

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. 2002a; 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. 2002a; 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 (≤ 4 th-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. 2002b) 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. 2002a), 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.

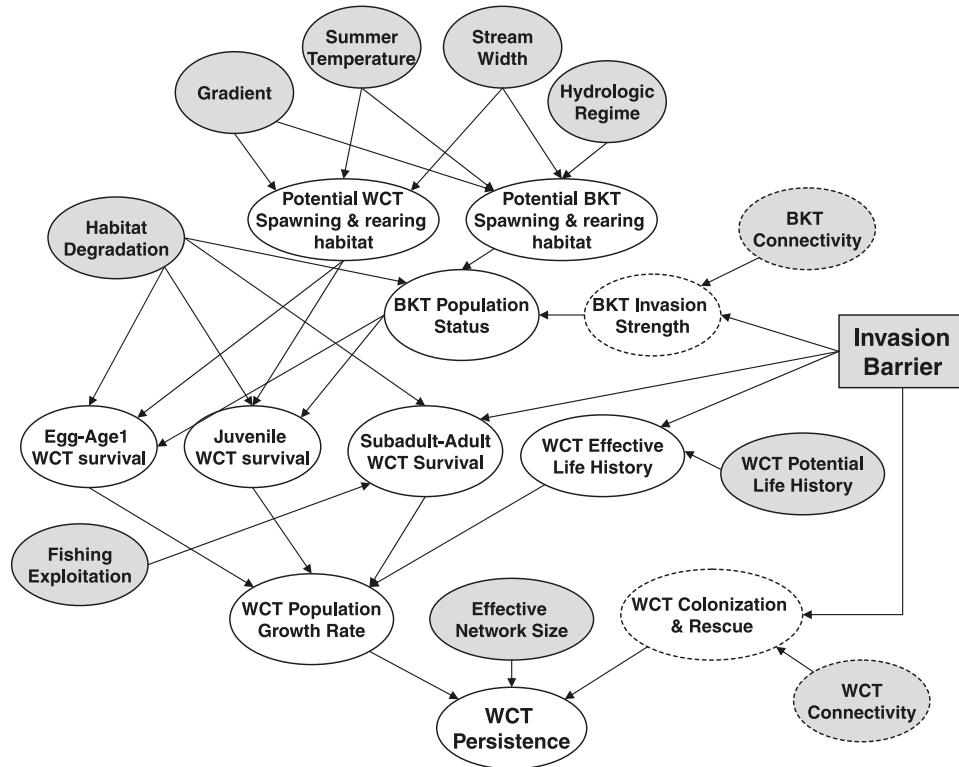
The model

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 S1⁴). 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-

⁴Supplementary 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 S1⁴ 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 resi-

dent life history, which defined the expected fecundity of spawning females. This demographic representation of stage-specific survival and reproductive output in the BBN is analogous 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 °C Low: 7–10 °C Optimum: 10–15 °C High: 15–18 °C Very high: >18 °C
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 (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: $\lambda = 0.85\text{--}0.95$ Moderate: $\lambda = 0.95\text{--}1.05$ High: $\lambda = 1.05\text{--}1.15$ 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 S1⁴.

^aInput 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 S1⁴). Habitat degrada-

tion 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. (2002b). 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. 2002b). 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 S1⁴) 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 S1⁴). 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 S1⁴). 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 S1⁴). 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 S1⁴). 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 S1⁴). 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 S1⁴). 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 S1⁴). 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 S2⁴), 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.

^aA 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.

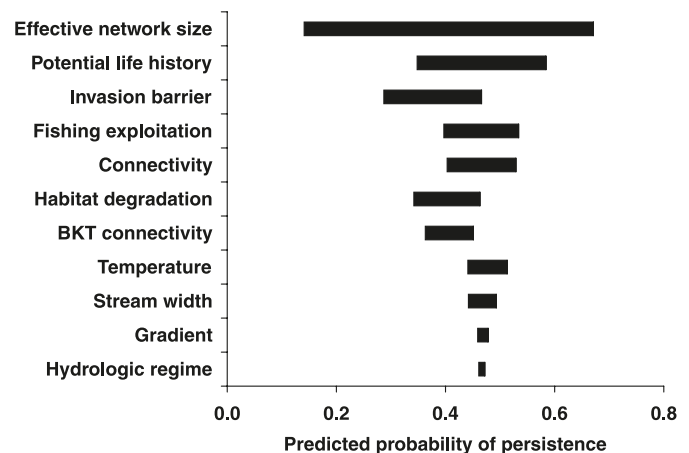
^bSensitivity values (entropy reduction) assumed a uniform prior probability distribution for each of the 11 input nodes and were calculated in Netica using the mutual information formula that appears in Pearl (1991, p. 321) that is implemented in Netica (B. Boerlange, Norsys Software Corporation, 3512 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

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*).



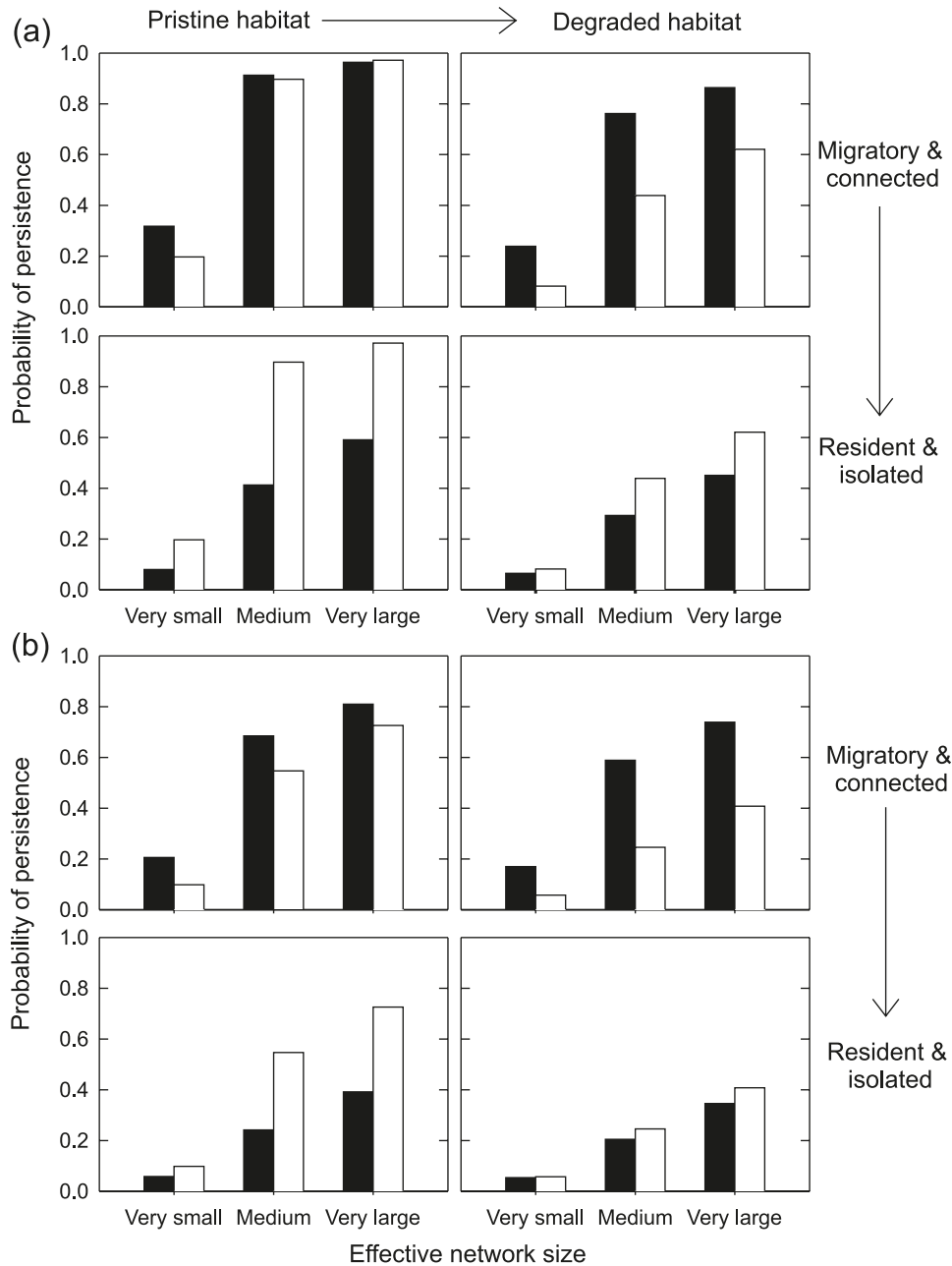
was predicted to increase from 0.81 to 0.97 if the existing barrier was removed. The apparent benefit resulted from the expectation that the existing population would re-express a migratory life history and connection with other populations in the Saint Regis River system. The relative increase was modest 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.

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.

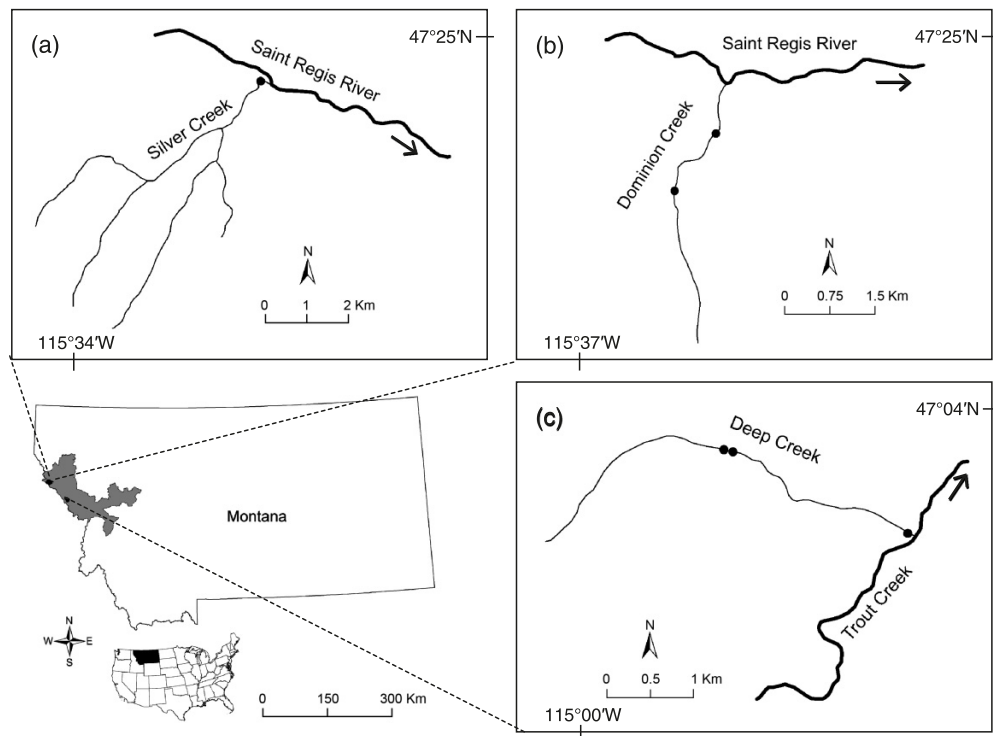


Table 5. Existing conditions for three westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) streams in Lolo National Forest that are threatened by invasion from nonnative brook trout (*Salvelinus fontinalis*) and possible management actions involving barrier maintenance or removal and habitat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

Node or factor affecting WCT persistence	State of node or existing condition ^a		
	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).

^aThe 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.

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.

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).

		Estimated probability of persistence	
		Habitat improvement	
Barrier removals	Nonnative trout invasion possible	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.

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; Ayllon 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. 2002b; 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 move-

ments. 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 hy-

bridization 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 $\times$ 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 isola-

tion 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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SUPPLEMENTAL APPENDIX S1.

**Definitions, justifications, and conditional relationships for variables (nodes)
comprising the isolation and invasion analysis and decision Bayesian belief
network (InvAD BBN)**

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Summary

Peterson et al. (2008) presented a tool to help biologists concerned with conservation of westslope cutthroat trout (or WCT, *Oncorhynchus clarkii lewisi*) quantify tradeoffs between the threats of isolation and invasion by nonnative brook trout (or BKT, *Salvelinus fontinalis*). The result was an isolation and invasion analysis and decision Bayesian belief network (*InvAD* BBN). We developed this Bayesian belief network (BBN) following the general procedures outlined elsewhere (Cain 2001; Marcot et al. 2006; Marcot 2007). We began with a series of meetings between several of 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, the authors developed conceptual models (i.e., box-and-arrow diagrams; synonymous with the terms “influence diagram” in Marcot et al. 2006 or “directed acyclic graph” in Pearl 1991) that depicted the hypothesized causal relationships and processes important to these species. The conceptual models were refined through iterative discussion to capture only the essential (and quantifiable) relationships in their simplest possible forms. The final conceptual model (Fig. 1 in Peterson et al. 2008) was converted to a Bayesian belief network (Fig. S1-1) 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. Arrows represented dependence or a cause-and-effect relationship between corresponding nodes. Conditional (quantitative) relationships 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. The completed BBN (*InvAD*) contained 22 variables (nodes), so for brevity Peterson et al. (2008) presented only concise definitions for each node (see Table 1 in Peterson et al. 2008), generalized each node’s influence, and summarized the quantitative conditional relationships among them. A representative example of these quantitative conditional relationships (i.e., CPTs) was given for a single node (see Table 2 in Peterson et al. 2008), but there are 11 such CPTs that underlie the *InvAD* BBN.

The following sections present more detailed node and state definitions along with the underlying scientific support for the ecological process or environmental condition represented by each of the 22 nodes in the *InvAD* BBN, and the quantitative conditional relationships (CPTs)

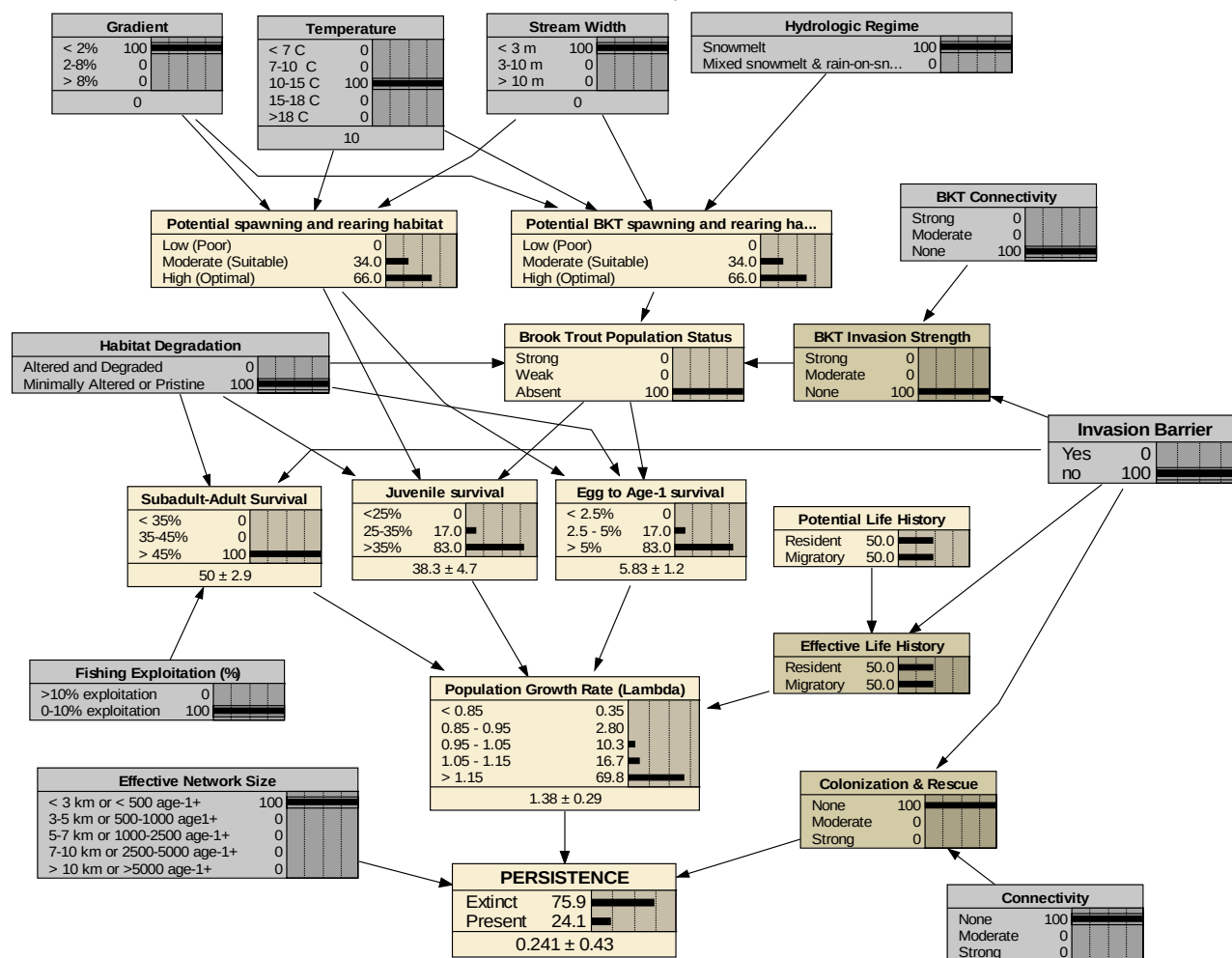
for each of the 11 nodes that have two or more parents (i.e., contributing nodes) (Tables S1-1 to Tables S1-11)⁴.

