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Population Viability Assessment of Salmonids by Using Probabilistic Networks

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Abstract.—Public agencies are being asked to quantitatively assess the impact of land management activities on sensitive populations of salmonids. To aid in these assessments, we developed a Bayesian viability assessment procedure (BayVAM) to help characterize land use risks to salmonids in the Pacific Northwest. This procedure incorporates a hybrid approach to viability analysis that blends qualitative, professional judgment with a quantitative model to provide a generalized assessment of risk and uncertainty. The BayVAM procedure relies on three main components: (1) an assessment survey in which users judge the relative condition of the habitat and estimate survival and reproductive rates for the population in question; (2) a stochastic simulation model that provides a mathematical representation of important demographic and environmental processes; and (3) a probabilistic network that uses the results of the survey to define likely parameter ranges, mimics the stochastic behavior of the simulation model, and produces probability histograms for average population size, minimum population size, and time to extinction. The structure of the probabilistic networks allows partitioning of uncertainty due to ignorance of population parameters from that due to unavoidable environmental variation. Although based on frequency distributions of a formal stochastic model, the probability histograms also can be interpreted as Bayesian probabilities (i.e., the degree of belief about a future event). We argue that the Bayesian interpretation provides a rational framework for approaching viability assessment from a management perspective. The BayVAM procedure offers a promising step toward tools that can be used to generate quantitative risk estimates in a consistent fashion from a mixture of information.

Public agencies such as the U.S. Forest Service (FS) and the U.S. Bureau of Land Management (BLM) must consider the potential effects of land management activities on aquatic species occurring on lands under their administration. Frequently, biological evaluations are based largely on the judgment and experience of local biologists because requisite information on local populations is unavailable and unlikely to be obtained within a reasonable time. Recent federal listings of several species under the U.S. Endangered Species Act (e.g., Snake River Chinook salmon *Oncorhynchus tshawytscha* and sockeye salmon *O. nerka*) have increased the importance and visibility of these analyses. In turn, the higher analytical profile has highlighted the need for more rigorous, consistent, and defensible analyses that recognize the uncertainty inherent in decisions made in information-poor environments. Watershed analysis has been proposed as the formal framework for assessing potential threats from land use decisions and for proposing mitigation measures that might be taken to ensure population viability (FEMAT 1993). To ensure the success of watershed-scale analysis, decision support tools are being developed by FS and BLM to guide evaluation of physical and biological systems.

We have developed a Bayesian viability assessment procedure (BayVAM) as a tool to characterize land use risks to salmonids. Two versions of the procedure exist, one for anadromous salmonids and one for potamodromous, or resident, trouts and chars. The BayVAM procedure incorporates a hybrid approach to viability analysis that blends qualitative judgment with quantitative models to provide a generalized assessment of risk and uncertainty. Herein we highlight distinguishing features of the BayVAM approach, using examples from the potamodromous version. A more specific application is discussed in the companion paper by Shepard et al. (1997, this issue).

Overview

The purpose of the BayVAM procedure is to provide a rigorous and repeatable method for examining watershed conditions in light of species' life history requirements in order to determine whether a population faces a serious risk of extirpation or significant decline. The BayVAM approach is an extension of the coarse filter approach presented by Rieman et al. (1993), which provides a concise method for distinguishing healthy populations from those at risk. In contrast to coarse

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TABLE 1.-Model parameters used in the Bay VAM simulations.

Parameter	Description	Range
fecund	Number of female eggs per adult female	50-1,250 eggs
incsuv	Spawning and incubation success	10-70%
alpha (α)	Fry survival at low density	10-40%
parrcap	Asymptotic parr capacity	1,000-10,000 parr
s_1	Juvenile survival	15-60%
s_2	Adult survival rate	15-90%
m	Age at maturity	3-6 years
s_0_CV	Coefficient of variation in fry survivals	15-90%
immigrant	Mean immigrants per generation	0-20 adult equivalents
intadt	Initial number of adult females	50-1,250 females
cat	Expected time between catastrophes	20-170 years

[a] 100·SD/mean.

filters, the BayVAM approach not only estimates risk, it clearly identifies presumed links between watershed conditions and life history parameters and distinguishes uncertainty due to natural random processes from uncertainty due to lack of knowledge or information (both of which contribute to overall assessed risk). The BayVAM procedure consists of three to five steps, the number depending on the scale of analysis, as follows.

Step 1.—Define the scale of analysis in terms of the populations under consideration and the landscape involved. Watershed boundaries form logical boundaries for many salmonid populations. Because the scales of administrative interest and population processes may not coincide (see Ruggiero et al. 1994), it is important to define individual populations or regional aggregations of populations clearly and in a biologically meaningful way. That is, the population boundaries should be consistent with the biology of the organism, not restricted by administrative boundaries. Boundaries placed on individual populations may vary widely by species and life history type.

Step 2.—Survey watershed conditions in terms of how they affect vital population parameters (see Shepard et al. 1997, this issue, for a survey example). Judge the relative condition of the habitat and estimate survival and reproductive rates for the population in question.

Guidelines normally are provided to help with drawing inferences from existing information and with designing data collection. For example, if an area has abundant silt-free gravel of the appropriate size for a salmon species' redd building and receives adequate instream flow during the egg and alevin incubation period, one might presume that spawning and incubation success are relatively high. Users of BayVAM do not choose precise parameter values; rather, they assign probabilities or likelihood values to specific ranges for each parameter (Table 1). The available parameter ranges span values consistent with salmonid populations in western North America. Parameter uncertainty due to lack of information or experience is incorporated in the probability distributions. As better information becomes available, responses can be updated to reflect the improved accuracy or precision of the information.

Step 3.—Complete a quantitative viability analysis for each population of interest using survey results from step 2. Central to this analysis are stochastic life cycle models, recast as probabilistic networks (details are provided below). The life cycle models integrate information on critical population processes and rates (e.g., fecundity, survival) and habitat capacity to simulate the dynamics of a population in a variable environment. These models track population numbers through annual time steps, introducing random fluctuations at each step. The probabilistic networks summarize and mimic the behavior of the life cycle model in a way that simplifies calculation and provides easily interpretable outputs. The probabilistic network is provided in the form of a simple spreadsheet. The BayVAM users enter the probability values generated in step 2, and the spreadsheet calculates corresponding probability values for a series of intermediate variables (algebraic combinations of the input parameters) and for three output variables: minimum population size, average population size, and time to extinction.

