A Bayesian belief network for modelling brown trout (*Salmo trutta*) populations in Switzerland

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Abstract: A Bayesian belief network is described that integrates the various scientific findings of an interdisciplinary research project on brown trout and their habitat in Switzerland. The network is based on a population model for brown trout, which is extended to include the effect of natural and anthropogenic influence factors. Uncertainty is included in the form of conditional probability distributions describing model relationships. The model is applied to brown trout populations at twelve locations in four river basins. Model testing consisted of comparing predictions of juvenile and adult density under current conditions to the results of recent population surveys. The relative importance of the various influence factors was then assessed by comparing various model scenarios, including a hypothetical reference condition. A measure of causal strength was developed based on this comparison, and the major stress factors were ranked according to this measure for each location. Results give an indication of the type of management actions that will be most effective in protecting or restoring brown trout populations.

Keywords: probability network, integrated modelling, population modelling, causal assessment

1. INTRODUCTION

In 1998, a nationwide research effort named "*Fischnetz" (Netzwerk Fischrückgang Schweiz)* was organized to evaluate the problem of reduced catch and health of brown trout in Swiss rivers (Burkhardt-Holm et al., 2002). A variety of field and laboratory studies were funded over a period of five years to investigate the various possible causal factors and consider opportunities for improvement. With the recent completion of these studies (Fischnetz, 2004), a method is required to integrate the results in a manner useful for causal assessment and management support.

We have developed a Bayesian belief network as a means for summarizing both the qualitative and quantitative information resulting from the *Fischnetz* projects. Belief networks have the advantage of making causal assumptions explicit and facilitating evaluation of effects, causal attribution, and uncertainty analysis. As with other attempts to model fish populations (Lee and Rieman, 1997; Nickelson and Lawson, 1998; Gouraud et al., 2001), the core of our network model is a dynamic representation of the species' life cycle. This is characterized by population parameters, such as growth, survival, and reproductive rates. These parameters are then linked to external indicators of habitat quality and anthropogenic influence using the results of the *Fischnetz* studies. In a belief network, these links take the form of conditional probability distributions, which capture the expected response of parameters to their immediate influences, including uncertainty and natural variability. For a given set of model inputs, these conditional probabilities are then propagated to model endpoints, giving users an indication of the consequences of inputs including the degree of uncertainty. While other authors have provided guidance on selecting appropriate parameter values for their models under various conditions (Shepard et al., 1997), our method is an attempt to formalize this procedure, making the scientific knowledge (and uncertainty) arising from recent studies an integral part of the model.

The model was applied to specific populations in Switzerland to assess the relative importance of different local stress factors in limiting brown trout populations. We used four river basins with varying characteristics to represent the range of conditions in the Swiss midlands. Model results corresponding to current conditions were compared to recent population surveys to assess the ability of the model to reproduce observed population variation across locations. The relative importance of stress factors was then estimated by comparing various model scenarios, including a hypothetical, pre-impact "reference" condition. A measure of causal strength was developed based on this comparison, and the major stress factors were ranked according to this measure for each location. Results give an indication of the type of management actions that would be most effective in protecting or restoring brown trout populations, and model predictions of the expected consequences of these actions are presented.

2. METHODS

2.1 Approach

Bayesian belief networks have been used in a variety of settings to compile information from various sources to generate probabilistic predictions (Varis, 1995; Borsuk et al., 2003). A key element in their use is a graphical representation. In this graph, nodes are used to represent important system variables (inputs, outputs, or intermediate variables), and arrows between nodes indicate a dependence between the corresponding variables. Such arrows can be drawn using conventional ideas of cause-and-effect (Pearl, 2000). 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 (Reckhow, 1999). This aspect of belief networks significantly facilitates their use for representing the results of multi-team, multi-disciplinary research projects such as *Fischnetz*.

Characterization of the relationships in a belief network consists of constructing conditional probability distributions that reflect the aggregate response of each variable to changes in its "up-arrow" predecessor together with the uncertainty in that response. Conditional probability relationships may be based on any available information, including: experimental or field results, process-based models, or the carefully elicited judgment of scientists.

Once all relationships in a network are quantified, probabilistic predictions of model endpoints can be generated conditional on certain values for "up-arrow" causal variables. These predicted endpoint probabilities, and the relative change in probabilities between alternative scenarios, convey the magnitude of expected system response to historical changes or proposed management while accounting for predictive uncertainties.