A hyperlinked list of nodes definitions (left column) and associated CPTs (right column) follows, and nodes refer to common environmental conditions or westslope cutthroat trout (WCT) unless specifically noted:

Node name	Conditional probability table (CPT)
Temperature	-
Gradient	-
Stream width	-
Hydrologic regime	-
Potential spawning and rearing habitat	Table S1-1
Potential BKT spawning and rearing habitat	Table S1-2
BKT connectivity	-
Invasion barrier	-
Invasion strength (for brook trout)	Table S1-3
Habitat degradation	-
Brook trout population status	Table S1-4
Fishing exploitation	-
Egg to age-1 survival	Table S1-5
Juvenile survival	Table S1-6
Subadult-adult survival	Table S1-7
Potential life history	-
Effective life history	Table S1-8
Population growth rate	Table S1-9
Connectivity	-
Colonization and rescue	Table S1-10
Effective network size	-
Persistence	Table S1-11

⁴ CPTs for three alternate or competing BBNs that have box-and-arrow identical to *InvAD* are also presented (see Tables S1-9 and S1-10). Analyses of results from the alternative models are presented in SUPPLEMENTAL APPENDIX S2, available on the Canadian Journal and Fisheries and Aquatic Sciences web site (cjfas.nrc.ca).

BBN to analyze tradeoffs between brook trout invasion versus intentional isolation of westslope cutthroat trout



InvAD Version 1.1, 13 February 2007

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Fig. S1-1. The isolation and invasion analysis and decision Bayesian belief network (*InvAD* BBN) as represented in the Netica modeling software. The black horizontal bars within each node (box) indicate the probability (%) of being in a particular state. (Note: the use of trade or firm names (e.g., Netica) is for reader information only and does not imply endorsement by the US Department of Agriculture or the US Department of Interior of any product or service.)

Node and state definitions - *temperature*

Temperature is defined as the mean “summer” temperature over the stream network approximately July 15 through September 15. This period is roughly symmetrical about the time of maximum temperatures observed in mountain streams of the northern interior western US (Rieman and Chandler 1998). Temperatures are believed to have an important influence on habitat potential for both brook trout and cutthroat trout primarily through growth and the demographic processes related to growth. The five states for the *temperature* variable (node) are:

<i>Temperature</i>	
State name	Values
Very low	<7°C
Low	7-10°C
Optimum	10-15°C
High	15-18°C
Very high	>18°C

The definition and states for *temperature* were authored by KDF and BER.

Background and justification - Temperature

Temperature can impose important constraints on growth (Bear 2005; Bear et al. 2007; McMahon et al. 2007) and demographic processes related to growth of both cutthroat and brook trout (Adams 1999; Coleman and Fausch 2007a, 2007b). Ultimately temperature is believed to constrain distributions, abundances and resilience of populations of these and related species in the stream habitats that are accessible to them (e.g., Paul and Post 2001; Rieman et al. 2006). Temperature can also mediate the interaction between species. In laboratory experiments De Staso and Rahel (1994) found that brook trout were able to dominate cutthroat trout at higher temperatures (20°C), but that neither species had an advantage at lower temperatures (10°C). For these reasons we believe that temperature will influence both the distribution and the interactions of cutthroat and brook trout even though they appear to have similar temperature optima. Both species can persist over a range of mean temperatures from approximately 7 to 18°C and perhaps even beyond (e.g., Adams 1999; Selong et al. 2001; Harig and Fausch 2002; Sloat et al. 2005;

Benjamin 2006; Coleman and Fausch 2007a, 2007b). In the laboratory the optimal range for growth appears to be between about 12 to 16°C for fish fed to satiation (Bear 2005; Bear et al. 2007; McMahon et al. 2007), but brook trout might have better performance at higher temperatures (our interpretation of these data). Given that temperatures for optimal growth are generally lower for fish with limited rations (Wootton 1998) we anticipate that optimal temperatures in the wild will be at least 1 or 2°C lower.

Node and state definitions - *gradient*

Gradient is defined as the mean percent gradient over the stream network. The three states for the *gradient* variable (node) are:

<i>Gradient</i>	
State name	Values
Low	<2%
Moderate	2%–8%
High	>8%

The definition and states for *gradient* were authored by KDF, DPP and BER.

Background and justification - gradient

Distribution and abundance of nonnative brook trout and native cutthroat trout are apparently related to stream gradient and habitat factors correlated with gradient. High gradient stream reaches may directly limit fish distribution where such reaches are impassible. High gradient stream reaches can also impose demographic constraints on fishes where spawning, rearing and survival are limited by habitat conditions (e.g., Fausch 1989). Studies of invasion and general habitat requirements for both species indicate that cutthroat trout populations may be less limited by increasing stream gradient than brook trout.

Several studies from the Rocky Mountains (USA) have observed an inverse relationship between stream gradient and biomass of brook trout (Chisholm and Hubert 1986; Fausch 1989; Rieman et al. 1999), and brook trout appear to have difficulty establishing populations in streams with gradients steeper than 4-7% (Fausch et al. 2006). Adult brook trout can move through and

occupy high gradient (e.g., >12%) stream reaches (Adams et al. 2000, 2001), leading to hypotheses that lack of upwelling ground water needed for egg incubation, scour of eggs or fry, and lack of off-channel or lateral nursery habitats in steep channel slopes may limit reproduction and recruitment (Fausch 1989; Adams 1999).

Small cutthroat trout have been observed over a wide range of stream gradients, and do not appear to be as constrained by moderate or even high gradient stream channels compared to brook trout. Moore and Gregory (1988) and Abbott (2000) associated the most productive natal areas for cutthroat trout with low gradient and unconfined channels, but Fausch (1989) and Rieman et al. (1999) found densities of small cutthroat trout were generally highest at intermediate gradients (e.g., 2%–8%). Interspecific competition whereby brook trout appear have an advantage in low gradient reaches may confound simple interpretation of a gradient-density relationships for cutthroat trout when the two species are sympatric (e.g., Fausch 1989).

We conclude that stream gradients >8% will represent marginal or even unsuitable natal habitat for brook trout while optimal spawning and rearing habitat will be more common in stream segments with gradient <2%. We assume that spawning and rearing habitat for cutthroat trout will be less strongly constrained by channel gradient.

Node and state definitions - *stream width*

Stream width is defined as the mean wetted width over the stream network during base flow. The three states for *stream width* are:

<i>Stream width</i>	
State name	Values
Small	<3 m
Medium	3-10 m
Large	>10 m

The definition and states for *stream width* were authored DPP and BER.

Background and justification – stream width

Geomorphic features such as stream size constrain the basic limits of fish habitat (Sheldon 1968), and stream size is believed to influence the distribution and abundance of stream salmonids in the western USA (Bozek and Hubert 1992; Mullan et al. 1992; Rieman and McIntyre 1995; Harig and Fausch 2002; Rich et al. 2003; but see Stritchert et al. 2001). Stream size is hypothesized to be an important correlate for the frequency and diversity of habitats need for reproduction and recruitment by brook trout and cutthroat trout.

Longitudinal patterns in the distribution of cutthroat trout and brook trout suggest that brook trout may better utilize larger natal habitats. Numerous studies have reported that cutthroat trout tend to occupy smaller streams in the upper watershed, while brook trout predominate in larger segments downstream (MacPhee 1966; Griffith 1972; Fausch 1989; Bozek and Hubert 1992; Paul and Post 2001; Peterson 2002), though exceptions are possible (Adams 1999). Data suggesting that brook trout are better able to utilize larger habitats, led Schroeter (1998) to hypothesize that habitat utilization and behavior differ between the two species. Brook trout exhibit a preference for pool habitats (Griffith 1972), and pools tend to be more frequent in larger, lower gradient streams (Hubert and Kozel 1993; Schroeter 1998).

Rieman et al. (1999) summarized the distribution and abundance of brook trout and westslope cutthroat trout from sites in Idaho and Montana, USA, in relation to geomorphic features. They found that small brook trout occur throughout streams 1-10 m wide, but that their density decreased in streams >10 m wide. A re-analysis of these data indicated they are most abundant when stream width was greater than 2-3 m (B.E. Rieman, unpublished data). Presence of competitors (brown trout, *Salmo trutta*) or habitat degradation in downstream segments may limit brook trout to smaller habitats in some cases (Kozel and Hubert 1989; Rahel and Nibbelink 1999). Westslope cutthroat trout are generally believed to spawn and rear in small tributary streams (Johnson 1963; Lukens 1978; Lewinsky 1986; McIntyre and Rieman 1995). Occurrence of age-0 (young of the year) westslope cutthroat trout was associated with streams less than 7.7 m wide (Abbot 2000) or less than 4th order (Dunnigan 1997). An inverse relationship between density of juveniles and stream width across a range of stream sizes (1.1-8.3 m width) has been reported for other cutthroat trout subspecies (Horan et al. 2000), but a positive relationship between cutthroat trout abundance and width has been observed where the range of mean widths was less (1.0-5.4 m, Harig and Fausch 2002). Densities of small westslope cutthroat trout in

Montana and Idaho were greatest in streams less than 3-5 m in width (Rieman et al. 1999; B.E. Rieman, unpublished data).

Based on our interpretation of the preceding data, we defined states for *stream width* whereby optimal natal habitats for cutthroat trout are most frequently found in small streams (<3 m), whereas optimal natal habitat for brook trout was slightly larger (3-10 m).

Node and state definitions – *hydrologic regime*

Hydrologic regime is defined as the seasonal patterns of runoff and flooding that might influence bed scour and subsequent incubation or emergence success of fall spawning salmonids like brook trout. The three states for *hydrologic regime* are:

<i>Hydrologic regime</i>	
State name	Description
Snowmelt	Peak flows generally ($\geq 80\%$ of years) occur during spring snow melt and after March 1.
Mixed rain-on-snow and snowmelt	Peak flows occur at least occasionally ($> 20\%$ of years) between early November and mid March.

The definition and states for *hydrologic regime* were authored BER and KDF.

Background and justification – hydrologic regime

Hydrologic regime and the patterns and timing of flooding vary across western North America, as influenced by climate and landform (Sanborn and Bledsoe 2006; Beechie et al. 2006). Distinct regimes including winter rain, snow melt, and rain-on-snow (or transitional) have been considered constraints on the distribution and diversity of stream fishes (e.g., Montgomery et al. 1999; Beechie et al. 2006). Regionally, we expect differences between snowmelt compared with mixed rain-on-snow and snowmelt hydrologic regimes to strongly

influence brook trout reproductive success. Several investigators have reported strong negative effects of winter flooding on brook trout embryo or fry survival (Elwood and Waters 1969; Seegrist and Gard 1972, Erman et al. 1988). Similar effects have been observed with other fall spawning salmonids (Strange et al. 1992; Strange and Foin 1999) where incubating embryos and pre-emergent alevins are vulnerable to bed mobilization and scour (Montgomery et al. 1999, Lapointe et al. 2000). Flooding that occurs shortly after emergence may also flush small fish from the stream, and elevated runoff has been shown to reduced recruitment of introduced stream salmonids in the Rocky Mountains, USA (Nehring and Anderson 1993; Laterell et al. 1998).

Presumably salmonids have adapted to minimize vulnerability to such events in their native range, but introduction to a novel environment may constrain reproductive success. For example, Fausch et al. (2001) showed that invasion of rainbow trout (*Oncorhynchus mykiss*) was more successful in regions where flow regimes more closely matched those in the native range (winter rain – summer low flow) than where they did not. Because brook trout did not evolve with a mixed hydrologic regime we assume that they will be less well adapted to those flow patterns. We anticipate that frequent or even occasional winter flooding will constrain the success of brook trout invasion, establishment, or the strength of a resulting population (if the first two occur), although that effect may also depend on geomorphic characteristics of available habitats (Montgomery et al. 1999). Anecdotal evidence suggests this mechanism could be important to explain the varied success of brook trout invasions in interior western North America and the Rocky Mountains (Fausch et al. 2006).

Node and state definitions - *potential spawning and rearing habitat*

Potential spawning and rearing habitat for westslope cutthroat trout is defined as the potential for successful reproduction and early rearing by cutthroat trout based on the physical template for natal habitat as influenced by stream gradient, summer water temperature and stream size (width). This definition assumes that cutthroat trout are or should be present and are not constrained by habitat degradation, barriers, competition, or other factors. The three states for *potential spawning and rearing habitat* are:

Potential spawning and rearing habitat

State name

Low (Poor)

Moderate (Suitable)

High (Optimal)

The definition and states for *potential spawning and rearing habitat* for cutthroat trout were authored DPP and BER.

Background and justification - potential spawning and rearing habitat

The potential for natal habitat to produce juvenile cutthroat trout is defined as a function of abiotic and physical factors defined in contributing (parent) nodes (Table S1-1). While westslope cutthroat trout and other salmonids are certainly affected by seasonal and interannual variability in flow conditions (e.g., Strange and Foin 1999), we assumed they were adapted to the prevailing flow conditions across the native range of the species so *hydrologic regime* was not designated as a variable influencing WCT in the *InvAD* BBN. We assumed that very low (<7°C) and very high (>18°C) mean summer temperatures impose major limitations on cutthroat trout reproduction and recruitment and will be a prevailing influence. We further assumed that cutthroat trout natal habitat will generally be poor in larger channels, and that their optimal natal habitat would be found in small, low to moderate-gradient stream channels where temperatures were 10-15°C.

Based on the distribution of observations of small cutthroat trout (<100 mm) in Idaho and Montana (Rieman et al. 1999), we estimate that low, moderate and high states are roughly equivalent with the potential for natal habitats to produce densities of <5, 5-15, and >15 small westslope cutthroat trout/100m², respectively.

Node and state definitions - *potential brook trout (BKT) spawning and rearing habitat*

Potential brook trout (BKT) spawning and rearing habitat is defined as the potential for successful reproduction and early rearing by brook trout based on the physical template for natal habitat as influenced by stream gradient, summer water temperature, stream size (width), and the

dominant hydrologic regime. This definition assumes that brook trout are or should be present and are not constrained by habitat degradation, barriers, competition, or other factors. The three states for *potential brook trout (BKT) spawning and rearing habitat* are:

Potential BKT spawning and rearing habitat

State name

Low (Poor)

Moderate (Suitable)

High (Optimal)

The definition and states for *potential brook trout (BKT) spawning and rearing habitat* were authored DPP and BER.

Background and justification - potential brook trout (BKT) spawning and rearing habitat

The potential for natal habitat to produce juvenile brook trout is defined as a function of abiotic and physical factors defined in contributing (parent) nodes (Table S1-2). We assumed that a mixed hydrologic regime imposes a major limitation on brook trout reproduction and recruitment and will be a prevailing influence even when other abiotic or physical factors are suitable. We further assumed that brook trout never do well in high-gradient channels of any size, and that their optimal natal habitat would be found in medium width low-gradient stream channels where temperatures were 10-15°C.

Based on the distribution of observations of small brook trout (<100 mm) in Idaho and Montana (Rieman et al. 1999), we estimate that low, moderate and high states are roughly equivalent with the potential for natal habitats to produce densities of <5, 5-15, and >15 small brook trout/100m², respectively. These values are within the range of densities observed by other investigators (Adams 1999).

Node and state definitions - *invasion barrier*

Invasion barrier is defined as a natural or human-constructed barrier that precludes upstream movement by stream fishes. The two states for *invasion barrier* are:

<i>Invasion barrier</i>	
State name	Description
Yes	Barrier is already present or will be constructed.
No	No barrier exists and none is planned.

The definition and states for *invasion barrier* were authored DPP.

Background and justification – invasion barrier

Whether or not to install an invasion barrier is the primary management decision considered by the *InvAD* BBN.

Node and state definitions - brook trout (BKT) connectivity and invasion strength

Brook trout (BKT) connectivity characterizes the potential for invasion by brook trout into the local stream network based on the magnitude and frequency of brook trout immigration. *Invasion strength* describes the realized connectivity as influenced by the number, distribution, and attributes of potential source brook trout populations outside the local stream network; and the characteristics of the movement corridor including whether or not an invasion barrier is present or will be installed.

The three states for *brook trout (BKT) connectivity*, and its dependent node, *invasion strength*, are:

<i>(BKT) connectivity and invasion strength</i>	
State name	Description
Strong	Potential for immigration of multiple adults into the local stream network on an annual basis. Robust neighboring populations are within 5 km (stream distance) or more distant populations (5-10 km) are known to exhibit jump dispersal, and the migration corridor is suitable.
Moderate	Immigration is episodic and/or includes few individuals because adjacent populations are weak or dispersal distances are far (>10 km), or partial migration barriers limit effective dispersal.
None	No immigration is expected because source populations either do not exist or are too far away, or because an upstream migration barrier is present in the movement corridor.

The definition and states for *brook trout (BKT) connectivity* and *invasion strength* were authored by DPP.

Background and Justification - brook trout (BKT) connectivity and invasion strength

Arrival of immigrants through natural dispersal or human intervention is the first phase of an invasion process that can lead to successful establishment and ecological effects in the

receiving ecosystem (Kolar and Lodge 2001; Dunham et al. 2002). The probability that invaders will successfully colonize a new habitat can depend strongly on the frequency and magnitude of immigration (i.e., propagule pressure) (Lockwood et al. 2005). The related concept of connectivity, or in the context of nonnative species its synonym invasion strength, describes the linkage between occupied or unoccupied habitat patches in terms of movement and the spatial structuring of populations.

A variety of metrics can be used to quantify connectivity, ranging from simple nearest-neighbor relationships to more explicit incidence functions that consider multiple source populations and patch characteristics (Moilanen and Nieminen 2002; Calabrese and Fagan 2004). The underlying considerations for connectivity or invasion strength will be distance to source populations, dispersal ability of the invader, propensity of source populations to produce immigrants, and physical (and perhaps biological) characteristics of the movement corridor that may influence the effective distance.

