

CHAPTER 12

Stochastic population dynamic models as probability networks

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1 Introduction

1.1 Population dynamic models

The dynamics of a population and its response to environmental change depend on the balance of birth, death and age-at-maturity, and there have been many attempts to mathematically model populations based on these characteristics. Historically, most of these models were deterministic, meaning that the results were strictly determined by the equations of the model and random variability was ignored. More recently, population modelers have moved away from deterministic models toward stochastic models that explicitly incorporate random variation and uncertainty [1, 2]. Stochastic models have the advantage of both characterizing the central tendencies of a population (similar to deterministic models) and addressing at least three sources of variability and uncertainty: (1) temporal or spatial variation in population structure and environmental conditions, (2) intrapopulation variation among individuals and (3) uncertainty in parameter estimates.

Representations of uncertainty and variability are especially critical for populations at risk of becoming extinct or losing significant genetic resources through declines. Chance occurrences can be catastrophic for species already on the brink of extinction. Conversely, some nuisance species may be of little concern on average, but can become major pests when population numbers periodically explode. Central tendencies or expected values resulting from deterministic models are insufficient for assessing these risks. The probabilities of catastrophic outcomes or population explosions can be considered using stochastic models that simulate temporal or spatial variation.

1.2 Stochasticity

With a stochastic model, an element of randomness is introduced for one or more processes of the model. As a result, every time the model is run, a different result is obtained. Running

it many times gives a measure of variability in results as represented by the model. Stochastic processes can be grouped into three categories: demographic, environmental and individual stochasticity [3].

Demographic stochasticity arises from random fluctuations in the sequence of births and deaths in a population. Even if the expected number of births and deaths is equal, there can be a sequence of consecutive births or deaths by random chance alone. Thus, the number of survivors present at a given time will be dictated by the actual sequence that occurs. This will have negligible effect on a large population, but can have a large effect on the persistence of a small population.

Environmental stochasticity is variation in habitat, weather, and other external factors that affect population survival and birth rates. Such variations can be attributed to typical variability in characteristics such as temperature, rainfall or stream flow, or to the occurrence of extreme events of low frequency, such as fire, flood or drought.

Individual stochasticity refers to genetic variability among members of a population (i.e., some members are inherently better able to survive than others). Phenotypic variation may also be important, such as effects of poor food availability at early life stages on growth rates and body size [3]. Individual stochasticity has typically been ignored in population models, but can have an important influence on the persistence of small populations. However, obtaining the relevant information is difficult and expensive. Therefore, we confine our discussion to demographic and environmental stochasticity, while acknowledging the potential importance of individual stochasticity.

The variance in the population growth rate resulting from the combination of demographic and environmental stochasticity directly influences the interannual variation in population abundance. For small populations, such variation is directly linked to risk of extinction. The expected time to extinction decreases as population size decreases and as the variation in the population growth rate increases. Small populations are at particular risk because they tend to vary relatively more than large populations [4]. Restricted populations also have less genetic or phenotypic diversity and fewer and less diverse refuges in available habitat. Thus, in variable environments these populations are likely to be less stable.

1.3 Stochastic models

Stochastic models are created in two basic ways. One option is to start with a deterministic model and recast the model parameters as random variables drawn from selected probability distributions. This option introduces little or no change in the basic model structure, but does require the specification of probability distributions for each model parameter. For nonlinear models, the expected or mean values of model outputs such as population size will differ from the output of a deterministic model that uses mean parameter values. This result, which arises from Jensen's inequality, illustrates the fallacy of assuming that the results of deterministic models using point estimates will be directly comparable to those of a properly constructed stochastic model.

The deterministic model with random parameters is conceptually weak because the deterministic relationships continue to be emphasized. Stochasticity in such models is essentially noise obscuring a deterministic signal. However, nature is inherently stochastic, not deterministic. Therefore, it seems appropriate to build this stochasticity into models in a more fundamental way. This can be accomplished by focusing on the state variables of the model rather than the parameters. Given the state of the system at time t , the likelihood or probability of all possible

future states at time $t + 1$ are assessed. The range of possible future states together with their probabilities defines a probability distribution, which is the fundamental building block of a stochastic process model.

1.4 Probability networks

Probability (or belief) networks have been used in a variety of settings to compile information from various sources to generate probabilistic inferences and predictions [5–8]. Their ease of use and graphical representation make them effective tools for constructing and applying stochastic population models. In the graphical representation, nodes represent important system variables (inputs, outputs or intermediate variables), and arrows between nodes indicate a dependent relationship between the corresponding variables. Such arrows can be drawn using conventional notions of cause-and-effect [9]. The interesting feature that is made explicit by the graph is the conditional independence implied by the absence of connecting arrows between some nodes. These independences allow the complex network of interactions from primary cause to final effect to be broken down into sets of relations, which can each be characterized independently [9]. This aspect of probability networks significantly facilitates their use for representing knowledge from multiple disciplines.

Characterization of the relationships in a probability network consists of constructing conditional distributions that reflect the aggregate response of each variable to changes in its immediate “up-arrow” predecessor, together with the uncertainty or variability in that response. In a stochastic population model, variables may represent abundance of various age-classes, population parameters, stochastic events or environmental conditions. As discussed in the next section, the conditional probability relationships may be based on any available information, including experimental or field results, simulation models or the elicited judgment of scientists. Once all relationships in a network are quantified, probabilistic predictions of model end points can be generated conditional on values (or distributions) of any “up-arrow” causal variables. These predicted end point probabilities, and the relative change in probabilities between alternative scenarios, convey the magnitude of expected population response to historical changes or proposed management while accounting for uncertainties and stochasticity.

2 Methods

2.1 Model construction

A key step in building a probability network is quantifying the relationship between each node and its parent(s). These relationships can be in the form of functional relations or discrete probability tables and can be derived from: (1) empirical data; (2) expert opinion or (3) simulation model outputs. Empirical data that consist of precise measurements in the field of the variable or relationship of interest are likely to be the most useful and least controversial form of information. Unfortunately, appropriate data may not always exist, especially at larger spatial scales. As a consequence, the elicited judgment of scientific experts may be required to quantify some of the probabilistic relationships. This approach is consistent with the Bayesian perspective, which states that probabilities are a useful way of expressing one’s degree of knowledge [10]. Established techniques exist for performing such elicitations [11, 12] and help assure accurate and honest assessments. A third, less typical, approach is to generate probabilities from many

runs of a stochastic simulation model external to the network. The probability network then serves as a kind of surrogate model that reproduces the probabilistic behavior of the underlying dynamics.

2.2 Communicating results

As mentioned earlier, representations of stochasticity are especially crucial when populations are being evaluated for their risk of extinction. Such an endeavor is known as population viability analysis (PVA), and a viable population was first defined by Shaffer [13] as one with a probability of extinction less than a certain value in a certain time period (e.g., <10% in 100 years).

