Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*)

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Abstract: Native salmonid fishes often face simultaneous threats from habitat fragmentation and invasion by nonnative trout species. Unfortunately, management actions to address one may create or exacerbate the other. A consistent decision process would include a systematic analysis of when and where intentional use or removal of barriers is the most appropriate action. We developed a Bayesian belief network as a tool for such analyses. We focused on native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and nonnative brook trout (*Salvelinus fontinalis*) and considered the environmental factors influencing both species, their potential interactions, and the effects of isolation on the persistence of local cutthroat trout populations. The trade-offs between isolation and invasion were strongly influenced by size and habitat quality of the stream network to be isolated and existing demographic linkages within and among populations. An application of the model in several sites in western Montana (USA) showed the process could help clarify management objectives and options and prioritize conservation actions among streams. The approach can also facilitate communication among parties concerned with native salmonids, nonnative fish invasions, barriers and intentional isolation, and management of the associated habitats and populations.

Résumé : Les poissons salmonidés indigènes font souvent face simultanément à une double menace représentée par la fragmentation des habitats et l'invasion de salmonidés non indigènes. Malheureusement, les aménagements faits pour régler un de ces problèmes peuvent faire surgir ou exacerber le second. Un processus de décision cohérent devrait inclure une analyse systématique du moment et de l'endroit les plus appropriés pour l'érection ou le retrait de barrières. Nous avons mis au point un réseau de croyance bayésien pour servir d'outil pour ces analyses. Nous nous sommes intéressés spécifiquement à la truite fardée (*Oncorhynchus clarkii lewisi*) indigène du versant occidental et à l'omble de fontaine (*Salvelinus fontinalis*) non indigène; nous avons tenu compte des facteurs du milieu qui influencent les deux espèces, de leurs interactions potentielles et des effets de l'isolement sur la persistance des populations locales de truites fardées. Les compromis entre l'isolement et l'invasion sont fortement influencés par la taille et la qualité des habitats du réseau de cours d'eau à isoler, ainsi que par les liens démographiques établis à l'intérieur des populations et entre elles. L'utilisation du modèle dans plusieurs sites de l'ouest du Montana (É.-U.) montre que le processus peut servir à éclaircir les objectifs et les options de l'aménagement et à établir les priorités des initiatives de conservation dans les différents cours d'eau. Cette méthode peut aussi faciliter la communication entre les divers intervenants préoccupés par les salmonidés indigènes, les invasions de poissons non indigènes, les barrières et l'isolement délibéré, ainsi que par l'aménagement des habitats et des populations associés.

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Introduction

Indigenous stream fishes, particularly salmonids, are in decline in many portions of western USA. Habitat fragmentation and invasion of nonnative fishes are primary contributors to these declines (Young 1995; Rieman et al. 2003; Fausch et al. 2006), but attempts to ameliorate their different effects may elicit different and often conflicting management approaches.

Widespread fragmentation of habitats and isolation of populations has been caused by habitat degradation (e.g., decreased water quality and quantity) and fish passage barriers associated with irrigation diversions, dams, and road crossings with impassable culverts that number in the thousands across the region (US General Accounting Office (US GAO) 2001; Clarkin et al. 2003). As a result, many populations of native salmonids are now restricted to headwater streams (Fausch et al. 2006; Neville et al. 2006). Population isolation can lead to loss of genetic diversity, limited expression of life history diversity, reduced population resilience, and ultimately to local extinction (see Fausch et al. 2006 for a review). Reversing habitat degradation can be slow, technically and politically difficult, and expensive (Williams et al. 1997). On the other hand, where habitats remain in relatively good condition, reversing habitat fragmentation and population isolation may only require removal or modification of a fish passage barrier. The ultimate cost and benefit, however, must be considered in the context of other threats, particularly encroachment by nonnative fishes.

Nonnative fishes have been widely introduced in western US streams since the late 1800s. Many nonnative species now occur in main-stem rivers (Lee et al. 1997), but of particular concern for native salmonids is the widespread invasion of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) into mid- and higher-elevation streams (e.g., Thurow et al. 1997; Schade and Bonar 2005). Nonnative trout can displace native species via hybridization (e.g., Allendorf et al. 2001), competition, or predation (e.g., Dunham et al. 2002*a*; Peterson and Fausch 2003). These nonnative species pose an acute threat to the native salmonids that are increasingly restricted to headwater streams (Dunham et al. 2002*a*; Fausch et al. 2006). Because nonnatives may continue to spread, many remnant populations of native salmonids remain at risk. As a result, many biologists install fish migration barriers, a strategy called isolation management (e.g., Kruse et al. 2001; Novinger and Rahel 2003).

The conundrum is that removal of migration barriers to connect native populations to larger stream networks could allow upstream invasions of nonnative fishes, while installing migration barriers to preclude these invasions may exacerbate effects of habitat fragmentation and population isolation. Both actions could threaten native species and integrity of aquatic systems, but fish biologists may employ both barrier installation and barrier removal strategies across the western USA without evaluation of the opposing threats. The potential conflicts highlight a challenge in native fish conservation.

Because resources for conservation management are limited, effective prioritization is important. Trade-offs may be relatively clear to biologists and managers with intimate knowledge of a particular system, and their efforts can be focused effectively. Elsewhere, the trade-offs may be more ambiguous or the data and experience more limited, and the result may be a decision that is influenced more by personal philosophy or public pressure than by knowledge. When the differences in these decisions cannot be clearly supported and articulated, the process can appear inconsistent and arbitrary to the public or the administrators controlling funding (US GAO 2001). A formal decision process could help.

Methods for assessment of barriers to fish passage are widely available (Clarkin et al. 2003), but tools to evaluate relative risks and trade-offs or to prioritize work are not. The limitation is not necessarily in knowledge of the relevant biology. Research on fish populations upstream of fish passage barriers, for example, showed the probability of extinction increases as a function of decreasing habitat area and time (e.g., Morita and Yamamoto 2002). Similar work exists on the distribution and interaction of nonnative and native salmonid species (e.g., Paul and Post 2001; Peterson et al. 2004). Existing knowledge, then, provides a foundation to consider the risks inherent in intentional isolation or continuing species invasions.

Fausch et al. (2006) synthesized much of the current knowledge, proposed a framework to consider trade-offs in the installation or removal of barriers, and provided general guidelines for individual decisions and prioritization of action among streams. A central conclusion was that trade-offs between the relative threats of invasion or isolation depend very much on environmental context. Application of these guidelines in complex environments, however, requires consideration of multiple interacting factors that may be difficult to address consistently, particularly when there is uncertainty about the conditions influencing the trade-offs. A Bayesian belief network (BBN) is one method that could be used to formalize the evaluation.

BBNs (Pearl 1991; Jensen 1996) increasingly are being used to provide formal decision support for natural resource issues (Reckhow 1999; Marcot et al. 2001; Marcot 2006), including fisheries management (e.g., Lee and Rieman 1997; Rieman et al. 2001; Borsuk et al. 2006). BBNs can be used to evaluate relative differences in predicted outcomes among management decisions. They are appealing because their basic structure (a box-and-arrow diagram that depicts hypothesized causes, effects, and ecological interactions) can be readily modified to reflect new information or differences in perceptions about key relationships. Moreover, BBNs can incorporate information from a variety of sources, such as empirical data, professional opinion, and output from process-based models. Outcomes also are expressed as probabilities, so uncertainty is explicit. In addition, BBNs are conceptually straightforward to build and use, so biologists can explore a variety of management scenarios in different ecological contexts and then quantify and communicate these options to decision makers (Marcot et al. 2006; Marcot 2007).

Our goal was to formalize an evaluation of trade-offs between intentional isolation and invasion, relevant to conservation of native salmonids. We focused on persistence of native westslope cutthroat trout (hereafter WCT, *Oncorhynchus clarkii lewisi*), potential invasion and subsequent effects of nonnative brook trout, and the primary environmental and anthropogenic factors influencing both species and their interactions. Our objectives were to develop and explore the application of a BBN as a decision support tool and highlight results that provide general guidance for biologists and managers. We focused this work on cutthroat trout and brook trout because they represent a widespread and well-defined problem in central and northern Rocky Mountain streams (Fausch et al. 2006), but we believe our approach can be readily adapted to other species.

