FEATURE:
FISH HABITAT

Making the Best Use of Modeled Data: Multiple Approaches to Sensitivity Analysis of a Fish-Habitat Model

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ABSTRACT: Fisheries management has become increasingly dependent on large and complex models; however, tools and technologies for model evaluation have lagged behind model development and application. Sensitivity analyses can test the degree to which particular model inputs or internal parameters affect model outputs and are recommended in model construction, calibration, and assessment. We describe three parallel sensitivity analyses of the Ecosystem Diagnosis and Treatment (EDT) model and draw combined conclusions. The details of how each agency conducted and utilized sensitivity analyses are outlined and the trade-offs between simpler and more intensive sensitivity analyses are described. Combined insights on the EDT model include identification of input parameters to which the model is surprisingly insensitive and quantification of prediction intervals. We conclude that known uncertainties in input data and internal parameters lead to large prediction intervals around estimates of population abundance and productivity but that the identification of high priority reaches for restoration and protection is relatively robust to these uncertainties. We recommend that sensitivity analyses are applied to all models used in fisheries management.

Haciendo mejor uso de los datos: múltiples enfoques al análisis de sensibilidad de un modelo de hábitat en peces

RESUMEN: El manejo de pesquerías se ha vuelto cada vez más dependiente de modelos grades y complejos; sin embargo, las herramientas y tecnologías para evaluarlos se han mantenido rezagados con respecto a su desarrollo y aplicación. Los análisis de sensibilidad, por un lado, pueden probar a qué grado los parámetros o entradas de un modelo en particular afectan las salidas y, por otro, se recomienda aplicarlos durante la construcción, calibración y evaluación del modelo. Aquí se describen en paralelo tres análisis de sensibilidad sobre el modelo de Tratamiento y Diagnóstico de Ecosistemas (TDE) y se llega a conclusiones comunes. Se destacan los detalles de cómo las agencias condujeron los análisis de sensibilidad y se describe el balance entre sus formas simples y complejas. Una introspección combinada de estos análisis aplicados al TDE incluye la identificación de aquellos parámetros de entrada a los que el modelo es particularmente insensible y la cuantificación de intervalos de predicción. Se concluye que tanto incertidumbre conocida en los datos de entrada como los parámetros internos dan como resultado amplios intervalos de predicción con respecto a las estimaciones de abundancia poblacional y productividad, pero la priorización de la restauración y protección es relativamente robusta a dicha incertidumbre. Se recomienda que los análisis de sensibilidad se apliquen a todos los modelos de manejo de pesquerías.

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INTRODUCTION

Fisheries management has become increasingly dependent on large and complex models. Such models are developed to help natural resource managers address complex issues by providing the estimates of ecosystem parameters or biological response that are necessary for making fisheries and habitat decisions. The challenge for scientists and managers is to develop models that enable informed and transparent decisions based on available scientific information, which is generally imperfect. The EcoPath/EcoSim framework, for example, has been used to study and understand foodwebs in hundreds of marine systems (Pauly et al. 2000 **QUERY: not in references**). ALFISH is a spatially explicit, age-structured model to explore fish density dynamics that has been applied in the Everglades (Gaff et al. 2004). Ihe Atlantis modeling framework, developed in Australia, has been employed to support integrated oceans management (Smith et al. 2007). These models are diverse but share a dependence on large numbers of parameters with complex interactions.

Advances in computing and mathematics have enabled such models to grow increasingly complex; however, tools and technologies for model evaluation have lagged behind model development and application. Sensitivity analyses provide objective criteria with which to evaluate model output, allowing users to explore how uncertainties in inputs and in parameter values propagate through the model. The results of sensitivity analyses can be used to provide more detailed model outputs, e.g., confidence intervals or precision estimates, to refine the model structure by removal of unnecessary parameters, and to improve the way modeled results are used to make decisions.

We employed a variety of sensitivity analysis techniques in the evaluation of a complex model used throughout the Pacific Northwest for salmon recovery planning, Ecosystem Diagnosis and Treatment (EDT). Sensitivity analyses were completed by three public agencies and provide an ideal opportunity for exploring the appropriate use of modeled predictions in salmon recovery and freshwater restoration planning, in specific, and environmental management in general. In this article, we explain sensitivity analyses and describe the EDT model before presenting three different sensitivity analyses of the EDT model (Table 1). In conclusion, we make explicit the trade-offs between these three types of sensitivity analyses, synthesize findings about the EDT model, draw conclusions about multi-agency analyses, and make recommendations about the use of sensitivity analyses for large and complex models.

SENSITIVITY ANALYSIS

Sensitivity analyses test the ability of inputs (data input into the model such as empirical observations), parameters (estimated relationships within the model), and model components (smaller sub-models or sets of parameters within the larger model) to affect model outputs and are a standard technique used in model construction, calibration, and assessment (Saltelli et al. 2000a). Sensitivity analyses can aid decision-makers by highlighting those inputs and components with the largest influence on the outputs. They are recommended when model output is used for decision making (Haefner 2005; ISAB 2001) and often provide insights into how the model arrived at a particular prediction and into potential biases in predictions. A further goal of sensitivity analyses is often to reduce the uncertainty in model output. In this case, a sensitivity analysis can identify those input factors or model parameters that, if measured more precisely, would provide the greatest reduction in model output uncertainty.

A useful byproduct of sensitivity analyses can be the estimation of the distribution of modeled outputs, often estimated through Monte Carlo simulations, which would result from incorporation of particular uncertainties. In this article, we refer to the percentile bounds, e.g., 90%, of that output distribution as a prediction interval; these bounds describe the range of predictions that the model produces when a set of known uncertainties are incorporated. As a practical matter, using a distribution of inputs rather than a single-point estimate illustrates that a given model will produce a range of predictions

Table 1. Comparison of EDT sensitivity analyses completed by three agencies.