Because of the difficulties in estimating Allee effects and demographic stochasticity influencing very small populations, some researchers have used stochastic models to simulate population declines not to extinction but to a low level that is still sufficiently large to neglect these influences. This is referred to as the *quasi-extinction* risk, which may be estimated more accurately than the risk of true extinction. A related concept is that of the *minimum viable population*, which is the population size that can sustain itself for at least a specified minimum period of time.

Serious biases may result in PVA when demographic stochasticity, environmental stochasticity, and uncertainty are not handled appropriately. To address this problem, Lande *et al.* [2] suggest the use of population prediction intervals (PPI). They define a PPI as “the stochastic interval that includes the unknown population size at a specified future time with a given probability or confidence level.” The approach uses fixed parameter values for each run of a stochastic population model, but varies the values of the parameters between runs randomly according to a specified probability distribution reflecting parameter uncertainty [2]. Desired quantities, such as (quasi)extinction time, that depend on population stochasticity can then be determined for each model run, and the variation across model runs will reflect epistemic uncertainty in model parameters. Thus, the width of the PPI will increase with both increasing stochasticity and increasing uncertainty. However, uncertainty in population parameters will not bias the estimated extinction risk; it will only affect our confidence in the estimate.

2.3 Use of probability networks

Probability networks represent a statistically rigorous way to incorporate diverse information on stochasticity and uncertainty into population predictions. There are a few key points here. First, empirical data often are lacking to assess, for example, the potential effects of some management action on key population parameters. However, there may be experts familiar with the location and species who could offer professional judgments based on their knowledge and experience. Probability networks incorporate these judgments as subjective probabilities, which are an expression of uncertainty about each relationship. Second, the process of assigning probabilities within the network forces one to think about the system, its uncertainties and its stochastic processes in an explicit manner. This can be especially instructive when conducted by a team of experts. Determination of probability relationships should be accompanied by supporting references, documentation or other description of why a particular relationship was chosen. This allows for an honest evaluation of the basis for a particular decision or finding. Third, probability networks can assist in the separate and appropriate handling of stochasticity and uncertainty [14]. Networks can be constructed with stochastic dynamics and static, yet probabilistic, parameters. Thus, PPIs can be determined according to the method described in the previous subsection. Alternatively, population statistics such as minimum population or extinction time can be represented as explicit nodes in the network, with conditional probability distributions determined

according to an external simulation model. Both methods will be demonstrated by the examples described in the next section. Finally, probability networks can be used effectively to identify data needs, including determination of which nodes have the most influence on results due to the uncertainty associated with them (i.e., sensitivity and value of information analysis).

3 Example models and their applications

3.1 BayVAM and westslope cutthroat trout in the Upper Missouri River Basin, USA

3.1.1 Overview

Bayesian Viability Assessment Module (BayVAM) is a stochastic, stage-structured demographic model that has been recast as a probability network by incorporating results from many Monte Carlo simulations over all possible combinations of model parameters [15]. This was done to enhance the model's utility in supporting population viability analyses in real time. In the following sections, we describe the structure of the underlying model and the representation of its results as a probability network. Details can be found in [15].

3.1.2 Underlying stochastic population model

The model underlying BayVAM is a stochastic life-cycle model (SLCM) of resident fish populations that operates on annual time steps (see [16] for a detailed description). The model uses information on critical population processes and rates (e.g., fecundity, survival) and habitat capacity to simulate the dynamics of a local population in a variable environment. For simplicity,

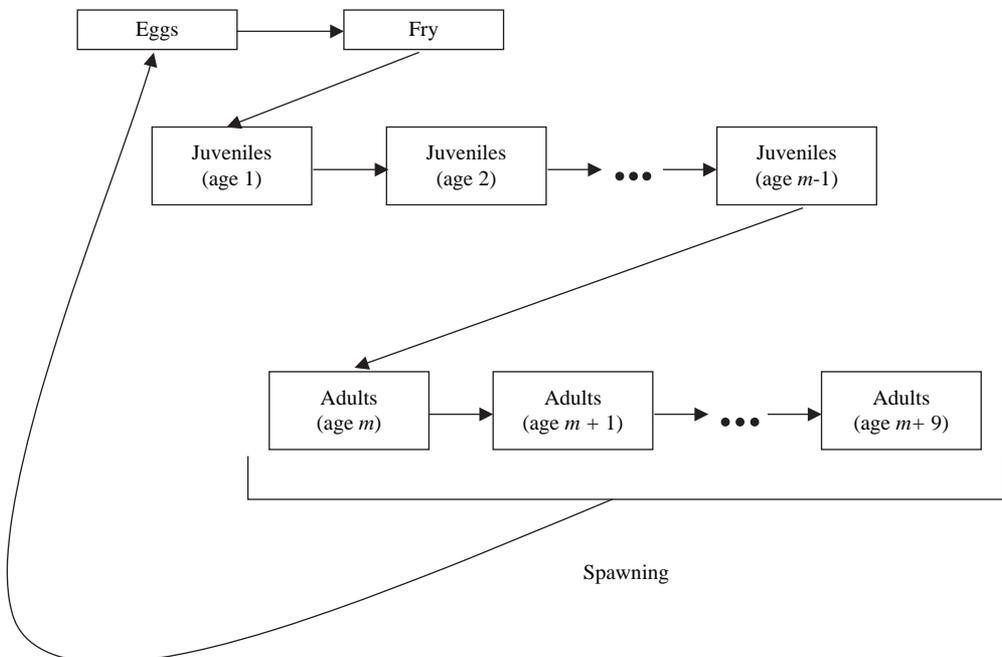


Figure 1: Structure of the population simulation model underlying BayVAM (reproduced from [15]).

modeled populations consist of females only, which avoids the necessity to track maturity and survival rates for both genders or to account for temporal changes in gender ratios. The population is divided into three main classes: 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 year-class cohorts, numbered from 1 to $m - 1$, and m to $m + 9$, respectively, where m is the age of maturity (Fig. 1).

The SLCM requires eight demographic parameters (Table 1) as well as estimates of the variation in subyearling survival, the expected frequency of major habitat disruptions (catastrophes) and the initial number of spawning adults. The model uses a 100-year simulation period, which is roughly 10–20 times the generation time of stream-dwelling salmonids. Although longer time frames may be appropriate for some species, 100 years proved sufficient to characterize the dynamics of the simulated populations and provide useful indices of risk. It is important to recognize that the time frame is only a standard of reference and the assessment is only for conditions at the time of analysis.

Spawning is initiated at the beginning of each simulated year. The number of eggs produced is the product of average fecundity and the number of adult females remaining at the end of the prior time step plus any immigrants. Immigrants are expressed as adult equivalents per spawning brood, i.e., 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 the chosen input value.