Invasion strength is presumed to be inversely related to distance between source and recipient habitats (Sheldon and Meffee 1995). However, the ability of stream fishes like brook trout to exhibit jump dispersal (e.g., Peterson and Fausch 2003a) means that nearest-neighbor relationships may not capture all significant immigration processes. There is little information to provide direct estimates of dispersal or dispersal kernels, but empirical studies of movement by brook trout indicates intra-annual movement distances can be at least 2 km even in small streams (Gowan and Fausch 1996a; Peterson and Fausch 2003a), and tens of kilometers for migratory forms (Curry et al. 2002). Similarly, demographic studies of stream salmonids indicate dispersal is more common among neighboring (within ~5-10 km) populations (Dunham and Rieman 1999; Koizumi and Maekawa 2004). Invasion strength (connectivity) can be weighted by patch or population size (Calabrese and Fagan 2004) on the assumption that larger populations produce more immigrants (e.g., Jager et al. 2001). Limited evidence indicates that immigration by brook trout can be proportional to source population density (Peterson and Fausch 2003a; Peterson et al. 2004). Physical (and in some cases biological) characteristics of the dispersal corridor, for example high-gradient reaches, may impede immigration by stream fishes and increase the effective distance between source and recipient habitat. Consequently, we assume a general relationship where *invasion strength* is inversely related to the distance and strength of source

populations, where active dispersal of 2-5 km is probable but distances of 10 km or more are less likely, and where migration barriers effectively stop upstream dispersal (Table S1-3).

Node and state definitions - *habitat degradation*

Habitat degradation is defined as whether salmonid habitat and the processes that create and maintain it have been altered by human activity. A central assumption is that watersheds without human disruption will tend to support more complex habitats resilient to disturbance.

The two state definitions for *habitat degradation* were based on differences between managed and unmanaged watersheds used by McIntosh et al. (2000) and Kershner et al. (2004):

<i>Habitat degradation</i>	
State name	Description
Altered and degraded	Activities that disrupt watersheds, such as logging, road construction, grazing, mining, water development, or other activities that influence erosion, wood loading, channel-floodplain connectivity, flood flows, or other hydrologic and geomorphic processes have been extensive and their effects persistent. The role of natural processes has been reduced.
Minimally altered or pristine	Activities disrupting watersheds have been infrequent, occurred historically, and were of limited extent and effect, or were entirely absent. Natural processes predominate in habitat formation and maintenance. The unmanaged state would be consistent with wilderness, roadless areas, or areas where previous or ongoing land management is relatively minor.

The definition and states for *habitat degradation* were authored by MKY, BER, and DPP.

Background and justification – habitat degradation

Abundance of adult cutthroat trout has frequently been associated with habitat quality and complexity, particularly the size and number of pools (Jakober et al. 1998; Harig and Fausch 2002). Low watershed or habitat integrity presumably results in habitat degradation and simplification that reduces carrying capacity and increases emigration. Poor habitat quality may increase predation rates on fish forced to occupy areas with less cover or may reduce survival during critical periods, for example during summer thermal maxima, floods, drought, and anchor ice formation, because refugia are few or lacking. Although watersheds that have been altered by natural disturbance may temporarily have poor habitat, recovery may be relatively rapid if natural processes that create and maintain habitat continue unabated and linkages between streams, riparian zones, and uplands remain intact (Beechie and Bolton 1999; Reeves et al. 2006). In contrast, human disturbance tends to be chronic and cumulative i.e., rarely restricted to a single effect at one point in time, and habitat quality may remain depressed indefinitely.

Because the quality and quantity of pools, large wood, and bank-related cover can be strongly influenced by land management (Young et al. 1994; McIntosh et al. 2000; Kershner et al. 2004), the degree of disruption in the watershed is expected to have at least some influence on the survival of juvenile, sub-adult, and adult cutthroat trout. Several studies have shown a negative relationship between indices of habitat disruption (e.g., clearcut logging or road density) and abundance or status of cutthroat trout (Lee et al. 1997; Abbott 2000), and there is some evidence that habitats in wilderness areas relatively free from human disturbance support more robust populations of cutthroat trout than do more heavily managed lands (Rieman and Apperson 1989; Kershner et al. 1997; Shepard et al. 2005). In addition, because habitat conditions might mediate individual growth or the availability of cover, they could also influence the outcome of the interactions between cutthroat trout and brook trout (DeStaso and Rahel 1994; Shepard et al. 2002; Shepard 2004), although we anticipate that this effect will be less important for cutthroat trout older than age 0 (Peterson et al. 2004). Overall, although we posit that habitat degradation resulting from watershed management leads to reduced juvenile, sub-adult, and adult cutthroat trout survival, empirical models quantifying the relationship between habitat condition and survival during these stages are lacking.

In contrast, there is a rich literature demonstrating that many land management activities lead to increases in fine sediment (Megahan et al. 1992; Hartman et al. 1996), which in turn can

reduce the survival to emergence of salmonids (Chapman 1988), including cutthroat trout (Young et al. 1991) and brook trout (Curry and MacNeill 2004).

Brook trout populations appear susceptible to effects of watershed degradation and habitat disruption within their native range (e.g., Hudy et al. 2004), and have been shown to respond positively to site-specific habitat improvements in the western USA (e.g., Gowan and Fausch 1996b). We infer that altered and degraded habitat will influence the population strength of nonnative brook trout populations through mechanisms similar to those affecting cutthroat trout, but assume that brook trout may be somewhat less sensitive based on their widespread distribution across a gradient of habitat quality in the western US (Schade and Bonar 2005).

Node and state definitions - *brook trout (BKT) population status*

Brook trout (BKT) population status is defined as the potential strength of a brook trout population in a stream segment as influenced by the realized condition of natal habitat and the likelihood of brook trout immigration. This node ultimately characterizes the potential for brook trout to become established in a stream segment, expand their population, and to exert biotic pressure, via competition and predation, on cutthroat trout. The three state definitions for *brook trout (BKT) population status* are:

<i>Brook trout (BKT) population status</i>	
State name	Description
Strong	Brook trout are established and maintain at least moderate densities [e.g., >5 small (<100 mm) brook trout per 100 m ²].
Weak	Brook trout are successfully established but maintain a population at low density (e.g., ≤ 5 small brook trout per 100 m ²).
Absent	Brook trout are not established

The definition and states for *brook trout (BKT) population status* were authored by DPP and BER.

Background and justification - brook trout (BKT) population status

The potential for brook trout to establish and maintain a robust population will depend on the ability of brook trout to arrive in the tributary network (a function of *BKT connectivity* and *invasion strength*) and the actual condition of the natal habitat (a function of *potential BKT spawning and rearing habitat* as influenced by *habitat degradation*) (Table S1-4). We made two general assumptions about how the contributing nodes influenced the potential population strength of brook trout. First, even moderate connectivity or invasion strength is expected to result in establishment of a strong population where natal habitat conditions are suitable or better. Second, strong connectivity and invasion strength can potentially overcome the effect of unfavorable natal habitat conditions and result in establishment, but the resulting population is expected to persist at low abundance.

Brook trout will be absent if they cannot immigrate into a tributary network. However, brook trout may also fail to successfully invade accessible habitats (e.g., Adams et al. 2002). We assume that brook trout may also be absent where *invasion strength* is moderate and habitat in the target segment is both inherently unsuitable and degraded. Similar to the rationale described under *potential brook trout spawning and rearing habitat*, general guidelines characterizing weak and strong populations would be average densities of small (juvenile or <100 mm) brook trout of ≤ 5 and > 5 fish/100 m², respectively. The evidence for these rough quantitative guidelines and their general applicability are not robust, however we expect the qualitative effect of brook trout population strength on cutthroat trout survival to be dose dependent whereby cutthroat trout survival and brook trout population strength are inversely related (e.g., Peterson et al. 2004).

Node and state definitions - *fishing exploitation*

Fishing exploitation is defined as the exploitation rate of subadult and adult (aged 2 and older) westslope cutthroat trout in a stream network. The two states for *fishing exploitation* are:

<i>Fishing exploitation</i>		
State name	Values	Description
Low	<10% annual exploitation	This often results from limited fishing pressure caused by poor or no roads or trails, long travel times from large towns and cities, or the fishery lacking notoriety. Exploitation may also be limited by special angling regulations.
High	>10% annual exploitation	Even modest levels of fishing pressure can lead to overexploitation, particularly for populations exhibiting low productivity, those lacking special regulations, or for which regulations are ignored or ineffective.

The definition and states for *fishing exploitation* were authored by MYK and BER.

Background and justification – fishing exploitation

Rieman and Apperson (1989) summarized much of the literature on the effects of fishing on westslope cutthroat trout which are believed to be particularly vulnerable to exploitation. Even modest angling effort can lead to overexploitation, but angling restrictions have been successful at mitigating this effect (Schill et al. 1986; McIntyre and Rieman 1995). Access to streams and public recognition of a fishery may also play an important role. For example, populations with easy road access and containing large-bodied migratory individuals are more likely to be fished at higher levels than those that are remote or support only small-bodied resident adults. Complex habitats, such as large accumulations of wood, or inaccessible reaches,

such as steep-sided canyons, may provide refuges from angling that reduce overall exploitation rates.

Fishing exploitation rates for depressed cutthroat populations that supported migratory life histories were between 27% and 30% (summary from Rieman and Apperson 1989). Simulations indicate that any exploitation will result in a change in the structure of the sub-adult and adult portion of the population, but persistence will depend on compensation in survival by other life stages and the intensity of exploitation (Rieman and Apperson 1989). For some populations where recruitment is limited by environmental conditions such as low summer water temperatures, there may be little or no compensatory increase in survival among other life stages and populations may rapidly decline. Under such circumstances, even incidental mortality from capture and release angling may not be sustainable (Paul et al. 2003). In other cases, populations with low adult survival but high juvenile survival may be highly resilient, particularly if fishing exploitation can be regulated. Fishing alone should not lead to reduced resilience unless the exploitation is of sufficient intensity and duration to result in the loss of diversity and adaptive potential in the population (e.g., Safina et al. 2005).

Node and state definitions - *egg to age-1 survival*

Egg to age-1 survival is defined as westslope cutthroat trout survival from egg to age 1 as influenced by realized habitat conditions and interactions with nonnative brook trout. The three states for *egg to age-1 survival* are:

<i>Egg to age-1 survival</i>		
State name	Values	Description
Low	<2.5%	The physical habitat template is poor for cutthroat trout spawning and rearing and/or the stream habitat is highly impacted by land use; or, if habitat conditions are suitable, then brook trout are present and relatively abundant.
Moderate	2.5%–5%	Realized habitat conditions may be suitable, with only minor degradation; or, if habitat conditions are optimal then brook trout are only present at low abundance.
High	>5%	No brook trout are present and habitat conditions are suitable to optimal (not degraded).

The definition and states for *egg to age-1 survival* were authored by DPP and BER.

Background and justification – egg to age-1 survival

The period from egg deposition and fertilization through first summer and winter is believed to be a key life stage influencing the resilience of salmonid populations. This life stage experiences relatively high mortality, so even modest changes in these rates can have profound

effects on the growth rate of a population (Rieman and Apperson 1989; Kareiva et al. 2000; Dambacher et al. 2001). There are at least three periods shown to be highly sensitive to environmental conditions and variability: incubation, emergence and early rearing, and overwintering. Salmonid fishes, including cutthroat trout, deposit and fertilize their eggs in nests (redds) constructed in stream gravels, and survival during incubation may be strongly affected by substrate composition and intragravel water flow that influences the oxygen supply to developing embryos (Irving and Bjornn 1984; Chapman 1988). Severe sedimentation can also limit survival by trapping or entombing emerging fry in the nest. Flooding during incubation or emergence can strongly influence survival through effects of scour or physical displacement (Strange et al. 1992; Nehring and Anderson 1993; Laterell et al. 1998; Strange and Foin 1999; Fausch et al. 2001). Early rearing and pre-winter growth conditions must be sufficient for salmonids to withstand metabolic deficits encountered during winter (Cunjak and Power 1987), but actual survival may be strongly influenced by winter severity (Meyer and Griffiths 1997; Coleman 2007).

The quality and quantity of complex habitats and refugia that might buffer against these effects (e.g., pools, off-channel or stream-margin nursery areas, interstices in substrate) can be strongly influenced by land management. Consequently, the magnitude of habitat degradation in a watershed is expected to have an important influence on survival during this life stage. Several studies have shown a negative relationship between indices of habitat disruption (e.g., clearcut logging, road building) and density or abundance of cutthroat trout (e.g., Rieman and Apperson 1989; Abbott 2000). Although reduced juvenile survival is a plausible mechanism to explain these observations, empirical models quantifying the relationship between habitat condition and juvenile survival are lacking, primarily because survival during this period is extremely difficult to measure with any precision.

Nonnative species invasions can strongly influence the population biology of native species, and competitive interactions leading to reduced survival rates, and is believed to be a key mechanism by which brook trout displace cutthroat trout in western North America (Dunham et al. 2002; Peterson and Fausch 2003b; Fausch et al. 2006). Competition and predation among salmonids has proven difficult to quantify in natural systems (Griffith 1988; Fausch 1988, 1998), but both direct (mark-recapture survival estimates, Peterson et al. 2004) and indirect evidence (abundance monitoring, Shepard et al. 2002) indicates that effects of brook

trout on cutthroat trout survival are most pronounced at juvenile life stages, especially during the first year of life, and that this relationship can be density-dependent (Peterson et al. 2004).

Habitat conditions can mediate interactions among competing species (condition-specific competition, Dunson and Travis 1991), and may influence the outcome of interactions between brook trout and cutthroat trout (DeStaso and Rahel 1994; Novinger 2000; Shepard 2004). While degraded habitat conditions are hypothesized to facilitate replacement or displacement of native species by nonnative species (Moyle and Light 1996), including cutthroat trout by brook trout; the widespread distribution of brook trout in undisturbed stream habitats (Schade and Bonar 2005) and displacement of cutthroat trout even in comparatively high-quality habitats (e.g., Shepard et al. 2002) suggests that biotic interactions have primacy under certain conditions.

Survival from egg to age 1 is difficult to precisely estimate for salmonid fishes, but demographic models that depend on these rates have typically approximated them by default based on empirical estimates for other stages (Rieman and Apperson 1989; Kareiva et al. 2000; Rieman and Allendorf 2001); or have used a range of possible values (Shepard et al. 1997), or a single plausible value (Hilderbrand 2003). A few empirical survival estimates for anadromous salmonids range from 2-15% (Dambaucher et al. 2001). An empirically-derived estimate of 2.6% was used in a modeling exercise for adfluvial Yellowstone cutthroat trout (*O.c. bouvieri*, (Stapp and Hayward 2002) and two species of charr averaged 4.5% (range 2.3-15.9%, geometric mean 3.5%, Morita and Yokota 2002). A simple approximation for westslope cutthroat based on general observations or assumptions of plausible rates of survival and fecundity in subadult and adult fish shows that survival to age 1 should be on the order of 1 to 7.5% for populations in equilibrium. The average survival rate necessary to maintain equilibrium will vary with survival at other stages, age at maturity, longevity, sex ratio, spawning frequency, and fecundity (e.g., higher survival will be necessary to support resident populations with small adults and low fecundity).

The *InvAD* BBN was developed assuming that survival of westslope cutthroat trout from egg to age 1 will depend on a suitable physical habitat template (*potential spawning and rearing habitat*), the condition of that habitat template (*habitat degradation*), and the potential presence and strength of a brook trout population (*BKT population status*) (Table S1-5). Degradation of suitable spawning and rearing habitat is assumed to reduce survival because of increases in fine sediment deposition, loss of lateral rearing habitats survival, and increased frequency and

intensity of flooding. Habitat degradation is irrelevant for survival if spawning and rearing habitat is inherently unsuitable. Biotic effects of brook trout are generally expected to override any buffering influence of high quality habitat, and strongly affect (reduce) survival of WCT to age 1.

Node and state definitions - *juvenile survival*

Juvenile survival is defined as westslope cutthroat trout survival from age 1 to age 2 as influenced by realized habitat conditions and interactions with nonnative brook trout. The three states for *juvenile survival* are:

<i>Juvenile survival</i>	
State name	Values
Low	<25% (assuming a range with a minimum of 15%)
Moderate	25%–35%
High	>35% (assuming a range with a maximum of 45%)

The definition and states for *juvenile survival* were authored by DPP and BER.

Background and justification – juvenile survival

Empirical data suggests that survival rates for cutthroat trout during the juvenile stage can be less than for adults, and estimates range from about 22 to 45% (Stapp and Hayward 2002; Peterson et al. 2004). Similar to egg to age-1 life stage, the juvenile life stage is expected to exhibit substantial variability in survival rates in response to environmental factors and ecological interactions with other fish species, such as brook trout. Demographic models suggest that population growth rates for cutthroat trout can be very sensitive to survival over this interval (Stapp and Hayward 2002; Hilderbrand 2003).

The factors believed to influence juvenile survival rates are similar to those described for the life stage from egg to age 1. Briefly, the quality and quantity of complex habitats, such as pools, off-channel and stream margin nursery areas, and interstices in streambed substrates, are hypothesized to influence growth and survival. Because watershed processes may strongly

influence these habitat characteristics, disruptive land management can reduce juvenile growth and survival (Suttle et al. 2004). Interactions with nonnative brook trout can also reduce survival of juvenile cutthroat trout (Peterson et al. 2004). Ecological interactions with brook trout may not reduce survival of juvenile cutthroat trout to the same extent as for young-of-the-year cutthroat trout (Peterson et al. 2004), perhaps because of improved competitive ability and reduced predation risk conferred by comparatively larger body size (e.g., Novinger 2000).