Agency	U.S. Bureau of Reclamation	Washington Department of Fish and Wildlife	NOAA Fisheries
Parameters varied **Region (species)**	Stream attributes Naches River (summer steelhead); Naches river (spring Chinook); American River (spring Chinook)	Stream attributes (All Puget Sound watersheds)	Stream attributes, habitat survival rules, benchmarks, adult parameters, all other internal parameters, East Fork Lewis River (fall Chinook), Snoqualmie River (fall Chinook), Germany Creek (coho), and Washougal River (winter steelhead)
Scale of sensitivity analysis	One at a time	All parameters simultaneously; groups of related parameters	All parameters simultaneously; groups of related parameters
Type of alternate parameter value selection	Systematic	Monte Carlo	Monte Carlo
Least sensitive parameters	Hydrologic regime natural, Hydrologic regime regulated, all flow attributes, Habitat-off-channel	Macroinvertebrates	Habitat inputs, internal habitat survival relationship parameters

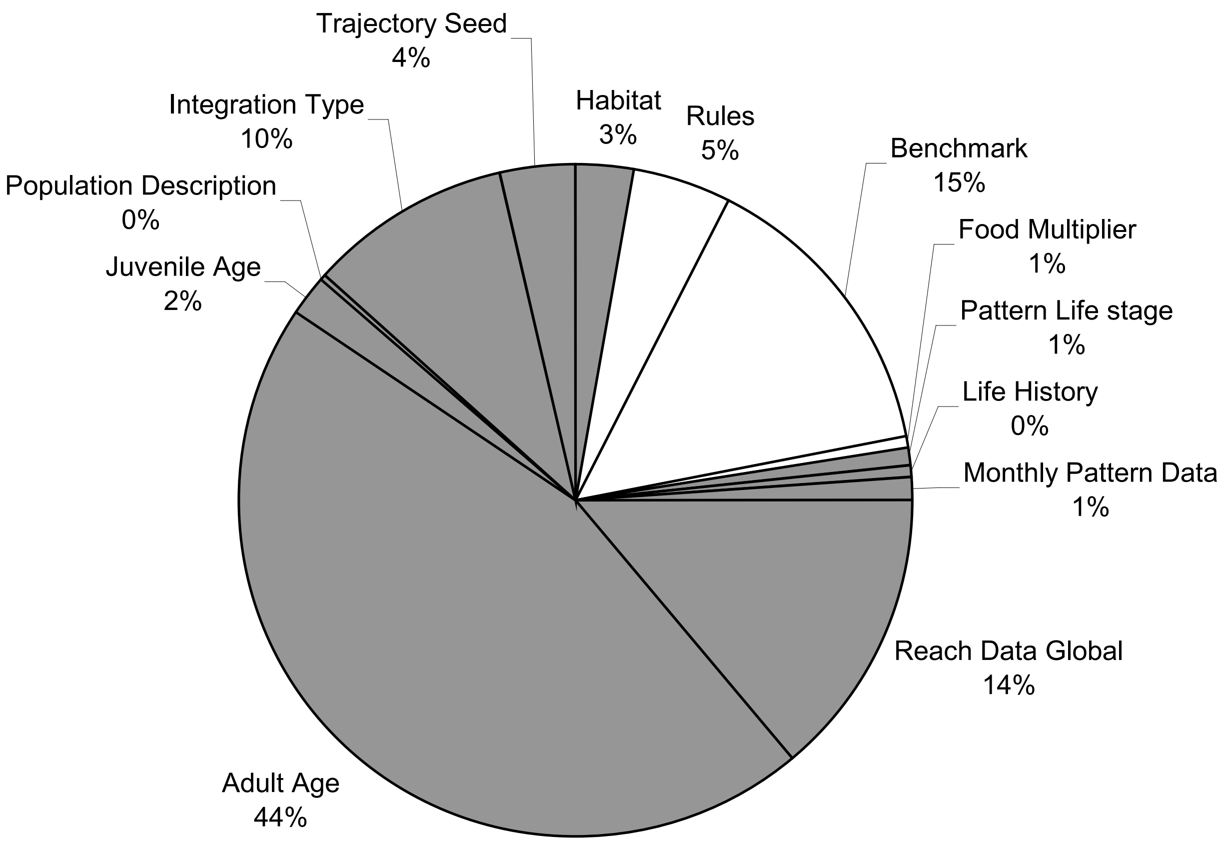
when all feasible inputs are considered. When modeled output is then used to estimate the effects of an on-the-ground action or group of actions, a decision-maker can make a better decision by considering the full range of plausible model outputs.

Consider an example application. In the Puget Sound Salmon Recovery Plan Executive Summary (Shared Strategy Development Committee 2007), EDT was used to predict that dam removal will improve North Fork Nooksack River Chinook salmon (*Oncorhynchus tshawytscha*) abundance by 30.8%. Managers tasked with deciding whether to invest in dam removal or other suites of habitat restoration actions would benefit from knowing (a) the range of modeled abundances given uncertainties in user input and internal model parameters, (b) whether and how often the model would predict a population decline post-dam-removal if uncertainty in all model parameters were considered, and (c) the likelihood that the model might have predicted an even more dramatic improvement in fish population performance. For example, should the value of 30.8% be interpreted to mean a range from 30.1 to 40.2% or from –10 to 70%?