Table 1: Description of the parameters of the SLCM and the range of values used in the BayVAM simulations (modified from [15]).

Model parameter	Description	Range of values
Fecundity	Number of female eggs per adult female	50–1250 eggs
Spawning/Incubation (<i>incsu</i>)	Spawning and incubation success rate; potential egg deposition to fry emergence	10–70%
Maximum fry survival (<i>a</i>)	Fry survival at low density; emergence to age 1	10–40%
Parr capacity (<i>parrcap</i>)	Asymptotic parr capacity	1000–10,000 parr
Juvenile survival (s_1)	Juvenile survival rate, age 1+ to adult	15–60%
Adult survival (s_2)	Adult survival rate	15–90%
Mature age (<i>m</i>)	Age at first maturity	3–6 years
Juvenile CV	Coefficient of variation (CV) in fry survival	15–90%
Immigration	Mean number of immigrants per genera- tion	0–20 adult equivalents
Initial number of adults	Initial number of adult females	50–1250 females
Catastrophic risk	Expected time between catastrophes	20–170 years

The number of fry produced is a random binomial variate with parameters N (number of eggs) and p (spawning and incubation success). Survival from fry to age 1 juveniles is modeled as the density-dependent relationship:

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

where s_0 is the expected survival, a is the maximum fry survival rate at 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. This results in an asymptotic production function where the number of age 1 juveniles produced approaches $a \cdot parrcap$ as fry numbers become large.

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 s_0 and coefficient of variation ($CV = 100 \cdot SD/mean$), specified as a model parameter. 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-dependent 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 pre-spawning mortality (which affects first-time and repeat spawners).

3.1.3 Modeling catastrophic disturbance

One aspect that has been added to the population model is the ability to include 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 user specifies the expected time period (in years) between catastrophes. This determines the probability of occurrence in a given year, assuming a Poisson process, i.e., the probability of catastrophe equals the reciprocal of the expected time between catastrophes. Occurrence of a catastrophe is modeled simply as a Bernoulli process each year: it either occurs or it does not.

When a catastrophe occurs, two things happen in the model. 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 ($incsv$) are also reduced, but return to their pre-catastrophe levels more slowly according to the equation:

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

where H is a scalar between 0 and 1 that is multiplied by $parrcap$ and $incsv$, 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 index is adjusted to reflect cumulative impacts (see [15] for details).

3.1.4 Stochastic model output

Each realization of the model produces a simulated time series of population abundances 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. This variation in a single time series arises from three components: (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 from annual variation in fry survival, independent of density-dependent variation and (3) catastrophic disturbances. Because of random fluctuation within the model, simulated extinctions can occur even when the overall trend in population numbers seems stable or increasing. Parameter uncertainty is not yet considered at this point in the analysis.

Four nodes within BayVAM are used to provide an indication of population viability: average population size, minimum population size, time to extinction and the adult CV.

3.1.5 Probability network construction

Uncertainty surrounding the future trajectory of a population comes from the combination of uncertainty in parameters with the demographic and environmental stochasticity inherent in the population. Demographic and environmental stochasticity is accommodated by the stochastic nature of the underlying model, i.e., the binomial transitions simulate demographic stochasticity, whereas the binomial-beta process used in subyearling survival together with the catastrophic disturbance function capture the essence of environmental stochasticity.

To explore the implications of parameter uncertainty, a series of Monte Carlo simulations are used in which various combinations of parameters are drawn from probability distributions defined for each parameter. Each realization represents a combination of randomly selected parameters (one set drawn for each realization) and a random sequence of annual fluctuations from natural processes (a different sequence for every realization). Combining large numbers of these realizations identifies the probability of various outcomes given parameter, demographic and environmental uncertainty.

The BayVAM module permits analysis of the combination of parameter, demographic and environmental uncertainties by recasting the simulation model described above as a probability network. This also provides a linkage between model parameters and real-world observation. A large number of simulations over all possible combinations of parameters are conducted once, and results of these simulations are used to build the network model.

The key to understanding the probability network within BayVAM is viewing the model as a graph, which includes all input parameters and output variables as nodes (Fig. 2). To efficiently capture the relationships between inputs and outputs that come from the underlying simulation model, four intermediate variables were used: *reproduction*, *replacement*, *equilibrium size*, and *resiliency*.

Reproduction is simply the product of fecundity and spawning and incubation success (*inc-suv*). Replacement is the hypothetical number of age 1 juveniles (*parr*) required to produce one adult spawner. Replacement (R) can be calculated from juvenile survival (s_1), age of maturity (m) and adult survival (s_2) as:

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

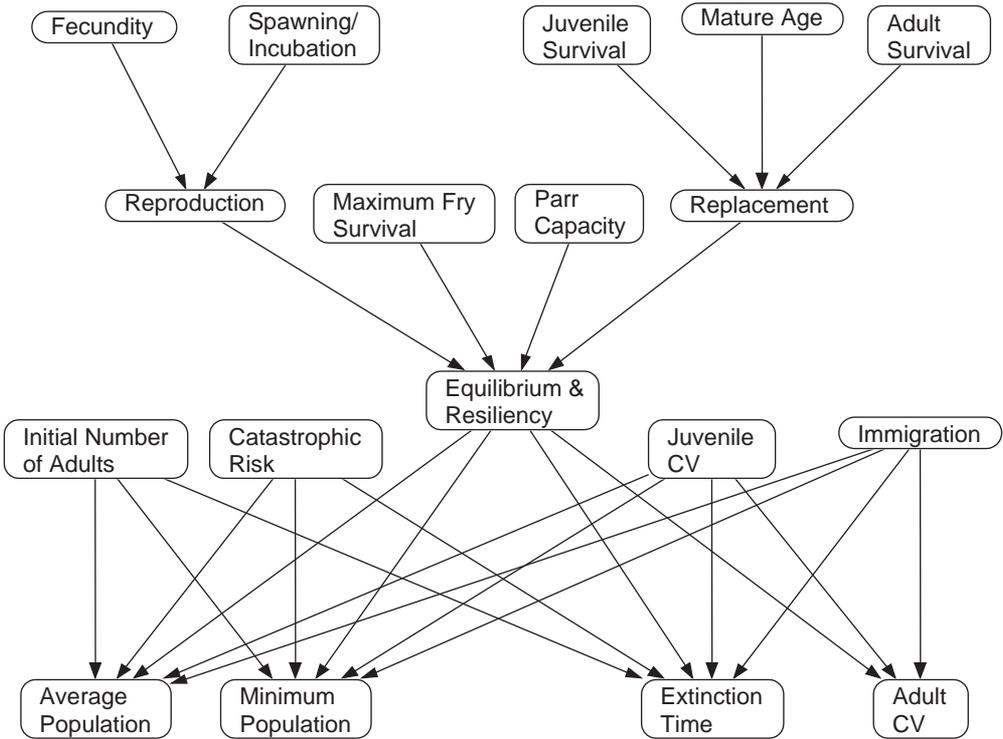


Figure 2: A graphical representation of the model within the BayVAM module. Input or root nodes (i.e., those with no arrows leading into them) and the diagnostic node (adult CV) can be manipulated by the user. All other nodes are either model intermediates or outputs (reproduced from [15]).