Materials and methods

Background and conceptual foundation

Cutthroat trout have declined throughout their range in the United States (e.g., Young 1995). There are six major extant subspecies in the Rocky Mountains (Behnke 1992), all of which have either been listed ($n = 3$) or petitioned for listing under the Endangered Species Act. WCT have been proposed for listing, but determined to be not warranted (US Fish and Wildlife Service (USFWS) 2003). That decision remains controversial (Allendorf et al. 2004, 2005; Campton and Kaeding 2005), but it is clear that many populations are at risk (Shepard et al. 2005), and managers are concerned with conservation of both the genetic and ecological integrity of remaining populations. We focus our analysis on WCT because they still inhabit large areas of connected habitat, because we have relatively good information about distributions and habitat use, and because there is considerable debate among biologists about the risks associated with isolation and invasion (Fausch et al. 2006). WCT are thought to occupy more than half of their historical range, with range losses attributed to overexploitation, habitat degradation and fragmentation, and nonnative fish invasions (McIntyre and Rieman 1995; Shepard et al. 2005). Considerable work on habitat use suggests that most spawning and early rearing is in small (≤4th-order) headwater tributaries. Resident individuals may spend their entire life in natal or nearby streams, but migratory individuals that move long distances (10–100 km) are important in many systems (McIntyre and Rieman 1995).

Our approach focused on persistence of WCT associated with individual tributaries or tributary networks representing spawning and early rearing habitat for any life history form. Natal habitat is discontinuous throughout a river basin, so tributaries can be viewed as local populations embedded in a larger metapopulation (Rieman and Dunham 2000; Dunham et al. 2002*b*) if migration and dispersal occur or as solitary isolates if this does not occur. Because brook trout invasion is considered a primary threat to persistence of WCT (and other cutthroat trout) across much of its range (Young 1995; Thurow et al. 1997; Dunham et al. 2002*a*), we developed a framework that considered trade-offs between the potential effects of intentional isolation (to preempt brook trout invasion) and of invasion, both mediated by habitat and environmental conditions. Invasion by rainbow trout is also a threat through hybridization and genetic introgression (Allendorf et al. 2001, 2004), but a formal consideration of genetic threats to WCT was beyond the scope of our primary objective. Although we did not attempt to directly model effects of rainbow trout invasion, our work evaluates the general risk from isolation; this could partially inform barrier considerations where threats of introgression are deemed important.

Fausch et al. (2006) framed the evaluation of isolation versus invasion as a series of questions that defined the trade-offs within individual stream networks and relative priorities among them. We formalized that process with a WCT population persistence model structured as a BBN. The probability of persistence for any local WCT population of interest can be estimated as a function of environmental conditions believed to influence the potential for successful invasion by brook trout, abundance of the resulting brook trout population, abundance and resilience of WCT, and the result of ecological interactions between the two species. Because of fundamental limitations in species persistence or viability models (Ralls et al. 2002), we viewed probabilities of persistence as relative measures useful for comparing alternatives within and among streams. For example, the probabilities could be used to evaluate the effect of a migration barrier on a WCT population and then compare conservation opportunities among a group of populations. The model represents a belief system founded on our collective understanding of WCT and brook trout biology and habitat requirements, but we are also attempting to validate this model with field data in a separate effort.

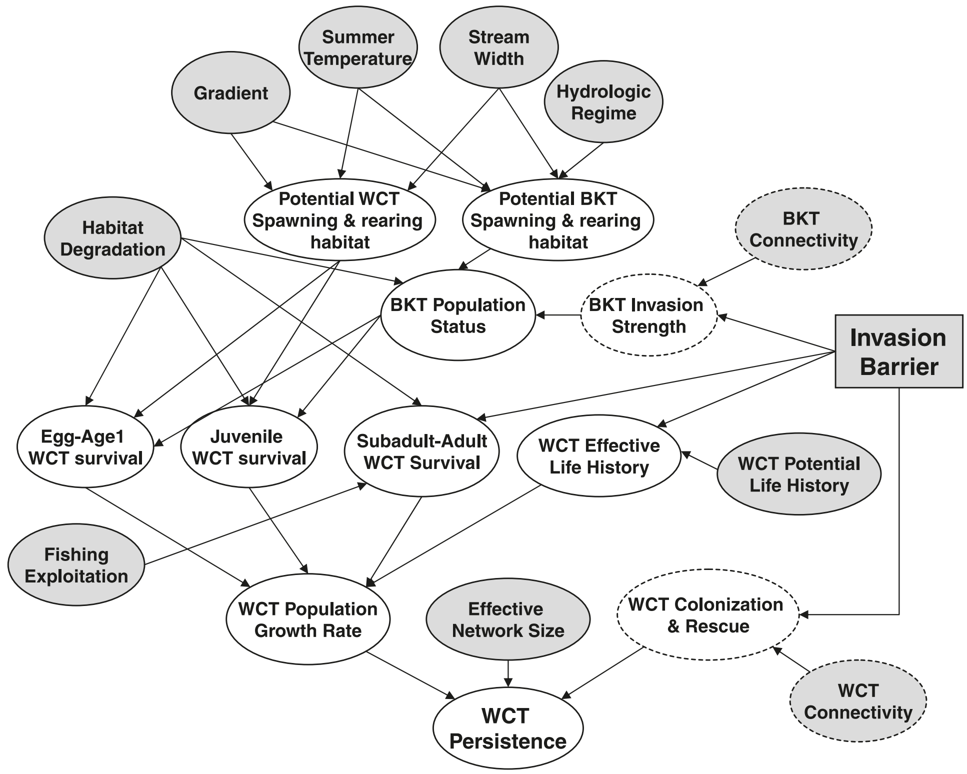
The model

We developed our BBN following general procedures outlined elsewhere (Cain 2001; Marcot et al. 2006; Marcot 2007). Briefly, we began with a series of meetings among the authors and biologists working with WCT throughout its range. We identified the primary environmental conditions associated with WCT, brook trout, and their ecological interactions. Subsequently, we developed conceptual models (box-and-arrow diagrams) that depicted the hypothesized causal relationships and processes important to these species. The conceptual models were refined through iterative discussion to capture only essential (and quantifiable) relationships in their simplest possible forms.

The final conceptual model (Fig. 1) was converted to a BBN by quantifying the conditional relationships among the attributes and processes represented by the diagram. Each network variable or “node” was described as a set of discrete states that represented possible conditions or values given the node’s definition (Table 1). Arrows represent dependence or a cause-and-effect relationship between corresponding nodes. Conditional dependencies among nodes were represented by conditional probability tables (CPTs) that quantify the combined response of each node to its contributing nodes, along with the uncertainty in that response (Supplemental Appendix S1[4]). Input nodes ideally represent proximate attributes of causal influence in the network, such as stream temperature or existence of a barrier, and do not have contributing nodes. The BBN was implemented in the modeling shell Netica (Norsys Software Corp., Vancouver, Brit-

[4] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3722. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 1. Conceptual model depicting environmental conditions and processes influencing persistence of westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) and the trade-offs between intentional isolation and invasion by brook trout (BKT, *Salvelinus fontinalis*). Shaded ovals indicate input variables or nodes (prior conditions) believed to affect WCT and BKT populations; dashed ovals indicate influences that originate outside the local stream network; the rectangle (invasion barrier) indicates the primary management decision; and arrows indicate conditional relationships among variables (nodes). See Table 1 for node definitions and range of values or categories (states) assigned to each node.



ish Columbia), which uses advanced algorithms to update the probability distributions of all variables in the network given evidence, findings, or presumed initial conditions entered at a variable or subset of variables.