There are a variety of methods for sensitivity analysis (Saltelli et al. 2000a). Local analyses, which alter factors "one at a time" (OAT), are the simplest to produce because all parameters, except those specifically being evaluated, are held constant. OAT analyses can determine how uncertainty in any one parameter or in any one input impacts model output but they ignore interactions among parameters. Often the results of an OAT sensitivity analysis can be calculated analytically but computer simulations may be necessary for complex models. Global analyses generally are more difficult to produce; they evaluate output uncertainty when all (or many) input factors are altered simultaneously. Variance partitioning methods take this a step further, producing an estimate of the proportion of the output variance attributable to each input factor. These methods are computationally demanding for complex models (Saltelli et al. 2000a) and have rarely, if ever, been applied to ecological models used in a management context.

Note that sensitivity analyses, in general, cannot estimate model accuracy (the distance between modeled output and the truth) but, rather, model precision (similarity of repeated model runs given a set of uncertainties which might include model structure, parameters, or inputs). In this article, we will report on three different and independent OAT analyses completed by the U.S. Department of the Interior/Bureau of Reclamation (Reclamation), the Washington Department of Fish and Wildlife, and the National Oceanic and Atmospheric Administration Fisheries Service (NOAA Fisheries) as well as global analyses completed by NOAA Fisheries. Because of the complexity of the EDT model, no agency evaluated whether the overall model structure was realistic nor did any agency

Figure 1. Results of the variance partitioning for the East Fork Lewis River, Washington, fall Chinook abundance (without harvest). The size of each pie wedge represents the proportion of total model output uncertainty (total effects) attributable to that group of parameters. Parameter groupings identified in white are internal parameters that do not vary from basin to basin. Solid shading indicates parameter groupings which model users can modify when running the model in a particular basin and for a particular population.



evaluate the sensitivity of modeled output to variations in model structure.

ECOSYSTEM DIAGNOSIS AND TREATMENT

EDT is a system for rating the quality, quantity, and diversity of stream habitat, relative to the species-specific needs of salmon (Lichatowich and Mobrand 1995; Mobrand et al. 1997; Blair et al. in press). EDT has been applied in nearly every salmon-bearing watershed in Washington and many in Oregon. In Puget Sound and in the Columbia Basin, the model has been widely used to assist in setting recovery goals (e.g., Lower Columbia Fish Recovery Board 2004; Northwest Power and Conservation Council 2005) for threatened and endangered salmonids and to predict consequences of proposed management actions (e.g., Shared Strategy Development Committee 2007). The EDT model compares estimated fish performance (e.g., population size or productivity) among current, historical, and potential habitat conditions. To do this, the EDT model requires thousands of data inputs and contains well over 1,000 internal parameters. Data inputs refer to those parameters which model users can modify when running the model in a particular basin and for a particular population. Internal parameters are those that do not vary from basin to basin (Figure 1). As described in the introduction, the EDT model is not unique in its complexity or size; we report the results of sensitivity analyses on the EDT model as a case study of how to conduct and interpret sensitivity analyses of large ecosystem models as well as to provide specific guidance on using EDT output in management decisions.

The EDT model consists of four major components (Blair et al. in press):

1. A reach level stream and environmental description. The reach level environmental description is based on 46 stream attributes (e.g., flow, stream temperature, macroinvertebrate abundance, and habitat types). Users are also asked to enter a "level of proof" rating for each stream attribute which describes the general method used to estimate that parameter (e.g., empirical data or expert opinion).
2. A set of "rules" that relate the environmental condition to life stage survival and capacity (as defined for the Beverton-Holt equation). The species-specific rules are rating curves for each salmonid species that link the stream attributes to life stage survival or density. The habitat rules reduce the predicted species-specific survival and maximum density to reflect local conditions in the stream.
3. Biological data on target species such as adult and juvenile age structure, run timing, sex ratio, fecundity, and ocean survival.
4. Integration of the reach by life stage estimates to the population level based on a disaggregated Beverton-Holt function (Beverton and Holt 1957; Moussalli and Hilborn 1986).

The outputs of an EDT analysis are the productivity and capacity parameters of a Beverton-Holt function, equilibrium abundance, and reach-level restoration and protection priorities. EDT is predominantly a deterministic model. There is no uncertainty in the relationships between fish habitat and fish production nor in population descriptors such as migration timing, fecundity, and ocean survival. An electronic library of EDT documentation is available from ICF Jones & Stokes (http://www.jonesandstokes.com/index.php?option=com_content&task=view&id=488&Itemid=784).

TESTING THE EXTREMES

Bureau of Reclamation biologists conducted a sensitivity analysis of the EDT model to determine how the EDT equilibrium abundance output for Chinook salmon and for steelhead (*O. mykiss*) varies as a function of stream attributes (Yoder et al. 2006). EDT was one model in a chain of hydrological, physical, and biological models employed by Reclamation to evaluate water storage and flow management options in the Yakima River, Washington. By exploring a wide range of input values (that included both plausible and implausible values for flow and habitat alterations), Reclamation analyses provided guidance for managers in how to use EDT output more effectively and in defining priorities for future data collection. Reclamation expected that productivity and abundance estimates would be sensitive to changes in stream attribute inputs; they aimed to discern the set of stream attributes to which the abundance and productivity estimates were most and least sensitive.

