

**Special Section:  
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**Articles**

# Adaptive Management of Bull Trout Populations in the Lemhi Basin

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## Abstract

The bull trout *Salvelinus confluentus*, a stream-living salmonid distributed in drainages of the northwestern United States, is listed as threatened under the Endangered Species Act because of rangewide declines. One proposed recovery action is the reconnection of tributaries in the Lemhi Basin. Past water use policies in this core area disconnected headwater spawning sites from downstream habitat and have led to the loss of migratory life history forms. We developed an adaptive management framework to analyze which types of streams should be prioritized for reconnection under a proposed Habitat Conservation Plan. We developed a Stochastic Dynamic Program that identified optimal policies over time under four different assumptions about the nature of the migratory behavior and the effects of brook trout *Salvelinus fontinalis* on subpopulations of bull trout. In general, given the current state of the system and the uncertainties about the dynamics, the optimal policy would be to connect streams that are currently occupied by bull trout. We also estimated the value of information as the difference between absolute certainty about which of our four assumptions were correct, and a model averaged optimization assuming no knowledge. Overall there is little to be gained by learning about the dynamics of the system in its current state, although in other parts of the state space reducing uncertainties about the system would be very valuable. We also conducted a sensitivity analysis; the optimal decision at the current state does not change even when parameter values are changed up to 75% of the baseline values. Overall, the exercise demonstrates that it is possible to apply adaptive management principles to threatened and endangered species, but logistical and data availability constraints make detailed analyses difficult.

Keywords: migratory; occupancy; patch network model; *Salvelinus confluentus*; *Salvelinus fontinalis*; stochastic dynamic programming



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## Introduction

The bull trout *Salvelinus confluentus* is a stream-living salmonid distributed in drainages of the northwestern United States. The decline of bull trout populations throughout their range, in concert with a number of other threats, has led to the species being listed as threatened under the Endangered Species Act (ESA, as amended 1973; Federal Register 63 [June 10, 1998]: 31647). Currently, the U.S. Fish and Wildlife Service (USFWS) has established four bull trout recovery objectives under the draft Recovery Plan (USFWS 2002), including 1) maintain current distribution of bull trout within bull trout core areas; 2) maintain a stable or increasing trend in abundance (distribution); 3) restore and maintain suitable habitat conditions for all bull trout life history stages; and 4) conserve bull trout genetic diversity and provide opportunity for genetic exchange.

In the Lemhi River drainage of eastern Idaho, the State of Idaho (State), National Oceanic and Atmospheric Administration (NOAA) Fisheries, and the USFWS are working together to address conservation needs of bull trout and other salmonids. The State is developing a conservation plan for federal approval under the Cooperative Agreement provisions of Section 6 of the ESA. The goal of the plan is to restore necessary water flows at appropriate times of year in key sections of the Lemhi watershed to protect salmon and bull trout and to allow fish passage. To recover bull trout populations in the Lemhi River Basin, the State has identified necessary conservation measures primarily involving changing water withdrawal activities, providing fish passage, protecting and restoring riparian buffers, conserving existing high quality stream habitats, and improving degraded streams (Batt 1996).

The Lemhi River Basin is 1 of 10 bull trout core areas in the Salmon River Recovery Unit. The recovery of bull trout in the Lemhi Basin may be hampered by fragmentation and isolation of existing populations, primarily as a result of irrigation water withdrawal. The development of effective and efficient strategies for protecting bull trout and allowing fish passage, however, are hindered by complexity and uncertainty associated with system behavior and multiple management

considerations (e.g., species conservation and socioeconomic needs). To aid the decision-making process, the USFWS requested a tool that would model the response of bull trout to reconnection of occupied and unoccupied streams. Although this is only one of the actions listed in the Section 6 agreement, we chose to focus on it as an example of a relatively tractable species recovery decision.

Here we describe an adaptive management framework for meeting bull trout recovery goals in the Lemhi Basin. Specifically, we consider adaptive management of stream reconnection, in which reconnection of stream reaches disconnected from the main drainage would be undertaken to support bull trout recovery. Adaptive management is a decision-making tool applicable to decisions that are iterated over time, wherein uncertainty in system dynamics is captured through competing models of system behavior and monitoring is used to reduce uncertainty over time (Williams et al. 2002). Optimization techniques applied to an adaptive management framework lead to recommendations for the best course of action given the state of the system and the level of uncertainty about it. We discuss the optimization approach we took and results of our optimization, as well as the adaptation portion of management, with detail on monitoring and feedback. We also discuss monitoring needs and the implications for management of bull trout in the Lemhi Basin, as well as our general approach and the process of developing an adaptive management framework. Our goals were to identify the best patches to reconnect for recovering bull trout in the Lemhi core area, and to elucidate some of the practical issues involved in taking an adaptive management approach to recovery planning.

## Biological Background

Bull trout populations have two distinct life history forms: resident and migratory. Both spawn in small headwater (second to fourth order) streams, typically from August through November (Rieman and McIntyre 1993). Eggs incubate over the winter and hatch between early April and May (Meehan and Bjornn 1991). Growth differs little between forms during their first 2 y of life in headwater streams but diverges as migratory fish move



into larger, more productive waters where growth rates are greater (Rieman and McIntyre 1993). Resident adults range from 150 to 300 mm in total length, whereas adult migratory fish commonly exceed 600 mm (Rieman and McIntyre 1993).

Although resident forms complete their life history entirely within headwater streams (Rieman and McIntyre 1993), migratory forms live in headwater streams for 1–3 y during their juvenile life stage and then migrate downstream to a larger river (fluvial individuals) or lake (adfluvial individuals; Rieman and McIntyre 1993; Saffel and Scarneccchia 1995). Migratory bull trout generally remain in downstream areas for 2–4 y before maturing and returning to spawn (Fraley and Shepard 1989; Rieman and McIntyre 1995). As is typical for a salmonid species, migratory bull trout usually spawn in their natal stream, although a small number of individuals spawn in different (nonnatal) streams (strays). Genetic data suggest that bull trout strays are less successful than for other salmonids (Kanda et al. 1997). Both life history forms become sexually mature at 5–7 y of age (Rieman and McIntyre 1993), and adults may spawn multiple times over their lifetimes.

All life history forms of bull trout initiate spawning activity in response to decreasing water temperatures (Swanberg 1997; Bonneau and Scarneccchia 1996; Jakober et al. 1998). Temperature also is an important factor influencing bull trout distribution (e.g., Fraley and Shepard 1989; Rieman and McIntyre 1996). Bull trout are rarely found in streams warmer than 19°C (Rieman and Chandler 1999); hence, resident populations and juvenile migratory fish less than 2 y old are generally restricted to higher elevation watersheds. These thermally suitable, high elevation watersheds, defined herein as patches, are discretely distributed within the bull trout range, particularly in the southern part of their range, such as south and central Idaho. Bull trout inhabiting these patches are considered distinct subpopulations and collections of subpopulations within defined geographical areas are believed to operate as metapopulations (patchily distributed populations sustained by recolonization events; Dunham and Rieman 1999), and limited genetic studies support this contention (Spruell et al. 1999, 2003; Whiteley et al. 2003). Bull trout presence in patches (occupancy) is influenced by patch size, distance to nearest occupied patch, and land use (Dunham and Rieman 1999).

Migratory life history forms are believed to be important components of bull trout populations. Migratory adults are much more fecund than resident adults due to their larger body size. Genetic studies of a congener, brook trout *Salvelinus fontinalis*, suggest that gene flow among subpopulations is primarily due to migratory forms (Rogers and Curry 2004), although both migratory and resident forms of rainbow trout *Oncorhynchus mykiss* contribute to gene flow (Olsen et al. 2006). It is widely assumed that the migratory individuals are also responsible for most colonization of unoccupied patches and demographic support of subpopulations (B. Rieman, U.S. Forest Services, personal communication). Consequently, reestablishing or increasing migratory components of bull trout populations might aid their recovery in the Lemhi Basin.

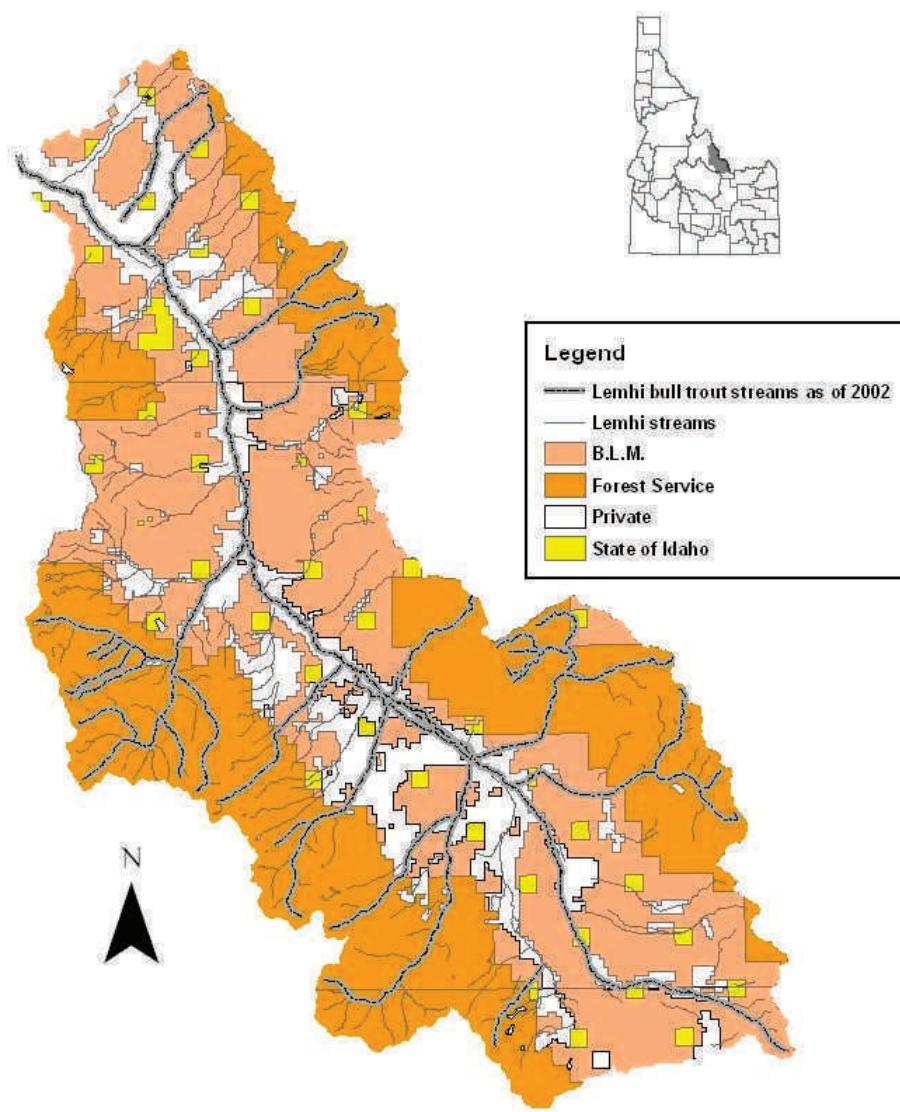
Considerable uncertainty exists about the mechanisms that determine bull trout life history strategy (Nelson et al. 2002), and two broad hypotheses have been proposed. The first hypothesis, based on studies of other *Salvelinus* species (Morinville and Rasmussen 2003), is that life history strategy is primarily determined by genetic factors. The second hypothesis is that the growth and survival of young fish influence the life history strategy (i.e., it is phenotypically plastic; Morita et al. 2000; Nelson et al. 2002). These two hypotheses can influence the development of effective recovery plans with respect to stream reconnection. For example, if the migratory life history is predominantly genetic and lost from disconnected patches, recovery efforts that focus on reconnecting occupied stream reaches will not lead to increased expression of the migratory life history and resulting colonization of streams. Alternatively, if life history strategy is phenotypically plastic, these streams could produce migratory individuals as soon as they are reconnected, and this would lead to an increase in colonization rates across the system. As a result, these two hypothesized responses might lead to different optimal strategies for reconnecting occupied patches.