General form of the model

Our final conceptual model (Fig. 1) and BBN included 22 nodes (Table 1; see Supplemental Appendix S1[4] for detailed node definitions and CPTs). The foundation of our approach was in two models of population persistence and demography. First, following Dennis et al. (1991) and application of these methods to threatened salmonid populations (Sabo et al. 2004), we considered the probability of persistence to be a function of population growth rate and population size, which was constrained by the effective network size defining a local population. Persistence also can be influenced by immigration represented through colonization and rescue from nearby populations. In essence, small populations confined to limited areas with highly variable or negative growth rates and little chance for support from surrounding populations will be less likely to persist than those that have stable or positive growth rates, large or complex areas of available habitat, and the potential for frequent demographic support from surrounding populations. Second, the population growth rate for WCT was estimated as a function of stage-specific survival rates (subadult–adult; juvenile; egg–age 1) and the expression of a migratory or resident life history, which defined the expected fecundity of spawning females. This demographic representation of stage-specific survival and reproductive output in the BBN is analagous to a stage-based matrix model commonly used to evaluate population response to changes in vital rates (Kareiva et al. 2000; Caswell 2001). We assumed no density dependence in estimates of population growth rate, primarily because there is little data to model that process for this species. Also, our objective was a model that focused on trade-offs and priorities among small populations that likely exist at densities below carrying capacity because of other constraints, such as habitat alteration. Although the lack of density dependence may bias our absolute estimates of persistence, others working with similar salmonid populations found this simplifying assumption does not substantially constrain utility of extinction probabilities used to consider relative vulnerabilities (Botsford and Brittnacher 1998; Sabo et al. 2004).

Our primary interest was to model the influence of brook trout invasion and the intentional use of barriers on cutthroat trout persistence. In our model, presence of an invasion barrier could influence persistence of WCT by eliminating migratory life histories and potential for colonization and rescue from surrounding tributaries and by stopping invasion by brook trout. We also assumed that a barrier could reduce survival of older (subadult–adult) WCT that are large enough for extensive movement (e.g., Bjornn and Mallett

Table 1. Node definitions and states for the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

Node name[a]	Definition	State
Temperature (I)	Mean summer water temperature over the stream network from 15 July to 15 September	Very low: <7 ºC Low: 7–10 ºC Optimum: 10–15 ºC High: 15–18 ºC Very high: >18 ºC
Gradient (I)	Mean percent gradient over the stream network	Low: <2% Moderate: 2%–8% High: >8%
Stream width (I)	Mean wetted width over the stream network during base flow	Small: <3 m Medium: 3–10 m Large: >10 m
Hydrologic regime (I)	Seasonal patterns of runoff and flooding that might influence bed scour and subsequent incubation or emergence success of fall spawning salmonids like BKT	Snowmelt Mixed rain-on-snow and snowmelt
Potential spawning and rearing habitat	The potential for successful reproduction and early rearing by WCT based on the physical template for natal habitat as influenced by stream gradient, summer water temperature, and stream size (width)	Low Moderate High
Potential BKT spawning and rearing habitat	The potential for successful reproduction and early rearing by BKT based on the physical template for natal habitat as influenced by stream gradient, summer water temperature, stream size (width), and the dominant hydrologic regime	Low Moderate High
Invasion barrier (I)	A natural or human-constructed barrier that precludes upstream movement by stream fishes	Yes No
BKT connectivity (I)	The potential for invasion by BKT into the local stream network based on the magnitude and frequency of BKT immigration as influenced by the number, distribution, and attributes of potential source BKT populations outside the local stream network and the characteristics of the movement corridor	Strong Moderate None
BKT invasion strength	Realized or effective "BKT connectivity" as influenced by whether or not an invasion barrier is present or will be installed	Strong Moderate None
Habitat degradation (I)	Whether salmonid habitat and the processes that create and maintain it have been altered by human activity	Altered and degraded Minimally altered or pristine
BKT population status	The potential strength of a BKT population in a stream segment as influenced by the realized condition of natal habitat and the likelihood of BKT immigration	Strong Weak Absent
Fishing exploitation (I)	Fishing exploitation rate of subadult and adult (aged 2 and older) WCT in a stream network	Low: <10% annual exploitation High: >10% annual exploitation
Egg to age-1 survival	WCT survival from egg to age 1 as influenced by realized habitat conditions and interactions with nonnative BKT	Low: <2.5% Moderate: 2.5%–5% High: > 5%
Juvenile survival	WCT survival from age 1 to age 2 as influenced by realized habitat conditions and interactions with nonnative BKT	Low: < 25% Moderate: 25%–35% High: >35%
Subadult–adult survival	Annual survival of subadult and adult WCT (ages 2 and older) as influenced by realized habitat conditions, fishing, and presence of an invasion barrier	Low: <35% Moderate: 35%–45% High: >45%

Table 1 (*concluded*).

Node name[a]	Definition	State
Potential life history (I)	The potential expression of migratory and resident life histories for WCT in a stream network; the potential influence of life history expression on the resilience of WCT is assumed to be primarily through the differential reproductive contribution of distinct migratory forms	Resident (low fecundity) Migratory (high fecundity)
Effective life history	Actual life history expression based on a "potential life history" and whether or not an invasion barrier is planned or installed (i.e., migratory life history is lost with installation of barrier)	Resident (low fecundity) Migratory (high fecundity)
Population growth rate	The potential finite rate of population increase (lambda or λ) for the local population of WCT as influenced by reproductive success and recruitment, stage-specific survival rates, and fecundity based on the predominant life history; the node defines population growth potential in the absence of density dependence and environmental variation	Very low: $\lambda < 0.85$ Low: $\lambda = 0.85–0.95$ Moderate: $\lambda = 0.95–1.05$ High: $\lambda = 1.05–1.15$ Very high: $\lambda > 1.15$
Connectivity (I)	The potential for immigration and demographic support for a local population of WCT based on the distribution, interconnection with, and independence of surrounding populations present in other stream networks; it is influenced by the expression of migratory life histories, barriers to movement, and the distribution and characteristics of neighboring populations	None Moderate Strong
Colonization and rescue	Realized or effective connectivity of WCT as influenced by "connectivity" and whether or not an invasion barrier is planned or installed	None Moderate Strong
Effective network size (I)[b]	Size or spatial extent of the local population and its vulnerability to environmental variation and catastrophic events; we use population size (age 1 and older) as our primary metric for the analysis, but assume that population size and network size (km) are directly related	Very small: <3 km or <500 WCT Small: 3–5 km or 500–1000 WCT Moderate: 5–7 km or 1000–2500 WCT Large: 7–10 km or 2500–5000 WCT Very large: >10 km or >5000 WCT
Persistence	The presence of a functionally viable local WCT population for at least 20 years	Absent Present

Note: Nodes that refer specifically to brook trout (BKT, *Salvelinus fontinalis*) population ecology are so noted (e.g., potential BKT spawning and rearing habitat, BKT invasion strength). Nodes without a species designation refer either specifically to westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) population ecology (e.g., fishing exploitation, potential spawning and rearing habitat, juvenile survival, persistence) or variables with a common influence on both species (e.g., temperature, habitat degradation, etc.). Details regarding definition of the nodes and information used to develop the associated conditional probability tables are in Supplemental Appendix S1[4].

[a]Input nodes (I) are those where the BBN user designates the prior probability of being in a particular state.

[b]"Effective network size" can be expressed as either length (km) of connected spawning and rearing habitat in a local stream network or the population size of individuals age 1 and older (age 1+) within the stream network.

1964; Zurstadt and Stephan 2004), because any fish moving downstream over a barrier will be lost from an isolated population. We assumed brook trout could influence juvenile survival and egg to age-1 survival of WCT directly by competition and (or) predation, but would not influence subadult–adult survival (Peterson et al. 2004).

A suite of other nodes was used to represent the influence of habitat and environmental conditions on these biological processes. Stream channel characteristics (gradient, temperature, and width) are commonly associated with the distribution and abundance of brook trout and WCT and were used here to delimit potential spawning and rearing habitat for both species (Supplemental Appendix S1[4]). Habitat degradation represented departure of habitat quality caused by land management, such as road building, grazing, mining, and timber harvest. Habitat degradation is believed to decrease survival of cutthroat trout and abundance of brook trout and to affect the outcome of ecological interactions between them (e.g., Shepard 2004). Hydrologic regime (timing and magnitude of flow) is hypothesized to have an important influence on population ecology of nonnative salmonids if high flows that scour streambeds coincide with egg incubation and alevin development (e.g., Strange et al. 1992; Fausch et al. 2001). We speculate that the effect of regional hydrologic patterns on reproduction may, in part, explain the variable success of brook trout invasion in some areas

(Fausch et al. 2006). Hydrologic regime was not considered important for WCT because the species presumably has adapted to flow patterns that exist within its native range. Fishing exploitation can reduce survival of WCT (McIntyre and Rieman 1995) and was included as an influence on subadult–adult survival. We did not consider fishing important for brook trout because they are believed to be less vulnerable than cutthroat trout (MacPhee 1966; Paul et al. 2003), and they are rarely targeted in major sport fisheries of this region. Connectivity for brook trout and for WCT represented size and proximity of surrounding tributary populations that could act as sources of invasion (brook trout) and immigration (cutthroat trout, via colonization and rescue). Potential life history represented the dominant life history (migratory or resident) expected in the WCT population, whereas effective life history indicated how life history expression could be constrained by an intentional migration barrier. Migratory life histories in salmonid populations may contribute to resilience and persistence of populations through enhanced growth and fecundity and through facilitation of gene flow and demographic support among tributaries (Rieman and Dunham 2000; Dunham et al. 2003; Neville et al. 2006). Generally, we anticipate tributary populations in large, relatively intact river basins will have an important if not dominant component of migratory individuals (McIntyre and Rieman 1995), but acknowledge that migratory forms may be lost, even when barriers don't exist, because of main-stem habitat degradation or other factors limiting suitability of downstream rearing or migratory habitat.

