited certainty. The sensitivity of modeled fish or habitat predictions to this imperfect knowledge base is often not thoroughly evaluated. In many cases, model accuracy (i.e., how well predictions match empirical observations) is not assessed before model outputs are incorporated into management decisions. Information about uncertainty associated with model predictions can inform managers about tradeoffs in model performance (i.e., how confident we are in predictions from each model) that will be instrumental in guiding development of robust watershed-level conservation plans and in refining future generations of models.

Steel et al. [36] developed an analytical tool to help managers evaluate potential effects of freshwater habitat restoration activities within a watershed by modeling watershed processes, habitat conditions, and salmonid population responses. The analytical tool is comprised of spatial datasets produced in a geographic information system (GIS) and a number of models (Fig. 1) that collectively predict responses of watershed features (e.g., riparian conditions, sediment delivery, hydrologic runoff), habitat conditions (e.g., bed scour, substrate composition, habitat suitability), and salmonid populations (e.g., spawner capacity, egg-to-fry survival, accessibility) to a variety of hypothetical watershed management strategies. For each management strategy, the analysis predicts spatially-explicit ecological conditions and fish responses. These predicted conditions can be compared to existing or best-case conditions to inform decision-makers about which options are both ecologically beneficial and economically feasible. The analytical tool is currently customized for Pacific salmonids in the Lewis River Basin, southwest Washington State, but can be modified for use in other watersheds or for other species.

For this tool to serve as a useful alternative to existing approaches for salmon recovery planning, decision-makers need to have a clear idea about how predictions relate to reality. There are five types of uncertainty encountered in modeling [33]: (1) uncertainty associated with choice of model structure (e.g., linear, non-linear, decision tree), (2) uncertainty in estimation of model parameters, (3) uncertainty in measurement of input data (e.g., measurement error), and (4) natural stochastic variation. All of these contribute to the fifth type of uncertainty: (5) accuracy with which model predictions represent reality. In this study, we investigated two of these sources of uncertainty for the analytical tool developed by Steel et al. [36]: (1) uncertainty associated with model parameters, and (2) the accuracy of predictions. Although we did not evaluate the effect of uncertainty associated with input data (e.g., landscape and instream conditions) used by models, nor of natural stochastic variability, this approach gave us a better understanding of how precise predictions are for the current parameterization in the Lewis River Basin.

With respect to model parameter uncertainty, we addressed three objectives. Our first objective was to evaluate the cumulative effect of uncertainty in all model parameters on predictions. To accomplish this, we simultaneously varied parameters by as much as 50% and generated a distribution of predictions which we used to interpret our confidence in predictions for a given level of collective parameter variance. Our second objective was to use sensitivity analysis to determine how uncertainty was partitioned among model parameters. We were interested in the relative influence each parameter had on variance in modeled predictions. We were especially interested in sensitivity of predictions by several models that used step functions to estimate relationships that are not completely understood because it is often assumed that predictions will be sensitive to the choice of step-delineating values. Our third objective was to investigate whether there was any spatial pattern in prediction uncertainty. We asked whether modeled predictions were more precise in some parts of the watershed compared to others. Finally, to evaluate model accuracy, we examined whether stream survey data fell within the range of model predictions. We explore how these analyses can (1) guide future model development (e.g., identification of areas where additional empirical data would increase prediction reliability) and (2) use results to describe how knowledge about uncertainty in modeled predictions can inform management decisions.

2 Methods

2.1 Basic Model Structure

We evaluated six independent geospatial models in the Lewis River Basin (described fully in [34, 36]) that each predicted unique outputs for each stream reach (Fig. 1). Models included (1) riparian functions (three sub-models), (2) sediment and water supply (three sub-models), (3) instream habitat conditions, (4) spawning habitat suitability (for Chinook (*O. tschawytscha*) and chum salmon (*O. keta*) and steelhead trout (*O. mykiss*)), (5) egg-to-fry survival (for three species; we evaluated only Chinook salmon), and (6) spawner capacity (Chinook salmon).

The riparian functions model is a three-part decision-tree model that predicts qualitative ratings for shade, pool-forming conifer abundance, and large woody debris recruitment provided by riparian vegetation within 60 m of each bank. The sediment and water supply model consists of three sub-models predicting the amount of surface erosion and hydrologic runoff from adjacent hillslopes that is supplied to streams, sediment input contributed by roads in adjacent drainage areas, and sediment derived from mass wasting. Surface erosion, hydrologic