The conditional relationships for this node are similar to that for *egg to age-1 survival*, in that survival rates will depend on a suitable physical habitat template (*potential spawning and rearing habitat*), the condition of that template (*habitat degradation*), and the potential presence and strength of a brook trout population (*BKT population status*) (Table S1-6). However, the relative magnitude of the effect of ecological interactions with brook trout will be comparatively less for juveniles, and effect of habitat quality and brook trout population strength is expected to be roughly equivalent.

Juvenile cutthroat trout have not yet recruited to the recreational fishery, and are less likely to be affected by presence of an invasion barrier because they presumably exhibit less ranging behavior than adults (because of lower metabolic demands) and do not migrate to spawn.

Node and state definitions - *subadult-adult survival*

Subadult-adult survival is defined as the annual survival of subadult and adult westslope cutthroat trout (ages 2 and older) as influenced by realized habitat conditions, fishing, and presence of an invasion barrier. The three states for *subadult-adult survival* are:

<i>Subadult-adult survival</i>	
State name	Values
Low	<35% (assuming a range with a minimum of 25%)
Moderate	35%–45%
High	>45% (assuming a range with a maximum of 55%)

The definition and states for *subadult-adult survival* were authored by MKY, BER, and DPP.

Background and justification – subadult-adult survival

Subadult-adult survival estimates the combined effects of realized habitat conditions, fishing mortality, and the presence of an invasion barrier on subadult and adult cutthroat trout survival (Table S1-7). Rieman and Apperson (1989) estimated that typical natural mortality rates for westslope cutthroat trout were 31-54% (i.e., without exploitation), but this increased to 70-73% in populations that were considered overexploited. Human-caused habitat degradation is expected to reduce the size and resilience of cutthroat trout populations, but we are not aware of good estimates relating natural mortality for subadult and adult cutthroat trout to habitat conditions. However we believe that effects of habitat degradation on this life stage of WCT will be less influential overall than fishing (where such fishing occurs). Evidence that brook trout can influence the survival of adult cutthroat trout is weak or absent (Griffith 1972; Cummings 1987; Schroeter 1998; Shepard et al. 2002; Peterson et al. 2004).

Installation of an invasion barrier to inhibit colonization by brook trout may also indirectly affect survival of cutthroat trout by disrupting movement patterns. Spawning migrations of resident cutthroat trout could be influenced by invasion barriers depending on the extent of such migrations relative to the location of the barrier. For example, decreased apparent survival will result where WCT move downstream over an (upstream) migration barrier, cannot return to their natal habitat to spawn, and are effectively lost from the local population in question (Note: the effect of an invasion barrier on cutthroat trout migratory life histories is considered under the nodes representing *potential life history* and *effective life history*). Invasion barriers can also influence cutthroat trout survival where they affect non-spawning movements, such as those movements to: summer feeding areas, refuges from ice and predation in winter, shelter from floods, or thermal refuges from high summer water temperatures. These movements may not be temporally predictable, but they are probably inevitable. For example, a local resource bottleneck may only happen once in a fish's lifetime, or several times in a single year. Also, some resource crises are likely to be ontogenetically driven i.e., larger individuals are more likely to outgrow food availability because their bioenergetic demands are greater, and they will more frequently be confronted with the choice of staying and suffering reduced growth or moving in an attempt to locate a bioenergetically favorable site and displace a smaller individual from it (because the best sites should always be occupied). Consequently, 5 km of

stream isolated by a barrier will contain fewer fish than 5 km of stream that remains connected to some undefined length of stream because, in the isolated stream, complementary habitats are fewer and the fish that seek them can be lost if they pass downstream over a migration barrier.

The physical habitat template for cutthroat trout defined in our model (i.e., the combination of *temperature*, *gradient*, and *stream width*) focuses on natal habitat. While these physical characteristics may, in part, influence the behavior, growth, and ultimately the survival of subadult and adult cutthroat trout, we assumed their effect on this older life stage was not quantifiable relative their influence on earlier life stages (egg through juvenile) which have more specific requirements. Accordingly, we assumed a priori that the physical habitat template at both the segment and stream network scales is suitable for subadult and adult cutthroat trout (i.e., the model has no explicit link between *potential spawning and rearing habitat* and *subadult-adult survival*), and that directed movement or ranging behavior links complementary feeding and refuge habitats distributed across the riverscape (e.g., Schlosser and Angermeier 1995; Northcote 1997; Gowan and Fausch 2002; Fausch et al. 2002). Degraded watershed conditions affect the quality and quantity of these complementary habitats.

The range of survival values used in the state definitions were consistent with those estimated for cutthroat trout estimated using mark-recapture methods (e.g., 23-57%, Peterson et al. 2004) or derived from long-term monitoring data (e.g., 37-48%, Stapp and Hayward 2002). Survival rates in moderate to high states encompassed values predicted to result in stationary or increasing populations using demographic models (e.g., Stapp and Hayward 2002; Hilderbrand 2002, 2003; D.P. Peterson, unpublished data).

Node and state definitions - *potential life history* and *effective life history*

Potential life history and *effective life history* characterize the potential and realized life history expression, respectively, for a local population of westslope cutthroat trout. The potential influence of life history expression on the resilience of cutthroat is assumed to be primarily through the differential reproductive contribution of distinct migratory forms. The two states for *potential life history*, and its dependent node, *effective life history* are:

<i>Potential life history and effective life history</i>	
State name	Description
Resident	There is no or very limited movement of fish into or out of the local tributary network. Adult females are likely to mature between 150 and 250 mm with fecundities ranging from 180 to 600 eggs per female.
Migratory	Movement of fish out of the local tributary network into larger rivers and lakes where accelerated growth occurs is extensive. Adult females are likely to mature between 250 and 450 mm (or larger) with fecundities ranging from 600 to 2,200 eggs per female.

The definition and states for *potential life history* and *effective life history* were authored by BER.

Background and justification - potential life history and effective life history

Most salmonids exhibit a diversity of movement patterns expressed in the timing and extent of migration among habitats. Cutthroat trout are often characterized as resident or migratory based on movements from natal habitats to sub-adult rearing areas (McIntyre and Rieman 1995; Fausch et al. 2006). The differential expression of migratory or non-migratory life histories may reflect the degree of movement needed to fulfill all life history requirements or the strategies necessary to maximize fitness along the environmental gradients influencing growth and survival (Northcote 1997; Fausch et al. 2002). The expression of life histories may vary

within and among streams and local populations. Faster growth, larger size at maturity and higher female fecundity is commonly associated with migratory life histories (Rieman and Apperson 1989; Downs 1995). These traits can influence on the demographic characteristics of a population and contribute to higher potential population growth rates (Rieman and Apperson 1989), resilience to disturbance (Rieman and Clayton 1997; Rieman and Dunham 2000) and possibly resistance to invasion (Dunham et al. 2002; Fausch et al. 2006).

We assumed that migratory and resident forms of cutthroat trout would exhibit substantially different growth and fecundities. We estimated the ranges of these characteristics from the summaries of Rieman and Apperson (1989), Downs (1995), and Downs et al. (1997). We anticipate that migratory life histories will be common where the interconnection between natal habitats and rearing areas in larger streams, rivers or lakes are complete and those rearing areas remain productive for cutthroat trout. We assumed resident life histories will dominate where barriers to migration exist between tributary streams (Table S1-8) and more productive downstream rearing environments or where those rearing environments are no longer conducive to rapid growth or survival of rearing individuals. A mix of life history forms may also exist in some streams (McIntyre and Rieman 1995) but we anticipate that the contribution from migratory individuals will likely dominate the demography of local populations where downstream conditions are still productive and conducive to expression of a migratory life history.

Node and state definitions - *population growth rate*

Population growth rate is defined as the potential finite rate of population increase (λ or λ) for the local population of westslope cutthroat trout 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. The five states for *population growth rate* are:

<i>Population growth rate</i>		
State name	Values	Description
Very low	$\lambda < 0.85$	The combination of low reproductive output, low survivorship and low fecundity from migratory individuals results in an annual decline of $>15\%$.
Low	$\lambda = 0.85-0.95$	Conditions intermediate to those in Very low and Moderate states.
Moderate	$\lambda = 0.95-1.05$	Vital rates are intermediate (resident or isolated populations) or low but sufficient demographic support is present to result in a stationary population.
High	$\lambda = 1.05-1.15$	Conditions intermediate to those in Moderate and Very High states.
Very high	$\lambda > 1.15$	Vital rates are high (resident or isolated populations) or vital rates are medium-to-high and migratory individuals provide strong demographic support such that the population can double within a generation (approx. 5 years).

The definition and states for *population growth rate* were authored by DPP and BER.

Background and Justification – population growth rate

A population's potential rate of growth is a function of birth rates and death rates which will depend on maturity schedule, fecundity, reproductive success and age specific survivorship. Growth rate can vary through space and time in response to environmental conditions and population density (Gotelli 1998). Population models provide a means to explore the demographic consequences of variation in vital rates (Noon and Sauer 1992). Matrix population models are particularly helpful because they can be used to estimate the finite rate of population increase (λ), a metric which integrates all vital rates into a single, easily interpreted value representative of a population's trajectory (Caswell 2000). A λ of 1.0 indicates a stationary population, whereas values above and below 1.0 represent increasing and declining populations, respectively. A population with a potential growth rate >1.0 is considered *resilient*, and has the demographic potential to respond and recover when its abundance is reduced through environmental or other factors. We estimated the combined effect of contributing nodes on *population growth rate* (i.e., developed its conditional probability table) using both a demographic model and expert opinion (Table S1-9).

Matrix model-based approach to define the conditional probabilities for *population growth rate*. A deterministic stage-based matrix model was used to approximate the combined influence of reproductive success (*egg to age-1 survival*), stage-specific survival (*juvenile survival* and *subadult-adult survival*), and fecundity (*effective life history*) on the expected population growth of cutthroat trout. We estimated the probability of *population growth rate* being in a particular state by calculating λ (i.e., the dominant eigenvalue of the matrix) based on all possible combinations of the states in four contributing (parent) nodes (Table S1-9).

Maturity schedules were consistent with Rieman and Apperson (1989), McIntyre and Rieman (1995), and Downs et al. (1997), such that female WCT first matured at age 3. Maturity rates varied between age-3 (10% mature) and age-4 (50% mature) classes, and all individuals age 5 and older were mature. The life cycle representing the population model is depicted in Fig. S1-2.

We simulated 1000 matrices for each combination of states for the four parent nodes. For each realization of the matrix, parameter values were randomly selected from a uniform distribution within the range of values for the appropriate state for each parent node. Vital rates

and matrix elements were uncorrelated. The random draw of vital rates reflects uncertainty in the parameter estimates rather than stochastic or demographic processes. We chose to account for environmental variation in population growth rate in another node (see *persistence*) and estimate the probability of persistence using the analytical model of Dennis et al. (1991) rather than a stochastic projection of the matrix population model because of the greater data requirements of the latter (e.g., Besseinger and Westphal 1998). Robust estimates of variance in the vital rates that would account for environmental variation are not available for the parameters in the matrix model. In contrast, empirical estimates of the variance in population growth rate following the analytical model of Dennis et al. (1991) are available for westslope cutthroat trout (McIntyre and Rieman 1995; see definition and justification for *persistence*).

Maturity schedules and rates were constant across all matrix model simulations, and a stable age distribution was assumed so there would be a dominant eigenvalue (λ) for each realized matrix. Accordingly, each matrix was considered a deterministic representation of a population based on the state of the parent nodes in the absence of density-dependent factors. The conditional probability table for *population growth rate* was parameterized based on the frequency distribution of simulation results. Matrix model simulations were implemented by spreadsheet (Microsoft Excel) using a Monte Carlo procedure and population analysis module developed for Excel (Hood 2004).

Mean simulated population growth rates ranged from 0.55 to 1.5 across a representative range of states for parent nodes (Fig. S1-3). Growth rates for resident populations never averaged greater than one unless at least two or three of the stage-specific survival rates (and including *subadult-adult survival*) were high. Increases in *subadult-adult survival* had a larger relative influence on population growth rate than either *egg to age-1* or *juvenile survival*. The presence of a migratory life history had a stronger relative influence than the combined effect of a one state increase in both *juvenile survival* and *subadult-adult survival* (i.e., from low to moderate or moderate to high survival). Presence of a migratory life history provided sufficient demographic support in some cases to compensate for survival rates that would otherwise result in deterministic extinction for a population.

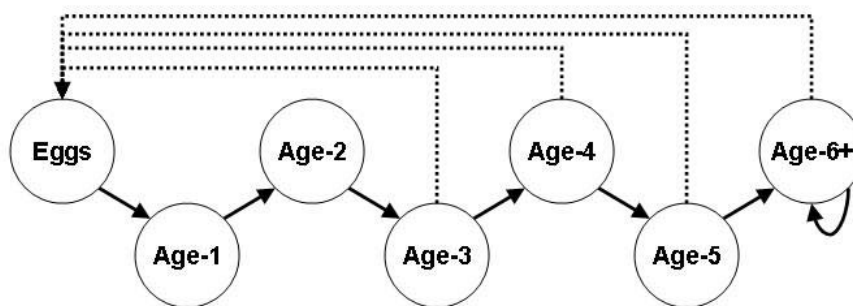


Fig. S1-2. Life cycle diagram of 7-stage matrix population model for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Stage-specific reproductive output (eggs) is denoted by dashed arrows and females begin reproducing at age-3. Survival between stages (transitions) are denoted by solid arrows.

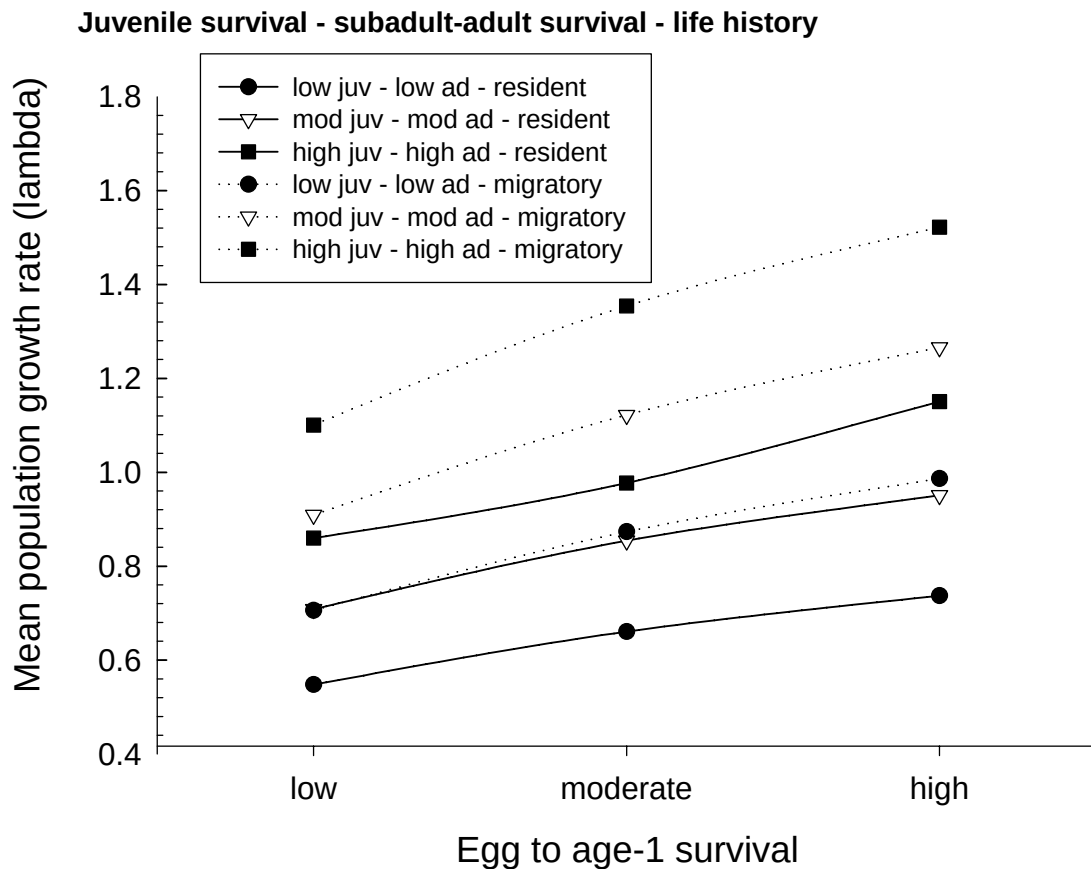


Fig. S1-3. Simulated mean population growth rate (λ) for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) across a representative range of values for *egg to age-1 survival*, *juvenile survival*, *subadult-adult survival*, and *effective life history* (resident or migratory life history, having low or high fecundity, respectively). For brevity, this figure depicts only results where the state values for *juvenile survival* (juv), *subadult-adult survival* (ad) co-varied (i.e., both low, moderate (mod) or high), but conditional probability tables were developed using all possible state combinations of the four contributing nodes (Table S1-9).

Opinion-based approach to define the conditional probabilities for *population growth rate*. In parallel to the matrix-model approach, two authors (BER and DPP) also estimated the probability of *population growth rate* being in a given state based on their interpretation of how the four contributing nodes (*egg to age-1 survival*, *juvenile survival*, *subadult-adult survival*, and *effective life history*) influence WCT populations. The probabilities for *population growth rate* under the assumption of intermediate (i.e., moderate) *egg to age-1 survival* and *juvenile survival* were interpolated based on the low and high estimates for each of those nodes. For the other two contributing nodes, all possible state combinations were directly estimated. Probabilities were averaged across authors to produce an alternate conditional probability table for *population growth rate* based entirely on opinion (Table S1-9).