The output variables are based on simulated 100-year periods, which are roughly 10-20 times the generation time of stream-dwelling salmonids. Although longer time frames may be appropriate for some species (Marcot and Murphy 1996), 100 years were sufficient for characterizing the dynamics of model populations and provide useful indices of risk for the species we examined. Changes in environmental conditions and management that

would make any projection moot are certain to occur within the next 100 years. Because ecosystems are dynamic, the chances of population increases or decreases will be different at any point in the future. Thus, time frame is only a standard of reference for an assessment based on conditions at the time of analysis.

The models consider only demographic features of populations; they incorporate no explicit representation of population genetics, including hybridization. Although small populations may be threatened by inbreeding depression and lost genetic diversity, it is difficult to incorporate genetic risks other than in qualitative terms (Hedrick and Miller 1992). An implicit assumption of the BayVAM approach is that most populations are at risk more from demographic processes than from genetic effects of small population size (see Shaffer 1987 and Lande 1988). Management actions aimed at natural reproduction (i.e., no hatchery fish are involved), which minimizes risks associated with population demographics, also should minimize most genetic risks, hybridization being a notable exception.

Step 4.—Identify, if desired, alternative hypotheses concerning population parameters and rerun the analysis. Multiple iterations can be used to evaluate the sensitivity of predictions to alternative hypotheses, determine the potential value of new information, or identify possible changes that might follow alternative management scenarios. For example, values for juvenile and adult survival might be adjusted upward to reflect a proposed management scheme to improve the number and quality of pool habitats through increased recruitment of large woody debris, if such action can legitimately improve habitat.

Step 5.—Complete analyses for all individual populations in the regional population, if a regional analysis is required, or for a representative subsample of populations. The examples below are limited to single populations. Shepard et al. (1997) provide an example of a regional analysis.

Quantitative Model Structure

The BayVAM procedure relies on stochastic population simulation models as the quantitative agents supporting the analysis. These models have been recast as probabilistic networks in order to enhance their utility. The following sections describe the structure of the underlying model used in the potamodromous version and the corresponding probabilistic network. The anadromous version is similar but is based on the life cycle model of Lee and Hyman (1992).

Underlying Model Structure

The underlying population viability model used in the potamodromous version is a stochastic, age-structured demographic model that tracks population numbers in annual time steps. To simplify matters, modeled populations consist of females only; any reference below to a specific life stage implies females only. This makes it unnecessary to track maturity and survival rates for both sexes or to account for time-varying sex ratios. The population is divided into three main stages: subyearlings (age 0), juveniles, and adults. Subyearlings progress from eggs to parr during the course of their first year, whereas juveniles and adults are further divided into discrete year-class cohorts, numbered from 1 to m - 1, and m to m + 9, respectively, where m is the age of maturity (Figure 1).

The model requires eight demographic parameters, an estimate of the variation in subyearling survival, the expected frequency of major habitat disruptions (catastrophes), and an initial number of spawning adults (Table 1). The length of the simulation period is variable. As mentioned above, a 100-year simulation period was used in developing the probabilistic network, but no such restriction is inherent in the simulation model itself.

Spawning initiates each simulated year. The number of eggs produced is the product of average fecundity and the number of adults remaining at the end of the prior time step plus any immigrants. Immigrants are expressed as adult equivalents per spawning brood; that is, any differences in reproductive success between immigrants and resident adults are incorporated by conversion to adult equivalents. For example, if immigrants are presumed to have a relative fitness of 0.8, then four adult equivalents would be added for every five immigrants. Immigrants contribute only to the number of eggs produced; they are not counted in adult numbers. Each year, the number of immigrant adult equivalents is generated as a Poisson random variate with expected value equal to immigrant.

The number of fry produced is a random binomial variate with parameters N (number of eggs) and p (spawning and incubation success). First-year survival of fry is modeled as the asymptotic, density-dependent relationship

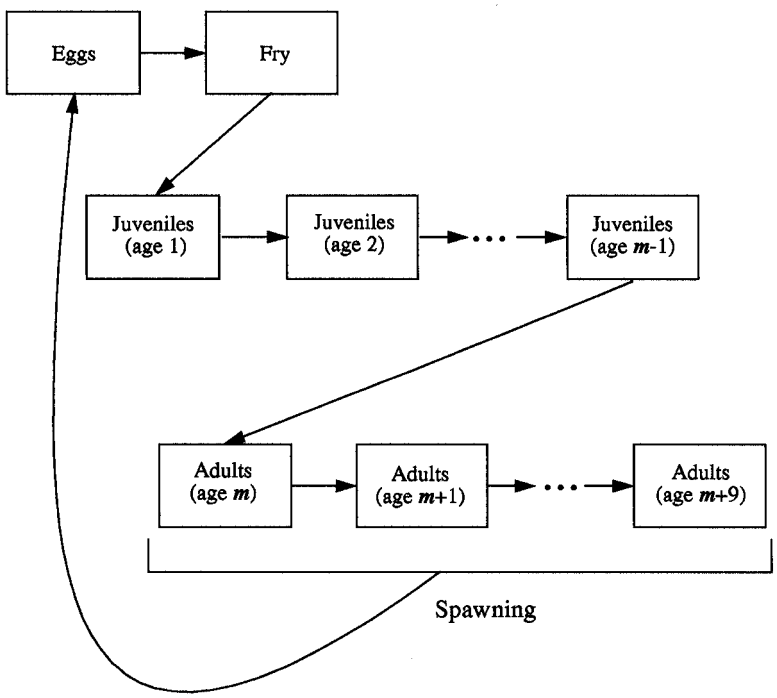

FIGURE 1.—Structure of the underlying population viability simulation model.

$$s_0 = \alpha\left(1 - \exp\left[\frac{-\text{parrcap}}{\alpha \cdot \text{fry}}\right]\right), \qquad (1)$$

where so is the expected survival, a is the maximum fry survival rate at a low density, parrcap is the maximum number of fry expected to survive the first year (i.e., the parr carrying capacity of the system), and fry is the number of fry or alevins hatching.