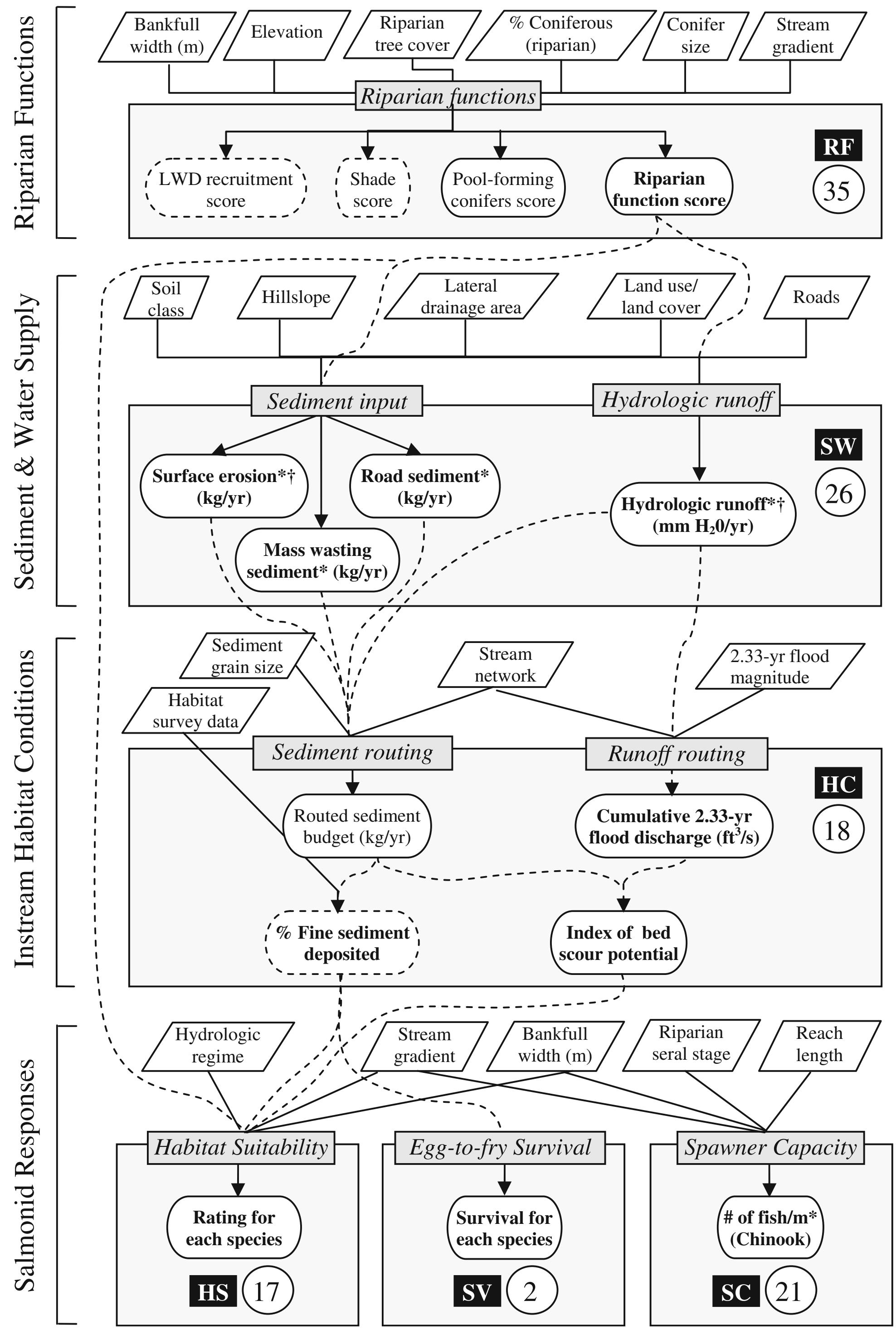

Fig. 1 Structure of the six ecological models evaluated (*shaded boxes*; see [36] for model descriptions), and number of parameters in each model (*circles to the right*). *Codes in black boxes* correspond with Table 1 to help identify parameters in each model. Data used by models were either derived independently from another source (e.g., landscape characteristics or other GIS data; *trapezoids connected with solid lines*) or were outputs predicted by one of these models (e.g., riparian function score; *ovals connected with dotted lines*). All predictions (*ovals*) were modeled for each individual stream reach. For sensitivity analyses, results were then summarized over all reaches historically accessible to winter steelhead (the most far-ranging species) for 13 predictions (ovals with bolded text; note that we summarized habitat suitability for three species). These output metrics were calculated as length-weighted reach averages or as sums of reach-specific values over all fish-accessible reaches (the latter are denoted by an asterisk). †Does not include WEPP model parameters (see text). Output metrics for which we had field data to validate are represented by *ovals outlined with a dotted line*

runoff, and road sediment models are adapted from the Water Erosion Prediction Project (WEPP [4]), and mass-wasting predictions are based on road density, land cover, and slope stability and verified by field surveys. Note that we did not evaluate parameters internal to the WEPP model, but we did evaluate parameters that quantified to what extent riparian conditions reduced the amount of predicted sediment and runoff reaching streams. The Instream Habitat Conditions model routes sediment and water contributed to each stream reach from the surrounding landscape and from an inverse-distance weighted area upstream to predict sediment transport and deposition rates. Substrate composition and bed scour are predicted from transport rates and local stream habitat survey data. The habitat suitability model combines species-specific spawning requirements (channel gradient, bankfull width, hydrologic regime) with anthropogenic effects (fine sediment in spawning gravels, altered riparian conditions) to predict spawning habitat suitability. The spawner capacity model uses remotely sensed (i.e., obtained from satellite data or areal photographs) riparian seral stage, bankfull width, and channel gradient to predict capacity for Chinook salmon spawners. Egg-to-fry survival for Chinook and coho salmon and steelhead are predicted from empirical relationships derived from meta-analyses of published relationships between percent fine sediment in spawning gravels and survival of eggs to fry [10].

We summarized predictions over all reaches accessible to anadromous fish to provide watershed-wide output metrics (depicted in Fig. 1). Several models yield multiple predictions (e.g., the Riparian Functions model predicts three individual responses plus a composite response), so we chose representative metrics from each model for evaluation. In certain cases, outputs from some models (e.g., riparian functions, sediment and water supply) were used as inputs to other models. These input data could have instead come from other sources such as independent external models, or empirical data if it existed. Although outputs from each model can be evaluated independently, in this study we evaluated uncertainty associated with parameters that both directly and indirectly (i.e., when model outputs were used as inputs) influenced predictions. Parameters in each model are listed in Table 1; due to the large number of parameters (119 total), we report only ones to which model outputs turned out to be sensitive.

2.2 Sensitivity Analysis

We used Monte Carlo simulations to evaluate how uncertainty in estimates of model parameters influenced predictions, both within and across models (objective #1). We created five ranges of input distributions, where error was assumed to be uniformly distributed around the original parameter value with the width equal to 10%, 20%, 30%, 40% or 50% of the nominal value. We used uniform distributions because we lacked data on the true underlying distributions. For each of the input distributions, we generated 500 samples to serve as input to the models. Each sample consisted of a set of parameter values, each drawn randomly and independently from its distribution. Using these datasets, we ran 500 simulations (applying the same set of parameters to all reaches in the watershed for a given run) and generated distributions of output metrics. We calculated the coefficient of variation of each output metric for each input distribution to compare the impacts of parameter uncertainty on model predictions.

To evaluate the relative effect of individual parameters on predictions (objective #2), we employed a quantitative sensitivity analysis using multiple linear regression [7, 27, 28]. We regressed each output metric generated from the Monte Carlo runs on all parameters for each input distribution (e.g., 10, 20, 30, 40, or 50% ranges). We used standardized-regression coefficients (SRCs) to evaluate the sensitivities of predictions to each parameter. SRCs were computed as $b\times(\mathrm{sd}\_x/\mathrm{sd}\_y)$, where b is the unstandardized regression coefficient, sd_x is the standard deviation of the parameter input values and sd_y is the standard deviation of the output. Standardization scaled the coefficients in units of standard deviations away from the nominal value [20], so that results were comparable across input distribution ranges. Final regression equations omitted parameters with a t-statistic less than 1 in absolute value (a p-value of about 0.3 for alpha=0.05). When input parameters are independent, as ours were, the square of each SRC is equal to the partial R^2, attributable to that factor in the model, and the squares are additive [7]. Values of $R^2>0.7$ suggest that relationships are linear enough to use regressions to assess sensitivities [29]. Thus, we assessed our regression models with R^2 using this benchmark. To protect against overfitting, we calculated the PRESS statistic (Predicted REsidual Sums of Squares) and checked to ensure that it decreased with the addition of each parameter to the model [7]. Once a final model was fit, we averaged the SRCs for models from all input distributions with $R^2>0.7$ to derive an estimate of the influence of each parameter on the variance of each output metric.