Replacement, reproduction and the parameters of fry survival then combine to determine equilibrium size and resiliency. Equilibrium size is the number of adults that would be expected to exactly replace themselves if there were no stochastic variation within the model. It is calculated as:

$$N_{\text{eq}} = \frac{-\text{parrcap}}{\log_c \left(1 - \frac{R}{a \cdot F} \right) a \cdot F}, \quad (4)$$

where N_{eq} is the equilibrium size, F is reproduction, and R , a and parrcap are as defined in previous equations. Equilibrium size is meaningful only if $a \cdot F$ is greater than R . If R exceeds $a \cdot F$, then there is no equilibrium point other than zero in the deterministic analogue of the model. In these situations, rapid population extinction is expected unless the population is supported by immigration.

Resiliency is defined as a normalized index of the average surplus production of juveniles over the range of spawners between zero and N_{eq} (i.e., the average distance between the spawner-to-recruit function and the replacement line in traditional stock-recruitment terms) divided by the

number of recruits produced at point $[N_{eq}, J_{eq}]$. Populations with high resiliency exhibit a high degree of density-dependence that tends to quickly return populations to near-equilibrium conditions following a perturbation. Because they are intrinsically linked, equilibrium size and resiliency are combined into a single node in the network model.

The addition of the intermediate variables representing reproduction, replacement, equilibrium size and resiliency, and their inherent relationship with other variables, allows for an interesting simplification in parameterizing the network model: once the values for reproduction and replacement are known, their parent nodes are not needed to estimate equilibrium size and resiliency. Also, once equilibrium size and resiliency are known, the only additional parameters needed to predict the output variables are initial adults, catastrophic risk, immigration rate and CV in juvenile survival (Fig. 2).

The next step in developing this probability network was specifying the conditional probabilities defining the relationships between a child node and the set of parent nodes. Because the network was designed to mimic the behavior of the simulation model, developing these probabilities involved analysis of the results of the Monte Carlo simulations. This process involved (1) randomly sampling model parameters from defined ranges and calculating intermediate variables; (2) running the model once for each random set of parameters; and (3) computing conditional probabilities based on the joint distribution of parameters, intermediate variables and

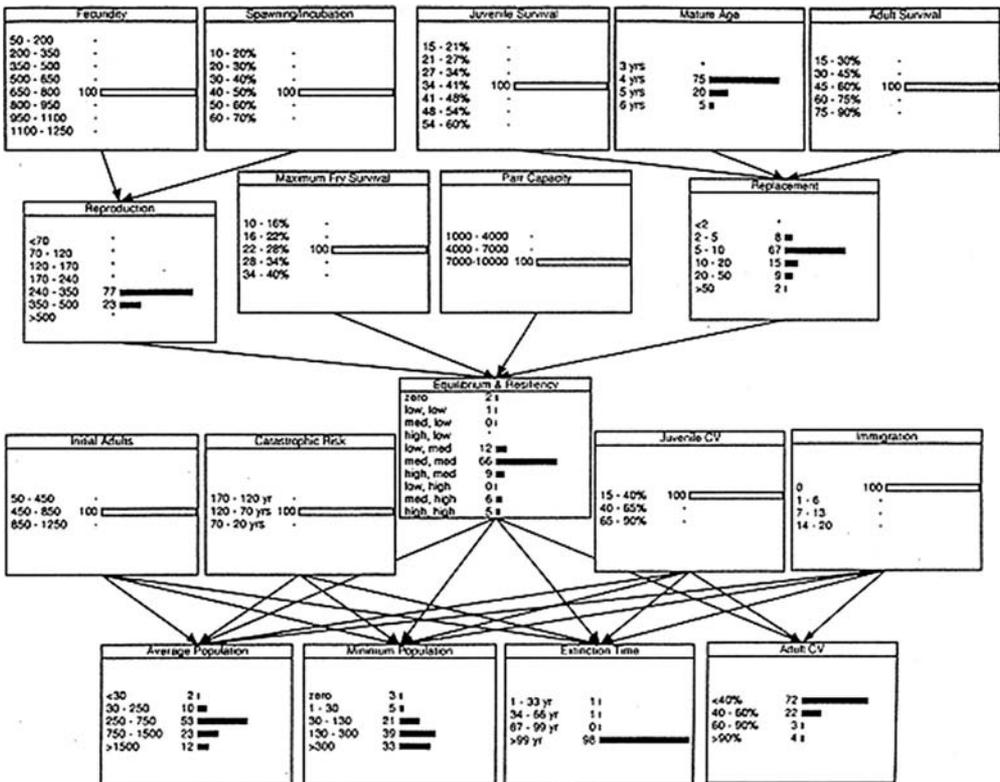


Figure 3: Graphical representation of the BayVAM results illustrating predicted intermediate and output probabilities (shaded nodes) given particular values of the inputs (unshaded nodes). A probability distribution was used for age at maturity (reproduced from [15]).

viability indices. Because all variables in BayVAM are represented by a finite number of discrete bins (rather than as continuous variables), these conditional probabilities are quantified as frequency histograms of the Monte Carlo simulations of the child nodes, given each combination of parent values. The simulation exercise involved 600,000 random combinations of parameters evenly distributed over the ranges specified in Table 1. Each simulation consisted of 100 years of dynamics.

To apply the BayVAM model, the user specifies the actual value (or uncertain distribution) of each input variable and the network then computes the resulting probability distributions for the intermediate and output variables (Fig. 3). This provides a quantitative assessment of relative risk and uncertainty for the population of interest.

3.1.6 Example BayVAM application

Shepard *et al.* [17] applied the BayVAM model to assess the risk of extinction of 144 distinct populations of westslope cutthroat trout in the Upper Missouri River Basin. The abundance and distribution of this subspecies have declined dramatically throughout their historical range due to introductions of non-native fishes, habitat alternations and overharvest. Federal land and state fish managers would like to know the relative extinction risk to each remaining population to justify and prioritize conservation and restoration efforts.

To determine the values of the input parameters for each population, an assessment questionnaire was completed by local fisheries biologists familiar with the individual fish populations, usually via field surveys or reviews of survey data. The questionnaire called for estimates of likelihood values for population demographic parameters and stream habitat capacity. Qualitative guidelines were given to provide a common set of assumptions for assigning values (see Appendix of ref. [17] for details).