Node and state definitions - *effective network size*

Effective network size defines the size or spatial extent of the local westslope cutthroat trout population and its vulnerability to environmental variation and catastrophic events. We use population size as our primary metric for the analysis, but assume that population size and stream network size (km) are directly related. Five states are defined because the risk of local extinction appears to increase rapidly as populations drop below moderate numbers. The five states for *effective network size* are:

<i>Effective network size</i>	
State name	Description
Very small	A local population supporting fewer than 500 individuals age 1 and older, or less than 3 km of interconnected stream segments of spawning and early rearing habitat. Populations with a very small <i>effective network size</i> could be highly vulnerable to catastrophic events that can be envisioned for the area in question in the next 20 years.
Small	A local population supporting 500 to 1000 individuals age 1 and older, or alternatively, 3 to 5 km of interconnected stream segments of spawning and early rearing habitat.
Moderate	A local population supporting 1000 to 2500 individuals age 1 and older, or alternatively, 5 to 7 km of interconnected stream segments of spawning and early rearing habitat.
Large	A local population supporting 2500 to 5000 individuals age 1 and older, or alternatively, 7 to 10 km of interconnected stream segments of spawning and early rearing habitat.
Very large	A local population supporting more than 5000 age 1 and older individuals, or alternatively, a network of more than 10 km of

inter- or closely connected stream segments representing suitable spawning and early rearing habitat. Populations with a very large *effective network size* are not likely to be vulnerable to catastrophic events that can be envisioned for the area in question within the next 20 years.

The definition and states for *effective population size* were authored by BER.

Background and justification – effective population size

The size of a network of interconnected stream segments that represents a local population can have an important influence on the persistence of that population. Small populations are more vulnerable to extinction due to loss of genetic variability, small random changes in demographic processes (demographic stochasticity), and normal environmental fluctuations (environmental stochasticity) (see Fausch et al. 2006 for a review), collectively known as small population phenomena (Caughley 1994). Larger-scale perturbations or catastrophes that severely reduce populations and habitats may be important for both small and large populations, particularly if populations are confined to a limited area, a single habitat, or a collection of habitats that could be affected by the same disturbance, such as fire, flood, drought, or temperature extremes. Disturbances that would pose little threat to larger, interconnected populations may become important when populations are small or highly fragmented (e.g., Dunham et al. 2003; Fausch et al. 2006).

We assumed that tributary network size and number of fish in the population will be positively related (e.g., Hilderbrand and Kershner 2000; Young et al. 2005), but the effective size of that tributary network also will be influenced by the complexity and heterogeneity of available habitats and the potential for catastrophic disturbances. Larger and/or more complex and productive habitats should support trout larger populations, and also should be better buffered against environmental variation (Rieman and McIntyre 1993) and catastrophic events if the population is broadly distributed. Recent work (Rieman et al. 1997) suggests that salmonids in tributary networks of more than approximately 10 km are likely large enough to persist following severe fires and subsequent catastrophic stream channel floods or scour events. Smaller populations appear far more vulnerable (e.g., Brown et al. 2001). For these reasons we assumed

that either population size or tributary (habitat) network size could be appropriate measures of *effective network size*. We equated the two based on estimated abundances of inland cutthroat trout from small streams (Hilderbrand and Kershner 2000; Young and Guenther-Gloss 2004; Young et al. 2005). When using the *InvAD* BBN, the probable state of this node can also be assigned by the user based on available local knowledge of the most constraining characteristic for the population in question. Our classification represents a generalization across habitats and environments assuming “moderate” densities ($\sim 0.2/\text{m}$) of fish (e.g., Hilderbrand and Kershner 2000; Young et al. 2005). Systems that are known to support unusually good or poor habitat, or are unusually vulnerable to potentially catastrophic events such as fire, flood or drought, could be rescaled as appropriate. For example, 10 km of degraded habitat that is unusually vulnerable to an extended drought and stream drying might be classified as having a moderate or small *effective network size*.

Node and state definitions - *connectivity* and *colonization and rescue*

Connectivity and *colonization and rescue* define the potential and realized immigration and demographic support, respectively, for a local population of westslope cutthroat trout based on the distribution, interconnection with, and independence of surrounding populations present in other stream tributary networks. It is influenced by the expression of migratory life histories, barriers to movement, and the distribution and characteristics of neighboring populations. The three states for *connectivity*, and its dependent node, *colonization and rescue* are:

<i>Connectivity</i> and <i>colonization and rescue</i>	
State name	Description
None	No immigration can (or will) occur because of a barrier to upstream movement, because neighboring populations are non-existent, too far away, or do not support migratory life histories.
Moderate	Immigration can (or will) occur, but is likely to occur only sporadically because surrounding populations are further than 10km, relatively weak or subject to simultaneous catastrophic disturbances, or do not have the full expression of migratory life histories.
Strong	Immigration of multiple adults into the local stream network can (or will) occur on an annual basis. Migratory life histories and the potential for immigration from surrounding populations are maintained through full connection of the stream network with the larger mainstem and other tributary systems. Healthy neighboring populations support migratory life histories, are not likely to experience simultaneous catastrophic events, and are within 5-10km (mouth to mouth) of the local stream network.

The definition and states for *connectivity* and *colonization and rescue* were authored by BER.

Background and justification - connectivity and colonization and rescue

Spatial structure and interconnection among local populations is believed to have a strong influence on the dynamics and persistence of animal populations. There is growing empirical evidence of the importance of such effects in salmonids (Dunham and Rieman 1999; Koizumi and Maekawa 2004; Ayllon et al. 2006; Isaak et al. 2007) including cutthroat trout (Dunham et al. 1997; Neville-Arsenault 2003; Neville et al. 2006). In essence, small isolated populations are far more prone to local extinctions than large or strongly interconnected populations. Theoretical work suggests even low levels of dispersal can dramatically increase the probability of persistence for local populations of cutthroat trout (Hilderbrand 2003) and other fishes (Jager et al. 2001). We assume, then, that dispersal among neighboring cutthroat trout populations can mitigate the effects of small population size and vulnerability to environmental stochasticity or catastrophic events (Dunham et al. 2003; Ayllon et al. 2006). If such dispersal is strong enough, then it could also serve to support populations that might otherwise be prone to deterministic extinction because of consistently negative population growth rates or low resilience (e.g., rescue effects, Brown and Kodric-Brown 1977; Gotelli 1991).

There is limited evidence to estimate dispersal directly, but genetic and demographic studies suggest dispersal is more common among neighboring populations of salmonids than more distant ones (Dunham and Rieman 1999; Koizumi and Maekawa 2004; Ayllon et al. 2006; Whiteley et al. 2006). The occurrence of migratory life histories also appears to influence the propensity for dispersal over longer distances in cutthroat trout (Neville-Arsenault 2003) and other salmonids (Ayllon et al. 2006). Others have suggested that dispersal in fishes is likely to be influenced by the relative size or density of the potential source populations (Jager et al. 2001). Accordingly we assume that effective dispersal into any local habitat of interest will depend directly on the distance to, number and relative strength of surrounding populations, access through a suitable dispersal corridor, and the occurrence of migratory life histories. Effective dispersal that could mitigate potential threats for a population over a period of 20 years will decline quickly as distances among populations exceed 5-10 km or migratory life histories are lost or precluded by migration barriers (Table S1-10).

Node and state definitions - *persistence*

Persistence is defined as presence of a functionally viable local westslope cutthroat trout population for at least 20 years. The two states for *persistence* are:

<i>Persistence</i>	
State name	Description
Absent	There are no fish left in the network or the population is so small that it is not expected to recover. Populations that drop below 20 adults are assumed to be functionally extinct because of severe genetic bottlenecks, Allee effects, depensation, or other mechanisms contributing to an extinction vortex such that complete extinction is simply a matter of time (e.g., Gilpin and Soulé 1986; Soulé and Mills 1998).
Present	A functioning population of more than 20 adults is present. A functioning population supports a complement of age classes that will reach maturity and likely reproduce.

The definition and states for *persistence* were authored by BER.

Background and justification - *persistence*

The expectation that a population will persist for a given period of time will be a function of demographic trends and resilience to environmental stochasticity (i.e., *population growth rate*), the size of the population and its vulnerability to environmental variation and catastrophic events (*effective network size*), and the potential for demographic support or recolonization through connectivity with other populations (*colonization and rescue*).

To approximate the combined effects of the three contributing nodes on the expectation of local extinction (i.e., conditional probability table for *persistence*) we used using both the analytic models of Dennis et al. (1991) and expert opinion (Table S1-11).

Model-based approach to define conditional probabilities for *persistence*.

We utilized a range of conditions consistent with our definitions of the states in the respective parental nodes to estimate the probabilities for functional extinction within 20 years. Our analysis followed those outlined by Rieman and McIntyre (1993) for bull trout (*Salvelinus confluentus*) populations, and McIntyre and Rieman (1995) for westslope cutthroat populations and similar applications with other salmonids (Sabo et al. 2004). The models require an estimate of the instantaneous population growth rate, variance in that growth rate, initial total population size, a threshold population size for effective extinction, and the period of time the population must persist. We assumed no density dependence. This could bias the estimates of extinction under optimistic growth rates and larger population sizes, but should be less important under the more constraining (and therefore critical) conditions of low or negative growth and small population size (Sabo et al. 2004) particularly if density dependence is tied primarily to habitat carrying capacities (Beissinger and Westphal 1998) as we suspect for these fishes. Population growth rates (transformed from finite to instantaneous) and initial population sizes (total age 1 and older fish) spanned those defined in the parental nodes. McIntyre and Rieman (1995) used a collection of population monitoring data to estimate the variance in population growth rates for seven different westslope cutthroat populations, with values ranging from 0.11 to 1.02 (mean $\cong$ 0.40). Because sampling error may inflate the apparent variation (e.g., Dunham et al. 2001; Holmes 2001) in population size or interannual growth rate, we assumed that populations would tend toward lower variation with larger population or stream tributary network size. Rieman and McIntyre (1993) found that variance in population growth rate for bull trout increased dramatically with smaller adult population sizes. Others have suggested that both population size and the area and heterogeneity of available habitat will buffer the effects of environmental variation (Pickett and Thompson 1978; Baker 1992). Accordingly we assumed that the variance in population growth rate was directly (and inversely) related to population size increasing from about 0.10 to 0.80 with populations ranging from more than 5000 to fewer than 100 total age-1 and older individuals (Fig. S1-4). Extreme differences in variance for a given population size and population growth rate were also tested (Fig. S1-5). To evaluate the sensitivity of the analytical results to our general assumption about the relationship between the variance in population growth rate and population size, we conducted identical analyses using both low (0.2) and high (0.8) constant variance independent of population size (Fig. S1-6). The sensitivity of

the *InvAD* BBN's predictions to these assumptions is evaluated elsewhere (Supplemental Appendix S2⁴).

We followed McIntyre and Rieman (1995) in setting a threshold for functional extinction at 100 total age 1 and older individuals which will equate to an adult population less than 20. We assumed that as numbers fall below this level the probability for severe small population effects (e.g., genetic bottlenecks, inbreeding, demographic stochasticity, depensatory mortalities) would virtually guarantee the eventual extinction of the population if it had no demographic or genetic support from outside populations. We used 20 years as our threshold for persistence because it is a more realistic period to anticipate the trends in a population or its habitat than have commonly been used (e.g., 50 to 100 years) in population viability analyses (Beissinger and Westphal 1998; Ralls et al. 2002). Twenty years is roughly the period associated with most land management planning, climatically forced environmental cycles that can influence hydrologic and thermal regimes, and significant changes in habitat associated with both restoration and degradation.

Our analyses with the Dennis et al. model indicated that the probabilities of persistence were strongly influenced by our assumptions of initial population size, population growth rate and variance in that growth rate (Figs. S1-4, S1-5 and S1-6). In general, the expected persistence of WCT declined dramatically as initial populations fell below about 1000 individuals (Figs. S1-4, S1-5 and S1-6). Population growth rate had the most dramatic influence on small- or intermediate-sized populations, and was less important among larger populations unless the growth rate was very low. Because the period over which persistence was evaluated was relatively short (e.g., 3 to 4 generations), larger populations had moderate or even higher probabilities of persistence with even negative growth rates as long as the variance in growth rate was relatively low. Our assumption that smaller populations have higher variance in their population growth rate is conservative when evaluating extinction, but we observed that small populations (500 or fewer individuals) experiencing strong population decline (e.g., $\lambda \leq 0.9$) were relatively insensitive to this assumption (Figs. S1-5 and S1-6). We used these results (i.e., Figs. S1-4 and S1-6) to directly estimate conditional probabilities for *persistence* associated with isolated populations represented by the midpoints of the classes in the parental nodes for *effective network size* and *population growth rate* (Table S1-11).

For conditions where *colonization and rescue* was possible we assumed that dispersal could maintain or recolonize populations that might otherwise be doomed to extinction through deterministic or stochastic processes (e.g., Ayllon et al. 2006). If *colonization and rescue* was strong we assumed that demographic support was virtually guaranteed and that populations not in severe population decline would essentially share the combined probability of simultaneous extinction of two independent populations (Table S1-11). We assumed that the benefits of weak connectivity or for populations in severe demographic decline would be less, and interpolated between the values for isolated and strongly connected conditions.

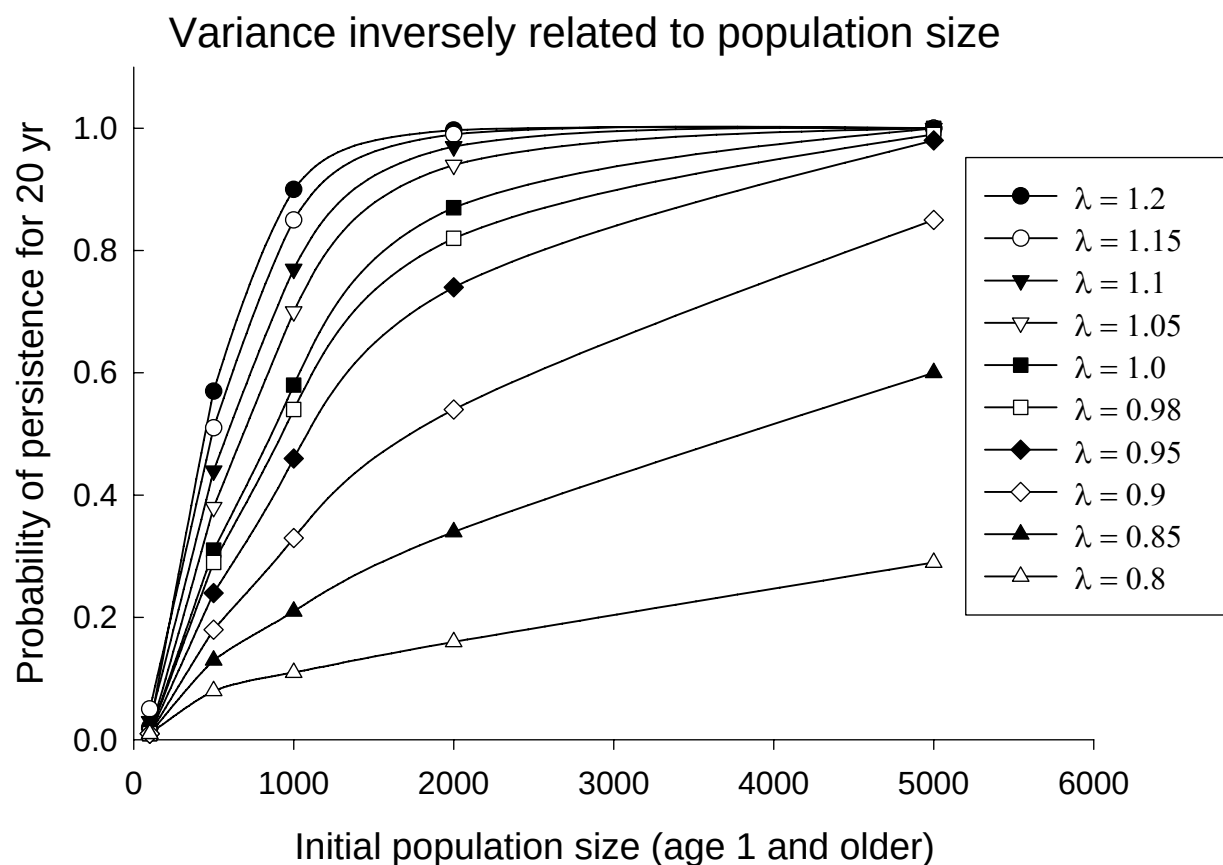


Fig. S1-4. Estimated probabilities of persistence for 20 years relative to initial population size and population growth rate (λ) assuming the variance in growth rate is inversely related to the initial population size, and using the model of Dennis et al. (1991). Population growth (λ) ranged from 0.8 to 1.15, and was transformed to the equivalent instantaneous rate for analysis. The variance in instantaneous growth rate was varied from 0.10 to 0.80 as initial population size decreased from 5000 (variance = 0.10) to 2000 (variance = 0.2) to 1000 (variance = 0.40) and to 500 or 100 (variance = 0.8). Results were used to develop the conditional probabilities (CPT) for *persistence* with the *InvAD* BBN (see Table S1-11).