To see how uncertainty is distributed spatially (objective #3), we mapped standard error of predicted egg-to-fry survival for Chinook salmon (*O. tshawytscha*) in each stream reach. We chose this metric as an example because the model that predicts egg-to-fry survival is simple and has fewer parameters than other models. In calculating standard errors, we used results from the 50% input distribution to be sure to capture spatial patterns in case variance was low. We investigated the relationship of standard error of egg-to-fry survival with the predictor variable, percent fine sediment deposited. Together, this relationship and the mapped uncertainty should highlight areas where management activities would be most effective.

2.3 Field Validation

We used instream habitat data from six streams (~1 km each) surveyed throughout the Lewis River Basin in 2005 (this study) and ten streams surveyed in 2003 (J. Burke, University of Washington, unpublished data) to estimate how well predictions from ecological models matched observed values. With the exception of substrate data from 2003 (see next paragraph), these data were not used to develop the underlying models. The Lewis River is a tributary to the Columbia River. The basin has high (nearly 200 cm) annual precipitation and drains 2,760 km^2 of the

Table 1 Definitions, nominal (i.e., initial) values, and units of the 71 parameters (of 119 total) to which predictions were found by regression analysis to be most sensitive

Parameter	Definition	Nominal value	Units
Riparian functions RF			
RF3	Shade: bankfull width	30	m
RF4	Shade: total % cover threshold #1	80	%
RF5	Shade: total % cover threshold #2	50	%
RF7	Shade: total % cover threshold #4	40	%
RF8	Shade: total % cover threshold #5	30	%
RF15	Pool-forming conifer: stream gradient threshold #1	0.04	–
RF19	Pool-forming conifer: conifer tree size threshold #3	2	in
RF22	Large woody debris: total % cover threshold #1	30	%
RF23	Large woody debris: total % cover threshold #2	50	%
RF24	Large woody debris: % of trees that are coniferous #1	70	%
RF25	Large woody debris: % of trees that are coniferous #2	50	%
RF26	Large woody debris: % of trees that are coniferous #3	30	%
RF29	Large woody debris: conifer tree size threshold #1	20	in
RF30	Large woody debris: conifer tree size threshold #2	10	in
Sediment & water supply SW			
SW1	Road: unpaved width	7.5	m
SW2	Road: paved width	15	m
SW3	Road: % sediment entering stream (poor riparian)	100	%
SW4	Road: % sediment entering stream (fair riparian, ash soil)	38	%
SW5	Road: % sediment entering stream (fair rip., paved roads)	45	%
SW6	Road: % sediment entering stream (fair rip., unpaved rds)	46	%
SW7	Road: distance to stream multiplier	2.47	m
SW9	Road: sediment yield (paved roads, non-ash soil)	0.64	$kg/m^2/yr$
SW10	Road: sediment yield (unpaved roads, ash soil)	24.7	$kg/m^2/yr$
SW11	Road: sediment yield (unpaved roads, non-ash soil)	5.8	$kg/m^2/yr$
SW12	Mass wasting: sediment yield (upper East Fork)	0.0318	$kg/m^2/yr$
SW14	Mass wasting: sediment yield (upper North Fork)	0.106	$kg/m^2/yr$
SW15	Mass wasting: sediment yield (lower North Fork)	1.4337	$kg/m^2/yr$
SW16	Mass wasting: road density threshold #1	0.0031062	m/m^2
SW18	Mass wasting: % 20-yr forest	75	%
SW19	Mass wasting: % of area considered highly stable #1	10	%
SW20	Mass wasting: % of area considered highly stable #2	4	%
SW21	Mass wasting: % of area considered highly stable #3	2	%
SW23	Mass wasting: % of area considered moderately stable #1	20	%
SW25	Mass wasting: % of area considered of low stability #1	85	%
Instream habitat conditions[a] HC			
HC1	Hydro: increase in Q from timber harvest	0.08	%
HC2	Hydro: increase in Q from roads	0.2	%
HC3	Hydro: increase in Q in agriculture (grass cover type)	0.36	%
HC6	Hydro: road density threshold	0.0012	m/m^2
HC7	Routing: hydro runoff coefficient a1	3	–
HC8	Routing: hydro runoff coefficient a2	0.93	–
HC9	Routing: fine-sediment coefficient a1	0.311034	–
HC10	Routing: fine-sediment coefficient b1	0.592983	–
HC11	Routing: fine-sediment coefficient a2	37.00906	–
HC12	Routing: fine-sediment coefficient b2	0.248506	–
HC13	Routing: fine-sediment coefficient a3	12.0335	–
HC14	Routing: fine-sediment coefficient b3	−0.69944	–
HC15	Routing: coarse sediment coefficient a1	110.5471	–
HC16	Routing: coarse sediment coefficient b	0.178887	–
HC17	Routing: coarse sediment coefficient a2	−0.23795	–
HC18	Routing: coarse sediment coefficient a3	−0.05387	–
Habitat suitability HS			
HS2	Intrinsic potential: bankfull width threshold #2	10	m

Table 1 (continued)

Parameter	Definition	Nominal value	Units
HS3	Intrinsic potential: stream gradient preference #1	0.01	–
HS4	Intrinsic potential: stream gradient preference #2	0.02	–
HS5	Intrinsic potential: stream gradient preference #3	0.03	–
HS8	Intrinsic potential: stream gradient preference #6	0.07	–
HS9	Intrinsic potential: stream gradient preference #7	0.12	–
HS10	Intrinsic potential: stream gradient preference #8	0.16	–
HS12	Modified physical function: fine-sediment score #1	5.9	(binned)
HS13	Modified physical function: fine-sediment score #2	13.3	(binned)
HS15	Modified physical function: bed scour score #2	0.0606	(binned)
HS16	Modified physical function: bed scour score #3	0.0835	(binned)
HS17	Modified physical function: bed scour score #4	0.1182	(binned)
Spawner capacity **SC**			
SC2	Spawners per redd #2	2.33	# fish
SC5	Redds per km #2	36.4	redds/km
SC10	Redd area #2	15.25	m^3
SC12	Percent of reach that is spawnable	0.06243	%
SC14	Stream gradient #2	0.04	–
SC15	Bankfull width #1	5	m
SC17	Bankfull width #3	25	m
Egg-to-fry survival[b] **SV**			
SV1	Chinook survival coefficient #1—regression intercept	0.236642	–
SV2	Chinook survival coefficient #2—regression slope	0.128547	–