Systematically varying model input values over a range and observing the amount of change in model output from a given baseline is one form of model sensitivity analysis (Haefner 2005). Reclamation analyses systematically varied EDT habitat inputs (e.g., maximum temperature, bed scour, etc.) for each river reach. These habitat attributes are typically input into EDT on a 0–4 scale. Reclamation started with the current set of attribute inputs and varied each attribute input, independently, by plus or minus 1, and then reran the model. They then varied each attribute input by plus and minus 2, 3 and 4, working within the limits of possible input values, which are 0–4 for most habitat attributes. Varying the input by ±4 quantified the sensitivity of the model to extreme changes in input attributes. Non-focal habitat attributes and all other parameters were held at their point estimates (Yoder et al. 2005).

Sensitivity ratings for most habitat inputs were calculated using the following equation (after Haefner 2005):

$$S = \frac{\left(\frac{(A_0 - A_1)}{A_1}\right)}{\left|P_{avg0} - P_{avg1}\right|}$$

where:

A_0 is the original EDT output point estimate;

A_1 is the new EDT output point estimate given a change in attribute value;

P_{avg0} is the mean initial input attribute value over all reaches;

P_{avg1} is the mean changed input attribute value over all reaches;

A similar equation was used for attribute responses on different numerical scales.

Results: Using sensitivity analysis results to inform decision-making

Reclamation found that model outputs for both steelhead and Chinook salmon populations in the Yakima River were most sensitive to variations in the following stream inputs: alkalinity, embeddedness, fine sediment, habitat backwater pools, habitat primary pools, miscellaneous toxins, temperature-daily maximum, temperature-daily minimum, and turbidity. Reclamation also identified stream inputs to which model results for all three focal populations in these river segments were relatively insensitive (Table 1), including a large number of flow parameters. Because of the non-linear mathematics within the model, sensitivity analyses were necessary to understand these relationships.

The relative insensitivity of EDT predictions of fish abundance to flow attributes provided valuable information about EDT usage in the evaluation of a proposed water storage and flow management project on the Yakima River. The relative insensitivity of EDT to direct flow attributes reflects the model assumption that flow has a small physiological effect on fish survival and that impacts of flow manifest themselves in other physical attributes. One of the most obvious potential impacts of the proposed water storage project would be the change in flow volumes and flow patterns. However, because flow effects almost all other physical stream attributes, the impact of a real-world change in flow on habitat conditions (e.g., stream wetted area, bed scour, embeddedness, and habitat-type distribution) would need to be determined independently and entered into the model as changes to non-flow attributes. Although Reclamation's conclusions about the flow attributes are applicable only to the Yakima basin, these conclusions are supported by research in other basins (Northwest Hydraulic Consultants 2005). Subsequently, Reclamation developed support models to calculate the values for those EDT inputs (i.e., flow, habitat and temperature attributes) most influenced by changes in stream flow. Furthermore, based on these findings, Reclamation facilitated the development of a customized version of EDT to address the major ways that flow regimes can be altered by land use practices (Lestelle et al. 2006).

Surveying users to estimate uncertainty in habitat ratings

Washington Department of Fish and Wildlife (WDFW) is responsible for co-managing 14 evolutionarily significant units (ESUs) of salmon including over 100 individual populations. WDFW has used EDT extensively to assist in the development of recovery goals and plans throughout Washington. Because EDT relies on detailed stream habitat input, there is concern that uncertainty in these stream habitat input variables might lead to large amounts of uncertainty in model output. The accuracy and precision of stream habitat data vary widely from stream attribute to stream attribute and from basin to basin depending on data collection methods and on the means of estimating model input values where no empirical data exists. One can then expect that the precision of modeled output will also be basin-specific.

This concern led WDFW to initiate a Monte Carlo simulation study to develop basin-specific estimates of model precision based on the quality of the stream input data (Busack and Thompson 2006). To identify the plausible range of stream attribute values, WDFW developed a survey and queried eight biologists with EDT experience to elicit ranges of plausible stream attribute scores based on both the reported stream attribute score and level of proof rating. For example, the survey asked "If a reach had a score of 2 for turbidity, with a level of proof of 3, what do you think the highest and lowest likely true value for turbidity might be?" WDFW then created triangular probability distributions, using the reported value as the mid-point and the survey's average range as the end-points, for each combination of attribute, level of proof, and stream attribute score.

The probability distributions were sampled in two ways. In the first analysis, all stream attribute parameters were varied simultaneously and in the second analysis, each of nine stream attribute parameter groupings were varied sequentially. In each analysis, 500 independent input stream attribute data sets were created for each of 10 Puget Sound watersheds supporting 15 Chinook salmon populations. Each of these 100,000 input data sets (2 analyses X 10 watersheds X 10 parameter groups X 500 iterations) represent plausible stream attribute input data sets, given the stream attribute values and levels of proof recorded in the original EDT runs for reach watershed (Busack and Thompson 2006).

Results: Using sensitivity analysis results to inform decision-making

Using the first WDFW approach, prediction intervals (range of 95% of Monte Carlo outputs) for Puget Sound Chinook populations generally had coefficients of variation of 3.5%, 7%, and 10.5% for productivity, capacity, and equilibrium abundance estimates respectively. WDFW concluded that, given the plausible range of stream-attribute inputs, variability in EDT output was generally low, although model results with larger prediction intervals were observed for some basins or populations (Busack and Thompson 2006). These results suggested that uncertainty in stream-attribute factors alone does not produce large uncertainties in model output. One conclusion from this result is that small errors in stream-attribute inputs will not propagate into large errors in model output, so long as model structure and other inputs such as fecundity, smolt-to-adult survival rates, etc., remain constant. Another possible explanation for these results is that some relationships between habitat inputs and population outputs are not captured in the model.