Reestablishing connectivity of existing isolated populations of bull trout also involves potential risk. Interactions between bull trout and nonnative fishes, primarily brook trout, are believed to be at least partially responsible for bull trout population declines (Nakano et al. 1998). Brook trout have been widely introduced throughout the Intermountain West and are present in the Lemhi Basin (Lee et al. 1997). They generally occur in warmer streams than bull trout populations. However, in streams where the species co-occur, bull trout distribution has been observed to shift toward colder stream reaches at higher elevations (Rich et al. 2003; Rieman et al. 2006). Additionally, hybridization between brook trout and bull trout is known to occur, apparently resulting in hybrids that are either sterile or have very low fecundity (Leary et al. 1993). Reestablishing connectivity of isolated bull trout populations may potentially allow brook trout to invade areas occupied by bull trout, resulting in local extinction. The empirical evidence of such an extreme interaction, however, is equivocal, and no study has demonstrated a direct connection between brook trout invasion and extinction of local bull trout populations. Rather, brook trout are believed to primarily displace bull trout from lower elevation streams, effectively reducing the size of suitable habitat patches (Leary et al. 1993). Further, brook trout invasion following reconnection is not predestined, and the likelihood of invasion will depend on the physical and thermal characteristics of the reconnected stream as well as the presence of brook trout source populations (Adams et al. 2001).

## Study Area

The Lemhi River Basin is a relatively large tributary of the Salmon River in eastern Idaho (Figure 1), 326,634 ha in size, with elevation averaging 2,200 m (range 1,244–3,429 m). Land ownership in the Basin is 78% Federal (U.S. Forest Service, Bureau of Land Management), 18%





**Figure 1.** Land ownership in the Lemhi River Basin and the known distribution of bull trout *Salvelinus confluentus*.

private, 3% State, and 0.5% municipal. The entire 66-mi (1 mi = 1.6 km) Lemhi River mainstem occurs on private land, and most of the lower elevation portions of the river's tributaries are also on private land. The Basin is primarily forested (48%), with most of the remaining land used to support livestock as croplands, pasture, or rangelands. Approximately 9% of the land is in irrigated agriculture, which produces alfalfa or hay for livestock (IDWR 1999). The Basin contains a total of 22 tributaries, 13 of which contain bull trout subpopulations. Of these 13 tributaries, only two, Hayden Creek and Big Timber Creek, support a migratory life history component (Table 1). These migratory individuals are believed to spawn in the tributaries and migrate to the Salmon River (Schoby 2006). Although Big Timber Creek is not connected throughout the year, the fact that the migratory life history is present in this subpopulation (Sutton and Morris 2004) suggests that it is connected when the fish migrate, thus we treat this tributary as connected and occupied.

## Adaptive Management Framework

Under the State conservation plan being developed, incentives would be provided to private landowners to encourage participation in bull trout conservation activities, including the reconnection of streams within the watershed to promote a greater bull trout distribution. Because not all landowners are expected to participate, the USFWS would like to prioritize restoration projects in advance of approaching landowners.

We define a tributary as connected if there is a year-round connection or the migratory life history is present. The decision context that we approach herein is how to prioritize the reconnection of 19 currently unconnected headwater streams in the Lemhi drainage, including 11 that are currently occupied by bull trout and 8 that are unoccupied. The time period for these activities is 10 y; however, the USFWS and State could extend the Cooperative Agreement (once finalized) for another 30 y beyond that. An important constraint is that funding and

**Table 1.** Characteristics of the 22 tributaries in the Lemhi River Basin, Idaho, that were considered in the bull trout *Salvelinus confluentus* adaptive management framework.

Tributary	Size (km <sup>2</sup> )	Road density (km/km <sup>2</sup> )	Seasonally connected?	Perennially connected?	Current bull trout status	Migratory life history present?
Geertson Creek	43.5	0.93	No	No	Occupied	No
Bohannon Creek	57.2	0.74	Yes	No	Occupied	No
Kenney Creek	NA <sup>a</sup>	NA	Yes	No	Occupied	No
Pattee Creek	81.8	1.11	Yes	No	Occupied	No
Little Eightmile Creek	78.0	0.68	No	No	Occupied	No
Hawley Creek	168.4	0.56	No	No	Occupied	No
Eighteenmile Creek	384.6	0.86	No	No	Occupied	No
Deer Creek	NA	NA	Yes	No	Occupied	No
Hayden Creek	392.8	0.46	Yes	Yes	Occupied	Yes
Big Timber Creek	223.8	0.49	Yes	No	Occupied	Yes
Big Eightmile Creek	166.7	0.68	No	No	Occupied	No
Lee Creek	NA	NA	No	No	Occupied	No
Mill Creek	79.8	0.86	No	No	Occupied	No
Big Springs Creek	NA	NA	Yes	Yes	Unoccupied	No
Pratt Creek	NA	NA	No	No	Unoccupied	No
Haynes Creek	NA	NA	No	No	Unoccupied	No
Agency Creek	107.8	0.93	Yes	No	Unoccupied	No
Mcdevitt Creek	60.6	0.93	No	No	Unoccupied	No
Canyon Creek	151.1	NA	No	No	Unoccupied	No
Kirtley Creek	56.5	1.11	No	No	Unoccupied	No
Texas Creek	257.1	0.43	No	No	Unoccupied	No
Little Springs Creek	NA	NA	No	No	Unoccupied	No

<sup>a</sup> NA indicates that the data were unavailable.

other resources are to be allocated for the reconnection of only 10 stream reaches in the 10-y period, as recommended in the draft bull trout recovery plan objectives for the Lemhi River recovery unit (USFWS 2002). In the following sections we describe elements of the adaptive management framework, including the management objective, the set of management actions under consideration, and the models used to predict system response to management.

## Objective

In a formal adaptive management approach, managers would have the ultimate responsibility for setting management objectives. Adaptive management cannot proceed without a clearly stated objective, formalized in an objective function. The bull trout recovery plan objectives are generally focused on maintaining species persistence and increasing populations based on either abundance or distribution (occupancy). The most direct measure of persistence is the risk of extinction or quasi-extinction over some relatively long time period (e.g., a few decades or longer) within a region. This cannot be directly observed, although it is straightforward to predict from a population model. Persistence ( $1 - \text{extinction risk}$ ) and occupancy are positively related, and occupancy can be both modeled using patch dynamic models and monitored directly. However, using occupancy as an optimization criterion assumes that each additional occupied patch is equal in value. In

general, the value of each additional occupied patch depends on whether it is connected or not and how many susceptible patches are available for colonization, as well as other ecologically important traits, such as the area of the patch and how far it is from other patches. Therefore, we set as an objective the persistence of at least one population 256 y after the end of the 10-y management horizon (i.e., the probability that at least 1 out of 22 tributaries would be occupied after 256 y).

In this demonstration, more than just management concerns informed how we determined our objective function. We used  $t = 256$  y because using a power of two ( $256 = 2^8$ ) minimized the number of matrix multiplications necessary to compute persistence; this is arbitrary and can be readily changed to meet any particular time frame considered relevant. We also found that the differences in the outcomes for the different models were relatively clear after at least 256 y; with shorter time horizons, there was not enough variation in persistence probability to distinguish between the results based on the different models (i.e., the uncertainty captured in the models did not have a large impact on our objective). Therefore, for demonstration of concept, we used a time horizon of 256 y.

## Alternative actions

Ultimately it would be desirable to prioritize individual streams for reconnection based on a suite of physical, biological, and hydrological characteristics. However, for



this initial prototype we only differentiated between streams based on their connectivity and occupancy by bull trout; that is, we considered a spatially implicit model of the system. This is clearly an oversimplification, but a spatially explicit model that tracked which specific patches were occupied would have a state space of  $2^{22}$ , well beyond the capability of today's computers to deal with in an optimization model. By limiting the state space, we can identify optimal strategies for the model and determine what affects their overall structure.

Therefore, in our formal decision context, it is possible each year either 1) to connect a stream that is currently occupied by bull trout, 2) to connect a stream that is currently unoccupied by bull trout, or if the system is in a state where neither of these actions is possible, and then the decision is forced to be 3) to do nothing.

### Predictive models

We modeled bull trout occupancy in Lemhi River Basin tributaries (henceforth, patch occupancy) using patch network models (Hanski et al 1996). Again, the basic model structure (which will form the basis of our alternative models) is spatially implicit, which means that all patches of a given type are equivalent—differences such as distance from other patches and area are ignored. Here we adopted nomenclature based on a four-patch epidemiological model described by Amarasekare and Possingham (2001). In this model, patch types are connected, occupied patches ( $I$ , infected); connected, unoccupied patches ( $S$ , susceptible); disconnected, occupied patches ( $L$ , latent); and disconnected, unoccupied patches ( $R$ , resistant). To this, we added an additional type of patch, a newly infected patch ( $N$ ), which is a patch that was formerly latent but has been connected through management and so is both connected and occupied. This patch type will express different dynamics in different models. Keeping the five types of patches straight is challenging; it helps to recall that we are casting bull trout in the role of the disease and patches of habitat in the role of hosts.

At present, the Lemhi Basin has 22 possible patches; 2 are infected, 0 are newly infected (by definition, because no connections have been made through management), 11 are latent, 1 is susceptible, and 8 are resistant. In the following, we will describe this state as  $\{I = 2, N = 0, L = 11, S = 1, R = 8\}$ . In this spatially implicit model structure, it is only necessary to track the number of patches in each state. The heart of our basic model structure is a Markov transition matrix,  $\mathbf{A}$ . This matrix is square with  $M$  rows and columns, where  $M$  is the number of states the system can occupy. Each entry  $a_{ij}$  in the matrix describes the probability that the system transitions from state  $i$  to state  $j$  between any two time steps. It is a first-order Markov chain because the probability of transition depends only on the state of the system now; the past history of the system does not affect the transition probability. Our patch model is an extension of a model widely known as the "chain binomial" model in both ecology and epidemiology (Hill and Caswell 1999, 2001). The general structure also works for individual births and deaths and is then useful for

decision making in small populations subject to demographic stochasticity (e.g., Tenhumberg et al. 2004).