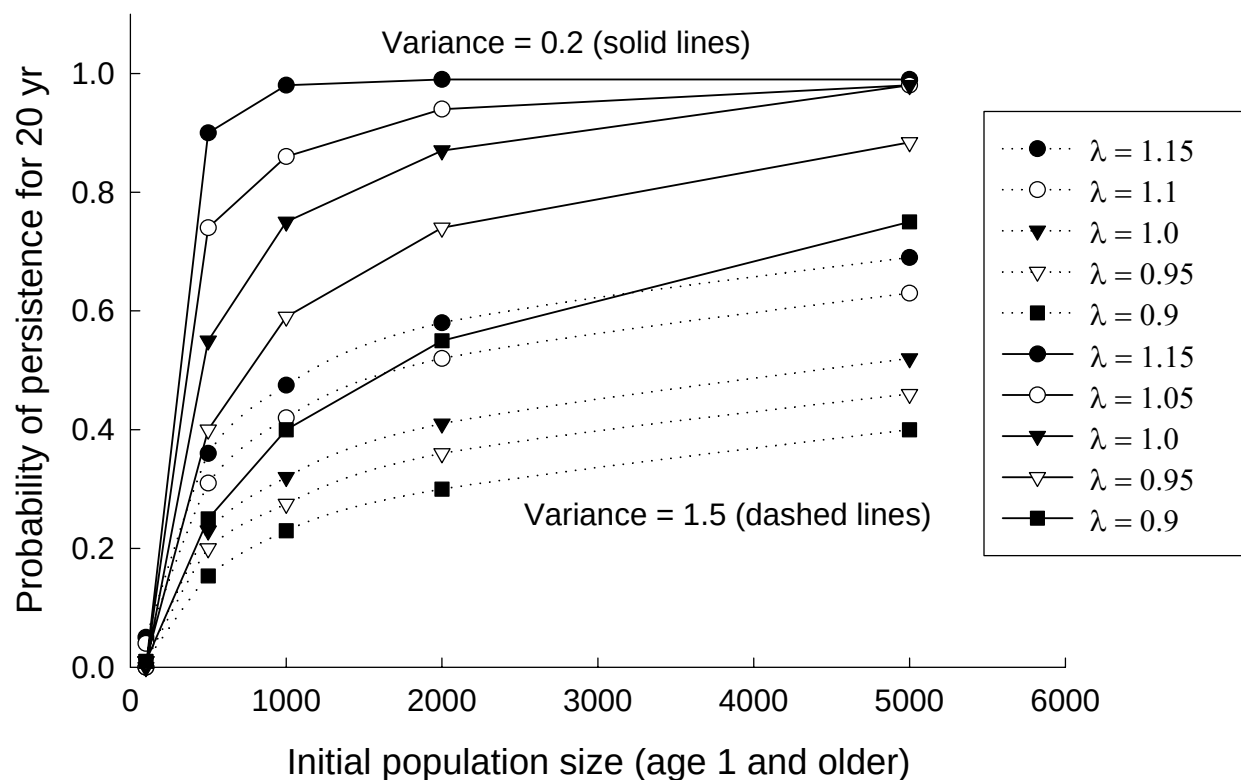


Fig. S1-5. Estimated probabilities of persistence for 20 years relative to initial population size, population growth rate (λ), and variance in growth rate, and using the model of Dennis et al. (1991). Finite population growth (λ) ranged from 0.9 to 1.15, and was transformed to the equivalent instantaneous rate for analysis. The variance in instantaneous growth rates was either 0.20 (solid lines) or 1.5 (dashed lines). Results show that persistence declines sharply below a population size of 1000 and with a higher variance in population growth rate.

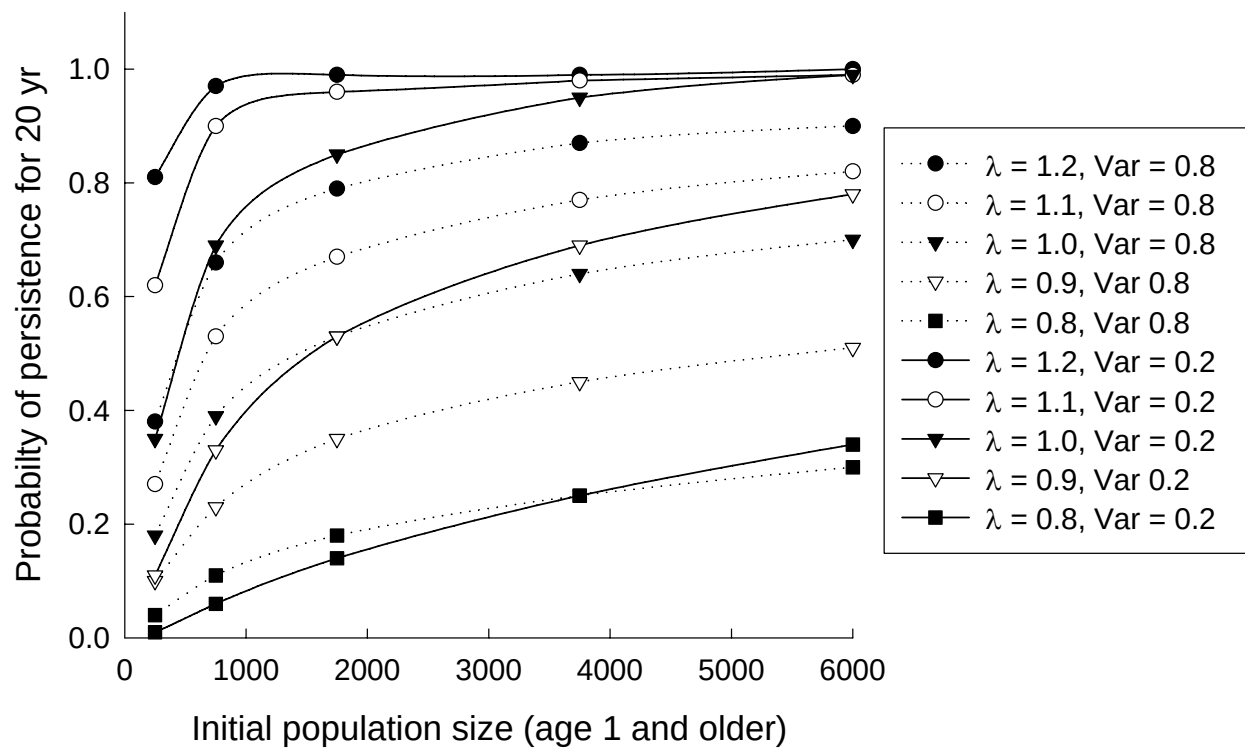


Fig. S1-6. Estimated probabilities of persistence for 20 years relative to population growth rate (λ) and initial population size assuming the variance (var) in growth rate is constant at low or high values, and using the model of Dennis et al. (1991). Finite population growth (λ) ranged from 0.8 to 1.2, and was transformed to the equivalent instantaneous rate for analysis. The variance in instantaneous growth rate was held constant at either low (var = 0.2, solid lines) or high (var = 0.8, dashed lines) values. These estimates of persistence were used to explore the implications of the fundamental uncertainty in the magnitude of the variance in relation to population growth rate. Results were used to develop the conditional probabilities (CPT) for *persistence* in two alternate BBNs (Table S1-11) that were used to evaluate the relative performance of the *InvAD* BBN (see Supplemental Appendix S2⁴).

Opinion-based approach to define conditional probabilities for *persistence*.

In parallel to the approach using the Dennis et al. model, four authors (BER, JBD, MKY, and DPP) also estimated the probability of *persistence* for WCT based on their interpretation of how the three contributing nodes (*effective network size*, *population growth rate*, and *colonization and rescue*) influence a local population in a stream network. The probabilities under the assumption of small (or low) and large (or high) *effective network size* and *population growth rate* were interpolated between values for very small (or very low) and moderate, and moderate and very large (or very high) estimates, respectively, for each of those nodes. Probabilities were averaged across authors to produce an alternate conditional probability table for *persistence* based entirely on expert opinion (Table S1-11).

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Table S1-1. Conditional probability table (CPT) for *potential spawning and rearing habitat* for westslope cutthroat trout.

<i>Potential spawning and rearing habitat</i>			Probability (%) of a given state for spawning and rearing habitat		
Contributing (parent) nodes					
Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
< 7	<2	<3	100	0	0
< 7	<2	3-10	100	0	0
< 7	<2	>10	100	0	0
< 7	2-8	<3	100	0	0
< 7	2-8	3-10	100	0	0
< 7	2-8	>10	100	0	0
< 7	>8	<3	100	0	0
< 7	>8	3-10	100	0	0
< 7	>8	>10	100	0	0
7-10	<2	<3	66	34	0
7-10	<2	3-10	66	34	0
7-10	<2	>10	100	0	0
7-10	2-8	<3	34	66	0
7-10	2-8	3-10	66	34	0
7-10	2-8	>10	100	0	0
7-10	>8	<3	66	34	0
7-10	>8	3-10	100	0	0
7-10	>8	>10	100	0	0
10-15	<2	<3	0	34	66
10-15	<2	3-10	34	66	0
10-15	<2	>10	100	0	0

<i>Potential spawning and rearing habitat</i>					
Contributing (parent) nodes			Probability (%) of a given state for spawning and rearing habitat		
Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
10-15	2-8	<3	0	0	100
10-15	2-8	3-10	33	34	33
10-15	2-8	>10	66	34	0
10-15	>8	<3	33	34	33
10-15	>8	3-10	66	34	0
10-15	>8	>10	100	0	0
15-18	<2	<3	66	34	0
15-18	<2	3-10	66	34	0
15-18	<2	>10	100	0	0
15-18	2-8	<3	34	66	0
15-18	2-8	3-10	66	34	0
15-18	2-8	>10	100	0	0
15-18	>8	<3	66	34	0
15-18	>8	3-10	100	0	0
15-18	>8	>10	100	0	0
>18	<2	<3	100	0	0
>18	<2	3-10	100	0	0
>18	<2	>10	100	0	0
>18	2-8	<3	100	0	0
>18	2-8	3-10	100	0	0
>18	2-8	>10	100	0	0
>18	>8	<3	100	0	0
>18	>8	3-10	100	0	0
>18	>8	>10	100	0	0

Note: The CPT for *potential spawning and rearing habitat* is based on the consensus opinion of two authors (DPP and BER).

Table S1-2. Conditional probability table (CPT) for *potential brook trout (BKT) spawning and rearing habitat*.

<i>Potential brook trout (BKT) spawning and rearing habitat</i>						
Contributing (parent) node				Probability (%) of a given state for BKT spawning and rearing habitat		
Hydrologic regime ^a	Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
Snowmelt	< 7	<2	<3	100	0	0
Snowmelt	< 7	<2	3-10	100	0	0
Snowmelt	< 7	<2	>10	100	0	0
Snowmelt	< 7	2-8	<3	100	0	0
Snowmelt	< 7	2-8	3-10	100	0	0
Snowmelt	< 7	2-8	>10	100	0	0
Snowmelt	< 7	>8	<3	100	0	0
Snowmelt	< 7	>8	3-10	100	0	0
Snowmelt	< 7	>8	>10	100	0	0
Snowmelt	7-10	<2	<3	34	66	0
Snowmelt	7-10	<2	3-10	0	100	0
Snowmelt	7-10	<2	>10	34	66	0
Snowmelt	7-10	2-8	<3	66	34	0
Snowmelt	7-10	2-8	3-10	34	66	0
Snowmelt	7-10	2-8	>10	66	34	0
Snowmelt	7-10	>8	<3	100	0	0
Snowmelt	7-10	>8	3-10	100	0	0
Snowmelt	7-10	>8	>10	100	0	0
Snowmelt	10-15	<2	<3	0	34	66
Snowmelt	10-15	<2	3-10	0	0	100

Potential brook trout (BKT) spawning and rearing habitat

Contributing (parent) node				Probability (%) of a given state for BKT spawning and rearing habitat		
Hydrologic regime ^a	Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
Snowmelt	10-15	<2	>10	0	34	66
Snowmelt	10-15	2-8	<3	34	66	0
Snowmelt	10-15	2-8	3-10	0	34	66
Snowmelt	10-15	2-8	>10	34	66	0
Snowmelt	10-15	>8	<3	100	0	0
Snowmelt	10-15	>8	3-10	100	0	0
Snowmelt	10-15	>8	>10	100	0	0
Snowmelt	15-18	<2	<3	0	100	0
Snowmelt	15-18	<2	3-10	0	66	34
Snowmelt	15-18	<2	>10	0	100	0
Snowmelt	15-18	2-8	<3	66	34	0
Snowmelt	15-18	2-8	3-10	0	100	0
Snowmelt	15-18	2-8	>10	66	34	0
Snowmelt	15-18	>8	<3	100	0	0
Snowmelt	15-18	>8	3-10	100	0	0
Snowmelt	15-18	>8	>10	100	0	0
Snowmelt	>18	<2	<3	66	34	0
Snowmelt	>18	<2	3-10	66	34	0
Snowmelt	>18	<2	>10	100	0	0
Snowmelt	>18	2-8	<3	100	0	0
Snowmelt	>18	2-8	3-10	100	0	0
Snowmelt	>18	2-8	>10	100	0	0
Snowmelt	>18	>8	<3	100	0	0

Potential brook trout (BKT) spawning and rearing habitat

Contributing (parent) node				Probability (%) of a given state for BKT spawning and rearing habitat		
Hydrologic regime ^a	Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
Snowmelt	>18	>8	3-10	100	0	0
Snowmelt	>18	>8	>10	100	0	0
Mixed	< 7	<2	<3	100	0	0
Mixed	< 7	<2	3-10	100	0	0
Mixed	< 7	<2	>10	100	0	0
Mixed	< 7	2-8	<3	100	0	0
Mixed	< 7	2-8	3-10	100	0	0
Mixed	< 7	2-8	>10	100	0	0
Mixed	< 7	>8	<3	100	0	0
Mixed	< 7	>8	3-10	100	0	0
Mixed	< 7	>8	>10	100	0	0
Mixed	7-10	<2	<3	100	0	0
Mixed	7-10	<2	3-10	100	0	0
Mixed	7-10	<2	>10	100	0	0
Mixed	7-10	2-8	<3	100	0	0
Mixed	7-10	2-8	3-10	100	0	0
Mixed	7-10	2-8	>10	100	0	0
Mixed	7-10	>8	<3	100	0	0
Mixed	7-10	>8	3-10	100	0	0
Mixed	7-10	>8	>10	100	0	0
Mixed	10-15	<2	<3	34	66	0
Mixed	10-15	<2	3-10	0	100	0
Mixed	10-15	<2	>10	100	0	0

Potential brook trout (BKT) spawning and rearing habitat

Contributing (parent) node				Probability (%) of a given state for BKT spawning and rearing habitat		
Hydrologic regime ^a	Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
Mixed	10-15	2-8	<3	100	0	0
Mixed	10-15	2-8	3-10	66	34	0
Mixed	10-15	2-8	>10	100	0	0
Mixed	10-15	>8	<3	100	0	0
Mixed	10-15	>8	3-10	100	0	0
Mixed	10-15	>8	>10	100	0	0
Mixed	15-18	<2	<3	100	0	0
Mixed	15-18	<2	3-10	100	0	0
Mixed	15-18	<2	>10	100	0	0
Mixed	15-18	2-8	<3	100	0	0
Mixed	15-18	2-8	3-10	100	0	0
Mixed	15-18	2-8	>10	100	0	0
Mixed	15-18	>8	<3	100	0	0
Mixed	15-18	>8	3-10	100	0	0
Mixed	15-18	>8	>10	100	0	0
Mixed	>18	<2	<3	100	0	0
Mixed	>18	<2	3-10	100	0	0
Mixed	>18	<2	>10	100	0	0
Mixed	>18	2-8	<3	100	0	0
Mixed	>18	2-8	3-10	100	0	0
Mixed	>18	2-8	>10	100	0	0
Mixed	>18	>8	<3	100	0	0
Mixed	>18	>8	3-10	100	0	0

Potential brook trout (BKT) spawning and rearing habitat

Contributing (parent) node				Probability (%) of a given state for BKT spawning and rearing habitat		
Hydrologic regime ^a	Temperature (°C)	Gradient (%)	Stream width (m)	Low (Poor)	Moderate (Suitable)	High (Optimal)
Mixed	>18	>8	>10	100	0	0

^a Mixed = *hydrologic regime* is mixed rain-on-snow and snowmelt

Note: The CPT for *potential BKT spawning and rearing habitat* is based on the consensus opinion of two authors (DPP and BER).

Table S1-3. Conditional probability table (CPT) for brook trout *invasion strength*.

<i>Invasion strength</i>		Probability (%) of a given state for		
Contributing (parent) nodes		invasion strength		
BKT connectivity	Invasion barrier	Strong	Moderate	None
Strong	Yes	0	0	100
Strong	No	100	0	0
Moderate	Yes	0	0	100
Moderate	No	0	100	0
None	Yes	0	0	100
None	No	0	0	100

Note: The CPT probabilities for *invasion strength* are a deterministic combination based on whether or not brook trout are expected to immigrate (*BKT connectivity*), and whether or not a physical migration barrier (*invasion barrier*) is present or planned. *Invasion barriers* are assumed to be 100% effective.

Table S1-4. Conditional probability table (CPT) for *brook trout (BKT) population status*.

<i>Brook trout (BKT) population status</i>			Probability (%) of a given state for BKT population status		
Contributing (parent) nodes					
BKT invasion strength	Potential BKT spawning and rearing habitat	Habitat degradation	Absent	Weak	Strong
Strong	Low	Degraded	35	45	20
Strong	Low	Minimally altered	20	45	35
Strong	Moderate	Degraded	10	60	30
Strong	Moderate	Minimally altered	0	35	65
Strong	High	Degraded	0	30	70
Strong	High	Minimally altered	0	0	100
Moderate	Low	Degraded	75	20	5
Moderate	Low	Minimally altered	40	45	15
Moderate	Moderate	Degraded	35	50	15
Moderate	Moderate	Minimally altered	10	40	50
Moderate	High	Degraded	10	45	45
Moderate	High	Minimally altered	5	20	75
None	Low	Degraded	100	0	0
None	Low	Minimally altered	100	0	0
None	Moderate	Degraded	100	0	0
None	Moderate	Minimally altered	100	0	0
None	High	Degraded	100	0	0
None	High	Minimally altered	100	0	0

Note: The CPT for *BKT population status* is based on opinion where the estimates of the five authors were averaged.