Using the second approach, in which they varied subsets of habitat parameters sequentially, WDFW identified a set of stream attributes which, across multiple watersheds, provided the largest contribution to the variance of model output for Puget Sound Chinook populations. Generally, Chinook capacity estimates were most sensitive to uncertainty in ratings for the habitat type group (e.g., relative amounts of primary pool, tailout, small cobble riffle) while productivity estimates were most sensitive to uncertainty in channel stability and sediment ratings. The precision of model estimates could best be improved by increasing accuracy and precision of attributes in these groups. Of these, only sediment was also identified in the Reclamation analysis (Yoder et al. 2006). The one stream attribute that consistently had little or no impact on model output was macroinvertebrate diversity (Busack and Thompson 2006). Therefore, if the management objective is to increase precision in EDT model outputs and habitat-sampling funds are limited, WDFW recommended not increasing the sampling intensity for macroinvertebrates, an expensive and time-consuming effort. Of course, there may be many important reasons to sample macroinvertebrates other than to improve EDT precision, as we have strong evidence from other sources that macroinvertebrates are a good indicator of salmon habitat quality (Quinn 2005).

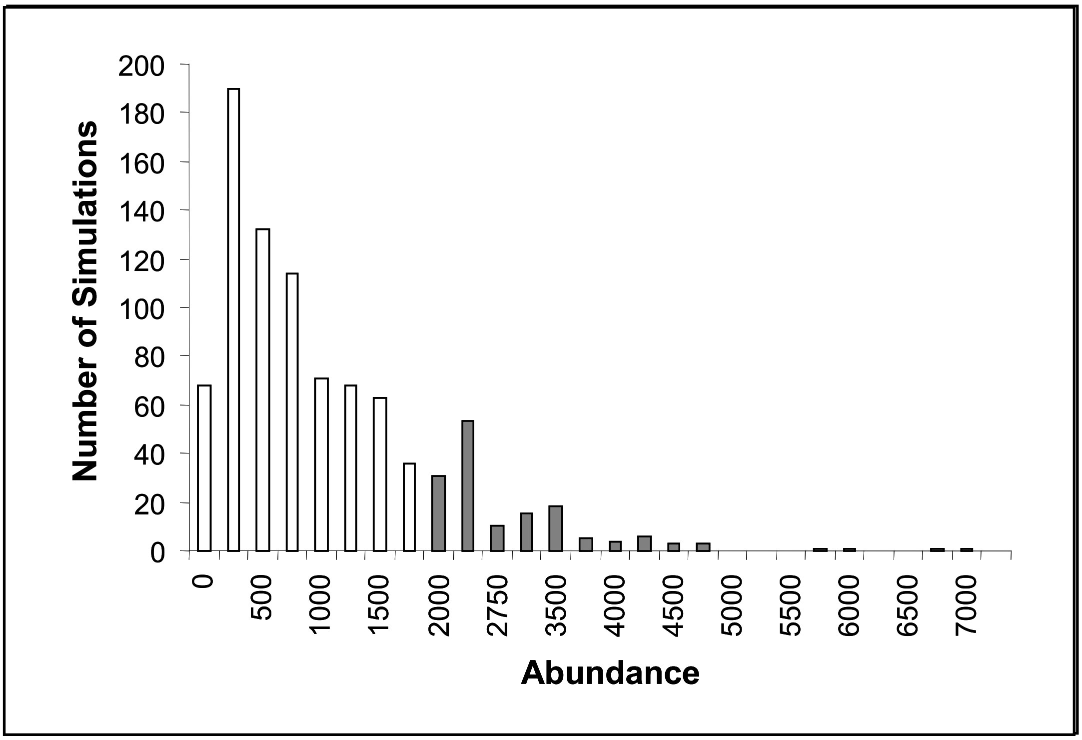
WDFW was also able to investigate the sensitivity of rankings of reaches for restoration or protection to habitat inputs. For Puget Sound watersheds, the top restoration and protection rankings were relatively stable within basins. In particular, uncertainty in stream attribute input data caused little shift in the predictions of where the best habitat restoration opportunities exist for Chinook within each watershed. They concluded that managers could be confident that modeled high priority reaches were consistent despite uncertainties in stream attribute input data. Restoration and protection rankings for reaches originally ranked as fourth or lower, however, were not as robust to the uncertainties in stream attribute inputs (Busack and Thompson 2006). Therefore, WDFW concluded that rankings for these mid-priority reaches should be used with caution in decision-making.

BEYOND HABITAT: SENSITIVITY ANALYSES OF ALL PARAMETERS

NOAA Fisheries is responsible for overseeing the development of recovery plans for most marine and anadromous species listed as threatened or endangered under the Endangered Species Act (ESA). NOAA Fisheries also contributes information to the management of freshwater and estuarine habitats and to the prioritization of freshwater and estuarine restoration and protection actions. Population parameters modeled using EDT and reach-specific restoration and prioritization actions are often used by state, tribal, and local groups in the processes of developing recovery plans and prioritized lists of restoration and protection actions. Therefore, NOAA needs the best possible understanding of the precision and accuracy of EDT output in order to evaluate whether model output is appropriately used to inform these decisions.