The actual number of juveniles produced is a random binomial-beta variate, whereby the probability of survival is randomly drawn from a beta distribution with mean so and coefficient of variation (CV = 100·SD/mean) specified within the model parameters. This random draw of the first-year survival probability introduces an element of variability consistent with annual environmental fluctuations in rearing conditions. Successive transitions within juvenile age-classes, from juveniles to adult class m, and within adult age-classes are density-independent, random binomial processes consistent with the stochastic, discrete nature of the model. Transitions within juvenile age-classes use the juvenile survival parameter s_1; juvenile-to-adult and adult-to-adult transitions use the adult survival parameter s_2, which includes prespawning mortality (which affects first-time and repeat spawners). These transition probabilities are constant across years for any realization of the model.

Modeling Catastrophic Disturbance

The simulation model also includes catastrophic disturbances. A catastrophic disturbance refers to a random event that substantially diminishes survival of all age-classes in the year of its occurrence and reduces spawning and incubation success and first-year survival for some years into the future. In the model, the expected time period (in years) between catastrophes (cat, Table 1) determines the probability of occurrence in a given year; the probability of catastrophe equals the reciprocal of the expected time between catastrophes. Occurrence of a catastrophe is modeled simply as a Bernoulli trial each year: a catastrophe either occurs or not.

When a catastrophe occurs, two things happen. First, the number of juveniles and adults is immediately reduced, but their survival rates in subsequent years remain the same as before. Second, the habitat carrying capacity for parr (reflected in parrcap) and the spawning and incubation success (incsuv) are also reduced but return to their pre-catastrophe levels more slowly according to the equation

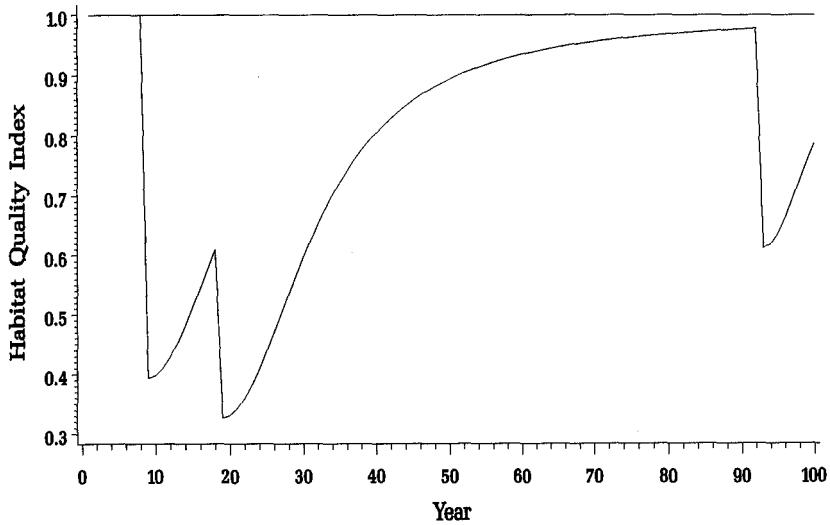

FIGURE 2.—Simulated habitat quality in an environment experiencing three catastrophic disturbances within a 100-year period (years 10, 19, and 93).

$$H = (1 - D) + D\left(\frac{t^2}{t^2 + 400}\right), \qquad (2)$$

where H is a scalar between 0 and 1 that is multiplied by parrcap and incsuv, D is the disturbance coefficient, and t is the time steps since disturbance. In model applications thus far, D is a random variate from a beta distribution with a mean of 0.5 and a standard deviation of 0.13. Thus, on average, each catastrophe reduces the population by one-half. Because multiple catastrophes can occur in sequence, the habitat quality index H is adjusted to reflect cumulative impacts (Figure 2).

Model Behavior

Each realization of the model produces a simulated time series of population abundance that exhibits random fluctuations. Conceptually, each time series reflects a combination of an underlying deterministic population trajectory with the annual variation introduced by the stochastic processes included in the model (Figure 3). This variation in a single time series arises from three parts: (1) demographic variability that arises because populations are composed of discrete individuals, and each individual independently contributes to birth and death processes through the binomial processes; (2) environmental variability that arises from the annual variation in fry survival, independent of density-dependent variation; and (3) catastrophic disturbances. Each time series is amenable to the same calculations that one can perform on empirical data. For example, summary statistics (e.g., mean and variance) or statistics designed for time series analysis can be used to summarize results. Because of random fluctuations within the model, simulated extinction can occur even when the overall trend in population numbers seems stable or increasing. Normally, multiple iterations of the model would be run for any given parameter set in order to identify central tendencies and the relative frequency of various outcomes such as extinction.

The relatively simple structure of the simulation model permits calculation of intermediate variables that can aid interpretation of model behavior. Two straightforward intermediate variables are reproduction and replacement. Reproduction is simply the product of fecundity and spawning and incubation success. Replacement is the hypothetical number of parr required to produce one adult spawner. Replacement (R) can be calculated from juvenile survival (s_1), maturation age (m), and adult survival (s_2) as

$$R = \left(s_1^{m-1} \sum_{i=1}^{9} s_2^i\right)^{-1}. \qquad (3)$$

Replacement, reproduction, and the parameters of the fry survival equation combine to determine two key intermediate variables, equilibrium size and resiliency. Equilibrium size is the number of adults that would be expected to exactly replace