The basic model structure was constructed in two parts. First, we calculated a matrix of transitions caused by colonization only. For example, the transition from  $\{I = 1, N = 0, L = 12, S = 1, R = 8\}$  to  $\{I = 2, N = 0, L = 12, S = 0, R = 8\}$  involves colonization of a susceptible patch, so this is a possible transition due to colonization. Susceptible patches are subject to colonization because they are both empty and connected to the network, and in certain models, newly infected patches are also subject to colonization. Note that resistant patches cannot be colonized because they are unconnected to the network.

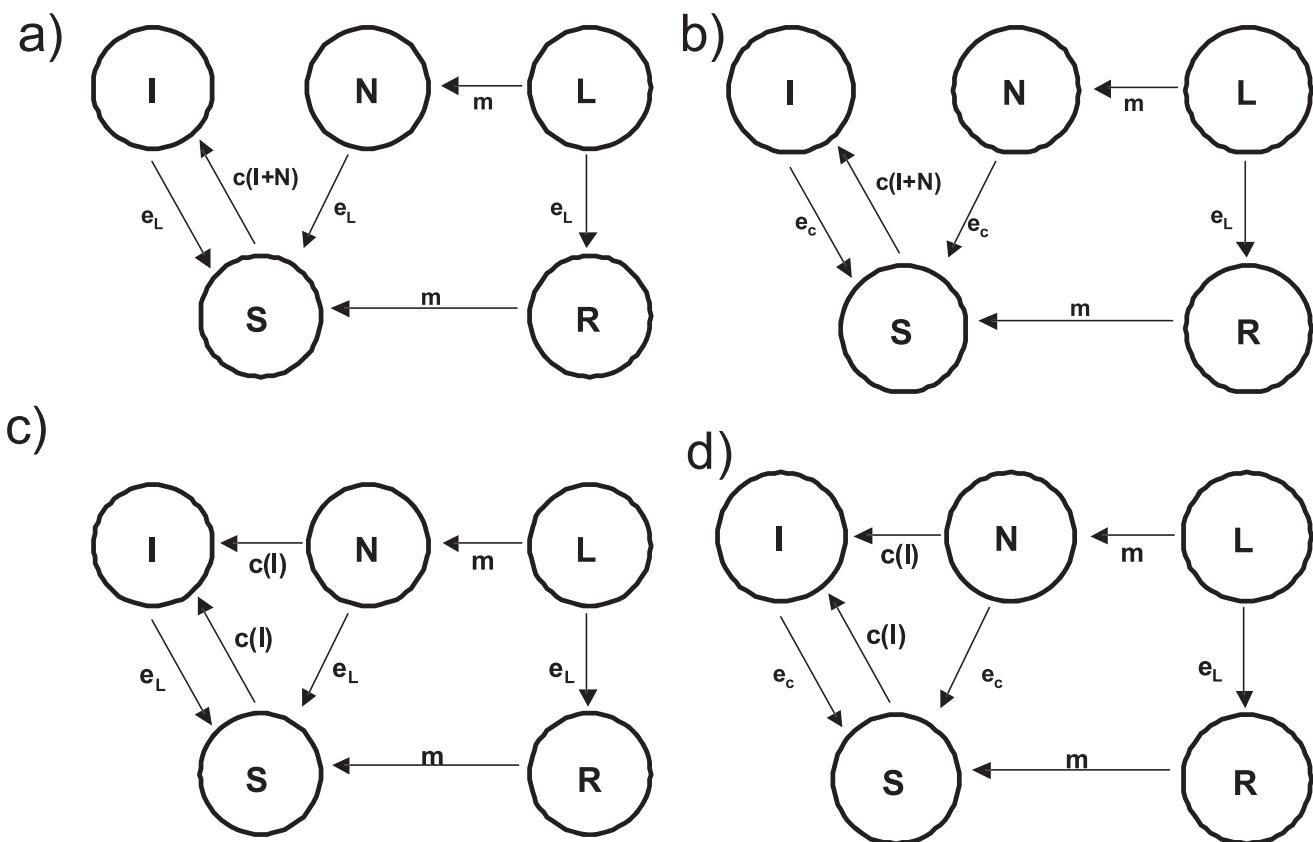
Second, we constructed a matrix of the probability of transitions involving local extinction. For example, transition from the current state  $\{I = 2, N = 0, L = 11, S = 1, R = 8\}$  to  $\{I = 0, N = 0, L = 11, S = 3, R = 8\}$ , which involves local extinction of the two infected patches, can be achieved through extinction. We then multiplied these matrices together, assuming independence between colonization and extinction, to obtain the full transition matrix  $\mathbf{A}$ .

We built four possible models to capture the two primary sources of uncertainty in the system. The first uncertainty we dealt with was in regard to the expression of the migratory life history trait. In the parameterization [MP], we assumed that the migratory life history will be expressed by individuals in a newly connected patch, such that some individuals in latent streams could immediately become migratory. In this model, the force of colonization is driven both by infected streams and newly infected streams because both will be able to provide migrants to the system, and migrants will be potential colonists. Alternatively, in parameterization [MS], we assumed that the migratory life history trait will not be expressed in formerly unconnected streams. In this parameterization, newly infected patches cannot provide colonists to the system immediately after they are connected—only after they are themselves colonized by infected patches will they contribute to the force of colonization.

The second source of uncertainty that we considered was the importance of brook trout to local extinction of patches. In parameterization [BN], we assumed no effect of brook trout on the extinction rate of connected patches, such that the extinction rate of all occupied patches is equal. Alternatively, in parameterization [BY], we assumed that the extinction rate in infected or newly infected patches is higher than in latent patches because of the impact of brook trout. The exact parameter values used are described later in this article.

We considered the four possible combinations of these four parameterizations, such that our models were Model [ME & BN], Model [ME & BY], Model [MS & BN], and Model [MS & BY]. Diagrams of the transitions in each of these models are shown in Figure 2 and described in the following text. In the analysis we considered that each of these parameterizations is equally likely; that is, the prior probability of each model is 0.25.





**Figure 2.** Alternative patch dynamics model for bull trout *Salvelinus confluentus* in the Lemhi Basin: **a** [MP & BN], **b** [MP & BY], **c** [MG & BN], and **d** [MG & BY]. Figures represent the differing contribution of newly infected (*N*) and infected (*I*) patches to the colonization of susceptible (*S*) patches (**a** and **b** vs. **c** and **d**) and the differing extinction rates (*e*) are for connected (*I*, *N*) and unconnected (latent, *L*) patches. Management actions are designated by “*m*” and involve connecting either a latent or resistant (*R*) patch.

Parameterizations [ME] and [MS] differ in their colonization matrices. In parameterization [ME], each infected and newly infected patch contributes colonists to a susceptible patch with a fixed probability  $c$  per time step. The probability that a susceptible patch is actually colonized then depends on the number of infected and newly infected patches available to contribute colonists. Therefore  $c_j$ , the probability a single susceptible patch is colonized in state  $j$ , is

$$c_j = 1 - (1 - c)^{l_j + N_j} \quad (1)$$

which is simply 1 minus the probability that none of the occupied, connected patches provides colonists. The probability of a colonization transition from a state  $j$  with  $S_j$  susceptible patches to a state  $k$  with  $S_k$  susceptible patches ( $S_k \leq S_j$ ) is then a binomial probability (hence the name “chain binomial model”):

$$c_{jk} = \begin{cases} \binom{S_j}{l_k - l_j} c_j^{l_k - l_j} (1 - c_j)^{S_j - l_k - l_j} \\ \text{if } l_j + N_j > 0, S_j > 0, l_k \geq l_j, S_k \leq S_j, (l_j + S_j) \\ = (l_k + S_k), N_j = N_k, \text{ and } R_j = R_k \\ 0 \text{ otherwise} \end{cases} \quad (2)$$

where  $I_m$ ,  $N_m$ ,  $S_m$ ,  $L_m$ , and  $R_m$  are the number of infected, newly infected, susceptible, latent, and resistant patches in state  $m$ . To clarify, we placed all colonized susceptible patches into the infected patch type—only management actions could move patches into the newly infected patch type. Because the patches work equivalently in this model, it is not critical to which type (*I* or *N*) an occupied, connected patch belongs (again, we assume in [ME] that bull trout in newly connected reaches have some nonzero probability of expressing the migratory life history trait). Note that the most difficult part of setting up a colonization matrix,  $\mathbf{C}$ , is identifying pairs of states that represent changes due to colonization—hence the long string of conditions described in the probabilities.

The colonization matrix for parameterization [MS] differs in that only infected patches contribute to colonization, such that

$$c_j = 1 - (1 - c)^{l_j} \quad (3)$$

and both susceptible and newly infected patches can be colonized (i.e., newly infected patches, *N*, must themselves be “colonized” by the migratory life history if they are to become infected patches). We then create two matrices, one for colonization of *S* patches, given here:

$$c_{jk}^S = \begin{cases} \left( \frac{S_j}{S_j - S_k} \right) c_j^{S_j - S_k} (1 - c_j)^{S_k} & \text{if } I_j > 0, S_j + N_j > 0, I_k \geq I_j, S_k \leq S_j, (I_j + N_j + S_j) \\ & = (I_k + N_k + S_k), N_j \leq N_k, \text{ and } R_j = R_k \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

and another for colonization of  $N$  patches ( $c_{jk}^N$ ), which has equivalent conditions but a probability of

$$\binom{N_j}{N_j - N_k} c_j^{N_j - N_k} (1 - c_k)^{N_k} \quad (5)$$

The product of these two colonization matrices then forms the overall colonization matrix for parameterization [MS].

The parameterizations [BN] and [BY] differ in their local extinction matrices,  $\mathbf{E}$ . The extinction matrix is constructed similar to the colonization matrix; infected, newly infected, and latent patches undergo transitions from occupied to unoccupied (local extinction) at a rate either  $e_{\text{connected}}$  (for infected and newly infected patches) or  $e_{\text{latent}}$  (for latent patches). Extinction in each of the three patch types occurs independently, so it is simplest to construct three extinction matrices, one for infected, one for newly infected, and one for latent patches, and then multiply these together to obtain all the requisite transitions in  $\mathbf{E}$ . The extinction matrix for infected patches is

$$e_{jk}^I = \begin{cases} \left( \frac{I_j}{I_j - I_k} \right) e_{\text{connected}}^{I_j - I_k} (1 - e_{\text{connected}})^{I_k} & \text{if } I_j + N_j > 0, I_k \leq I_j, N_k \leq N_j, S_k \geq S_j, (I_j + N_j + S_j) \\ & = (I_k + N_k + S_k), \text{ and } R_j = R_k \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

and the extinction matrix for newly infected patches follows the same conditions as for infected patches, but with the probability

$$\binom{N_j}{N_j - N_k} e_{\text{connected}}^{N_j - N_k} (1 - e_{\text{connected}})^{N_k} \quad (7)$$

For latent patches, the extinction matrix is

$$e_{jk}^L = \begin{cases} \left( \frac{R_j}{R_k - R_j} \right) e_{\text{latent}}^{R_k - R_j} (1 - e_{\text{latent}})^{R_j - R_k - R_j} & \text{if } L_j > 0, L_k \leq L_j, R_k \geq R_j, (L_j + R_j) \\ & = (L_k - R_k), S_j = S_k, \text{ and } I_j = I_k \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

The extinction transition matrix  $\mathbf{E}$  is formed by the product of these 3 matrices. In parameterization [BN] we set  $e_{\text{connected}} = e_{\text{latent}}$ , whereas in parameterization [BY], we set  $e_{\text{connected}} > e_{\text{latent}}$ ; that is, in the [BY] parameterization, the risk of brook trout invasion increases the relative risk of extinction in connected patches.