The goals of the NOAA analyses were to quantify a more complete prediction interval, by incorporating uncertainty in non-habitat inputs and in internal parameters, and to identify which input parameters are responsible for the majority of output variability (McElhany et al. in press). NOAA Fisheries designed a global sensitivity analysis (Sobol 1993; Saltelli et al. 2000a, 2000b) that incorporated known or estimated uncertainty on nearly every parameter in the EDT model. In the first step, a potential distribution was defined for each input and internal model parameter. Distributions for stream attributes were defined using WDFW's survey results (Busack and Thompson 2006). Distributions for other parameters were defined during collaborative meetings (including scientists from Snohomish County, Pierce County, NOAA Fisheries, WDFW, Reclamation, and Mobrand, Jones & Stokes) at which measurement errors, empirical data, simulation studies, and expert opinion were considered. To estimate one prediction interval, the model was run at least 250 times. For each parameter in each run, a value was randomly and independently selected from the distributions defined above. Using this approach, all possible combinations of parameters, both internal and user-defined, had a possibility of being included in the simulation study (McElhany et al. in press). The resulting prediction interval therefore reflects the distribution of model outputs given known and estimated

Figure 2. Histogram of the 894 successful Monte Carlo simulations of abundance (Neq) for the East Fork Lewis fall Chinook population, calculated without harvest. The solid bars represent abundance estimates of 2000 or greater. Note that 1,000 Monte Carlo simulations were attempted but 106 resulted in unusable parameter combinations.



uncertainties in the stream attributes (from WDFW), the population descriptors, and the internal model parameters.

In conducting the global sensitivity analysis, NOAA Fisheries was also able to estimate the effect of uncertainty in any one parameter, or group of parameters, on the final prediction distribution. The total prediction interval was partitioned using an approach that is analogous to an analysis of variance (ANOVA) to identify the contribution of each parameter or set of parameters to the total output uncertainty (Sobol 1993; Satelli et al. 2000a). Because of the large number of parameters, NOAA applied a hierarchical approach, varying sets of parameters (e.g., all stream attributes) together. Once the most sensitive groups of parameters were identified, the analysis focused on determining which specific parameters in these sensitive groups contributed most to prediction uncertainty (McElhany et al. in press).

Results: Using sensitivity analysis results to inform decision-making

NOAA created prediction intervals for multiple populations. For example, the 80% prediction interval for fall Chinook abundance (equilibrium abundance of a Beverton-Holt model) under current conditions without harvest in the East Fork Lewis River, Washington, using the global sensitivity analysis, ranged from 35 to 2,274 fish with a mean predicted abundance of 941 (median = 635). In other words, given uncertainties in the input data and internal parameters, model output for this scenario was between about 35 and 2,274 fish in 80% of EDT simulations (McElhany et al. in press).

In addition to providing a more informed estimate of the mean model prediction, the analysis also provides managers with a distribution of model predictions (Figure 2). If one needed to know whether the population prediction exceeds, for example, 2,000 fish, inferences based on the mean estimate would suggest not. In contrast, inferences using the prediction intervals indicate that, given the input data, model parameters, and the uncertainty distributions, there is a 17% chance that EDT will produce an estimate greater than 2,000 fish (Figure 2). In this way, prediction intervals for population abundance, productivity, and capacity can provide increased information for model-supported decision-making (Steel et al. in press).

Assessments of the reach priorities for restoration and protection suggest that these may also shift as uncertainty is incorporated into the modeling process but that the suite of high priority restoration reaches is relatively robust to uncertainties in inputs (McElhany et al. in press). These results are consistent with those of WDFW (Busack and Thompson 2006).

Like the other agencies, NOAA was also able to identify groups of parameters to which the model appears less sensitive, at least for the basins examined (Table 1). When a model is not sensitive to variation in particular parameters, it may be because those parameters are not important for estimating the output of interest, the parameter is already estimated with a high degree of precision, the model is not capturing a relationship as expected, or another factor is limiting model output and until this bottleneck is removed the parameter of interest can have no effect. The variance partitioning provided initially unexpected results. Much of the emphasis of EDT critique and evaluation has been on the use of expert opinion to generate stream attributes and on the formulation of the rules or equations linking stream attributes to survival (ISAB 2001). It might have been expected that the uncertainty in stream attributes would have a relatively large effect on the size of the final prediction interval. As shown in an example using East Fork Lewis River fall Chinook (Figure 1), uncertainty in stream attribute inputs had a small relative impact on the size of the prediction interval. Other parameter groups, such as the adult parameters (e.g., fecundity, ocean survival) and the benchmarks, contributed most to the variability in the model prediction.

Variance partitioning results were consistent across all three basins for which NOAA ran the sensitivity analysis (McElhany et al. in press). Although there is variation among populations in which parameter groups have the greatest sensitivities, stream attributes have consistently lower sensitivities than other groups of parameters (McElhany et al. in press). This should not be interpreted to mean that instream habitat is not important to salmon or that stream attribute parameters do not affect EDT results. The importance of the adult parameter group should not be surprising as adult parameters include ocean survival, fecundity, sex ratio, and age structure. This group of parameters defines the reproductive potential of the species and needs to be captured with high precision if estimates of fish production from any model are to reflect observed data.

CONCLUSIONS: SYNTHESIZING MULTIPLE APPROACHES

Trade-offs between types of sensitivity analyses

Each of the sensitivity analyses described above took a different mathematical approach to questions about the impacts of model inputs on model outputs and about model precision. The Reclamation approach, simply varying an input and observing the response in model output, provided invaluable insights to the first question. As a result of their sensitivity analyses, they were able to avoid misuse of the EDT model, in isolation, for predicting the fisheries response to a range of proposed management actions. Simple sensitivity analyses such as these have limitations. They cannot identify interactions between uncertainties in multiple inputs or between inputs and internal parameters. As well, they provide only crude estimates of model precision, a range rather than a distribution of potential outputs. Reclamation's systematic sensitivity analyses represent a large amount of work because of the large number of inputs considered. However, often these systematic variations in inputs and internal parameters can be conducted with a minimum of computer programming or specialized software. Failure to conduct such simple sensitivity analyses in model development and before using modeled predictions in management decisions severely reduces the value of modeling for decision making.