Table S1-5. Conditional probability table (CPT) for *egg to age-1 survival* of westslope cutthroat trout.

<i>Egg to age-1 survival</i>			Probability (%) of a given state for egg to age-1 survival		
Contributing (parent) nodes					
BKT population status	Potential spawning and rearing habitat	Habitat degradation	Low	Moderate	High
Strong	Low	Degraded	100	0	0
Strong	Low	Minimally altered	100	0	0
Strong	Moderate	Degraded	100	0	0
Strong	Moderate	Minimally altered	90	10	0
Strong	High	Degraded	95	5	0
Strong	High	Minimally altered	75	25	0
Weak	Low	Degraded	85	15	0
Weak	Low	Minimally altered	75	25	0
Weak	Moderate	Degraded	65	35	0
Weak	Moderate	Minimally altered	50	50	0
Weak	High	Degraded	45	45	10
Weak	High	Minimally altered	20	55	25
Absent	Low	Degraded	75	25	0
Absent	Low	Minimally altered	45	50	5
Absent	Moderate	Degraded	15	60	25
Absent	Moderate	Minimally altered	0	50	50
Absent	High	Degraded	5	40	55
Absent	High	Minimally altered	0	0	100

Note: The CPT for *egg to age-1 survival* is based on opinion where the estimates of the five authors were averaged.

Table S1-6. Conditional probability table (CPT) for *juvenile survival* of westslope cutthroat trout.

<i>Juvenile survival</i>			Probability (%) of a given state for juvenile survival		
Contributing (parent) nodes					
BKT population status	Potential spawning and rearing habitat	Habitat degradation	Low	Moderate	High
Strong	Low	Degraded	100	0	0
Strong	Low	Minimally altered	75	25	0
Strong	Moderate	Degraded	75	25	0
Strong	Moderate	Minimally altered	37.5	62.5	0
Strong	High	Degraded	62.5	37.5	0
Strong	High	Minimally altered	25	50	25
Weak	Low	Degraded	100	0	0
Weak	Low	Minimally altered	50	50	0
Weak	Moderate	Degraded	50	50	0
Weak	Moderate	Minimally altered	0	87.5	12.5
Weak	High	Degraded	25	62.5	12.5
Weak	High	Minimally altered	0	37.5	62.5
Absent	Low	Degraded	75	25	0
Absent	Low	Minimally altered	25	75	0
Absent	Moderate	Degraded	25	62.5	12.5
Absent	Moderate	Minimally altered	0	50	50
Absent	High	Degraded	12.5	50	37.5
Absent	High	Minimally altered	0	0	100

Note: The CPT for *juvenile survival* (i.e., survival from age-1 to age-2) is based on opinion where the estimates of two authors (DPP and BER) were averaged.

Table S1-7. Conditional probability (CPT) table for *subadult-adult survival* of westslope cutthroat trout.

<i>Subadult-adult survival</i>			Probability (%) of a given state for subadult-adult survival		
Contributing (parent) nodes					
Fishing exploitation	Habitat degradation	Invasion barrier	Low	Moderate	High
High	Degraded	Yes	100	0	0
High	Degraded	No	50	50	0
High	Minimally altered	Yes	50	50	0
High	Minimally altered	No	37.5	50	12.5
Low	Degraded	Yes	25	75	0
Low	Degraded	No	12.5	37.5	50
Low	Minimally altered	Yes	0	10	90
Low	Minimally altered	No	0	0	100

Note: The CPT for *subadult-adult survival* (i.e., survival of individuals age-2 and older) is based on opinion where the estimates of two authors (DPP and BER) were averaged.

Table S1-8. Conditional probability table (CPT) for *effective life history* of westslope cutthroat trout.

<i>Effective life history</i>		Probability (%) of a given state for	
Contributing (parent) nodes		effective life history	
Potential life history	Invasion barrier	Resident	Migratory
Resident	Yes	100	0
Resident	No	100	0
Migratory	Yes	100	0
Migratory	No	0	100

Note: The CPT probabilities for *effective life history* are a deterministic combination based on the expectation of a local westslope cutthroat trout population expressing a resident or migratory life history (*potential life history*), and whether a migration barrier (*invasion barrier*) would preclude actual expression of a migratory life history.

Table S1-9. Conditional probability tables (CPTs) for *population growth rate* of westslope cutthroat trout based on (a) the frequency distribution of output from a matrix population model (demographic model), and (b) expert opinion (opinion).

<i>Population growth rate</i>									
Contributing (parent) nodes ^a				Probability (%) of a given state for population growth rate					
Eff.				(a) Demographic model				(b) Opinion	
	Egg to age-1 surv	Juv surv	Subadult surv						
				Very low	Low	Mod	High	Very high	Very high
Res	Low	Low	Low	100	0	0	0	0	0
Res	Low	Low	Mod	99.9	0.1	0	0	75	25
Res	Low	Low	High	86.5	13.1	0.4	0	50	37.5
Res	Low	Mod	Low	100	0	0	0	68.75	31.25
Res	Low	Mod	Mod	96.3	3.7	0	0	50	37.5
Res	Low	Mod	High	64.5	30	5.5	0	25	43.75
Res	Low	High	Low	100	0	0	0	50	37.5
Res	Low	High	Mod	87.32	12.36	0.32	0	25	50
Res	Low	High	High	46.5	36.19	16.16	1.15	0	50
Res	Mod	Low	Low	99.9	0.1	0	0	50	50
Res	Mod	Low	Mod	80.1	18.8	1.1	0	37.5	37.5
Res	Mod	Low	High	25.3	46.3	25.7	2.7	25	31.25
Res	Mod	Mod	Low	95.9	4.1	0	0	31.25	43.75

Population growth rate

Contributing (parent) nodes ^a				Probability (%) of a given state for population growth rate										
Eff	life history	Egg to age-1 surv	Juv surv	Subad- adult surv	(a) Demographic model					(b) Opinion				
					Very low	Low	Mod	High	Very high	Very low	Low	Mod	High	Very high
Res	Mod	Mod	Mod	Mod	48	40.5	11.1	0.4	0	9.375	46.875	43.75	0	0
Res	Mod	Mod	Mod	High	6.8	31.5	41	19.4	1.3	0	28.125	68.75	3.125	0
Res	Mod	High	High	Low	85.1	14.4	0.5	0	0	12.5	37.5	50	0	0
Res	Mod	High	High	Mod	27	42.2	26.4	4.4	0	0	37.5	43.75	18.75	0
Res	Mod	High	High	High	1.4	17	37.2	34.2	10.2	0	6.25	56.25	37.5	0
Res	High	Low	Low	Low	93.7	6.3	0	0	0	25	50	25	0	0
Res	High	Low	Low	Mod	38.65	44.22	16.47	0.66	0	0	50	50	0	0
Res	High	Low	Low	High	3.8	26.9	41.8	24.5	3	0	25	75	0	0
Res	High	Mod	Mod	Low	69.4	27	3.6	0	0	0	50	43.75	6.25	0
Res	High	Mod	Mod	Mod	12.48	36.38	38.9	11.96	0.28	0	25	43.75	31.25	0
Res	High	Mod	Mod	High	0	7.7	29.1	39.2	24	0	0	62.5	31.25	6.25
Res	High	High	High	Low	44.2	39.7	15.5	0.6	0	0	12.5	62.5	25	0
Res	High	High	High	Mod	3.57	23.16	38.34	29.1	5.83	0	12.5	25	50	12.5
Res	High	High	High	High	0	1.1	14.9	31.9	52.1	0	0	25	37.5	37.5
Migr	Low	Low	Low	Low	93.23	6.52	0.25	0	0	37.5	37.5	25	0	0
Migr	Low	Low	Low	Mod	56.2	29.3	12.8	1.7	0	12.5	62.5	25	0	0

Population growth rate													
Contributing (parent) nodes ^a				Probability (%) of a given state for population growth rate									
Eff. life history	Egg to age-1 surv	Juv surv	Subad- adult surv	(a) Demographic model					(b) Opinion				
				Very low	Low	Mod	High	Very high	Very low	Low	Mod	High	Very high
Migr	High	Low	Low	10.03	27.42	34.27	22.4	5.88	0	25	62.5	12.5	0
Migr	High	Low	Mod	0	3.9	16.8	28.4	50.9	0	0	62.5	37.5	0
Migr	High	Low	High	0	0	1.33	11.14	87.53	0	0	50	37.5	12.5
Migr	High	Mod	Low	1.53	11.32	25.36	31.99	29.8	0	6.25	56.25	31.25	6.25
Migr	High	Mod	Mod	0	0.08	4.05	15.2	80.67	0	0	31.25	50	18.75
Migr	High	Mod	High	0	0	0	1.2	98.8	0	0	12.5	50	37.5
Migr	High	High	Low	0	3.7	15.8	25.1	55.4	0	0	37.5	37.5	25
Migr	High	High	Mod	0	0	0.4	7.2	92.4	0	0	12.5	37.5	50
Migr	High	High	High	0	0	0	0	100	0	0	0	12.5	87.5

^a Abbreviations: Mod = moderate, Eff life history = *effective life history*, Egg to age-1 surv = *egg to age-1 survival*, Juv surv = *juvenile survival*, and Subad-adult surv = *subadult-adult survival*.

Note: The CPT for *population growth rate* based on (a) the demographic model (by DPP), and (b) opinion was based on the mean estimates of two authors (DPP and BER).

Table S1-10. Conditional probability table (CPT) for *colonization and rescue* of westslope cutthroat trout.

<i>Colonization and rescue</i>		Probability (%) for a given state of colonization and rescue		
Contributing (parent) nodes				
Connectivity	Invasion barrier	None	Moderate	Strong
None	Yes	100	0	0
None	No	100	0	0
Moderate	Yes	100	0	0
Moderate	No	0	100	0
Strong	Yes	100	0	0
Strong	No	0	0	100

Note: The CPT probabilities for *colonization and rescue* are a deterministic combination based on whether or not cutthroat trout from other populations are expected to provide demographic support to the local population of interest (*connectivity*), and whether or not a physical migration barrier (*invasion barrier*) is present or planned. An *invasion barrier* is assumed to be 100% effective at stopping such demographic support.

Table S1-11. Conditional probability tables (CPTs) for 20-year *persistence* of westslope cutthroat trout based on either output from the analytical model of Dennis et al. (1991) where the variance in population growth rate was (a) inversely related to population size (used for the *InvAD* BNN), (b) a constant value of 0.2 ($\text{Var}=0.2$), (c) a constant value of 0.8 ($\text{Var}=0.8$); or (d) where probabilities for a given state were based entirely on expert opinion (Opinion).

<i>Persistence</i>		Probability (%) for a given state of persistence ^b											
Contributing (parent) nodes		(a) InvAD				(b) Var=0.2				(c) Var=0.8			
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization		(a) InvAD		(b) Var=0.2		(c) Var=0.8		(d) Opinion			
		and rescue		Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
< 3 km or <500 age-1+	<0.85	None		95	5	99	1	96	4	100	0		
< 3 km or <500 age-1+	<0.85	Moderate		92.5	7.5	98.5	1.5	94.1	5.9	81.3	18.8		
< 3 km or <500 age-1+	<0.85	Strong		90	10	98	2	92.2	7.8	56.3	43.8		
< 3 km or <500 age-1+	0.85-0.95	None		92	8	89	11	90	10	84.4	15.6		
< 3 km or <500 age-1+	0.85-0.95	Moderate		88.5	11.5	84.1	15.9	85.5	14.5	68.8	31.3		
< 3 km or <500 age-1+	0.85-0.95	Strong		85	15	79.2	20.8	81	19	40.6	59.4		
< 3 km or <500 age-1+	0.95-1.05	None		87	13	65	35	82	18	68.8	31.3		
< 3 km or <500 age-1+	0.95-1.05	Moderate		81.5	18.5	53.6	46.4	74.6	25.4	56.3	43.8		
< 3 km or <500 age-1+	0.95-1.05	Strong		76	24	42.3	57.8	67.2	32.8	25	75		

Persistence		Probability (%) for a given state of persistence ^b									
Contributing (parent) nodes		(a) InvAD		(b) Var=0.2		(c) Var=0.8		(d) Opinion			
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization and rescue		Abs	Pres	Abs	Pres	Abs	Pres		
< 3 km or <500 age-1+	1.05-1.15	None		82	18	38	62	73	27	62.5	37.5
< 3 km or <500 age-1+	1.05-1.15	Moderate		74.5	25.5	26.2	73.8	63.1	36.9	46.9	53.1
< 3 km or <500 age-1+	1.05-1.15	Strong		67	33	14.4	85.6	53.3	46.7	15.6	84.4
< 3 km or <500 age-1+	>1.15	None		72	28	19	81	62	38	56.3	43.8
< 3 km or <500 age-1+	>1.15	Moderate		62	38	11.3	88.7	50.2	49.8	37.5	62.5
< 3 km or <500 age-1+	>1.15	Strong		52	48	3.6	96.4	38.4	61.6	6.3	93.8
3-5 km or 500-1000 age-1+	<0.85	None		90	10	94	6	89	11	96.9	3.1
3-5 km or 500-1000 age-1+	<0.85	Moderate		85.5	14.5	91.2	8.8	84.1	15.9	78.1	21.9
3-5 km or 500-1000 age-1+	<0.85	Strong		81	19	88.4	11.6	79.2	20.8	50	50
3-5 km or 500-1000 age-1+	0.85-0.95	None		70	30	67	33	77	23	78.1	21.9
3-5 km or 500-1000 age-1+	0.85-0.95	Moderate		59.5	40.5	55.9	44.1	68.1	31.9	60.9	39.1
3-5 km or 500-1000 age-1+	0.85-0.95	Strong		49	51	44.9	55.1	59.3	40.7	35.9	64.1
3-5 km or 500-1000 age-1+	0.95-1.05	None		50	50	31	69	61	39	59.4	40.6
3-5 km or 500-1000 age-1+	0.95-1.05	Moderate		37.5	62.5	20.3	79.7	49.1	50.9	43.8	56.3
3-5 km or 500-1000 age-1+	0.95-1.05	Strong		25	75	9.6	90.4	37.2	62.8	21.9	78.1

<i>Persistence</i>		Probability (%) for a given state of persistence ^b											
Contributing (parent) nodes		(a) InvAD				(b) Var=0.2				(c) Var=0.8			
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization		(a) InvAD		(b) Var=0.2		(c) Var=0.8		(d) Opinion			
		and rescue		Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
3-5 km or 500-1000 age-1+	1.05-1.15	None		29	71	10	90	47	53	53.1	46.9		
3-5 km or 500-1000 age-1+	1.05-1.15	Moderate		18.5	81.5	5.5	94.5	34.5	65.5	35.9	64.1		
3-5 km or 500-1000 age-1+	1.05-1.15	Strong		8	92	1	99	22.1	77.9	12.5	87.5		
3-5 km or 500-1000 age-1+	>1.15	None		15	85	3	97	34	66	46.9	53.1		
3-5 km or 500-1000 age-1+	>1.15	Moderate		8.5	91.5	1.5	98.5	22.8	77.2	28.1	71.9		
3-5 km or 500-1000 age-1+	>1.15	Strong		2	98	0.1	99.9	11.6	88.4	3.1	96.9		
5-7 km or 1000-2500 age-1+	<0.85	None		83	17	86	14	82	18	93.8	6.3		
5-7 km or 1000-2500 age-1+	<0.85	Moderate		76	24	80	20	74.6	25.4	75	25		
5-7 km or 1000-2500 age-1+	<0.85	Strong		69	31	74	26	67.2	32.8	43.8	56.3		
5-7 km or 1000-2500 age-1+	0.85-0.95	None		48	52	47	53	65	35	71.9	28.1		
5-7 km or 1000-2500 age-1+	0.85-0.95	Moderate		35.5	64.5	34.5	65.5	53.6	46.4	53.1	46.9		
5-7 km or 1000-2500 age-1+	0.85-0.95	Strong		23	77	22.1	77.9	42.3	57.8	31.3	68.8		
5-7 km or 1000-2500 age-1+	0.95-1.05	None		15	85	15	85	47	53	50	50		
5-7 km or 1000-2500 age-1+	0.95-1.05	Moderate		8.5	91.5	8.6	91.4	34.5	65.5	31.3	68.8		
5-7 km or 1000-2500 age-1+	0.95-1.05	Strong		2	98	2.3	97.8	22.1	77.9	18.8	81.3		