For each population, the associated set of likelihood values for the population parameters was used in BayVAM to calculate the probabilities associated with minimum population size, average population size and time to extinction. Populations were classified into three risk groups based on their estimated probabilities of persistence over 100 years ($p100$): very high risk ($p100 \leq 50\%$), high risk ($50\% < p100 \leq 80\%$) or moderate risk ($80\% < p100 \leq 95\%$).

The BayVAM model predicted that most (103/144 or 71%) of the populations had a very high risk of extinction ($p100 \leq 50\%$), 27 populations (19%) exhibited a high risk of extinction ($50\% < p100 \leq 80\%$) and 14 (10%) of the populations had a moderate risk of extinction ($80\% < p100 \leq 95\%$) (Fig. 4). More detailed analysis revealed that extinction risk was most strongly correlated with livestock grazing, mineral development, angling and the presence of non-native fish. These findings have led the state and federal land managers to develop an ambitious conservation and restoration program for this subspecies in the Upper Missouri River Basin. Special focus was placed on tributaries with genetically pure populations with a moderate to high probability of extinction.

3.1.7 Discussion

The BayVAM model reproduces the behavior of the underlying simulation model with one important difference – the sensitivities of outputs to changes in inputs are reduced. The reason for this lies in the way that a signal (i.e., the change in output due to a change in input) is attenuated as it passes through the network. In the probability 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 or attenuation of the signal as it passes from one node to the other. This phenomenon is worsened by the representation of variables as

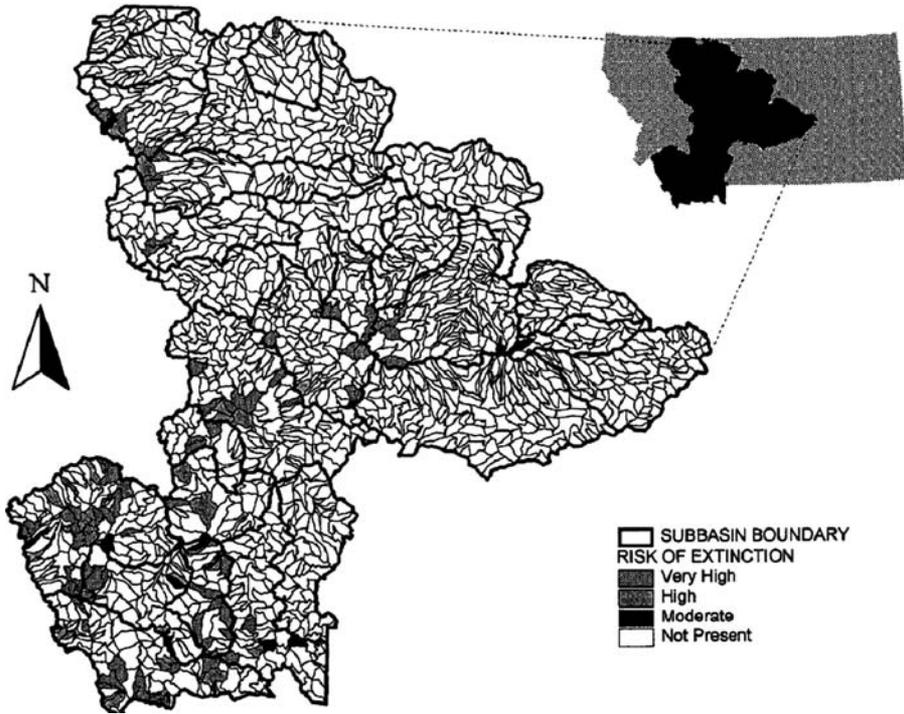


Figure 4: Extinction risk classes for populations of westslope cutthroat trout are shown by watershed within subbasins of the Upper Missouri River Basin (reproduced from [17], with permission of the American Fisheries Society).

discrete quantities because no distinction is made between higher and lower values in the same bin of the frequency histogram. This imprecision enhances the dampening effect.

The relative insensitivity means that substantive changes in parameter distributions are required to change the distributions of the viability indices. Relative to initial conditions of no information, the network requires considerable information about population parameters to achieve acceptably high probabilities of persistence or low levels of uncertainty. Thus, BayVAM implicitly places the burden of proof on the network user to demonstrate that a watershed can support a given population.

Because of these limitations inherent in the BayVAM approach (and in PVA in general), one should not read too much into the risk values for a single population. Rather, these values are better used as a basis for ranking the *relative* viability of populations at risk to provide some guidance with respect to which populations are seemingly in greater need of immediate attention [18]. This was the perspective adopted in the case study application.

3.2 CATCH-Net and brown trout in the Rhine River Basin, Switzerland

3.2.1 Overview

Causal Assessment of Trout Change using a Network model (CATCH-Net) is a probability network model developed to assess the relative importance of different local stress factors in limiting brown trout density in Swiss rivers [19]. Unlike BayVAM, CATCH-Net does not rely on an

external simulation model, but rather includes a dynamic representation of the fish life cycle within the network itself. This is accomplished by creating dynamic nodes for which the values at one time step depend on the values of other nodes at a previous time step. In this way, direct cycles, which are not allowed in probability networks, are avoided.

Additionally, while BayVAM provides qualitative guidance on selecting appropriate population parameters as inputs, CATCH-Net attempts to formalize this procedure by making the links with habitat quality and anthropogenic influence integral parts of the model. These links take the form of conditional probability distributions describing the expected response of parameters to their external influences, including the effects of uncertainty or natural variability. The following sections provide a brief overview of the model, and details are reported in [19].

3.2.2 Population model

At the heart of the model (Fig. 5) is a representation of the fish life cycle with five major stages: eggs, newly emergent fry (age 0), late summer fry (age 0+), immature juveniles and adult spawners. The distinction between emergent and late summer fry was made to differentiate the period of greatest density dependence (see below).

The number of viable eggs deposited in the gravel depends on the total number produced by females and the joint deposition and fertilization success rate (referred to here as a combined “spawning rate”). The total number of eggs produced is the product of average fecundity and the number of mature females. Females were assumed to comprise half of the simulated adult population. Fecundity was described by the following relationship with weight:

$$F = 6.26 \times W^{0.89}, \quad (5)$$

where F is fecundity (eggs/female) and W is weight (g).

The number of emergent fry is the product of the number of deposited eggs and the average survival rate in the gravel. Referred to as “incubation survival,” this rate includes the incubation, hatching and gravel emergence processes. After emerging from the gravel substrate, the first year of life for brown trout can be divided into two distinct periods: the first period covers the density-dependent transition from emergent to late summer fry, and the second covers the density-independent transition from late summer fry to 1+ juveniles (overwinter survival).