Using a Monte Carlo approach to sensitivity analysis adds two levels of complexity to the sensitivity analysis but provides more robust information. The first added complexity is the necessity of quantifying not only the range but also the distribution of possible values for the inputs and internal parameters of interest. WDFW used an opinion survey to estimate the range of plausible values around each estimated stream attribute. In the future, empirical data from pilot studies or other regions could also be used to estimate these input distributions. The second complexity is simply the Monte Carlo sampling routine that requires programming or software support. The added value of the Monte Carlo approach is the quantification of a distribution of plausible outputs that can be used to quantify particular risks of interest (Figure 2).

Variance partitioning is particularly important for complex models because it quantifies not only independent impacts of particular parameters or groups of parameters but interactions between parameters. Variance partitioning allowed NOAA to compare the total impacts of suites of parameters on model outputs and to identify those parameters or groups of parameters whose uncertainty had the greatest impact on model output. Variance partitioning methods require customized programming and more advanced mathematics (Sobol 1993). Their value in complex ecological models is just beginning to be explored.

Value of multi-agencies collaborations

The three analyses described here were conducted in parallel by three public agencies with differing goals and responsibilities. Clear communication between agencies about how the EDT model would be used, about how sensitivity analyses were conducted, and about interpretation of sensitivity analyses has greatly improved each individual analysis. For example, the NOAA analyses were able to build on WDFW's opinion survey of habitat input distributions. And, sharing of information was required to come to a consensus about the appropriate distribution of plausible parameters for the remaining inputs and internal parameters. Since the final value of sensitivity analyses depends on agreement of these distributions, such consensus building was essential. For example, if one agency felt that the uncertainty around parameter X varied between 5 and 20 while another agency believed that the parameter uncertainty only varied between 16.5 and 17.5, it would be difficult to design one sensitivity analysis that would be considered valid by both agencies. In addition, these complex collaborations enabled all available empirical data to be brought to bear on the discussion.

Each agency has a different mandate for natural resource management and therefore, different objectives for sensitivity analyses. WDFW, for example, calculated customized prediction intervals for every watershed in Puget Sound for which EDT analyses have been completed (Busack and Thompson 2006). They are now able to provide guidance on the best opportunities to reduce model output variance in each Puget Sound watershed, if additional funding were available for habitat research. By working together, each agency was also able to benefit from the combined results of the three sensitivity analyses and to synthesize the results into one set of conclusions about appropriate uses of the EDT model.

Using sensitivity analyses to draw conclusions about EDT

By combining results from the three sensitivity analyses, we are able to draw several robust conclusions about the EDT model given known and unavoidable uncertainties. First, the model is less sensitive to uncertainties in stream attributes than might have been expected. Investments in increased data collection on habitat may not yield increased precision in EDT output. Using the EDT model in isolation to predict the effects of some environmental changes, such as impacts of flow alterations, can provide misleading results, especially where strong interactions with other stream attributes are expected and not explicitly included in the model. Sensitivity analyses have guided the development of new models in the Yakima Basin and can continue to guide the collection of data to improve model precision. Second, the model is most sensitive to parameters that describe adult populations and reproductive potential. The NOAA sensitivity analysis suggests that most of the uncertainty in model predictions of salmon abundance and productivity does not derive from uncertainty about habitat condition but from uncertainty in the other parameters—even knowing stream attributes perfectly, most of the model uncertainty would remain. Research can provide refined estimates of adult population parameters or rules linking specific stream attributes to survival that would improve model precision. Third, as expected for a complex ecosystem model, prediction intervals for the EDT-based estimates of abundance, productivity, and capacity are large. The size of the prediction intervals suggests that decisions based on point estimates for these fish performance metrics alone are risky. Fourth, the highest priority reaches for restoration and protection are relatively robust to known parameter uncertainties

Implications for the use of models in fisheries management

The use of models in fisheries management has a long history and models will continue to play an integral role in fisheries and fish habitat management for the foreseeable future. The combination of these three sensitivity analyses and an investigation of the implications of their combined results provide an opportunity for general guidelines on the use of models in fisheries management.

First, managers can improve their use of modeled data by requesting prediction intervals (and if possible confidence intervals). Distributions of model output provide increased information on the risks of achieving or failing to achieve particular thresholds. Confidence or prediction intervals are particularly important where modeled output is passed on as input to another model.

Second, since most models provide predictions that are imperfect, the use of multiple independent models can provide a stronger basis on which to base decisions (ISAB 2001). When multiple independent models provide similar conclusions, it suggests that that conclusion is robust to the architecture and assumptions of any one model. Where competing models are unavailable, sensitivity analyses can suggest whether model output is robust to particular assumptions.

Third, where possible, models must be evaluated with respect to both precision and accuracy. It is frustrating that years of analyses on one model can only produce information about model precision yet this is a common situation. Models are developed to assist decision-makers in exactly the sort of situations for which data to quantify predictive accuracy are unavailable. In these circumstances, it is important to maintain skepticism until empirical data can be collected.

Finally, models should not be used in management decisions without at least some sensitivity analyses. Sensitivity analyses provide essential information when using modeled predictions in a decision-making context. They enable an assessment of the probability of making a wrong conclusion as a result of uncertainties in the data used to run the model and of uncertainties in the parameters used to build the model. Sensitivity analyses can be used to focus research and data collection efforts on parameters that will result in better decision-making and, hopefully, increased cost efficiency and improved fish populations. Sensitivity analyses are particularly important for complex models where the relationships between inputs and outputs are not transparent and for models that rely on inputs or internal parameters that are known to be uncertain. Models are often also used to provide evidence for a specific thesis or as a rationale for specific actions. In these cases, a sensitivity analysis serves to provide transparency to the analysis and can be included as an important element of evidence building (Saltelli et al. 2000b). As increasingly complex management decisions demand increasingly complex models, sensitivity analyses become essential tools in appropriately using modeled predictions in decision-making.