2.2 Brown trout life cycle

Resident, stream-dwelling brown trout in Switzerland deposit their eggs during late autumn or early winter. The eggs incubate over winter, hatch in early spring, and emerge from the gravel around May. Soon after gravel emergence, these fry disperse locally and establish territories, which they defend vigorously against other fry, and from which they gather their food. The availability of territories is believed to be an important factor limiting populations, as evidence of density dependence is most frequently observed at this stage. After about two to three years, depending on growth rate, juvenile trout become reproductively mature and begin to spawn. Brown trout in Switzerland rarely live longer than 5-7 years.

2.3 Model

A graphical belief network representing the key factors influencing brown trout was drawn in collaboration with the twelve members of the *Fischnetz* leadership committee through a series of individual and group meetings (Figure 1). The members of the committee have been responsible for overseeing 73 research projects covering all major aspects of the brown trout and its environment in Switzerland (Burkhardt-Holm et al., 2002). At the heart of the resulting graph is a representation of the trout's life cycle with five major stages: eggs, newly emergent spring fry (age 0), autumn fry (age 0), immature juveniles, and adult spawners. The distinction between spring and autumn fry was made to delineate the period of greatest density dependence, modelled using a Ricker curve (Ricker, 1954). The number of individuals in each life stage is influenced by the number in the previous life stage as well as appropriate population parameters, such as survival and reproductive rates. These parameters are influenced in turn by intermediate variables, such as body size, growth rate, and health indices, or by external controls, including environmental conditions, temperature, water quality, stocking practices, angling, prey resources, and competing species.

With the basic structure of the model determined, the next step is to develop the conditional probabilities characterizing the dependences among the variables. A dynamic, age-structured population model can be used to relate the nodes representing the various life stages and population parameters. However, these parameters must still be related to the environmental and anthropogenic factors that represent the root causes of population decline, and which may differ across streams. This is where the recent data and experience resulting from the *Fischnetz* projects are most valuable. The development of the relations leading to each life stage is described by Borsuk et al. (2004).

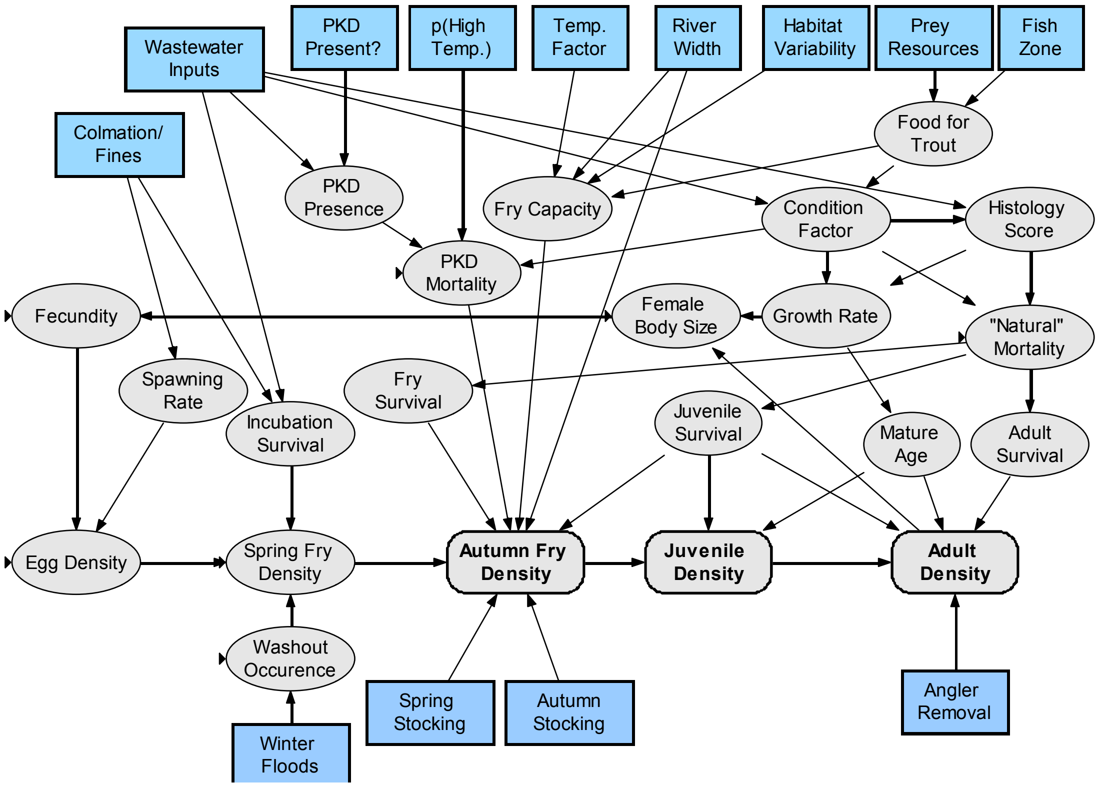

Figure 1. A belief network indicating the causal relations between brown trout life stages and anthropogenic influence factors. PKD is an abbreviation for proliferative kidney disease, a parasite-borne disease.