Consistent with the findings of Elliott [20], CATCH-Net employs the Ricker model of density dependence to describe survival during the first period, in which the relationship between stock (S) and recruitment (R) is:

$$R = aSe^{-bS}. \quad (6)$$

The specification of the parameters a and b of the stock-recruitment curve can be facilitated by viewing them in terms of two features:

1. The slope of the curve at the origin, i.e., the survival rate of fry at low population density ($R_s = a$), and
2. The maximum of the curve, i.e., the maximum capacity of the stream for late summer fry ($K_f = 0.3679 \times a/b$).

Fry survival at low density ($<10 \text{ ind/m}^2$) has been estimated to be between 0.08 and 0.10 [21]. We therefore used a symmetric triangular distribution with these values as limits. The maximum recruitment capacity K_f of a population is generally believed to be limited by the availability of consumable habitat resources, such as space, cover and food availability [22]. The relationship with habitat is described in the next subsection.

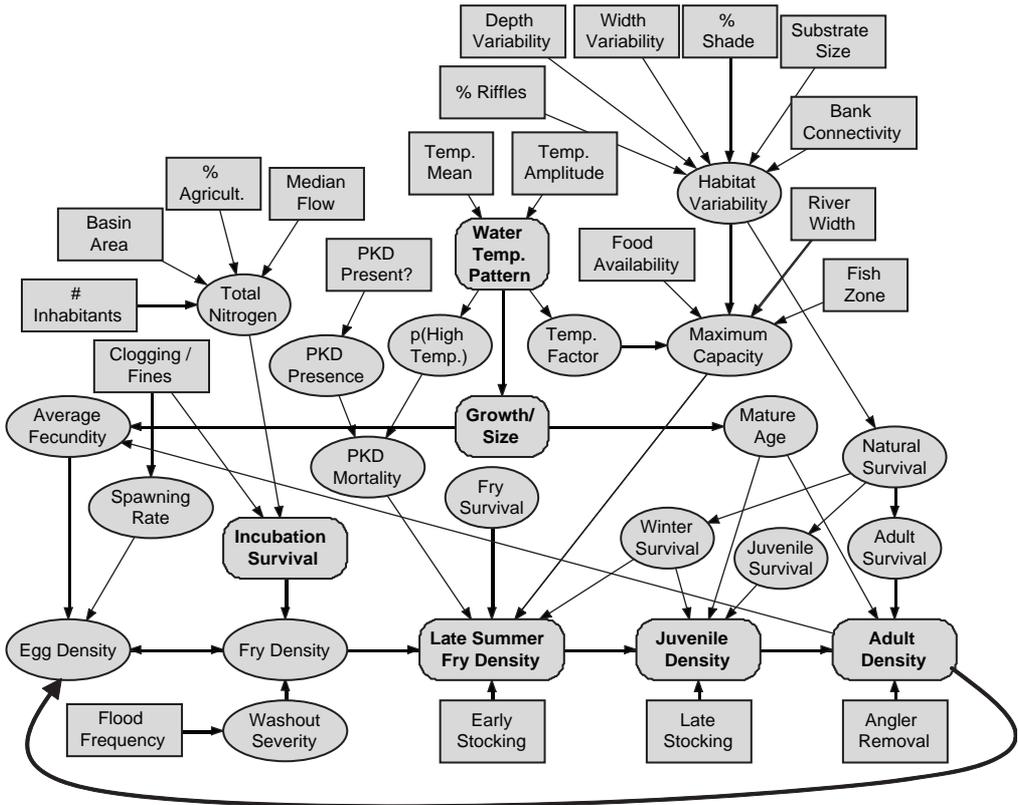


Figure 5: Graphical representation of CATCH-Net. Shaded nodes represent variables that are part of the dynamic, age-structured population model. Unshaded nodes represent variables describing external influences. Square nodes represent model inputs (modified from [19], with permission of Elsevier).

Young-of-year fish in Switzerland are vulnerable to proliferative kidney disease (PKD), a serious parasitic infection of salmonids. An interviewed expert believed that mortality of fry due to PKD would typically be between 0% and 20% in rivers in which the PKD parasite is present. However, if water temperature exceeds 15°C for more than 2 weeks and PKD is present, then mortality is expected to increase to between 10% and 70%. These assessments were used as the limits for uniform probability distributions for PKD-induced mortality of fry in the model. This mortality is assumed to occur after the density-dependent stage, and so cannot be compensated.

After the critical first period, the survival rate increases and is no longer density-dependent. Based on literature estimates, the maximum survival rate of juvenile and adult brown trout is represented by a symmetric triangular distribution with lower and upper bounds of 0.3 and 0.5, respectively. Survival is then reduced in proportion to the habitat quality, as described in the next subsection.

Many female brown trout in Switzerland are reproductively mature by their third year (age 2+) and almost all are mature by their fourth year (age 3+), although there is some variation. It is generally observed that early maturity is associated with higher growth rates and therefore the

proportion of the population that is expected to be reproductively mature at age 2+ was dependent on average size.

To determine size-at-age, we used a modified version the brown trout growth model developed by Elliott *et al.* [23] in which the specific growth rate is expressed as a function of weight and water temperature.

3.2.3 External influences

Population parameters are influenced by external controls, including substrate quality, habitat conditions, temperature, water quality, disease, stocking practices, angling, prey resources and competing species.

Substrate composition and water quality are the most commonly cited factors influencing the rate of spawning success and incubation survival. The composition of the substrate determines the permeability, which, in turn, influences the interstitial water flow and oxygen concentration. Additionally, poor substrate composition can hinder the successful emergence of hatched fry. The probabilistic relationship between spawning, incubation survival and substrate composition was elicited independently from three experts who based their answers on their research experience and the literature [19]. The relationship between incubation survival and water quality was based on egg incubation experiments performed *in situ* at various locations in Switzerland [24]. The proportion of surviving eggs was related to the estimated mean annual concentration of total nitrogen, used as an integrated measure of water quality. Zobrist and Reichert [25] found that mean annual concentrations of total nitrogen could be accurately predicted from basin land use and population size and their relationship was incorporated into the CATCH-Net model.

The hydrologic regime may also have an important influence on incubation survival. High flows during the intra-gravel period can cause egg pocket scouring. For a particular streambed, the flow magnitude at which scour occurs (Q_s) can be estimated using river width, bed slope and gravel size [26]. The extent of scour can then be expected to increase with higher flows, reaching 20% scour at a flow value of $2.5Q_s$, consistent with the results of Lapointe *et al.* [27].