We did not explicitly represent survival and population growth rates for brook trout as we did for WCT, but rather used brook trout population status as an index of population size. In essence, we tried to predict whether brook trout would be established, and if they were, we assumed that competitive or predatory effects of brook trout would be directly related to the density of the resulting population (i.e., strong populations had a greater effect than weak ones).

Issues of scale

The BBN represented factors influencing a WCT population at several spatial scales. Persistence was considered at the scale of a local population defined by its associated spawning and rearing habitats. This is consistent with the patch concept of Dunham et al. (2002*b*). The spatial extent of the local stream network (effective network size) is ultimately defined by the presence of a barrier or a demographically important discontinuity in habitat, such as a dramatic change in stream size at a tributary junction (e.g., Dunham et al. 2002*b*). The stream channel characteristics (gradient, temperature, and stream width) that define potential spawning and rearing habitat are commonly measured at the scale of individual habitat units and averaged over longer segments of streams. Because a local stream network that defines a population would generally consist of multiple stream segments, there is a potential mismatch in scale between these habitat characteristics and the resulting estimates of WCT persistence. In application of the BBN, we considered a range of values associated with stream channel characteristics representative of the larger stream network. We broadly categorized channel characteristics (see Table 1; Supplemental Appendix S1[4]) to encompass variation among stream segments within many habitat networks. In the case of unusually large stream networks with substantial variation in conditions, the range of variation must be represented in the BBN by the distribution of probabilities reflecting average conditions in that system.

We defined the temporal scale for our BBN as 20 years. We chose this interval because it is difficult to anticipate population trends over much longer periods (Beissinger and Westphal 1998; Ralls et al. 2002). This also is roughly the time scale associated with federal land management planning and with substantial changes in habitat associated with both restoration and degradation. The BBN was not dynamic in the sense that cyclic biological processes are expressed through time steps, as often used in population simulation (Marcot et al. 2001). Rather, time dependence was explicitly considered in the population growth model used to parameterize the BBN (e.g., Lee and Rieman 1997; Shepard et al. 1997). Conditional probabilities in each node reflected our belief about future states once physical and biological processes have played out. In developing the CPTs, we assumed that initial conditions established in the input nodes represented the present, and these factors influenced the outcome (i.e., WCT persistence) expected after 20 years (Supplemental Appendix S1[4]). For example, any population with a negative population growth rate is deterministically fated to extinction if conditions influencing the growth rate do not change and the evaluation is not bounded in time. However, if growth rate is not strongly negative or if the population is initially large, it may well persist for 20 years.

Conditional relationships

The CPTs represent our belief about the probability of a node being in a state given information in the contributing nodes. By default, we used uniform prior probabilities for input nodes during model development and entered specific values during analyses to represent conditions in a watershed or stream network of interest. We crafted CPTs based on published and unpublished data, output from analytical models, expert opinion, and personal experience (Table 1; Supplemental Appendix S1[4]). The relationships between potential natal habitat for both species and channel characteristics (i.e., gradient, temperature, and stream width) were based on field observations and laboratory experiments summarized from the literature and our own work (Supplemental Appendix S1[4]). The CPTs for most other input nodes relied largely on a synthesis of existing theory and empirical observation (see Fausch et al. 2006 for an overview). For example, the CPT that represents how potential spawning and rearing habitat, habitat degradation, and brook trout population strength affect egg to age-1 survival of WCT was derived from our observations and discussion in the context of available work on these and similar species (Table 2; Supplemental Appendix S1[4]). Lack of detailed information on key processes that influence invasion dynamics and species interactions led us to draw on a variety of information types (e.g., data, opinion, experience) to specify conditional relationships. The CPTs for most nodes where opinion was required were developed by two or more authors independently, but after full discussion and review of available infor-

Table 2. Conditional probability table (CPT) for egg to age-1 survival of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) as an example of the conditional relationships underlying connected nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

Contributing (parent) nodes			Probability of a given state for survival		
Brook trout population status	Potential spawning and rearing habitat	Habitat degradation	Low	Moderate	High
Strong	Low	Degraded	1.00	0	0
		Minimally altered	1.00	0	0
	Moderate	Degraded	1.00	0	0
		Minimally altered	0.90	0.10	0
	High	Degraded	0.95	0.05	0
		Minimally altered	0.75	0.25	0
Weak	Low	Degraded	0.85	0.15	0
		Minimally altered	0.75	0.25	0
	Moderate	Degraded	0.65	0.35	0
		Minimally altered	0.50	0.50	0
	High	Degraded	0.45	0.45	0.10
		Minimally altered	0.20	0.55	0.25
Absent	Low	Degraded	0.75	0.25	0
		Minimally altered	0.45	0.50	0.05
	Moderate	Degraded	0.15	0.60	0.25
		Minimally altered	0	0.50	0.50
	High	Degraded	0.05	0.40	0.55
		Minimally altered	0	0	1.00

Note: This CPT was populated by expert opinion based on the probabilities averaged across the five co-authors.

mation. Where consensus for a CPT was not achieved, we accounted for uncertainty arising from differences of opinion among us by averaging the conditional probabilities among possible outcomes to arrive at a final CPT. More generally, the distribution of probabilities for any CPT represented uncertainty about the ecological processes depicted in the BBN as well as the expected variability in the response or outcome (e.g., Table 2).

The CPTs for population growth rate and persistence were developed using output from the two population models described earlier. We estimated conditional probabilities associated with potential population growth rate based on 1000 replicate simulations of a stage-based matrix model using vital rates drawn randomly from distributions representing the range of conditions possible in the parent nodes (e.g., stage-specific survival and fecundity associated with effective life history; Supplemental Appendix S1[4]). Simulations were implemented by spreadsheet using a Monte Carlo procedure and population analysis module developed for Excel (Hood 2004). Variation in output among replicates for a set of initial conditions represented uncertainty in vital rate estimates rather than environmental or demographic stochasticity (Supplemental Appendix S1[4]). We estimated the probability of persistence using the method of Dennis et al. (1991) based on our estimates of population growth rate, variance in that growth rate, initial population size, and the 20-year time horizon. Growth rate and initial population size could be inferred directly from the contributing (parent) nodes (Fig. 1). We used the analytical method to estimate persistence rather than a stochastic simulation with the matrix model because we have no information to guide estimates of the environmentally forced variances associated with each vital rate. We do, however, have estimates of the range in variances associated with population growth rates for WCT (e.g., McIntyre and Rieman 1995) and assumed that this variance was inversely related to population size (e.g., Rieman and McIntyre 1993). We refer to the completed BBN as InvAD (isolation and invasion analysis and decision) or the InvAD BBN.

To consider the importance of uncertainty in our assumptions about the conditional relationships for population growth rate and persistence, we developed three alternative BBNs that were identical conceptually to the InvAD BBN (i.e., having the same box-and-arrow diagrams as Fig. 1) but with different CPTs (Supplemental Appendix S1[4]). The first two alternates had CPTs for persistence where the variance in population growth rate was either assumed to be independent of population size with a constant value of 0.2 (low constant variance) or to be independent of population size with a value of 0.8 (high constant variance). To determine if expert judgment strongly deviated from the output of the two demographic models, we developed a third alternative where the CPTs for population growth rate and persistence were both based on opinion as informed by empirical data and professional experience (opinion only). We subsequently compared the performance of these alternative models with the InvAD BBN. We concluded that predictions were generally consistent (Supplemental Appendix S2[4]), so we only present analyses and results from the original model.