Codes in black boxes are abbreviations for each model, and correspond with Fig. 1, which depicts model structures

[a] Coefficients for routing sediment are from the following equations: (1) % Fine sediment=$a_1 P_F^{b\,1}$ $(1+a_2\text{VWI}^{b\,2}+a_3\text{QS}^{b\,3})$, and (2) Coarse fraction of sediment=a_1 D^b $(1+a_2 P_F+a_3\text{VWI})$, where P_F=percent of sediment <1 mm contributed from lateral hillslopes and from an upstream zone of influence, *VWI* valley width index, *QS* stream power, and *D* characteristic grain size

[b] Models also predicted survival for steelhead trout and coho salmon but were not included

western slope of the Cascade Mountain range. Natural disturbances have included forest fires and volcanic activity, and anthropogenic influences have included timber harvest, agriculture, residential development, and gravel mining [11]. Four species of federally listed anadromous salmonids are found in the watershed: Chinook, coho (*O. kisutch*), and chum salmon, and steelhead trout.

Stream habitat survey data included unit-specific (i.e., pool, riffle) measures of substrate composition (including percent fine sediment deposited in stream beds), counts of large woody debris, and percent of the stream shaded by riparian vegetation; see [23] for survey methods. Surveyed reaches were chosen to be broadly representative of conditions in the Lewis River Basin. Large woody debris was both modeled and observed for all 16 stream reaches. Observed substrate composition data from the 2003 surveys were used to parameterize the model predicting percent fine sediment deposited in streams. Therefore, we could only use substrate composition data from the 2005 surveys for validation of this metric. Shade was estimated in the field for the 2005 surveys only. For Chelatchie Creek, we recorded observations of percent fine-sediment deposition made by two independent observers.

Modeled and observed data were not directly comparable due to discrepancies in spatial resolution or in the way that data were represented (e.g., modeled categorical levels of good, fair, or poor versus numerical surveyed values). Thus, we did not compute any formal statistics, but instead compared results qualitatively. For large woody debris recruitment and riparian shade, we report whether the field observations fell within the range of model predictions. A translation step was required to compare modeled scores to observed values. For example, observed counts of large woody debris in the bankfull channel could best be compared to predictions by the riparian large woody debris recruitment sub-model, and observations of percent shade over streams due to riparian vegetation were compared to predicted riparian shade scores. We assumed that a modeled score of 'poor' (represented as a value of 1) indicates less than or equal to two pieces of large wood per 100 m, a score of 'fair' (value of 2) represented two to five pieces, and a score of 'good' (value of 3) represented greater than or equal to five pieces [21]. Similarly for shade, we assumed that a score of 'poor' represented <20% shade over the stream channel, a score of 'fair'=20–50%, and a score of 'good'=>50% [31]. These assumptions resulted in the following equations: (a) LWD score=0.884 ln(observed

LWD count)+1.0647, and (b) Shade score=0.8464 ln (observed % shade)−0.8039. Observed data were summed over the entire surveyed reach and compared to modeled data for the same stretch (if N>1 modeled reaches, we used a length-weighted average of modeled scores). To estimate the range of modeled predictions, we calculated the minimum and maximum predictions from the Monte Carlo simulations when variance of input parameters was set to 30% (the midpoint of the five input distributions we tested) for the same georeferenced stream reaches.

3 Results

3.1 Sensitivity Analysis

Certain model output metrics (e.g., 2.3-year flood discharge, hydrologic runoff, riparian functions, and habitat suitability) exhibited little variation, regardless of the amount of uncertainty in parameters (Fig. 2). The coefficients of variation for these metrics were linearly related to input distribution ranges. Variances in other metrics, most notably bed scour, were highly influenced by even low levels of uncertainty in input distributions, and relationships appeared to increase exponentially.

Average R^2 values were greater than 0.75 for nearly all output metrics analyzed with the regression analysis (Table 2), suggesting that the models were largely additive and that multiple linear regression was an appropriate method of sensitivity analysis. The only model regressions with an R^2 less than 0.7 were bed scour using input distribution ranges of 30%, 40% and 50% (R^2=0.66, 0.52, and 0.52, respectively). In seven out of the 13 output metrics, R^2 was at least 0.9 for all regressions. Of the initial 119 parameters, model output was sensitive to 71 (60%). Parameters that had |SRC| >0.1 were limited to 52 (44%), with only 11 (9%) having |SRC| >0.5. Sensitive metrics were directly or indirectly influenced by fewer than half of the parameters (Table 2). Predicted riparian conditions were sensitive to 34% of parameters, sediment from surface erosion to 17%, hydrologic runoff to 17%, sediment from roads to 30%, sediment from mass wasting to 20%, percent fine sediment deposited to 23%, bed scour to 8%, 2.3-year flood discharge to 9%, habitat suitability (spring Chinook) to 32%, spawner capacity to 41%, and egg-to-fry survival to 21%.