2.4 Simulations

The fully characterized model was implemented using Analytica, a commercially available software program for evaluating graphical probability models (Lumina, 1997). Other, non-commercial software packages are also available. We chose Analytica because it allows for the use of continuous or discrete variables related by any functional expression. Conditional probabilities can be represented by a wide variety of distributions and are propagated through the network using Monte Carlo or Latin hypercube sampling.

Bayesian belief networks are required to be acyclic. However, the population model requires a cycle linking adults back to eggs. This was handled in Analytica by creating dynamic nodes for the variables representing the various life stages. The values of these variables at one time step can then depend on the values of other, down-arrow variables at a previous time step. In this way, cycles are avoided (Haas et al., 1994).

One hundred simulations were performed for each scenario to represent the effects of uncertainty on results. Each simulation consisted of 120 years, with only the last 100 years used for analysis. The variables “PKD Mortality”, “Washout Occurrence”, and “Fecundity” were modelled as dynamic variables, with new values drawn in each year. The other variables, which are interpreted as average values, differed across simulations but were assumed to have constant values for each year of a simulation. The Latin hypercube sampling method was used to draw random samples from all probability distributions.

Model results represent the density of the various life stages of a brown trout population at a particular location, given values for the different primary influence factors. The predicted density is a long-term summary for that location and may be very different during a particular year, depending on annual conditions. However, the results include predictions of the variability across years, expressed as a distribution of predictions.

Four river basins were chosen to represent the range of conditions in Switzerland: the Emme, Lichtenstein Binnenkanal (LBK), Necker, and Venoge (Table 1). These four basins served as case studies for other parts of the *Fischnetz* project. Data on brown trout density and the relevant influence factors are available for three survey sites (upstream, middle, and downstream) in each river basin. The *Emme* basin is comprised of approximately 50% agriculture, 40% forest and 10% developed land. Most of the development is in the lower portion, where the two largest of six total wastewater plants discharge. Natural habitat variability along the river is fairly low, and PKD has been detected in downstream section. Historical records show a nearly 60% decline in angler catch of brown trout since 1989. *LBK* is a largely human-influence canal, with poor habitat structure in the downstream sections, a high level of fines, and a generally low angler catch of brown trout. There is only one treatment plant discharging to LBK. The *Necker* system is largely healthy, with high habitat quality, relatively low wastewater discharge, and no evidence of PKD. Fines may, however, be a problem in the lower reaches. Finally, the *Venoge* has high habitat quality, but also high fines, high wastewater inputs, and presence of PKD. Catch reductions have not been as severe as at other locations, but stocking is also high.

Table 2. Summary of basin characteristics for the four study sites.

	Emme	LBK	Necker	Venoge
Area	963 km^2	138 km^2	123 km^2	231 km^2
Length	ca. 80 km	29 km	ca. 31 km	ca. 80 km

2.4.1 Model Testing

To assess the ability of the model to reproduce observed population patterns, model results were first generated for current conditions (Table 2) at the twelve survey sites and compared to the recent population surveys. For stocking and catch values, the annual average for the period 1996 to 2000 was used. Model predictions were recorded for juvenile and adult density at each location and compared against the average of the observed values over the three survey dates.

2.4.2 Causal Assessment

To assess the current relative impact of each major stress factor at each survey site, a quantitative measure of causal strength was developed. This was defined as the reduction in adult density that would result if that stress factor were the only one present at that location, divided by the reduction resulting from all the stress factors that are actually present. This gives a relative causal strength ranging from 0 to 100%. Because the measure depends on the other site-specific characteristics, such as width, temperature, and fish zone designation, it can be used as an indication of the relative importance at a particular site but not compared across different sites.

2.4.3 Effects of Management

To consider the effect of management measures to improve conditions, model predictions were generated assuming the removal of the one or two most important stressors at each site. Other site-specific conditions, such as temperature, width, and fish zone were maintained at the current values. The recent levels of stocking and angler catch were also maintained.