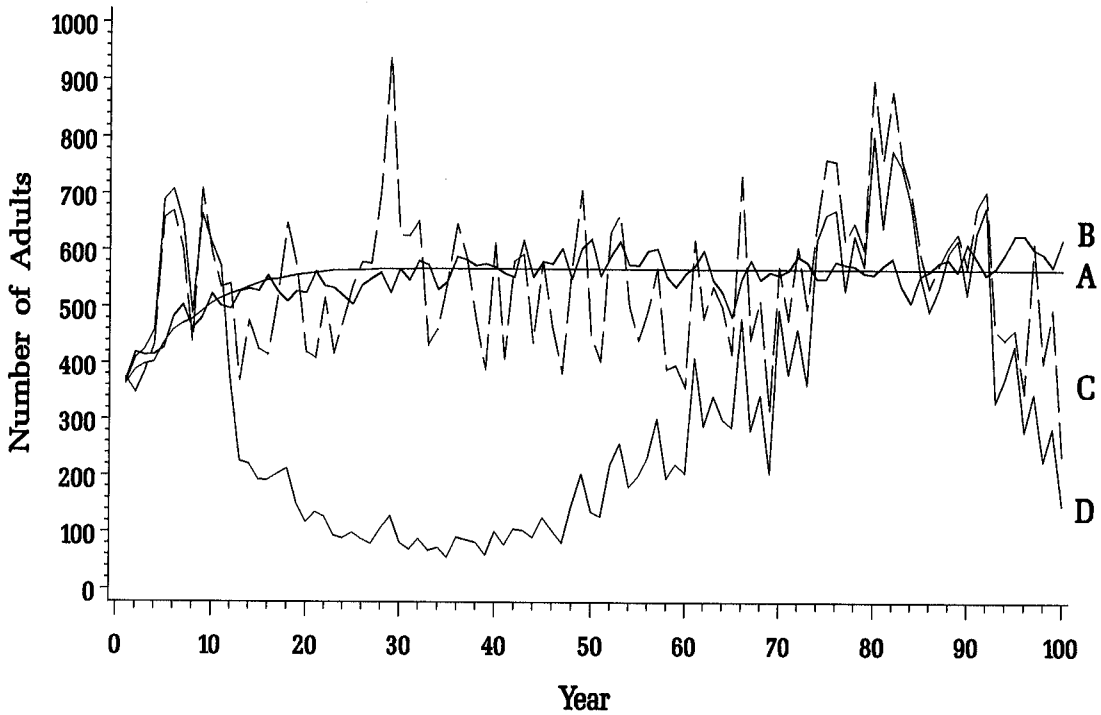

FIGURE 3.—Simulated time trace of population abundance with various levels of random variation included: deterministic model with no random variation (A), model A plus demographic variation (B), model B plus environmental variation in first-year survival (C), and model C plus catastrophic disruptions from Figure 2 (D).

themselves if there were no stochastic variation within the model (Figure 4). It is calculated as

$$\text{Neq} = \frac{-\text{parrcap}}{\log_e\left(1 - \frac{R}{\alpha \cdot F}\right)\alpha \cdot F}, \qquad (4)$$

where Neq is the equilibrium size, R is replacement, F is reproduction, and α and parrcap are as defined in equation (1). Equilibrium size is meaningful only if $\alpha \cdot F$ is greater than R. If R exceeds $\alpha \cdot F$, then there is no equilibrium point other than zero in the deterministic analog of the model. In these situations, rapid population extinction is expected unless the population is supported by immigration.

Resiliency also plays an important role in population persistence. Resiliency is defined as a normalized index of the average surplus production of juveniles over the range of spawning adults between zero and Neq, divided by the number of recruits produced at point [Neq, Jeq]. This is equivalent to the shaded area in Figure 4 divided by Neq·Jeq. Populations with high resiliency exhibit a high degree of density dependence that tends to quickly return populations to near-equilibrium conditions following a perturbation. Resiliency and equilibrium size are linked because zero equilibrium size implies zero resiliency as well. For any positive equilibrium value, a range of resiliency values is possible.

Probabilistic Networks

In real-world applications, model parameters are never known with certainty. As described in step 2 above, this uncertainty in parameters is quantified in the BayVAM procedure during the survey of watershed conditions. When ample data are available to estimate model parameters, uncertainty in the parameters can be estimated through conventional means such as confidence limits. When data are lacking, professional judgment is used to identify the probability of various parameter ranges. The use of professional judgment to estimate parameters and their uncertainty is much discussed in the literature (Morgan and Henrion 1990; Ludwig 1996) and is not without its detractors (see also Dennis 1996). There is no disagreement, however, that parameter uncertainty works in concert

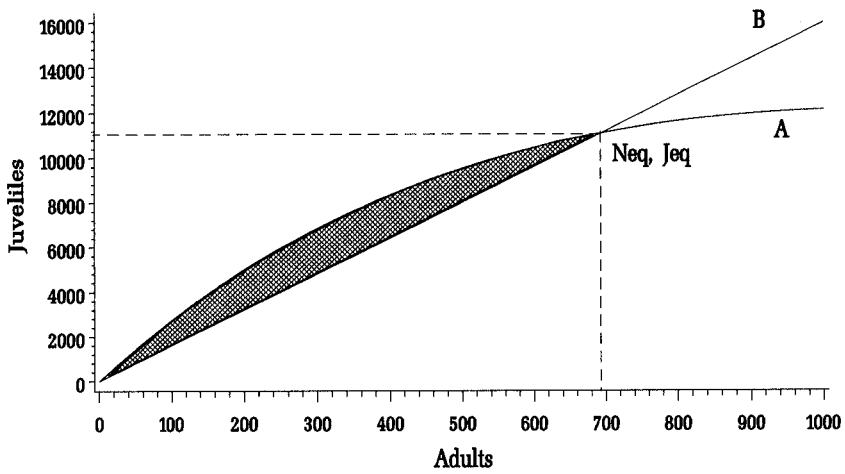

FIGURE 4.—Graphical representation of the underlying relationship between juveniles and adults. Curve A represents the expected number of juveniles produced for each level of spawning adults; curve B is the reciprocal number of adults that are expected from a given level of juvenile recruits to the population. The point [Neq, Jeq] represents the equilibrium point of the deterministic analog of the model. The shaded area between the two curves reflects the degree of population resiliency present.

with natural variability to reduce the certainty with which one can anticipate future states of nature.

In the current context, uncertainty arises from the combination of parameter uncertainty and the three sources of natural variability addressed above (demographic variability, environmental variability, and catastrophes). To explore the implications of this uncertainty with the population simulation model, a series of Monte Carlo simulations can be used in which various combinations of parameters are drawn from the probability distributions defined for each parameter. Each realization would represent a combination of randomly selected parameters (one set drawn per realization) and a random sequence of annual fluctuations from natural processes (a different sequence for every realization). Combining large numbers of such realizations would identify the probability of various outcomes given all four sources of uncertainty. (There is additional uncertainty due to alternative model forms, but we ignore this for now.)