Riparian function output was sensitive to parameters in the shade and large woody debris sub-models, especially those related to the amount of canopy cover (RF4, RF5) and the percent of cover that was coniferous (RF24), but not to parameters in the pool-forming conifer sub-model (Table 2). Out of 35 step-function parameters in riparian models, outputs were at least weakly sensitive to only seven parameters (20%). Surface erosion (both sediment and hydrologic runoff) were sensitive to riparian parameters describing total canopy cover (RF5, RF22) and the proportion of cover that was coniferous (RF25). Note again that we did not test parameters internal to the WEPP model, which predicted inputs for surface erosion and runoff. The amount of sediment coming from roads was most sensitive to width of unpaved roads (SW1), sediment yield coming from unpaved roads (SW11), distance of roads from streams (SW7), and the degree to which riparian conditions could reduce sediment from unpaved roads (SW6). The amount of sediment contributed by mass wasting was most sensitive to parameters relating to sediment yield expected from the upper North Fork (SW14), the amount of hillslope area in various stages of stability (SW19, SW23, SW25), as well as road density (SW16). The 2.3-year flood discharge was most sensitive to parameters related to road density (HC2, HC6). Fine-sediment deposition predictions were sensitive to the fine sediment coefficients b3 (HC14) and a1

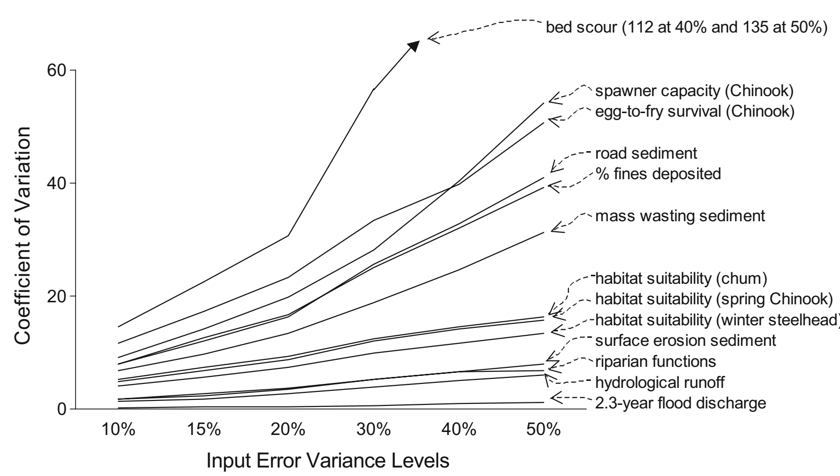

Fig. 2 Coefficients of variation for each model output metric across the five ranges of input distributions (i.e., uncertainty in parameters)

Table 2 Results of multiple regressions indicating parameters to which predicted output metrics were sensitive (|SRC|>0.1)

Output metric	R^2	Total[a] no. sensit. params.	Highly sensitive (|SRC| >0.5)	Moderately sensitive (|SRC| 0.3–0.5)	Weakly sensitive (|SRC| 0.1–0.3)
Riparian	0.897	12 of 35 (35)	RF4 (−0.611)	RF24 (0.455) RF5 (−0.348)	RF29 (−0.240) RF30 (−0.219) RF26 (0.155) RF8 (−0.119)
Sediment from surface erosion	0.839	6 of 35 (0[b])	RF5 (0.543)	RF25 (0.452) RF22 (0.423)	RF26 (−0.331)
Hydrologic runoff	0.850	6 of 35 (0[b])	RF5 (0.556)	RF22 (0.456) RF25 (0.389)	RF26 (−0.286) RF8 (0.218) RF24 (−0.129)
Sediment from roads	0.972	14 of 46 (11)	SW1 (0.632)	SW11 (0.475) SW7 (0.365) SW6 (0.352)	SW3 (0.183) SW10 (0.151) SW4 (0.130)
Sediment from mass wasting	0.850	10 of 50 (15)		SW14 (0.408) SW23 (−0.377) SW19 (−0.366) SW16 (−0.326) SW25 (0.304)	SW15 (0.232) SW12 (0.228) SW18 (0.217) SW20 (−0.151)
2.3-year flood discharge	0.997	6 of 69 (8)	HC2 (0.913)	HC6 (−0.302)	HC1 (0.139) HC8 (0.135) HC7 (0.107) HC3 (0.102)
% Fines	0.986	17 of 75 (14)	HC14 (−0.650) HC9 (0.538)		HC13 (0.290) HC10 (−0.288) HC11 (0.239) HC12 (0.130)
Bed scour	0.759	6 of 79 (18)	HC18 (−0.618)	HC15 (−0.478)	HC17 (−0.238) HC16 (0.174)
Habitat suitability for steelhead, Chinook, and chum	0.964 0.963 0.967	28 31 30 of 96 (17)	HC15 (0.714, 0.713, 0.705)	HC18 (0.408, 0.408, 0.432)	HS16 (0.209, 0.200, 0.190) HC9 (−0.197, −0.193, −0.184) HC10 (0.158, 0.156, 0.138) HC16 (−0.138, −0.141, −0.146) HS13 (0.140, 0.142, 0.129) HS15 (0.133, 0.148, 0.171) HC17 (0.115, 0.115, 0.115) HC11 (−0.120, −0.117, −0.113) HS2 (−0.107, n/a, n/a)
Chinook spawner capacity	0.955	7 of 17 (17)	SC2 (0.606) SC10 (−0.514)	SC12 (0.496)	SC15 (−0.187) SC14 (0.165 SC5 (0.105)
Chinook egg-to-fry survival	0.985	16 of 77 (2)	SV2 (−0.534) HC9 (−0.533)	HC10 (0.410) HC11 (−0.317)	HC14 (0.285) HC13 (−0.207) HC12 (−0.123)

SRC Standardized regression coefficients. See Table 1 for parameter definitions.
[a] Number of parameters to which results were sensitive (i.e., |SRC|>0), out of the total number of parameters capable of influencing each metric (both directly and indirectly through other models); the number of parameters capable of directly influencing each metric is in parentheses.
[b] Does not include WEPP model parameters (see text); influenced indirectly by riparian parameters.

(HC9; coefficients obtained from regression to a calibration data set), and bed scour was most sensitive to coarse sediment coefficients a3 (HC18) and a1 (HC15; Table 2).

Habitat suitability predictions were sensitive to a similar set of parameters for each species evaluated (Table 2). These results were more dependent on parameters that predicted how sediment was routed (effects of bed scour were largest; HC15 and HC18) than on step-function parameters related to bankfull width, stream gradient, or riparian functions. Chinook salmon spawner capacity was most sensitive to local fish population characteristics (e.g., spawners per redd (SC2), redd area (SC10), and percent spawnable (SC12)). These were more sensitive than stream gradient or bankfull width, and riparian seral stage had no influence. Chinook salmon egg-to-fry survival was sensitive to the slope of the relationship between survival and fine sediment (SV2) as well as indirectly to fine-sediment deposition parameters (HC9, HC10, and HC11) in the habitat conditions model.