Analyses

To characterize the behavior of the InvAD BBN, we conducted two analyses under a standard set of conditions. First, to understand how predictions were influenced by a particular environmental or biological condition, we conducted general sensitivity analyses assuming no prior knowledge about

Table 3. Variables representing standard environmental conditions and inputs manipulated under the hypothetical example to explore trade-offs between invasion and isolation of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) threatened by brook trout (*Salvelinus fontinalis*).

Node	State
Standard variables	
Gradient	<2%
Stream width	<3 m
Temperature	10–15 °C
Hydrologic regime	Snowmelt
Brook trout connectivity	Strong
Manipulated variables	
Invasion barrier	Yes, no
Potential life history	Migratory, resident
Connectivity	High, none
Habitat degradation	Yes, no
Fishing exploitation	High, low
Effective network size	Very small, medium, very large

Note: The isolation and invasion analysis and decision Bayesian belief network (InvAD BBN) was used to generate estimates for westslope cutthroat trout persistence for 48 different scenarios based on the state combinations of the manipulated variables. The standard conditions were selected so that habitat was equally suitable for both species.

states of input nodes (i.e., uniform prior probabilities or complete uncertainty) by estimating entropy reduction values (i.e., based on mutual information formulae in Pearl (1991) and implemented in Netica) for all nodes and by changing the initial conditions of input nodes and plotting the range of predicted responses. Second, to assess the relative changes in persistence from barriers and other management options, we generated a series of predictions for 48 scenarios using a standard set of initial conditions typical of WCT streams in the northern Rocky Mountains while manipulating a subset of input conditions that might vary in response to management history or population characteristics (Table 3).

To explore application of the model in real-world management, we used the InvAD BBN to predict WCT persistence in three streams in the northern Rocky Mountains within the Lolo National Forest in western Montana, where conservation efforts focus on WCT and where brook trout were a known threat. These examples focused on changes in persistence (from current conditions) relative to barrier construction or removal and other management options. The Lolo National Forest is roughly situated at the geographic center of WCT's historical range in the United States (Shepard et al. 2005). WCT populations in the region occupy both isolated tributary streams and larger interconnected stream systems (Shepard et al. 2005). For each scenario we analyzed, fishery biologists from Lolo National Forest were asked to describe the invasion threat from brook trout and existing or proposed migration barriers, define environmental and physical conditions required as BBN inputs, and provide any additional contextual information relevant to the biology of WCT (e.g., presence of other nonnative fish species). The model was used to generate predictions and explore alternative management actions based on the site-specific information.

Results

Sensitivity analyses and model behavior

Sensitivity analyses indicated that the BBN generally behaved as we intended based on its structure and the relative influences of the variables we believed were important. Population size (or extent of habitat) and demographic characteristics strongly affect predicted probability of persistence. Entropy reduction estimates considering all 21 variables indicated that predictions of persistence were two–three times more sensitive to information about population growth rate (0.188) than the next most influential variables: effective network size (0.092) and subadult–adult survival (0.054) (Table 4). Results generally reflected a proximity effect, where the influence of a particular node is inversely related to the number of intervening links (Fig. 1, Table 4). In one exception, persistence was more sensitive to one of its grandparents (subadult–adult survival) than to one of its parents (colonization and rescue).

Among input variables only, both analytical (Table 4) and graphical representations (Fig. 2) demonstrated that effective network size was most influential. Four of the seven most important nodes either represent or directly influence habitat connectivity, migration, and dispersal (e.g., potential life history, invasion barrier, connectivity, BKT connectivity; Fig. 2). However, their relative effect was, on average, about one-third that of effective network size (e.g., compare width of bars in Fig. 2).

Relative effect of isolation management on persistence

In the generalized examples that explored isolation management in response to brook trout invasion threats across a range of initial conditions (Table 3), the relative influence of invasion barriers depended strongly on effective network size, habitat conditions in the network, and potential expression of migratory life histories (Fig. 3). The probability of persistence of a local WCT population increased as the effective network size increased (Fig. 3). This pattern was consistent across all combinations of variables in the examples, including installation of a migration barrier. A barrier always increased the probability of persistence for a population with no migratory component or no potential for immigrants from other WCT populations. In contrast, a barrier almost always reduced the probability of persistence when the existing population expressed a migratory life history and was strongly connected to other populations.

Although direction of change in persistence with a barrier depended consistently on life history and connectivity, the magnitude of change depended on other conditions as well. Habitat degradation and fishing, for example, tended to increase risk for migratory, connected populations beyond that resulting from barrier installation and to reduce the relative benefits of intentional isolation for a resident, nonmigratory population threatened by invasion. Habitat degradation had a similar influence and was more important than fishing averaged across other factors (Fig. 3).

Case studies: intentional isolation and other management options in three streams

The range of conditions in the three streams from Lolo National Forest allowed us to explore the nature of trade-offs

Table 4. Sensitivity of predicted persistence for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) to all contributing nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN) relative to the number of intervening links.

Node	No. of links to persistence[a]	Sensitivity[b]
Population growth rate	1	0.188
Effective network size	1	0.092
Subadult–adult survival	2	0.054
Effective life history	2	0.043
Egg to age-1 survival	2	0.031
Invasion barrier	2–5	0.025
Colonization and rescue	1	0.023
Juvenile survival	2	0.020
Habitat degradation	3–4	0.016
Fishing exploitation	3	0.014
Potential spawning and rearing habitat	3	0.012
Potential life history	3	0.011
Brook trout invasion strength	4	0.007
Temperature	4–5	0.003
Connectivity	2	0.002
Brook trout population status	3	0.002
Stream width	4–5	0.002
Brook trout connectivity	5	0.001
Potential brook trout spawning and rearing habitat	4	<0.001
Gradient	4–5	<0.001
Hydrologic regime	5	<0.001

Note: Survival and population growth rate nodes refer to westslope cutthroat trout.

[a]A value of 1 indicates a direct connection between nodes. Some nodes have a range of links because they affect more than one variable in the Bayesian belief network (BBN); thus their effect can cascade through the network by different paths.

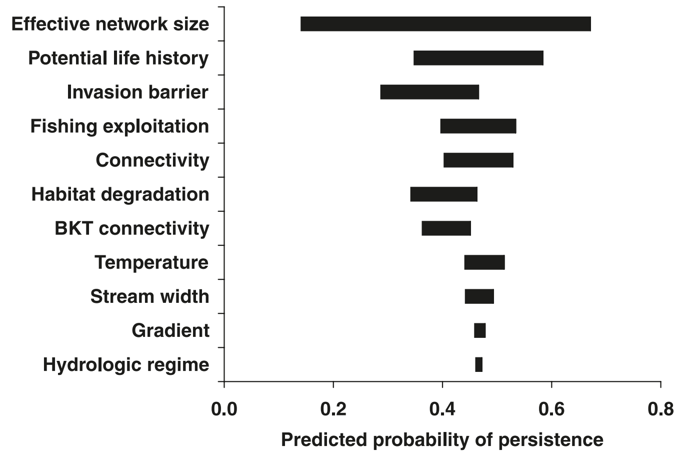
[b]Sensitivity values (entropy reduction) assumed a uniform prior probability distribution for each of the 11 input nodes and were calculated in Netica using the mutual information formula that appears in Pearl (1991, p. 321) that is implemented in Netica (B. Boerlange, Norsys Software Corporation, 3512 West 23rd Avenue, Vancouver, BC V6S 1K5, personal communication). Marcot et al. (2006) present the same formula. Values integrate the influence of nodes having a range of links.

biologists and managers might encounter when trying to assess what could be achieved through installation or removal of barriers relative to other management actions (Fig. 4, Tables 5 and 6).

Silver Creek

Silver Creek contains a genetically pure WCT population isolated above a culvert in a large stream network (>10 km) (Fig. 4). Invasion by brook trout that occur immediately downstream was considered imminent without a barrier. Potential management actions were to remove the existing culvert barrier (and replace with a bridge or passable culvert), thereby reconnecting the isolated population to populations in adjacent stream networks and downstream habitats, or to modify or replace the barrier with a structure that can withstand extreme environmental conditions (e.g., floods) and ensure continued isolation. The probability of persistence was predicted to increase from 0.81 to 0.97 if the existing barrier was removed. The apparent benefit resulted from the expectation that the existing population would re-express a migratory life history and connection with other populations in the Saint Regis River system. The relative increase was modest because the existing isolated network was already relatively large and habitat was good. The analysis suggested that the local population was likely to persist with or without a barrier. If maintenance of genetic purity were a priority, then intentional isolation would also preclude invasion by rainbow trout and WCT × rainbow trout hybrids.