The BayVAM procedure permits analysis of the combination of parameter uncertainty and natural variability, not by requiring Monte Carlo simulation in each analysis, but by recasting the simulation model as a probabilistic network. A large number of simulations over all possible combinations of parameters are done once, and the results of these simulations are used to build a probabilistic network. Probabilistic networks, also called Bayesian belief networks or causal probabilistic networks, are relatively new developments in the field of artificial intelligence and form a special class of graphical models that are becoming increasingly popular in statistics (see Whittaker 1990). Examples of probabilistic networks used in natural resource management are rare; Haas (1991) is a notable exception. Pearl (1988), Olson et al. (1990), and Haas (1991) provide useful introductions to the topic.

Key to understanding the probabilistic network is viewing the simulation model as a graph (Figure 5), wherein each input parameter, intermediate variable, and output variable defines a node or point on the graph. Because they are intricately linked, equilibrium size and resiliency are captured in a single node. Nodes are connected by directed arcs (arrows), which indicate the causal relationships and the conditional dependencies among nodes. For example, replacement is a function of juvenile survival, age at maturity, and adult survival. This relationship, which was defined mathematically in equation three, is depicted graphically in the upper right portion of Figure 5. Reproduction is a similar function of fecundity and spawning and incubation success. The relationship between reproduction, α, parrcap, replacement, and equilibrium size and resiliency raises an interesting point that is made explicit in the graph: once the values for reproduction and replacement are known, their antecedent parameters are not needed to estimate equilibrium size and resiliency. The graphical view of the model also suggests that once equilibrium size and resiliency are known,

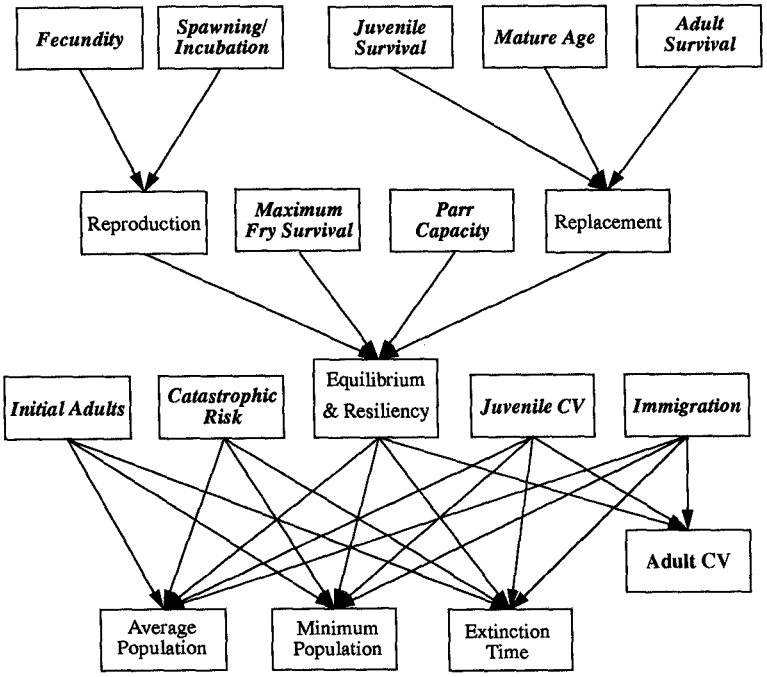

FIGURE 5.—Schematic diagram of the BayVAM probabilistic network. Input nodes (highlighted in boldface italic) and a diagnostic node (Adult CV) correspond to elements assessed in a watershed and population survey. All others are either model intermediates or outputs.

the only additional parameters needed to project the output variables are initial adults, catastrophic frequency, immigration rate, and the coefficient of variation in first-year survival (Figure 5).

In order to depict the uncertainty associated with each node, nodes are subdivided into 3-10 discrete levels. Generally, these levels refer to a specified range of a continuous variable. At a given point in time, each node has one true value that reflects the state of nature. This true value, however, will not be known with absolute certainty. In the probabilistic network, this uncertainty is displayed by assigning a degree of belief (i.e., Bayesian probability) to each value within each node. Each node then has an array of probability values associated with it, creating a probability histogram that is known as a belief vector (Figure 6). These vectors are constrained such that the sum of all values within each vector is 100%. The allocation of beliefs within a node is used to quantify the strength or quality of the available information. For example, if several years of data provide good estimates of juvenile survival that vary around a mean of 30%, the belief vector for juvenile survival might be concentrated in the 27-34% range. Conversely, if there are no data for a particular watershed, but survival values in similar systems have been reported that uniformly range from 20 to 40%, a belief vector spread over the lower four classes might be appropriate. If there is absolutely no information available to judge juvenile survival, the default uniform probability distribution (equal probability assigned to each class) would be appropriate. Biologists with some knowledge of the watershed, the species and life history, and the relevant fish habitat relations should be able to make classifications that fall somewhere between the extremes of no information and a value known with certainty.

The purpose of a probabilistic network is to rigorously track these belief vectors and to systematically update them as information is added to the system. It does this using the calculus of conditional probability first articulated by Bayes (1763). Information is added to the system by changing the belief vectors associated with the input parameters. This information is then propagated through the probabilistic network to update beliefs about the intermediate and output variables. Essential to propagation are link matrices of conditional probabilities that define the relationships between nodes. Wherever there is a directed arc, there is a