The specification of the maximum capacity K_f of the stock-recruitment curve was based on the method of Vuille [28]. Vuille proposed that maximum production per unit area is proportional to the abundance of prey, an index of habitat quality, a temperature coefficient and a width correction factor. This relationship, when considered as an upper limit, has been supported by electro-fishing and angler catch data in rivers throughout the Swiss canton of Bern. If it is assumed that the limits imposed by these resources are primarily manifest during the critical period, then the maximum recruitment capacity of late summer fry can also be assumed to show such a proportionality. Therefore, this relation was used in the CATCH-Net model.

In Switzerland, brown trout are often stocked in rivers popular with anglers. Stocking of 0+ fry is most common, but may occur in either spring or autumn. As these periods are before and after the critical period of density dependence, respectively, they are handled separately in the model. Fry stocked before the critical period are simply added to the number of newly emergent fry for the year in which they are stocked, thus contributing to density-dependent mortality. Fry stocked after the critical period are assumed to initiate a new phase of density-dependent mortality, which follows a “hockey stick” shape [29], with a width correction that assumes narrow rivers are fully suitable for juveniles, while the centre channel of rivers wider than 8 m provides habitat that is only half as suitable. The hockey stick shape was chosen for this phase of density dependence because, while habitat may still set the upper limit to the population, there are no theoretical reasons to expect overcompensation at this age.

Anglers in Switzerland are required to record and submit to the appropriate canton the number, size, location and date of all fish caught and retained. Therefore, in the model, the total

recorded catch is simply removed from the adult population at the end of each year, proportional to the relative abundance of each adult age class.

3.2.4 Stochastic model output

A large number of simulations are performed for each set of inputs to represent the effects of uncertainty on results. The Latin hypercube sampling method is used to draw random samples from all probability distributions. Each simulation consists of 120 years, with only the last 100 years used for analysis. The variables “Average Fecundity,” “Spawning Rate,” “Incubation Survival,” “PKD Mortality,” “Fry Survival,” “Natural Survival,” and “Washout Severity,” are modeled as dynamic variables, with new values drawn in each year. The other variables, which are interpreted as average values, differ across simulations but are assumed to have constant values for each year of a simulation. Water temperature variables, including the term used to estimate maximum recruitment capacity and the probability of more than 2 weeks greater than 15°C, are calculated from sinusoidal curves describing seasonal variation with site-specific estimates of mean and amplitude.

Model results represent the density of the various life stages of a particular brown trout population given values for the different primary influence factors. The predicted density is a long-term summary for that location, and significant annual variability may underlie this summary depending on annual conditions. Regular fluctuations can also be an inherent property of populations controlled by the Ricker function [30]. To capture this variability and oscillation, our results include estimates of the variability across years, expressed as a distribution of predictions.

3.2.5 Example CATCH-Net application

Borsuk *et al.* [19] applied CATCH-Net to four sub-basins of the Rhine River in Switzerland: the Emme, Lichtenstein Binnenkanal, Necker and Venoge (Fig. 6). These basins were selected for study because they all show a considerable decline in brown trout catch over the last 10–20 years. In addition, they are typical in that they exhibit a multitude of stress factors. In each basin, three distinct brown trout populations were modeled.

Model results were generated for current conditions at the 12 sites and compared to population surveys taken in 2002 and 2003 [31]. Mean model predictions with 90% uncertainty intervals were compared against the mean, minimum and maximum of the observed values.

To assess the relative impact of each major stress factor at each survey site, a quantitative measure of causal strength was used. This was defined as the change in adult density that would result if that stress factor were the only one present at that location, divided by the predicted adult density in the absence of any of the investigated stress factors.

Model predictions showed a reasonable correspondence with observations for juveniles when uncertainty and variability are taken into account (Fig. 7). Both predictions and observations show clear upstream to downstream trends in brown trout density in all four rivers. The model predicts near extinction of the local populations at the two downstream Venoge sites, which have high levels of clogging, poor water quality, PKD, high water temperature, high angler catch and high competition with other fish species. Despite all this, however, population surveys have found a reasonable number of juvenile brown trout. Stocking is fairly high at these locations and, although discontinued for the years of the survey, may still contribute to the density of 2+ or late maturing 3+ juveniles. The two downstream populations on the Emme area also predicted to be near extinction, an expectation that the population surveys support. These populations experience poor water quality, PKD and high angler removal, which are not counterbalanced by the limited stocking efforts. With data available for only 2 years, it is difficult to distinguish whether

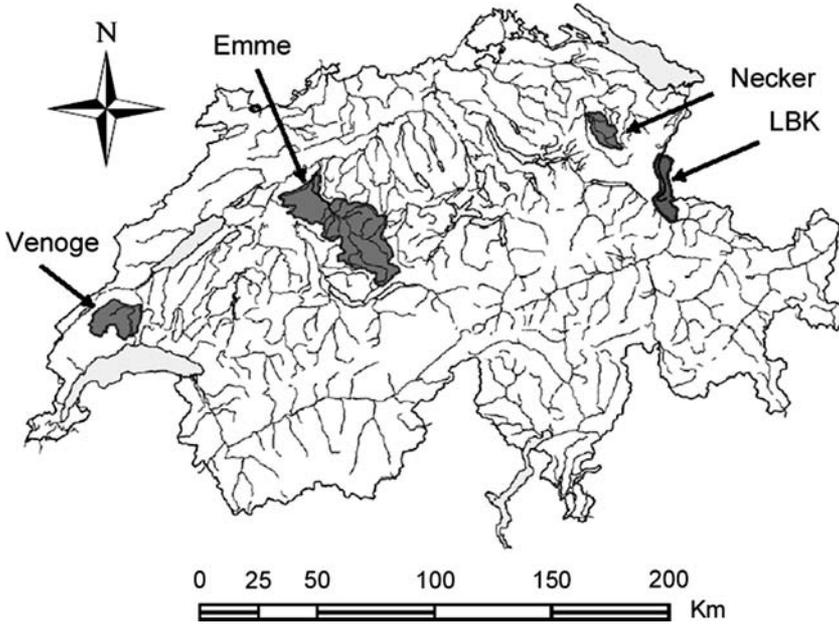


Figure 6: Map of Switzerland showing the four river basins used in the case study (reproduced from [19], with permission of Elsevier).

mismatches between predictions and observations at the other sites are due to model weaknesses or natural variability.

Causal strength estimates showed that habitat degradation is very important at nearly all sites, potentially responsible for reductions relative to optimal conditions of over 50% in nine of the populations. PKD is also fairly important at sites where it occurs, causing reductions over 25% in most cases. Angler catch is important at some locations, such as all the sites in the Emme and downstream sites in the Venoge, and may be responsible for reductions as high as 50%. The effects of gravel bed clogging and water quality are much more ambiguous, probably due to the fact that their impact occurs before the critical period of density dependence. Total reductions caused by all of the stress factors together are at least as great as the observed declines in angler catch over the last 10–15 years. This suggests that there is at least the potential to explain the declines by a degradation in conditions.