When examined reach-to-reach, we found that prediction certainty varied spatially for Chinook salmon egg-to-fry survival (Fig. 3a,b). Uncertainty was highest when fine-sediment deposition was approximately 10 to 20% (Fig. 3c). When sediment was higher than this range, survival dropped quickly and when sediment was <10% fines, survival was predicted to be high. Within the 10–20% range, spatial variance was highest because this is where the predictive relationship exhibited a threshold effect. Thus, spatial differences in landscape characteristics that influenced sediment deposition in the 10–20% range correlate to spatial uncertainty for this metric. Predictions were less variable in the lower basin, where low-gradient channels are surrounded by altered landscapes (e.g., urban, rural residential, and agriculture) and sediment inputs are higher than in high-gradient channels with vegetated landscapes in the upper basin (Fig. 3a). We found no relationships between prediction standard error in sub-basins and sub-basin area, stream length, or stream density.

3.2 Field Validation

Fine-sediment deposition values were within predicted ranges for all six reaches for which we had data. Four of the six streams for which we visually estimated shade had values within the range predicted by models. Observed counts of large woody debris were within modeled ranges for half (8 of 16) of the stream reaches (Table 3).

Observations of percent fine-sediment deposition in Chelatchie Creek made by two observers differed for some habitat types (scour pools, plunge pools, and riffles), but were similar for others (glides and dam pools). Average differences between observer estimates ranged from 4% (glides) to 30% (plunge pools); only eight of 34 individual habitat unit estimates differed by more than 25%. Differences between observer estimates did not appear to be related to type of habitat unit.

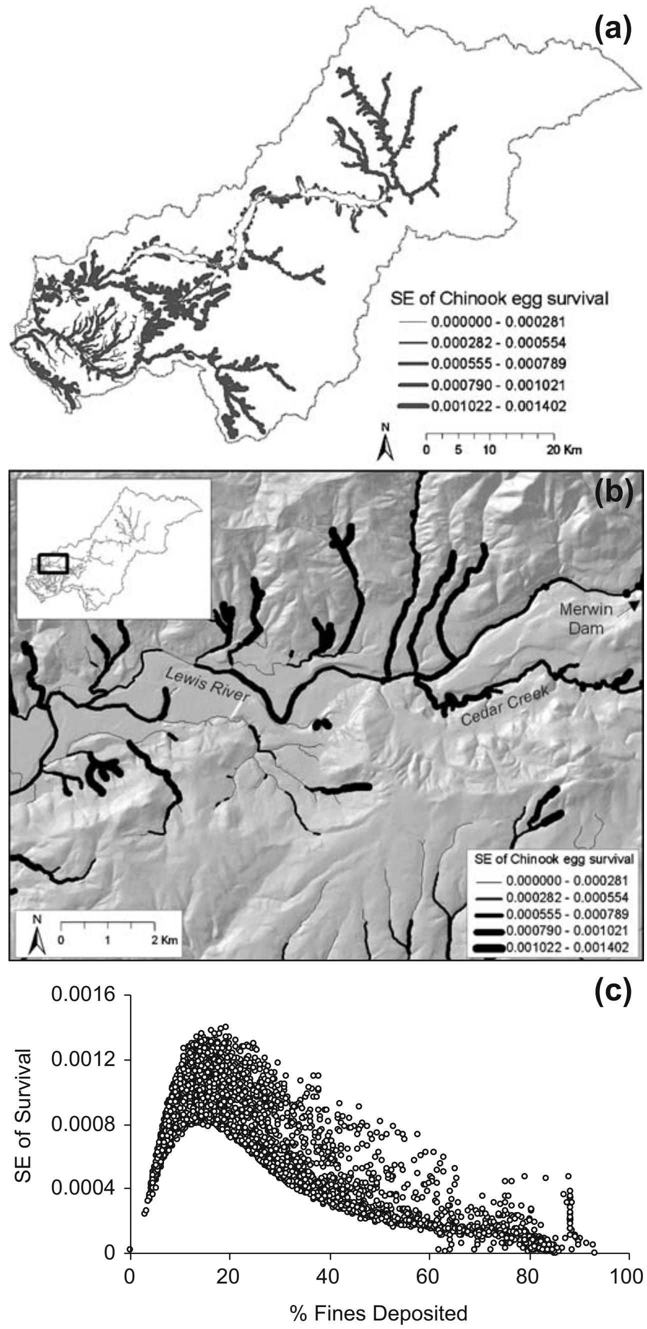

Fig. 3 Spatial distribution of uncertainty (standard error, SE, represented by line thickness) in predictions for Chinook salmon egg-to-fry survival, shown (**a**) throughout all reaches in the Lewis River Basin accessible to anadromous fish and (**b**) as a close-up in the lower watershed. The graph (**c**) depicts standard error of egg-to-fry survival predictions in relation to the primary predictor, percent of stream beds covered in fine sediment

4 Discussion

4.1 Insights from Sensitivity Analyses

Multiple approaches exist for evaluating sensitivity of predictions to uncertainty in model components. The most thorough approach is a variance-based global sensitivity analysis [27, 32], which partitions variation into that caused by main effects and that caused by interactions. This type of analysis can be unwieldy if models are very complex. However, if a model is expected to be linear, a regression analysis provides a quantitative sensitivity analysis where regression coefficients indicate the effect of varying that particular parameter away from the nominal value by a

Table 3 Comparison of instream habitat conditions assessed from field surveys and models

Stream	Year	Length (km)	LWD[a]		Shade		% Fines	
			Obs.	Pred.	Obs.	Pred.	Obs.	Pred.
Chelatchie Creek	2005	1.17	1.1	2–3	1.7	1.3–2.5	27[b]	15–58
Lockwood Creek	2005	0.73	1.3	1–2.8	2.5	2–3	29	9–30
Muddy River	2005	0.39	1.2	1–1.7	1.6	1–1.7	12	7–23
Rock Creek (EF)	2005	0.86	0.9	1–2	2.4	1–2	17	10–34
upper Siouxon Creek	2005	0.90	1.8	2.2–3	2.8	2–3	6	2–11
Smith Creek	2005	0.20	1.8	1–2	0.1	1–2	14	7–22
Clear Creek	2003	1.12	3	2–3	–		–	
Copper Creek	2003	1.95	1.6	1.8–2.5	–		–	
EF Lewis River	2003	0.87	0.1	1–3	–		–	
Johnson Creek	2003	1.49	2.1	1–3	–		–	
Mason Creek	2003	1.20	0.1	1–3	–		–	
Miller Creek	2003	0.60	2.6	1.4–2.8	–		–	
NF Lewis River	2003	0.358	0.9	3	–		–	
Pine Creek	2003	2.13	1.6	1–3	–		–	
Rock Creek (NF)	2003	1.42	0.1	1.8–2.9	–		–	
lower Siouxon Creek	2003	0.91	1.2	2–3	–		–	

LWD Counts of large woody debris per 100 m, *Shade* percent shade over stream due to riparian canopy cover, and *%Fines* percent fine sediment (<1 mm) in the substrate. For comparison, large woody debris counts and riparian shade percentages observed in survey data were represented as scores predicted by models. Ranges for predictions were based on Monte Carlo runs where variance in parameter distributions was set to 30%. Shade was not assessed in 2003, and fine-sediment data from 2003 were used to parameterize models and therefore could not be used to assess model accuracy.