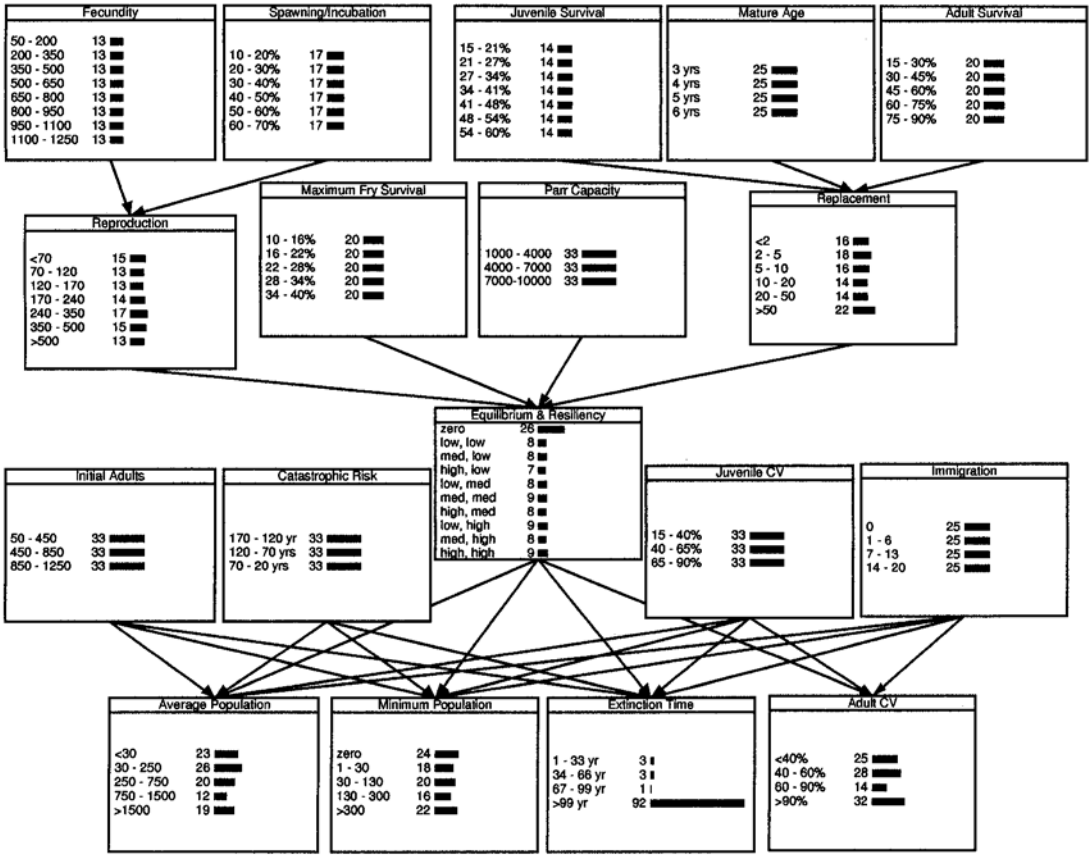

FIGURE 6.—Graphical representation of the BayVAM probabilistic network in the initialized state, wherein no prior information regarding the condition of the model input parameters is given. Histograms at each node reflect the marginal probabilities (i.e., belief vectors) associated with each node, expressed as percentages.

link matrix that explicitly defines the conditional relationship between the two nodes. For example, if a hypothetical node A is connected to node B through a directed arc from A to B, then there is an explicit statement of the form, "given that A has a value *a,* then the probability that B has the value *b is P*," for all combinations of possible values of A and B. Generally, the values within link matrices come from empirical evidence, or if that is lacking, from expert opinion. The BayVAM probabilistic networks are unconventional in that the link matrices are derived from simulation results (see below).

Viability Indices

Three variables are used within the BayVAM procedure to reflect viability: average population size, minimum population size, and time to extinction. These variables are generated from each realization of the simulation model. In the probabilistic network, the belief vectors associated with each viability index are comparable to the frequency distributions produced in a Monte Carlo analysis as described above, in that they represent the observed frequency of outputs given a large number of simulations involving random sampling of parameters from the parameter space defined by the parameter belief vectors.

The viability indices can be used to assess risk, where "risk" is used in the colloquial sense that implies a probabilistic loss (i.e., there is something of value which could be lost, though the loss is uncertain). On these terms, risk is expressed in two dimensions, one dimension expressing the magnitude of potential loss and the second expressing the probability of loss. Because the magnitude of loss can be described in an infinite number of ways depending on the circumstances, direct comparisons of risks measured on different scales are not possible. There is no such ambiguity with proba-

bility, which can be defined rigorously on a scale of zero to one, where one implies certainty. As Ramsey (1926), de Finetti (1974), and others have shown, the rules of probability apply even when the probability merely reflects one's subjective degree of belief (Press 1989; Howson and Urbach 1991).

In the case of fish populations, any decline would represent loss, be it loss of recreational fishing opportunities, aesthetic values, or unique genetic resources. The extent of the potential loss is reflected in average adult numbers and minimum population size; the probability of the loss is reflected in the belief vectors. Where populations may go extinct, the urgency of the situation is reflected in the belief vector of time to extinction.

Diagnostic Nodes

Most of the inferences within the probabilistic network follow causal pathways; that is, information about parameters is used to infer belief about intermediate variables and viability indices. One exception is the adult CV node, which is a fourth output of the simulation model that tracks the coefficient of variation in adult numbers for extant populations. This node can be used optionally to provide additional information about the variation in first-year survival when time series information on adult counts is available. If this option is invoked, the probabilistic network uses (1) the relationships defined in the link matrices among equilibrium size and resiliency, immigration, first-year variation in survival, and adult CV, (2) the calculated belief vectors for equilibrium size and resiliency and immigration given the other input parameters, and (3) adult CV values from empirical data to update belief vectors for first-year survival.

Developing Link Matrices

A key step in developing the probabilistic network was specifying the link matrices that define the relationships between a target or receptor node and the set of donor nodes that conditionally affect the belief vector of the receptor node. (Within the graphical model, directed arcs connect donor nodes to receptor nodes.) Because the probabilistic network was designed to mimic the behavior of the simulation model, developing the link matrices involved analyzing the results of Monte Carlo simulation. This process involved (1) randomly sampling model parameters from defined ranges and calculating intermediate attributes, (2) running the model once for each random set of parameters, (3) mapping the parameter values into discrete levels consistent with the ranges used in the assessment survey and mapping intermediate attributes and model outputs into similar variables that were used as nodes within the probabilistic network, and (4) computing contingency tables based on the joint distribution of parameters, intermediate variables, and viability indices. These contingency tables then were translated into the link matrices needed in the probabilistic network. The matrices that link each receptor node to donor nodes are based on the relative frequency with which each level of the receptor node was observed during the simulation exercise, given each combination of donor values.