Finally, the full transition matrix is then constructed from the component matrices by multiplication:

$$\mathbf{A} = \mathbf{C} \times \mathbf{E} \quad (9)$$

One additional useful classification of states in the system is to identify *absorbing* states—states from which the system cannot return by either colonization or extinction. In this model, the absorbing states are ones in which all occupied patches have gone extinct (i.e.,  $I = N = L = 0$ ).

We can use this simple model to examine the potential payoffs for the reconnection projects as changes in the probability of regional extinction. Using the transition matrix  $\mathbf{A}$  appropriate to one of the four specified models, we can calculate the probability that the system passes from its current state to any state with 0 occupied patches (i.e., regional extinction) at some point in the future. This is not species extinction—just extinction in the Lemhi Basin assuming no rescue colonization from outside the Lemhi. This is simply the sum of transitions from current state  $j$  to all absorbing states. We can obtain this regional extinction probability over any required time frame by raising  $\mathbf{A}$  to the power  $t$ , where  $t$  is the number of years over which we would like to assess extinction risk. This assumes that we make no additional reconnections during time  $t$ . Again, we used  $t = 256$  y in our analyses (i.e., 256 y after any reconnections are completed).

We developed initial parameter estimates for the models by fitting incidence function models (O'Hara et al. 2002) to existing data on bull trout patch occupancy in the Boise River Basin, Idaho (Dunham and Rieman 1999). The models were fit using Monte Carlo Markov Chain as implemented in BUGS software, version 1.3 (Lunn et al. 2000). The models were fit using 100,000 iterations, 25,000 iteration burn-in, and diffuse priors.

### Optimization

The modeling goal of this effort was to use predictive models to prioritize patches for reconnection. We began by assuming that at any given time step, only one patch can be reconnected. The question then was which type of patch would contribute the most to increasing occupancy and the probability of metapopulation persistence. This decision may be state dependent and certainly depends on the degree to which structural uncertainty about migratory behavior and the effect of brook trout has been resolved.

We used stochastic dynamic programming (SDP; Bellman 1957) to identify reconnection strategies that maximize persistence of the metapopulation. This approach identifies an optimal decision for every single state the system could be in. It begins at the final time period by selecting the decision for each state that maximizes the “terminal value function” (Clark and Mangel 2000). In our case the terminal value function is the probability that the system persists (i.e., has at least one patch occupied) without any additional intervention for the next 256 y:

$$V(T, T, s) = 1 - \sum_{s'} a_{ss'}^{256} \quad (10)$$



where  $T$  is the final time period,  $s$  is the current state of the system,  $s'$  is a state from the set of absorbing states, and the superscript 256 indicates the transitions come from  $\mathbf{A}^{256}$ . The transition  $a_{ss'}$  is the probability of transitioning from state  $s$  to  $s'$ , and the sum is taken over all possible absorbing states. The value of any absorbing state is 0, because the probability that the system remains in that state is 1. To clarify, we assigned 0 value if 256 y after the 10-y management horizon, the species was extinct in the Lemhi Basin; we assigned full value if at least one patch was occupied. This is only one possible terminal value function; any function with a defined value for each state could be used.

The SDP algorithm proceeds by stepping back one time period and recalculating for each state the decision that maximizes future value

$$V(t, T, s) = \max_{d \in D} \left\{ \sum_{s''} a_{ds''} V(t+1, T, s'') \right\} \quad (11)$$

where  $t$  is the current time period,  $s$  is the current state,  $s''$  is the state at the next time period, and  $d$  is the state after making one of the decisions in the set  $D$ . Equation (11) essentially averages the value of all states the system might reach after making a decision  $d$ . The set  $D$  includes two possibilities at present: reconnect a latent patch and reconnect a resistant patch. Reconnecting a latent patch changes the state from  $s = \{I, N, L, S, R\}$  to  $d = \{I, N+1, L-1, S, R\}$ , and reconnecting a resistant patch changes the state from  $s = \{I, N, L, S, R\}$  to  $d = \{I, N, L, S+1, R-1\}$ . We also subtracted a small constant  $\delta = 1 \times 10^{-10}$  from the value for the decision to reconnect a resistant patch. This represented a small preference for reconnecting a latent patch, because the added value of the decision to reconnect a resistant patch has to exceed this amount before that option is selected. Not including this tiny constant would mean that the choice between the two strategies is made based on numerical rounding error when the value function is very flat. We chose this constant as the smallest value that stabilized the results in preliminary runs.

The algorithm proceeds iteratively back in time. When  $t$  is close to the terminal time  $T$ , the decisions are often highly dependent on time. Initially we discussed the decisions for the first year only; later we showed with forward simulations that the decisions for the current state are relatively consistent across time. The optimization was programmed in R and run on a desktop PC. The sensitivity analysis was run on R compiled for the University of Nebraska-Lincoln Holland Computer Center's PrairieFire cluster.

## Results

The incidence function parameter estimates (on a logit scale) are shown in Table 2. Incidence function models allow for differences among patches in both location and patch size, which in this initial prototype we ignored (the model is spatially implicit). However, ignoring the between patch differences in the incidence function model would lead to biased parameter estimates for the values we are

**Table 2.** Parameter estimates calculated from bull trout *Salvelinus confluentus* presence data from Boise River Basin, Idaho (Dunham and Rieman 1999) using a Bayesian incidence function model.

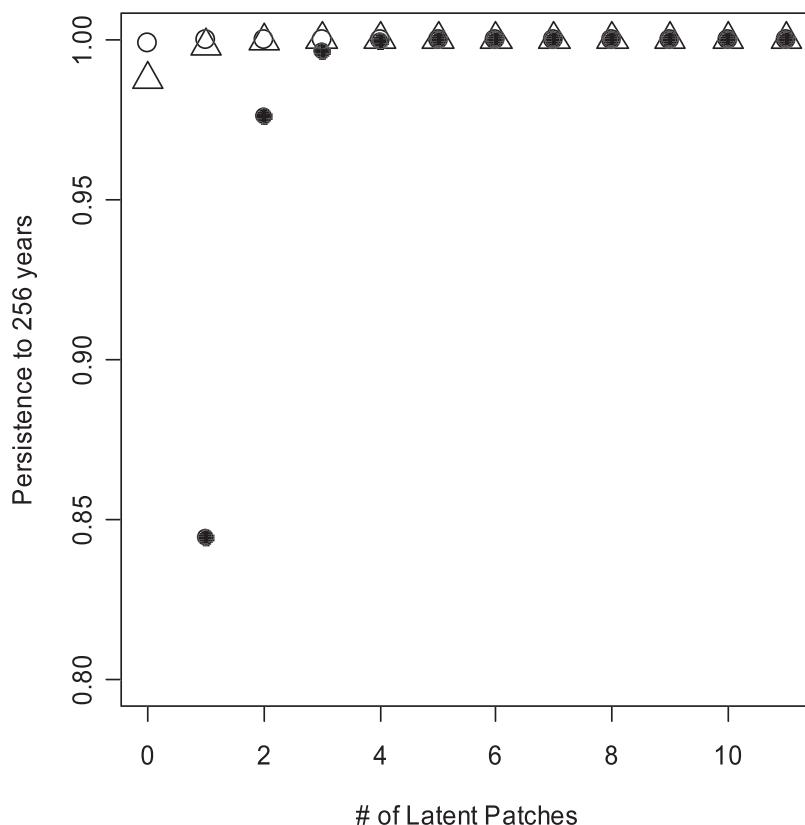
Parameter	Estimate	Standard deviation
Extinction		
Intercept	-1.070	0.071
Patch size	-0.025	0.010
Road density	-2.961	0.905
Colonization		
Intercept	-1.071	0.367
Distance from nearest infected	-0.048	0.020

interested in—the extinction rate for an average size patch and the colonization rate at the average separation. We used the average patch size ( $159 \text{ km}^2$ ) to obtain an estimate for  $e_{\text{latent}} = 0.0075$  per year, and for parameterization [BN], we assumed  $e_{\text{latent}} = e_{\text{connected}}$ . For parameterization [BY], we assumed the negative effect of brook trout was similar to a 30% reduction in patch size (i.e., approximately  $111 \text{ km}^2$ ); with this value, we calculated  $e_{\text{connected}} = 0.03$ . This assumed that the additional risk from exposure to brook trout outweighs any genetic “rescue effect” provided by movement of migratory fish. The 30% reduction in patch size is based on the expert judgment of bull trout experts familiar with the region (B. Rieman, U.S. Forest Services; J. Dunham, U.S. Geological Survey, personal communication). Distance from nearest infected patch was the predictor used for colonization; the average separation among patches in the Lemhi is 22.6 km, so  $c = 0.104$ . The current state of the system is  $\{I = 2, N = 0, L = 11, S = 1, R = 8\}$ , and with no additional reconnections the probability of persistence to 256 y is greater than 0.9999 for all parameterizations. With two infected patches the system could lose all of the latent patches without greatly affecting persistence; however, if there are fewer infected patches the probability of persistence decreases abruptly with fewer than four latent patches (Figure 3).

First, assume we know which model is correct. In general, if migration is phenotypic, the decision space is symmetrical between the  $N$  and  $I$  states (symmetric over the  $x$  and  $y$  axes, Figures 4 and 5) because these states are equivalent under the [ME] parameterization. Clearly, when there are no latent patches, the decision is always to connect a resistant patch (left-most column, Figure 4 and Figure 5). Resistant patches are also connected if there is an effect of brook trout ([BY] parameterization), relatively few latent patches, and a small number of infected or newly infected patches (second-to-left column, Figure 4). This represents the “lifeboat” effect of latent patches as protection from the effects of invasive species. If we assume there is no effect of brook trout ([BN] parameterization; Figure 5) then the area where resistant patches are connected when there are latent patches available is nearly completely eliminated.