3. RESULTS

3.1 Model Testing

Model predictions show a reasonable correspondence with observations for juveniles (Figure 2a). At the middle and upstream locations (2 and 3, respectively) for all three rivers, predictions are close to observed values. At the upstream Venoge location, there is high uncertainty in the model predictions. This is primarily due to the presence of PKD and the fact that temperatures only occasionally exceed a threshold for PKD-induced mortality of approximately two weeks greater than 15ºC (see Table 2). The observed value of 1445 ind/ha is within the range of model prediction uncertainty. Model predictions of juvenile density consistently exceed observed values at the most downstream locations. This may indicate that downstream sites are somehow less favourable for brown trout than the factors included in the model

Table 2. Current values of the important input variables for each of the basins. Survey locations are numbered from 1 to 3 from downstream to upstream.

Location	Level of Fines	% Waste-water	PKD	p(T> 15ºC)	Temp. Factor	Width (m)	Habitat Variability	Species Zone	Prob. of Flood	Spring Stocking (ind/ha/y)	Autumn Stocking (ind/ha/y)	Angler Catch/ha (ind/ha/y)
Emme 1	Low	10-30	Yes	0.9	1.25	23.6	Low	Grayling	0.22	0	150	38
Emme 2	Low	<10	Yes	0.7	1.25	32	Low	Trout	0.22	331	178	55
Emme 3	Low	<10	No	0.5	1	11.7	Med	Trout	0.22	987	136	76
LBK 1	High	<10	?	0	1	8.5	Low	Trout	0.18	0	1,954	5
LBK 2	High	<10	No	0	1	4.9	Low	Trout	0.18	0	1,954	0
LBK 3	Med	<10	No	0	1	3.9	High	Trout	0.18	0	1,954	0
Necker 1	Med	<10	No	0.7	1.25	13.3	Med	Grayling	0.185	7,303	0	28
Necker 2	Med	<10	No	0.7	1.25	15.4	High	Trout	0.185	4,753	0	90
Necker 3	Low	<10	No	0.1	0.75	5.7	High	Trout	0.185	2'418	0	9
Venoge 1	High	10-30	Yes	0.9	1.5	11.8	Med	Barbel	0.273	1,437	803	150
Venoge 2	High	10-30	Yes	0.9	1.5	14	High	Barbel	0.273	1,437	803	150
Venoge 3	Med	<10	Yes	0.3	1.25	6.1	High	Trout	0.273	8,114	0	170

would suggest. The effects of width, wastewater input, temperature, habitat quality, and biological fish zone are already included in the model. It is possible that neglected effects, such as bird predation or immigration, have a greater influence downstream than upstream.

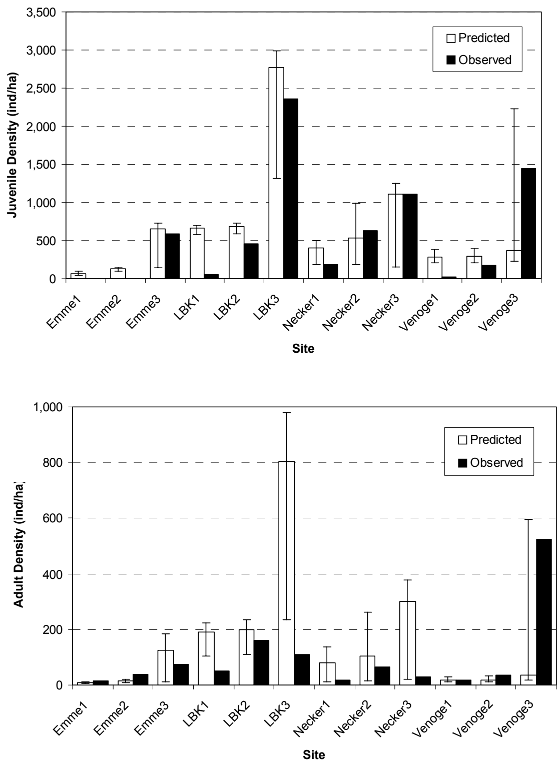

Figure 2. A comparison of model predictions and observations for (a) juvenile and (b) adult density. Vertical error bars represent the 10 and 90% predictive limits, indicating the effects of uncertainty and variability. Observed values are the average of the three survey dates in 2002. The density of juveniles was not recorded at the two downstream sections of the Emme.

There is less correspondence between predictions and observations for adults (Figure 2b). The most upstream site in the LBK is especially overpredicted. However, this was not the case for juveniles, suggesting that some cause for loss of adult fish may have been neglected. This may be bird predation, unrecorded angler catch, or emigration. Such losses may also account for the overprediction at the upstream Necker site.