Persistence		Probability (%) for a given state of persistence ^b													
Contributing (parent) nodes		(a) InvAD				(b) Var=0.2				(c) Var=0.8				(d) Opinion	
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization and rescue		Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres		
5-7 km or 1000-2500 age-1+	1.05-1.15	None		4	96	4	96	33	67	43.8	56.3				
5-7 km or 1000-2500 age-1+	1.05-1.15	Moderate		2	98	2.1	97.9	21.9	78.1	25	75				
5-7 km or 1000-2500 age-1+	1.05-1.15	Strong		0	100	0.2	99.8	10.9	89.1	9.4	90.6				
5-7 km or 1000-2500 age-1+	>1.15	None		2	98	1	99	21	79	37.5	62.5				
5-7 km or 1000-2500 age-1+	>1.15	Moderate		1	99	0.5	99.5	12.7	87.3	18.8	81.3				
5-7 km or 1000-2500 age-1+	>1.15	Strong		0	100	0	100	4.4	95.6	0	100				
7-10 km or 2500-5000 age-1+	<0.85	None		77	23	75	25	75	25	75	25				
7-10 km or 2500-5000 age-1+	<0.85	Moderate		68	32	65.6	34.4	65.6	34.4	65.6	34.4				
7-10 km or 2500-5000 age-1+	<0.85	Strong		59	41	56.3	43.8	56.3	43.8	34.4	65.6				
7-10 km or 2500-5000 age-1+	0.85-0.95	None		26	74	31	69	55	45	59.4	40.6				
7-10 km or 2500-5000 age-1+	0.85-0.95	Moderate		16.5	83.5	20.3	79.7	42.6	57.4	46.9	53.1				
7-10 km or 2500-5000 age-1+	0.85-0.95	Strong		7	93	9.6	90.4	30.3	69.8	21.9	78.1				
7-10 km or 2500-5000 age-1+	0.95-1.05	None		5	95	5	95	36	64	43.8	56.3				
7-10 km or 2500-5000 age-1+	0.95-1.05	Moderate		2.5	97.5	2.6	97.4	24.5	75.5	28.1	71.9				
7-10 km or 2500-5000 age-1+	0.95-1.05	Strong		0	100	0.3	99.8	13	87	9.4	90.6				

<i>Persistence</i>		Probability (%) for a given state of persistence ^b											
Contributing (parent) nodes		(a) InvAD				(b) Var=0.2				(c) Var=0.8			
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization and rescue		Abs		Pres		Abs		Pres		Abs	
7-10 km or 2500-5000 age-1+	1.05-1.15	None		1	99	2	98	23	77	35.9	64.1		
7-10 km or 2500-5000 age-1+	1.05-1.15	Moderate		0.5	99.5	1	99	14.1	85.9	20.3	79.7		
7-10 km or 2500-5000 age-1+	1.05-1.15	Strong		0	100	0	100	5.3	94.7	4.7	95.3		
7-10 km or 2500-5000 age-1+	>1.15	None		1	99	1	99	13	87	28.1	71.9		
7-10 km or 2500-5000 age-1+	>1.15	Moderate		0.5	99.5	0.5	99.5	7.3	92.7	12.5	87.5		
7-10 km or 2500-5000 age-1+	>1.15	Strong		0	100	0	100	1.7	98.3	0	100		
>10 km or > 5000 age-1+	<0.85	None		70	30	66	34	70	30	56.3	43.8		
>10 km or > 5000 age-1+	<0.85	Moderate		59.5	40.5	54.8	45.2	59.5	40.5	56.3	43.8		
>10 km or > 5000 age-1+	<0.85	Strong		49	51	43.6	56.4	49	51	25	75		
>10 km or > 5000 age-1+	0.85-0.95	None		15	85	22	78	49	51	46.9	53.1		
>10 km or > 5000 age-1+	0.85-0.95	Moderate		8.5	91.5	13.4	86.6	36.5	63.5	40.6	59.4		
>10 km or > 5000 age-1+	0.85-0.95	Strong		2	98	4.8	95.2	24	76	12.5	87.5		
>10 km or > 5000 age-1+	0.95-1.05	None		1	99	1	99	30	70	37.5	62.5		
>10 km or > 5000 age-1+	0.95-1.05	Moderate		0.5	99.5	0.5	99.5	19.5	80.5	25	75		
>10 km or > 5000 age-1+	0.95-1.05	Strong		0	100	0	100	9	91	0	100		

<i>Persistence</i>		Probability (%) for a given state of persistence ^b															
Contributing (parent) nodes		(a) InvAD				(b) Var=0.2				(c) Var=0.8				(d) Opinion			
Effective network size (km or age-1 and older) ^a	Population growth rate (λ)	Colonization and rescue		Abs		Pres		Abs		Pres		Abs		Pres			
>10 km or > 5000 age-1+	1.05-1.15	None		1		99		1		99		18		28.1		71.9	
>10 km or > 5000 age-1+	1.05-1.15	Moderate		0.5		99.5		0.5		99.5		10.6		89.4		84.4	
>10 km or > 5000 age-1+	1.05-1.15	Strong		0		100		0		100		3.2		96.8		100	
>10 km or > 5000 age-1+	>1.15	None		0		100		0		100		10		90		81.3	
>10 km or > 5000 age-1+	>1.15	Moderate		0		100		0		100		5.5		94.5		93.8	
>10 km or > 5000 age-1+	>1.15	Strong		0		100		0		100		1		99		100	

SUPPLEMENTAL APPENDIX S2.

Comparison of alternative Bayesian belief networks to analyze assumptions about the variance in population growth rate for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and the consistency of predictions under the isolation and invasion analysis and decision Bayesian belief network (*InvAD* BBN)

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Introduction

The goal of the research reported in Peterson et al. (2008) was a tool to help biologists concerned with conservation of westslope cutthroat trout (WCT, *Oncorhynchus clarkii lewisi*) and to quantify trade-offs between the threats of isolation and invasion by nonnative brook trout. The result was the isolation and invasion analysis and decision (*InvAD*) Bayesian belief network (BBN, collectively *InvAD* BBN).

The *InvAD* BBN was based on two underlying population models used to characterize the growth and persistence of WCT – a stage-based matrix population model and the diffusion-approximation persistence model of Dennis et al. (1991) (see Peterson et al. 2008; see Supplemental Appendix S1⁴). The range of population growth rates and the range of variances in population growth rates were based on the synthesis of McIntyre and Rieman (1995). Given the underlying models, the *InvAD* BBN assumed that the variance in population growth rate for WCT was inversely related to population size, citing evidence of this relationship in populations of another wide-ranging salmonid species native to the region (e.g., Rieman and McIntyre 1993). The conditional probabilities in the link matrices (CPTs) for nodes representing *population growth rate* and *persistence* of WCT were estimated with the stage-based matrix and Dennis et al. models, respectively. Because little work has been done to quantify population growth rates or variances in WCT or any salmonid populations, our assumptions about the variance in those growth rates are uncertain. Conceivably, the variance in population growth rate for WCT may range widely among populations and may even be independent of population size. Differences in the characteristics of population growth and the underlying CPT had the potential to affect the BBN's predictions and resulting management guidance, so we constructed several alternate BBNs to examine the importance of our assumptions.

Methods

Concurrent with the development of *InvAD*, we developed three competing BBN's conceptually identical to *InvAD* (i.e., with the same box-and-arrow diagram as Figure 1 in Peterson et al. 2008) but different CPTs for one or two nodes. We compared the behavior of these alternative models to *InvAD* as summarized in Peterson et al. (2008). To contrast our basic

⁴ Additional supplementary information for Peterson et al. (2008) can be found in SUPPLEMENTAL APPENDIX S1, available on the Canadian Journal and Fisheries and Aquatic Sciences web site (cjfas.nrc.ca).

assumption that the variance in population growth rate is inversely related to population size, we built alternate BBNs where the CPT for *persistence* assumed that the variance in population growth rate was either independent of population size with a constant value of 0.2 (low constant variance) or 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 matrix and Dennis et al. models, we also developed a BBN where the CPT for *population growth rate* and *persistence* were based on opinion as informed by empirical data, professional experience, etc. (opinion only).

We conducted two analyses using *InvAD* and the three alternate models. First, we compared the overall agreement in the sensitivities of *population growth rate* and *persistence* to information at other nodes using Kendall's coefficient of concordance (Sokal and Rohlf 1981). Sensitivities were based on entropy reduction values appropriate for discrete or categorical variables (see Marcot et al. 2006). This concordance test indicates whether the relative influence of particular variables (nodes) differed among the alternative models. Second, we compared qualitative model behavior (i.e., general patterns in predictions) among alternatives using the hypothetical management scenario from Peterson et al (2008). Briefly, we generated a set of predictions for each alternative model using 48 different scenarios based on a range of initial environmental conditions typical of WCT streams in the northern Rocky Mountains (see Table 3 in Peterson et al. 2008). We subsequently examined whether the predictions and general patterns resulting from each model were generally consistent (i.e., would provide similar guidance to biologists).

Results and Discussion

We did not find strong differences in the predicted invasion-isolation trade-off among the four BBNs. Under uniform prior probabilities for all input nodes, the rank order in sensitivities of *persistence* (to other nodes) were highly concordant among the four models (Kendall's $W = 0.921$, $p < 0.001$, $n = 21$ variables, where $W = 1$ is perfect concordance; Table S2-1 and Table 4 of Peterson et al. 2008). Similarly, the sensitivity of *population growth rate* (to other nodes) was concordant between *InvAD* and the opinion only alternative ($W = 0.982$, $p = 0.012$, $n = 17$ variables). The low constant variance and high constant variance alternatives were not included in the comparison for the *population growth rate* node because they had identical CPTs.

Predictions generated with *InvAD* were generally consistent with trends and trade-offs observed with the other three alternatives (cf. Table S2-2 with Figure 3 in Peterson et al. 2008). That is, all four BBNs predicted that: probability of WCT persistence increased with increasing *effective network size*, an *invasion barrier* either increased (for resident, isolated population) or decreased (for migratory, connected population) the probability of persistence, and *habitat degradation* and *fishing exploitation* either moderated benefits or increased threats from intentional isolation. Nonetheless, relative differences in predictions among models indicated that alternatives could be either more or less optimistic about expected fate of WCT populations than the *InvAD* BBN in particular situations (cf. Table S2-2 with Figure 3 in Peterson et al. 2008).

The opinion only BBN made no explicit assumption about the variance in population growth rate and produced results qualitatively similar to the other three BBNs. Differences in the influence of certain variables were apparent, but again the general predictions and trade-offs identified by using the opinion only BBN were consistent with the other BBNs. The opinion only alternative was more optimistic about the fate of all smaller populations in the absence of an invasion barrier and about the benefits of an invasion barrier for small, resident populations. This alternative was slightly more pessimistic about the fate of isolating smaller, migratory populations connected to other WCT populations (cf. Table S2-2 with Fig. 3 in Peterson et al. 2008).

Predictions were generally consistent among models, but comparative differences could be attributed to the relative influence of a few key variables. In general, predictions from the opinion only BBN were more sensitive to the presence of and connection with other populations, whereas the other three models were more sensitive to the target population's inherent demographic characteristics. For the three BBNs (*InvAD*, low constant variance, and high constant variance) that had two of their CPTs directly based on output from analytical models, the probability of *persistence* was most sensitive to the state probabilities at the node for *population growth rate* (e.g., Table 4 in Peterson et al. 2008). In contrast, for the opinion only BBN *persistence* was most sensitive to probabilities at *colonization and rescue* (Table S2-1).

We concluded that basic results and potential application of our model (i.e., *InvAD* BBN) are not seriously constrained by our key assumptions regarding population growth rates. Clearly, more research is needed to refine the estimates for this process and our understanding of the

details in WCT population dynamics. As with any population viability model based on the approximations of complex population dynamics, our results cannot be viewed as estimates of the true probabilities of persistence; they can, however, provide a measure of relative differences in threats associated with isolation and brook trout invasion (Beissinger and Westphal 1998; Reed et al. 2002).

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Table S2-1. Sensitivity of *persistence* and *population growth rate* for westslope cutthroat trout (WCT) to all contributing nodes in four alternative BBNs (*InvAD*, low constant variance, high constant variance, and opinion only) based on the conceptual model presented in Figure 1 of Peterson et al. (2008). Survival and population growth rate nodes refer to WCT. Sensitivity values were calculated using a uniform prior probability distribution for each of the 11 input nodes. Nodes refer to common environmental conditions or westslope cutthroat trout unless otherwise noted.

Sensitivity (entropy reduction values) ^a					
Node ^c	Persistence ^b		Population growth rate		
	Low constant	High constant			
	variance	variance	Opinion	InvAD	Opinion
Population growth rate	0.27322	0.11268	0.07663	-	-
Effective network size	0.07173	0.0608	0.04662	-	-
Subadult-adult survival	0.07231	0.03148	0.01889	0.21536	0.13675
Effective life history	0.05816	0.03385	0.03089	0.13597	0.11113
Egg to age-1 survival	0.044	0.01686	0.00995	0.14783	0.23167
Invasion barrier	0.02986	0.02302	0.04053	0.04815	0.02675
Colonization and rescue	0.02583	0.02664	0.07866	-	-
Juvenile survival	0.02881	0.01123	0.00856	0.09396	0.18305

Sensitivity (entropy reduction values) ^a						
Node ^c	Persistence ^b			Population growth rate		
	Low constant variance	High constant variance		InvAD	Opinion	Opinion
Habitat degradation	0.02177	0.00841	0.00601	0.06927	0.07463	
Fishing exploitation	0.01891	0.00757	0.00248	0.0585	0.03052	
Potential spawning and rearing habitat	0.01668	0.00732	0.00651	0.0489	0.09689	
Potential life history	0.01557	0.00757	0.00281	0.05471	0.03737	
Invasion strength (of brook trout)	0.00782	0.00671	0.01575	0.0008	0.00786	
Temperature	0.00419	0.00186	0.00166	0.01327	0.02953	
Connectivity	0.000184	0.00374	0.01963	-	-	
BKT population status	0.00208	0.002	0.00651	0.00319	0.00771	
Stream width	0.0023	0.00103	0.00088	0.00757	0.01625	
BKT connectivity	0.00137	0.00072	0.00029	0.00559	0.00533	
Potential BKT spawning and rearing habitat	0.00064	0.00026	0.00032	0.0019	0.00496	
Gradient	0.00043	0.00019	0.00017	0.00141	0.0031	
Hydrologic regime	0.00003	0.00001	0.00001	0.0001	0.0001	

^a Sensitivity values (entropy reduction) calculated using the software program Netica following the formula presented in Marcot et al. (2001; 2006). Note that the use of trade or firm names (e.g., Netica) is for reader information only and does not imply endorsement by the US Department of Agriculture or the US Department of Interior of any product or service.

^b Sensitivities for *persistence* under the *InvAD* BBN are presented in Table 4 of Peterson et al. (2008).

^c The rank order of nodes preserved after Table 4 of Peterson et al. (2008).

Table S2-2. Predicted probability of presence for westslope cutthroat trout (WCT) after 20 years under three alternative BBNs and the scenarios portrayed in the hypothetical management example described in Table 3 of Peterson et al. (2008). “Low constant variance” and “High constant variance” networks have conditional probability tables for *persistence* developed assuming a population growth rate variance of 0.2 and 0.8, respectively, and using the model of Dennis et al. (1991). The “opinion only” network has conditional probability tables for *population growth rate* and *persistence* parameterized using expert opinion.

Node and state		Probability of WCT being present after 20 yr									
		Effective network size									
		Very small		Medium		Very large					
BBN	Fishing	Life history/ Connectivity	Habitat degradation	No	Barrier	No	Barrier	No	Barrier	No	Barrier
Low constant variance	Low	Migratory/Connected	Pristine	0.67	0.58	0.91	0.90	0.96	0.97		
			Degraded	0.46	0.14	0.75	0.43	0.87	0.62		
	High	Resident/Isolated	Pristine	0.13	0.58	0.40	0.90	0.59	0.97		
			Degraded	0.068	0.14	0.27	0.43	0.47	0.62		
High	Low	Migratory/Connected	Pristine	0.36	0.21	0.67	0.54	0.82	0.72		
			Degraded	0.25	0.037	0.56	0.22	0.76	0.43		
	High	Resident/Isolated	Pristine	0.042	0.21	0.22	0.54	0.42	0.72		
			Degraded	0.024	0.037	0.18	0.22	0.38	0.43		

Node and state			Probability of WCT being present after 20 yr								
			Effective network size								
			Very small		Medium		Very large				
BBN	Fishing	Life history/ Connectivity	Habitat degradation	No	Barrier	No	Barrier	No	Barrier	No	Barrier
High constant var	Low	Migratory/Connected	Pristine	0.42	0.28	0.80	0.65	0.90	0.79	0.90	0.79
			Degraded	0.31	0.097	0.67	0.32	0.79	0.46	0.79	0.46
		Resident/Isolated	Pristine	0.094	0.28	0.31	0.65	0.45	0.79	0.45	0.79
			Degraded	0.067	0.097	0.25	0.32	0.38	0.46	0.38	0.46
	High	Migratory/Connected	Pristine	0.26	0.13	0.60	0.39	0.74	0.53	0.74	0.53
			Degraded	0.20	0.054	0.52	0.22	0.68	0.35	0.68	0.35
		Resident/Isolated	Pristine	0.055	0.13	0.22	0.39	0.34	0.53	0.34	0.53
			Degraded	0.047	0.054	0.20	0.22	0.32	0.35	0.32	0.35
Opinion only	Low	Migratory/Connected	Pristine	0.75	0.36	0.82	0.55	0.97	0.70	0.97	0.70
			Degraded	0.69	0.23	0.77	0.38	0.94	0.58	0.94	0.58
		Resident/Isolated	Pristine	0.19	0.36	0.33	0.55	0.55	0.70	0.55	0.70
			Degraded	0.12	0.23	0.24	0.38	0.51	0.58	0.51	0.58

Node and state		Probability of WCT being present after 20 yr							
		Effective network size							
BBN	Fishing	Life history/ Connectivity	Habitat degradation	Very small		Medium		Very large	
				No	Barrier	No	Barrier	No	Barrier
High		Migratory/Connected	Pristine	0.68	0.30	0.76	0.47	0.93	0.64
			Degraded	0.65	0.19	0.73	0.32	0.91	0.55
		Resident/Isolated	Pristine	0.11	0.30	0.22	0.47	0.51	0.64
			Degraded	0.076	0.19	0.17	0.32	0.48	0.55