If the migratory life history is suppressed in unconnected patches, the decision space is no longer





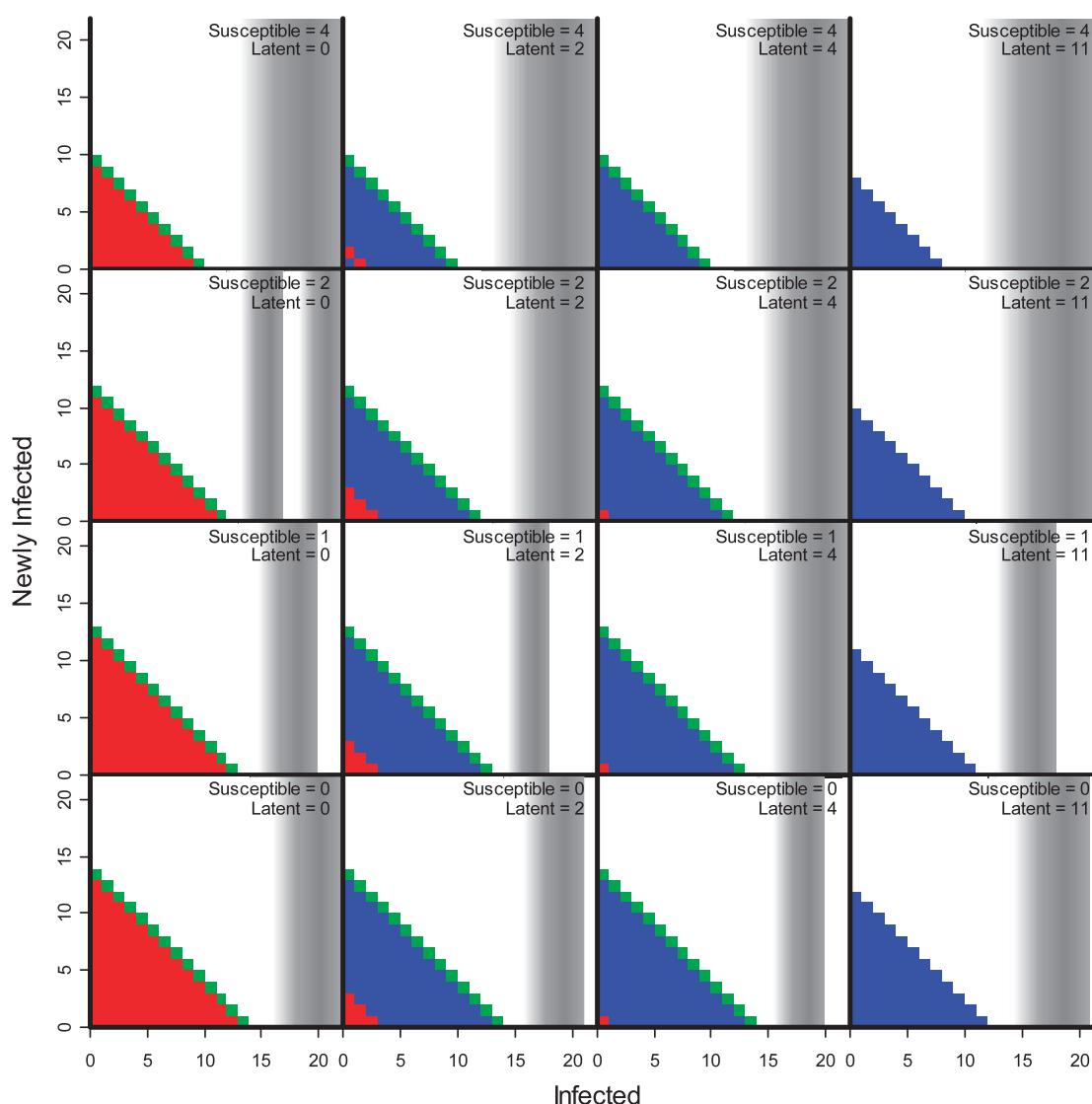
**Figure 3.** Probability of persistence for bull trout *Salvelinus confluentus* in the Lemhi Basin over 256 y as a function of the number of latent patches. Each set of points shows the change in persistence as the number of latent patches changes from the current state ( $L = 11$ ) to zero while the number of infected and susceptible patches remains constant. Open circles are the nominal state  $l = 2$ , open triangles are  $l = 1$ , and closed circles are  $l = 0$ .

symmetric between the  $l$  and  $N$  states. In particular, when there is a brook trout effect ([MS & BY]; Figure 6), connecting resistant patches is a better strategy for low numbers of infected patches regardless of how many newly infected patches there are. Thus, if there is a delay in expressing the benefits of the migratory life history strategy, the lifeboat effect gets stronger. As before, if there is no brook trout effect the decision space for connecting resistant patches shrinks dramatically (Figure 7).

In fact, we do not know which of the four parameterizations is true. We can construct an SDP that incorporates this uncertainty into the decision process by calculating an average outcome for each decision, in which the value associated with each parameterization is weighted by the uncertainty attached to it. If the uncertainty is assumed to be equal across all four parameterizations, the results reflect features of all parameterizations (Figure 8); the decision space is not symmetric and there is a moderate lifeboat effect when the number of latent patches is less than five. The difference in value at the current state for the “averaged” SDP versus each of the “known” SDP outcomes is less than  $2 \times 10^{-12}$ . This is one estimate of the “value” of information, measured in units of the terminal fitness function (i.e., the probability of the population persisting for 256 y). This value is much less than the minimum

difference imposed between the two decisions, suggesting that resolving the uncertainties between the parameterizations is of little value in the current system state. In contrast, the value of information is about 100 times greater than  $\delta$  at the state  $\{l = 2, N = 0, L = 2, S = 0, R = 18\}$ , for which the optimal decision is to connect a resistant patch. In that case, information about which parameterization is correct will have a large impact on which decision is optimal.

It is difficult to visualize the consequences of following the optimal policy by examination of the complete decision space; much of the information in that policy may not be realized in most circumstances because the system will not visit much of the state space. Instead, to understand the consequences of following the optimal policy, it is possible to imagine a limited “forward simulation” from the current state under the proposed plan of reconnecting one stream each year. We can assume for purposes of this limited simulation that no colonization or extinction events take place—for all parameterizations under the baseline parameters there is an 80% chance that the system will remain in its current state for the next year. In that case, the only change in state arises from management decisions to connect latent or resistant patches. In the present state the optimal decision is to reconnect a latent patch, increasing the number of newly infected patches by



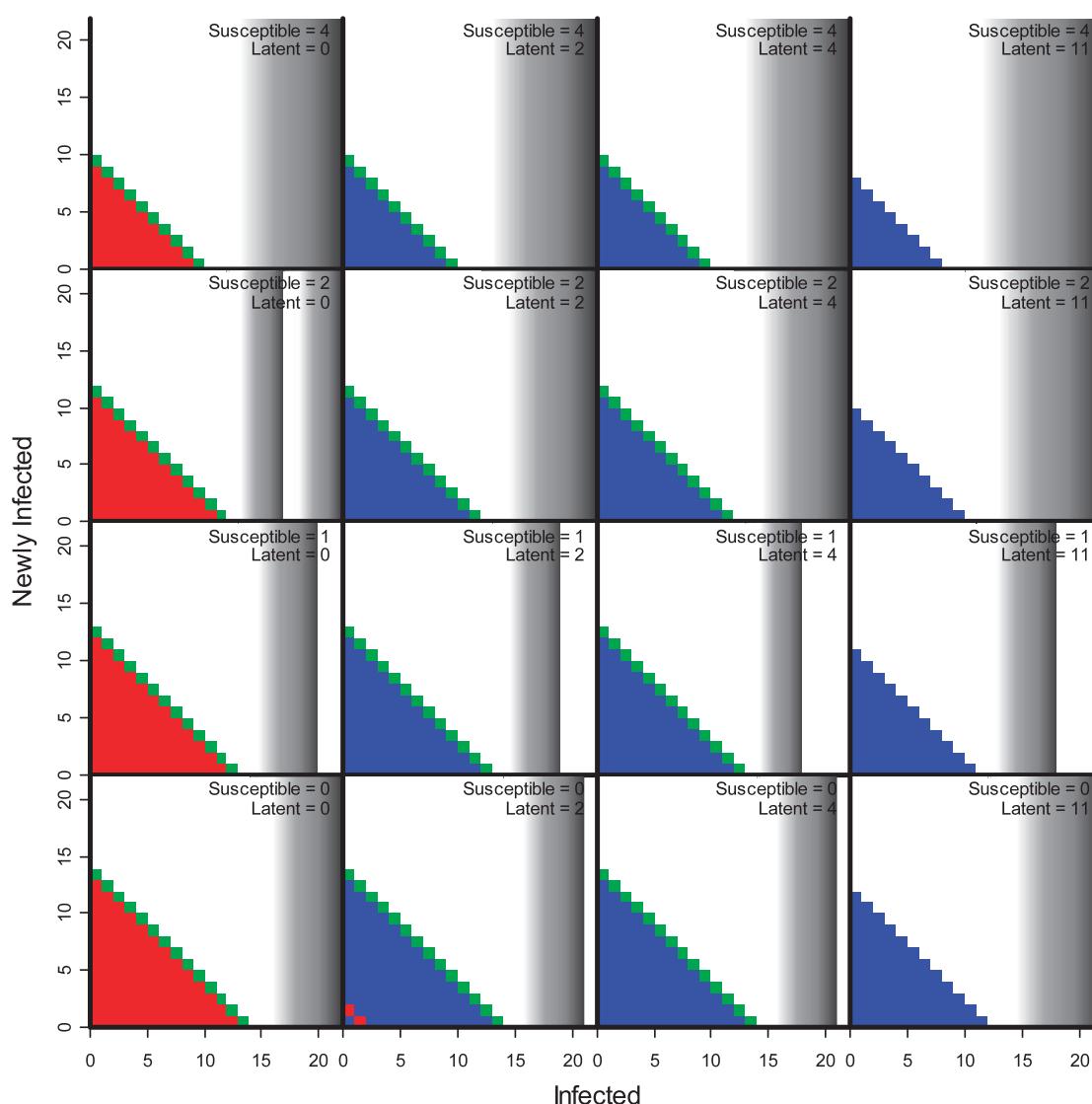
**Figure 4.** Results for the [ME] & [BY] parameterization in year 1 for bull trout *Salvelinus confluentus* in the Lemhi Basin. Red = connect a resistant patch; blue = connect a latent patch. Green indicates states from which no connections are possible (maximum number of actions exceeded or no available patches); white space also indicates combinations of states that are impossible. The current state is in the rightmost column, third row from the top. Each panel has the number of infected patches on the x axis, and the number of newly infected patches on the y axis. The number of susceptible and latent patches are fixed for each panel, with the actual number displayed in the top right corner of the panel.

one, to one. At that point, the optimal decision is still to connect a latent patch, increasing the number of newly infected patches to two. For three of the parameterizations the decision to connect a latent patch remains optimal as long as there are no local extinctions or recolonizations until all latent patches are connected. For the [MS & BY] parameterization (Figure 6), the decision switches to connecting resistant patches after two latent patches are connected.

We also simulated the process forward in time from the current state allowing local extinctions and recolonizations, using the model averaged optimal policy to obtain the current decision, and then sampling from the range of future states that could occur from the [ME & BY] parameterizations. By repeating this process 1,000 times we can build up a picture of what the next 10 y are predicted to look like

under the optimal policy. In fact, despite the apparent complexity of the optimal policy, given our current initial state and the average predicted dynamics, the median trajectory for the number of infected patches is practically a straight line (Figure 9). Furthermore, the number of latent patches undergoes an identical decrease, indicating that in most cases, the decisions are to connect latent patches. This result is consistent across all four combinations of migratory behavior and brook trout effects.