Fig. 2. Sensitivity of persistence to input nodes in the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN). Values were generated by sequentially manipulating the state probabilities of each input node to produce the lowest and highest predicted values for persistence while maintaining uniform prior probabilities for all the other input nodes (except invasion barrier). Invasion barrier was set to "no" for all input variables to represent a default condition. The value for invasion barrier represents sensitivity to the management decision under complete uncertainty about the most likely state of other inputs. Unless otherwise noted, nodes refer to westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) or environmental conditions common to both species. BKT, brook trout (*Salvelinus fontinalis*).

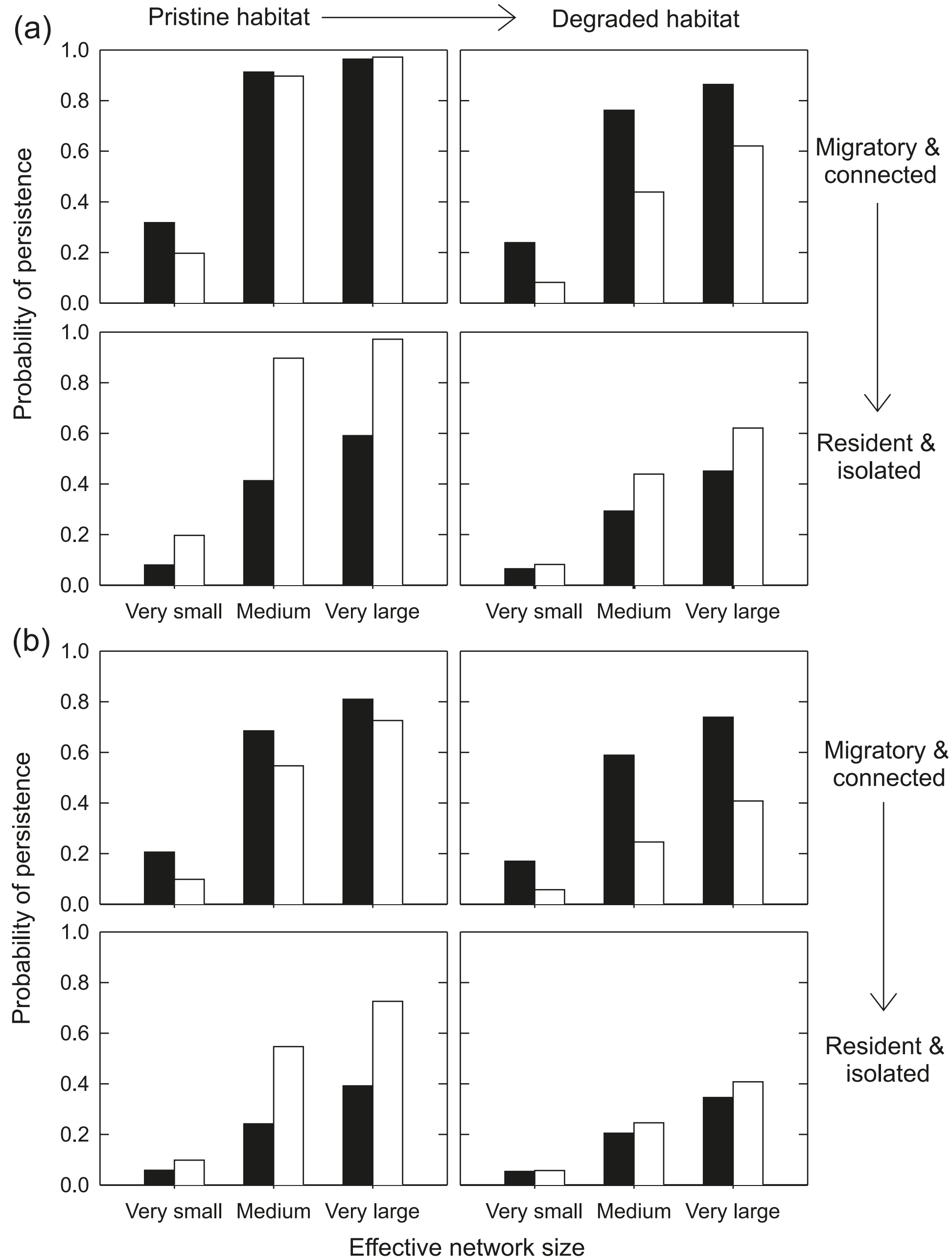


Dominion Creek

Dominion Creek contains a WCT population believed to be genetically pure and fragmented by two culvert barriers (Fig. 4). There was a total of approximately 4.25 km of suitable habitat between the lower (near the stream's mouth) and upper barrier (1.5 km) and above the upper barrier (2.75 km). Brook trout are already established between the lower and upper barriers. Potential management actions were to (1) remove the upper barrier to increase the effective network size for the WCT population above the lower barrier, (2) remove the lower barrier to connect the lower population fragment to other stream networks, (3) remove both barriers, (4) eradicate brook trout between the two barriers, and (5) eradicate brook trout and remove the upper barrier (i.e., actions 1 and 4).

Under existing conditions in Dominion Creek, the estimated persistence in the lower (brook trout established) and upper (brook trout absent) stream segments was 0.11 and 0.22, respectively. Removing the upper barrier increased the

Fig. 3. Predicted response of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) to installation of an invasion barrier based on the management scenarios described in Table 3 and using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN). Bars denote the predicted probability of persistence with (open bars) or without (solid bars) a barrier relative to habitat size and quality, life history expression, connection to other populations, and low (*a*) or high (*b*) fishing exploitation.



estimate for the combined segment to 0.38, but brook trout are then expected to become established throughout the stream. Removing the lower barrier increased the estimate for the lower segment to 0.37, but the largest relative benefit was expected through removing both barriers (estimated persistence = 0.86). The eradication of brook trout in the lower segment increased estimated WCT persistence from 0.11 to 0.22, whereas eradication plus removal of the upper barrier substantially decreased risk (i.e., estimated persistence = 0.75).

Intentional isolation with two barriers did not appear to be a highly effective alternative in Dominion Creek. The single-barrier option offered substantial benefit only if implemented in conjunction with brook trout eradication. The cost and effort required to attempt eradication can be substantial (Shepard et al. 2002) and the ultimate success uncertain (Meyer et al. 2006), but the combination of brook trout removal and isolation (which would also preempt introgression with rainbow trout) might be considered if the WCT population was considered an unusually important contribution to total genetic diversity for the species (Fausch et al. 2006). If the Dominion Creek population does not represent an important element of genetic diversity and (or) brook trout eradication is not feasible, then conservation ef-

Fig. 4. General location and orientation of three streams (*a–c*) in Lolo National Forest (shaded area in inset) used for the case study analysis. Streams contain populations of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) threatened with invasion by brook trout (*Salvelinus fontinalis*). Circles indicate locations of existing fish migration barriers; darker lines denote the main stem, and arrows show the direction of stream flow.