The simulation exercise involved 600,000 random combinations of parameters chosen from selected ranges (Table 1). Uniform distributions were used to describe the distribution of parameters within each range. Each simulation consisted of 100 years of dynamics. Several summary statistics were calculated for each simulation, including the mean and variance of the population size over the entire period and for only those years when adults were present. Extinction time was defined as the first year in which there were neither adults nor juveniles; runs that did not result in extinction were assigned an extinction time of more than 100 years.

Parameter ranges generally were chosen to span the range of expected values for trout and char populations in a variety of conditions. One exception is the part capacity parameter, parrcap. Parr capacity was used as a scaling parameter to set the range of possible equilibrium sizes. Our intent was to develop a model that would be applicable to self-sustaining populations in small to moderately sized watersheds (<20,000 ha). Thus, the upper limit on parrcap was set to correspond to an Neq value of roughly several thousand, given median values of the other parameters. The lower limit was set to correspond to Neq values of a few hundred under good conditions. Obviously, application of the model to populations outside these ranges would be inappropriate.

The link matrix for the diagnostic node, adult CV, was derived from the subset of simulations in which the simulated population did not go extinct and there were no catastrophes. In such cases, the observed adult CV is sensitive to population resiliency and variation in juvenile survival; adult CV declines as resiliency increases and variation in juvenile survival decreases.

Interpreting Belief Vectors

The principal outputs of the probabilistic networks are the belief vectors associated with the viability indices. As stated above, these vectors represent the expected frequency of results given a large number of simulations involving random sampling of parameters from the parameter space defined by the parameter belief vectors. The interpretation of these vectors thus must be guided by an understanding of the model. Interpretation also must be tempered by an understanding of uncertainty, how it is propagated through a probabilistic network, and what the belief vectors imply in terms of ecological risk.

For starters, remember that any model is, at best, nothing more than a caricature of reality; it will exaggerate some features of the system while understating or ignoring others. Even models parameterized with the best of data and ecological understanding should not be confused with real ecosystems. Similarly, model outputs such as estimated probability of extinction should not be confused with any true system parameter. The survival of a particular species or stock is not a controlled experiment that will be repeated infinite times, leading to an empirical probability of persistence. Time will proceed only once and the species will either persist or not. Thus, the only defensible interpretation of probability of extinction is in the Bayesian sense of a measure of our belief about a future event (see Howson and Urbach 1991; Ludwig 1996). Even staunch frequentist statisticians cannot claim a non-Bayesian interpretation of future species extinction or quasiextinction. Frequentists can define probability distributions only in terms of the long-term behavior of known statistical models or the result of an infinite series of identical trials (Dennis 1996; Ludwig 1996). Translating the behavior of a statistical model to a degree of belief about a future event in the real world is uniquely Bayesian.

For those who value species persistence, it seems prudent to manage natural resources cautiously and to proceed with changes in a natural system only when the weight of available evidence convincingly suggests that future actions will not jeopardize a species (i.e., the species has a high Bayesian probability of persistence). Any uncertainty, whether it arises from unpredictable events in nature, or from an inability to identify or measure ecosystem parameters, lessens the certainty with which one can anticipate future states of nature. In the probabilistic network, increased uncertainty translates into more even probability distributions at each node. For example, when no information is available, the belief vectors for parameter nodes are uniform distributions (Figure 6). In this initial state, the belief vectors for average population size and minimum population size are fairly uniform and the belief vector for extinction time suggests a low probability of extinction, mainly due to the high probability of the population being supported by immigration. Closer inspection reveals that the probability of zero equilibrium and resiliency is 26%, which would lead one to expect that at least 26% of the populations are ultimately doomed, while simultaneously 75% of the simulated populations are being augmented by immigration (Figure 6). Multiplying 26% times 25% (the fraction unsupported by immigration) gives 7%, which is essentially the fraction that went extinct.

In this example, the probability of extinction means little. The larger lesson is that uncertainty begets uncertainty. Without information, nothing can be said with certainty concerning the future status of the stock. When all combinations of parameters (over the ranges used here) are equally likely, then the odds favor unforeseen combinations of parameters that can either enhance or inhibit populations in an unpredictable fashion.

From a management perspective, knowing how much uncertainty is due to ignorance (i.e., parameter uncertainty) and how much is due to random environmental fluctuations can be important because of the different management strategies needed to address each. While parameter uncertainty can be decreased simply through increased information, a certain level of uncertainty is due to processes that may be beyond the control of management. The role of management in this case is to plan for that uncertainty and mitigate negative effects to the extent this is practical.

The probabilistic network is structured such that the uncertainty in viability indices that arises from parameter uncertainty can be partitioned partially from that due to random environmental fluctuations. For example, if the parameter nodes that determine equilibrium and resiliency are set to single-value histograms, then the probability vector for the equilibrium-resiliency node is concentrated over a narrow range (Figure 7). In this example, the uncertainty in the viability indices (Figure 7) arises primarily from random processes. It is straightforward to iteritavely adjust the parameter uncertainty and the level of random fluctuations