[a] Observations were counts in stream channels whereas predictions were for recruitment rates

[b] Represents the average of two observers

fixed fraction of its variance [2]. The models we evaluated were highly linear, as evidenced by R^2 values close to unity for several metrics, and all mean R^2 values>0.75. In fact, the top three most sensitive parameters found by regression analysis agreed well with preliminary analyses using other sensitivity analysis approaches (A. Fullerton, unpublished data). We found that R^2 values declined with increasing parameter uncertainty. For most of these, the decrease in R^2 was not substantial and the SRCs were fairly constant. In others, particularly bed scour, the decrease in R^2 was substantial (to a low of 0.52 at 50% parameter uncertainty) and some changes in SRCs were observed when uncertainty increased. This suggests that there were either some interactions or nonlinearities occurring at higher levels of uncertainty which cannot be investigated using regression methods.

A limitation of our approach is that we used uniform distributions for parameter uncertainty because we lacked information on true parameter distributions. It is likely that some parameters are more uncertain than others. Several ways in which uncertainty estimates could be improved include (1) convening a panel of experts, (2) collecting more empirical data in the basin, (3) fitting parameters from statistical correlations in similar basins, or (4) conducting uncertainty analysis on cross-combinations of uncertainty levels using best-available distributions (e.g., hold uncertainty at 10% for one parameter and vary the others across all levels of 10%, 20%, 30%, and 50%). Despite this limitation, we feel that our approach provided a general assessment of the effect of uncertainty on modeled predictions.

Understanding how certain we are about parameters is clearly important for interpreting predictions. Our analysis indicated that less than half of the parameters in the six models we evaluated contributed to uncertainty in predictions in the Lewis River Basin. Six parameters to which model output was most sensitive (|SRC|>0.5) affected multiple output metrics. Three were parameters describing riparian canopy thresholds—percent cover (RF22 and RF5) and percent coniferous (RF25)—and three were coefficients in the Habitat Conditions model—a multiplier of incoming fine sediment (HC9), and multipliers of sediment grain size (HC15) and valley width index (HC18). Assessing accuracy of these parameter values could be a relatively inexpensive way to improve model performance.

It is tempting to identify sensitive parameters as the most important or most influential, but it is essential that model users distinguish between parameters to which outputs were sensitive and parameters that are ecologically important. A parameter insensitive to uncertainty may be a very important part of our mechanistic understanding of ecosystem processes and their contribution to population viability (see, e.g., [38]). If we have reasonable evidence that a relationship exists in nature but do not see sensitivity of results to parameters in that relationship, we should reconsider whether the model was developed to adequately represent the relationship. For example, sensitivity analysis of the Ecosystem Diagnosis and Treatment (EDT) model [16, 37] found little sensitivity of predictions to habitat parameters, yet biologists firmly believe that habitat features such as flow contribute significantly to salmon population performance. As a direct response to their sensitivity analysis results, the Bureau of Reclamation developed support models for EDT in the Yakima River Basin to provide increased precision to modeled stream attributes most influenced by changes in flow [37]. Barring this possibility for the models we evaluated in the Lewis River Basin, parameters with $|SRC| < 0.1$ (i.e., those not listed in Table 2) could reasonably be either removed from models or set to static values, since predictions were not sensitive to their values. This would reduce model complexity considerably, yet it is unclear whether predictions would be sensitive to these parameters under other conditions where values of input data may be beyond the range we tested.

The influence of a parameter is related to the spatial extent and accuracy of input data estimates (see Fig. 1 for input data used by each model). We did not assess this source of uncertainty, but it should be evaluated before these models are used in other watersheds for two reasons. First, predictions may be sensitive to uncertainty in input data. For example, the remotely sensed data that were used to model vegetation in the Lewis River watershed classified riparian areas as largely coniferous in the upper watershed. It is likely that at a higher resolution we would find riparian areas dominated with deciduous or mixed forests. If vegetation was classified this way, models would rate such areas lower quality for riparian functions. Second, because model input data may differ substantially in other watersheds, predictions may be sensitive to different parameters in another area. For example, in the Lewis River watershed, sediment entering streams from roads was much greater in magnitude than sediment coming from mass wasting or surface erosion; thus, parameters describing the contribution from roads would be expected to be more sensitive to uncertainty than those from other sources of erosion. But in another basin where sediment is contributed more by natural processes than by roads, the sensitivity of parameters relating to roads may be reduced. For these reasons, models should be adapted to the extent possible and tested under appropriate local conditions before being simplified.

Our analyses have identified ways to improve these models in the Lewis River Basin, but have also elucidated several insights for future model development in general. First, characterization of sensitivity of predictions to different types of uncertainty should be incorporated in model construction from the start. By identifying how to reduce model complexity and improve precision and accuracy, a more robust model can be developed in the next iteration. Second, estimates of uncertainty and expected variability should be included as standard model outputs (e.g., as prediction intervals). Consideration of which measures of uncertainty will best aid interpretation and use of model results can influence model design. For example, it may be equally important for decision-makers to understand how model results represent natural variability in addition to prediction uncertainty contributed by other factors.

4.2 Spatial Distribution of Uncertainty

In the Lewis River Basin, variance in predictions was unevenly distributed spatially, with less sensitivity in the lower part of the river basin. This might simply reflect the magnitude of predicted values; i.e., we would expect lower variance in predictions if the value being predicted is low. For example, egg-to-fry survival for Chinook salmon was predicted to be poor in the lower watershed in lower gradient areas where sediment scoured from higher gradients is deposited, and where concentrated roads contribute high levels of sediment; we would expect these predictions to be more certain than those in areas where survival is expected to be high (e.g., where sediment levels are below or near critical survival thresholds). Alternatively, we would expect predictions in less disturbed areas to have higher variance due to higher levels of landscape complexity and habitat heterogeneity (or possibly due to paucity of data in this part of the range). This result again emphasizes that the range of input data affects the sensitivity of predictions. Identifying spatial uncertainty allows targeting data collection in areas that will improve model precision. In the Lewis River Basin, this means collection of more data in areas where fine-sediment deposition is predicted to be 10–20%.