Although we constructed the SDP using a probability of persistence criterion, the State conservation plan that is being developed for consideration by NOAA Fisheries and the USFWS under Section 6 of the ESA has identified a goal of achieving 10 occupied and connected patches through management actions. This seems likely to be achieved over the 10 y of direct activity (Figure 9) since



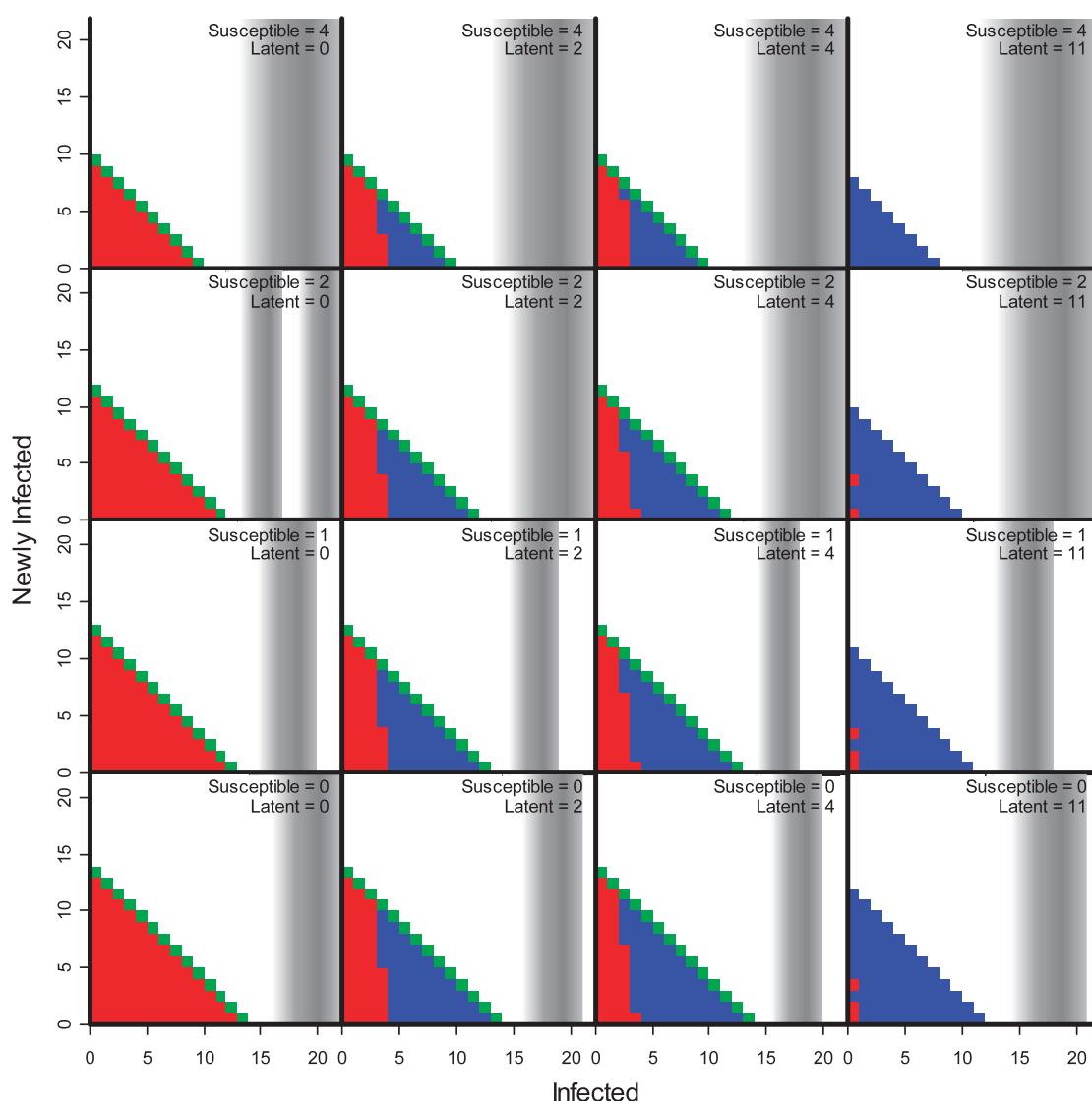
**Figure 5.** Results for the [ME] & [BN] parameterization in year 1 for bull trout *Salvelinus confluentus* in the Lemhi Basin. Red = connect a resistant patch; blue = connect a latent patch. Green indicates states from which no connections are possible (maximum number of actions exceeded or no available patches).

the minimum number of connected, occupied patches at 10 y, based on 1,000 forward simulations, is 11. However, given the assumed dynamics, how likely is it that this strategy would continue to perform to the end of the 30-y Cooperative Agreement currently under development? It appears as though the number of connected patches is adequate to maintain a quasistationary distribution with a minimum of 10 connected occupied patches for at least that length of time (Figure 10).

We conducted a sensitivity analysis by perturbing all three parameters ( $e_{\text{latent}}$ ,  $e_{\text{connected}}$ ,  $c$ ) of the spatially implicit model up to 75% of their nominal values (see *Supplemental Material*, Figures S1 and S2, for details; <http://dx.doi.org/10.3996/022011-JFWM-012.S1>). From a decision-making perspective, the most important result of the sensitivity analysis that could occur is for the optimal decision to change as the parameters changed. The model-averaged optimal decisions are the most sensitive; however, most decisions are robust

up to 75% perturbations in the parameters. In the portion of the state space where the decision is to connect a resistant patch, the optimal decisions change with only a 1% change in the parameters. This mirrors the “value of information” calculations. However, for the current state of the system, the optimal decision of connecting latent patches is highly robust to parameter uncertainty.

The results of our optimization suggest that, under current conditions, the optimal policy for the Lemhi Basin is, in most cases, to connect latent patches; that is, connect currently occupied patches back into the metapopulation. This result is highly robust to structural uncertainty expressed by the four different models we examined, and also to parametric uncertainty within those models. However, in other parts of the state space (i.e., if the system was starting from a different place) the optimal decisions would be different and would also be quite sensitive to uncertainty.



**Figure 6.** Results for the [MS] & [BY] parameterization in year 1 for bull trout *Salvelinus confluentus* in the Lemhi Basin. Red = connect a resistant patch; blue = connect a latent patch. Green indicates states from which no connections are possible (maximum number of actions exceeded or no available patches); white space also indicates combinations of states that are impossible.

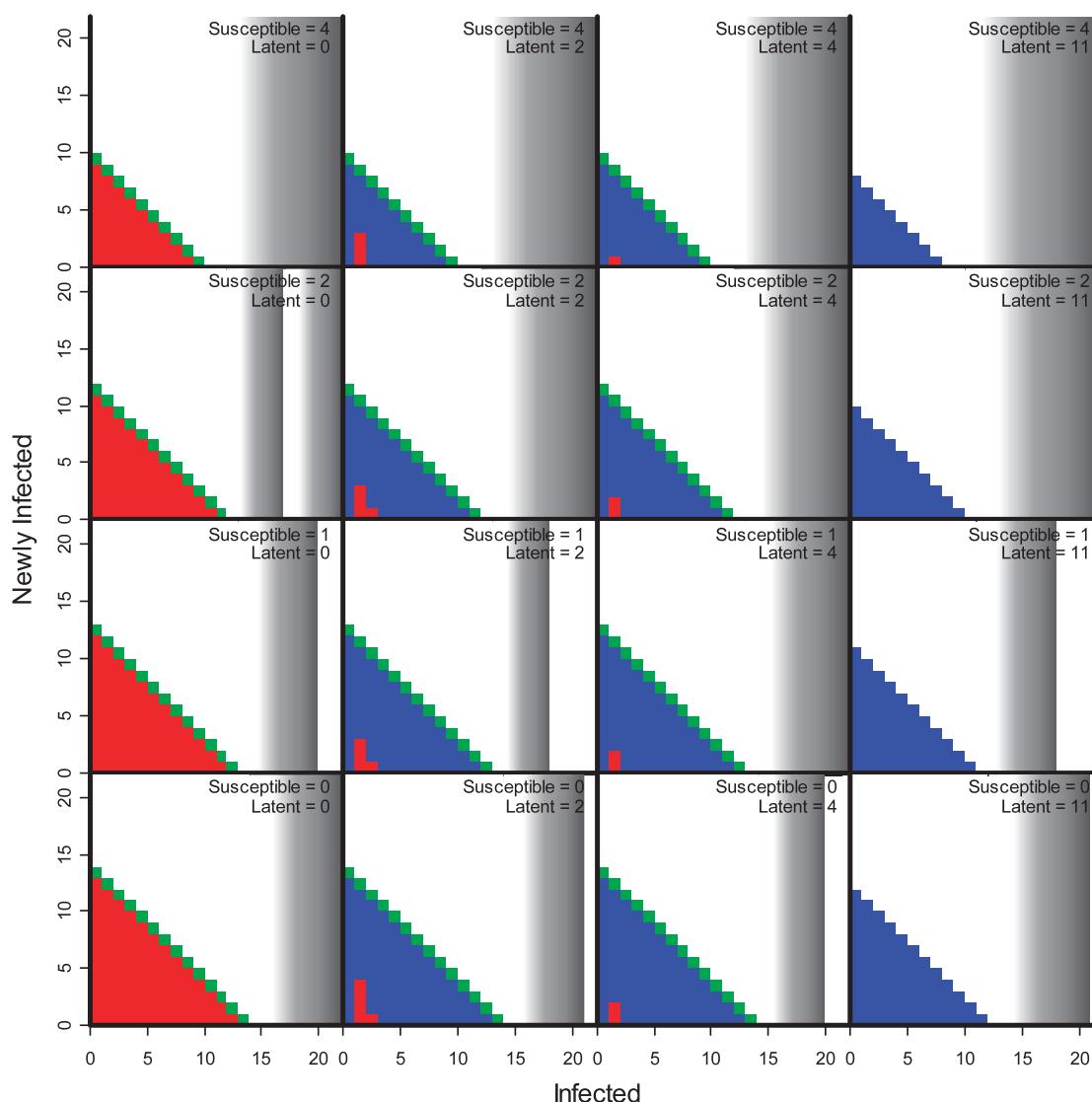
### Monitoring and Adaptation

Monitoring the result of a chosen management action, including, at a minimum, the resulting system state (in this case the number of patches in each of the five patch types), is critical to the conduct of adaptive management for several reasons. First, when decisions are potentially state dependent (as they are here), monitoring provides the data needed for making the next decision. In addition, monitoring permits an evaluation of the predictive ability of the chosen system models. That is, it is also possible to use monitoring data to update model weights (here we assume equal weight given to the four models), and so potentially improve decision-making. Finally, monitoring allows for evaluating the effectiveness of the chosen management action with respect to the objective function. Given the current system state in the Lemhi Basin, the value of information (i.e., evaluating the system models) is low. However, in

other system states, the value of monitoring information may be quite high. In addition, the two other roles of monitoring (evaluating system state and evaluating effectiveness of management) are still relevant in this situation. Tools exist, including both occupancy and mark-recapture monitoring, for reducing uncertainty in this system. Patch occupancy is the currency of the objective function, and so is the natural choice for a monitoring program in the context of this exercise.