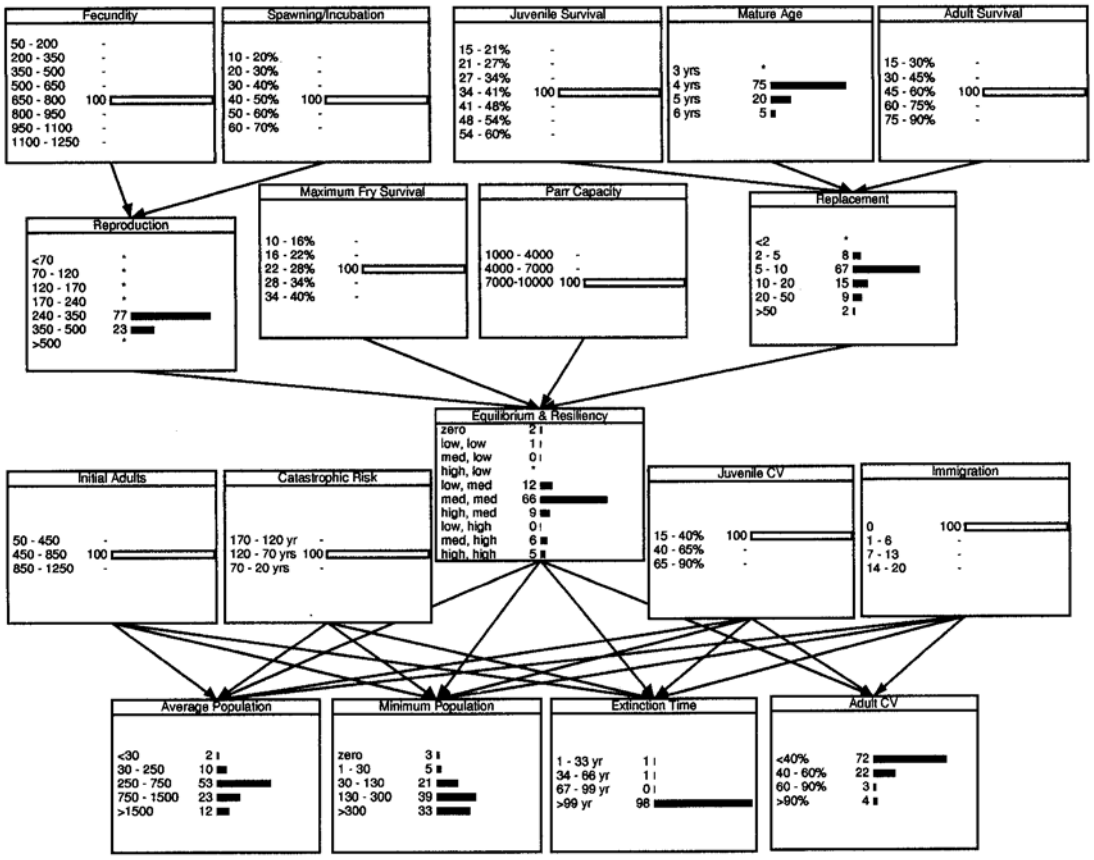

FIGURE 7.—Graphical representation of the BayVAM probabilistic network illustrating updated belief vectors given information on population parameters. Information input to the network is shown as unshaded bars with a belief value of 100. A probability distribution for age at maturity was added also.

in order to discern the relative contribution of each to the final uncertainty in viability indices.

The probabilistic network displays sensitivities to changes in parameter inputs that are consistent with the behavior of the analytical model, with one important difference: the magnitude of those sensitivities may be reduced. In general, the probabilistic network exhibits less sensitivity to changes in parameters than would be exhibited in a more conventional simulation approach. The reason for this lies in the way that a signal (i.e., the change in an output due to a change in input) is attenuated as it passes through a probabilistic network. In the probabilistic network, parameter nodes are connected to intermediate nodes in probabilistic fashion, as opposed to the precise algebraic connection within the analytical model. This results in a dampening in signal as it passes from one node to the other. Changing the mode of the belief vector for incubation success slightly, for example, does not change the belief vector for extinction time to the same extent that an equivalent change in a point estimate for incubation success does in the simulation model.

This relative insensitivity lends a certain inertia to the probabilistic network, in that substantive changes in parameter belief vectors are required to shift the belief vectors or reduce the uncertainty exhibited in the viability indices. Relative to initial conditions of no information (Figure 6), the probabilistic network requires considerable information about population parameters to achieve acceptably high probabilities of persistence or low levels of uncertainty (e.g., Figure 7). Thus, the probabilistic network implicitly places the burden of proof on the network user to demonstrate that a watershed can support a given population. In workshops where we have presented the BayVAM procedures and asked participants to apply them, we've noticed a tendency on the part of partici-

pants to skew the belief vectors toward the less optimistic parameter ranges. Whether this represents either an unintentional or strategic bias is unknown, but clearly it contributes further to the conservative nature of the procedure.

Application

We evaluated the BayVAM procedure in a series of test applications in watersheds throughout the Pacific Northwest in a cooperative effort with FS and BLM biologists. Participating biologists received rudimentary training and then were asked to apply the procedure to populations familiar to them. The most extensive application of the BayVAM procedure to date is the application described by Shepard et al. (1997).

Results from the early testing phase are instructive. Although the procedure seemed well received by those in training, there was an apparent reluctance by some to apply it. Much of this reluctance undoubtedly is due to the novel nature of this procedure and the natural hesitancy to use an approach that one does not fully understand, yet is expected to explain to others. As the procedure is more widely applied and the results become more familiar, we expect wider acceptance.

One of the more encouraging results of our experience thus far with the BayVAM procedure is the extent and focus of discussions that are generated by each application. The transparent nature of the probabilistic network makes explicit all of the assumptions made by a user. If such assumptions seem in conflict with the evidence presented to justify those assumptions, or inconsistent with other assumptions, others are quick to notice. This often leads to a focused discussion of a particular assumption. The overall structure of the simulation model has not been seriously questioned, although it is a legitimate concern. For example, our underlying assumption is a population driven by age-structured dynamics, a conventional approach that can be traced to the age-structured models of Leslie (1945, 1948) and the stock recruitment models of Ricker (1954). Alternative, habitat-structured models have been proposed (Bartholow et al. 1993; Bowers 1993) that might lead to different results. As our understanding of population dynamics improves, corresponding changes and enhancements in the BayVAM procedure are anticipated.

We have identified the BayVAM procedure as a tool for population viability assessment (PVA). As such, many of the questions and concerns that have been raised about PVA may apply (e.g., Simberloff 1988; Boyce 1992; Caughley 1994). In his critique of conservation biology, Caughley (1994) characterizes many PVAs completed on threatened species as, "essentially games played with guesses" (see also Hedrick et al. 1996). Caughley (1994) correctly notes that most PVAs are based on computer simulations with simplistic models, and the basic model parameters are rarely known with precision. In the BayVAM approach, we have tried to mitigate this limitation by making the guesswork an explicit source of uncertainty in results and by incorporating sufficient detail into the population model to force users to think systematically about the factors affecting multiple life stages. When used within an integrated assessment of land use activities (e.g., Shepard et al. 1997), the procedure helps to more fully identify population threats as well as quantify risks.

Whatever its shortcomings, the BayVAM procedure offers a promising step towards tools that are widely applicable and can be used to assess the population viability of salmonid populations in a rigorous and consistent fashion with a mixture of information. For this reason, we believe that combining qualitative judgments with quantitative models using probabilistic networks is an approach deserving of a second look by the wider resource management community.

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