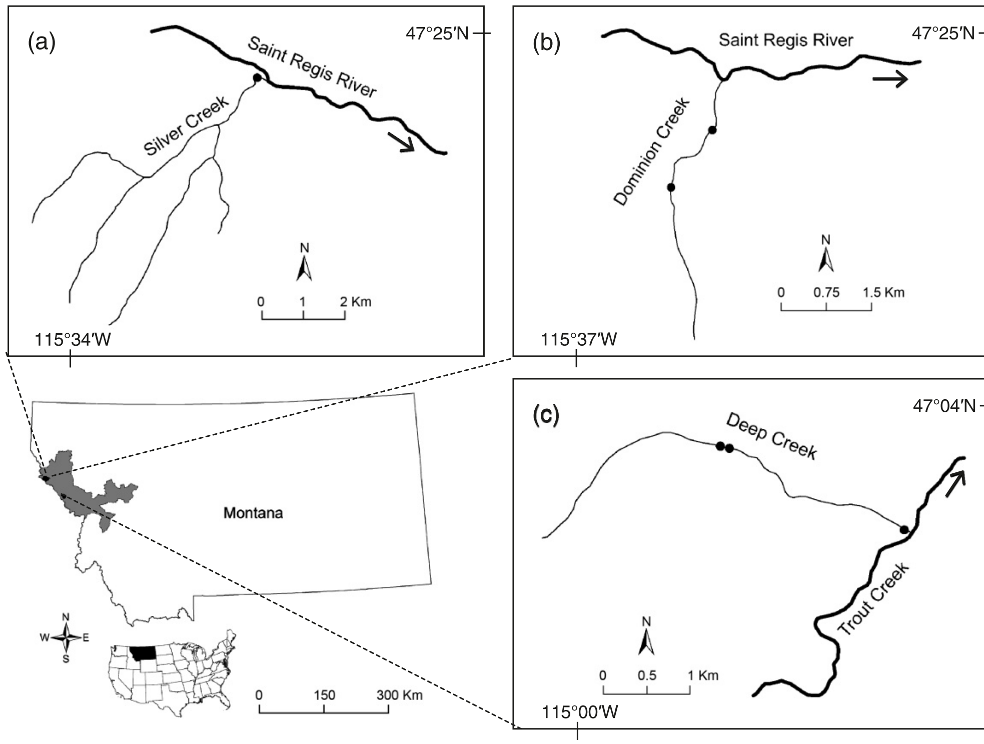


Table 5. Existing conditions for three westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) streams in Lolo National Forest that are threatened by invasion from nonnative brook trout (*Salvelinus fontinalis*) and possible management actions involving barrier maintenance or removal and habitat restoration that were analyzed using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

	State of node or existing condition[a]		
Node or factor affecting WCT persistence	Silver Creek	Dominion Creek	Deep Creek
Gradient	2%–8%	2%–8%	2%–8%
Temperature	7–10 °C, 10–15 °C	10–15 °C	10–15 °C
Stream width	3–10 m	<3 m	<3 m
Hydrologic regime	Mixed	Snowmelt	Snowmelt
Habitat degradation	Pristine	Pristine	Degraded
Potential life history	Migratory	Migratory	Migratory
(Potential) connectivity	Strong	Strong	Strong
Effective network size	>10 km	<3 km	<3 km
Brook trout connectivity	Moderate	Strong	Strong
Additional nonnative trout threats	RBT, WCT × RBT hybrids	WCT × RBT hybrids	—
No. of existing barriers	1	2	3

Note: Information on streams elicited from B. Riggers and S. Hendrickson, Lolo National Forest, Fort Missoula Building 24, Missoula, MT 59804, USA (August 2006, personal communication).

[a]The probabilities were 1.0 for referenced state in each input node with the exception of temperature in Silver Creek, which was split (0.5, 0.5) between two states. Rainbow trout (RBT, *Oncorhynchus mykiss*) and (or) WCT × RBT hybrids are present below, or in the larger stream below, the downstream barrier in both Silver and Dominion creeks.

forts might be better served by focusing efforts in other larger tributary systems (e.g., Silver Creek).

Deep Creek

Deep Creek contains a WCT population fragmented by a series of three culverts (Fig. 4). Approximately 4.1 km of suitable WCT habitat was collectively distributed between lower (near the stream's mouth) and middle barriers (2.4 km), between the middle and upper barrier (0.1 km), and above the upper barrier (1.6 km). The habitat has been affected by land use and was classified as degraded. Cutthroat trout were not present above the upper barrier. Brook trout were a known invasion threat. Potential management actions were to (1) remove the lower barrier to connect the lower habitat fragment to other stream networks; (2) remove the middle and upper barriers to increase the effective network size isolated by the lower barrier; (3) remove all three barriers to both reconnect the fragmented populations and increase the effective network size; and (4) implement general habitat restoration efforts either in conjunction with barrier removals (1–3 above) or instead of barrier removals.

In Deep Creek, management actions involving both barriers and habitat restoration could be important. Any combination of barrier removal was estimated to increase the probability of persistence for the existing population (Table 6), though there are important differences among them. Removal of all three barriers was estimated to increase the probability of persistence from 0.09 to 0.72 by the combined effect of increasing the network size (from <3 to 3–5 km) and reestablishing the migratory pathway to the larger system (Table 6). The benefits of reconnection appeared to be substantial, whereas removal of the middle and upper barriers provided some benefit, but the risks appeared to remain high (i.e., probability of persistence = 0.30). Removal of the two upper barriers in conjunction with habitat restoration over 4 km of stream could approach the benefit expected with removal of all three barriers (Table 6).

It appears that considerable expense of either removing all barriers or coupling the removal of two barriers with habitat restoration will be required to substantially reduce the risks in Deep Creek. Alternatively, managers could forgo work in this stream and allocate resources to another system where greater benefits might be realized at lower cost.

Table 6. Estimated probability of persistence for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in Deep Creek, Lolo National Forest, under four alternative management actions analyzed using the isolation and invasion analysis and decision Bayesian belief network (InvAD BBN).

Barrier removals	Nonnative trout invasion possible	Estimated probability of persistence — Habitat improvement: No	Yes
None	No	0.09	0.22
Lower	Yes	0.30	0.38
Middle and upper	No	0.30	0.73
All three	Yes	0.72	0.86

Note: Predictions considered removal of existing barriers, alone and in combination, with and without habitat improvement.

Discussion

Conservation strategies for inland cutthroat trout including WCT often advocate a combination of efforts to either isolate or reconnect populations to reduce threats from nonnative trout or isolation, respectively (Lentsch et al. 2000; May et al. 2003; Shepard et al. 2005). An objective analysis of the issues and opportunities for either action, however, can be a challenge. We found that development and application of a BBN could help explore the trade-offs between intentional isolation and invasion for WCT populations threatened by invasion. It also provides a foundation for further work in both management and research.

General guidance and further work

The assumptions inherent in the BBN and subsequent analyses suggest two generalizations for management of barriers and invasions. First, a barrier will be more likely to increase the probability of persistence for a WCT population as the expression of migratory life histories becomes limited, demographic links to other populations are reduced, and invasion by brook trout becomes more likely. The relative benefits associated with any barrier, however, can depend primarily on habitat quality and size of the isolated stream network and secondarily on other environmental effects. These general results follow from our understanding of stream salmonid biology (see review by Fausch et al. 2006 and references therein), and the behavior of the model supports the perspective of many biologists that intentional isolation can be an important tool, but with limitations.

Many WCT populations, especially those east of the Continental Divide in Montana, are functionally and demographically isolated by habitat degradation, dewatering, and loss of downstream rearing habitats (e.g., Shepard et al. 2005) even though a permanent migration barrier may not exist. Other inland cutthroat trout face similar situations (e.g., May et al. 2003; Hirsch et al. 2006; Pritchard and Cowley 2006). Intentional migration barriers could be important tools to reduce any additional threat of invasion in these systems, but priorities might favor isolation of the largest populations and best habitats. For example, continued isolation of Silver Creek could provide an excellent opportunity to conserve a WCT population threatened by brook trout invasion because the existing barrier isolates >10 km of stream habitat, and the processes that create and maintain aquatic habitats in that watershed are intact. In contrast, Deep Creek would require both removal of multiple barriers and habitat restoration (and thus much greater cost) to achieve a comparable result.

Second, maintenance or restoration of fish passage appears to most strongly influence persistence of WCT when the full expression of life histories and strong connection with other populations are anticipated, even if brook trout are expected to invade. In essence, more robust and resilient WCT populations were believed likely to resist displacement by brook trout (i.e., biotic resistance). The relative benefit of maintaining or restoring passage again was dependent principally on the size and quality of the available habitat. Our general results imply that WCT should resist brook trout invasion in the right circumstances.