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REFERENCES

Beverton, R. J. H., and **S. J. Holt.** 1957. On the dynamics of exploited fish populations. Fishery Investigations 2: 1-533.

Blair, G. R., L. C. Lestelle, and **L. E. Mobrand.** In press. The Ecosystem Diagnosis and Treatment Model: a tool for assessing salmonid performance potential based on habitat conditions. *In* E. Knudson and H. Michael, eds. Pacific salmon environment and life history models: advancing science for sustainable salmon in the future. American Fisheries Society, Bethesda, Maryland.

Busack, C. A., and **B. E. Thompson.** 2006. Improving salmon habitat productivity models for setting escapement goals and prioritizing habitat recovery funding. Final report to the Pacific Salmon Commission, Project SF-2006-H-27, Dec 15. Washington Department of Fish and Wildlife, Olympia.

Gaff, H., J. Chick, J. Trexler, D. DeAngelis, L. Gross, and **R. Salinas.** 2004. Evaluation of and insights from ALFISH: a spatially explicit, landscape-level simulation of fish populations in the Everglades. Hydrobiologia 520:73-87.

Haefner, J. W. 2005. Modeling biological systems: principles and applications. 2nd Edition. Springer, Inc., New York.

Independent Science Advisory Board (ISAB). 2001. Model synthesis report: an analysis of decision support tool used in Columbia River basin salmon management. ISAB, Portland, Oregon. Available at: www.nwcouncil.org/library/isab/isab2001-1.pdf (Accessed 15 Nov 2007).

Lestelle, L. C., B. Watson, and **G. Blair.** 2006. Species-habitat rules: Supporting documentation for updated flow rules for application in EDT. Mobrand, Jones & Stokes, Vashon, Washington. Available at: www.jonesandstokes.com/index.php?option=com_docman&task=doc_download&gid=121 (Accessed 15 Nov 2007).

Lichatowich, J. A., and **L. E. Mobrand.** 1995. Analysis of Chinook salmon in the Columbia River from an ecosystem perspective, Mobrand Biometrics. Bonneville Power Administration, Portland, Oregon. Available at: http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=25105-2 (Accessed 15 Nov 2007).

Lower Columbia Fish Recovery Board. 2004. Lower Columbia salmon recovery and fish and wildlife plan. Lower Columbia Fish Recovery Board, Longview, Washington. Available at: www.lcfrb.gen.wa.us/December%20Final%20%20Plans/lower_columbia_salmon_recovery_a.htm (Accessed 14 June 14, 2007).

McElhany, P., E. A. Steel, D. W. Jensen, K. Avery, N. Yoder, B. Thompsen, and **C. Busack.** In press. Dealing with uncertainty in ecosystem models: lessons from a complex salmon model. Ecological Applications.

Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and **T. S. Vogel.** 1997. An approach to describing ecosystem performance "through the eyes of salmon." Canadian Journal of Fisheries and Aquatic Sciences 54: 2964-2973.

Moussalli, E., and **R. Hilborn.** 1986. Optimal stock size and harvest rate in multistage life history models. Canadian Journal of Fisheries and Aquatic Sciences 43(1):135-141.

Northwest Hydraulic Consultants. 2005. Final report—Instream flow assessment pilot project. Prepared for Shared Strategy for Puget Sound, USA. Available at: www.sharedsalmonstrategy.org/resources.htm#water_quantity (Accessed 14 June 2007).

Northwest Power and Conservation Council. 2005. Subbasin plans in Columbia River basin fish and wildlife program. Northwest Power and Conservation Council, Portland, Oregon. Available at: www.nwcouncil.org/library/2000/2000-19/FullReport.pdf (Accessed 15 Nov 2007).

Quinn, T. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society and University of Washington Press, Seattle.

Saltelli, A., K. Chan, and **E. M. Scott (editors).** 2000a. Sensitivity analysis. John Wiley and Sons, Ltd., Chichester, UK.

Saltelli, A., S. Tarantola, and **F. Campolongo.** 2000b. Sensitivity analysis as an ingredient of modeling. Statistical Science 15(4):377-395.

Shared Strategy Development Committee. 2007. Puget Sound salmon recovery plan. Shared Strategy Development Committee, Seattle, Washington. Available at: www.nwr.noaa.gov/Salmon-Recovery-Planning/Recovery-Domains/Puget-Sound/PS-Recovery-Plan.cfm (Accessed 14 June 2007).

Sobol, I. M. 1993. Sensitivity estimates for nonlinear mathematical models. Mathematical Modelling and Computational Experiment 1:407-414.

Smith, A.D.M., E.J. Fulton, A.J. Hobday, D.C. Smith, and **P. Shoulder.** 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES Journal of Marine Science 64: 633-639.

Steel, E. A., T. J. Beechie, M. Ruckelshaus, A. H. Fullerton, P. McElhany, and **P. Roni.** In press. Mind the gap: uncertainty and model communication between managers and scientists. *In* E. Knudson and H. Michael, eds. Pacific salmon environment and life history models: advancing science for sustainable salmon in the future. American Fisheries Society, Bethesda, Maryland.

Yoder, N. J., M. D. Bowen, K. P. Zehfuss, J. Hubble, B. Watson, B G. R. Blair. 2006. Systematic sensitivity analysis