3.2.6 Discussion

The quantitative results of the CATCH-Net model can be expected to be sensitive to the choice of a function describing density-dependent survival in the first year. The Ricker curve was used because it has been conceptually and empirically supported for brown trout populations. However, it has the distinctive feature of overcompensation at high stock densities leading to a lower number of resulting recruits. Another recruitment curve without this property could lead substantially different results. Density dependence can also lead to sustained oscillations or even chaotic fluctuations in density with time. In our model, such behavior was not readily apparent in the results because many controlling parameters were also assumed to vary with time.

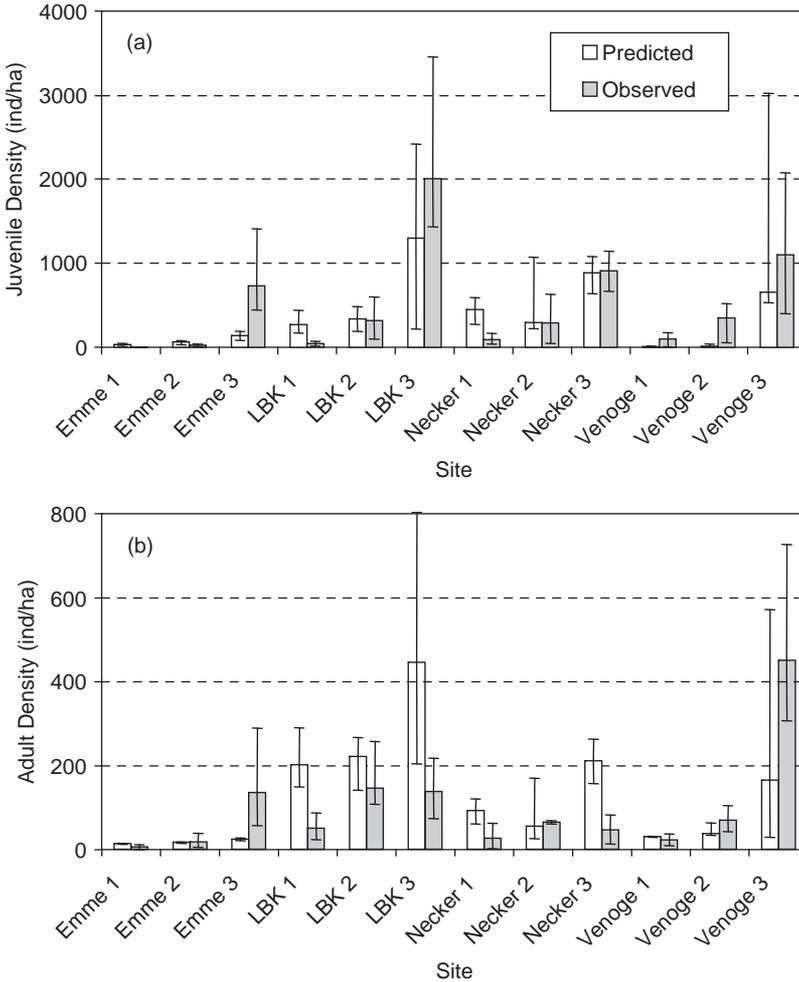


Figure 7: A comparison of model predictions and observations for (a) juvenile and (b) adult density at the case study locations. Vertical error bars represent the 10% and 90% predictive limits, indicating the effects of uncertainty and variability. Observed values are the average, minimum and maximum of the sampling dates in 2002–2003. Numbering of the sites corresponds to relative position: 1 = downstream, 2 = midstream, 3 = upstream (reproduced from [19], with permission of Elsevier).

Compared to BayVAM, CATCH-Net has some distinctive features. Variables are represented as continuous, rather than discrete, quantities, thus helping to avoid the relative imprecision and signal attenuation that occur when uncertainty is propagated through discretized variables. Population dynamics are also incorporated directly into the model, which should ease future updating. Finally, population parameters are explicitly linked to external influences as part of the model, while in BayVAM, this linkage is external. While this choice may help formalize the reasoning procedure in CATCH-Net, it may limit its flexibility relative to BayVAM.

4 Availability of models and software

4.1 BayVAM/Netica

The SLCM underlying BayVAM is available in the SAS programming language from the U.S. Forest Service [16]. The recasting of the model as a probability network was implemented in Netica, a software program that is commercially available from Norsys (www.norsys.com). Netica has a simple user interface for creating graphical networks and allows the conditional relationships between nodes to be entered as either discrete probabilities or functions. Conditional probability relationships can also be learned directly from data files, including files containing the results of external model simulations.

All nodes in Netica must be described by discrete quantities, but the program includes facilities for discretization of naturally continuous variables. Results of models are displayed as easy-to-understand bar graphs or a true/false meter for each node.

Regarding dynamics, it is possible in Netica to have links with time delays, indicating that the value of one node depends on the value of another at an earlier time. Because probability networks are required to be acyclic, after specification, the network is expanded so that dynamic nodes in the original network become multiple nodes in the expanded version, indicating the value of that variable at multiple points in time. While conceptually this allows for the representation of cycles, such as those inherent in dynamic population models, using such networks to represent long time periods in Netica can be a bit cumbersome.

In addition to its Netica implementation, the BayVAM network has been implemented in spreadsheet form for Excel and Quattro Pro. In these versions, the user simply assigns probabilities to each input variable, and the spreadsheet then computes the corresponding probability values for the intermediate variables and the three output variables: minimum population size, average population size and time to extinction. While this version does not have the graphical advantages of the network implementation, it may be more accessible for users familiar with spreadsheets.

4.2 CATCH-Net/Analytica

CATCH-Net was implemented using Analytica, a software program available from Lumina (www.lumina.com). Analytica also has a very easy to use graphical interface and allows for the use of continuous or discrete variables that can be related by any functional expression. Conditional probabilities can be represented by a wide variety of distributions and are propagated through the network using random or Latin hypercube sampling.

Analytica handles changes over time using dynamic nodes. These nodes are represented by arrays with an explicit time index. Such arrays can also be conveniently used with other indices, such as those representing multiple populations, species or age classes.

Unfortunately, the flexibility offered by Analytica comes at the cost of being able to perform probabilistic inference on parent nodes from observations of children. The ability to introduce findings at any point in the network and see how they affect the probabilities of all other nodes can be a useful advantage of Netica. For example, in BayVAM, the user can use observations of the variation in adults (“Adult CV”) to provide diagnostic inference about the variation in juveniles (“Juvenile CV”). This is not possible to do in Analytica.

The CATCH-Net model is available from the authors in English or German, and a detailed user’s manual is available in German [32].

Acknowledgements

Sections of this chapter, including figures, have been previously published in [15, 17, 19] and are reproduced here with the permission of the publishers.

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