### Occupancy monitoring

Occupancy estimation entails a sampling and modeling procedure whereby the presence of a species in a set of habitat patches is evaluated while simultaneously accounting for imperfect detectability of the species, yielding two sets of parameters: 1)  $\Psi$ , the estimated proportion of sampled sites occupied by the species of interest; and 2)  $p$ , the conditional detection probability; that is, the probability of detecting the species during a



**Figure 7.** Results for the [MS] & [BN] parameterization in year 1 for bull trout *Salvelinus confluentus* in the Lemhi Basin. Red = connect a resistant patch; blue = connect a latent patch. Green indicates states from which no connections are possible (maximum number of actions exceeded or no available patches); white space also indicates combinations of states that are impossible.

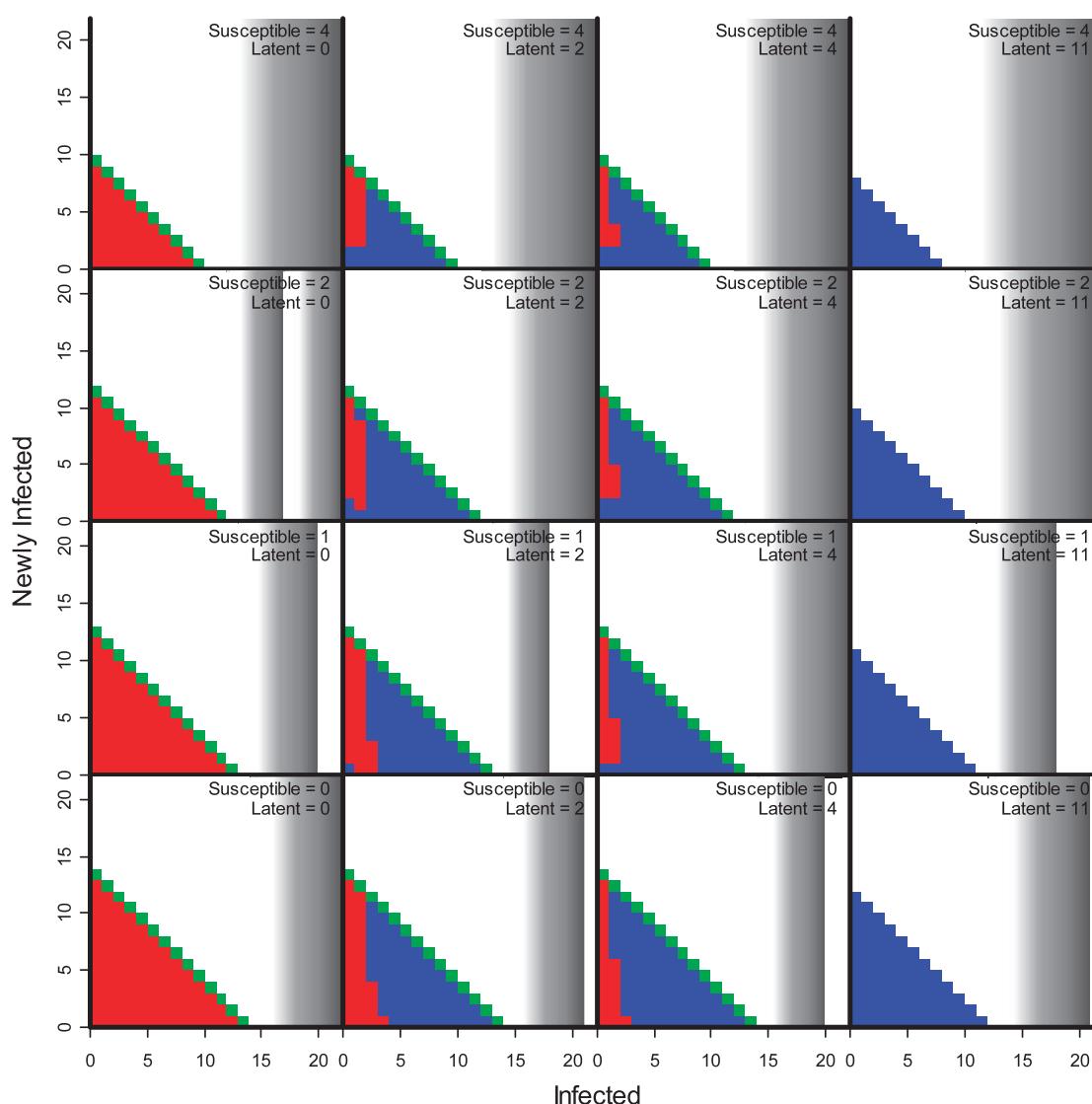
survey, given that the species is present in the patch (MacKenzie et al. 2002, 2005). Joint estimation of these parameters requires collecting multiple samples in each patch during a time period in which the population can be assumed to be closed to demographic processes (i.e., closed to colonization and extinction of the patch). A sampling procedure for estimation of occupancy and patch dynamics could be conducted whereby connected ( $I$  and  $S$ ), newly connected ( $N$  and  $S$ ), and latent ( $L$ ) patches were monitored for occupancy. The proportion of occupied patches of each type would then be used as an updated estimate of the system state.

Sampling infected and newly infected patches is necessary to detect extinction events in these patches. Sampling in susceptible patches is of primary interest for observing the process of colonization. Sampling in latent patches is necessary to determine whether the patch still contains the species before a reconnection action (i.e.,

only latent patches that will be reconnected in the near future need be sampled in this scheme).

Large (spawning) trout are susceptible to electrofishing injury (Sharber and Carothers 1988; Hemmingsen et al. 1996), so sampling would likely be restricted to snorkeling or other minimally intrusive survey techniques for sampling trout. Ideally, occupancy estimation would be conducted at each of these sites during the fall spawning season, August–September (Schobey 2006), with two or more replicate samples collected during the sampling period. This would be conducted preferably over the course of the season, so that sampling of both juvenile and adult migratory fish is possible.

Recent theory has extended patch occupancy to include estimation of patch dynamics across multiple seasons and multiple species (MacKenzie et al. 2003, 2005). A multiple-season approach consists of occupancy sampling at multiple points in time, separated by periods



**Figure 8.** Model averaged decision space assuming equal weights on the four models for bull trout *Salvelinus confluentus* in the Lemhi Basin. Red = connect a resistant patch; blue = connect a latent patch. Green indicates states from which no connections are possible (maximum number of actions exceeded or no available patches); white space also indicates combinations of states that are impossible.

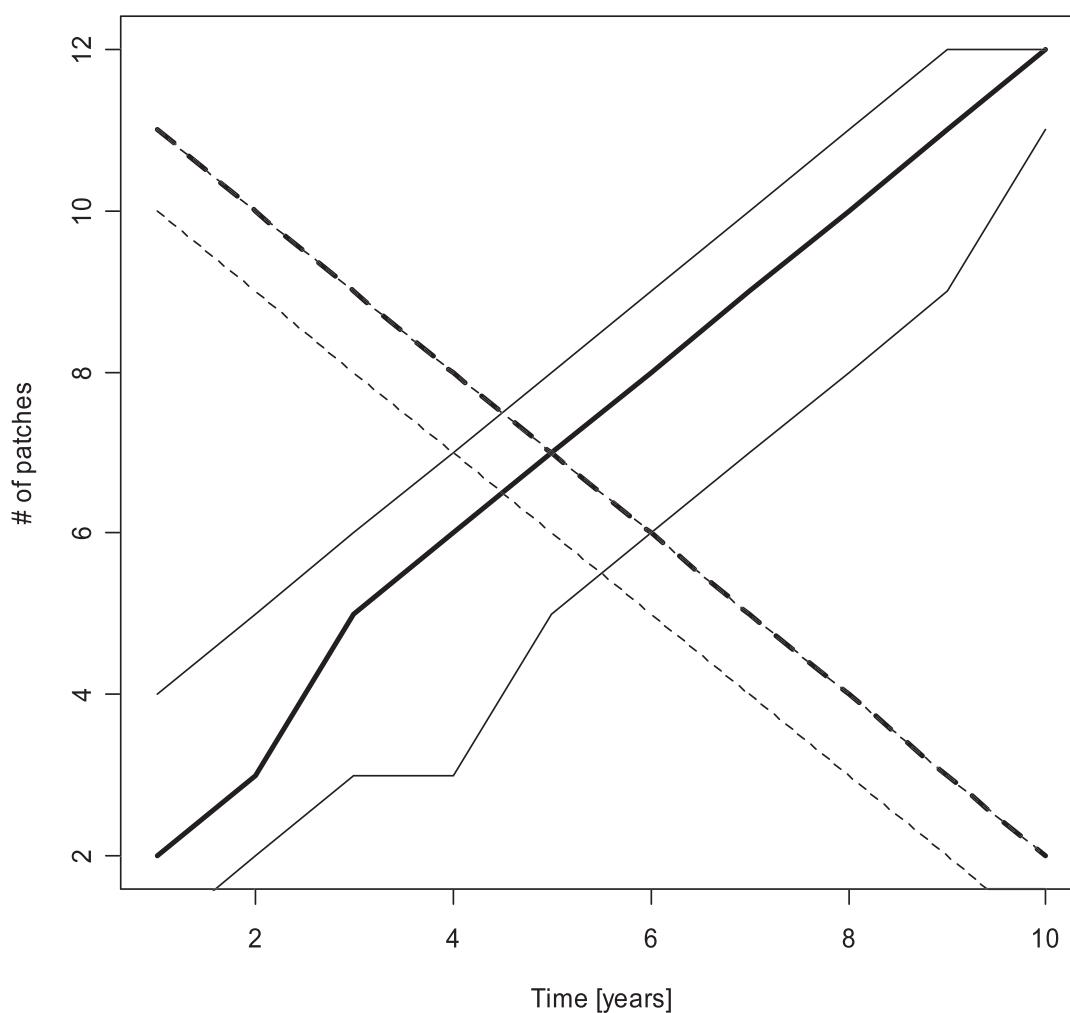
during which demographic processes may occur. Multiple seasons of data allow estimation of two additional parameters, including 1)  $\gamma_t$ , the probability that an unoccupied patch becomes occupied between time  $t$  and  $t + 1$ ; and (2)  $\varepsilon_t$ , the probability that an occupied patch at time  $t$  is not occupied at time  $t + 1$ . Linking the colonization parameter to the system state could provide some information on the mechanisms leading to colonization. An additional uncertainty is the potential interaction between bull trout and brook trout. Multi-species occupancy and dynamics estimation approaches have been described (MacKenzie et al. 2005) that allow for inference about interspecies interactions. Such approaches would update the information state relative to the [BN] and [BY] model parameterizations.