With data available for only one year, it is difficult to distinguish whether mismatches between predictions and observations are due to model weaknesses or natural variability. Data from multiple years will be required to better assess the long-term average density.

3.2 Causal Assessment

Causal strength estimates show that the relative impact of the different causal factors differs by location (Figure 3). Habitat is very important at all but the most unimpaired sites. Sediment clogging by fines and PKD are also very important at sites where they occur. However, in the Venoge, it seems that the effect of these stress factors on the population is partially offset by stocking. Wastewater inputs are a contributing factor at three of the locations.

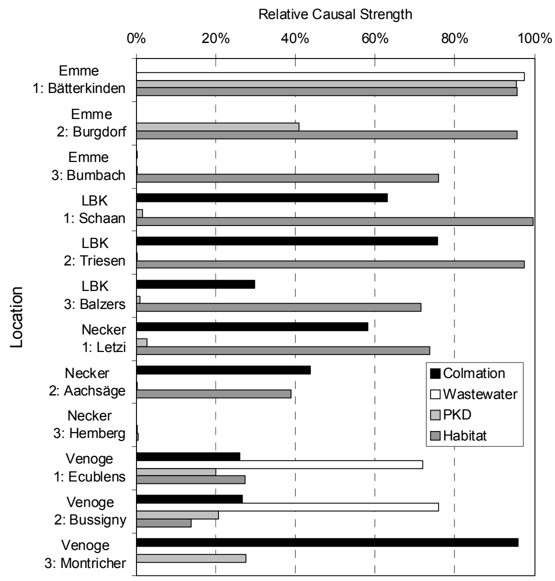

Figure 3. The estimated causal strength of the four most important stress factors at each location. Relative causal strength for a particular stress factor is defined as the reduction in adult density that would result if that stress factor were the only one present at a location, divided by the reduction resulting from all the stress factors that are actually present. If a bar is not shown for a location, then the stressor is not present.

3.3 Effects of Management

Predictions show that significant improvements can be expected to result from management measures at some of the sites (Figure 4). The downstream LBK populations would benefit greatly from an improvement in the habitat score and the elimination of sediment clogging by reducing the input of fines. The midstream Necker population would also benefit if the sediment clogging level could be reduced to “low.” The adult density of other populations would not increase substantially, even if the major stress factors could be removed. The two downstream Emme sites, for example, are severely limited by the presence of PKD. The downstream Necker and two downstream Venoge sites cannot be expected to support high brown trout densities because of their classification as Grayling or Barbel zones. Under conditions of "low" clogging, the most upstream Venoge site shows a predicted population density close to the actual observed density (see Figure 2b). This suggests that actual sediment conditions may not generally be as bad as found in the habitat survey. The presence of PKD at this location does not severely limit the population, because temperatures are not very high. Other upstream locations are already close to their optimal level, so further improvements are not likely.

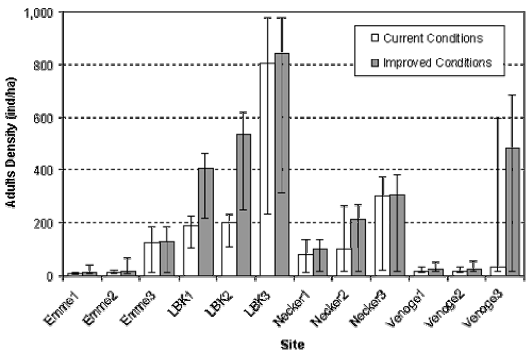

Figure 4. The predicted effect of management measures to eliminate the two major stress factors at each location. Vertical error bars represent the 10 and 90% predictive limits of adult population density.

4. DISCUSSION

Many of the populations in the study locations are exposed to more than one stress factor. Our causal assessment showed that, in most cases, even if only one of the important stress factors is present, the population density could be severely reduced. This implies that if multiple factors are present, then all of them would have to be eliminated in order to achieve a significant recovery. This result was confirmed by the predicted response of the populations to management measures (see Figure 4); locations with PKD, for example, did not show an improvement.

The conditions observed at the study locations are common throughout the midlands of Switzerland. Sediment clogging, wastewater inputs, PKD, and poor habitat are common problems. Therefore, the results of this modelling study can be expected to be generally applicable. However, the response of a population to the introduction or removal of a particular stressor will depend highly on existing conditions, including the presence of other stressors. The model developed in this study based upon the results of recent research can be used to provide these site-specific assessments.

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