Such spatial effects can alter the usefulness of modeled data, depending on the spatial scale at which predictions are being used. For example, if the resolution of interest is individual stream reaches (1–10 km), uncertainty in modeled predictions may be too large to make predictions useful for making decisions (e.g., in locating individual restoration projects). However, if predictions are made over a range of 10–100 km, predictions can elucidate influential regional trends that may affect project performance, and at the scale of >100 km (i.e., at the watershed or subwatershed level), spatial uncertainty may be less important.

4.3 Field Validation

We found reasonable agreement between observed and modeled data for the few streams for which we had empirical data. Several factors limited our ability to do a more rigorous validation. The most serious problem was that we had very small sample sizes of stream survey data (N=6 to 16). Other than this small dataset, basin-specific data do not exist at an appropriate spatial resolution for most instream habitat characteristics that were modeled (e.g., bed scour, riparian functions, substrate composition, large woody debris, and flow). Lack of empirical data on instream habitat characteristics is a common problem. Busack and Thompson [1] evaluated the quality of data for ten Puget Sound (Washington, USA) watersheds that were used as inputs to the Ecosystem Diagnosis and Treatment model (EDT; [12, 18]). Categories of data quality ranged from empirical to purely hypothetical or expert opinion. They found that for most data types evaluated, only one-quarter or less of model inputs were based on empirical data. When the EDT model was applied in the Lewis River Basin, about two-thirds of these characteristics were estimated by experts or derived from theory [3]. The paucity of empirical data is precisely why models are often used to make management decisions, and is also why testing models is essential.

In many cases, even when data are available, there is a spatial disconnect between the resolution of empirical data and predictions, or a difference in the way data are represented. Field observations may be collected over hundreds of meters or only at point locations whereas modeled predictions may be for thousands of meters. A problem we encountered was that we were unable to directly compare modeled and observed data due to a difference in metrics. For example, field observations of large woody debris consisted of counts of wood in stream channels whereas predictions were for relative recruitment rates from riparian areas. Although these metrics are related, wood in channels can include old pieces that predate the current stand (e.g., [9]), pieces carried to the channel by mass wasting from outside the riparian zone (e.g., [26]), and fluvial transport from upstream (e.g., [14]), all of which can confound correlations between current riparian stand type and instream wood counts and complicate efforts to quantify uncertainty. And finally, empirical data are subject to generally unquantified measurement error and observer bias [33], as we found when two biologists independently estimated percent fine sediment in Chelatchie Creek.

Users cannot assess model results if predictions cannot be compared to observations due to lack of empirical data or differences in currency or spatial resolution. These points compel us to suggest that models be built with components that can be validated. Early in model design, as the quantities to be predicted are decided on, it is important to consider how these predictions can be tested, given the format of available or easily obtainable data. It is often not possible to completely validate model results; after all, one goal of such models is to estimate quantities that cannot be measured (e.g., future population levels), but our ability to assess and interpret model results will be improved if we include components whose predictions can be compared to observations. Additionally, modelers should demand that collection of field data used to parameterize models include quantification of observer error, measurement error, and natural variability. By partitioning error to its various components, users can better identify how model precision can be improved such as by increasing sample size or implementing observer training.

4.4 Management Implications of Uncertainty

An understanding of uncertainty in modeled data (i.e., the potential magnitude of model errors) can be used to improve management decisions in several ways. First, when models include estimates of input errors (e.g., using Monte Carlo simulations), the resulting distribution of predictions can provide more robust information about the likelihood of a particular outcome [35]. Restoration decisions are classically based on analyses that compare point estimates of means (e.g., a particular set of reaches having 3.2 times less fine sediment than another set of reaches). If managers instead used the entire distribution of predictions, they would be able to estimate the likelihood of exceeding a critical threshold. For example, it might be more useful to say that given estimated uncertainty in the model, there is a 63% chance of exceeding 10% fine-sediment deposition, a value above which egg-to-fry survival declines rapidly. In the Lewis River Basin, our analyses can suggest which management approaches are “sure bets” and which have too much uncertainty associated with them to be useful. We are more certain that management strategies that focus on reducing sediment input to improve egg-to-fry survival will be successful than we are of strategies that focus on improving bed scour conditions because of greater variability in predictions for the latter. This insight would not have been possible without sensitivity analyses; management decisions would have had to be made using only point estimates.

Second, by using multiple models to make predictions and assessing a variety of output metrics, managers will rely less on any one model and the accuracy of its inputs. Rather, decisions can be made based on what the majority of models (or metrics) suggest. When decisions are based on multiple models, it is not necessary to have a model that is complex enough to be biologically realistic. For example, we found that predictions from many of the models using step functions were fairly insensitive to the choices of thresholds between steps. If these models were instead mathematical equations, we may have found additional parameters to which outputs were sensitive. However, this simple solution provided predictions that were relatively robust to the choice of the exact step, and in combination with other metrics can increase decision accountability. Also, by including models that predict multiple response metrics, managers can further boost their confidence because we are often more certain about some relationships than others. Compare, for example, the level of uncertainty associated with egg-to-fry survival and spawner capacity with the lower uncertainty in many of the habitat metrics in Fig. 2. Predictions about habitat conditions are based on fundamental relationships that are well understood whereas predictions about fish populations are based on estimates that are often quite uncertain, and are often based on a larger number of inputs.

A final way to acknowledge model uncertainty is to predict a variety of alternate future scenarios, since the exact future is unknowable [24]. Due to the paucity of empirical data, models are an inevitable part of the decision-making process. The issue that remains is not whether or not to use models, but how to incorporate uncertainty into predictions. Ultimately, the utility of using models like the ones analyzed here to help make management decisions will depend on the willingness of managers to acknowledge data and model limitations [6, 30] and to embrace uncertainty information (e.g., by asking that predicted restoration action responses be stated as probabilities of success). Uncertainty in modeled predictions, if communicated clearly (i.e., framed as probabilities), should not be a reason for stalling on important decisions [8, 13].

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