Although occupancy is the obvious focus of monitoring in this situation, there exists a potentially long lag time between reconnecting a resistant patch and observing

colonization of the resultant susceptible patch (or between reconnecting a latent patch and observing colonization of an existing susceptible patch). The presence of two connected, apparently suitable, but unoccupied patches in the Lemhi suggests that colonization events are uncommon. A long lag time such as this reduces the effectiveness of monitoring for learning and adaptation. Given this problem, there are a number of advantages that could be gained by using mark-recapture sampling in the infected, newly-infected, and latent patches. Most critically, with mark-recapture, movement of migratory individuals out of infected and newly infected patches can be observed, leading to reduced time to distinguishing between model parameterizations [ME] and [MS].

#### Mark-recapture monitoring

A program of marking bull trout and recapturing or detecting these marked fish can provide multiple benefits.



**Figure 9.** The median (thick line), minimum and maximum number of infected (solid lines) or latent (dashed lines) from 1,000 Monte Carlo forward simulations for bull trout *Salvelinus confluentus* in the Lemhi Basin. The optimal policy from the model averaged stochastic dynamic programming was used, and the forward dynamics used the [ME] & [BY] parameterizations.

First, by marking individuals with Passive Integrated Transponder (PIT) tags in the headwaters of a patch during spawning each year and setting up an array of PIT readers at a point of demarcation from the patch, one could immediately detect movement out of a latent patch after reconnection.

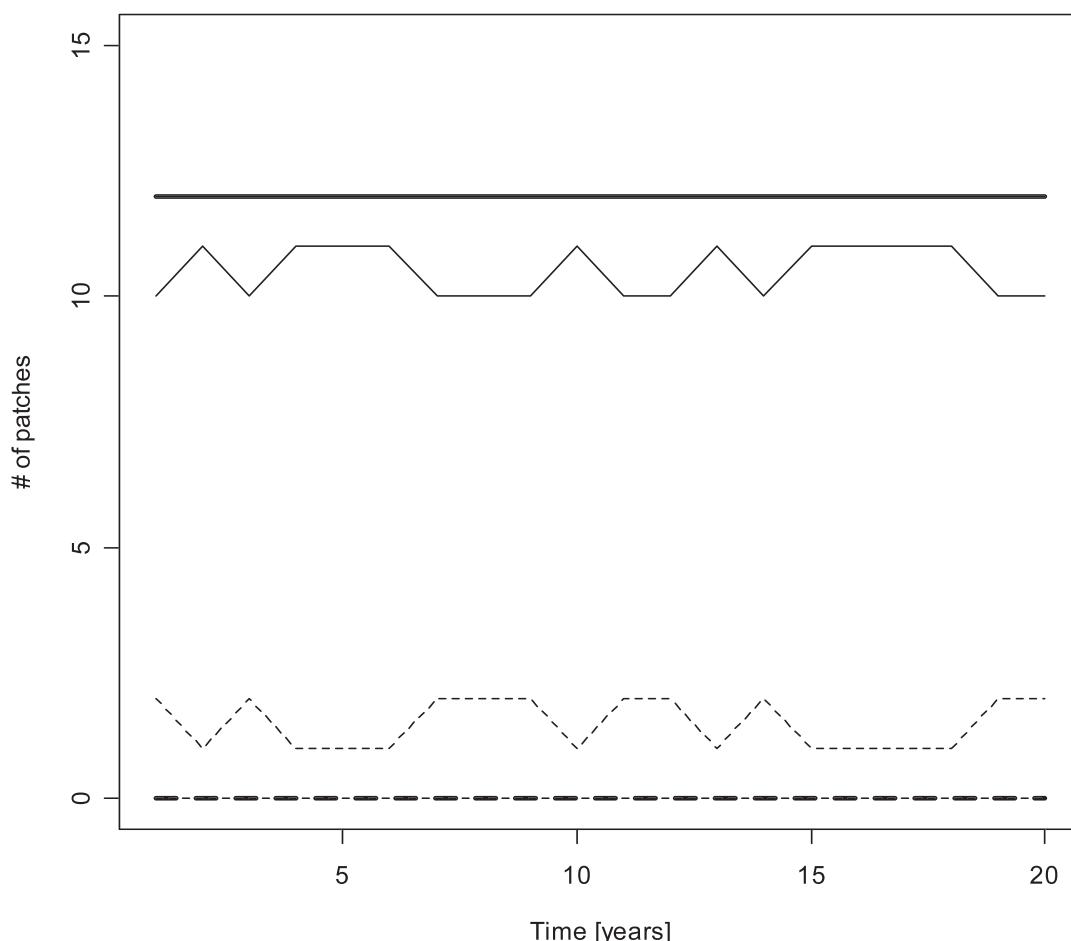
In addition, the data used to make this simple assessment of whether fish are leaving an occupied patch would also permit assessment of vital rates and breeding probabilities. The use of captures and PIT readers for a given patch constitutes a gateway robust design (Bailey et al. 2004; Kendall 2004), which allows for the estimation of survival probabilities and, for breeders that only use the patch to spawn, the probability of breeding in a given year. When captures and PIT readers are implemented at multiple patches, the combination of data permits the estimation of dispersal among patches (Hestbeck et al. 1991; Kendall 2004).

Taken together, these data can be used to estimate the parameters of a metapopulation model. Because patch dynamics are ultimately an artifact of the survival and movements of individuals, by increasing knowledge about this individual movement, improved models for

patch dynamics can be developed. Therefore, the implementation of a marking program provides both short-term (detects some movement between patches) and long-term (models rates of survival and movements among patches) benefits to the management of bull trout.

Finally, it will be possible to address uncertainty in mechanisms causing migratory behavior and potential effects of brook trout by linking the relevant parameters (i.e., dispersal probability) to patch disturbance and productivity levels. Developing proxies for these patch characteristics will be necessary in order to undertake a formal analysis of dispersal mechanisms and interspecific interactions.

Challenging the predictions of the alternative models with the observed colonization data would allow us to update our confidence in the different models. This can be done formally by assigning probabilities to the models and updating these probabilities annually with Bayes' theorem. These updated probabilities, which reflect the degree of accumulated learning, could then be used at the next time step, to produce a revised prioritization scheme for subsequent decision making. Over time, we would hope these model probabilities would converge to the best predictive model(s), and the



**Figure 10.** Forward simulation starting from the most common state at the end of restoration activity  $\{I = 12, N = 0, L = 2, S = 0, R = 8\}$ , to the end of the Habitat Conservation Plan for bull trout *Salvelinus confluentus* in the Lemhi Basin. The median (thick line), minimum and maximum number of infected (solid lines) or latent (dashed lines) from 1,000 Monte Carlo forward simulations. The optimal policy from the model averaged stochastic dynamic programming was used, and the forward dynamics used the [ME] & [BY] parameterizations.

prioritization scheme would stabilize to an optimal policy. However, given a 10-y management time horizon, it is possible that limited learning will be achieved in this system to directly benefit management.

### Lessons Learned

Aside from the technical results relevant to the Lemhi Basin, we also are interested in communicating our most critical “lessons learned” in implementing an adaptive approach to recovery planning. The actual implementation of adaptive management has generally been thought to fall short of the promise of adaptive management (e.g., Williams et al. 2007); we believe that such practical advice may well be critical for increasing the use of this powerful tool. Therefore, we hope to provide some practical information on the strategies that we found to be most useful in developing this adaptive management application, and to highlight portions of the problem-solving process we went through in order to complete this work.

The identification of objectives is the first and critical step in developing an adaptive management plan; these

objectives are then formalized in an objective function. Typically, managers would have the largest influence on setting the objective function; in this case, we set our objective function based on conversations with the entire group. It is important to note that we considered not just the management and regulatory context in determining our objective function, but also the value of this exercise as a case study. In particular, we worked to develop an objective function that was reasonably sensitive to management decisions, so that we could illustrate state-dependent decisions. We considered two different objective functions—one in which our objective was to maximize the number of sites that were occupied at the end of the 30-y management horizon. The second candidate function, and the one we eventually decided upon, was the probability of having at least one occupied patch (i.e., population persistence) at some time frame after the end of the management horizon. This objective function was attractive because the ESA is primarily concerned with long-term species persistence, rather than with maximizing species density. However, this second objective was overall less sensitive to management options because the probability of having

at least one occupied site was generally quite high in any case. In order to illustrate state-dependent decisions, therefore, we chose a relatively long time span of 256 y. Determining a time span over which the objective function was sensitive to management required some experimentation with the SDP. In a fully real-world application, this process might include what is known as “double-loop learning” (Lee 1993). If the objective function was found, after it was agreed upon by stakeholders, to be relatively insensitive to management decision making, after a number of years of application the objective function itself could be considered for modification.

Developing the modeling framework was the most technically challenging part of this project. We began by developing a four-state model, which did not include the newly infected state. However, we came to realize that this was a necessary state if we were going to develop the model parameterization [MS]. Adding a patch type to the model increased our state space so much that computation was not possible on a typical desktop computer. Only after we limited the state space so that all possible states with a total of 22 patches were not included and instead only states that we could possibly reach (i.e., we could never have more latent states than we started with) did this problem become possible to solve on a desktop computer. In essence, developing the SDP for this application required relatively advanced programming skills. We recommend that if such skills are not available on a team interested in developing an adaptive management plan based on SDP, seeking outside assistance should be considered. However, it is important to note that SDP itself is not necessary to all adaptive management applications, and less technically challenging tools could have been used for this problem as well.

Challenges in development and implementation of this framework included not having the same level of information on study area tributaries and not having comprehensive baseline data on existing environmental conditions. Other uncertainties included the presence, distribution, and abundance of brook trout in the Lemhi River and the differential probabilities that brook trout would invade a specific stream reach. There are also uncertainties concerning flows available or needed to reconnect each of the 10 stream reaches, and whether or not any specific tributary would have adequate support from landowners, water users, or other stakeholders to recover bull trout in the Lemhi basin (i.e., partial management control). Absent additional resources to collect needed data, and in light of the identified limitations, we were unable to construct a spatially explicit model (e.g., to provide a decision tool to prioritize the reconnection of specific tributaries in the Lemhi basin). Better scientific information and data would improve our understanding of the environmental baseline for specific stream reaches, and the potential effects of brook trout invasion. Nonetheless, the process of defining the problem and making even limited predictions sharply clarified scientific constraints that ultimately affect stream reconnection prioritizations.

## Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

**Figure S1.** Scatterplot of the relative perturbations to the three parameters at the 75% level of uncertainty. Lighter colored points have negative perturbations to  $e_{\text{connected}}$ . The largest perturbations to each parameter occur when the perturbations to the other two parameters are zero.

**Figure S2.** Minimum perturbation magnitude to change the nominal decision by state, for the model averaged output. Red = 1%, green = 50%, blue = 75%, and black indicates the decision did not change under any perturbation.

All found at DOI: <http://dx.doi.org/10.3996/022011-JFWM-012.S1> (118 KB DOC).

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