Results also reflect our assumptions about migratory life histories in WCT and their association with higher individual and population growth rates (Rieman and Apperson 1989), demographic resilience, and connectivity among populations (Rieman and Clayton 1997; Dunham and Rieman 1999; Aylion et al. 2006). These advantages are consistent with faster growth, larger body size, higher female fecundity, and higher propensity for dispersal among populations that presumably will help WCT resist brook trout invasions or increase their resilience to disturbances (Fausch et al. 2006). Our assumptions and results are consistent with current understanding of demographic process. As yet, however, there is limited empirical evidence that connected, migratory WCT populations actually do better resist invasion, so further investigation is needed to reveal any patterns and characterize the proximate mechanisms (Fausch et al. 2006). We also assumed that isolated WCT populations can fully re-express migratory life histories if connection is restored, but we have little empirical evidence to gauge how quickly this might occur (but see Thrower et al. 2004; Olsen et al. 2006). In the interim, managers might exercise caution and view the benefits of reconnection as a topic for exploration through adaptive management. In some cases, for example, managers have multiple opportunities to maintain or remove barriers. When uncertainty is high, experimentation and monitoring (i.e., remove some barriers, retain others, and monitor the response) could be the most efficient way forward (Fausch et al. 2006).

The BBN and analyses also rest heavily on the assumption that habitat area or population size, particularly for very small tributary systems, will have an important influence on persistence of isolated populations. There are many examples of WCT persisting above barriers (Shepard et al. 2005), but virtually no information on those populations that have disappeared, so our assumptions are based largely on the observations and results with similar species (e.g., Morita and Yamamoto 2002; Fausch et al. 2006). An empirical evaluation of the minimum habitat area (patch size) that will sustain isolated WCT populations for a given period of time would help biologists identify populations at high risk of extirpation from so-called isolation effects such as demographic, genetic, and environmental uncertainty (Caughley 1994). Limited data for other salmonids suggest that patch size–persistence relationships could be species-specific (e.g., Rieman and McIntyre 1995; Dunham et al. 2002*b*; Morita and Yamamoto 2002). Many WCT populations are now isolated by artificial (e.g., culvert) or natural barriers with a known time of construction or formation. An inventory of existing isolates could provide a simple test of the effects of isolation and extinction risk analogous to the work of Morita and Yamamoto (2002) with white-spotted char (*Salvelinus leucomaenis*). Such information could directly extend the utility of the models developed here.

Lessons from BBN development and application

The process of building and applying the BBN to the invasion–isolation issue was useful because it forced both the developers and users to think in greater detail about fundamental mechanisms and processes, ecological context, the logic and conservation values involved in the decision process, and other possible management actions that might complement barriers.

First, the model-building exercise forced us to explicitly define the links between habitat conditions and brook trout and how these factors interact with migration barriers to affect WCT demography. For example, the iterative process of describing key variables and their influences (e.g., Jensen 1996; Cain 2001; Marcot et al. 2006) led us to formally define stage-specific mortality for WCT. In doing so, we partitioned the effect of brook trout invasion within the early life stages of WCT. Following that, we realized we also needed to represent the effect of an invasion barrier on mortality of adult WCT through disruption of nonreproductive movements. The general approach led us to consider the complexity of the barrier–invasion interactions that we might not have anticipated otherwise.

Accounting for these effects in model structure also made it easier to see the detail in intermediate responses, which provided insight into how a particular set of conditions affect risk to WCT populations. For example, use of the InvAD BBN helped visualize how installation of a barrier was predicted to affect survival rates of WCT at different life stages and whether these changes would interact with or potentially compensate for the effect of losing a migratory life history in their influence on the population growth rate (intermediate response). In turn, changes in population growth rate interacted with the loss of connection to other WCT populations to determine the probability that WCT will ultimately persist in the local stream network.

Second, use of a model like the InvAD BBN in a decision process forces the user to evaluate their assumptions and to clearly define the conservation priorities motivating a management choice. USDA Forest Service biologists working through the exercise of critiquing and using the model have routinely commented that the model structure helped them think about all the important processes, not just those they may have emphasized in the past. A broader consideration of ecological process in the context of personal experience can promote communication among biologists that work in different systems or have different professional backgrounds and between research and management. The case study from Deep Creek revealed that some biologists were more optimistic about the resilience of isolated, allopatric WCT populations in a degraded watershed than predicted by the model. The discrepancy initiated a discussion about whether the difference resulted from a relatively imprecise definition of degraded habitat or a possible context dependency in the effect of habitat quality on isolation. Further investigation may be needed to address either possibility, but application of the BBN can initiate the discussion.

Perhaps more importantly, the InvAD BBN compels users to define the conservation priorities underlying a particular decision and how those values relate to the overall conservation strategy. An initial step in a manager's decision process may be to describe conservation values for populations of interest in terms of evolutionary, ecological, and socio-economic characteristics (e.g., Fausch et al. 2006). If, for example, a manager is willing to accept an increased risk through intentional isolation, then he or she must explain that the most important conservation value is the maintenance of an evolutionary legacy (e.g., an irreplaceable component of species' genetic diversity). It follows then that ecological function (connectivity and multiple life history expression) and socio-economic concerns (recreational fishing) either are irrelevant because these characteristics do not exist, or they are secondary concerns. A clear statement of management objectives is particularly important where individual WCT populations face multiple nonnative threats and where these threats vary across a group of populations (e.g., Silver and Deep creeks) managed under a common framework. Our model was not designed to quantify the threat of hybridization, but if a manager placed greater emphasis on the genetic integrity of a WCT population and perceived hybridization as a major threat, then he or she could still explore the relative risk of isolation that came from an interest in avoiding introgression.

This exercise naturally leads to a series of questions that should sharpen the decision process: What are you hoping to conserve? Is the proposed action worth it? What is the relative benefit of taking action with this population versus another? Overall, the model induces biologists and managers to clearly describe the assumptions, logic, and values leading to a decision, which fosters communication (e.g., Steventon et al. 2006).

Caveats

The InvAD BBN is a belief system based on current understanding of brook trout invasion processes and effects and the consequences of incidental or intentional isolation for WCT; potential users should be aware of its limitations. Predictions should be interpreted in terms of the relative differences between management options for a set of environmental conditions, not as absolute probabilities (e.g., Ralls et al. 2002). A BBN provides guidance during the decision process, but does not supplant or replace a human decision (Marcot 2006) nor does it substitute for the professional knowledge of an experienced fishery biologist. It does, however, allow biologists and managers to more clearly think about the relative effects of brook trout and isolation on WCT populations and to quickly visualize and evaluate the effects of complex interactions. As a working hypothesis, it can be directly tested, updated, or modified using examples from fishery management or challenged and revised based on new empirical or theoretical results. Though beyond the scope of the current effort, the model could also be extended to explicitly represent the cost and benefit of particular decisions by adding utility nodes that, for example, depict the financial cost of barrier management or the value derived from increasing the representation of a desired WCT population characteristic such as genetic purity, life history variation, or large body size.

BBNs are relatively straightforward to understand and use, but developing one may be a lengthy, iterative process. We found that a lack of empirical information about certain ecological processes led to extensive debate about which variables to include in the model. Moreover, justifying these variables and their conditional relationships became a major endeavor.

The InvAD BBN was developed to characterize threats to WCT from brook trout and the risk of losing a local population of WCT, but analogous models could be developed to address similar threats to other native species like threatened bull trout (*Salvelinus confluentus*) and to consider effects of multiple invaders or other threats. For example, introgression with rainbow trout (or rainbow trout × cutthroat trout hybrids) is a recognized threat to WCT (e.g., Allendorf et al. 2001, 2004; Shepard et al. 2005) and was a contextual consideration in two of our case study examples. The considerable variation in patterns of introgressive hybridization observed for WCT in some cases (Weigel et al. 2003; Ostberg and Rodriguez 2006) may belie a conservative, simplifying assumption that hybridization will ultimately occur wherever rainbow trout invasion is possible (e.g., Hitt et al. 2003). We caution that although InvAD BBN can quantify the relative risk of isolation that follows from an interest in preventing invasion by nonnative salmonids, the model neither formally considers nor quantifies the threat of hybridization. A synthesis of WCT hybridization dynamics across environmental gradients, for example, would be the first step to an extension that formally quantified such a threat.

The InvAD BBN obviously does not solve the often opposing problems of brook trout invasion and habitat fragmentation facing WCT or other native fishes in western North America. Rather, it provides a process and framework for thinking through the issues, clearly documenting and defining knowledge and uncertainty, and identifying conservation values and objectives. Site-specific analysis using the InvAD BBN or similar BBNs may help identify management options and trade-offs in a particular stream. The greater utility, however, may be using the model to explore the relative benefits of isolation or connection across a collection of WCT populations and using that information to implement more strategic conservation programs and prioritize limited resources.

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